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CHECKLIST

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Hydroides Gunnerus, 1768 (Annelida, Serpulidae) is feminine: a nomenclatural checklist of updated names

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Abstract

As a service to taxonomists and ecologists using names in the well-known and species-rich ship-fouling serpulid genus *Hydroides* we present an update of all 107 non-synonymised scientific names, with additional information on *Hydroides* nomenclature, original names, etymologies, and type localities derived from original literature, and in accord with the World Register of Marine Species (WoRMS) database. An update is needed because the gender of genus *Hydroides* has from 1 January 2000 reverted to the original feminine, due to a change in the wording of International Code of Zoological Nomenclature which was overlooked at that time, and is contrary to the usage in practice of *Hydroides* as masculine which had started about 1992, although Code-required from the 1960s. We match 31 further original names of current WoRMS subjective junior synonyms to each non-synonymised name, and also report on the world distribution of the genus as illustrated by type localities of the valid names. We include notes on seven *species inquirenda*. The correct rendering is given of six names that have been altered for gender agreement for the first time herein. *Hydroides gottfriedi* **nom. n.** replaces junior homonym *H. rostrata* Pillai, 1971. Currently there are 41 non-synonymised species-group names in *Hydroides* which should be gender invariant, and 23 names which would only change if moved to a neuter genus; the remaining 43 names are fully gender variable. Place-names (23), and personal names (16) make up more than a third (36%) of the species names, with most of the remainder (68) being descriptive of species character states, usually of operculum morphology (54). All species, except *H. norvegica* (63°N), have type localities in shallow-water coastal locations in temperate to tropical waters below latitude 44°, with the highest number of new species (54) from the adjoining Western Pacific and Indian Ocean areas. The other concentration of new species (31) are those first found on the Pacific and Atlantic coasts of North America and in the Caribbean.

Keywords

Etymology, gender agreement, geolocation, ICZN, type locality

Introduction

An unusual situation has arisen concerning the correct formulation and spelling of historic species-group names in *Hydroides* Gunnerus, 1768 (Serpulidae) with respect to the established requirement of the International Code of Zoological Nomenclature (hereafter the Code) that the suffix spelling of a Latin or Latinized adjectival species-group name must agree in gender with its genus (ICZN 1999: Article 31.2). The stability of *Hydroides* names is important for tracking name usages as it is the largest serpulid genus, currently with 107 non-synonymised names, and also a further 31 original names currently placed as subjective synonyms. *Hydroides* includes *H. elegans* (Haswell, 1883), a model organism for settlement and genetic study (e.g., Hadfield 1998), and some other economically important species such as *H. ezoensis* Okuda, 1934, *H. dianthus* (Verrill, 1873), *H. dirampha* Mörch, 1863, and *H. sanctaecrucis* Krøyer [in] Mörch, 1863, which are foulers of ship hulls, harbour structures, and aquaculture equipment (Sun et al. 2015).

Hydroides species are easily recognisable by the morphology of the plug which closes the mouth of their calcareous tubes. It is a two-tier operculum with a basal funnel and a distal spinous structure called the verticil. The distinctive and varied structure of the verticil spines has enabled many *Hydroides* species to be detected. Identification from tubes alone is problematic, thus past diversity is difficult to determine from the fossil record in the absence of the opercula. *Hydroides* has no current subgenera, but *Eupomatus* Philippi 1844, the most prominent junior synonym of *Hydroides*, and the little-used *Eucarphus* Mörch, 1863, were both at times used as subgenera defined by verticil morphology. The taxonomic history is reviewed in Bastida-Zavala and ten Hove (2002).

We recently realised that the gender agreement serpulid taxonomists had been applying to adjectival *Hydroides* species-group names for the last 16 years was the opposite of that required by the fourth edition of the Code (ICZN 1999, effective 1 January 2000), in that authors since that date had continued using or creating masculine instead of feminine Latin forms. Additionally, taxonomists had not consistently observed the different Code rule applicable prior to 1999, with one author producing new *Hydroides* names seemingly of both genders in the same publication (Straughan 1967a). Therefore we have compiled a checklist of *Hydroides* name spellings we believe are currently correct, including also identifying the names not subject to gender agreement.

The derivation of *Hydroides* as an Annelida genus name is known. Stearn (1983: 266) explains that substantives derived from *-oides* were commonly used for new genera before and during Linnæus' era to indicate resemblance to a genus already known, sometimes just as temporary names. The *-oides* suffix is originally adjectival, transliterated from Greek *οειδης*. Gunnerus had at first used the cnidarian genus of *Hydra* (named for the creature of Greek myth) as the genus name for his new tubedwelling worm in 1766 correspondence with Linnæus, but shortly thereafter changed it to *Hydroides* for his new species *H. norvegica* as published in 1768, "until Mr. v. Linné makes its genus known" (Gunnerus 1768, Moen 2006). The link to hydrozoans was spurious, but the genus name persisted. Usage of the same spelling applied to true hydrozoans persists in Romance language works, where "hydroïdes" (hydroids) can substitute for the formal higher group name, Hydrozoa. The pair of usages are not homonyms in the strict Code sense, but there is some false positive reporting of the *Hydroides* annelid genus in bioinformatics search results (e.g., from some of the Hydrozoa works of Billard, such as Billard 1907).

Hydroides was feminine because Gunnerus clearly treated it as feminine when he used the feminine '*norvegica*' as epithet for the worm instead of the masculine '*norvegicus*' (likewise the calcareous tube was separately named *Serpula norvegica* by Gunnerus). However, in recent years Gunnerus's original feminine gender assignment for *Hydroides* became not obvious to most. This is exemplified by Moen (2006), who in the summary of her historical paper on Gunnerus reports without qualification that "in 1768 J. E. Gunnerus first described the species *Hydroides norvegicus*". Although Moen was well aware Gunnerus did not use that spelling she perhaps believed the 'correct' masculine ending (although incorrect since 2000) was always to be used, regardless of what was originally written.

The Code in its first edition indicated that genus names ending in *-oides* were to be treated as masculine (ICZN 1961: 33, Article 30(a)(ii) Examples), whereas in botany they were treated as feminine (Stearn 1983: 265). By the time of the Code third edition (ICZN 1985: 30, Article 30(b) Examples) the article text was the same, with the examples text explaining that these masculine genus names were substantivated adjectives, thus for *Hydroides* the adjectival descriptive of 'hydra-like' was functioning as a noun. Mandatory gender agreement, although much debated, was retained in the Code fourth edition, but changes were made in order "to simplify the identification of gender in genus-group names" (ICZN 1999: XXVI).

Unexpectedly one of the qualifying clauses now included in the Code fourth edition (ICZN 1999) had a major effect on *Hydroides* Gunnerus by reverting it to feminine status after almost 40 years as the opposite gender. The wording of Article 30.1.4.4 in full is "A compound genus-group name ending in the suffix *-ites*, *-oides*, *-ides*, *-odes*, or *-istes* is to be treated as masculine unless its author, when establishing the name, stated that it had another gender or treated it as such by combining it with an adjectival species-group name in another gender form." Why the Code editorial group thought the refinement was necessary is unknown, but presumably it was regarded as better matching contemporary practice with the original 18–19th century usages.

Hydroides began as feminine in 1768, and feminine adjectival endings matching this were usual for over 220 years but not universal (e.g., *H. bifurcatus* Pixell, 1913). Hartman (1965: 79) had maintained original feminine endings in her supplementary world catalogue, although not long later she had used the masculine for *H. pacificus* Hartman (Hartman 1969). Masculine endings, which the Code had required from the early 1960s onwards, otherwise only became common around 1992 (Moen 2006:

121), although *H. bifidus* Imajima, 1982 and *H. bisectus* Imajima & ten Hove, 1989 were newly described somewhat earlier. Ben-Eliahu and ten Hove (1992: 37) correctly pointed out that the Code third edition (ICZN 1985) had *Hydroides* as masculine (actually in place since the first edition). Serpulid taxonomists then adopted the use of masculine endings and continued with this right up to August 2015, unaware of the change back to feminine required from 1 January 2000 when the new Code came into effect. The fourth edition Code was incorrectly cited as continuing masculine endings in ten Hove and Ben-Eliahu (2005: 128). In summary, for nearly 40 years species names in *Hydroides* were required to have masculine endings according to the ICZN Code, although largely ignored for about 30 years, and now for the last 16 years they were required to have the feminine ending as begun by Gunnerus, also ignored. The conflict was first reported in WoRMS by one of us (GBR) in July 2015, after a misinterpretation of the Code requirement for *Hydroides* names was published in Tovar-Hernández et al. (2016, as first online July 2015, p.8). Gender-corrected names were subsequently used in Sun et al. (2015), Kupriyanova et al. (2015), and Sun et al. (2016).

Code Article 31 (ICZN 1999) explains some of the requirements and exceptions regarding species-group Latin name formation. In general, most species-group names ending in the suffixes *-us, -a, -um* are declinable and likely to be adjectives. There are some exceptions applicable here such as *-spina*, which is a noun in apposition and should not change with gender, and most other name endings will not change. The only possible endings of changeable adjectives are -a, -us (these two make up over 60% of all names), -is, -um, -e, -er, -ior, whereas nouns can have all endings (Welter-Schultes 2013). Personal names as species-group names are usually (exceptions) formed as genitive-case nouns (ICZN 1999, Article 31.1). Nouns with Latin adjectival suffixes can become adjectives, notably non-Latin place-names with the suffixes *-ensis* (masculine/feminine) or *-ense* (neuter), indicating of that place, or suffix '*-anus -a*', indicating belonging to. However, nouns compounded with dictionary Latin adjectives are treated as noun phrases in apposition (ICZN 1999, glossary).

Here we present an update of all non-synonymised names, and additional information on *Hydroides* nomenclature, as derived in conjunction with the World Register of Marine Species (WoRMS) Polychaeta database (Read and Fauchald 2016), where further details are available. Certain *species inquirenda* (seven names which are otherwise valid but require taxonomic clarification due to inadequate original descriptions) are included and examined in the checklist for analytic purposes, while noting (as explained by ICZN 1999, Article 23.9.6) that the inclusion of these names should not later be considered as new usages.

We have taken this opportunity to investigate type localities of all the species, and to geolocate them to modern standards if possible. Prior to satellite-based navigation only vessel-based collections were likely to provide type-locality geolocations, and the descriptions used to pinpoint coastal sites could be vague or problematic. For instance Treadwell (1939: 164) gave an update that the "precise position" of his Mayagüez Bay station 6062 of 1902 could be relocated based on using a red buoy at the harbour entrance as a reference point, but we are doubtful of the 100 year longevity of this buoy. We have been able to suggest placements for at least three species for which only a vague location was previously available. Type localities are mapped to show the world distribution.

Methods

The checklist is based on a review of original literature for all *Hydroides* species-group names, and a review of about 250 *Hydroides*-related name records at WoRMS (Read and ten Hove 2016). Under Code Article 34.2 (ICZN 1999), prior usages in literature are not required—here we simply formulate and present correct spellings. Gender agreement is mandatory, which means that non-agreeing scientific names strictly do not exist as valid spellings, and can be updated without explanation (to the bewilderment of many in the past, so we strongly advise annotation of new gender-spelling variants to avoid uncertainty). It is also worth noting that, while gender-agreement variants obviously are minor spelling changes, the Code is worded so that these different spellings are not treated as separate usages under prevailing usage rules.

All original literature for *Hydroides* names was examined. Names as given are our derivations of correct endings for gender agreement, and are followed as necessary with the original binominal combination and comments on current status. The etymology (author's and/or interpreted dictionary entries) is given, followed by our evaluation of the type of name (adjective, invariant noun in apposition, etc.) from available information. The derivation of names is unambiguous when authors give full etymologies, but this is rare for old names, and often sketchy for modern ones. Derivations are frequently only evident by matching likely character states mentioned, and occasionally there seems no obvious basis for the name chosen. The sources we have used to study derivations include online dictionaries and meta Greek/Latin language resources (Harper's Etymonline; Logeion; Lexilogos), the Lewis and Short (1891) Latin dictionary (print, also online), as well as analytical dictionaries on the classical languages in science (Brown 1956; Stearn 1983). We have included the current subjective synonyms at WoRMS (if any) of each name (and their type localities), but have not included the other superseded recombinations, nor any misspellings of the valid name (these are fully listed at WoRMS and links to the current and original name records at WoRMS are in the Suppl. material 1 which also summarises the name analysis).

The type locality names have been investigated and their geolocations are included, usually derived by retrospective georeferencing. They are mapped to place the original discoveries in a geographic context and to locate where topotype material could be sought. Current place-names were geolocated using several web-based gazetteers (e.g., GeoNames, GEOLocate, Marineregions (WoRMS), Wikipedia). Disused historic names were sought via general web searches and Wikipedia. Holotype georeference information in online collections databases and in subsequent publications was evaluated if available (these data can be based on retrospective approximations, rather than information supplied by authors on labels). Occasionally modern authors have published geolocations that are obviously imprecise or displaced, and we have pointed these out. The point-geolocations of the older taxa are our informed coastal assignments (indicated as map estimates) if derived from place-names which are towns, islands, or occasionally only known as strips of coast or other imprecise geographic extents. Sometimes positioning was assisted by further information from or about authors. A few times we were unable to narrow the collection site to any point and we indicate when we have given a general geolocation instead. We are unable to calculate the uncertainties (in extent) of our derived coordinates, and caution that each is a precise point location of the possible site, the nearest logical coastal geolocation at this time, as adjusted with satellite image overlay of terrain using the Wikipedia GeoLocator mapping tool. A list of geolocations is in the Suppl. material 1.

Results

Checklist of *Hydroides* species original names

Family SERPULIDAE Rafinesque, 1815

Hydroides Gunnerus, 1768

Type species. *Hydroides norvegica* Gunnerus, 1768 (original binomen)

Includes *Eupomatus* Philippi, 1844, type species *E. uncinatus* Philippi, 1844 (by subsequent designation), *Eucarphus* Mörch, 1863 (as *Hydroides* (*Eucarphus*)), type species uncertain (full synonymy in WoRMS)

***Hydroides adamaformis* Pillai, 2009** (original binomen)
Etymology: The author states the name for *H. adamaformis* is derived from Latin *adamas* 'diamond' in reference to the diamond-shaped appearance of the verticil spines "although their distal ends are curved inwards". The suffix *-formis* 'shaped' is used to form an adjective.
Evaluation: Masculine/feminine invariant adjective (*formis,* neuter *forme*) (Stearn 1983: 94).
Type locality: Lucas Island (south west corner), near Dampier Archipelago, Kimberley region, Western Australia.
Geolocation: -15.2167°, 124.5167° (author, but is east of Lucas).
WoRMS: 555194
Synonyms: No subjective synonyms.

***Hydroides affinis* (Marion, 1875) (originally as *Eupomatus affinis*)**
Status: Name now disused and representing a *species inquirenda* possibly senior to *Hydroides helmata* (Iroso, 1921).
Etymology: Not stated, but *E. affinis* is named from the Latin adjective *affinis* 'related to'.
Evaluation: Masculine/feminine invariant adjective (*affinis -e*) (Stearn 1983: 94).
Type locality: Golfe de Marseille, France, Mediterranean Sea. No further precision, but likely to be coastal close to Marseille, possibly at or near Île Ratonneau, which the author mentions frequently (Marion and Bobretzky 1875). However, a stone pier off Arenc, Marseille is also mentioned (as *Hydroides uncinata* habitat).
Geolocation: 43.2872°, 5.3143° (map estimate, Île Ratonneau).
WoRMS: 383237
Synonyms: As *species inquirenda* has no synonyms although *H. helmata* has been suggested (Zibrowius 1971: 713–714).

***Hydroides alatalateralis* (Jones, 1962) (originally as *Eupomatus alatalateralis*)**
Etymology: The author states that *E. alatalateralis* is named for "limbations that are to be found on the sides of the spines of the distal opercular circlet", thus combining the Latin adjectives *alata* 'furnished with wings' and *lateralis* 'lateral'.
Evaluation: Masculine/feminine invariant adjective (*lateralis -e*) (Stearn 1983: 94).
Type locality: Port Royal, Jamaica, Caribbean Sea.
Geolocation: 17.9369°, -76.8439° (map estimate).
WoRMS: 369228
Synonyms: No subjective synonyms.

***Hydroides albiceps* (Grube, 1870) (originally as *Serpula* (*Eupomatus*) *albiceps*)**
Etymology: Not stated, but *S. albiceps* may be named for the *operculum album* mentioned by Grube (1870: 521) by combining the Latin adjective *albus* 'white' with *-ceps* derived from Latin noun *caput* 'head'.
Evaluation: Noun in apposition (cf. noun '*quadriceps*'), or if treated as adjectival *-ceps* endings are invariant.
Type locality: 'Tor' (El Tor), Gulf of Suez, Red Sea.
Geolocation: 28.2365°, 33.6130° (map estimate).
WoRMS: 130997
Synonyms: *Hydroides spiratubus* Pillai, 2009 (Fenelon Island, Kimberley, Australia)
Serpula (Hydroides) multispinosa ternatensis Fischli, 1903 (Ternate, Indonesia)

***Hydroides amri* Sun, Wong, ten Hove, Hutchings, Williamson & Kupriyanova, 2015 (original binomen)**
Etymology: The authors state the name for *H. amri* is in honour of the Australian Museum Research Institute (AMRI).

Evaluation: Invariant non-Latinized noun in apposition '*amri*' from an acronym, pronounced as a single word, not letter by letter as if an initialism (ICZN 1999, Article 11.3).
Type locality: Bass Point south, south of Wollongong, NSW, Australia.
Geolocation: -34.6033°, 150.8953° (authors).
WoRMS: 852781
Synonyms: No subjective synonyms.

Hydroides ancorispina* Pillai, 1971 (original binomen)
Etymology: Not stated, but *H. ancorispina* may be named from Latin nouns *ancora* 'anchor', *spina* 'thorn', referring to the fact that both radii and verticil spines have anchor shaped tips.
Evaluation: Invariant noun in apposition.
Type locality: Wellawate, Colombo, Sri Lanka.
Geolocation: 6.8746°, 79.8569° (map estimate).
WoRMS: 328434
Synonyms: No subjective synonyms.

***Hydroides arnoldi* Augener, 1918 (original binomen)**
Etymology: Not stated, but *H. arnoldi* is evidently named after one of its collectors, Arnold Schultze.
Evaluation: Invariant genitive noun *arnoldi* from modern personal name of Arnold.
Type locality: Reported as two worms from two collection sites, Lome, Togo and Isla Annobón, Equatorial Guinea, both in Gulf of Guinea, West Africa. However, only the Annobón occurrence remains in *H. arnoldi* (see WoRMS for further explanation).
Geolocation: -1.4063°, 5.6373° (Annobón, map estimate).
WoRMS: 338000
Synonyms: No subjective synonyms.

***Hydroides augeneri* Zibrowius, 1973 (original binomen)**
Etymology: Not stated, but *H. augeneri* is evidently named after Hermann Augener.
Evaluation: Invariant genitive noun *augeneri* from modern personal name of Augener.
Type locality: "Malembe" in Zaire (now Democratic Republic of Congo), but a coastal instance of the name could not be found, either in DR Congo or its neighbours. Zaire (DR Congo) has a very narrow access to the coast, and a coastal georeference was derived from "Vista", the only other named collection site.
Geolocation: -5.8763°, 12.283° (map estimate for Vista).
WoRMS: 328435
Synonyms: No subjective synonyms.

Hydroides azorica **Zibrowius, 1972b (original binomen)**

Etymology: Not stated, but evidently *H. azorica* is named after the Azores archipelago where collected.
Evaluation: Latinized adjectival form *azorica* with correct feminine ending. *H.* '*azoricus*' usages exist (e.g., Bellan 2001).
Type locality: On shipwreck "Doria" east of Ponta Delgada port, Ilha de Sao Miguel, Açores (Azores).
Geolocation: 37.7410°, -25.6478° (map estimate).
WoRMS: 328436
Synonyms: No subjective synonyms.

Hydroides bandaensis **Zibrowius, 1972a (original binomen)**

Etymology: Not stated, but evidently *H. bandaensis* is named after the Banda Islands where collected.
Evaluation: Masculine/feminine invariant '*-ensis*' adjective created from non-Latin geographic name Banda.
Type locality: Banda Islands (exact location unknown), Banda Sea, Indonesia.
Geolocation: -4.525°, 129.9089° (gazetteer, for Banda Islands).
WoRMS: 369229
Synonyms: No subjective synonyms.

Hydroides bannerorum **Bailey-Brock, 1991 (original binomen)**

Etymology: The author named *H. bannerorum* after biologists Albert H. (Hank) and Dora May (Dee) Banner.
Evaluation: Invariant plural genitive adjective *bannerorum* from Banner family name.
Type locality: Near Banners Point (Kalaeloa) sewage outfall, near Pearl Harbour, Oahu, Hawaii, Pacific Ocean.
Geolocation: 21.2719°, -158.1213° (map estimate).
WoRMS: 328437
Synonyms: No subjective synonyms.

Hydroides basispinosa **Straughan, 1967a (originally as *H. basispinosus*)**

Status: The synonymy of *H. basispinosa* and *H. gradata* Straughan, 1967a with *H. operculata* Treadwell, 1929 was re-confirmed by Sun et al. (2015: 63), but is being re-examined, and we provisionally include the *H. basispinosus* original name analysis separately.
Etymology: Not stated, but the compound name for *H. basispinosus* means 'spiny-pedestal' as derived from Latin (originally Greek) feminine noun *basis* 'pedestal' and adjective *spinosus -a -um* 'spiny'. Basal internal spinules on opercular spines are mentioned (not figured).

Evaluation: Gender-variable adjective (in practice). Elsewhere in the article Straughan used feminine adjectival new species names, and in relation to the basal spinules Straughan probably intended another adjectival compound name. Her error in gender ending can be corrected to '*-spinosa*'. However, she used the feminine Latin noun '*basis*' (pedestal), not the adjectival '*basalis*' (basal) which would have become '*basalispinosa*'. If a noun phrase with a feminine noun then '*basispinosus*' was incorrect Latin (it should also have been '*basispinosa*'), and the original spelling must be maintained (ICZN 1999, Article 31.2.1). While this can be noted, Straughan is not the only author to adopt '*basis*' as if adjectival, and it seems best not to apply the strictest interpretation here. Usage as '*basispinosa*' already exists (e.g., Sun et al. 2015: 63).
Type locality: Mouth of Ross River, Townsville, Queensland, Australia.
Geolocation: -19.2569°, 146.8494° (map estimate).
WoRMS: 881640
Synonyms: See *H. operculata* comments.

Hydroides bifurcata Pixell, 1913 (originally as *H. bifurcatus*)

Etymology: Not stated, but the name for *H. bifurcata* is adjectival from Latin *furcatus* 'forked', likely referring to the bifid verticil spines.
Evaluation: Gender-variable adjective. The original incorrect masculine ending as *H. bifurcatus*, repeated in Day (1951: 64), was silently corrected to '*bifurcata*' in Day (1967: 808).
Type locality: Minicoy/Maliku (as Minikoi), south Lakshadweep archipelago, north of the Maldive Islands.
Geolocation: 8.2854°, 73.0673° (map estimate).
WoRMS: 873900
Synonyms: No subjective synonyms.

Hydroides bisecta Imajima & ten Hove, 1989 (originally as *H. bisectus*)

Etymology: Not stated, but *H. bisecta* is likely named based on *bisectus* 'bisected', a New Latin past participle used as an adjective, derived from Latin *bis* 'two', *secare* 'to cut', and referring to the bifid tips of verticil spines.
Evaluation: Gender-variable adjective, corrected herein to '*bisecta*'.
Type locality: off Sesoko Marine Station, Sesoko Island, Okinawa Islands, Japan.
Geolocation: 26.6365°, 127.8661° (map estimate).
WoRMS: 880526
Synonyms: No subjective synonyms.

Hydroides bispinosa Bush, 1910 (original binomen)

Etymology: Not stated, but the name for *H. bispinosa* is likely referring to the pair of lateral spinules on the verticil spines described by Bush, based on Latin *bis* 'two' with adjective *spinosus* 'spined'. Bush compared *H. bispinosa* with *H. multispinosa*.

Evaluation: Gender-variable adjective with correct original feminine ending. Usage as ‘*bispinosus*’ exists (e.g., Bastida-Zavala and ten Hove 2002: 125).

Type locality: Bermuda. The Yale Peabody Museum type (syntype? YPM IZ 001367.AN) from the Verrill Bermuda Expedition in 1898, evidently has no further location data, but Castle Harbour is a collection site mentioned by Bush (1910).

Geolocation: Imprecisely known (possible place of origin, Castle Harbour, 32.3472°, -64.6872°, Bermuda).

WoRMS: 421083

Synonyms: No subjective synonyms.

Hydroides brachyacantha **Rioja, 1941a (original binomen)**

Etymology: Not stated, and the description of *H. brachyacantha* does not indicate why the name derives from Greek βϱαχυ (brachy) ‘short’, αϰανθα (akantha) ‘spine’, feminine noun, thus short-spine. In New Latin *acantha* has frequently been used as part of feminine compound names in both genera and species-group names. An identical spelling might be expected to be a noun form in both, but species-group names ending as *-acantha -acanthus* have regularly been treated as Latinized Greek adjectives, and that may have been the intention of the author.

Evaluation: Gender-variable adjective with correct feminine ending. Usages as ‘*brachyacanthus*’ exist (e.g., Bastida-Zavala and ten Hove 2003: 73).

Type locality: Marina Mazatlán, Mazatlán, Sinaloa, Gulf of California, Mexico.

Geolocation: 23.2797°, -106.4611° (original author, with neotype of Sun et al. (2016: 49) from the same geolocation).

WoRMS: 328441

Synonyms: No subjective synonyms.

Hydroides bulbosa **ten Hove, 1990 (originally as *H. bulbosus*)**

Etymology: Not stated, but *H. bulbosa* is evidently named for the bulbous (Latin *bulbosus -a -um*) dorsal verticil spine.

Evaluation: Gender-variable adjective, corrected herein to ‘*bulbosa*’.

Type locality: Khor Ghubb ’Ali, Musandam Peninsula, Oman, Strait of Hormuz, in a sheltered bay at 18 m.

Geolocation: 26.2633°, 56.3572° (map estimate).

WoRMS: 882354

Synonyms: No subjective synonyms.

Hydroides calopoma **Zibrowius, 1973 (original binomen)**

Etymology: Not stated, but the name for *H. calopoma* is a compound noun which may be referring to the operculum, from Greek ϰαλος (kalos) ‘beautiful’, πωμα (poma) ‘lid’.

Evaluation: Invariant noun in apposition (indeclinable because ending in a transliterated Greek word).

Type locality: Isla Tortuga, off Isla Annobón, Equatorial Guinea, Gulf of Guinea.
Geolocation: -1.4055°, 5.6562° (map estimate).
WoRMS: 369230
Synonyms: No subjective synonyms.

***Hydroides capensis* Zibrowius, 1972b (original binomen)**
Etymology: Not stated, but *H. capensis* is evidently named after the Cape Provinces of South Africa.
Evaluation: Masculine/feminine invariant '*-ensis*' adjective created from non-Latin geographic name.
Type locality: Offshore from Lambert's Bay, north of Cape Town, western coast of South Africa.
Geolocation: -32.0833°, 17.9333° (author).
WoRMS: 338003
Synonyms: No subjective synonyms.

***Hydroides chilensis* Hartmann-Schröder, 1962 (original binomen)**
Etymology: Not stated, but *H. chilensis* is evidently named after the country of collection.
Evaluation: Masculine/feminine invariant '*-ensis*' adjective created from non-Latin geographic name.
Type locality: Arica (coastal port city), Chile.
Geolocation: -18.4815°, -70.3333° (map estimate).
WoRMS: 328444
Synonyms: No subjective synonyms.

***Hydroides crucigera* Mörch, 1863 (originally as *Hydroides* (*Eucarphus*) *crucigera*)**
Etymology: Not stated, but the name for *H. crucigera* is likely referring to the verticil spines, which are cross-bearing, from feminine Latin noun *crux, crucis* 'cross', with Latin suffix *ger, gera* 'to bear'.
Evaluation: Gender-variable adjective with correct original feminine ending. Usages as incorrect suffix '*crucigerus*' and as masculine '*cruciger*' exist (e.g., de León González 1990: 336, Bastida-Zavala and ten Hove 2003: 78). Names ending in *-ger* may be nouns or masculine adjectives (ICZN 1999, Article 31.2.2). The usage of Mörch was adjectival as he used feminine *-gera*.
Type locality: Puntarenas, Gulf of Nicoya, Costa Rica Pacific coast (Mörch, 1863 as "*oceano pacifico, juxta* Puntarenas").
Geolocation: 9.9739°, -84.8330° (map estimate).
WoRMS: 333637
Synonyms: *Hydroides californicus* [sic] Treadwell, 1929 ("Lower California" (Baja California) Mexico)

Hydroides dafnii (Amoureux, Rullier & Fishelson, 1978) (originally as *Eupomatus dafnii*)

Etymology: Not stated, but *Eupomatus dafnii* as “trouvé par Mr. Dafni” is evidently named after the collector, Yaacob Dafni (Amoureux et al. 1978: 60, 148).
Evaluation: Invariant genitive form *dafnii* of the modern personal name Dafni.
Type locality: Eilat, Gulf of Aqaba (of Eilat), Israel, Red Sea, on reef coral. The site is mapped by the authors, but not georeferenced.
Geolocation: 29.5266°, 34.9377° (map estimate).
WoRMS: 369231
Synonyms: No subjective synonyms.

Hydroides deleoni Bastida-Zavala & ten Hove, 2003 (original binomen)

Etymology: The authors state *H. deleoni* is named after Jesús A. de León-González.
Evaluation: Invariant genitive form *deleoni* constructed from the personal name de Leon.
Type locality: Punta San Juanico, Western coast of Baja California Sur, Mexico. Authors’ georeference (26°13'N, 112°13'W, inland, ~26 km off target) is herein corrected to 26°15'9"N, 112°28'33"W).
Geolocation: 26.2524°, -112.4757° (San Juanico, map estimate).
WoRMS: 328445
Synonyms: No subjective synonyms.

Hydroides dianthus (Verrill, 1873) (originally as *Serpula dianthus*)

Etymology: Verrill (1873: 28) states for *S. dianthus* that the name alludes to the resemblance to *Dianthus* flowers as the colours of its branchiae “recalls the varied hues and forms of different kinds of pinks, (*Dianthus*.)”. The botanical generic name *Dianthus* (flower of Zeus) is New Latin (Linnæus and earlier) from Greek Δηοσ (Dios), genitive of Zeus, and ανθος (anthos) ‘flower’. As *Serpula* is feminine and *dianthus* is masculine it seems Verrill intended the name as a noun (*Actinia dianthus* Ellis, 1768 is an earlier similar pairing).
Evaluation: Invariant noun in apposition.
Type locality: Great Egg Harbor to New Haven and Cape Cod, Atlantic coast USA.
Geolocation: Unknown (New Haven, 41.2520°, -72.9086°, as a central possible place of origin on Atlantic coast USA).
WoRMS: 131000
Synonyms: Possibly *Hydroides hexagonus sensu* Pratt, 1916 and others [*non* Bosc, 1802]
Serpula dianthus citrina Verrill, 1873 (for Verrill’s colour variant specimens)
Hydroides (Eupomatus) dianthoides Augener, 1922 [*partim*, *fide* Bastida-Zavala and ten Hove 2002: 143) (Haiti, Caribbean Sea)

Hydroides diplochone **(Grube, 1878a) (originally as *Serpula* (*Hydroides*) *diplochone*)**
Status: Name now disused and representing a *species inquirenda*. A single subsequent valid usage of the name was later identified as an occurrence of *Hydroides ezoensis* (a junior name), but it is uncertain that Grube's original serpulid (type missing) was the same (*fide* Zibrowius 1978: 144; Sun et al. 2015: 37).
Etymology: Not stated, but the name for *Serpula diplochone* derives from Greek Latinized as *diplos* 'two-fold' and feminine Greek noun χοάνη (choani) 'funnel', thus double funnel, evidently in reference to the two-tier operculum that Grube describes (a generic character). There are no other names based on *chone* in Serpulidae, but it is part of several generic names in Sabellidae.
Evaluation: Invariant noun in apposition.
Type locality: Askold Island, outer Peter the Great Gulf, North Japan Sea. We infer this to be the type locality. Grube does not present location information beyond that the material was from "nordjapanischen Meeres", but it is also mentioned that the collector was the Siberian-based Polish naturalist Dybowski, whose travels in the region are documented. In 1874 Benedykt Dybowski collected fauna at Askold Island, near Vladivostok, Primorsky Krai (*fide* Zoological Museum, University of Lliv [no date]).
Geolocation: 42.7333°, 132.3333° (map estimate, Askold Island).
WoRMS: 333639
Synonyms: As *species inquirenda* has no synonyms, although *H. ezoensis* has been suggested.

Hydroides dipoma **(Schmarda, 1861) (originally as *Eupomatus dipoma*)**
Etymology: Not stated, but in the description for *Eupomatus dipoma* Schmarda (1861: 29) describes in Latin "*Operculum duplex infundibuliforme*" (double funnel lid) and in German "Das Thier hat zwei Deckel" (has two lids), evidently referring to the two opercula figured in his plate, and based on Greek δις (dis) 'twice', and πωμα (poma) 'cap' (see ten Hove and Ben-Eliahu (2005) for an analysis of records of bi-operculate specimens in *Hydroides*).
Evaluation: Invariant compound noun in apposition (indeclinable because ending in a transliterated Greek word).
Type locality: Cape of Good Hope, South Africa ("Vorgebirge der Guten Hoffnung").
Geolocation: -34.3583°, 18.4725° (Cape of Good Hope (gazetteer), although Schmarda more likely was indicating a general coastal area).
WoRMS: 369232
Synonyms: *Eupomatus spinosus* Pixell, 1913 (Gulf of Suez)
Hydroides uncinatus macronyx Ehlers, 1913 (Simonstown, False Bay, South Africa)

Hydroides dirampha **Mörch, 1863 (originally as *H.* (*Eucarphus*) *dirampha*)**
Etymology: Not stated, but for *H. dirampha* Mörch describes "*utrinque inflexione obsoleta, unde lateraliter adunco-rostrato*" (rudimentary bend both sides, hence laterally-curved beak), with the Latinization *dirampha* evidently referring to the twin sharp lateral points of the blunt tip of the verticil spines, ultimately from Greek δις (dis) 'twice',

and ϱαμφος (rampos) 'beak', the latter modified through New Latin masculine noun forms *rhamphus* and the lesser-used *ramphus* (both with a number of usages as part of compound genus names) to *rampha*, a usage seemingly unique to Mörch.

Evaluation: Treated here as an invariant noun in apposition, because an incorrect Latinization. While Mörch consistently modified his *Hydroides* names as feminine, and the name seems intended as feminine adjectival rather than a noun, it looks like a misspelled Latinization which should be left unaltered. Usages in *Hydroides* as '*diramphus*' exist (e.g., Bastida-Zavala and ten Hove 2002: 161).

Type locality: Saint (St.) Thomas Island, United States Virgin Islands, Lesser Antilles ("*in portu urbis St. Thomae Antillarum*"), most likely the Saint Thomas port town of Charlotte Amalie.

Geolocation: Imprecisely known (near to 18.34°, -64.92° if harbour at Charlotte Amalie, St Thomas Island).

WoRMS: 131001

Synonyms: *Eucarphus serratus* Bush, 1910 (Bermuda, western Atlantic)
Eupomatus lunulifer Claparède, 1870a (Gulf of Naples, Italy, Tyrrhenian Sea)
Hydroides (Eucarphus) benzoni Mörch, 1863 (Bahia coast, Brazil)
Hydroides (Eucarphus) cumingii Mörch, 1863 (Philippines unspecified)
Hydroides (Eucarphus) cumingii navalis Mörch, 1863 (New Zealand unspecified)
Hydroides malleophorus [sic] Rioja, 1942 (Mazatlán, Gulf of California, Mexico Pacific coast)

Hydroides dolabrus **Tovar-Hernández, Villalobos-Guerrero, Kupriyanova & Sun, 2016 (original binomen)**

Etymology: The authors state for *H. dolabrus* that "*dolabrus* is from the Latin *dolabra*, a sort of pickaxe that resembles the shape of the verticil spines".

Evaluation: Invariant noun in apposition. The Latin *dolabra* is a feminine noun, and cannot become a masculinised adjective as '*dolabrus*' to match a masculine *Hydroides*. This is not a word as listed in classical Latin dictionaries, and should be considered as an invariant combination of letters. A suitable adjectival equivalent would have been *dolabratus -ata*.

Type locality: Mazatlan Marina, Mazatlan, Gulf of California, Mexico Pacific coast.

Geolocation: 23.2798°, -106.4611° (authors).

WoRMS: 851651

Synonyms: No subjective synonyms.

Hydroides elegans **(Haswell, 1883) (originally as *Eupomatus elegans*)**

Status: The much-used name *H. elegans* is *nomen protectum* with respect to *nomen oblitum H. abbreviata* Krøyer [in] Mörch, 1863 (Bastida-Zavala and ten Hove, 2002).

Etymology: Not stated, but the *Eupomatus elegans* name is likely derived from the Latin adjective *elegans -antis* (genitive) 'elegant'.

Evaluation: Invariant adjective (masculine/feminine/neuter '*-ans*').

Type locality: Port Jackson, NSW, Australia (not further specified).

Geolocation: -33.8456°, 151.2622° (gazetteer).
WoRMS: 131002
Synonyms: *Hydroides abbreviata* Krøyer [in] Mörch, 1863 [*nomen oblitum*] (Saint Croix island, Virgin Islands, Caribbean Sea)
Hydroides incrustans Monro, 1938 (Shoreham Harbour Canal, Sussex, England)
Hydroides pacificus Hartman, 1969 (Velero station 1452-42, Ship hull & pier, Long Beach, California)
Hydroides spinalateralis Straughan, 1967a (Shoal Point, Mackay, Queensland, Australia)

***Hydroides elegantula* (Bush, 1910) (originally as *Eupomatus elegantulus*)**
Etymology: Not stated, but the *E. elegantulus* name is likely derived from Latin adjective *elegans -antis* 'elegant', combined with the Latin suffix *-ulus*, a male diminutive adjectival form.
Evaluation: Gender-variable adjective, corrected in *Hydroides* to feminine '*elegantula*' by Zibrowius (1971: 695).
Type locality: Bermuda. The Yale Peabody Museum holotype YPM IZ 001323.AN from the Verrill Bermuda Expedition in 1898, evidently has no further location data, but Castle Harbour is a collection site mentioned by Bush (1910).
Geolocation: Imprecisely known (possible place of origin, Castle Harbour, 32.3472°, -64.6872°, Bermuda).
WoRMS: 873929
Synonyms: No subjective synonyms.

***Hydroides euplaeana* (Delle Chiaje, 1828) (originally as *Sabella euplaeana*)**
Status: Name now disused and representing a *species inquirenda* that has been compared to *H. pseudouncinata* Zibrowius, 1968. It is not a candidate *nomen oblitum* (used as valid by Zibrowius, 1972c: 116–117). If suppression is desirable prevailing usage of *H. pseudouncinata* would be maintained (ICZN 1999, Recommendation 23A).
Etymology: Not stated, but *Sabella euplaeana* was evidently named after the Latin name for Caiola Island, Naples, where Delle Chiaje states it was collected. Caiola is modern day Gaiola, in Roman times known as Euplaea. The name as combined with feminine adjectival suffix *-ana* indicates from Euplaea.
Evaluation: Gender-variable geographical Latin adjective (*-anus*, *-ana*) from place-name, with correct original feminine ending.
Type locality: Caiola (Gaiola/Euplaea) Island, Naples, Italy, Tyrrhenian Sea, Mediterranean.
Geolocation: 40.7917°, 14.1869° (map estimate).
WoRMS: 381073
Synonyms: As *species inquirenda* has no synonyms, although *H. pseudouncinata* has been suggested.

Hydroides exaltata **(Marenzeller, 1885) (originally as *Eupomatus exaltatus*)**
Etymology: Not stated, but Marenzeller (1885: 217) described the character of the opercular verticil spines for *E. exaltatus* as being elevated on a central column ("einer centralen Säule"). The Latin *exaltatus* '(up) lifted' species-group name is perhaps in reference to this.
Evaluation: Gender-variable adjective, corrected to feminine '*exaltata*' as recombined (e.g., Imajima 1976b: 232). Usages in *Hydroides* as '*exaltatus*' exist (e.g., Dew 1959: 27).
Type locality: East coast of Enoshima Island ("Ostküste der Insel Eno-sima"), Sagami Bay, Honshu, Japan. There is an Enoshima-rettō Island, also off Honshu, but the Sagami Bay Enoshima Island (only ~0.5 km long) is the most likely visited.
Geolocation: 35.3008°, 139.4839° (map estimate).
WoRMS: 873938
Synonyms: No subjective synonyms.

Hydroides exaltata vesiculosa **Fauvel, 1919 (originally as *H. exaltatus* var. *vesiculosus*)**
Status: Name now disused and representing a *species inquirenda*. Similarities of the original description to *Hydroides albiceps* have been noted, but the name is yet to be synonymised.
Etymology: Not stated, but *H. exaltata vesiculosa* was evidently named for its vesicular dorsal verticil spine.
Evaluation: Gender-variable adjective with incorrect original ending, corrected to feminine (e.g., Monro 1937: 316).
Type locality: Gatavaké (Baie de Gatavaké), Mangareva Island, Mangareva/Gambier Islands, French Polynesia, South Pacific.
Geolocation: -23.1188°, -134.9798° (map estimate).
WoRMS: 875068
Synonyms: As *species inquirenda* has no synonyms.

Hydroides externispina **Straughan, 1967b (original binomen)**
Etymology: Not stated, but for *H. externispina* it is likely the Latin *spina* 'thorn' refers to the external (curved outwards) spines of the verticil.
Evaluation: Invariant noun in apposition.
Type locality: Heron Island, Queensland, Australia, collected close to the marine station by Dew (map in Straughan 1967b).
Geolocation: -23.4430°, 151.9110° (map estimate).
WoRMS: 328446
Synonyms: No subjective synonyms.

Hydroides ezoensis **Okuda, 1934 (original binomen)**
Etymology: Not stated, but *H. ezoensis* is evidently named after its area of collection, as Ezo (also as Yezo) is a former name for the island of Hokkaido, Japan. The species-group name '*ezoensis*' has often been used for Japanese taxa, along with '*yezoensis*'.

Evaluation: Masculine/feminine invariant '-*ensis*' adjective created from non-Latin geographic name.
Type locality: Not fixed by author. Original records are from "Akkeshi, Muroran, and Oshoro", which are widely separated places around the coast of Hokkaido Island, with the first two having marine stations.
Geolocation: Imprecisely known (possibly as 43.0209°, 144.8368° for Akkeshi Marine Station).
WoRMS: 131003
Synonyms: See comments for *H. diplochone*.

Hydroides floridana (Bush, 1910) (originally _Eupomatus floridanus_, new name for _Eupomatus uncinatus_ non Philippi _sensu_ Ehlers, 1887)
Etymology: Not stated, but *E. floridanus* is evidently named after its purported region of collection. 'Florida' is Spanish for flowery land and is here combined with the Latin adjectival suffix *-anus -a -um*, indicating from Florida.
Evaluation: Gender-variable adjective based on a non-Latin geographic name, corrected to feminine herein. Usages in *Hydroides* as '*floridanus*' exist (e.g., Bastida-Zavala and ten Hove 2002: 118) but not previously as '*floridana*'.
Type locality: Unknown, not certain to be off namesake Florida. When Ehlers (1887: 286) described the Polychaeta collected from voyages of Coast Survey Steamer "Blake" he wrote in his native German but recorded the two locations for the *Eupomatus* specimens literally in English as "inside fishing ground Cape Rear" and also "off W. down Cape Dear Rio" (both at 7 fathoms). However, these place-names seem to be misreadings as they could not be found in the Caribbean or Florida, nor do the "Blake" voyage reports include the names. The similarity of names suggests the location is possibly off Cape Fear, North Carolina, with its associated Cape Fear (Rio) River, disregarding that Ehlers' monograph title appears to exclude Atlantic coast voyages the "Blake" also made. As the types are believed lost the original label cannot be checked. No specimens are currently listed in the Yale Peabody Museum online catalogue although Bush (1910: 498) earlier saw a mass of several hundred tubes, indicating an aggregation.
Geolocation: Unknown (if off Cape Fear, North Carolina then that place-name is at (gazetteer) 33.84°, -77.96°).
WoRMS: 369234
Synonyms: *Eupomatus decorus* Treadwell, 1931 (Grand Isle, Louisiana, Gulf of Mexico)
Hydroides rostrata Iroso, 1921 [junior objective synonym (same specimen)]

Hydroides furcifera (Grube, 1878b) (originally as _Serpula furcifera_)
Etymology: Not stated but Grube described for *S. furcifera* forked spines in the opercular funnel as well as the verticil, thus Latin *furca* 'fork', combined with adjectival

suffix *-fer -a -um* ‘bear’. Lewis and Short (1891: 795) include *furcifera* as a feminine noun meaning phallus, but it is unlikely this was Grube’s intention. A more common adjectival form would be *furcillata* ‘forked’.
Evaluation: Gender-variable adjective with correct original feminine ending. Names ending in *-fer* may be nouns or masculine adjectives (ICZN 1999, Article 31.2.2 example). The usage of Grube was adjectival as he used feminine *-fera*. A listing-only usage in *Hydroides* as ‘*furcifer*’ exists (ten Hove and Kupriyanova 2009: 53).
Type locality: “Ubay, Pandanon”, Philippines. Ubay (10.0606°, 124.4707°) is a small port on Bohol Island, and Pandanon Island (10.1779°, 124.0839°) is a small reef ~45 km to the west of Ubay.
Geolocation: 10.0606°, 124.4707° (map estimate, Ubay).
WoRMS: 369235
Synonyms: *Hydroides bifidus* [sic] Imajima, 1982 (off Arumonogui, Palau Islands, Micronesia)

Hydroides fusca **Imajima, 1976a (original binomen)**

Etymology: Not stated, but the species-group name for *H. fusca* from Latin *fuscus* ‘dark’ is evidently in reference to the “glossy black” verticil spines.
Evaluation: Gender-variable adjective with correct original feminine ending. A listing-only usage in *Hydroides* as ‘*fuscus*’ exists (ten Hove and Kupriyanova 2009: 53).
Type locality: Offshore east off northern tip of Tanegashima (island), Southern Japan, 80 m.
Geolocation: 30.8225°, 131.1335° (map estimate from author’s map).
WoRMS: 369236
Synonyms: No subjective synonyms.

Hydroides fusicola **Mörch, 1863 (as *H.* (*Eupomatus*) *fusicola*)**

Etymology: Not stated, but *H. fusicola* is evidently named after the gastropod genus *Fusus* (now *Fusinus*) combined with *-cola* ‘dweller’, as it was found attached to a ‘*Fuso*’ sp.
Evaluation: Invariant compound noun in apposition with *-cola* as a substantival suffix. The Code has a stipulation (ICZN 1999, Article 30.1.4.2) that genera with *-cola* endings be treated as masculine compound nouns (or mostly so treated, similar to the *-oides* situation). It has no advice for species-group names with *-cola* suffixes, but they are recommended to be treated similarly (David and Gosselin 2002: 34), not declined to agree with the first noun or the genus.
Type locality: Japan (not further specified). Mörch only knew the specimen was from the collection of Wessel in Hamburg.
Geolocation: Unknown (gazetteer Japan central point as 37°, 138°).
WoRMS: 369237

Synonyms: *Hydroides okudai* Pillai, 1972 [*nom. n.* for "*H. uncinata* (*sensu* Okuda et Uschakov)"] (location not fixed by author, but the Okuda (1937: 63) usage was for Ishihama, Japan, a name for at least four possible Honshu coastal locations)

Hydroides gairacensis **Augener, 1934 (originally as *H.* (*Eupomatus*) *gairacensis*)**

Status: Candidate *nomen protectum* against senior name *Hydroides* (*Eupomatus*) *dunkeri* Mörch, 1863 (*fide* Bastida-Zavala and ten Hove, 2002: 132). Prevailing usage maintained pending proof of sufficient usage of *H. gairacensis*, but *H. dunkeri* is a *nomen oblitum*, not used as a valid name after 1899 (listings are excluded as usages under ICZN 1999, Article 23.9.6).
Etymology: Not stated, but *H. gairacensis* is evidently named after its place of collection, Gairaca.
Evaluation: Masculine/feminine invariant '*-ensis*' adjective created from a non-Latin place-name.
Type locality: Gairaca, near Santa Marta, Caribbean Sea coast of Colombia.
Geolocation: 11.3184°, -74.1084° (map estimate).
WoRMS: 369238
Synonyms: *Hydroides (Eupomatus) dunkeri* Mörch, 1863 [*nomen oblitum*] (La Guayra, Panama, Caribbean Sea)

Hydroides glandifera **Rioja, 1941a (originally as *H. glandiferum*)**

Status: Type taxon by monotypy of *Olgaharmania* Rioja 1941b, a synonym of *Hydroides*.
Etymology: Not stated, but as Rioja (1941a: 174) writes of "una robusta protuberancia . . .en forma de glande" for *H. glandifera*, it is likely to be a functional name for the bulbous dorsal verticil spine from Latin *glans* 'acorn' combined with adjectival suffix *-fer -a -um* 'bear'. It is unclear why Rioja (incorrectly) used the neuter form '*glandiferum*' at first, but he later (Rioja 1941b: 733) modified the spelling for his feminine *Olgaharmania glandifera* combination.
Evaluation: Gender-variable adjective with corrected feminine ending. Usages in *Hydroides* as '*glandifer*' and '*glandiferum*' exist (e.g., Bastida-Zavala and ten Hove 2003: 89).
Type locality: Caleta (Playa Caleta), Acapulco, Mexico.
Geolocation: 16.8313°, -99.9031° (map estimate).
WoRMS: 338016
Synonyms: No subjective synonyms.

Hydroides glasbyi **Sun, Wong, ten Hove, Hutchings, Williamson & Kupriyanova, 2015 (original binomen)**

Etymology: The authors dedicated *H. glasbyi* to Christopher J. Glasby.
Evaluation: Invariant genitive form *glasbyi* of the personal name Glasby.
Type locality: Fort Hill Wharf, Darwin, Northern Territory, Australia.

Geolocation: -12.4714°, 130.8467° (authors, 12°28'17"S, 130°50'48"E).
WoRMS: 852813
Synonyms: No subjective synonyms.

***Hydroides gracilis* (Bush, 1905) (originally as *Eupomatus gracilis*)**
Etymology: Not stated, but the Latin *gracilis* 'slender' name for *H. gracilis* is likely referring to the simple verticil spines.
Evaluation: Invariant adjective (masculine/feminine '*gracilis*').
Type locality: Pacific Grove, California, Pacific coast USA.
Geolocation: 36.6236°, -121.9119° (map estimate).
WoRMS: 333640
Synonyms: *Eupomatus intereans* Chamberlin, 1919 (Laguna Beach, California coast)

***Hydroides gradata* Straughan, 1967a (original binomen)**
Status: The synonymy of *H. basispinosa* and *H. gradata* Straughan, 1967a with *H. operculata* Treadwell, 1929 was followed by Sun et al. (2015: 63), but is being re-examined, and we provisionally include the *H. gradata* record separately.
Etymology: Not stated, but for *H. gradata* the Latin *gradata* 'gradual' is evidently describing the gradual size change of the ring of opercular spines.
Evaluation: Gender-variable adjective with correct original feminine ending.
Type locality: Pretty Beach, 40 km north of Cairns, Queensland, Australia
Geolocation: -16.6111°, 145.5318° (map estimate).
WoRMS: 384604
Synonyms: See *H. operculata* comments.

***Hydroides helmata* (Iroso, 1921) (originally as *Eupomatus helmatus*)**
Status: Zibrowius (1971: 713–714) synonymised an older name, *Eupomatus affinis* Marion, 1875, under *H. helmata*. This is not possible on priority, nor does *H. affinis* qualify as a *nomen oblitum* as it was used as valid (Zibrowius 1968: 115) post 1899. We include both names (see entry for *H. affinis* as *species inquirenda*).
Etymology: Not stated, but *E. helmatus* is likely named after the larger helmet-like dorsal verticil spine as Iroso (1921: 54) describes "che ricade sugli altri ad elmo" (which falls on others [spines] helmet-like). Helm and helmet are not from Latin, though the author's construction appears to be intended as adjectival, with adjectival suffix *-atus* added to mean helm-like.
Evaluation: Gender-variable adjective corrected to feminine in *Hydroides* in Zibrowius (1971: 713).
Type locality: Unspecified Gulf of Naples (Golfo di Napoli), Italy.
Geolocation: Imprecisely known (a Golfo di Napoli mid-point (gazetteer) is 40.8°, 14.2°).
WoRMS: 131004
Synonyms: No subjective synonyms, but has been linked to *H. affinis* (see above).

***Hydroides heterocera* (Grube, 1868) (originally as *Serpula* (*Eupomatus*) *heterocerus*)**
Etymology: Not stated but the name for *S. heterocerus* is likely describing the dimorphism in verticil spines, from Greek hετεϱοσ (*heteros*) 'different' and ϰεϱασ (*keras*) 'horn'. The Latinized *heterocerus* is an adjectival form to be declined.
Evaluation: Gender-variable adjective corrected to feminine in Zibrowius (1971: 715). Grube (1868: 639) originally incorrectly created a masculine '*heterocerus*' in agreeing with the masculine subgenus *Eupomatus* rather than the feminine genus *Serpula*. Usages exist in *Hydroides* as '*heterocerus*' (e.g., Ben Eliahu and ten Hove 2011: 26), and as the misspelling '*heteroceros*' (e.g., Day 1967: 807).
Type locality: Unspecified Red Sea. Grube's report title refers to Red Sea worms collected by Georg Ritter von Frauenfeld. Grube states in his opening sentence that the worms were handed to him without any other information, and it seems he did not investigate this further. In the narrative of his visit von Frauenfeld (1855) mentions Suez, the Sinai Peninsula, and seeing countless annelids on the Red Sea shore, but he does not match observation to locality.
Geolocation: Imprecisely known, but perhaps northern Red Sea (a gazetteer Red Sea mid-point is 20.3°, 38.6°).
WoRMS: 851900
Synonyms: No subjective synonyms. However, the misidentification *Serpula* (*Hydroides*) *uncinata non* Philippi, *sensu* Gravier, 1906, has been assigned to *H. heterocera* (e.g., Pixell 1913: 75).

***Hydroides heterofurcata* Pillai, 1971 (original binomen)**
Etymology: Not stated, but evidently *H. heterofurcata* is named because there are two types of furcate verticil spines of the operculum (Pillai 1971: 114).
Evaluation: Gender-variable adjective with correct original feminine ending. Usages as '*heterofurcatus*' exist (e.g., ten Hove and Kupriyanova 2009: 53).
Type locality: near Talaimannar Pier, Sri Lanka, 4 m depth.
Geolocation: 9.1079°, 79.7292° (map estimate from author map).
WoRMS: 328449
Synonyms: No subjective synonyms.

***Hydroides hexagona* (Bosc, 1802) (originally *Serpula hexagona*)**
Status: A name disused by taxonomists and representing a *species inquirenda*. The original description and figure are rudimentary and the species Bosc saw will remain indeterminable unless original specimens are found (unlikely). However, the name cannot be a *nomen oblitum* as it was revived as *H. hexagonus* [sic] in three widely used manuals on invertebrates of the United States eastern coast (Pratt 1916, Grave 1937, Costello et al. 1957). These instances should be considered misidentifications, and might be referable either to the junior name *H. dianthus* (*fide* Zibrowius 1971: 697, Bastida-Zavala and ten Hove 2002: 108), or to other similar species. Nevertheless, there are multiple

modern citations of the research on *Hydroides* sperm (e.g., Colwin and Colwin 1961) in which the name appeared.
Etymology: Bosc described the tube of *Serpula hexagona* as “montrant la moitié d’un prisme hexagone …”, and the name is a New Latin adjectival form for six-sided, modified from Greek. Bosc’s figure shows two ridges so the tube cross-section would be trapezoidal, not literally hexagonal as named, but half (la moitié) of that.
Evaluation: Gender-variable adjective with correct feminine ending herein. Usages in *Hydroides* as ‘*hexagonus*’ and ‘*hexagonis*’ exist (e.g., Pratt 1916: 302, Grave and Oliphant 1930: 234) but not previously as ‘*hexagona*’.
Type locality: Charleston Harbour, Charleston, South Carolina, Atlantic coast USA.
Geolocation: 32.8186°, -79.9279° (gazetteer).
WoRMS: 384606
Synonyms: As *species inquirenda* has no synonyms.

Hydroides homoceros Pixell, 1913 (original binomen)
Etymology: Not stated, but for *H. homoceros* it is likely that the Greek hομοσ (*homos*) ‘uniform’ and κερασ (*keras*) ‘horn’, refers to the opercular verticil spines. Pixell appears to have named ‘*homoceros*’ as the opposite to ‘*heteroceros*’ (her error for the existing ‘*heterocerus*’) which she mentions.
Evaluation: Incorrect Latinization treated here as an unchanging noun in apposition. Usages exist as ‘*homocera*’ (e.g., Ben-Eliahu and ten Hove 1992: 35) and ‘*homocerus*’ (e.g., Bellan 2001: 226).
Type locality: Multiple Indian Ocean localities as the syntypes (aggregated as only one NHM specimen lot 1924.6.13.147 received from the Cyril Crossland Collection) came both from the Maldive area (specified as Miladhunmadulu Atoll and Minikoi), and from off Zanzibar.
Geolocation: Unknown (map estimate 6.02°, 73.19° for Noonu, the southern Miladhunmadulu Atoll).
WoRMS: 238212
Synonyms: No subjective synonyms.

Hydroides huanghaiensis Sun & Yang, 2000 (original binomen)
Etymology: Not stated, but *H. huanghaiensis* is evidently named after the sea in which the worm was collected as “Huanghai” means Yellow Sea in Chinese.
Evaluation: Masculine/feminine invariant ‘*-ensis*’ adjective created from a non-Latin geographic name, Huanghai.
Type locality: Northern Yellow Sea, off the Chinese coast near Dalian.
Geolocation: 39.00°, 122.1167° (as authors, 39°00'N, 122°70'E [? error for 7']).
WoRMS: 328450
Synonyms: No subjective synonyms.

Hydroides humilis (Bush, 1905) (originally as _Eupomatus humilis_)
Etymology: Not stated, but for *E. humilis* possibly the name, from Latin *humilis* 'humble' (or 'low'), is referring to the small size of the single specimen collected.
Evaluation: Masculine/feminine invariant adjective (*humilis -e*) (Stearn 1983: 94).
Type locality: Guaymas, Gulf of California coast, Sonora state, Mexico. Bush provides no other details other than the name Guaymas (Mexico).
Geolocation: 27.9087°, -110.8931° (map estimate).
WoRMS: 369239
Synonyms: No subjective synonyms.

Hydroides inermis Monro, 1933 (original binomen)
Etymology: Not stated, but for *H. inermis* it is likely that the Latin *inermis* 'unarmed', is referring to the verticil spines without spinules. Monro stated the operculum "lacks spines both on the lower and the upper calix".
Evaluation: Masculine/feminine invariant adjective (*inermis -e*).
Type locality: James Bay, Isla Santiago (was James Island), Galapagos, Ecuador.
Geolocation: -0.1959°, -90.8424° (map estimate).
WoRMS: 338017
Synonyms: No subjective synonyms.

Hydroides inornata Pillai, 1960 (original binomen)
Status: The current synonymy of *H. inornata* with *H. operculata* is being re-evaluated, and meantime it is included separately here.
Etymology: Not stated, but for *H. inornata* it is likely that the Latin *inornatus* 'unadorned' is referring to the verticil spines without side spinules.
Evaluation: Gender-variable adjective with correct original feminine ending. Usages as '*inornatus*' exist (e.g., Amoureux et al.: 57).
Type locality: Maha Alamba (not found, perhaps disused), "about a mile" from the Negombo Lagoon entrance (an aquatic research institute is nearby), north of Colombo, west coast of Sri Lanka.
Geolocation: 7.1945°, 79.8392° (map estimate).
WoRMS: 338018
Synonyms: No subjective synonyms, and has been regarded as junior to *H. operculata* (e.g., Sun et al. 2015: 62).

Hydroides kimberleyensis Pillai, 2009 (original binomen)
Etymology: The author named *H. kimberleyensis* after the Kimberley region of Western Australia.
Evaluation: Masculine/feminine invariant '*-ensis*' adjective created from a non-Latin geographic name.

Type locality: Off east side of Fenelon Island (main island of Institut Islands) at 6 m, Kimberley, Western Australia.
Geolocation: -14.1167°, 125.7167° (author).
WoRMS: 555195
Synonyms: No subjective synonyms.

Hydroides lambecki **Bastida-Zavala & ten Hove, 2002 (original binomen)**
Etymology: The authors named *H. lambecki* after Hugh J.P. Lambeck (entomologist, deceased, one time assistant to ten Hove), who first noted this as a species different from *H. mongeslopezi*.
Evaluation: Invariant genitive form *lambecki* of the personal name Lambeck.
Type locality: Vaarsenbaai (cove), Boca Sami, Curaçao, Netherlands Antilles.
Geolocation: 12.15°, -69.00° (gazetteer).
WoRMS: 328452
Synonyms: No subjective synonyms.

Hydroides lirs **Kupriyanova, Sun, ten Hove, Wong & Rouse, 2015 (original binomen)**
Etymology: The authors named *H. lirs* after the Australian Museum's Lizard Island Research Station (LIRS).
Evaluation: Invariant non-Latinized noun in apposition '*lirs*' from an acronym, pronounced as a single word.
Type locality: Front of reef between Bird and South Islands, Lizard Island, Queensland, Australia, -14.6978°, 145.4639° (station MI QLD 2354 in Ribas and Hutchings, 2015).
Geolocation: -14.6978°, 145.4639° (station list).
WoRMS: 877990
Synonyms: No subjective synonyms.

Hydroides longispinosa **Imajima, 1976b (original binomen)**
Etymology: Not stated, but *H. longispinosa* evidently is named after the "conspicuous, long central spine" (long in comparison with *H. elegans*), based on Latin adjectives *longus* 'long' with *spinosus* 'spined'.
Evaluation: Gender-variable adjective with correct original feminine ending. Usages as '*longispinosus*' exist (e.g., Bailey-Brock 1987: 282).
Type locality: Koniya, Amami-Oshima, Amami Islands, Southern Japan.
Geolocation: 28.1472°, 129.3078° (map estimate).
WoRMS: 328453
Synonyms: *Hydroides centrospina* Wu & Chen, 1981 (Yulin Harbour, Hainan Island, South China Sea)

Hydroides longistylaris Chen & Wu, 1980 (original binomen)
Etymology: Not stated, but for *H. longistylaris* evidently the Latin *longus* 'long' and adjectival Latinization of Greek στυλος (stylos) 'pillar' refers to the long, elongated basis of the opercular funnel, thus 'pillar-like'.
Evaluation: Masculine/feminine invariant adjective (*-stylaris -e*).
Type locality: Shellfish farms, Zhangpu (Zhangzhou), Fujian Province, China.
Geolocation: 24.4379°, 117.9762° (map estimate).
WoRMS: 328454
Synonyms: No subjective synonyms.

Hydroides malleolaspina Straughan, 1967a (original binomen)
Etymology: Not stated, but the name for *H. malleolaspina* is evidently a compound noun from Latin *malleolus* 'small hammer', referring to the dorsal hammer-shaped verticil spine, and *spina* 'thorn'.
Evaluation: Invariant noun in apposition. Usages as '*malleolaspinus*' exist (e.g., Murray et al. 2010: 393).
Type locality: Pialba, Hervey Bay, Queensland, Australia.
Geolocation: -25.2747°, 152.8345° (map estimate).
WoRMS: 369240
Synonyms: "*Hydroides trihamulatus*" [sic] Pillai, 2009 [unavailable name (no type-designation), assignment by Murray et al. 2010] (Australia)

Hydroides microtis Mörch, 1863 (originally as _H._ (_Eucarphus_) _microtis_)
Etymology: Not stated, but for *H. microtis* the '*micro*' derives from Greek μικρος (micros) 'small', and perhaps is combined with Greek neuter noun genitive οτοσ (otos) 'ear'. The Latinizations '*microtis*' and '*microtus*' are in use as both genus and species-group names for small-eared biota. Whether the same derivation applies for *H. microtis* is unclear, as the verticil spines are knob-tipped and not notably small or ear-like.
Evaluation: Invariant whether a noun in apposition or (masculine/feminine) intended as adjectival.
Type locality: North America (unspecified) as "*ad Americam borealem*" on *Argopecten irradians* (was as *Pecten*), collected by A. B. Mayer, presumably on the Atlantic coast as *A. irradians* is the bay scallop of that region.
Geolocation: Unknown (unspecified Atlantic coast of North America, with 44°, -68° the mid point of the coastal extent).
WoRMS: 333641
Synonyms: No subjective synonyms.

Hydroides minax (Grube, 1878b) (originally as _Serpula minax_)
Etymology: Not stated, but for *S. minax* the Latin adjective *minax -acis* meaning 'jutting out' is likely referring to the enormous dorsal verticil spine.
Evaluation: Invariant adjective (masculine/feminine '*minax*').
Type locality: Philippines (unspecified).
Geolocation: Unknown (12°, 122° (gazetteer) is central to the Philippines Islands).
WoRMS: 131007
Synonyms: *Serpula* (*Hydroides*) *monoceros* Gravier, 1906 (Bonhoure Recif, Djibouti, Gulf of Aden)

Hydroides mongeslopezi Rioja, 1958 (original binomen)
Etymology: The author named *H. mongeslopezi* after Ricardo Monges López of Veracruz.
Evaluation: Invariant genitive noun *mongeslopezi* from modern personal name of Monges López.
Type locality: On floating pumice, Playa Norte, Isla Santiaguillo, Veracruz, Gulf of Mexico.
Geolocation: 19.1634°, -95.8502° (map estimate).
WoRMS: 328456
Synonyms: No subjective synonyms.

Hydroides monroi Zibrowius, 1973 (original binomen)
Etymology: Not stated, but the species *H. monroi* is evidently named after C. C. A. (Charles Carmichael Arthur) Monro, who had studied the specimens earlier.
Evaluation: Invariant genitive noun *monroi* from modern personal name of Monro.
Type locality: Pointe Noire, Congo, West Africa.
Geolocation: -4.7858°, 11.8361° (map estimate).
WoRMS: 328457
Synonyms: No subjective synonyms.

Hydroides mucronata Rioja, 1958 (original binomen)
Etymology: Not stated, but the name for *H. mucronata* is evidently referring to the pointed (Latin *mucronatus*) side spines of the verticil spines "que tienen forma de mucron" (Rioja 1958: 256).
Evaluation: Correct original adjectival feminine ending. Usages as '*mucronatus*' exist (e.g., Bastida-Zavala and ten Hove 2002: 141).
Type locality: Isla de Sacrificios, Veracruz, Gulf of Mexico.
Geolocation: 19.1749°, -96.0929° (map estimate).
WoRMS: 328458
Synonyms: No subjective synonyms.

Hydroides multispinosa Marenzeller, 1885 (original binomen)
Etymology: Not stated, but the name for *H. multispinosa* evidently refers adjectivally to multiple lateral spinules on the verticil spines.
Evaluation: Correct original adjectival feminine ending. Usages as masculine '*multispinosus*' exist (e.g., ten Hove and Kupriyanova 2009: 54).
Type locality: Shore at Eno-sima (Enoshima), Sagami Bay, Honshu, Japan. There is an Enoshima-rettō Island, also off Honshu, but the Sagami Bay Enoshima is the most likely visited.
Geolocation: 35.2977°, 139.4817° (map estimate).
WoRMS: 335316
Synonyms: No subjective synonyms.

Hydroides nanhaiensis Wu & Chen, 1981 (original binomen)
Etymology: Not stated, but *H. nanhaiensis* is evidently named broadly geographically as "Nanhai" is the South China Sea in Chinese.
Evaluation: Masculine/feminine invariant '*-ensis*' adjective created from a non-Latin geographic area name.
Type locality: Xi River estuary, Pearl River Delta, Macao, Guangdong, China coast, South China Sea, 58m, fixed on rock, stations 6016, 6044 (*fide* Sun and Yang 2014: 218 (map), 241; no locality in the original text).
Geolocation: 22.0602°, 113.4792° (map estimate, Xi River mouth).
WoRMS: 328459
Synonyms: No subjective synonyms.

Hydroides nigra Zibrowius, 1971 (original binomen)
Etymology: Not stated, but the name for *H. nigra* is evidently referring to the dark colour of the operculum, especially of the opercular constriction ("un anneau noir à la base de l'opercule") and the verticil spines, and derived from the Latin adjective *niger, nigra, nigrum* 'black'.
Evaluation: Gender-variable adjective with correct original feminine ending. Usages as '*niger*' exist (e.g., Bellan 2001: 226)).
Type locality: Tabarka "au large de l'ile [Tabarka] et de la Pointe Meloula [4 km west]", Tunisia, Mediterranean Sea.
Geolocation: 36.9666°, 8.7588° (map estimate for north end of Tabarka).
WoRMS: 328460
Synonyms: No subjective synonyms.

Hydroides nikae Sun, Wong, Tovar-Hernández, Williamson & Kupriyanova, 2016 (original binomen)
Etymology: The authors named *H. nikae* after Nika Mikhin, daughter of Kupriyanova.

Evaluation: Invariant feminine genitive form *nikae* of given name Nika.
Type locality: Edithburgh Jetty, Edithburgh, St Vincent Gulf, South Australia.
Geolocation: -35.0848°, 137.7488° (adjusted to jetty from authors' inland 35°05'S, 137°44'(should be 45') E).
WoRMS: 871949
Synonyms: No subjective synonyms.

Hydroides nodosa Straughan, 1967a (original binomen)

Etymology: Not stated, but *H. nodosa* is likely named for the internal "rounded projection" at the base of each verticil spine, from the adjective *nodosus -a -um* 'knotty'.
Evaluation: Gender-variable adjective with correct original feminine ending. Usages as '*nodosus*' exist (e.g., ten Hove and Kupriyanova 2009: 54).
Type locality: Tannum Sands, Gladstone, Queensland, Australia.
Geolocation: -23.93°, 151.37° (map estimate *fide* Australian Museum holotype W.4013 catalogue record).
WoRMS: 328461
Synonyms: No subjective synonyms.

Hydroides norvegica Gunnerus, 1768 (original binomen)

Status: The type species of the genus (by monotypy).
Etymology: Not stated, but the name for *H. norvegica* is evidently derived from the country of collection, Norway (Latin *Norvegia*), from which the feminine-suffix adjective '*norvegica*' is derived.
Evaluation: Gender-variable adjective based on a geographic name. *H. norvegica* was given a species-group name with a feminine ending. Many usages as '*norvegicus*' exist (e.g., Moen 2006: 115).
Type locality: Trøndelag region, Norway. Trondheimsfjord off Statsbygd is one of three locations mentioned by Gunnerus (see Moen, 2006: 118).
Geolocation: Imprecisely known (map estimate 63.4687°, 10.011° for off Statsbygd).
WoRMS: 131009
Synonyms: There is an extensive list by McIntosh (1923: 347) of early serpulid names and usages in *Eupomatus*, *Hydroides, Serpula*, and *Vermilia* that are suggested to be *Hydroides norvegica* synonyms. Nine of the placements were repeated later in a world catalogue (Hartman 1959), but only two can be confirmed here (see Read and Fauchald 2016 for status of the remainder). Also Mörch, 1863 named a subspecies *H. norvegica gronlandica*, based on a Fabricius MS, but it is a *nomen dubium* unlikely to be a *Hydroides*.
Eupomatus trypanon Claparède, 1870b (Gulf of Naples, Italy, Tyrrhenian Sea)
Serpula solitaria Bean, 1844 (Scarborough, North Yorkshire, England)

Hydroides novaepommeraniae Augener, 1925 (originally as _Hydroides_ (_Eupomatus_) _novae-pommeraniae_)

Etymology: Not stated, but the name for *H. novaepommeraniae* is evidently a Latinized form of the former name of the island of collection, New Britain, Bismarck Archipelago, now part of Papua New Guinea, once a German colony named Neupommern, after the Baltic (Ostsee) coastal lands besides Pommersche Bucht.
Evaluation: Invariant noun in the genitive case created from a non-Latin geographic name Latinized as '*novaepommeran*'.
Type locality: "Hanam-Hafen" (Hannan or Garua Harbour), north coast of New Britain, Papua New Guinea.
Geolocation: -5.2833°, 150.0333° (map estimate).
WoRMS: 131010
Synonyms: *Hydroides grubei* Pillai, 1965 (Binakayan, Cavite, Manila Bay, Philippines)

Hydroides ochotereana Rioja, 1941a

Etymology: Rioja (1941a: 167) stated the name for *H. ochotereana* was "dedicar esta especie al Maestro D. Isaac Ochoterena", but he used the spelling '*ochotereana*' for the species-group name.
Evaluation: Incorrect Latinization to be treated as a noun in apposition. The use of *H. ochotereana* has been regarded as an accidental incorrect original spelling by Bastida-Zavala and ten Hove (2003), who cited Article 32.5 (ICZN 1999) as justification for using '*ochoterena*', although that would be an unchanged noun in apposition, rather than a genitive. Instead, we cannot reject the likelihood that Rioja had intentionally used the altered '*-eana*' ending (after all he used it consistently five times but correctly spelled the name of dedicatee Ochotorena) aiming to create an adjectival form of Ochotorena. His adaptation could be intended as a rendering using the suffix '*-anus*' *-ana*' (belonging to), frequently used for adjectival Latinization of nouns based on personal and geographic names. As it was the author who was responsible for an incorrect Latinization (ICZN 1999, Article 32.5.1) his original spelling is not corrected (also see Welter-Schultes, 2013: 77). This also avoids the name looking like an authorship (ICZN 1999, recommendation 31A).
Type locality: La Aguada and La Quebrada beaches, Acapulco, Mexico.
Geolocation: 16.8461°, -99.9156° (La Quebrada, map estimate).
WoRMS: 328462
Synonyms: No subjective synonyms.

Hydroides operculata (Treadwell, 1929) (originally as _Eupomatus operculata_ [sic])

Etymology: Not stated, but the name for *E. operculata* derives from the Latin verb *operculo -avi -atum* 'to cover', and in New Latin *operculata* is used as an adjectival form. It is unclear why Treadwell chose the name as all *Hydroides* have opercula. His specimen was endowed with two, but he didn't name it '*bioperculata*'.

Evaluation: Gender-variable adjective with incorrect original feminine ending for *Eupomatus*. Usages in *Hydroides* as '*operculatus*' exist (e.g., Bellan 2001: 226).
Type locality: Berbera, Somaliland, Gulf of Aden.
Geolocation: 10.441°, 45.0075° (map estimate).
WoRMS: 131011
Synonyms: *Hydroides basispinosa* Straughan, 1967a [re-evaluating, see listing herein]
Hydroides gradata Straughan, 1967a [re-evaluating, see listing herein]
Hydroides inornata Pillai, 1960 [re-evaluating, see listing herein]

Hydroides panamensis Bastida-Zavala & ten Hove, 2003 (original binomen)
Etymology: The authors state that *H. panamensis* is named "for its distribution, as far as known yet restricted to the Pacific side of Panama (and adjacent areas)."
Evaluation: Masculine/feminine invariant '*-ensis*' adjective created from a non-Latin geographic name.
Type locality: Paitilla Beach (Punta Paitilla), Panama City, Western Panama.
Geolocation: 8.9733°, -79.5183° (map estimate).
WoRMS: 328464
Synonyms: No subjective synonyms.

Hydroides parva (Treadwell, 1902) (originally as _Eupomatus parvus_)
Etymology: Not stated, but Treadwell (1902: 210) stated the specimens of *E. parvus* were "very small" (6 mm) thus Latin *parvus* 'small'.
Evaluation: Gender-variable adjective recombined in *Hydroides* with correct feminine ending (e.g., Zibrowius 1971: 712, 717). Usages in *Hydroides* as '*parvus*' exist (e.g., Hartman 1956: 250).
Type locality: West coast of Puerto Rico, Caribbean Sea, at both Boqueron Bay and nearby Mayagüez Harbour (station 6062, estimated 18.2°, -67.17°), as Treadwell had specimens from both locations. No station geolocations appear to have been available for the various *Fish Hawk* 'Porto Rico' stations (Treadwell 1939). Syntypes (USNM 16173) in the Smithsonian National Museum of Natural History are recorded as from Boqueron Bay (Bahia de Boqueron).
Geolocation: 18.0208°, -67.1987° (map estimate, Bahia de Boqueron).
WoRMS: 876557
Synonyms: No subjective synonyms.

Hydroides pectinata (Philippi, 1844) (originally as _Eupomatus pectinatus_)
Status: Name now disused and representing a *species inquirenda.* It is not eligible as a candidate *nomen oblitum* (used in taxonomy by Iroso 1921: 49, Naples), but is indeterminable unless original specimens are found. The operculum figured by Philippi is similar to that of *H. elegans* (Haswell, 1883) (*fide* Zibrowius 1971: 718).

Etymology: Philippi's brief Latin description of *E. pectinatus* describes the operculum spines as '*utrinque pectinatis*' (pectinate both sides) with three sharp teeth. The Latin adjective *pectinatus* indicates comb-like divisions.
Evaluation: Gender-variable adjective recombined in *Hydroides* with correct feminine ending (e.g., Mörch, 1863: 377).
Type locality: Unspecified Mediterranean, but can be narrowed to the Tyrrhenian Sea coast of Italy as Philippi's activities were in western Italy, and plausibly to Naples as he was based there prior to 1844.
Geolocation: Unknown (Tyrrhenian Sea, with Naples shore (40.8327°, 14.2358° map estimate) a possible point location).
WoRMS: 393822
Synonyms: As *species inquirenda* has no synonyms although *H. elegans* has been suggested.

Hydroides perezi Fauvel, 1918 (original binomen)

Etymology: Fauvel announces on the first page of his article that *H. perezi* is dedicated to "M. Ch. Pérez", who collected the worms off the Arabian coast.
Evaluation: Invariant genitive form *perezi* from personal name Pérez.
Type locality: Pearling banks (within 24°55'N–25°10'N, 54°40'E–55°10'E) dredged ~15 miles from the coast of Oman (currently near Dubai, UAE) (Fauvel 1918: 329).
Geolocation: 25.0417°, 54.9167° (map estimate, mid point of bounds given by author).
WoRMS: 209947
Synonyms: No subjective synonyms.

Hydroides plateni (Kinberg, 1867) (originally as *Eupomatus plateni*)

Etymology: Not stated, but *E. plateni* is evidently named after its La Plata collection station of the Swedish frigate *Eugenie* expedition.
Evaluation: Invariant genitive from Old Frankish 'platen', ultimately from Greek πλατυσ (platus) 'flat', relating to the Spanish La Plata placename, which plausibly had derived from a once widespread use of 'plate' to signify precious metals. Other '*plateni*' species group names of the period may relate to the German zoological collector Carl Platen (1843–1899) but clearly not this one.
Type locality: Offshore off the La Plata ("*prope ostium fluvii* La Plata") embayment, Argentina/Uruguay (the *Eugenie* berthed at Montevideo, Uruguay).
Geolocation: Imprecisely known (map estimate -35.3°, -56.3° for mid La Plata, offshore of Montevideo).
WoRMS: 369242
Synonyms: No subjective synonyms.

Hydroides protulicola **Benedict, 1887 (original binomen)**
Etymology: Not stated, but *H. protulicola* is evidently named from *Protula* (serpulid genus) combined with *-cola* 'dweller', because it was fastened on the tube of *Protula diomedeae* Benedict, 1887.
Evaluation: Invariant compound noun in apposition with *-cola* as a substantival suffix.
Type locality: Northeast off Cape Hatteras, North Carolina, Atlantic coast USA, 86 m.
Geolocation: 35.7°, -74.9083° (from author as 35°42'00"N, 74°54'30"W).
WoRMS: 338020
Synonyms: No subjective synonyms.

Hydroides pseudexaltata **Pillai, 2009 (originally as *H. pseudexaltatus*)**
Etymology: The author states he named *H. pseudexaltatus* after the superficial similarity of the operculum to that of *H. exaltatus.*
Evaluation: Gender variable adjective, with usage as corrected feminine '*pseudexaltata*' in Sun et al. (2015: 65).
Type locality: Shoreline on "island off north east Heywood Island" Kimberley, Western Australia. The author's given geolocation (15°05'S, 124°25'E) is oceanic and clearly incorrect. This is not a rounding error. The island north east of Heywood is the closely adjacent and much larger Jungulu Island.
Geolocation: -15.3167°, 124.3493° (map estimate, Jungulu shore adjacent Heywood Island).
WoRMS: 882697
Synonyms: No subjective synonyms.

Hydroides pseudouncinata Zibrowius, 1968 (original binomen)
Status: Currently valid but it is possibly the same as the disused *H. euplaeana* (see above).
Etymology: Not stated, but evidently *H. pseudouncinata* was named because it represents one of the taxa previously confounded under *H. uncinata* (see below), a name regarded as of indeterminable identity from its original description (*fide* Zibrowius 1971: 709).
Evaluation: Gender-variable adjective with correct original feminine ending. Usages as '*pseudouncinatus*' species (or nominal subspecies) exist (e.g., ten Hove and Kupriyanova 2009: 54).
Type locality: East off Île Gaby (also Degaby), Marseille, France, Mediterranean Sea (not in Zibrowius 1968, *fide* Zibrowius 1971: 708).
Geolocation: 43.2776°, 5.3449° (map estimate).
WoRMS: 131012
Synonyms: No subjective synonyms.

***Hydroides pseudouncinata africana* Zibrowius, 1971 (original trinomen)**
Etymology: The author named subspecies *H. pseudouncinata africana* after its continent of collection, Africa.
Evaluation: Gender-variable adjective with correct original feminine ending. Usages as '*africanus*' exist (e.g., ten Hove and Kupriyanova 2009: 54).
Type locality: Off Rio de Oro, Mauritania, Atlantic coast of Africa.
Geolocation: 21.0833°, -17.4° (author, 21°05'N, 17°24'W).
WoRMS: 335489
Synonyms: No subjective synonyms.

***Hydroides qiui* Sun, Wong, ten Hove, Hutchings, Williamson & Kupriyanova, 2015 (original binomen)**
Etymology: The authors dedicated *H. qiui* to Jian-Wen Qiu.
Evaluation: Invariant genitive form *qiui* from personal name Qiu.
Type locality: East Arm Port, Darwin Harbour, Northern Territory, Australia.
Geolocation: -12.4917°, 130.8831° (authors, 12°29'30"S, 130°52'59"E).
WoRMS: 852783
Synonyms: No subjective synonyms.

***Hydroides ralumiana* Augener, 1927 (originally (incorrectly) as *H.* (*Eupomatus*) *ralumianus*)**
Etymology: Not stated, but *H. ralumianus* is named after Ralum plantation, near its place of collection.
Evaluation: Gender-variable adjective, based on a non-Latin place-name, corrected by Day (1967: 806) from the masculine. The suffix '*-anus -a*' is frequently used for Latinization of names based on localities and personal names.
Type locality: Ralum, Kokopo, Blanche Bay, New Britain (Neu-Pommern), Bismarck Archipelago of Papua New Guinea. The plantation "Ralum" was briefly the base for Friedrich Dahl, who collected the worms in 1896–97 (*fide* Augener 1927).
Geolocation: -4.3371°, 152.2674° (map estimate).
WoRMS: 209951
Synonyms: No subjective synonyms.

***Hydroides recta* Straughan, 1967a (original binomen)**
Etymology: Not stated, but the name for *H. recta* is perhaps a reference to the 8th enlarged dorsal verticil spine with its "pointed process perpendicular to it" from Latin *rectus* 'perpendicular'.
Evaluation: Gender-variable adjective with correct original feminine ending. Usages as masculine '*rectus*' exist (e.g., Pillai 2009: 132).
Type locality: Pretty Beach, north of Cairns, Queensland, Australia.

Geolocation: -16.6111°, 145.5318° (map estimate, a beach 40 km north of Cairns).
WoRMS: 328466
Synonyms: No subjective synonyms.

***Hydroides recurvispina* Rioja, 1941a (original binomen)**
Etymology: Not stated, but the name for *H. recurvispina* is likely referring to the verticil spines which are sharply curving backwards on themselves. Thus the name is formed from Latin *recurvus* 'backward curved' combined with *spina* 'thorn'.
Evaluation: Invariant noun in apposition. Bastida-Zavala and ten Hove (2003: 99) maintained the original spelling.
Type locality: La Aguada, Acapulco, Mexico.
Geolocation: 16.8398°, -99.9009° (map estimate).
WoRMS: 328467
Synonyms: No subjective synonyms.

***Hydroides rhombobula* Chen & Wu, 1980 (originally as *H. rhombobulus*)**
Etymology: Not stated, but the name for *H. rombobulus* may be referring to the shape of the verticil spines, derived from a combination of Greek ϱομβος (rombos) '*rhombus*', which is a parallelogram with only opposite angles equal, and Latin *-ulus*, which is a diminutive in masculine-form.
Evaluation: Clearly intended as an adjectival name, so it is corrected herein to feminine *rhombobula.*
Type locality: Dongshan, Fujian Province, China
Geolocation: 23.6689°, 117.3969° (map estimate).
WoRMS: 882579
Synonyms: No subjective synonyms.

***Hydroides rostrata* Pillai, 1971 (original name, junior homonym, replacement name *Hydroides gottfriedi* nomen novum)**
Status: Previously unreplaced junior homonym preoccupied by the invalid *Hydroides rostrata* Iroso, 1921, which was a *n. nom*. for the specimen of *Eupomatus uncinatus non* Philippi, *sensu* Ehlers, 1887, but a junior objective synonym of *Hydroides floridana* (Bush, 1910) as Bush had already re-named it. Replaced by *Hydroides gottfriedi* **nom. n.** here.
Etymology: Not stated, but *H. rostrata* is likely named after the large rostrum-like verticil spine figured by the author. The adjective *rostratus -a -um*, means having a beak. The genitive replacement name *H. gottfriedi* is in memory of Telesphore Gottfried Pillai (1930–2013), the original-name author.
Evaluation: Gender-variable adjective with correct original feminine ending. Usages as '*rostratus*' exist (e.g., ten Hove and Kupriyanova 2009: 54).

Type locality: Hikkaduwa, Sri Lanka. Types were collected at both Hikkaduwa and Wellawatte. These localities are separated by some considerable distance, but the holotype at the Natural History Museum, London BM 1968–148, is from Hikkaduwa.
Geolocation: 6.1324°, 80.1000° (map estimate).
WoRMS: 328469
Synonyms: No subjective synonyms.

***Hydroides salazarvallejoi* Bastida-Zavala & ten Hove, 2002 (original binomen)**
Etymology: The authors named *H. salazarvallejoi* as a dedication to Sergio Salazar-Vallejo.
Evaluation: Invariant genitive form *salazarvallejoi* from personal name Salazar-Vallejo.
Type locality: Cabo de la Aguja, Santa Marta region, Colombia, Caribbean Sea.
Geolocation: 11.3040°, -74.1937° (map estimate).
WoRMS: 328470
Synonyms: No subjective synonyms.

***Hydroides sanctaecrucis* Krøyer [in] Mörch, 1863 (originally *Hydroides (Eucarphus) sanctae crucis*)**
Etymology: Not stated, but *H. sanctaecrucis* is clearly named after its type locality, Saint Croix Island, and the syntypes at the Zoological Museum, University of Copenhagen are labelled "Kr. St. Croix, legit Oerstedt". The genitive of the feminine Latin noun *crux* 'cross' is *crucis*.
Evaluation: Place-name translated into Latin. The genitive-case noun *sanctaecrucis* is invariant.
Type locality: Saint Croix (unspecified further), Virgin Islands, Caribbean Sea.
Geolocation: 17.6949°, -64.7416° (map estimate for the port area).
WoRMS: 333645
Synonyms: *Hydroides (Eupomatus) dianthoides* Augener, 1922 [*partim*, *fide* Bastida-Zavala and ten Hove 2002: 147] (Haiti, Caribbean Sea)

***Hydroides similis* (Treadwell, 1929) (originally as *Eupomatus similis*)**
Etymology: Not stated, but an instance of the Latin adjective *similis* 'similar to'. Later in the same work Treadwell (1929: 12) considered his *H. californicus* (now *H. crucigera*) as similar to his *E. similis*, which isn't compared to any taxon, so the more logical application of the names would have been in reverse.
Evaluation: Masculine/feminine invariant adjective (*similis -e*) (Stearn 1983: 94).
Type locality: Unspecified beyond a "Lower California" location on label (Baja California, Mexico). The collector was Townsend, on the 'Albatross' voyage of 1911, and the location is perhaps more likely the Gulf of California than off the Pacific coast. Gulf coast sites mentioned by Treadwell where other polychaetes were collected include

Isla Carmen and Isla San José, but there are many other possibilities (see Townsend 1916: 399, end map).
Geolocation: Unknown (30°, -115° (gazetteer) as Baja California general region, but perhaps inner coast).
WoRMS: 369244
Synonyms: No subjective synonyms.

***Hydroides similoides* Bastida-Zavala & ten Hove, 2002 (original binomen)**

Etymology: The authors state they named *H. similoides* for its resemblance to *H. similis* (type locality Baja California) thus combining the Latin adjective *similis* 'similar to' with the suffix *-oides*, also 'similar to'.
Evaluation: Invariant adjectival suffix *-oides.*
Type locality: La Parguera (jetty of marine institute), Isla Magueyes, Puerto Rico.
Geolocation: 17.9700°, -67.0463° (map estimate).
WoRMS: 328471
Synonyms: No subjective synonyms.

***Hydroides simplidentata* Pillai, 2009 (originally as *Hydroides simplidentatus*)**

Etymology: The author states the name *H. simplidentatus* "refers to the simple unmodified spines at the base of the enlarged coronal [verticil] spine", combining Latin adjectives *simplus -a -um* 'simple' and *dentatus -a -um* 'toothed'.
Evaluation: Corrected to the feminine form *simplidentata* in Sun et al. (2015: 79) as clearly an adjectival name.
Type locality: Unnamed reef north-west of Buffon Island (but cf. author's supplied geolocation which is non-reef and east of Buffon Island), Kimberley, Western Australia.
Geolocation: -14.9167°, 124.8° (author as stated, but likely displaced incorrectly by ~13 km to the East).
WoRMS: 882648
Synonyms: No subjective synonyms.

***Hydroides sinensis* Zibrowius, 1972a (original binomen)**

Etymology: Not stated, but *H. sinensis* is evidently named for its occurrence on the coast of China.
Evaluation: Masculine/feminine invariant Latin adjective ('*sinensis*') referring to China, a non-Latin geographic name.
Type locality: Off Qingdao (Zibrowius as 'Tsindao'), China coast, northern Yellow Sea.
Geolocation: 36.0565°, 120.38° (map estimate).
WoRMS: 328472
Synonyms: No subjective synonyms.

Hydroides spongicola Benedict, 1887 (original binomen)
Etymology: Not stated but *H. spongicola* is evidently named from English 'sponge' as stem *spongi-* combined with *-cola* 'dweller', because of its association as "frail calcareous tubes in living sponges".
Evaluation: Invariant compound noun in apposition with *-cola* as a substantival suffix.
Type locality: West offshore from Venice, Florida, Gulf of Mexico, USA, 48 m.
Geolocation: 27.0667°, -83.3542° (as from author as 27°04'00"N, 83°21'15"W).
WoRMS: 338021
Synonyms: No subjective synonyms.

Hydroides steinitzi Ben-Eliahu, 1972 (original binomen)
Etymology: The species *H. steinitzi* is dedicated to Heinz Steinitz.
Evaluation: Invariant genitive form *steinitzi* from personal name Steinitz.
Type locality: Sinai bank of Little Bitter Lake, Suez Canal, opposite Al-Kabrit on Egyptian bank.
Geolocation: 30.2662°, 32.5066° (opposite Al-Kabrit, map estimate).
WoRMS: 131014
Synonyms: No subjective synonyms.

Hydroides stoichadon Zibrowius, 1971(original binomen)
Etymology: Not stated, but *H. stoichadon* is from Greek Στοιχαδας (Stoichadas), an old name for Îles d'Hyères, an archipelago of small islands near Toulon, Mediterranean coast of France (H. Zibrowius pers. comm.).
Evaluation: Invariant Latinization created from Greek place-name, having the form of a noun in apposition.
Type locality: Cap du Merlan, the south west corner of Parc Nacional de Port Cros (island), off the Mediterranean coast of France.
Geolocation: 42.9960°, 6.3718° (map estimate).
WoRMS: 131015
Synonyms: No subjective synonyms.

Hydroides tambalagamensis Pillai, 1961 (original binomen)
Etymology: Not stated but *H. tambalagamensis* is evidently named after its place of collection, Tambalagam.
Evaluation: Masculine/feminine invariant '*-ensis*' adjective created from a non-Latin place-name.
Type locality: Nachchikuda, Tambalagam Lake (a bay), eastern Sri Lanka.
Geolocation: 8.5333°, 81.1667° (map estimate).
WoRMS: 328474
Synonyms: *Hydroides spiculitubus* [noun in apposition] Pillai, 2009 (Long Reef, Kimberley, Western Australia)

Hydroides tenhovei **Bastida-Zavala & de León González, 2002 (original binomen)**
Etymology: The authors dedicated the name *H. tenhovei* to Harry ten Hove.
Evaluation: Invariant genitive form *tenhovei* from personal name ten Hove.
Type locality: Cabo San Lazaro, western coast of Baja California Sur, Mexico.
Geolocation: 24.7813°, -112.2905° (authors 24°50'N, 112°15'W, adjusted to be coastal).
WoRMS: 328475
Synonyms: No subjective synonyms.

Hydroides trilobula **Chen & Wu, 1978 (originally *H. trilobulus*)**
Etymology: Not stated, but the name for *H. trilobulus* evidently refers to three vesicular verticil spines (three lobes), which are small ones, hence the diminutive Latin suffix *-ulus*.
Evaluation: Clearly meant as an adjectival name, so it is corrected herein to *trilobula.*
Type locality: Xisha Islands (Paracel Islands, unspecified further), South China Sea, of which Yongxing Island is the largest.
Geolocation: Imprecisely known (16.8833°, 112.2833° if Yongxing Island, map estimate).
WoRMS: 882593
Synonyms: No subjective synonyms.

Hydroides trivesiculosa **Straughan, 1967b (originally *H. trivesiculosus*)**
Etymology: Not stated, but the name for *H. trivesiculosus* is evidently referring to the three lobes of the enlarged dorsal spine of the verticil, thus *tri* with Latin adjective *vesiculosus -a um* 'full of blisters'.
Evaluation: Gender-variable adjective with ending feminine as in Sun et al. (2015: 85) and Kupriyanova et al. (2015; 293), both mistakenly reporting the original name as '*trivesiculosa*'). Usages as '*trivesiculosus*' (besides original) exist (e.g., ten Hove and Ben Eliahu 2005: 134).
Type locality: Heron Island, Queensland coast, Australia, collected close to the marine station by Dew (map in Straughan 1967b).
Geolocation: -23.4430°, 151.9110° (map estimate).
WoRMS: 882647
Synonyms: No subjective synonyms.

Hydroides trompi **Bastida-Zavala & ten Hove, 2003 (original binomen)**
Etymology: The authors named *H. trompi* dedicated to Jossy S. Tromp, a student of ten Hove.
Evaluation: Invariant genitive form *trompi* from personal name Tromp.
Type locality: Lower chamber wall and floor, Miraflores Locks, Panama Canal, Panama.
Geolocation: 8.9967, -79.5964 (authors).
WoRMS: 328478
Synonyms: No subjective synonyms.

***Hydroides tuberculata* Imajima, 1976a (original binomen)**

Etymology: Not stated, but the name for *H. tuberculata* may refer to tubercles (knobs) on each verticil spine as the Latin noun *tuberculum* refers to a swelling or lump.

Evaluation: Gender-variable adjectival form of *tuberculum* with correct original feminine ending. Usages as '*tuberculatus*' exist (e.g., Bailey-Brock 1987: 282).

Type locality: Urata (beach), Tanegashima (island), Southern Japan. Imajima (1976a) also gives records for Sumiyoshi, and off Nishinoomote Harbour, Tanegashima, but a Urata specimen is the holotype (NSMT-Pol. H-120) at the National Museum of Nature & Science, Tokyo.

Geolocation: 30.8233°, 131.0409° (map estimate, Urata).

WoRMS: 871950

Synonyms: No subjective synonyms.

***Hydroides uncinata* (Philippi, 1844) (originally as *Eupomatus uncinatus*)**

Status: Name now disused and representing a *species inquirenda* which is the type species of *Eupomatus*. It is not a candidate *nomen oblitum* (used in taxonomy as valid by Zibrowius 1968: 109, Hartman 1969: 757, Gibbs 1971: 202, Pillai 1972: 15, Day 1973: 132, and others), but the taxon it represents may be indeterminable unless original specimens are found. Zibrowius (1968) named *H. pseudouncinata* to establish a separation from *H. uncinata*, and Pillai (1972) did likewise with *H. okudai*. The name does not obviously threaten the validity of subsequent names, but it is notable that several *H. uncinata* usages have been assigned elsewhere, e.g., *Serpula* (*Hydroides*) *uncinata non* Philippi, *sensu* Gravier, 1906 to *H. heterocera*.

Etymology: Not stated, but Philippi described the verticil spines as with "*cornubus octo, apice incurvo uncinatis*" (eight horns, curved tip hooked), thus the name refers to the hooked spines, from the Latin adjective *uncinatus* 'hooked'.

Evaluation: Gender-variable adjective with correct feminine ending. Usages in *Hydroides* as '*uncinatus*' exist (e.g., Ehlers 1913: 582).

Type locality: Unspecified Mediterranean, but can be narrowed to the Tyrrhenian Sea coast of Italy as Philippi's activities were in western Italy, and plausibly to Naples as he was based there prior to 1844.

Geolocation: Unknown (Tyrrhenian Sea, with Naples shore (40.8327°, 14.2358° map estimate) a possible point location).

WoRMS: 156135

Synonyms: As *species inquirenda* has no synonyms.

***Hydroides uniformis* Imajima & ten Hove, 1986 (original binomen)**

Etymology: Not stated, but the name *H. uniformis* evidently refers to the straight, thick, unornamented spines of the verticil which are described as "uniform".

Evaluation: Masculine/feminine invariant adjective (*uniformis -e*) (Stearn 1983: 94).

Type locality: Kesao, Guadalcanal, Solomon Islands, Pacific Ocean.
Geolocation: -9.25°, 159.6667° (map estimate).
WoRMS: 369245
Synonyms: No subjective synonyms.

Hydroides vizagensis **Lakshmana Rao, 1969 (original binomen)**
Etymology: Not stated, but the name *H. vizagensis* likely derives from the collection location, Visakhapatnam, which has the nickname Vizag.
Evaluation: Masculine/feminine invariant '*-ensis*' adjective created from a non-Latin place-name.
Type locality: Naval Base (collected off settlement panels), Visakhapatnam Harbour, east coast of India, Bay of Bengal.
Geolocation: 17.6938°, 83.2739° (map estimate).
WoRMS: 870503
Synonyms: No subjective synonyms.

Hydroides xishaensis **Chen & Wu, 1978 (original binomen)**
Etymology: Not stated, but *H. xishaensis* is evidently named after its area of collection, the Xisha Islands.
Evaluation: Masculine/feminine invariant '*-ensis*' adjective created from a non-Latin geographic name.
Type locality: Xisha Islands (Paracel Islands, unspecified further), South China Sea, of which Yongxing Island is the largest.
Geolocation: Imprecisely known (16.8833°, 112.2833° if from Yongxing Island, map estimate).
WoRMS: 328480
Synonyms: No subjective synonyms.

Discussion

Name characteristics and potential variation

Place-names (23), and personal names (16) make up more than a third (36%) of the 107 non-synonymised species-group names in *Hydroides*, with most of the remainder (68) being descriptive of species character states, with a remarkable number relating to operculum morphology (54). The (perhaps) 'small-eared' *H. microtis* was the only species where the reason for the author's choice was not obvious. Otherwise three species were named for their attractive appearance (*H. dianthus, H. elegans, H. elegantula*), three were named for the animals they were found on (*H. fusicola, H. protulicola,* *H. spongicola*), four names are comparative (*H. affinis, H. pseudouncinata, H. similis, H. similoides*), two species names probably relate to body size (*H. humilis, H. parva*), and one species name relates to the tube form (*H. hexagona*).

Currently the 107 names include 41 which should be gender invariant (including 17 nouns in apposition, including two acronyms), and 23 with adjectival masculine/feminine endings in *-is*, which would only change (to *-e*) if moved to a neuter genus (13 of these are place-names). The remaining 43 names are fully gender variable. There are 68 adjectival names in total (including 19 adjectival place-names), with only two adjectival names completely invariant.

Type locality distribution

Type localities of the *Hydroides* serpulids listed are, with one exception, in shallow-water coastal locations in temperate to tropical waters between 43.3°N and 35.3°S (Figs 1–2). *Hydroides norvegica* is the exception from deeper water (but still inshore), and occurred at the highest latitude at 63.4°N. It is the most cold tolerant based on type locality, with a 20° latitudinal gap to all other species type localities, although its distribution extends south into the Mediterranean (Zibrowius 1971). The western Pacific Ocean (Australia

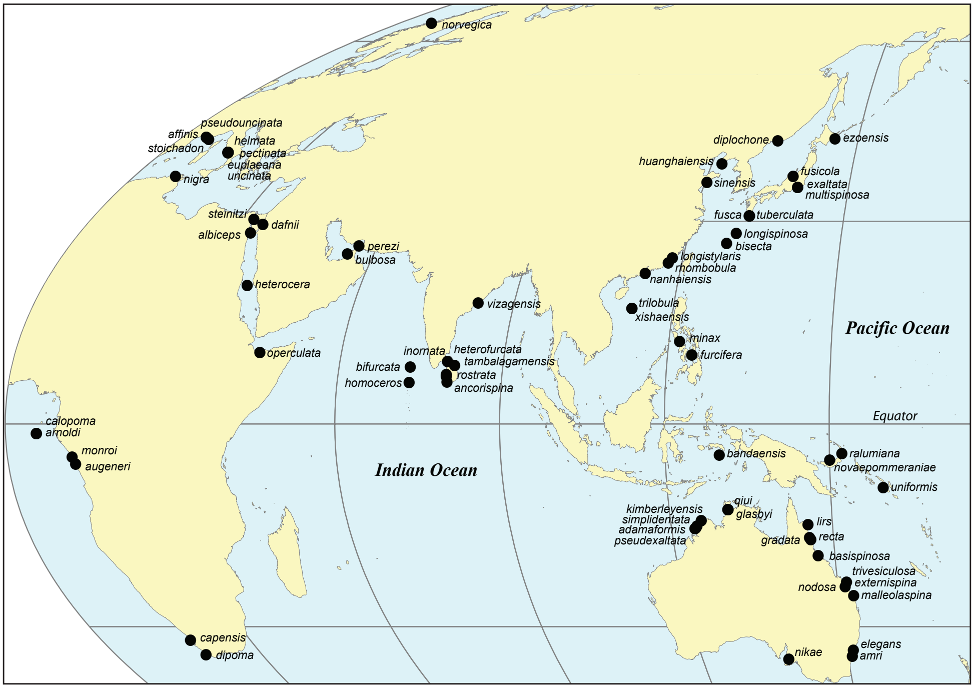

Figure 1. *Hydroides* species type localities of the Eastern Hemisphere (Indian Ocean and Western Pacific). Labels are current species-group names (except homonym *H. rostrata* renamed herein as *H. gottfriedi* nom. n.)

to northern Japan) has the biggest group of new species at 39, with another 15 species in the northern Indian Ocean and Red Sea (Fig. 1), a total of 54 for the greater Indo-Pacific. The Americas north of the equator have 13 new species on the East Pacific coast, and 18 on the Western Atlantic coast and the Caribbean/Gulf of Mexico area (Fig. 2), a total of 31 for North American and Caribbean coasts combined. Europe (including Azores) has only 10 new species, mostly in the Mediterranean Sea (Fig. 1). This leaves only 12 other species described from elsewhere. Notably, few new species (9) have been reported from the major continental coasts of the South American coast south of the equator, and the African coast (outside of the Red Sea and Mediterranean, and including Madagascar), but this may be partly a reflection of lesser sampling effort, and also the consequence of other areas being examined first, given that *Hydroides* species are readily translocated on the floating objects and vessel hulls they colonise.

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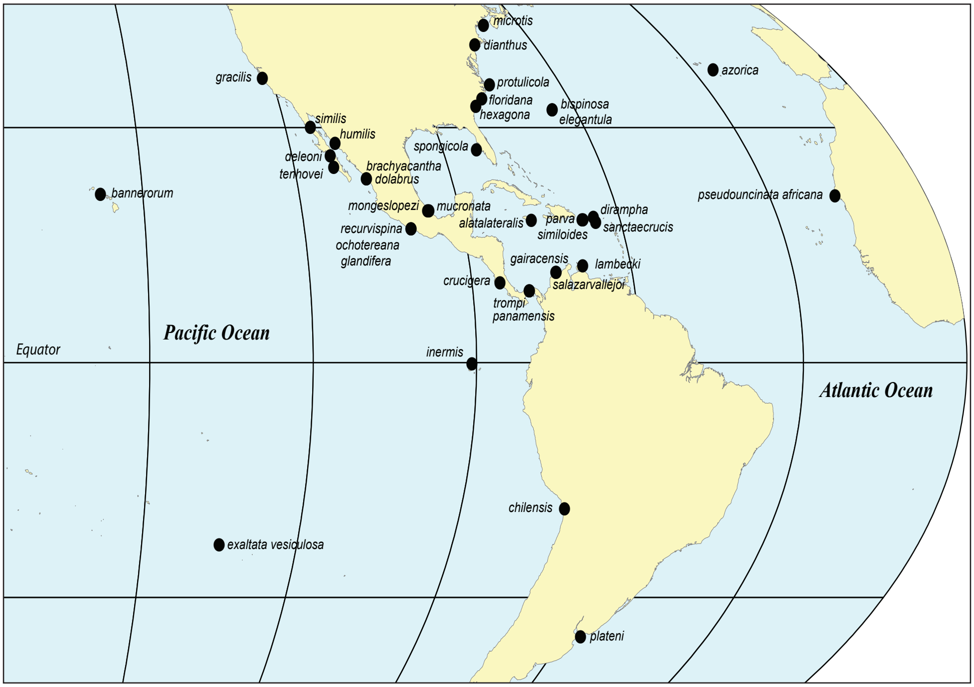

Figure 2. *Hydroides* species type localities of the Western Hemisphere (Americas and Eastern Pacific). Labels are current species-group names. Map grids 30° intervals.

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References

Amoureux L, Rullier F, Fishelson, L (1978) Systématique et Écologie d'Annélides Polychètes de la presqu'îl du Sinai. Israel Journal of Zoology 27(2–3): 57–163.

Augener H (1918) Polychaeta. Beiträge zur Kenntnis der Meeresfauna Westafrikas 2(2): 67–625. http://biodiversitylibrary.org/page/7172280

Augener H (1922) Über litorale polychaeten von Westindien. Sitzungsberichte der Naturforschender Freunde zu Berlin 1922(3–5): 38–53. http://biodiversitylibrary.org/page/43656381

Augener H (1925) Die Polychaeten der Südsee-Expedition der Hamburgischen wissenschaftliche Stiftung 1908–1909. Mitteilungen der Zoologisches Staatsinstitut und zoologisches Museum, Hamburg 41: 53–70.

Augener H (1927) Polychaeten von Neu-Pommern. Sitzungsberichte der Gesellschaft der naturforschende Freunde zu Berlin 1926: 119–152.

Augener H (1934) Polychaeten aus den Zoologischen Museen von Leiden und Amsterdam. IV (Schluss). Zoölogische Mededeelingen Rijks Museum van Natuurlijke Historie Leiden 17: 67–160. http://www.repository.naturalis.nl/record/318471

Bailey-Brock JH (1987) The polychaetes of Fanga'uta Lagoon and coral reefs of Tongatapu, Tonga, with discussion of the Serpulidae and Spirorbidae. Bulletin of the Biological Society of Washington 7: 280–294.

Bailey-Brock JH (1991) Tubeworms (Serpulidae, Polychaeta) collected from sewage outfalls, coral reefs and deep waters off the Hawaiian Islands, including a new *Hydroides* species. Bulletin of Marine Science 48(2): 198–207. http://www.ingentaconnect.com/contentone/umrsmas/bullmar/1991/00000048/00000002/art00006

Bastida-Zavala JR, ten Hove HA (2002) Revision of *Hydroides* Gunnerus, 1768 (Polychaeta: Serpulidae) from the Western Atlantic Region. Beaufortia 52(9): 103–178.

Bastida-Zavala JR, ten Hove HA (2003) Revision of *Hydroides* Gunnerus, 1768 (Polychaeta: Serpulidae) from the Eastern Pacific Region and Hawaii. Beaufortia 53(4): 67–110.

Bastida-Zavala JR, de León González JA (2002) A new species of *Hydroides* (Polychaeta: Serpulidae) from western Mexico. Journal of the Marine Biological Association of the United Kingdom 82(3): 389–393. doi: 10.1017/S0025315402005623

Bean W (1844) A supplement of new species. In: Thorpe C. British Marine Conchology, Edward Lumley, London, 263–267. doi: 10.5962/bhl.title.11208

Bellan G (2001) Polychaeta. In: Costello MJ et al. (Eds) European register of marine species: a checklist of the marine species in Europe and a bibliography of guides to their identification. Collection Patrimoines Naturels 50: 214–231. http://www.vliz.be/imisdocs/publications/77636.pdf

Benedict JE (1887) Descriptions of ten species and one new genus of annelids from the dredgings of the U.S. Fish Commission Steamer Albatross. Proceedings of the United States National Museum 9: 547–553. doi: 10.5479/si.00963801.9-594.547

Ben-Eliahu MN (1972) A description of *Hydroides steinitzi* n. sp. (Polychaeta: Serpulidae) from the Suez Canal with remarks on the serpulid fauna of the Canal. Israel Journal of Zoology 21(2): 77–81. http://www.tandfonline.com/doi/abs/10.1080/00212210.1972.10688351

Ben-Eliahu MN, Hove HA ten (1992) Serpulids, Annelida: Polychaeta, along the Mediterranean coast of Israel—New population build-ups of Lessepsian migrants. Israel Journal of Zoology 38(1): 35–53. http://www.tandfonline.com/doi/abs/10.1080/00212210.1992.10688664

Ben-Eliahu MN, Hove HA ten (2011) Serpulidae (Annelida: Polychaeta) from the Suez Canal—From a Lessepsian Migration Perspective. Zootaxa 2848 (Monograph): 1–147. http://www.mapress.com/zootaxa/list/2011/2848.html

Billard A (1907) Hydroïdes de la Collection Lamarck du Muséum de Paris. I Plumulariidae. Annales des sciences naturelles. Zoologie (Series 9) 5: 319–335. http://biodiversitylibrary.org/page/34908193

Bosc LAG (1802) Histoire naturelles des vers, contenant leur description et leurs moeurs; avec figures dessinées d'après nature. Tome Premiere. De l'imprimerie de Guilleminet, chez Deterville, Paris, 324 pp. doi: 10.5962/bhl.title.64025

Brown RW (1956) Composition of scientific words. Reprint edition. Smithsonian Institution Press, Washington, 882 pp.

Bush KJ (1905) Tubicolous annelids of the tribes Sabellides and Serpulides from the Pacific Ocean. Harriman Alaska Expedition 12: 169–346. doi: 10.5962/bhl.title.27846

Bush KJ (1910) Description of new serpulids from Bermuda with notes on known forms from adjacent regions. Proceedings of the Academy of Natural Sciences, Philadelphia 62: 490–501. http://biodiversitylibrary.org/page/26294605

Chamberlin RV (1919) New polychaetous annelids from Laguna Beach, California. Journal of Entomology and Zoology. Pomona College 11(1): 1–23. http://biodiversitylibrary.org/page/12263520

Chen M, Wu BL (1978) Two new species of the genus *Hydroides* (Polychaeta, Serpulidae) from the Xisha Islands, Guandong Province, China. Studia Marina Sinica 12: 141–145.

Chen M, Wu BL (1980) Two new species of the genus *Hydroides* (Polychaeta, Serpulidae). Oceanologia et Limnologia Sinica 11(3): 247–250.

Claparède E (1870a) Les Annélides Chétopodes du Golfe de Naples. Seconde partie. Ordre IIme. Annélides Sédentaires. Mémoires de la Société de physique et d'histoire naturelle de Geneve 20(1): 1–225. http://biodiversitylibrary.org/page/2071623

Claparède E (1870b) Les Annélides Chétopodes du Golfe de Naples. Supplement. Mémoires de la Société de physique et d'histoire naturelle de Geneve 20(2): 365–542. http://biodiversitylibrary.org/page/2094031

Colwin AL, Colwin LH (1961) Fine structure of the spermatozoon of *Hydroides hexagonus* (Annelida), with special reference to the acrosomal region. Journal of Biophysical and Biochemical Cytology 10(2): 211–230. doi: 10.1083/jcb.10.2.211

Costello DP, Davidson ME, Eggers A, Fox MH, Henley C (1957) Methods for Obtaining and Handling Marine Eggs and Embryos. Marine Biological Laboratory & Lancaster Press, Woods Hole, Massachusetts, 247 pp. doi: 10.5962/bhl.title.1023

David N, Gosselin, M (2002) Gender agreement of avian species names. Bulletin of the British Ornithologists' Club 122: 14–49.

Day JH (1951) The Polychaet [sic] Fauna of South Africa. Part I. The intertidal and estuarine Polychaeta of Natal and Mosambique. Annals of the Natal Museum 12(1): 1–67. http://content.ajarchive.org/cdm4/document.php?CISOROOT=/03040798&CISOPTR=905&REC=12

Day JH (1967) A monograph on the Polychaeta of Southern Africa. Part 2. Sedentaria. Trustees of the British Museum (Natural History) London, 459–878. doi: 10.5962/bhl.title.8596

Day JH (1973) New Polychaeta from Beaufort, with a key to all species recorded from North Carolina. National Oceanic and Atmospheric Administration Technical Report NMFS CIRC-375: 1–140. doi: 10.5962/bhl.title.62852

Delle Chiaje S (1828) Memorie sulla storia e notomia degli animali senza vertebre del Regno di Napoli. vol. 3. Stamperia della Societa' Tipografica, Napoli, 232 pp. [plates published separately in 1830, dated "1822"] http://www.biodiversitylibrary.org/item/40491

Dew B (1959) Serpulidae (Polychaeta) from Australia. Records of the Australian Museum 25: 19–56. doi: 10.3853/j.0067-1975.25.1959.654

Ehlers E (1887) Reports on the results of dredging, under the direction of L. F. Pourtalès, during the years 1868–1870, and of Alexander Agassiz, in the Gulf of Mexico (1877–78), and in the Caribbean Sea (1878–79), in the U.S. Coast Survey steamer "Blake", Lieut-Com. C. D. Sigsbee, U.S.N. and Commander J. R. Bartlett, U.S.N., commanding. XXXI. Report on the Annelids. Memoirs of the Museum of Comparative Zoology, Harvard 15: 1–335. doi: 10.5962/bhl.title.65639

Ehlers E (1913) Die Polychaeten-Sammlungen der Deutschen Südpolar-Expedition 1901–1903. Deutsche Südpolar-Expedition 13(Zoologie V): 397–598. http://biodiversitylibrary.org/page/2139283

Fauvel P (1918) Annélides polychètes des côtes d'Arabie récoltées par M. Ch. Pérez. Bulletin du Muséum d'Histoire Naturelle, Paris 24(5): 329–344. http://biodiversitylibrary.org/page/5037658

Fauvel P (1919) Annélides polychètes des îles Gambier et Touamotou. Bulletin du Muséum National d'Histoire Naturelle, Paris 25(5): 336–343. http://biodiversitylibrary.org/page/5027005

Fischli H (1903) Polychäten von Ternate. Senckenbergische Naturforschende Gesellschaft Abhandlungen 25(1): 90–136. http://biodiversitylibrary.org/page/25232322

Frauenfeld G von (1855) Naturhistorische Fragmente: gesammelt auf einer Reise am Rothen Meere im Frühjahre 1855. Sitzungsberichte der Mathematisch-Naturwissenschaftlichen Classe der Kaiserlichen Akademie der Wissenschaften (Wien) 18: 66–87. http://biodiversitylibrary.org/page/6441585

Gibbs PE (1971) The polychaete fauna of the Solomon Islands. Bulletin of the British Museum (Natural History) Zoology 21(5): 101–211. doi: 10.5962/bhl.part.10154

Grave BH (1937) *Hydroides hexagonus*. In: Galtsoff PS, Lutz FE, Welch PS, Needham JG (Eds) Culture methods for invertebrate animals. Comstock Publishing Company, Ithaca, New York, 185–187. doi: 10.5962/bhl.title.6012

Grave BH, Oliphant JF (1930) The longevity of unfertilized gametes. Biological Bulletin (Woods Hole) 59(3): 233–239. doi: 10.2307/1536993

Gravier C (1906) Sur les Annélides Polychètes de la Mer Rouge (Serpulides). Bulletin du Muséum d'Histoire Naturelle, Paris 12: 110–115. http://biodiversitylibrary.org/page/5021287

Grube AE (1868) Beschreibungen einiger von Georg Ritter von Frauenfeld gesammelter Anneliden und Gephyreen des rothen Meeres. Verhandlungen der kaiserlich-königlichen zoologisch-botanischen Gesellschaft in Wien 18: 629–650. http://biodiversitylibrary.org/page/25254604

Grube AE (1870) Beschreibungen neuer oder weniger bekannter von Hrn. Ehrenberg gesammelter Anneliden des rothen Meeres. Monatsbericht der Koniglich Preussischer Akademie der Wissenschaften zu Berlin 1869: 484–521. http://www.biodiversitylibrary.org/page/36276705

Grube AE (1878a) Einige neue anneliden aus Japan. Jahres-Bericht der Schlesischen Gesellschaft für Vaterländische Cultur 55 [1878 for 1877 year]: 104–106. http://biodiversitylibrary.org/page/37206819

Grube AE (1878b) Annulata Semperiana. Beiträge zur Kenntniss der Annelidenfauna der Philippinen. Memoires de L'Académie Impériale.des Sciences de St.-Pétersbourg VII Série 25(8): 1–300. doi: 10.5962/bhl.title.85345

Gunnerus JE (1768) Om nogle Norske Coraller. Det Kongelige Norske Videnskabernes Selskabs Skrifter 4: 38–73. http://gdz.sub.uni-goettingen.de/dms/load/img/?PPN=PPN481641912_0004&IDDOC=273812

Hadfield MG (1998) The D P Wilson lecture. Research on settlement and metamorphosis of marine invertebrate larvae: past, present and future. Biofouling 12(1–3): 9–29. doi: 10.1080/08927019809378343

Harper D (2001–2016). Online Etymology Dictionary. http://www.etymonline.com/index.php

Hartman O (1956) Polychaetous annelids erected by Treadwell, 1891 to 1948, together with a brief chronology. Bulletin of the American Museum of Natural History 109(2): 239–310. http://hdl.handle.net/2246/1145

Hartman O (1959) Catalogue of the polychaetous annelids of the world. Parts 1 & 2. Allan Hancock Foundation Occasional Paper 23: 1–628

Hartman O (1965) Supplement and index to the catalogue of the polychaetous annelids of the World, including additions and emendations since 1959. Allan Hancock Foundation Occasional Paper 23 Supplement and Index: 1–197. http://digitallibrary.usc.edu/cdm/ref/collection/p15799coll82/id/19369

Hartman O (1969) Atlas of the sedentariate polychaetous annelids from California. Allan Hancock Foundation, University of Southern California, 812 pp.

Hartmann-Schröder G (1962) Die Polychaeten des Eulitorals. In: Hartmann-Schröder G and Hartmann G. Zur Kenntnis des Eulitorals der chilenischen Pazifikküste und der argentinischen Küste Südpatagoniens unter besonderer Berücksichtigung der Polychaeten und Ostracoden. Mitteilungen aus dem Hamburgischen zoologischen Museum und Institut 60: 57–270.

Haswell WA (1883) On some new Australian tubicolous annelids. Proceedings of the Linnean Society of New South Wales 7: 633–638. http://biodiversitylibrary.org/page/6462370

Hove HA ten (1990) Description of *Hydroides bulbosus* sp. n. (Polychaeta, Serpulidae), from the Iranian Gulf, with a terminology for opercula of *Hydroides*. Beaufortia 41(16): 115–120.

Hove HA ten, Ben-Eliahu MN (2005) On the identity of *Hydroides priscus* Pillai 1971—Taxonomic confusion due to ontogeny in some serpulid genera (Annelida: Polychaeta: Serpulidae). Senckenbergiana Biologica 85(2): 127–145.

Hove HA ten, Kupriyanova, EK (2009) Taxonomy of Serpulidae (Annelida, Polychaeta): The state of affairs. Zootaxa 2036: 1–125. http://www.mapress.com/j/zt/issue/view/2173

Imajima M (1976a) Serpulid polychaetes from Tanega-shima, southwest Japan. Memoirs of the National Science Museum 9: 123–143. http://ci.nii.ac.jp/naid/110004313275

Imajima M (1976b) Serpulinae (Annelida, Polychaeta) from Japan I. the genus *Hydroides*. Bulletin of the National Science Museum, Tokyo, Series A (Zoology) 2(4): 229–248. http://ci.nii.ac.jp/naid/40005325183

Imajima M (1982) Serpulinae (Polychaetous Annelids) from the Palau and Yap Islands, Micronesia. Proceedings of the Japanese Society of Systematic Zoology 23: 37–55. http://ci.nii.ac.jp/naid/110002339223

Imajima M, ten Hove HA (1986) Serpulinae (Annelida, Polychaeta) from Nauru, the Gilbert Islands (Kiribati) and the Solomon Islands. Proceedings of the Japanese Society of Systematic Zoology 32: 1–16. http://ci.nii.ac.jp/naid/110002339356

Imajima M, ten Hove HA (1989) Two new species of serpulids (Annelida, Polychaeta) from Sesoko Island, Okinawa. Bulletin of the National Science Museum, Tokyo, Series A (Zoology) 15(1): 11–17. http://ci.nii.ac.jp/naid/110004311713

International Commission on Zoological Nomenclature [ICZN] (1961) International Code of Zoological Nomenclature, adopted by the XV International congress of Zoology. The International Trust for Zoological Nomenclature, London, 176 pp. doi: 10.5962/bhl.title.50303

ICZN (1985) International Code of Zoological Nomenclature Third Edition adopted by the XX General Assembly of the International Union of Biological Sciences. The International Trust for Zoological Nomenclature, London, 338 pp. doi: 10.5962/bhl.title.50611

ICZN (1999) International Code of Zoological Nomenclature Fourth edition adopted by the International Union of Biological Sciences. The International Trust for Zoological Nomenclature, London, 306 pp. doi: 10.5962/bhl.title.50608

Iroso I (1921) Revisione dei Serpulidi e Sabellidi del Golfo di Napoli. Pubblicazioni della Stazione Zoologica di Napoli 3: 47–91.

Jones ML (1962) On some polychaetous annelids from Jamaica, the West Indies. Bulletin of the American Museum of Natural History 124(5): 169–212. http://hdl.handle.net/2246/1213

Kinberg JGH (1867 (or late 1866)) Annulata nova. [Continuatio.]. Öfversigt af Kongl. [sic] Vetenskapsakademiens förhandlingar, Stockholm 23(9): 337–357. http://biodiversitylibrary.org/page/32287795

Kupriyanova EK, Sun Y, Hove, HA ten, Wong E, Rouse GW (2015) Serpulidae (Annelida) of Lizard Island, Australia. Zootaxa 4019(1): 275–353. doi: 10.11646/zootaxa.4019.1.13

Lakshmana Rao MV (1969) Fouling serpulids from some Indian harbours. Journal of the Timber Development Association of India 15(2): 1–20.

de León González JA (1990) Dos serpúlidos nuevos para el Pacifico Mexicano y duplicidad opercular en *Hydroides crucigerus* [sic] (Polychaeta: Serpulidae). Revista de biologia tropical 38(2A): 335–338. http://revistas.ucr.ac.cr/index.php/rbt/article/view/25383

Lewis CT, Short C (1891) Harpers Latin dictionary. A new Latin dictionary: founded on the translation of Freund's Latin-German lexicon Harper, New York, 2019 pp. https://archive.org/details/LewisAndShortANewLatinDictionary

Marenzeller E von (1885) Südjapanische Anneliden. II. Ampharetea, Terebellacea, Sabellacea, Serpulacea. Denkschriften der Akademie der Wissenschaften Mathematisch-Naturwissenschaftliche Classe. Wien. 49(2): 197–224. http://biodiversitylibrary.org/page/7102598

Marion AF (1875) Sur les Annélides de Marseille. Revue des sciences naturelle. Montpellier 4(1): 301–312. http://biodiversitylibrary.org/page/14526461

Marion AF, Bobretzky N (1875) Étude des Annélides du golfe de Marseille. Annales des Sciences Naturelles, Paris (series 6) 2: 1–106. http://biodiversitylibrary.org/page/33155516

McIntosh WC (1923) A monograph of the British marine annelids. Volume IV Part II. Polychaeta. Sabellidae to Serpulidae with additions to the British marine Polychaeta during the publication of the monograph. Ray Society 4(2): 251–538.

Moen TL (2006) A translation of Bishop Gunnerus' description of the species *Hydroides norvegicus* with comments on his *Serpula triqvetra*. Scientia Marina 70 (Supplement 3): 115–123. doi: 10.3989/scimar.2006.70s3115

Monro CCA (1933) The Polychaeta Sedentaria collected by Dr. C. Crossland at Colón, in the Panama Region, and the Galapagos Islands during the Expedition of the S.Y. 'St. George'. Proceedings of the Zoological Society of London 103(4): 1039–1092. doi: 10.1111/j.1096-3642.1933.tb01640.x

Monro CCA (1937) Polychaeta. The John Murray Expedition 1933–1934 Scientific Reports. 4(8): 243–321. http://biodiversitylibrary.org/page/49518757

Monro CCA (1938) On a new species of serpulid polychate from the Shoreham Harbour Canal, Sussex. Annals and Magazine of Natural History (Series 11) 1(1): 73–78. doi: 10.1080/00222933808526742

Mörch OAL (1863) Revisio critica Serpulidarum. Et Bidrag til Rørormenes Naturhistorie. Naturhistorisk Tidsskrift, København, Ser. 3, 1: 347–470. http://www.archive.org/details/naturhistoriskti01copeuoft

Murray A, Hutchings P, Pillai TG (2010) Note on *Hydroides malleolaspinus* from the Kimberleys of Western Australia (Polychaeta: Serpulidae). Records of the Australian Museum 62(3): 393–394. doi: 10.3853/j.0067-1975.62.2010.1564

Okuda S (1934) Some tubicolous annelids from Hokkaido. Journal of the Faculty of Science, Hokkaido University, Series 6, Zoology 3(4): 233–246. http://hdl.handle.net/2115/26971

Okuda S (1937) Annelida polychaeta in Onagawa Bay and its vicinity. I. Polychaeta Sedentaria. Science Reports of the Tohoku Imperial University. Fourth Series Biology 12(1): 45–69.

Philippi A (1844) Einige Bemerkungen über die Gattung *Serpula*, nebst Aufzählung der von mir im Mittelmeer mit dem Thier beobachteten Arten. Archiv für Naturgeschichte Berlin 10(1): 186–198. doi: 10.5962/bhl.part.29558

Pillai TG (1960) Some marine and brackish water serpulid polychaeta from Ceylon, including new genera and species. Ceylon Journal of Science (Biological Sciences) 3(1): 1–40.

Pillai TG (1961) Annelida Polychaeta of Tambalagam Lake, Ceylon. Ceylon Journal of Science (Biological Sciences) 4(1): 1–40. http://dl.nsf.ac.lk/handle/1/7600

Pillai, TG (1965) Annelida Polychaeta from the Philippines and Indonesia. Ceylon Journal of Science (Biological Sciences) 5(2): 112–177. http://dl.nsf.ac.lk/handle/1/7733

Pillai TG (1971) Studies on a collection of marine and brackish-water polychaete annelids of the family Serpulidae from Ceylon. Ceylon Journal of Science (Biological Sciences) 9(2): 88–130.

Pillai TG (1972) A review and revision of the systematics of the genera *Hydroides* and *Eupomatus* together with an account of their phylogeny and zoogeography. Ceylon Journal of Science (Biological Sciences) 10(1): 7–31. http://dl.nsf.ac.lk/handle/1/7815

Pillai TG (2009) Descriptions of new serpulid polychaetes from the Kimberleys of Australia and discussion of Australian and Indo-West Pacific species of *Spirobranchus* and superficially similar taxa. Records of the Australian Museum 61(2): 93–199. doi: 10.3853/j.0067-1975.61.2009.1489

Pixell HLM (1913) Polychaeta of the Indian Ocean, together with some species from the Cape Verde Islands. The Serpulidae, with a classification of the genera *Hydroides* and *Eupomatus*. Transactions of the Linnean Society of London, Series 2 16: 69–92. doi: 10.1111/j.1096-3642.1914.tb00125.x

Pratt HS (1916) A manual of the common invertebrate animals, excluding insects. A. C. McClurg and Co., Chicago, 737 pp. doi: 10.5962/bhl.title.1245

Read GB, Fauchald K (Ed.) (2016) World Polychaeta database. http://www.marinespecies.org/polychaeta

Read GB, Hove HA ten (2016) *Hydroides* Gunnerus, 1768. http://www.marinespecies.org/polychaeta/aphia.php?p=taxdetails&id=129566

Ribas J, Hutchings PA (2015) Lizard Island Polychaete Workshop: sampling sites and a checklist of polychaetes. Zootaxa 4019(1): 7–34. doi: 10.11646/zootaxa.4019.1.4

Rioja E (1941a) Estudios Anelidologicos. II. Observaciones acerca de varias especies del genero *Hydroides* Gunnerus (sensu Fauvel) de las costas Mexicanas del Pacifico. Anales del Instituto de Biologia (Mexico) 12(1): 161–175.

Rioja E (1941b) Estudios Anelidologicos. III. Datos para el conocimiento de la fauna de poliquetos de las costas del pacifico de Mexico. Anales del Instituto de Biologia, Mexico 12(2): 669–746.

Rioja E (1942) Estudios Anelidologicos. IV. Observaciones sobre especies de serpulidos de las costas del Pacifico de Mexico, con descripcion de una especie nueva del genero *Hydroides*. Anales del Instituto de Biologia (Mexico) 13(1): 125–135.

Rioja E (1958) Estudios Anelidologicos. XXI. Observaciones acerca de algunas especies de serpulidos de los generos *Hydroides* y *Eupomatus* de las costas Mexicanas del Golfo de Mexico. Anales del Instituto de Biologia, Mexico 28(1/2): 247–266 [1957 issue]

Schmarda LK (1861) Neue wirbellose Thiere beobachtet und gesammelt auf einer Reise um die Erdr [sic] 1853 bis 1857 von Ludwig K. Schmarda. Erster Band. Turbellarien, Rotatorien und Anneliden. Zweite Hälfte. Wilhelm Engelmann, Leipzig, 164 pp. doi: 10.5962/bhl.title.14426

Stearn WT (1983) Botanical Latin. 3rd edition revised. David & Charles, London, 566 pp.

Straughan D (1967a) Marine Serpulidae (Annelida: Polychaeta) of eastern Queensland and New South Wales. Australian Journal of Zoology 15(1): 201–261. doi: 10.1071/ZO9670201

Straughan D (1967b) Some Serpulidae (Annelida: Polychaeta) from Heron Island, Queensland. University of Queensland Papers [Great Barrier Reef Committee, Heron Island Research Station] 1(2): 27–45.

Sun R, Yang D (2000) Study on *Hydroides* (Polychaeta: Serpulidae) from waters off China. I. Studia Marina Sinica 42: 116–135. [Chinese with English summary]

Sun R, Yang D (2014) Annelida Polychaeta III Sabellida. Fauna Sinica Invertebrata 54: 1–493.

Sun Y, Wong, E, Hove HA ten, Hutchings PA, Williamson JE, Kupriyanova EK (2015) Revision of the genus *Hydroides* (Annelida: Serpulidae) from Australia. Zootaxa 4009(1): 1–99. doi: 10.11646/zootaxa.4009.1.1

Sun Y, Wong E, Tovar-Hernández MA, Williamson JE, Kupriyanova EK (2016). Is *Hydroides brachyacantha* (Serpulidae : Annelida) a widespread species? Invertebrate Systematics 30(1): 41–59. doi: 10.1071/IS15015

Tovar-Hernández MA, Villalobos-Guerrero TF, Kupriyanova EK, Sun Y (2016 [online 2015]). A new fouling *Hydroides* (Annelida, Sabellida, Serpulidae) from southern Gulf of California. Journal of the Marine Biological Association of the United Kingdom 96(3): 693–705. doi: 10.1017/S0025315415000764

Townsend CH (1916) Voyage of the 'Albatross' to the Gulf of California in 1911. Bulletin of the American Museum of Natural History 35(24): 399–476. http://hdl.handle.net/2246/1019

Treadwell AL (1902) The polychaetous annelids of Porto Rico. Bulletin of the United States Fish Commission. 20, 2: 181–210. http://www.marinespecies.org/polychaeta/aphia.php?p=sourcedetails&id=126990

Treadwell AL (1929) New species of polychaetous annelids in the collections of the American Museum of Natural History from Porto Rico, Florida, Lower California, and British Somaliland. American Museum Novitates 392: 1–13. http://hdl.handle.net/2246/3789

Treadwell AL (1931) Three new species of polychaetous annelids in the collections of the United States National Museum. Proceedings of the U.S. National Museum 80(2902): 1–5. http://biodiversitylibrary.org/page/7614489

Treadwell AL (1939) Polychaetous Annelids of Porto Rico and Vicinity. New York Academy of Sciences. Scientific Survey of Porto Rico and the Virgin Islands 16(2): 151–319. https://archive.org/details/scientificsurvey160104newy

Verrill AE (1873) VIII. Report upon the invertebrate animals of Vineyard Sound and the adjacent waters, with an account of the physical characters of the region. Report of the United States Commission of Fish and Fisheries, 757 pp. doi: 10.5962/bhl.title.11688

Welter-Schultes FW (2013) Guidelines for the Capture and Management of Digital Zoological Names Information. Version 1.1, [Version 1.0 released 2012] 126 pp. http://www.gbif.org/orc/?doc_id=2784

Wu BL, Chen M (1981) Two new species of *Hydroides* (Polychaeta: Serpulidae) from South China Sea. Oceanologia et Limnologia Sinica 12(4): 354–357.

Zibrowius H (1968) Étude morphologique, systématique et écologique des Serpulidae (Annelida Polychaeta) de la région de Marseille. Recueil des Travaux de la Station Marine d'Endoume 43(59): 81–252.

Zibrowius H (1971) Les espèces Méditerranéennes du genre *Hydroides* (Polychaeta Serpulidae). Remarques sur le pretendu polymorphisme de *Hydroides uncinata*. Tethys 2: 691–746. http://paleopolis.rediris.es/benthos/REF/som/T-pdf/1970_2-3-691.pdf

Zibrowius H (1972a) Deux espèces nouvelles du genre *Hydroides* (Polychaeta, Serpulidae) de la Mer Jaune et des Iles Banda. Bulletin de la Société Zoologique de France 97(1): 89–93.

Zibrowius H (1972b) *Hydroides norvegica* Gunnerus, *Hydroides azorica* n.sp. et *Hydroides capensis* n. sp. (Polychaeta Serpulidae) espèces vicariantes dans l'Atlantique. Bulletin du Muséum d'Histoire Naturelle, Paris, Series 3, 33(39): 433–446.

Zibrowius H (1972c) Mise au point sur les espèces Méditeranéennes de Serpulidae (Annelida Polychaeta) décrites par Stefano delle Chiaje (1822–1829, 1841–1844) et Oronzio Gabriele Costa (1861). Tethys 4(1): 113–126. http://paleopolis.rediris.es/benthos/REF/som/T-pdf/1972_4-1-113.pdf

Zibrowius H (1973) Serpulidae (Annelida Polychaeta) des côtes ouest de l'Afrique et des archipels voisins. Annales Musee Royal de l'Afrique Centrale, Ser. 8, Sciences Zoologique 207: 1–93.

Zibrowius H (1978) Introduction du polychète Serpulidae Japonais *Hydroides ezoensis* sur la côte Atlantique Française et remarques sur la propagation d'autres espèces de Serpulidae. Tethys 8(2): 141–150. http://paleopolis.rediris.es/benthos/REF/som/T-pdf/1976_8-2-141.pdf

Zoological Museum, Ivan Franko National University of Lviv (undated) Benedykt Dybowski (12.V.1833–31.I.1930). http://zoomus.lviv.ua/en/dybovsky/ [Accessed on 28 July 2016]

Supplementary material 1

Hydroides type-species data summary

Authors: Geoffrey B. Read, Harry A. ten Hove, Yanan Sun, Elena K. Kupriyanova

Data type: spreadsheet

Explanation note: Name categories, original-name WoRMS links, geolocations, locations, etc.

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RESEARCH ARTICLE

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First record of *Rhopalophthalmus longipes* Ii, 1964 from Malaysian waters (Crustacea, Mysida)

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Abstract

The marine mysid species *Rhopalophthalmus longipes* Ii, 1964 is reported from Malaysian waters for the first time. Specimens are described and illustrated in detail based on material collected by epibenthic sledge from the seagrass meadows of Pulau Tinggi, Johor. Specimens exhibit a slight difference from Ii's type material by possessing a rounded process bearing two small protrusions apically near the middle distal end of the third segment of antennal peduncle. In addition, its telson armed with 7-9 moderately strong setae at the lateral margin.

Keywords

Malaysian waters, Mysidae, new record, *Rhopalophthalmus longipes*, taxonomy

Introduction

The genus *Rhopalophthalmus* was established in 1906 by Illig in his preliminary report on the Valdivia Expedition with *R. flagellipes* as its type species collected from Congo Estuary, Africa. Later in 1910, Hansen allocated another species to this genus, *R. egregius* from Bawean Island in the Java Sea, Indonesia, from the Siboga Expedition.

Currently, the genus *Rhopalophthalmus* contains 27 nominal species (Mees 2010). The previous records of the genus *Rhopalophthalmus* in Malaysian waters were restricted to *R. egregius*, *R. orientalis* and *R. hastatus* (Tan et al. 2014).

Rhopalophthalmus longipes was first described from Ajiro, Shizuoka Prefecture, Japan by Ii (1964) during the South China Sea expedition that was conducted by the Imperial Fisheries Experimental Station of Japan. It was then found in the adjacent waters of Nansha Islands, the Spratlys (Wang and Liu 1994) and East China Sea (Wang and Liu 1997). In 2011, Hanamura et al. recorded the occurrence of *R. longipes* from Amami Island, south-western Japan, south-western part of the South China Sea, and also the western part of Timor Sea. Since Ii's original description of *Rhopalophthalmus longipes* is relatively brief and literature from different areas noted morphological variability, the present paper provides a full redescription of *R. longipes* collected from Malaysian waters.

Materials and methods

Specimens were collected from two sites (Kampung Pasir Panjang and Kampung Sebirah Kechil) of seagrass beds from Pulau Tinggi, Sultan Iskandar Marine Park (SIMP), Johor (Fig. 1) by using an epibenthic sledge with a mouth opening of 20 cm height and 60 cm width, mesh size 140 µm. Three replicates were obtained for each station. The appendages and mouthparts were dissected and mounted on glycerol gel slides and then drawn under an optical microscope (Olympus BX43) and stereomicroscope with

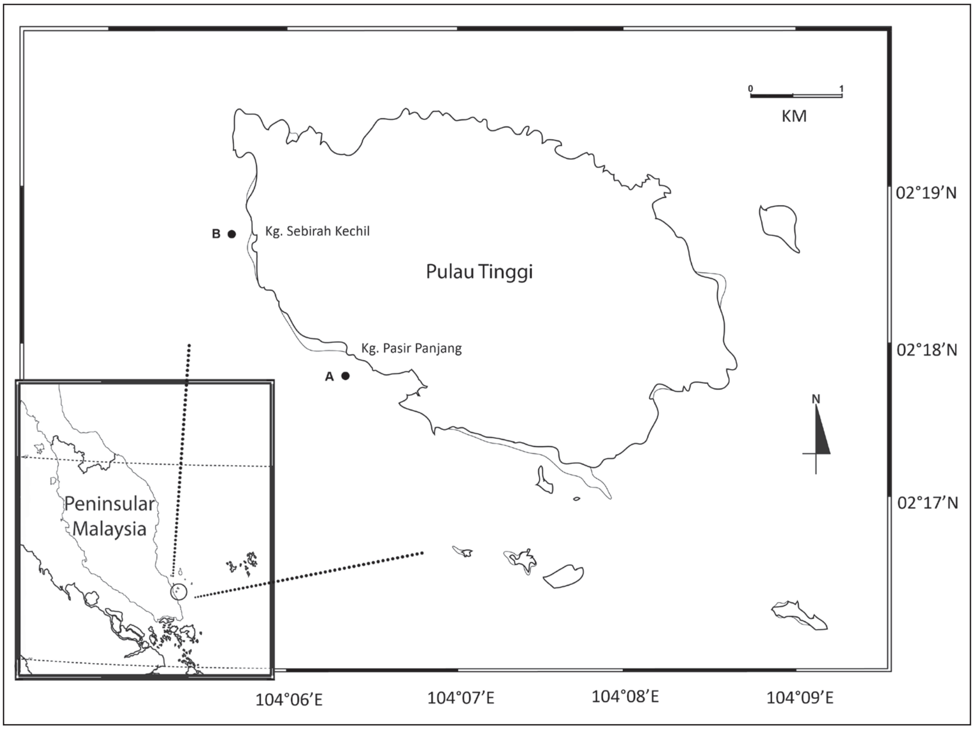

Figure 1. Map of the study area, **A** Kampung Pasir Panjang and **B** Kampung Sebirah Kechil, Pulau Tinggi, Sultan Iskandar Marine Park, Johor.

camera lucida. The drawings were digitized on Adobe Illustrator CC using the methods described in Coleman (2003). Material was deposited in Universiti Kebangsaan Malaysia Muzium Zoologi (**UKMMZ**).

Systematics

Order MYSIDA Boas, 1883
Family MYSIDAE Haworth, 1825
Subfamily RHOPALOPHTHALMINAE Hansen, 1910
Genus *Rhopalophthalmus* Illig, 1906

Rhopalophthalmus longipes Ii, 1964

Figs 2–5

Rhopalophthalmus longipes Ii, 1964, 180, figs 46, 47; Mauchline and Murano 1977, 75 [catalogue]; Muller 1993, 49 [catalogue]; Wang and Liu 1994, 91, figs 14; 1997, 204; 2000, 114, figs 27; Hanamura et al. 2011, 14, figs 8-10.

Material examined. One immature female, 6.5 mm, UKMMZ-1553, Kampung Sebirah Kechil, Pulau Tinggi, Sultan Iskandar Marine Park, Johor, 02°18.581'N, 104°05.624'E, epibenthic sledge, 25th March 2012, 30.1 °C, depth 7 m, coll. Azman, B.A.R., Tan, H.S. and Shamsul, B.; eight immature females, six juveniles, UKMMZ-1554; three juveniles, UKMMZ-1555; two immature females, four juveniles, UKMMZ-1556; same station. Largest immature female, 6.9 mm, juveniles, 1.9-3.5 mm, males not collected. In the females, smaller than 5.9 mm, the pleopods are not fully developed. Juveniles: in the smallest specimens at our disposal, measuring 1.9 mm, the eyes are somewhat larger and with stouter stalk than in the adult.

Description. Based on immature female, 6.5 mm, UKMMZ-1553, Figs 2A, 5A.

Carapace short; anterior dorsal part of carapace between postorbital spines slightly produced, forming evenly rounded rostral plate; the postorbital spines sharp, supported by very short, feebly developed carina; antero-lateral angles of the carapace (“cheeks”) somewhat sinuous or slightly concave; posterior dorsal margin excavate, leaving the last two to three posterior thoracic somites exposed completely in dorsal view; cervical sulcus well marked dorsally and laterally around anterior one-third, nodules not present on the dorsal surface of carapace, just posterior to cervical groove in addition to posterior one.

Eyes large and globular, somewhat shorter than the first joint of antennular peduncle; cornea well pigmented; the whole eye, including the stalk, nearly 1 ½ times as long as broad, stalk nearly cylindrical, cornea occupying ⅓ of the eye and somewhat narrower than the distal end of the stalk (Fig. 3A).

Antennular peduncle somewhat slender, first segment of antennular peduncle 1 ⅓ times as long as the combined length of distal two segments, armed with several setae along lateral margin; second segment shortest, slightly shorter than wide; third segment longer than wide, with three moderate setae, distal outer corner produced into a

Figure 2. *Rhopalophthalmus longipes* Ii, 1964, **A** immature female, 6.5 mm, UKMMZ-1553 **B** juvenile, 2.4 mm, UKMMZ-1554, Pulau Tinggi, Malaysia.

triangular process under the base of the outer flagellum and a rounded process bearing two protrusions (Fig. 3B) apically near the middle distal end (Fig. 3C).

Antennal scale extending beyond the distal end of the antennular peduncle, approx. 6⅓–7 times as long as wide, the margins nearly parallel and equal width throughout; apex almost truncate; a distinct oblique suture marking off the small distal segment; disto-lateral spine slender, prominent and extending beyond the apex of the scale; sympod composed of four spines on the inner ventral face at the base of peduncle (Fig. 3E), two longer and two short spines, the most inner lateral spine around five times longer than the mesial one (Fig. 3D).

Labrum transverse, without process in front, mandibles with moveable lacinia thick, molar process thick, slightly produced, with teeth on the end, the palp moderately short, very feebly expanded. Maxilla (Fig. 3F) with the lobe from third segment deeply cleft, the palp elongated, the exopod rather small.

Abdominal somites smooth, second to fifth somites nearly sub-equal in length, first and sixth somites 1 ½ times as long as fifth one (Fig. 5A).

Endopods of *pereopods* (Figs 4A, B, C, D, E, F, 5B) slender and gradually increase in length posteriorly, remarkable in having proportionately long endopod particularly in seventh one; endopod of third to sixth pereopods similar in shape but length increasing posteriorly; endopod of third pereopod (Fig. 4C) slightly stouter than the

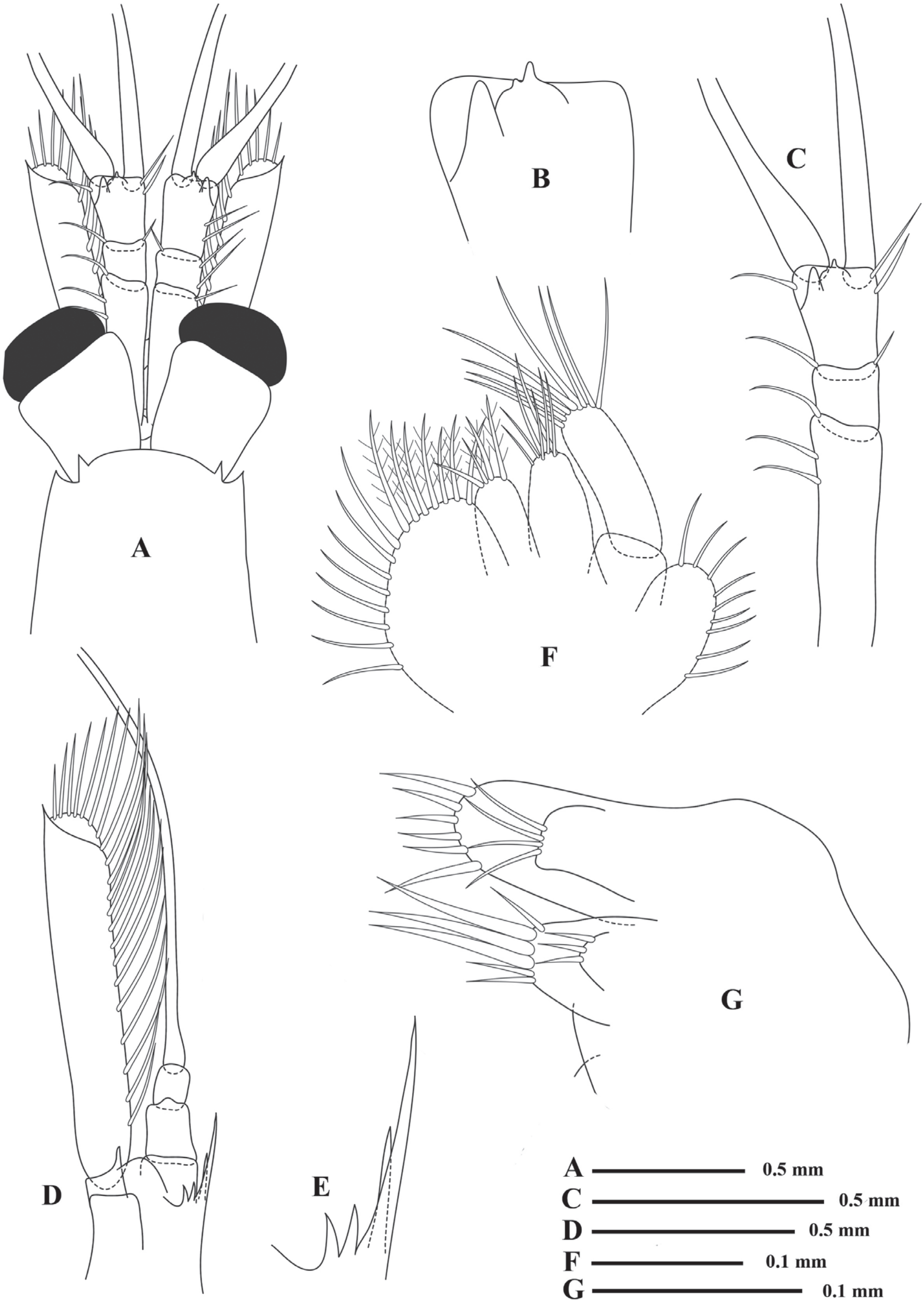

Figure 3. *Rhopalophthalmus longipes*; **A** anterior part of carapace **B** third segment of antennular peduncle **C** antennule **D** antenna and antenna scale **E** sympod spines of antenna **F** maxilla **G** maxillule.

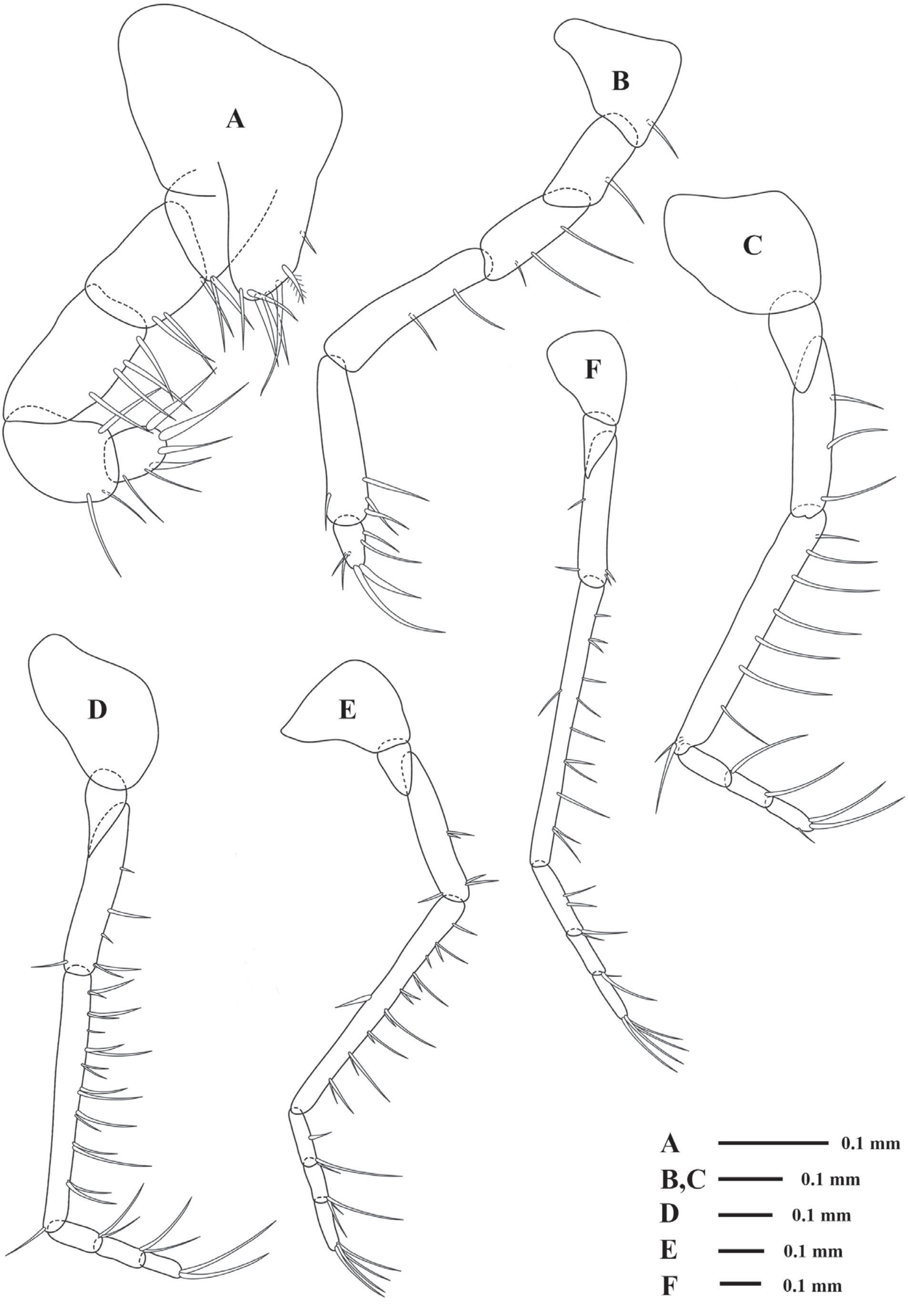

Figure 4. *Rhopalophthalmus longipes*; **A** endopod of first pereopod **B** endopod of second pereopod **C** endopod of third pereopod **D** endopod of fourth pereopod **E** endopod of fifth pereopod **F** endopod of sixth pereopod.

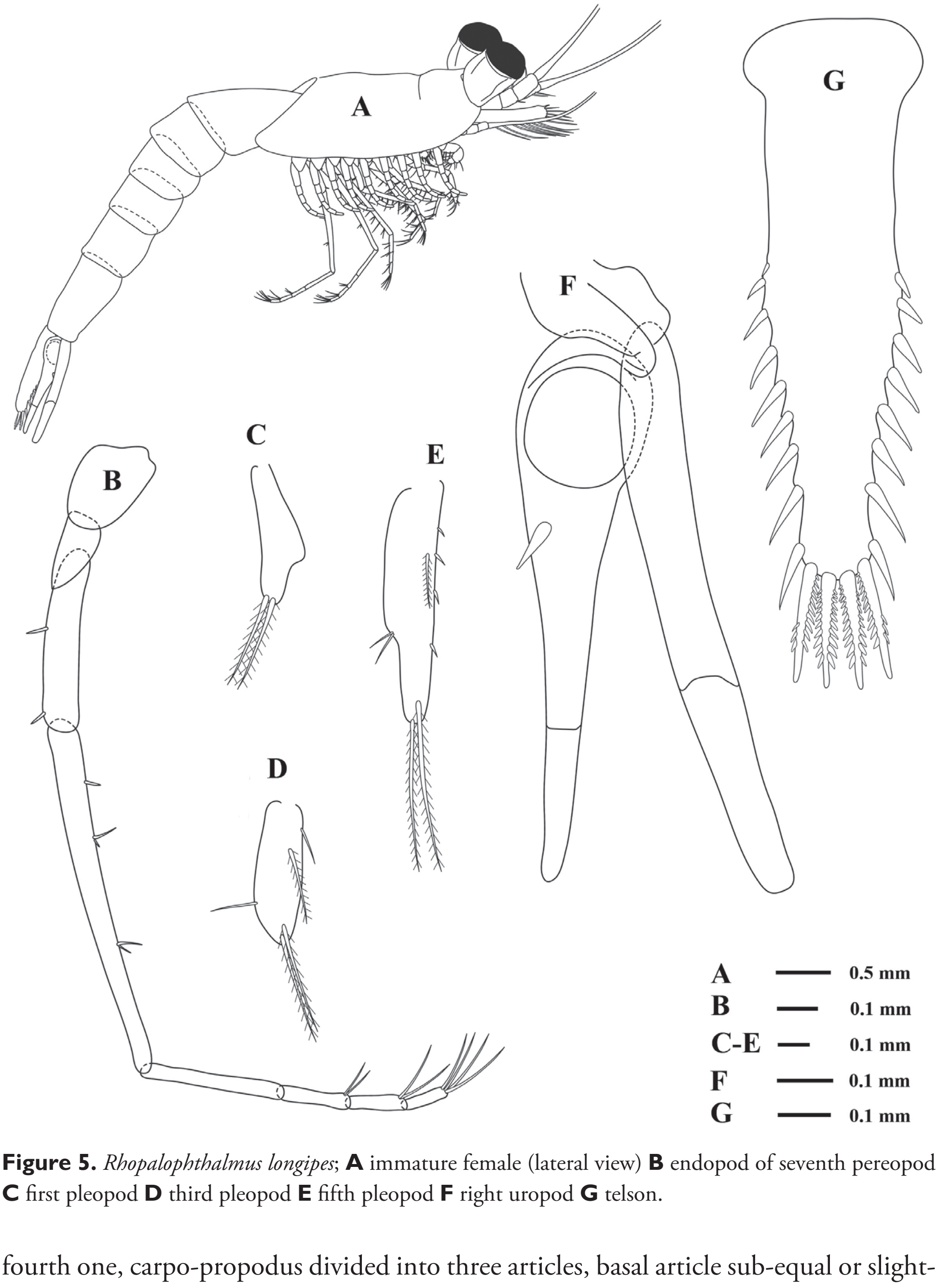

Figure 5. *Rhopalophthalmus longipes*; **A** immature female (lateral view) **B** endopod of seventh pereopod **C** first pleopod **D** third pleopod **E** fifth pleopod **F** right uropod **G** telson.

fourth one, carpo-propodus divided into three articles, basal article sub-equal or slightly longer than the carpo-propodus; endopod of fourth to sixth pereopods (Figs 4D, 4E, 4F) having three-segmented carpo-propodus; endopod of seventh pereopod (Fig. 5B) longest, approx. 2½ times as long as the exopod, carpo-propodus divided into four articles, carpus noticeably long, as long as or longer than pereopod normally unarticulated, barely reaching mid-length of basal plate of exopod.

Pleopods un-articulated, length generally increasing on posterior somites but that on third pleopod somewhat short, comparable to first one (Figs 5C, 5D, 5E).

Uropod two-segmented in both endopod and exopod; endopod sub-equal in length with telson, proximal segment with a strong stout seta at the middle of the ventral inner margin, distal segment ¼ of the endopod in length; exopod with outer margin very fine setose, somewhat longer than endopod with distal segment ⅖ of the exopod in length and 10½ times as long as wide (Fig. 5F).

Telson comparatively narrow and slender, 4 ⅖ times as long as basal wide, nearly same length as the sixth abdominal somite, extends distinctly beyond the articulations of the uropod, abruptly constricted beyond the articulations of the uropod but not forming discernible waist, and hardly broadens to first ½ point with the lateral margins nearly parallel, in the next half gradually narrows distally with convex margins somewhat concave, and accordingly rather slightly broadens distally near the apex; distal half of the lateral margin armed with 7–9 strong spines, increasing in length posteriorly in the distal part but become again somewhat shorter towards the apex; apex narrowly rounded and armed with four extremely strong spines; the apical spines nearly equal in length with each other, ⅕ of the total length of the telson and furnished with secondary spinules, which are flattened like saw-teeth (Fig. 5G).

Type locality. Shizuoka, Japan

Distribution. Shizuoka, Nagasaki, Japan (Ii, 1964); Nansha Islands, the Spratlys (Wang and Liu, 1994); East China Sea (Wang and Liu, 1997); off Amami Island, south-western Japan; south-western part of South China Sea and western part of Timor Sea (Hanamura et al., 2011) and Pulau Tinggi, Johor, Malaysia (present study).

Remarks. *Rhopalophthalmus longipes* was first described by Ii (1964) based on the specimens collected from Japan. This species can be easily distinguished from others species in having a very narrow telson and secondary spinules on the apical spines of telson. Another distinct character within the genus is the endopod of third to seventh thoracopods gradually increasing in length posteriorly and the seventh endopod of thoracopod being more than twice as long as the exopod.

Rhopalophthalmus longipes resembles *Rhopalophthalmus orientalis*, which was described by Tattersall (1957) from Japanese waters by having two long spines and two shorter spines at the antennal sympod and possessed peculiarly flattened teeth-saw like secondary spinules on the apical spines of telson. However, the seventh endopod of thoracopod in latter species is not as long as twice the length of exopod compared to *R. longipes* and the telson is conspicuously slender in the distal half compared to *R. orientalis*, which is moderately broad in distal half. In addition, *R. orientalis* has small triangular rostrum, which is not found in the *R. longipes*. *R. longipes* also shows resemblance to *R. terranatalis* O. Tattersall, 1957 collected from estuarine waters around the coasts of Natal from Richard's Bay (on the east to Langebaan Bay of the south-west coast), but seventh thoracic endopod of the latter species has seven sub-segments instead of four sub-segments with an unusually elongated carpus in *R. longipes*.

The specimens found in this study exhibit some slight differences from the *Rhopalophthalmus longipes* of Hanamura et al. (2011) as the small nodules near the cervical sulcus of the carapace were absent. The specimens at hand also differ from the specimens described by Ii (1964) and Hanamura et al. (2011) by the combination of these characters; 1) presence of a triangular process under the base of the outer flagellum; 2) presence of a rounded process bearing two protrusions apically near the middle distal end of third segment of antennule peduncle; and 3) telson armed with only 7-8 moderately strong setae.

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References

Coleman CO (2003) "Digital inking": How to make perfect line drawings on computers. Organisms Diversity and Evolution 3(14): 1–14. https://doi.org/10.1078/1439-6092-00081

Hanamura Y, Murano M, Man A (2011) Review of eastern Asian species of the mysid genus *Rhopalophthalmus* Illig, 1906 (Crustacea, Mysida) with descriptions of three new species. Zootaxa 2788: 1–37.

Hansen HJ (1910) The Schizopoda of the Siboga Expedition. Siboga Expedition 37: 1–77.

Ii N (1964) Fauna Japonica, Mysidae (Crustacea). Biogeographical Society of Japan, Tokyo, 610 pp.

Illig G (1906) Bericht über die neuen Schizopodengattungen und -arten der deutschen Tiefsee-Expedition, 1898–1899. Zoologisher Anzeiger 30: 194–211.

Mauchline J, Murano M (1977) World list of the Mysidacea, Crustacea. Journal of the Tokyo University of Fisheries 64(1): 39–88.

Mees J (2015) *Rhopalophthalmus longipes*. In: Mees J, Meland K (Eds) World List of Lophogastrida, Stygiomysida and Mysida. World Register of Marine Species. http://www.marinespecies.org/aphia.php?p=taxdetails&id=226630 [accessed on 2016-07-11]

Tan HS, Azman BAR, Othman BHR (2014) Taxonomic status of mysid shrimps (Crustacea) from Peninsular Malaysia waters. Malayan Nature Journal 66 (3&4): 103–116.

Tattersall OS (1957) Report on a small collection of Mysidacea from the Sierra Leone estuary together with a survey of the genus *Rhopalophthalmus* Illig and a description of a new species of *Tenagomysis* from Lagos, Nigeria. Proceedings Zoological Society London 12: 81–128. https://doi.org/10.1111/j.1096-3642.1957.tb00282.x

Wang S, Liu JY (1994) A faunal study of Mysidacea of Nasha Islands and its adjacent waters. Marine Fauna and Flora and Biogeography of the Nansha Islands and Neighbouring Waters I. Ocean Press 1: 61–111. [In Chinese]

Wang S, Liu JY (1997) Mysidacea fauna of the East China Sea. Studia Marina Sinica 38: 191–222. [In Chinese]

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CHECKLIST

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Bees of the Azores: an annotated checklist (Apidae, Hymenoptera)

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Abstract

We report 18 species of wild bees plus the domesticated honeybee from the Azores, which adds nine species to earlier lists. One species, *Hylaeus azorae*, seems to be a single island endemic, and three species are possibly native (*Colletes eous*, *Halictus villosulus*, and *Hylaeus pictipes*). All the remaining bee species are most likely accidental introductions that arrived after human colonization of the archipelago in the 15th century. Bee diversity in the Azores is similar to bee diversity of Madeira and Cape Verde but nearly ten times lower than it is in the Canary Islands.

Keywords

Apidae, Azores, *Hylaeus azorae*, Hymenoptera, pollination

Introduction

The Azores are an archipelago of nine islands and several small islets which range in age from 5.5 million years for Santa Maria (Feraud et al. 1981) to 0.27 million years for Pico (Demand et al. 1982). They are in a very isolated position in the North Atlantic, c. 1300 km from the European continental coast, 1900 km from Newfoundland and 880 km from Madeira, the closest archipelago (Fig. 1).

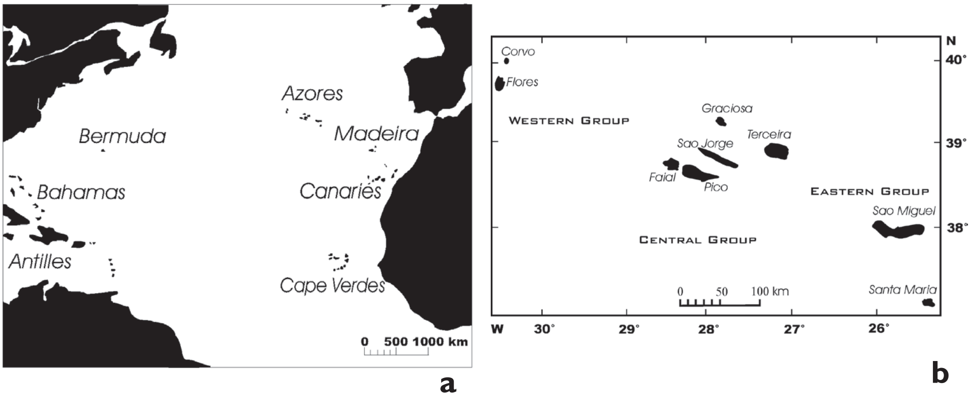

Figure 1. **a** Map of the Northern Atlantic islands **b** Azores archipelago (modified from Schaefer et al. 2011).

It is therefore not surprising that a strictly terrestrial insect group such as the bees (Hymenoptera, Apidae) is represented with a low number of lineages in the Azores. According to the latest published checklist (Franquinho de Aguiar et al. 2010) only nine species plus the honeybee (*Apis mellifera*) occur in the archipelago. The latter is kept by apiculturists on most islands but currently not known to exist in the wild on any of the Azorean islands. Even though the number of species is low, wild bees are relatively common in the Azores and can occur in high numbers of individuals in natural vegetation, often visiting endemic plant species like the Azores goldenrod (*Solidago azorica*, Asteraceae) or Azores bellflower (*Azorina vidalii*, Campanulaceae) (Weissmann and Schaefer, unpubl. data), but also exotic invasive plant species (Picanço et al., unpubl. data). Their importance for pollination, a key ecosystem service, and thus for survival of the endemic flora and crop production in the Azores has not been studied very well so far. As mentioned by Borges et al. (2010), Hymenoptera in general are poorly studied in the Azores, and there is the urgent need to address the Linnean shortfall and carry out basic inventory and taxonomic work, later followed by more advanced ecological and behavioural studies.

One of the reasons for the lack of pollinator studies in the Azores could be their difficult taxonomy and the challenge to identify wild bee species in the field. Our aim therefore is to provide a comprehensive up-to-date checklist of the bee species of the Azores and highlight characters suitable for field identification, without the need to collect the bee and examine e.g. the male genital apparatus or micropunctures on the scutum. We try to avoid jargon and complicated technical terms as much as possible to allow ecologists and botanists who are not experienced entomologists to identify all bees of the Azores to species- or at least genus-level. In this way, we hope to stimulate more research on bees and pollinators in general in the archipelago, in order to improve conservation management of endangered plants as well as fruit production.

Material and methods

To obtain a comprehensive species list, we combined observation data of almost two decades of fieldwork by all authors with a review of the available literature, discussions with many experts (see acknowledgements) and visits to the bee collections in Linz (Biology Center, Oberösterreichisches Landesmuseum Linz) and Munich (Bavarian State Collection of Zoology, ZSM). Most of our field work was done on Corvo, Flores, Faial, Graciosa, Santa Maria, and Terceira, with occasional bee observations on the three remaining islands of the archipelago. We made thousands of bee observations during all these years but did not collect large numbers of voucher specimens. Instead, we just took a few selected individuals every year, often animals found dead on roadsides, in spider webs or in Japanese beetle traps (Azores Agriculture Services monitoring plan for *Popillia japonica*). These were identified using the latest morphological identification keys for Europe (e.g., Amiet 1996, Amiet et al. 2001, Amiet et al. 2004, Amiet and Krebs 2014, Falk and Lewington 2015, Scheuchl and Willner 2016). We tried to obtain photographs of living individuals in addition to the voucher specimens, since these are an important source of ecological and behavioural information (e.g., flower visitation, phenology, nesting and mating behaviour) not available from collected material.

For all species, except *except Apis mellifera*, *Bombus pratorum*, *Halictus lativentris*, *Hylaeus azorae*, *Megachile concinna*, *Megachile pyrenaica*, and *Osmia niveata*, we used DNA barcoding to obtain some sort of molecular confirmation of the species identity. We extracted DNA from legs or the thorax of up to six dry or ethanol-preserved individuals per species using a NucleoSpin tissue kit (Macherey-Nagel, Germany) following the manufacturer's protocol. Then we used polymerase chain reaction (PCR) to amplify c. 600 nucleotides of the mitochondrial cytochrome c oxidase I (COI) gene as described in Schmidt et al. (2015). For PCR we relied on the Kapa2G Fast ready mix (Kapa Biosystems, Wilmington, USA) following the suggested standard protocol. Following Smith et al. (2012), we first worked with the primer combination LepF1 and LepR1, and for poor quality DNA samples added the internal primers C_ANTMR1D and RonMWASPdeg_t1. Because of problems with *Wolbachia* (see below), we designed a new forward primer Hym-COI-F (TAA GAA TAA TTA TTC GWA TAG AAT TAA G), which was used together with LepR1 for all halictid and colletid bees. We cleaned the PCR products enzymatically with ExoSAP-IT mix (Affymetrix, Santa Clara, USA) and sent them to a private company (GATC, Konstanz, Germany) for Sanger sequencing. We edited and assembled the raw sequence reads using Geneious 6.1.8 (Biomatters, Auckland, New Zealand). Then we performed BLAST (Basic Local Alignment Search Tool) searches in GenBank (www.ncbi.nlm.nih.gov/genbank/) to compare our sequences to all publicly available bee sequences. Furthermore, we aligned the obtained COI sequences with additional sequences from other parts of the species ranges downloaded from GenBank in Geneious 6.1.8 using the Geneious alignment algorithm. We added COI sequences from GenBank of the six species, for which no sequence from Azorean material was available and *Vespula germanica* (introduced invasive in the Azores) as an outgroup and used RAxML v. 8.1.18 (Stamatakis, 2014) on the CIPRES Science Gateway v.3.3 (http://phylo.org) to estimate a maximum likelihood (ML) phylogeny.

Results

In total, we found evidence for occurrence of 18 wild bee species from seven genera (*Anthidium*, *Bombus*, *Colletes*, *Halictus*, *Hylaeus*, *Megachile*, and *Osmia*) and four families (Apidae, Colletidae, Halictidae, and Megachilidae) plus the domesticated honeybee *Apis mellifera* in the Azores. For 15 species, we have detailed photographs from the field in the Azores and for 17 species, at least one specimen from the Azores exists in our collections or in other public collections. For one species, *Osmia niveata*, we found only literature data (see species accounts for details).

We managed to produce COI sequence data for ten species, which we used for comparison with GenBank sequences, mostly those from the study of Schmidt et al. (2015). A match of 98-100% to at least two GenBank sequences with the same species identity was interpreted as support of our morphological identification (see species accounts for exceptions). DNA extraction from both ethanol and air dried specimens of different age (up to 17 years) was successful. However, we observed that PCR reactions with the standard barcoding primer combination LepF1-LepR1 resulted mostly in sequences of *Wolbachia* parasites, whereas the use of internal primers or our more specific newly designed forward primer gave 100% bee sequences (see also Smith et al. 2012). All sequences have been deposited in GenBank (acc. no. KX824760-80). The ML community phylogeny (Fig. 2) is well resolved and all genera and species are recovered as monophyletic, with very little intraspecific genetic variation. Four of the three families are also recovered as monophyletic. The only exception is Colletidae, where the *Hylaeus* lineage and the *Colletes* lineage do not form a clade. However, the bootstrap values are very low at these nodes and it should be kept in mind that all this is based on just 657 nucleotides of the mitochondrial COI gene. To obtain a more robust phylogeny estimate, additional mitochondrial and nuclear DNA sequences would be necessary but this is beyond the scope of our checklist.

The current state of knowledge regarding the distribution per island within the archipelago is shown in Table 1. Most species (14) are known from the largest island, São Miguel, followed by Faial with 12 species and the small islands Corvo and Flores with 11 species each. Only seven species are currently known from São Jorge. Most species seem to occur on several or all islands. Just one species, *Hylaeus azorae*, might be a single-island endemic, known only from Pico island. *Megachile pyrenaica* and *Bombus pratorum* are also restricted to a single island, Santa Maria and Faial respec-

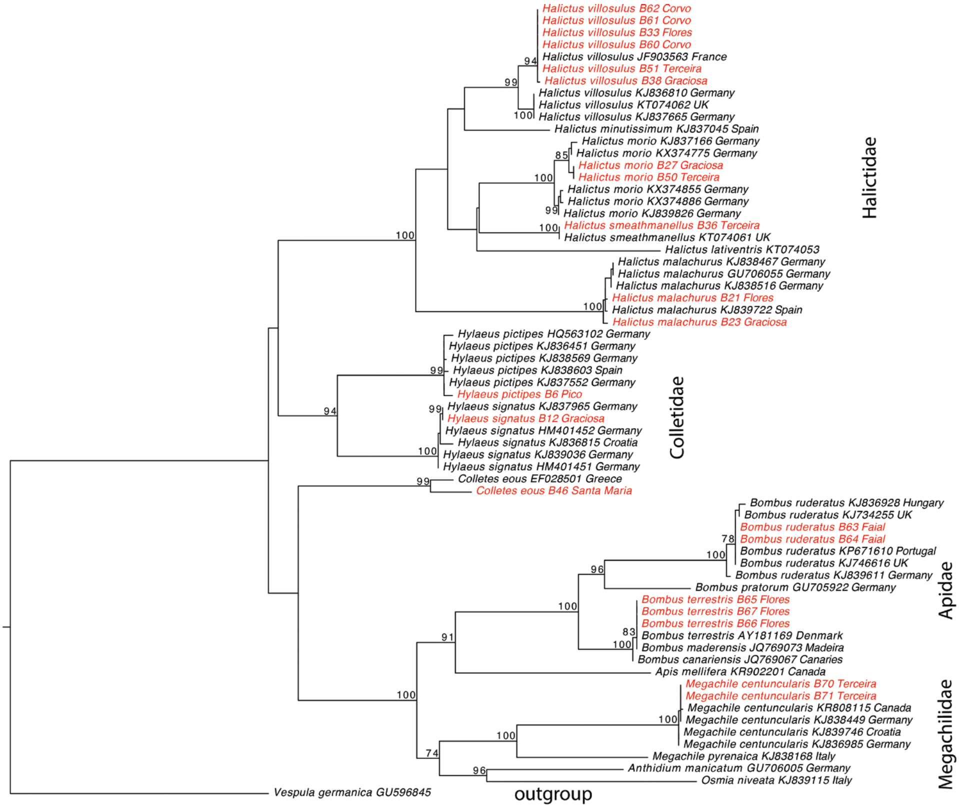

Figure 2. ML phylogeny estimate of the bee species of the Azores archipelago based on 657 nucleotides of the COI gene; sequences of Azorean samples in red, those from other regions in black; the phylogeny is rooted on the Azorean invasive *Vespula germanica*; for sequences downloaded from GenBank, the accession numbers are given, for new Azorean sequences we give the collection number of TUM; the two species *Megachile concinna* and *Hylaeus azorae* are missing in the tree because of lack of material from the Azores for sequencing and lack of sequences from other sources.

tively, but certainly recent introductions. *Megachile concinna* is known only from the islands of the western group, *Colletes eous* only from the eastern group.

Our current state of data with regards to foraging is summarized in Table 2. It is based on the observations over the past decades but is certainly not exhaustive. For several species, e.g. *Bombus pratorum*, a much wider host plant spectrum can be assumed. Only one species, *Hylaeus signatus*, is known to be a specialist in other parts of its range but it seems to be less strict in the Azores (see below). Foraging preferences of four species (*Megachile pyrenaica*, *Halictus lativentris*, *Hylaeus azorae*, *Osmia niveata*) are unknown in the Azores.

Table 1. Species list with distribution per island and presumed status in the archipelago.

Species	Corvo	Flores	Faial	Pico	Graciosa	S. Jorge	Terceira	S. Miguel	Sta. Maria	Status
Anthidium manicatum (Linnaeus)			X					X		introduced
Apis mellifera Linnaeus	X	X	X	X	X	X	X	X	X	domesticated
Bombus pratorum (Linnaeus)			X							introduced
Bombus ruderatus (Fabricius)	X	X	X	X	X	X	X	X	X	probably introduced
Bombus terrestris (Linnaeus)	X	X	X	X	X	X	X	X	X	probably introduced
Colletes eous (Morice)								X	X	possibly native
Halictus lativentris (Schenk)			X					X		probably introduced
Halictus malachurus (Kirby)	X	X	X	X	X	X		X	X	probably introduced
Halictus minutissimus (Kirby)			X				X	X		probably introduced
Halictus morio (Fabricius)	X	X		X	X	X	X	X	X	probably introduced
Halictus smeathmanellus (Kirby)	X	X		X			X	X		probably introduced
Halictus villosulus (Kirby)	X	X	X	X	X	X	X	X	X	possibly native
Hylaeus azorae (Warncke)				X						**endemic**
Hylaeus pictipes (Nylander)	X	X	X	X	X			X		possibly native
Hylaeus signatus (Panzer)	X	X	X	X	X		X	X	X	introduced
Megachile centuncularis (Linnaeus)	X	X	X			X	X	X		probably introduced
Megachile concinna (Smith)	X	X								introduced
Megachile pyrenaica Lepeletier									X	introduced
Osmia niveata (Fabricius)							?	?		doubtful

Table 2. Flowering plant groups visited by wild bee species in the Azores.

Bee species	Plant family
Anthidium manicatum	Asteraceae, Fabaceae, Lamiaceae
Bombus pratorum	Lamiaceae
Bombus ruderatus	Aizoaceae, Asteraceae, Boraginaceae, Brassicaceae, Elaeagnaceae, Ericaceae, Fabaceae, Hydrangeaceae, Hypericaceae, Lamiaceae, Myrtaceae, Plantaginaceae, Polygonaceae, Primulaceae, Resedaceae, Rosaceae, Scrophulariaceae, Solanaceae, Tropaeolaceae, Verbenaceae, Zingiberaceae
Bombus terrestris	Aizoaceae, Asteraceae, Boraginaceae, Brassicaceae, Campanulaceae, Caprifoliaceae, Elaeagnaceae, Ericaceae, Frankeniaceae, Iridaceae, Lamiaceae, Myrtaceae, Pittosporaceae, Plantaginaceae, Primulaceae, Resedaceae, Rosaceae, Solanaceae, Tropaeolaceae, Zingiberaceae
Colletes eous	Asteraceae
Halictus lativentris	Unknown
Halictus malachurus	Apiaceae, Asteraceae, Campanulaceae, Ericaceae, Resedaceae, Tamaricaceae
Halictus minutissimus	Asteraceae (*Erigeron karvinskianus*)
Halictus morio	Apiaceae, Asteraceae, Campanulaceae, Fabaceae, Hydrangeaceae, Hypericaceae, Lamiaceae, Lythraceae, Oxalidaceae, Polygonaceae, Ranunculaceae, Rosaceae, Scrophulariaceae, Zingiberaceae
Halictus smeathmanellus	Asteraceae (*Solidago azorica*), Campanulaceae (*Azorina vidalii*), Fabaceae
Halictus villosulus	Asteraceae, Ericaceae, Fabaceae, Frankeniaceae, Gentianaceae, Hydrangeaceae, Hypericaceae, Lamiaceae, Plantaginaceae, Primulaceae, Rosaceae
Hylaeus azorae	Unknown
Hylaeus pictipes	Asteraceae (*Solidago azorica*, *Helminthotheca echioides*), Ranunculaceae (*Ranunculus cortusifolius*)
Hylaeus signatus	Resedaceae (*Reseda luteola*), Tamaricaceae (*Tamarix africana*)
Megachile centuncularis	Asteraceae, Fabaceae
Megachile concinna	Fabaceae (*Lotus corniculatus*)
Megachile pyrenaica	Unknown
Osmia niveata	Unknown

Annotated checklist

In the following, we provide short species accounts for all 19 bee species for which we found evidence that they exist or have existed in the Azores. General distribution data and most information on nesting and social behaviour is based on literature (Amiet and Krebs 2014, Falk and Lewington 2015, Scheuchl and Willner 2016). Information on foraging and phenology is based on observations by the authors unless other sources are indicated. This information was compiled during fieldwork in the Azores since 1998 and is therefore much more comprehensive than the data from the collected individuals. The specimen numbers refer to the collections at Technical University of Munich (TUM) and University of Azores, Entomoteca Dalberto Teixeira Pombo (EDTP).

Apidae

Bombus Latreille

Large, hairy, predominantly black, yellow- or white-banded eusocial bees. Nests are built in cavities in the ground, preferably old mouse nests. Females collect pollen with special structures, pollen baskets, on the tibiae of their hind legs. These are absent in parasitic bumblebees of which none are known in the Azores. Three species in the Azores.

Bombus pratorum (Linnaeus)

Description. Large black bee (wing length 13 mm in queens and 10 mm in workers and males), queens and workers with a bright yellow band on the thorax close to the head, a second one in the middle of the abdomen on tergite 2 (often paler or missing in workers), and orange tip of the abdomen; males with yellow head, large bright yellow band in the upper part of the abdomen, and orange tip of the abdomen (Fig. 3g–h).

Distinguishing features. Smallest bumblebee of the Azores and only bee species with orange tip of abdomen in the archipelago.

General distribution. From Portugal in the West to Kamchatka in the East, and from northern Scotland in the North to northern Iran in the South.

Distribution in the Azores. Faial.

First record. 2015.

Nesting. No nests observed in the Azores, elsewhere the species has colonies of 50-120 individuals in existing cavities on the surface or in the soil.

Social behaviour. Primitively eusocial.

Foraging. The only observation in the Azores was on *Prunella vulgaris* (Lamiaceae), elsewhere the species is polylectic.

Phenology. August.

Material. None.

Note. One single observation by Valter Jacinto on Faial Island, Miradouro da Caldeira (c. 850 m asl.), 13 August 2015, (http://www.inaturalist.org/observations/1910834).

Bombus ruderatus (Fabricius)

Description. Large black bee; wing length 18 mm and total length up to 22 mm in queens, workers with wing length of 13 mm and total length up to 16 mm, males with wing length of 14 mm; queens and workers with two brownish-yellow bands on the thorax, a narrow yellow band and white tip of the abdomen (Fig. 3a, c); males with paler yellow bands, more white abdomen and white hairy face pattern (Fig. 3e).

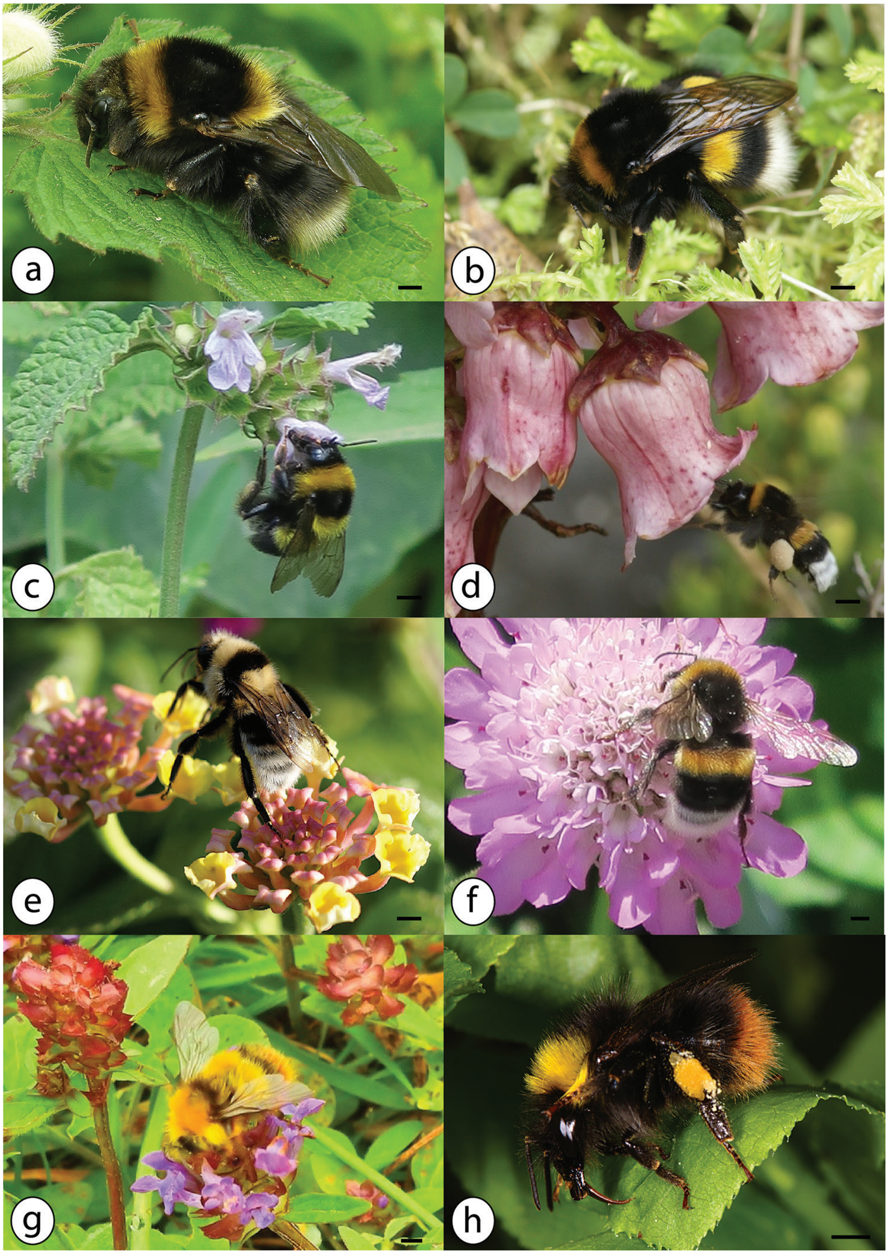

Figure 3. Azorean *Bombus* species: **a** *Bombus ruderatus* queen, UK **b** *Bombus terrestris* queen, July 2016, Terceira; c) *Bombus ruderatus* worker on *Ballota nigra* (Lamiaceae), July 2016, Terceira (Angra do Heroísmo) **d** *Bombus terrestris* worker on *Azorina vidalii* (Campanulaceae), July 2015, Corvo **e** *Bombus ruderatus* male on *Lantana camara* (Verbenaceae), September 2010, São Miguel **f** *Bombus terrestris* male, July 2016, Flores **g** *Bombus pratorum* male on *Prunella vulgaris* (Lamiaceae), August 2015, Faial (Miradoura da Caldeira) **h** *Bombus pratorum* worker, Norway; photos: Steven Falk (**a**), Hanno Schaefer (**b, c, e, f**), Julie A. Weissmann (**d**), Valter Jacinto (**g**) and Kjetil Fellheim on wikipedia (creative commons license) (**h**); scale bars 2 mm.

Distinguishing features. Of the two bumblebee species in the archipelago, *B. ruderatus* is the paler species and can be recognized by the different colour pattern (two yellow bands on the thorax vs. one yellow thorax band in *B. terrestris*).

General distribution. Madeira; throughout Europe from the Iberian Peninsula to southern Scandinavia; North Africa; Asia to Siberia in the East; introduced and invasive in New Zealand and South America (Chile, Argentina).

Distribution in the Azores. All islands.

First record. 1865 (Godman 1870, as *B. hortorum*).

Nesting. Colonies of up to 50-100 workers in existing holes in the ground.

Social behaviour. Primitively eusocial.

Foraging. Polylectic, visits a wide range of species, including exotic invaders like *Lantana camara*, Verbenaceae (Fig. 3e).

Phenology. All year.

Material. Faial (Horta), August-September 1930, leg. L. Chopard, det. Benoist (Benoist et al. 1936, not seen) Faial (Castello Branco, from Japanese beetle trap), 1999, 1 worker, 9 males, leg. H. Schaefer, coll. TUM (specimens B48-B49, B52-B56, B63-B64, B72).

COI sequences of specimens B63-64 (TUM), acc. no. KX824771-72, are identical to *B. ruderatus* sequences from Portugal and UK in GenBank (see Fig. 2).

Note. Reports of *Bombus hortorum* L. by Benoist et al. (1936) refer to this species.

Bombus terrestris (Linnaeus)

Description. Large black bee (wing length 18 mm, total length 20–22 mm in queens; wing length 13 mm, total length 11–17 mm in workers; wing length 14 mm, total length 11–17 mm in males) with one strong brownish-yellow band on the thorax close to the head, a second one in the middle of the abdomen (tergite 2), and bright white tip of the abdomen (Fig. 3b, d, f).

Distinguishing features. In contrast to *B. ruderatus*, only one yellowish band on the thorax, which is deeper in colour than in the previous species.

General distribution. North Africa, Eurasia (Portugal to Norway in the North and Japan in the East), populations on the Canaries and Madeira have been described as distinct species but at least for Madeira, this is not supported (Widmer et al. 1998, Williams et al. 2012); introduced and invasive in parts of Asia, New Zealand, Tasmania, and South America.

Distribution in the Azores. All islands.

First record. Williams et al. 2012 (no island specified).

Nesting. Colonies of several 100 workers in existing holes in the ground.

Social behaviour. Primitively eusocial.

Foraging. Polylectic, visits a wide range of species, including endemics like *Azorina vidalii* (Campanulaceae, Fig. 3d), and invasive exotics like *Hedychium gardnerianum* (Zingiberaceae) and *Leycesteria formosa* (Caprifoliaceae).

Phenology. All year (queens flying December/January to March).

Material. Graciosa, 1 worker; Flores (Santa Cruz and Lajes das Flores, from Japanese beetle trap), July 2016, 9 queens, 9 workers, all leg. H. Schaefer, coll. TUM (specimens B2, B47, B65-B67, B73-B87).

COI sequences of specimens H. Schaefer B65-B67 (TUM), acc. no. KX824773-75, are identical to a *B. terrestris* sequence from Denmark and a *B. maderensis* sequence from Madeira in GenBank but differ slightly from *B. canariensis* JQ769067 (see Fig. 2).

Colletidae

Colletes Latreille

Medium-sized solitary bees. Most species have conspicuous bright hair bands on the abdomen. Nests are built in light soil, often in aggregation. The chambers are lined with a cellophane-like substance. Females collect pollen on the hind legs and the sides of the propodeum. One species in the Azores.

Colletes eous (Morice)

Description. Medium-sized bee (total length 10–13 mm in both sexes, wing length c. 8 mm in females) with orange brown hairy thorax and dark abdomen with white hairy tergite margins (Fig. 4a–b).

Distinguishing features. Medium-sized bee with light brown thorax and conspicuously black and white ringed abdomen.

General distribution. Mediterranean region to Central Asia (Kuhlmann 2005).

Distribution in the Azores. São Miguel and Santa Maria.

First record. 1972.

Nesting. See above.

Social behaviour. Solitary.

Foraging. Based on literature polylectic.

Phenology. June-July.

Material. Santa Maria (Vila do Porto), July 1972, 1 male, leg. N.L.H. Krauss, coll. Snow Entomological Museum, Lawrence, Kansas; São Miguel (Mosteiros), 24.07.2004, 1 male, leg. A. Kroupa, coll. Kroupa (M. Kuhlmann, pers. comm., 28.09.2016); Santa Maria, July 2001, 1 female, leg. H. Schaefer, det. M. Kuhlmann, coll. TUM (B46).

Note. According to M. Kuhlmann, Kiel (pers. comm., 23.11.2015) earlier reports of *C. canescens* Smith 1853, from the islands, most likely refer to this species.

DNA barcoding of specimen B46 (acc. no. KX824776) and BLAST search in GenBank resulted in *C. eous* from Greece as best match (acc. no. EF028501). However, the similarity is only 94%, which means that there are 23 nucleotide differences distributed over the entire COI sequences (see also branch length difference in the ML tree, Fig. 2).

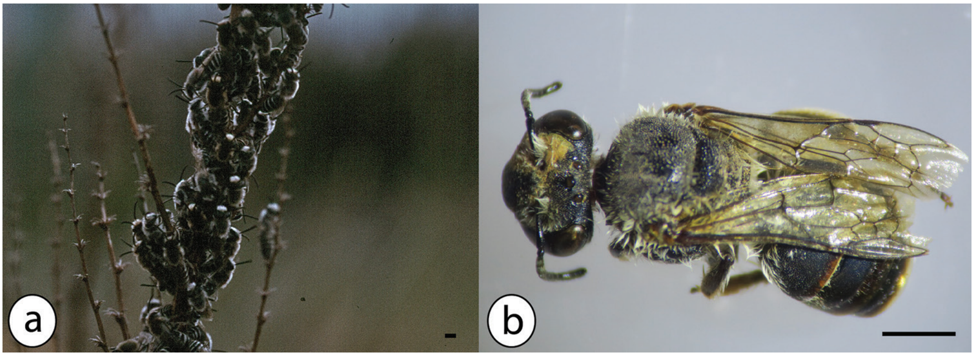

Figure 4. Azorean *Colletes* species: **a** aggregation of more than 50 males of *Colletes eous*, June 2001, Santa Maria (pasture near airport) **b** *Colletes eous* female from Santa Maria (B46, TUM); photos: Hanno Schaefer (**a**) and Julie A. Weissmann (**b**); scale bars 2 mm.

This suggests that the Azorean *Colletes* is not the same species as the one sequenced from Greece but more morphological and genetic data is needed to solve this question.

Hylaeus Fabricius, (*Prosopis*)

All Azorean *Hylaeus* species are small black bees with whitish or yellow face patterns, the males with a mask-like pattern (Fig. 5a–c), the females usually with two dots (Fig. 5d–e). They are solitary bees and build their nests in hollow twigs or other cavities in wood, stone or vertical soil banks. Females collect pollen in their crop. Three species in the Azores, none of them mentioned in the previous lists for Macaronesia (Erlandsson 1983) or the Azores (Franquinho de Aguiar et al. 2010).

Hylaeus (*Prosopis*) *azorae* (Warncke)

Description. Male 6–7 mm, female unknown; sternite 7 with winged appendages, sternite 8 deeply V-shaped (Fig. 6a).

Distinguishing features. Male with +/- rectangular yellowish face pattern (Fig. 5a); female unknown.

General distribution. Endemic to the Azores.

Distribution in the Azores. Pico, Montanha do Pico.

First record. 1938 (described in Warncke 1992b, known only from the type).

Nesting. Unknown, probably in hollow twigs.

Social behaviour. Unknown, but probably solitary.

Foraging. Unknown.

Phenology. July.

Material. Pico, 10.07.1938, 1 male, leg. Ragnar Storå, coll. Linz.

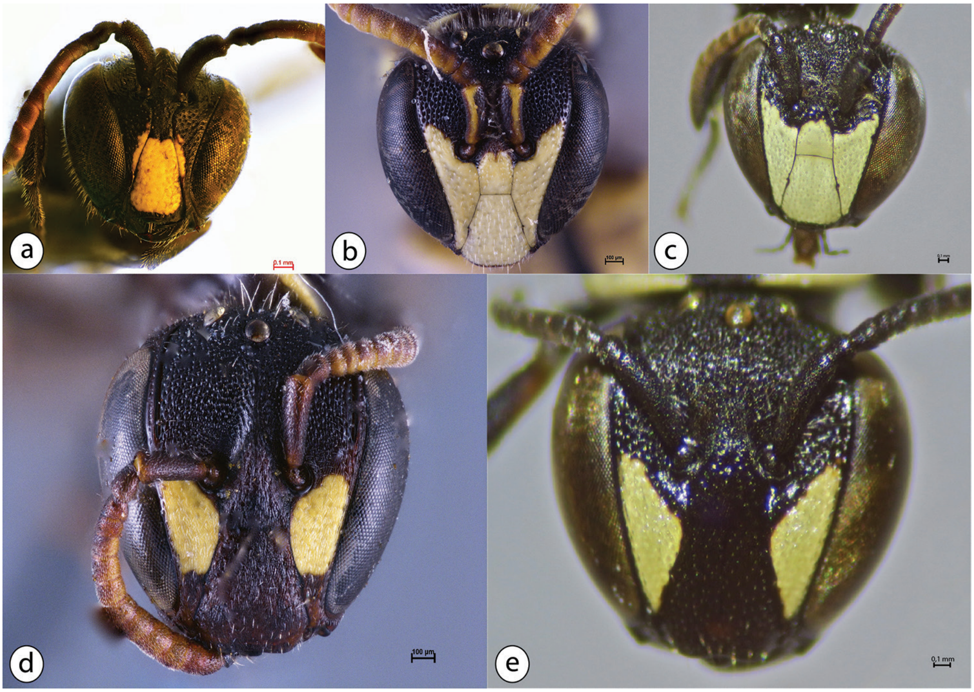

Figure 5. Face patterns of the Azorean *Hylaeus* species; males in the top row, females below: **a** *Hylaeus azorae* **b** *Hylaeus pictipes* **c** *Hylaeus signatus* **d** *Hylaeus pictipes* **e** *Hylaeus signatus*; photos: Esther Ockermüller (Oberösterreichisches Landesmuseum Linz) (**a, b, d**) and Julie A. Weissmann (**c, e**); scale bars 0.1 mm.

Hylaeus (*Prosopis*) *pictipes* (Nylander)

Description. Small black bee (wing length 3.5 mm, total length c. 5 mm) with elongate face, yellow face patterns, and black mandibles (Fig. 5b, d, 6c); groove (fovea) alongside inner eye margin curved towards lateral ocelli (cf. Falk and Lewington 2015, p. 81).

Distinguishing features. Smallest *Hylaeus* in the Azores, male with yellow face pattern exceeding insertion point of antennae, female face pattern with two small trapezoidal yellow spots; legs of males mainly yellow.

General distribution. Eurasia, from Portugal to the Caucasus.

Distribution in the Azores. Corvo, Faial, Flores, Graciosa, Pico, São Miguel.

First record. 1938 (first mentioned in Warncke 1992b).

Nesting. Builds nests in pithy stems or uses existing cavities (e.g., hollow twigs, holes of wood-boring beetles).

Social behaviour. Solitary.

Foraging. Polylectic, observed on Ranunculaceae (*Ranunculus cortusifolius*) (Fig. 6d) and Asteraceae (*Solidago azorica*, *Helminthotheca echioides*).

Phenology. June-August.

Material. Faial (Horta), 30.06.–05.07.1938, 1 female, leg. Richard K. H. Frey; Pico (Madalena), 6–9.07.1938, 1 male, leg. Ragnar Storå; Pico (Madalena), 6–9.07.1938, 1

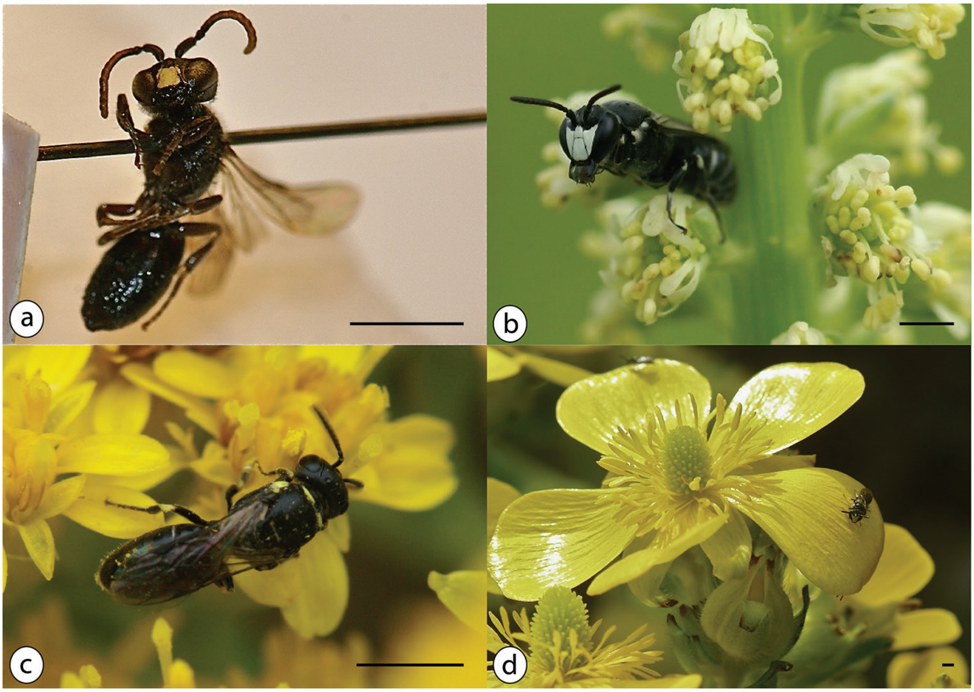

Figure 6. Azorean *Hylaeus* species: **a** *Hylaeus azorae* male, Holotype from Pico, Oberösterreichisches Landesmuseum Linz **b** *Hylaeus signatus* male in *Reseda luteola* (Resedaceae), regurgitating nectar, June 2012, Graciosa **c** *Hylaeus pictipes* female, dorsal view, on *Solidago azorica* (Asteraceae), July 2015, Corvo **d** *Hylaeus pictipes* male (second male in the background) on *Ranunculus cortusifolius* (Ranunculaceae), June 2012, Corvo; photos: Hanno Schaefer (**a, b, d**); Julie A. Weissmann (**c**); scale bars 2 mm.

female, leg. Richard K. H. Frey; S. Miguel (San Roque), 21.07.1938, 1 male, leg. Richard K. H. Frey, all det. and coll. Warncke (Linz). Corvo, 3 males; Graciosa (rim of Caldeira), 1 male; Pico (São Roque), 2 females, all leg. H. Schaefer, coll. TUM (B3-B7, B44).

The COI sequence of specimen H. Schaefer B6 (TUM), acc. no. KX824777, differs in 1–7 positions from the five *H. pictipes* sequences from Spain and Germany in GenBank (see Fig. 2).

Hylaeus signatus (Panzer)

Description. Medium-sized black bee (total length 7–9 mm in both sexes, wing length 4.5–5.5 mm in females and 4–6 mm in males) with roundish face and conspicuous yellowish-white face markings, without curved grooves (fovea) along eye margin; mandibles and legs black; white hair bands on lateral sides of tergite 1 (Fig. 6b).

Distinguishing features. Relatively large; male with mask not exceeding insertion point of antennae (Fig. 5 c), female face pattern with the two spots larger than in *H. pictipes* and more triangular in outline (Fig. 5e); *Reseda* specialist.

General distribution. Madeira (introduced); North Africa; Eurasia, from Portugal in the West to northern Scandinavia and Uzbekistan in the East.

Distribution in the Azores. All islands except São Jorge.

First record. 2001 (Santa Maria; H. Schaefer, unpublished data).

Nesting. In existing cavities (twigs, earth, abandoned nests of other hymenoptera, etc.), sometimes in dense aggregations.

Social behaviour. Solitary bee.

Foraging. Oligolectic, usually *Reseda* specialist, but in the Azores also observed on *Tamarix africana* (Tamaricaceae).

Phenology. June-August.

Material. Corvo (Vila do Corvo), 04.08.2014, 1 male; Graciosa, June 2012, 3 females, 7 males on *Tamarix*; Terceira (airport), 08.08.2014, 1 female, 1 male; Santa Maria, 1 female, all leg. H. Schaefer, coll. TUM (B8-B20; B45).

The COI sequence of specimen H. Schaefer B12 (TUM), acc. no. KX824778, is identical to a *H. signatus* sequence from Germany (KJ837965, see Fig. 2).

Halictidae

Halictus Latreille

All Azorean *Halictus* species are small brownish bees, often occurring in large numbers and nesting in the ground. Males are elongate bees with long antennae (Fig. 7a). Females of the genus can be recognized by a median furrow on the otherwise hairy tergite 5 near the tip of the abdomen (Fig. 7d) and relatively short antennae. Females collect pollen with help of pollen brushes on their hind legs. Both solitary and eusocial species of this genus exist in the Azores. The Azorean species are commonly treated as members of the genus *Lasioglossum* but we follow Amiet and Krebs (2014) and include *Lasioglossum* in a broadly circumscribed *Halictus*. Six species in the Azores.

Halictus lativentris (Schenk), (*Lasioglossum lativentre*)

Description. Small, dark brown bee (total length 8–9 mm in both sexes, wing length 5,5–6 mm in females and 4,5–5,5 mm in males), with narrow bands of pale hair on the abdomen; stigma light brown (Fig. 7a–b).

Distinguishing features. Unknown.

General distribution. West- and Central Europe.

Distribution in the Azores. Faial, São Miguel.

First record. 1984 (first mentioned by Stöckl 1988).

Nesting. Probably in light soils.

Social behaviour. Solitary.

Foraging. No observation data from the Azores available, probably polylectic.

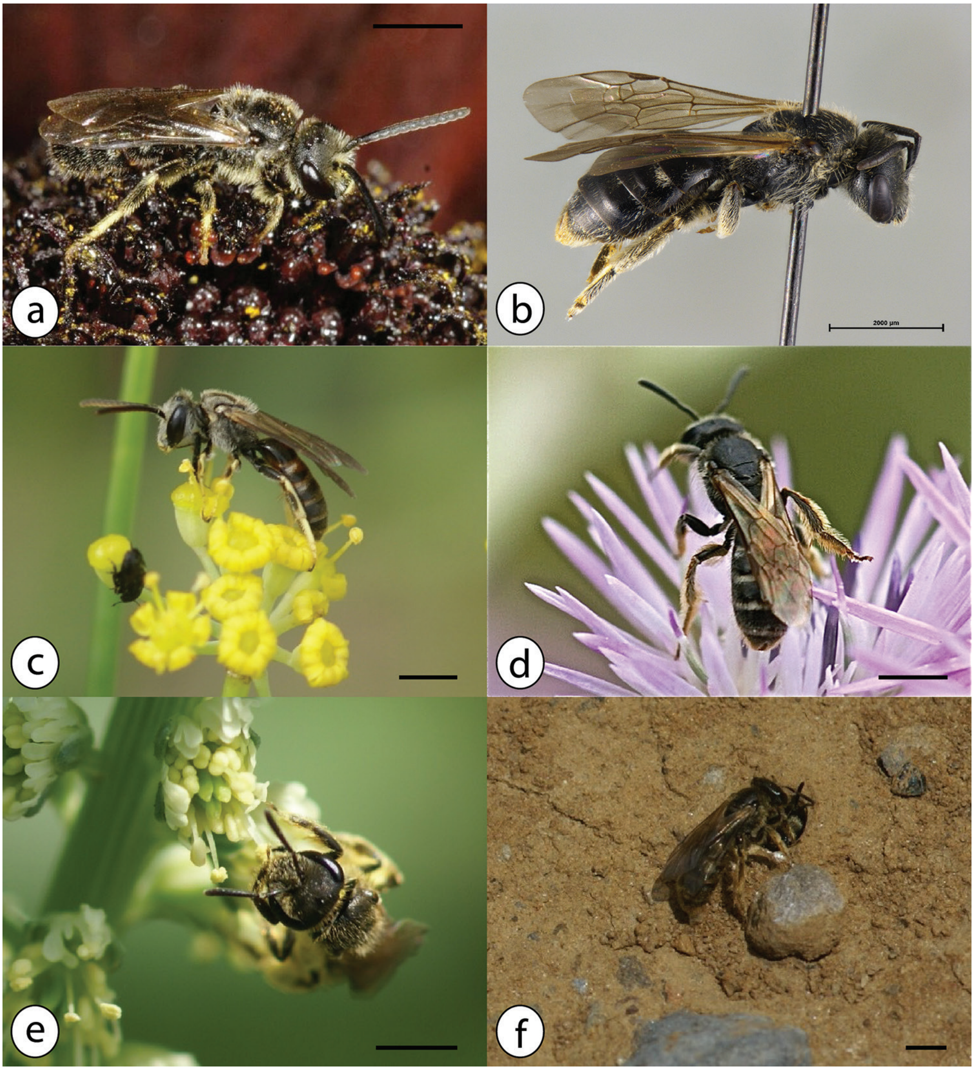

Figure 7. Azorean *Halictus* species: **a** *Halictus lativentris* male, UK **b** *Halictus lativentris* female from Faial, leg. P. Wirtz **c** *Halictus malachurus* male on *Foeniculum vulgare* (Apiaceae) with *Brassicogethes* beetle in the foreground, July 2016, Corvo **d** *Halictus malachurus* female on *Galactites tomentosus* (Asteraceae), June 2012, Graciosa; **e** *Halictus malachurus* female on *Reseda luteola* (Resedaceae), July 2016, Corvo **f** *Halictus malachurus* female approaching nest, while another female guards the entrance hole and touches the antennae of the arriving bee to control its scent, July 2016, Corvo; photos: Jeremy Early (**a**), Esther Ockermüller (Oberösterreichisches Landesmuseum Linz) (**b**), Julie A. Weissmann (**c, e, f**); Hanno Schaefer (**d**); scale bars 2 mm.

Phenology. July-August.

Material. São Miguel (Remédios), 10.08.1984, 1 male, leg. La Roche, det. Ebmer (Ebmer, pers. comm., 20.09.2016); Faial (Horta), 22.07.1992, 1 female, leg. P. Wirtz, det. Ebmer, coll. Warncke (Linz).

Halictus malachurus (Kirby), (*Lasioglossum malachurum*)

Description. Small dark brown bee (total length 7–10 mm in both sexes, wing length 5,5–6,5 mm in females and 4,5–6,5 mm in males); males and females with densely punctuated scutum and top of propodeum with angulate hind corner; males with black or extensively red abdomen, particularly long antennae and extensively yellow legs (Fig. 7c–f).

Distinguishing features. The largest representative of the genus in the Azores; "shoulders" of the thorax strongly angled (Fig. 7e).

General distribution. North Africa; Eurasia, from Portugal to Iran and North to Denmark.

Distribution in the Azores. All islands except Terceira (where probably overlooked).

First record. 1930 (first mentioned by Benoist et al. 1936).

Nesting. Ground nesting (mostly in compacted soil), often in large aggregations; sentinel bee closes access with her head (Fig. 7f).

Social behaviour. Eusocial, sometimes polygynous, and sometimes (in warmer environments) with several broods of workers.

Foraging. Polylectic, observed e.g., on Apiaceae (*Foeniculum vulgare*), Asteraceae (*Galactites tomentosus*, *Helminthotheca echioides, Solidago azorica*, *Tolpis azorica*) and Resedaceae (*Reseda luteola*).

Phenology. July-September.

Material. São Miguel (Furnas) and Faial (Horta), August-September 1930, leg. L. Chopard, det. Blüthgen (Benoist et al. 1936, not seen). São Miguel, September 1954, 5 males, leg. M. Diñiz. São Miguel (Lagoa das Furnas), 07.08.1984, 1 female; São Miguel (Ponta Delgada), 12.08.1984, 2 females; São Miguel (Ginetes), 11.08.1984, 2 females; São Miguel (São João), 09.08.1984, 2 females, 2 males; São Miguel (Feteiras), 11.08.1984, 4 males, all leg. La Roche, det. Ebmer (Ebmer, pers. comm.). Flores, 02.08.2014, 1 female; Graciosa, 3 females, 1 male, all leg. H. Schaefer, coll. TUM (specimens B21-B25).

The COI sequences of specimens H. Schaefer B21 and B23 (TUM), acc. no. KX824763-64, differ in 1–5 positions from the *H. malachurus* sequences from Spain and Germany in GenBank (see Fig. 2).

Halictus minutissimus (Kirby), (*Lasioglossum minutissimum*; *Evylaeus minutissimus*)

Description. Tiny blackish bee (total length c. 5 mm in both sexes, wing length 3,5–4 mm in females and 3–3,5 mm in males); males with entirely dark hind legs (Fig. 8a–b).

Distinguishing features. Smallest of the *Halictus* species in the Azores, behaviour more hectic than other bees.

General distribution. West- and Central Europe.

Distribution in the Azores. Faial, São Miguel, Terceira.

First record. 1986 (first mentioned by Ebmer 1988).

Nesting. Ground nests, sometimes in large aggregations.

Social behaviour. Solitary.

Foraging. Polylectic, observed on Asteraceae (*Erigeron karvinskianus*).

Phenology. July.

Material. Faial (Horta), July 1986, 1 female, leg. Aptroot, det. Ebmer, coll. Mus. Leiden (Ebmer 1988); São Miguel (Ponta Delgada), July 1992, leg. Wirtz, det. Warncke (Wirtz 1994, not seen).

Halictus morio (Fabricius), (*Lasioglossum morio*)

Description. Small black bee (total length 7–8 mm, wing length 4 mm), in the sun often shining metallic green; with narrow bands of whitish hair on the abdomen (Fig. 8c–d).

Distinguishing features. With *H. smeathmanellus*, one of the two small and greenish representatives of the genus in the Azores, but smaller in size than the former species; thorax and abdomen metallic green; males with entirely black tarsi.

General distribution. North Africa; Eurasia, from Portugal to Kazakhstan and north to Finland.

Distribution in the Azores. All islands except Faial (where probably overlooked).

First record. 1930 (first mentioned by Benoist et al. 1936).

Nesting. On bare or sparsely vegetated surfaces on south-facing slopes or flat areas (here, the entrance often with small conical tumuli), often in large aggregations.

Social behaviour. Primitively eusocial.

Foraging. Polylectic, observed on Asteraceae (*Helminthotheca echioides, Sonchus asper*) and Oxalidaceae (*Oxalis corniculata*).

Phenology. April-September.

Material. São Miguel (Furnas), August-September 1930, leg. L. Chopard, det. Blüthgen (Benoist et al. 1936, not seen). São Miguel (2 km SE Feteiras), 11.08.1984, 3 females 1 male; São Miguel (Feteiras), 11.08.1984, 3 females, 2 males; São Miguel (Santana), 07.08.1984, 1 male; São Miguel (Ponta Delgada), 12.08.1984, 1 male, São Miguel (Vila Franca), 07.08.1984, 1 male, all leg. La Roche, det. Ebmer (Ebmer, pers. comm.). São Miguel (Lagoa das Furnas), 23.04.1984, 1 male, leg. Suko, det. Ebmer, coll. Mus. Bremen (Ebmer, pers. comm.). São Miguel (Ponta Delgada), July 1992, leg. Wirtz, det. Warncke (Wirtz 1994, not seen). Santa Maria (Vila do Porto), July 1972, 1 female, det. Ebmer, coll. Senckenberg Frankfurt (Ebmer, pers. comm.). Graciosa (Serra Branca), 4 females; Graciosa (Serra dos Fontes), 3 females; Terceira, 08.08.2014, 1 female, all leg. H. Schaefer, coll. TUM (specimens B26-B32, B50).

The COI sequences of specimens H. Schaefer B27 and B50 (TUM), acc. no. KX824760-61, differ in 1–2 positions from the closest *H. morio* sequences in GenBank, which are of German origin (see Fig. 2).

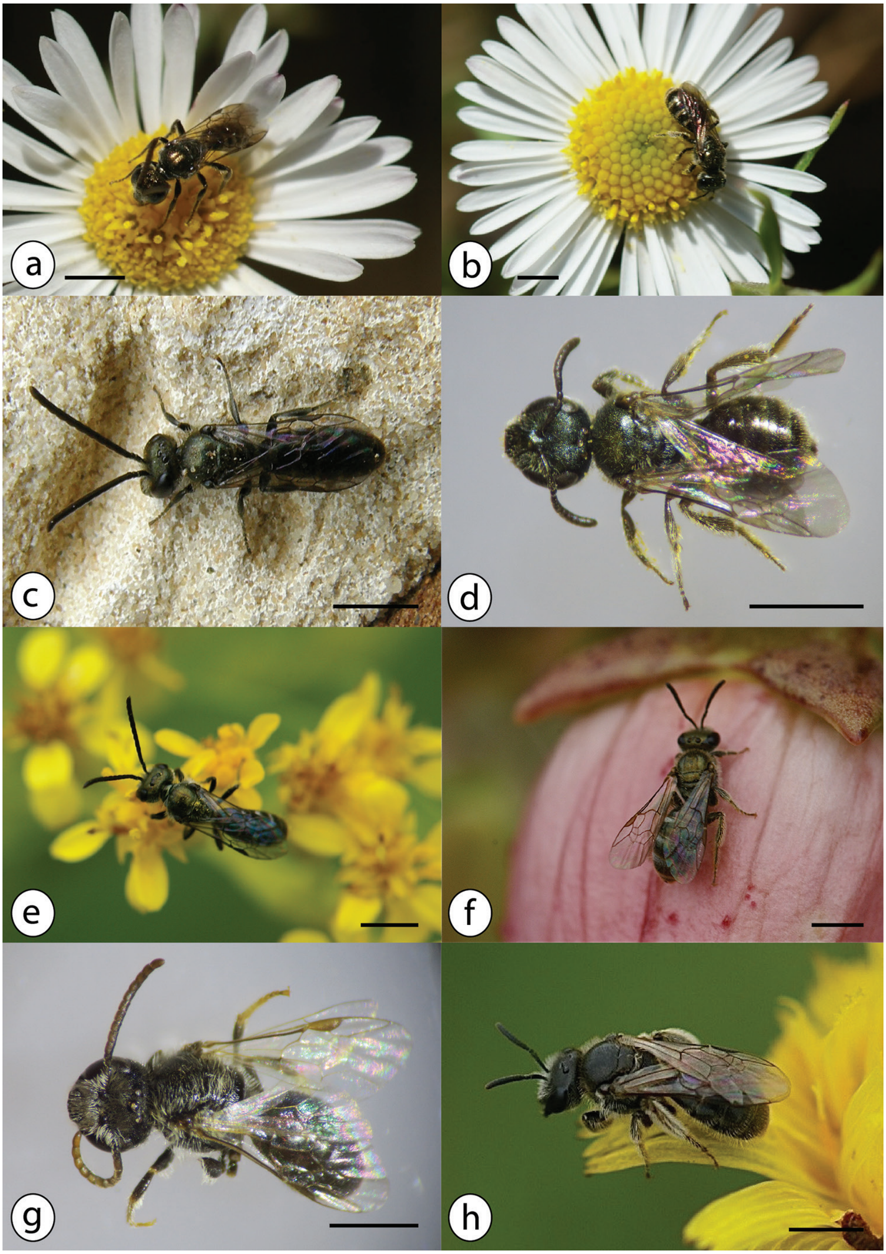

Figure 8. Azorean *Halictus* species (continued): **a** *Halictus minutissimus* male on *Erigeron karvinskianus* (Asteraceae), July 2016, Terceira (Monte Brasil) **b** *Halictus minutissimus* female on *Erigeron karvinskianus* (Asteraceae), July 2016, Terceira (Monte Brasil) **c** *Halictus morio* male, UK **d** *Halictus morio* female from Graciosa (B29, TUM) **e** *Halictus smeathmanellus* male on *Solidago azorica* (Asteraceae), August 2015, Flores **f** *Halictus smeathmanellus* female on *Azorina vidalii* (Campanulaceae), July 2015, Corvo **g** *Halictus villosulus* male from Corvo (B60, TUM) **h** *Halictus villosulus* female on *Leontodon taraxacoides* (Asteraceae), June 2012, Graciosa; photos: Julie A. Weissmann (**a, d, e, f, g**); Hanno Schaefer (**b, h**); Steven Falk (**c**); scale bars 2 mm.

Halictus smeathmanellus (Kirby), (*Lasioglossum smeathmanellum*)

Description. Small black bee (wing length 4.5 mm in females and 4–4.5 mm in males), in the sun shining metallic green, scutum sparsely punctuated (Fig. 8e–f).

Distinguishing features. With *H. morio*, one of the two small and greenish representatives of the genus in the Azores, but larger in size than the former species.

General distribution. North Africa (Morocco); in Europe from the Iberian Peninsula to Scotland and SW Germany.

Distribution in the Azores. Corvo, Flores, Pico, São Miguel, Terceira.

First record. First mentioned in Blüthgen (1944), no island specified.

Nesting. Mostly in vertical structures (sparsely vegetated slopes, crevices in cliffs or walls), often in large aggregations.

Social behaviour. Probably solitary (http://www.bwars.com/bee/halictidae/lasioglossum-smeathmanellum) but no observations from the Azores available.

Foraging. Polylectic, observed on Asteraceae (*Solidago azorica*).

Phenology. July-August.

Material. Pico (Madalena), July 1986, 6 females, 1 male, det. Ebmer, coll. Museum Leiden (Ebmer, pers. comm.). Terceira (airport), 1 female, leg. H. Schaefer, B36 (TUM).

The COI sequence of specimen H. Schaefer B36 (TUM), acc. no. KX824762, is identical to a *H. smeathmanellus* sequence from England in GenBank (KT074061, see Fig. 2).

Halictus villosulus (Kirby), (*Lasioglossum villosulum*)

Description. Medium-sized bee (total length 6–9 mm in females and 6–8 mm in males, wing length 4.5–5.5 mm in females and 4–4.5 mm in males,); scutum with unusually large punctures, top of propodeum roundish; head and thorax hairy; abdomen shiny black (Fig. 8g–h).

Distinguishing features. Medium-sized *Halictus* (similar in size to *H. smeathmanellus* but not metallic green); head densely white villous, thorax and abdomen blackish dark with scattered long white hairs.

General distribution. Madeira, Canaries; North Africa; Eurasia, from Portugal to Nepal and Malaysia in the East and Finland in the North.

Distribution in the Azores. All islands.

First record. 1930 (first mentioned by Benoist et al. 1936).

Nesting. In various substrates on sparsely vegetated slopes, cliffs or flat areas (in the latter, the entrance often with small tumuli); often in large aggregations.

Social behaviour. Solitary.

Foraging. Polylectic, observed on Asteraceae (*Helminthotheca echioides*, *Hypochaeris radicata, Leontodon taraxacoides, Sonchus asper)* and Frankeniaceae (*Frankenia laevis*).

Phenology. June-September; *H. villosulus* is known to be bivoltine (two generations per year) elsewhere but no detailed observational data is available from the Azores.

Material. São Miguel (Furnas) and Terceira (Monte Brasil), August-September 1930, leg. L. Chopard, det. Blüthgen (Benoist et al. 1936, not seen). São Miguel (Ponta Delgada), July 1992, leg. Wirtz, det. Warncke (Wirtz 1994, not seen). São Miguel (Ponte), July 1986, 3 females; Faial (Horta), July 1986, 5 females, 5 males; Pico (Magdalena), July 1986, 1 male, all det. Ebmer, coll. Museum Leiden (Ebmer, pers. comm.). São Miguel (S. João), 09.08.1984, 1 female, 1 male; São Miguel (Ponta Delgada), 12.08.1984, 1 female; São Miguel (Vila Franca), 07.08.1984, 1 male; São Miguel (Remedios), 10.08.1984, 1 male, all leg. La Roche, det. Ebmer (Ebmer, pers. comm.). Santa Maria (Vila do Porto), July 1972, 2 females, det. Ebmer, coll. Senckenberg Frankfurt (Ebmer, pers. comm.). Corvo (lighthouse), 5 females, 1 male; Flores (Ponta da Faja), 05.08.2014, 3 females; Graciosa, June 2012, 6 females; Terceira (airport), 1 male; Terceira, 08.08.2014, 1 female, all leg. H. Schaefer, coll. TUM (specimens B33-B35, B37-B43, B51, B57-B62).

The COI sequence of specimens H. Schaefer B33, B38, B51, B60-B62 (TUM), acc. no. KX824765-70, are (near) identical to a *H. morio* sequence from France in GenBank (JF903563), but they differ in at least 15 positions from the remaining *H. morio* sequences in GenBank (see Fig. 2).

Megachilidae

The females of all representatives of this group collect pollen with a pollen brush beneath their abdomen.

Anthidium Fabricius

The genus is characterised by a specialised nesting behaviour: females build their nests from plant hairs or rarely resin and can be recognised when transporting such balls of plant fibres or resin in their mandibles. The males show territorial behaviour. Solitary. One species with limited distribution in the Azores, likely an introduction.

Anthidium manicatum (Linnaeus)

Description. Total length 11–12 mm in females and 14–18 mm in males, wing length 8–10 mm in females and 9,5–12 mm in males; wings dark, face and legs yellow, body black with yellow spots and bands, tergite 7 of males with five black spine-like extensions (Fig. 9a–b).

Distinguishing features. Both sexes with conspicuous yellow-black abdominal patterns; can be confused only with similar looking syrphid flies or species of wasps, especially the introduced *Vespula germanica*, but differs from all these taxa in flight behaviour and abdominal pollen collection (in females).

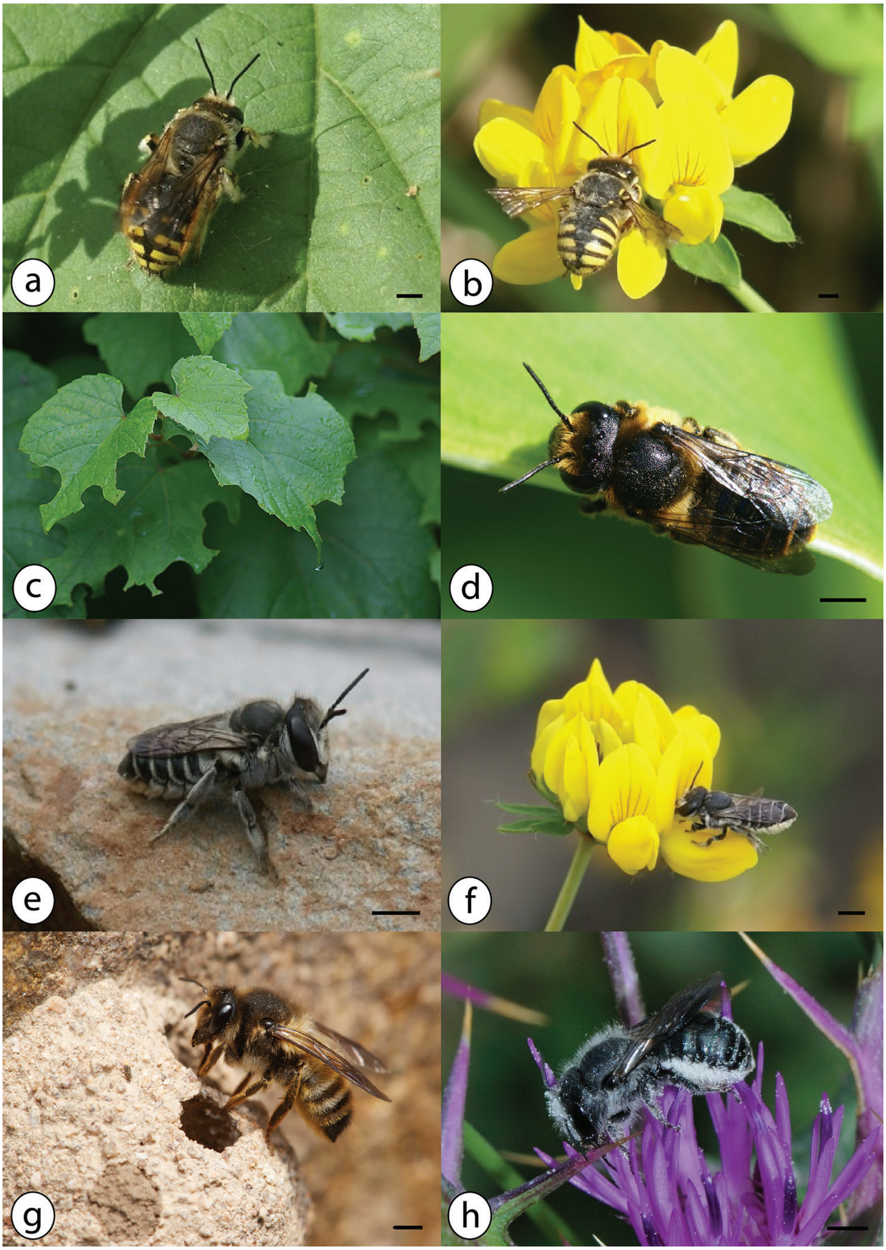

Figure 9. Azorean Megachilidae: **a** *Anthidium manicatum* male, note the spine-like extensions at the tip of the abdomen, July 2016, Faial **b** *Anthidium manicatum* female on *Lotus corniculatus* (Fabaceae), July 2016, Faial **c** grapevine, *Vitis vinifera* (Vitaceae), leaves with oval and circular cuts made by leafcutter bees, probably *M. centuncularis*, June 2013, Corvo **d** *Megachile centuncularis* female resting on leaf of Kahili ginger, *Hedychium gardnerianum* (Zingiberaceae), August 2015, Flores **e** *Megachile concinna* female, July 2016, Flores **f** *Megachile concinna* female on *Lotus corniculatus* (Fabaceae), July 2016, Corvo **g** *Megachile pyrenaica/rufescens*, female on its clay nest, 26.04.2010, France (Le Muy) **h** *Osmia niveata*, female on *Centaurea* spec., Israel; photos: Julie A. Weissmann (**a, b, d, e, f**), Hanno Schaefer (**c**), Nico J. Vereecken (**g**), Gideon Pisanty on wikipedia (creative commons license) (**h**); scale bars 2 mm.

General distribution. Eurasia, North Africa; introduced in the Canaries, North and South America, New Zealand.

Distribution in the Azores. Faial, São Miguel.

First record. 1857 (Drouët 1861).

Nesting. In existing holes; cell walls and closing plugs are built out of plant fibres.

Social behaviour. Solitary.

Foraging. Polylectic; preference for Lamiaceae, where the females also collect plant hairs for their nest, observed on *Lotus corniculatus* (Fabaceae).

Phenology. July-September.

Material. Faial (Horta), September 1952, 1 female (Carthy 1955, not seen). São Miguel (Ponta Delgada), July 1992, leg. Wirtz, det. Warncke (Wirtz 1994, not seen).

Megachile Latreille

The genus is known for two different types of specialised nesting behaviour (Trunz et al. 2016). In subgenus *Megachile*, the female bees build their nests in holes of wood or stone and use pieces of cut-out sections of leaves or petals ("leaf-cutter bees"). Their cuttings are quite conspicuous (Fig. 9c) and can help to locate the bees in the field. In subgenus *Chalicodoma*, females construct nests of mud and sand instead of leaf pieces (Fig. 9g). Females of the genus are easy to recognize by their strong mandibles and by their tendency to bend the abdomen upwards when visiting flowers. Solitary. Three species in the Azores.

Megachile centuncularis (Linnaeus)

Description. Medium-sized (total length 11–12 mm in females and 9–11 mm in males, wing length 7–8,5 mm in females and 7–8 mm in males) dark brown bees with yellowish hair and reddish abdominal pollen collecting brushes (Fig. 9d).

Distinguishing features. Females with conspicuous ventral pollen brushes and strong mandibels.

General distribution. West- and Central Europe.

Distribution in the Azores. Corvo, Faial, Flores, São Jorge, São Miguel, Terceira.

First record. 1865 (Godman 1870).

Nesting. In existing holes (e.g. in dead wood, walls, soil or twigs); cell walls and closing plugs are built of leaf sections.

Social behaviour. Solitary.

Foraging. Polylectic, Asteraceae, Fabaceae.

Phenology. July-September.

Material. São Miguel (Furnas, Ponta Delgada), August-September 1930, leg. L. Chopard, det. Benoist (Benoist et al. 1936, not seen). Faial (Horta), August-September 1952, 2 females (Carthy 1955, not seen). Terceira, 2 females, leg. A. Picanço MF22.1, MF22.2 (EDTP).

The COI sequences of specimens MF22.1, MF22.2 (EDTP), acc. no. KX824779-80, are identical to a *M. centuncularis* sequence from Germany in GenBank (KJ838449), and very similar to others from Canada, Croatia, and Germany (see Fig. 2).

Megachile concinna Smith; syn.: *M. atratula* Rebmann (see Gonzalez et al. 2010)

Description. Smallest of the leafcutter bees in the Azores (total length 9 mm in females and 7 mm in males). Strongly banded tergites, silvery-brown appearance. Females have a silvery pollen brush underneath the abdomen (Fig. 9e).

Distinguishing features. Smallest of the leafcutter bees on the Azores, silvery-brown appearance; fast flyer.

General distribution. Mediterranean region.

Distribution in the Azores. Corvo, Flores, Faial.

First record. Ornosa et al. (2007), as *M. atratula*.

Nesting. Probably in sandy ground near the coast but no nest observations available from the Azores.

Social behaviour. Solitary.

Foraging. Polylectic, with strong preference for Fabaceae, especially *Lotus* species (Fig. 9f).

Phenology. Observed in July-August.

Material. None seen; listed in the AMNH database for the Azores - http://www.discoverlife.org/mp/20l?id=AMNH_BEES67697

Note. The *M. concinna* complex is currently focus of phylogenetic analyses by C. Praz but no Azorean material was included in the study (C. Praz, pers. comm., Sept. 2016).

Megachile pyrenaica Lepeletier, (*Chalicodoma pyrenaicum*)

Description. Medium-sized (total length 13–16 mm), dark, very hairy bees (Fig. 9g).

Distinguishing features. Only bee species in the Azores that builds large clay nests.

General distribution. Mediterranean region.

Distribution in the Azores. Santa Maria.

First record. 2012 (see: http://www.gba.uac.pt/media/press&events/ver.php?id=126)

Nesting. Unknown.

Social behaviour. Solitary.

Foraging. Probably oligolectic on Fabaceae (Scheuchl and Willner 2016) but no observational data available from the Azores.

Phenology. June-July.

Material. Santa Maria (near airport), 2 specimens, 2012, det. Kratochwil, coll. Kratochwil (pers. comm., 30.09.2016).

Note. Easily confused with the morphologically very similar *C. rufescens*, from which it differs mainly by its orange tarsi (M. Aubert, pers. comm., Sept. 2016).

Osmia Panzer

Build their nest in existing cavities in wood or stone. Solitary. One species in the Azores but no recent confirmation.

Osmia niveata (Fabricius), syn. *Osmia fulviventris* (Panzer)

Description. Small dark bee (total length 8–10 mm; wing length 7–8 mm in females and 6–7 mm in males) with conspicuous orange red pollen collecting brushes on the underside of the abdomen (Fig. 9h).

General distribution. Madeira, West Palaearctic.

Distribution in the Azores. Probably São Miguel and Terceira (see below).

First record. 1865 (Godman 1870).

Nesting. Probably in existing cavities in wood or stone but no observations from the Azores available.

Social behaviour. Solitary.

Foraging. Oligolectic on Asteraceae, with preference for thistles and relatives (Scheuchl and Willner 2016) but no foraging observations from the Azores available.

Phenology. Unknown.

Material. No specimens seen/known to us.

Note. Records of *Osmia emarginaria* St. Farg from São Miguel and Terceira (Godman, 1870) most likely refer to this species.

Domesticated species

Apis Linnaeus

Apis mellifera Linnaeus

Description and distinguishing features. Honeybees are larger than most wild bees in the islands (total length 11–13 mm in workers, 13–16 mm in males; wing length 9–10 mm in workers and 12–13,5 mm in males) but can be confused with some syrphid flies (e.g., *Eristalis tenax*). They differ from superficially similar *Megachile* by their pollen-collecting mode: scopae on the legs (Fig. 10), not abdominal brushes.

General distribution. Probably native to the Mediterranean region but kept by beekeepers in temperate regions worldwide for honey production.

Distribution in the Azores. Apiculture is declining in the Azores (maybe as a result of accidental introduction of *Varroa destructor* mites) but honeybee colonies are still kept on all islands; in 2010, the number of bee colonies in the Azores was c. 3850, belonging to 255 beekeepers (source: Paulo Miranda at http://montedomel.blogspot.de).

First record. 16th century (Frutuoso 2005); according to Marques (cited in Crane 1999: 219) "[b]eekeeping was started in 1554 (…), the bees probably being taken there from Portugal."

Nesting. Today, honeybees are not known to occur as escaped/feral bees in the archipelago but Drouët (1861) reported wild honeybees from São Miguel.

Social behaviour. Highly eusocial.

Foraging. Polylectic.

Phenology. All year.

Figure 10. *Apis mellifera* worker on *Azorina vidalii* (Campanulaceae), August 2015, Flores; photo: Julie A. Weissmann; scale bar 2 mm.

Material. São Miguel (Furnas) and Terceira (Monte Brasil), August-September 1930, leg. L. Chopard, det. Benoist (Benoist et al. 1936, not seen).

Note. De la Rúa et al. (2006) analysed genetic diversity of Azorean honeybees and found a comparably low number of mitochondrial haplotypes, some of them shared with Madeiran honeybees, other probably recent introductions from the mainland.

Discussion

We add nine species to the latest list of Franquinho de Aguiar et al. (2010), which doubles the number of bee species in the archipelago. This massive increase is most likely not the result of numerous introduction or colonization events in the past few years but rather reflects the lack of research on Hymenoptera in the Azores (see also Borges et al. 2010). However, the origin of most species remains rather doubtful and some, e.g. *Bombus pratorum* and *Megachile pyrenaica*, are probably very recent introductions, which will perhaps not establish a permanent population and disappear after a few years.

The total number of now 18 wild bee species plus *Apis mellifera* is similar to Madeira, where Kratochwil et al. (2008) reported 15 species plus honeybee and

Fellendorf et al. (1999) reported 18 species plus honeybee. In the Cape Verdes, the currently known species number is also similar (21 according to Báez et al. 2005, Straka and Engel 2012, Schaefer, unpubl. data). However, it is likely that more fieldwork in the Cape Verdes will lead to an increase of species numbers, especially in the halictid bees, where so far very few species are listed. In the well surveyed Canary Islands, bee diversity is much higher than elsewhere in Macaronesia, with 124 species, many of them with several subspecies (Báez et al. 2004). A comparison of species number per genus in the four archipelagos (Table 3) shows that the Canaries have a much higher number of genera, probably a result of the close proximity to the North African/Mediterranean bee diversity centre. Furthermore, several of them (e.g., *Andrena*, *Halictus*, *Osmia*) seem to have radiated in the Canaries, whereas no species rich bee radiations have been discovered so far in the remaining archipelagos.

When comparing bee species numbers per island in the Azores, it is important to keep in mind that our fieldwork on Pico, São Jorge, and São Miguel was less extensive than in the rest of the archipelago, so species numbers on these four islands are likely an underestimate of the true diversity. So far, it seems that bee diversity is fairly similar on all islands (seven to 14 species) and does not depend on classical biogeographical and ecological variables (island size, amount of natural vegetation, flowering plant diversity or altitude). More fieldwork is needed to confirm distribution per island and also assess altitudinal ranges and habitat preferences of the different bee species in the islands. There is recent evidence from Terceira that many bee species are foraging in disturbed habitats (Picanço et al., unpubl. data) but it is unclear if they can survive without natural vegetation. Further research on the impact of land use changes and the effects of invasive plant species on the long term survival of each of the Azorean bee species seems particularly important.

Five of the wild species (and the domesticated honeybee) are social, *Bombus pratorum*, *Bombus ruderatus*, *Bombus terrestris*, *Halictus malachurus*, and *Halictus morio*. The remaining species are solitary but three of them, *Halictus minutissimus*, *Halictus smeathmanellus*, and *Halictus villosulus* nest in aggregations. As pollen sources, most of the Azorean bees seem to visit a broad range of flowering plants. The only exception is *Hylaeus signatus*, which is mainly found on *Reseda* but not strictly specialized in the Azores, because it also visits *Tamarix africana*. None of the species in our list has a parasitic life form, which is remarkable given the high number of parasitic "cuckoo bees" on the mainland. The cuckoo bee *Sphecodes pseudofasciatus* Blüthgen (historically confused with *Sphecodes croaticus* Meyer) was listed for the Azores in the AMNH Bees database (http://www.discoverlife.org/mp/20l?id=AMNH_BEES44929), but this entry seems to be an error (J. Ascher, pers. comm., Sept. 2016). However, the occurrence of *Sphecodes* in the Azores would not be too surprising since several potential host species (halictids) exist and the genus is known from Cape Verde (Pauly et al. 2002, Straka and Engel 2012 [*S. capverdensis* = *S. pinguiculus*]) and the Canary Islands (Bogusch and Straka 2012, Warncke 1992a [*S. atlanticus*, *S. hirtellus*, *S. marginatus*, *S. punctipes*, *S. ruficrus*]) but apparently not from Madeira.

The Apidae of the Azores are another case where it seems important to caution against the uncritical use of checklist data. The number of bees in the Azores has

Table 3. Comparison of species number per genus in the four Macaronesian archipelagos; for Madeira based on Fellendorf et al. (1999), for Canaries on Báez et al. (2004) and for Cape Verdes based on Báez et al. (2005), Straka and Engel (2012), and Schaefer, unpubl. data.

Genus	Azores	Madeira	Canaries	Cape Verdes
Amegilla	--	1	3	4
Ammobates	--	--	2	--
Andrena	--	3	21	--
Anthidium	1	--	2	--
Anthophora	--	--	4	--
Apis	[1]	[1]	[1]	[1]
Bombus	3	2	1	--
Ceratina	--	--	1	--
Ceylalictus	--	--	--	3
Chiasmognathus	--	--	--	1
Colletes	1	--	2	--
Dasypoda	--	--	1	--
Dioxys	--	--	2	--
Dufourea	--	--	2	--
Epeolus	--	--	1	--
Eucera	--	--	2	--
Halictus (incl. *Lasioglossum*)	6	3	16	2
Heliophila	--	--	3	--
Hoplitis	--	2	--	--
Hylaeus	3	2	5	--
Megachile	3	1	8	2
Melecta	--	--	5	--
Melitta	--	--	2	--
Nomada	--	--	5	--
Nomioides	--	--	4	2
Osmia	1	3	14	--
Panurgus	--	--	2	--
Parammobatodes	--	--	1	--
Sphecodes	--	--	6	1
Stelis	--	1	2	--
Tetralonia	--	--	4	--
Thyreus	--	--	3	4
Xylocopa	--	1	--	1
Total species number (excl. *Apis mellifera*)	**18**	**19**	**124**	**20**

been underestimated a lot so far. Moreover, while the latest checklist (Franquinho de Aguiar et al. 2010) classifies all bee species except the honeybee as "native", none of them were seen as "natives" in the previous version by Borges et al. (2005). Currently, it seems best to classify only one species as endemic, the poorly known *Hylaeus azorae*, collected only once on Pico island but clearly morphologically distinct from any other

Macaronesian *Hylaeus*. The related *H. pictipes* is found mainly in natural habitats on native plants and shows some genetic differentiation compared to mainland material. Therefore, we suggest to classify it as "possibly native" species, even if this is still a bit speculative. Based on the same reasoning, we also suggest to classify *Halictus villosulus* as "possibly native", because it is mainly found in the higher altitudes of the islands in more natural vegetation than the other halictids and is also known from Madeira and the Canaries. For several of the remaining species, it seems clear that they are recent introductions because they are restricted to disturbed habitats at low altitudes, often on just a single island (e.g.: *Anthidium manicatum*, *Megachile pyrenaica*, *Hylaeus signatus*). Most of the halictid bees, of which endemic and native species are known in Madeira and the Canaries, are currently best classified as "probably introduced" until comprehensive phylogeographic analyses allow to make a more informed decision. The genetic data available so far, shows hardly any differentiation of the island populations from the mainland, which seems to reject the hypothesis of long isolated evolution following colonization prior to the arrival of human settlers in the 15th century. The available material from the Azores also does not show any significant morphological differentiation from mainland populations (A. Ebmer, pers. comm.). Notably, we also do not find any evidence for an undescribed endemic *Halictus* species, which had been reported as "endemic super generalist" pollinator from Flores (Olesen et al. 2002). The widespread and probably introduced *Halictus malachurus* is today the most common bee in the study site of Olesen et al. (2002) on Flores and material collected by Olesen has been identified as *H. malachurus* (A. Ebmer, pers. comm.). This would suggest that contrary to the interpretation of Olesen et al. (2002), instead of endemic super generalists, an introduced pollinator complex, consisting mainly of *H. malachurus* and *H. morio* plus the less abundant *H. smeathmanellus* and *H. lativentris* might be most important for pollination networks in the Azores today. However, detailed observations, ideally on several islands and in different plant communities are needed before any definitive conclusion should be drawn.

From an evolutionary biology perspective, it is interesting that the percentage of endemic bees in the Azores (one endemic species, 5%) seems to be much lower than in Madeira (six endemic species, 33% (Fellendorf et al. 1999)) and the Canaries (46 endemic species, 37% (Báez et al. 2004)) or Cape Verdes (eleven endemic species, 55% (Báez et al. 2005, Straka and Engel 2012)). Whether this pattern is real and a result of e.g., the comparably young geological age or low habitat heterogeneity of the Azores, or simply reflects differences in the research intensity in the different archipelagos remains to be seen.

Conclusions

With 18 wild species plus the domesticated honeybee, the bee diversity in the Azores seems similar to that of Madeira and Cape Verde but much lower than in the Canaries. The small number of endemic/native species suggests that the endemic flora of the Azores might have evolved mainly without presence of pollinating bees and adapted to other pollinator groups but more research is needed to confirm this hypothesis. More generally, we show that detailed taxonomic work and comprehensive fieldwork is needed before any checklist data can be used for macroecological studies (biodiversity comparisons) and ecological studies, e.g. pollination network analyses.

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References

Amiet F (1996) Insecta Helvetica Band 12. Apidae, 1. Teil: Allgemeiner Teil, Gattungsschlüssel, die Gattungen *Apis*, *Bombus* und *Psithyrus*. Schweizerische Entomologische Gesellschaft (SES/SEG), Neuchâtel, 98 pp.

Amiet F, Herrmann M, Müller A, Neumeyer R (2001) Fauna Helvetica Band 6. Apidae 3: *Halictus*, *Lasioglossum*. Schweizerische Entomologische Gesellschaft (SES/SEG), Neuchâtel, 208 pp.

Amiet F, Herrmann M, Müller A, Neumeyer R (2004) Fauna Helvetica Band 9. Apidae 4: *Anthidium*, *Chelostoma*, *Coelioxys*, *Dioxys*, *Heriades*, *Lithurgus*, *Megachile*, *Osmia*, *Stelis*. Schweizerische Entomologische Gesellschaft (SES/SEG), Neuchâtel, 274 pp.

Amiet F, Krebs A (2014) Bienen Mitteleuropas. Gattungen, Lebensweise, Beobachtung. 2nd ed. Haupt Verlag, Berne, 423 pp.

Báez M, Koponen M, García A, Martín E (2004) Hymenoptera. In: Izquierdo I, Martín JL, Zurita N, Arechavaleta M (Eds) Lista de especies silvestres de Canarias (hongos, plantas y animales terrestres). Consejería de Medio Ambiente y Ordenación Territorial, Gobierno de Canarias, 281–300.

Baéz M, García A, Koponen M (2005) Hymenoptera. In: Arechavaleta M, Zurita N, Marrero MC, Martín JL (Eds) Lista preliminar de especies silvestres de Cabo Verde (hongos, plantas y animales terrestres). Consejería de Medio Ambiente y Ordenación Territorial, Gobierno de Canarias, 96–100.

Benoist R, Berland L, Blüthgen P (1936) Voyage de MM. L. Chopard et A. Méquignon aux Açores (Août-Septembre 1930). Annales de la Société Entomologique de France 105: 9–10.

Blüthgen P (1944) Neue oder für Deutschland neue Bienen und Wespen und neue deutsche Fundorte einiger Arten (Hym. Apid., Sphecid., Vespid.). Mitteilungen der deutschen entomologischen Gesellschaft 12: 24–31.

Bogusch P, Straka J (2012) Review and identification of the cuckoo bees of central Europe (Hymenoptera: Halictidae: *Sphecodes*). Zootaxa 3311: 1–41.

Borges PAV, van Achterberg K, Askew RR, Zwakhals K, Oliveira O, Santos AMC (2005) Apidae (Hymenoptera). In: Borges PAV, Cunha R, Gabriel R, Martins AF, Silva L, Vieira V (Eds) A list of the terrestrial fauna (Mollusca and Arthropoda) and flora (Bryophyta, Pteridophyta and Spermatophyta) from the Azores. Direcção Regional do Ambiente and Universidade dos Açores, Horta, Angra do Heroísmo and Ponta Delgada, 218 pp.

Borges PAV, Bried J, Costa A, Cunha R, Gabriel R, Gonçalves V, Martins AF, Melo I, Parente M, Raposeiro P, Rodrigues P, Santos RS, Silva L, Vieira P, Vieira V, Mendonça E, Boieiro M (2010) Description of the terrestrial and marine Azorean biodiversity. In: Borges PAV, Costa A, Cunha R, Gabriel R, Gonçalves V, Martins AF, Melo I, Parente M, Raposeiro P, Rodrigues P, Santos RS, Silva L, Vieira P, Vieira V (Eds) A list of the terrestrial and marine biota from the Azores. Princípia, Cascais, 9–33.

Carthy JD (1955) Aspects of the Fauna and Flora of the Azores. IX. Hymenoptera. Annals and Magazine of Natural History, series 12, 8: 834–839.

Crane E. (1999) The world history of beekeeping and honey hunting. Routledge, New York, Abingdon, 704 pp.

De la Rúa P, Galián J, Vest Pedersen B, Serrano J (2006) Molecular characterization and population structure of *Apis mellifera* from Madeira and the Azores. Apidologie 37: 699–708. https://doi.org/10.1051/apido:2006044

Demand J, Fabriol R, Gerard F, Lundt F, Chovelon P (1982) Prospection géothermique, íles de Faial et de Pico (Açores). Rapport géologique, geochimique et gravimétrique. Technical report, BRGM 82 SGN 003 GTH.

Drouët H (1861) Éléments de la faune açoréenne. Mémoires de la Société d'Agriculture, des Sciences, Arts et Belles-Lettres du Département de l'Aube 12: 287–523.

Ebmer AW (1988) Kritische Liste der nicht-parasitischen Halictidae Österreichs mit Berücksichtigung aller mitteleuropaischen Arten (Insecta: Hymenoptera: Apoidea: Halictidae). Linzer biologische Beiträge 20: 527–711.

Erlandsson S (1983) The *Hylaeus* species from the Macaronesian islands. Vieraea 12: 113–120.

Falk S, Lewington R (2015) Fieldguide to the bees of Great Britain and Ireland. Bloomsbury, London, New York, 432 pp.

Fellendorf M, Mohra C, Roberts S, Wirtz P, van der Zanden G (1999) The bees of Madeira (Hymenoptera, Apoidea). Bocagiana 197: 1–17.

Feraud G, Gastaud J, Schmincke HU, Pritchard G, Lietz J, Bleil U (1981) New K-Ar ages, chemical analyses and magnetic data of rocks from the islands of Santa Maria (Azores), Porto Santo and Madeira (Madeira Archipelago) and Gran Canaria (Canary Islands). Bulletin Volcanologique 44: 359–375. https://doi.org/10.1007/BF02600570

Franquinho de Aguiar A, van Achterberg K, Askew RR, Zwakhals K, Santos AMC, Borges PAV (2010) Apidae (Hymenoptera). In: Borges PAV, Costa A, Cunha A, Gabriel R, Gonçalves V, Martins AF, Melo I, Parente M, Raposeiro P, Rodrigues P, Santos RS, Silva L, Vieira P, Vieira V (Eds) A list of the terrestrial and marine biota from the Azores. Princípia, Cascais, 244 pp.

Frutuoso G (2005) Livro quarto das saudades da terra. (1589). (Volume IV). Instituto Cultural de Ponta Delgada, Ponta Delgada, 554 pp.

Godman F du Cane (1870) Natural History of the Azores, or Western Islands. J. Van Voorst, London, 377 pp.

Gonzalez VH, Engel MS, Hinojosa-Díaz IA (2010) A new species of *Megachile* from Pakistan, with taxonomic notes on the subgenus Eutricharaea (Hymenoptera: Megachilidae). Journal of the Kansas Entomological Society 83: 58–67. https://doi.org/10.2317/JKES0905.16.1

Kratochwil A, Franquinho Aguiar AM, Smit J (2008) Apoidea. In: Borges PAV, Abreu C, Aguiar AMF, Carvalho P, Jardim R, Melo I, Oliveira P, Sérgio C, Serrano ARM, Vieira P (Eds) A list of the terrestrial fungi, flora and fauna of Madeira and Selvagens archipelagos. Direcção Regional do Ambiente da Madeira and Universidade dos Açores, Funchal and Angra do Heroísmo, 346 pp.

Kuhlmann M (2005) Faunistik und Zoogeographie der Bienengattung *Colletes* Latreille 1802 (Hymenoptera: Apidae: Colletinae) in Mittelasien. Linzer Biologische Beiträge 37/2: 1353–1396.

Olesen JM, Eskildsen LI, Venkatasamy S (2002) Invasion of pollination networks on oceanic islands: importance of invader complexes and endemic super generalists. Diversity and Distribution 8: 181–192. https://doi.org/10.1046/j.1472-4642.2002.00148.x

Ornosa C, Ortiz-Sánchez FJ, Torres F (2007) Catálogo de los Megachilidae del Mediterráneo occidental (Hymenoptera, Apoidea). II. Lithurgini y Megachilini. Graellsia 63: 111–134. https://doi.org/10.3989/graellsia.2007.v63.i1.85

Pauly A, Pesenko YA, La Roche F (2002) The Halictidae of the Cape Verde Islands (Hymenoptera Apoidea). Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Entomologie 72: 201–211.

Schaefer H, Moura M, Belo Maciel G, Silva LF, Rumsey F, Carine MA (2011) The Linnean shortfall in oceanic island biogeography: a case study in the Azores. Journal of Biogeography 38: 1345–1355. https://doi.org/10.1111/j.1365-2699.2011.02494.x

Scheuchl E, Willner W (2016) Taschenlexikon der Wildbienen Mitteleuropas. Alle Arten im Portrait. Quelle & Meyer, Wiebelsheim, 917 pp.

Schmidt S, Schmid-Egge C, Morinière J, Haszprunar G, Hebert PDN (2015) DNA barcoding largely supports 250 years of classical taxonomy: identifications for Central European bees (Hymenoptera, Apoidea partim). Molecular Ecology Resources 15: 985–1000. https://doi.org/10.1111/1755-0998.12363

Smith MA, Bertrand C, Crosby K, Eveleigh ES, Fernandez-Triana J, Fisher BL, Gibbs J, Hajibabaei M, Hallwachs W, Hind K, Hrcek J, Huang D-W, Janda M, Janzen DH, Li Y, Miller SE, Packer L, Quicke D, Ratnasingham S, Rodriguez J, Rougerie R, Shaw MR, Sheffield C, Stahlhut JK, Steinke D, Whitfield J, Wood M, Zhou X (2012) *Wolbachia* and DNA Barcoding Insects: Patterns, Potential, and Problems. PLoS ONE 7: e36514. https://doi.org/10.1371/journal.pone.0036514

Stamatakis A (2014) RAxML version 8: a tool for phylogenetic analyses and post-analyses of large phylogenies. Bioinformatics 30(9): 1312–1313. https://doi.org/10.1093/bioinformatics/btu033

Stöckl P (1998) Die Wildbienen ausgewählter Xerothermstandorte des Oberinntales (Nordtirol, Österreich) (Hymenoptera: Apidae). Berichte des naturwissenschaftlich-medizinischen Vereins in Innsbruck 85: 287–327.

Straka J, Engel MS (2012) The apid cuckoo bees of the Cape Verde Islands (Hymenoptera, Apidae). ZooKeys 218: 77–109. doi: 10.3897/zookeys.218.3683. https://doi.org/10.3897/zookeys.218.3683

Trunz V, Packer L, Vieu J, Arrigo N, Praz CJ (2016) Comprehensive phylogeny, biogeography and new classification of the diverse bee tribe Megachilini: Can we use DNA barcodes in phylogenies of large genera? Molecular Phylogenetics and Evolution 103: 245–259.

Warncke K (1992a) Die westpaläarktischen Arten der Bienengattung Sphecodes Latr. (Hymenoptera, Apidae, Halictinae). Bericht der Naturforschenden Gesellschaft Augsburg 52: 9–64.

Warncke K (1992b) 2. Beitrag zur Systematik und Verbreitung der Bienengattung *Prosopis* F. in der Westpaläarktis (Hym., Apidae). Linzer biologische Beiträge 24: 747–801.

Widmer A, Schmid-Hempel P, Estoup A, Scholl A (1998) Population genetic structure and colonization history of *Bombus terrestris* s.l. (Hymenoptera, Apidae) from the Canary Islands and Madeira. Heredity 81: 563–572. https://doi.org/10.1046/j.1365-2540.1998.00407.x

Williams PH, Brown MJF, Carolan JC, An J, Goulson D, Aytekin AM, Best LR, Byvaltsev AM, Cederberg B, Dawson R, Huang J, Ito M, Monfared A, Raina RH, Schmid-Hempel P, Sheffield CS, Šima P, Xie Z (2012) Unveiling cryptic species of the bumblebee subgenus *Bombus* s. str. worldwide with COI barcodes (Hymenoptera: Apidae). Systematics and Biodiversity iFirst: 1–36.

Wirtz P (1994) A note on Bees from the island of Madeira and from the Azores – with a call for help in identification. Melissa 7: 5.

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A review of *Lista* Walker, 1859 in China, with descriptions of five new species (Lepidoptera, Pyralidae, Epipaschiinae)

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Abstract

Ten species of the genus *Lista* are recognized from China. Among them, five species are described as new to science, namely, *L. angustusa* **sp. n.**, *L. gilvasa* **sp. n.**, *L. longifundamena* **sp. n.**, *L. menghaiensis* **sp. n.**, and *L. sichuanensis* **sp. n.** Diagnoses are provided for the genus and five previously described species, *L. haraldusalis* (Walker, 1859), *L. insulsalis* (Lederer, 1863), *L. ficki* (Christoph, 1881), *L. plinthochroa* (West, 1931), and *L. variegata* (Moore, 1888), that occur in China. Two species, *L. plinthochroa* and *L. variegata*, are reported from China for the first time. All adults and their genital structures are illustrated. A key to the Chinese species is provided.

Keywords

China, new record, new species, Pyraloidea, taxonomy

Introduction

The genus *Lista* was erected by Walker in 1859, based on *Lista genisusalis* Walker, 1859 as the type species. Subsequently Lederer (1863) erected *Paracme* for *insulsalis* (Lederer, 1863) from Ningbo (Zhejiang, China), Christoph (1881) erected *Craneophora* for *ficki* (Christoph, 1881) from Heilongjiang (China), and Butler (1889) proposed *Belonepholis* for the species *striata* from Dharmsala (India) as a junior synonym of *ficki*. These genera were synonymized with *Lista* by Solis (1992), a paper which also listed seven species under *Lista* by Solis (1992), *L. carniola* (Hampson, 1916), *L. ficki*, *L. haraldusalis* (Walker, 1859), *L. insulsalis*, *L. sumatrana* (Hering, 1901), *L. variegata* (Moore, 1888) and *L. plinthochroa* (West, 1931). Yamanaka described a new species, *L. monticola* Yamanaka, 2000, from Nepal. At present, eight species of *Lista* have been reported all over the world and are distributed in the Palaearctic and Oriental Regions.

In China, three species were previously recorded, *L. ficki*, *L. insulsalis* and *L. haraldusalis* (Caradja 1925; Wang et al. 2003; Li and Ren 2008). In this paper, two species, *L. plinthochroa* and *L. variegata*, are newly recorded from China, and an additional five species are described as new to science.

Material and methods

The specimens examined and the types of the new species are deposited in the collection of the Institute of Zoology, Chinese Academy of Sciences (IZCAS), Beijing, P. R. China. The specimens were collected with different methods, but mainly by light traps. The photographs of moths and their genitalia were taken with a NIKON D7000 digital camera connected to a NIKON SMZ 1500 stereomicroscope. Methods of dissection, morphometrics, and terminology follow Wang et al. (2003) and Slamka (2006).

Taxonomic account

Lista Walker, 1859

Lista Walker, 1859: 877. Type species: *Lista genisusalis* Walker, 1859
Paracme Lederer, 1863: 338. Type species: *Poracme insulsalis* Lederer, 1863
Craneophora Christoph, 1881: 1. Type species: *Craneophora ficki* Christoph, 1881
Belonepholis Butler, 1889: 89. Type species: *Belonepholis striata* Butler, 1889

Diagnosis. The genus is very special in its external characters. It can be easily distinguished from other genera of the subfamily by having a much brighter and conspicuous wing pattern. The valva usually has spines or sclerotized plate medially located in the male genitalia and the oval or rounded corpus bursae have the rounded signa in the female genitalia, which are same as in the genus *Stericta*. But it differs from the latter by the shapes of valva and juxta. In general, the wings have an orange to yellow postmedial fascia with dark brown edges. In the male genitalia, the uncus usually has long or short spines laterally located, the sacculus always has two sclerotized processes medially located, and the valva usually has a variously-shaped sclerotized plate in the central area distal to the saccular processes.

Description. Head covered with dense scales; labial and maxillary palpi upturned; antennae filiform, male with a scape extension covered with dense scales. Both wings with similar patterns, fasciae indistinct except postmedial fascia, postmedial fasciae conspicuous, and smooth at border.

Male genitalia. Uncus broad, gnathos various. Valva broad, and outer margin usually truncated; costa sclerotized; sacculus well developed, often with hook-like or spine-like processes, usually extending backward to base of valva. Phallus slender, slightly curved.

Female genitalia. Ovipositor covered with dense setae. Sterigma associated with the ostium bursae appears to be sclerotized. The papillae analis are not extruded and are located within the 8th segment; the sterigma is lightly sclerotized and the lamella postvaginalis is variously sclerotized. Apophysis anterior nearly same length or longer than apophysis posterior. Ductus bursae slender, usually membranous. Corpus bursae elliptic or rounded, usually with two rounded or oval-shaped signa consisting of many minute spines.

Distribution. China, Russia, Korea, Japan, India, Nepal, Sri Lanka, Vietnam, Myanmar, Malaysia, Indonesia, Philippines, New Guinea.

Key to the species of *Lista* in China

1 Uncus with two spines **2**

– Uncus without spines **6**

2 Uncus with spines laterally located, hindwing with pink-fuscous scales **3**

– Uncus with spines medially located, hindwing with pale-yellow scales .... ***L. variegata***

3 Spines nearly as long as uncus; forewing covered with more fuscous scales than yellow .... ***L. insulsalis***

– Spines half as long as uncus; forewing with more yellow scales than fuscous **4**

4 Juxta with spines about 1/2 of length of juxta at apex .... ***L. longifundamena* sp. n.**

– Juxta with spines about 1/3 of length of juxta at apex **5**

5 Base of juxta broad, postmedial fascia slightly curved, ductus bursae as same as in width .... ***L. haraldusalis***

– Base of juxta narrow, postmedial fascia straight, lower ductus bursae broader than upper .... ***L. gilvasa* sp.n.**

6 Gnathos with two spines 7

– Gnathos without spines **8**

7 Middle of sacculus with a serrated sclerotized plate, bent towards outer margin of plate and with a short thorn-like process .... ***L. angustusa* sp. n.**

– Middle of sacculus with a spine-like process, bent towards outside .... ***L. sichuanensis* sp. n.**

8 Juxta with apex rounded **9**

– Juxta with apex pointed .... ***L. ficki***

9 Male with long hair scales nearly 2/3 of abdomen length at abdomen end. Middle of sacculus with a long spine and a short thorn-like process, Top of ductus bursae slightly sclerotized..***L. plinthochroa***

– Male with short hair scales nearly 1/4 of abdomen at abdomen end, middle of sacculus with a long sclerotized plate and a short thorn-like processes, the sclerotized plate with apex serrated, ductus bursae membranous .... ***L. menghaiensis* sp. n.**

***Lista angustusa* sp. n.**

http://zoobank.org/12F9A4BB-E225-442F-BE21-2104F358766D

Figs 1, 13, 23

Diagnosis. The new species is very similar to *L. haraldusalis* in wing pattern, but the wing color of the new species is darker than the latter. In the male genitalia, it can be distinguished from the latter by the narrower valva, having two lateral spines in the gnathos, and lacking spines in the uncus.

Description. Adult. Forewing length 8.5–11.0mm (*n* = 7). Head pale yellow, mixed with brown; labial palpus upturned, third segment pointed; antenna brown, scape extension black, with pale grey scales on inner side, and blackish-brown on outer side. Thorax mixed with pale yellow, blackish-brown and pale grey scales. Forewing covered with brown, yellow and pink scales; base mixed with yellow and black scales; postmedial fascia orange with dark brown edges, outer area covered with fuscous and dark pink scales; cilia brown. Hindwing with same pattern as forewing.

Male genitalia (Fig. 13). Uncus broad, densely suffused with setae, apex truncated. Gnathos incurved apically, with three spines at apex and a long spine laterally located. Valva nearly the same width from base to apex, apex obliquely truncated; costa obviously sclerotized, apex swollen; sacculus expanded at base, with two processes in middle, the inner one larger, with serrated edge, the outer one small thorn-like, a sclerotized plate from sacculus to valva medially located. Juxta constricted and bifurcated, two pointed plates at apex. Phallus cylindrical, curved slightly.

Female genitalia (Fig. 23). Ovipositor nearly round, suffused with setae. Apophysis anterior and apophysis posterior nearly same length. Ductus bursae short, membranous. Corpus bursae elliptic, with two rounded signa.

Holotype. ♂, Jiangxi: Jiulianshan, 11.VI.1975, Song Shimei (gen. slide. no. Ep540).

Paratypes. 5♀♀, locality and collector same as holotype, 21.VI–8.VIII.1975, (gen. slide. no. Ep562). Guangdong: Ruyuan, Nanling, 1♂, 20.VII.2008, Chen Fuqiang (gen. slide. no. Ep549); Chebaling, 1♂, 22.VII.2008, Chen Fuqiang (gen. slide. no. Ep543).

Distribution. China (Jiangxi, Guangdong).

Etymology. The specific name is derived from Latin *angustus* (= narrow) in accordance with its narrow valva.

Figures 1–6. Adults. **1** *Lista angustusa* sp. n., male, holotype **2** *L. ficki* (Christoph, 1881), male **3** *L. gilvasa* sp. n., male, holotype **4** *L. haraldusalis* (Walker, 1859), female **5** *L. insulsalis* (Lederer, 1863), male **6** *L. longifundamena* sp. n., male, holotype.

Lista ficki (Christoph, 1881)

Figs 2, 14, 24

Craneophora ficki Christoph, 1881: 2; Janse 1931: 439–491; Inoue 1982: 379, pl. 45, fig. 40; Yamanaka and Yoshiyashu 1992: 91.
Belenopholis striata Butler, 1889: 90, pl. 134, f. 3.
Lista ficki (Christoph): Solis 1992: 283.

Diagnosis. The species is different from congeners by paler scales on the forewing, the tip of the gnathos without denticulation, and the juxta swollen, the apex bifurcated with two pointed processes.

Material examined. Guangdong: Dinghushan, 1♀, 7.VII.1973, Li Tiesheng. Jiangxi: Jiulianshan, 1♂, 23.IX.1979, Song Shimei. Hubei: Shennongjia, 3♂♂1♀, 950–1250m, 3–16.VII.1980, Yu Peiyu & Han Yinheng (gen. slide no. Ep552); Xingshan, 1♂3♀♀, 1350m, 18.VII.1993, Song Shimei (gen. slide no. Ep532). Gansu: Wenxian, 1♀, 720m, 28.VII.1999, Yao Jian; Zhouqu, 1♀, 2400m, 14.VII.1999, Zhu Chaodong.

Distribution. China (Heilongjiang, Gansu, Hubei, Jiangxi, Guangdong, Guangxi); India, Japan, Philippines.

Remarks. Yamanaka (2000) reported this species in Nepal. However, according to the related literature, the genitalia are quite different from those of *L. ficki* (Christoph, 1881) provided by Janse (1931). Meanwhile, their structure of the male genitalia matches the figure of *L. haraldusalis* (Walker, 1859) provided by Marumo (1942). Therefore, his reported species actually is *L. haraldusalis* (Walker, 1859) rather than *L. ficki* (Christoph, 1881).

***Lista gilvasa* sp. n.**

http://zoobank.org/AB832BCC-54D7-4147-BC89-20B306FE65A6
Figs 3, 15, 25

Diagnosis. The new species is similar to *L. longifundamena* sp. n. Both species are different from other congeners by the straight postmedial fascia on the forewing; however, *L. longifundamena* sp. n. has the valva slightly constricted from the middle to the apex, the sacculus with the inner processes at middle more slender, and the apex of the juxta bifurcated with two strongly sclerotized slender arms.

Description. Adult. Forewing length 9.5–10.5mm (n = 4). Head yellow; labial palpus upturned, mixed with yellow and black scales; maxillary palpus pale yellow; antenna pale brown, scape extension black, mixed with golden scales in male. Thorax mixed with blackish-brown and a small number of yellow scales. Forewing covered with brown, yellow, black and pink scales; postmedial fascia straight, pale yellow with brown edges, outer area covered with fuscous and dark pink scales; cilia brown. Hindwing with similar pattern to forewing, but more brown scales than forewing in central area, and outer area covered with pink scales.

Male genitalia (Fig. 15). Uncus broad, densely covered with setae, two spine-like processes at base laterally. Gnathos narrower and more sclerotized than uncus. Valva slightly broader from base to apex, apex rounded; costa slightly sclerotized, apex swollen; sacculus with two processes in middle, the inner one spine-like, the outer one thorn-like, a thin sclerotized plate from sacculus to center of valva. Juxta peltate and bifurcated, apex pointed. Phallus curving slightly, with a crescent-shaped cornutus at apex.

Female genitalia (Fig. 25). Ovipositor slightly narrow, suffused with setae. Apophysis anterioris longer than apophysis posterioris. Ductus bursae slender, membranous. Corpus bursae round, with two signa, nearly oval.

Holotype. ♂, Guangxi: Napobeidou, 550m, 22.VI.2000, Zhu Chaodong (gen. slide no. Ep524).

Paratayes. Guangxi: Longzhou, 1♂, 550m, 22.VI.1963, Wang Chunguang (gen. slide no. Ep529); Jinxiu, Luoxiang, 1♀, 200m, 15.V.1999, Han Hongxiang; Shangsi, 1♀, 300m, 29.V.1999, Zhang Xuezhong (gen. slide no. Ep563).

Distribution. China (Guangxi).

Etymology. The specific name is derived from Latin *gilvas* (= pale yellow), in accordance with the yellow postmedial fascia of the new species.

Lista haraldusalis (Walker, 1859)

Figs 4, 16, 26

Locastra haraldusalis Walker, 1859: 160.
Lista genisusalis Walker, 1859: 877.
Stericta haraldusalis (Walker): Hampson 1896: 121; Lu and Guan 1953: 109.
Craneophora haraldusalis (Walker): Janse 1931: 473–474.
Lista haraldusalis (Walker): Solis 1992: 283.
Lista ficki (nec. Christoph): Yamanaka 2000: 67–69 (misidentified).

Diagnosis. The species can be distinguished from other species of the genus by its specific gnathos. In this species, the gnathos is broader and more sclerotized than that in other species and it has a serrated apex that is located medially.

Material examined. Hubei: Shennongjia, 2♂♂, 950m, 3–17.VII.1980, Yu Peiyu; Shennongjia, 1♀, 500m, 30.V.1981, Han Yinheng; Shennongjia, 2♂♂4♀♀, 500–1250m, 16.VI–4.VII.1981, Han Yinheng (gen. slide no. Ep556); Shennongjia, 2♂♂2♀♀, 860–920m, 28.VII–17.VIII.1981, Han Yinheng; Xingshan, 3♂♂, 1350m, 18.VII.1993, Song Shimei (gen. slide no. Ep75, Ep527); Digui, 5♂♂5♀♀, 110–117m, 3–6.IX.1994, Han Yinheng (gen. slide no. Ep73, Ep526, Ep551, Ep74, Ep522). Shaanxi: Zhenba, 1♀, 5.VI.1981; Zhouzhi, 2♀♀, 1350m, 24.VI.1999, Zhu Chaodong; Foping, 1♀, 900m, 27.VI.1999, Zhang Youwei (gen. slide no. Ep516); Foping, 4♂♂6♀♀, 867m, 15.VIII.2007, Li Wenzhu (gen. slide no. Ep515). Zhejiang: Linan, 3♀♀, 1350m, 28–29.VII.2003, Xue Dayong & Han Hongxiang (gen. slide no. Ep517). Gansu: Wenxian, 2♂♂, 720–1000m, 20–28.VII.1999, Yao Jian (gen. slide no. Ep541). Guangxi: Longsheng, 1♀, 11.VI.1980, Xue Dayong; Napo, Baihe, 2♀♀, 440m, 6–7.IV.1998, Wu Chunsheng & Li Wenzhu (gen. slide no. Ep557); Jinxiu, 1♀, 300m, 29.IV.1999, Yao Jian. Yunnan: Pingbian, 1♀, 1500m, 19.VI.1956, Huang Keren; Menghai, Xishuangbanna, 1♀, 1200–1600m, 20.VII.1958, Pu Fuji; Xishuangbanna, 1♂, 650m, 25.VII.1962, Song Shimei; Da Menglong, Xishuangbanna, 1♀, 650m, 29.V.1962, Song Shimei; Xishuangbanna, 1♀, 15.V.1978, Wang Shuyong; Weixi, 1♀, 2500m, 25.VII.1981, Wang Shuyong; Lufeng, 1♀, 23.VI.1982; Daguan, 1♂1♀, 780m, 1.VII.1982, Luo Feijin (gen. slide no. Ep559); Nabanhe, 1♀, 1083m, 25.VI.2014, Liu Xiuwei (gen. slide no. Ep566). Anhui: Jiuhuashan, 1♂, 1979m, 24.VII.2003 (gen. slide no. Ep565). Guizhou: Congjiang, 5♂♂1♀, 1–10.VIII.2013, Yang Maofa (gen. slide no. Ep567). Fujian: Sangang, 1♀, 740m, 30.VI.1960, Zhang Yiran; Sangang, 1♀, 18.IX.1979, Yu Chunren; Wuyishan, 1♀, 650m, 27.V.2000, Wang Jiashe; Wuyishan, 1♀, 650m, 27.VII.2000, Song Shimei; Xianfengling, 1♀, 500m, 4.VI.1981, Qi Shicheng. Sichuan: Emeishan, 1♀, 800–1000m, 13.VI.1957, Zhu Fuxing. Xizang: Motuo, 1♂1♀, 1.VI.1983, Han Yinheng. Hainan: Jianfengling, 1♀, 26.X.1982; Wuzhishan, 1♂, 9.XII.2007, Chen Fuqiang (gen. slide no. Ep577).

Distribution. China (Shaanxi, Gansu, Anhui, Zhejiang, Hubei, Jiangxi, Fujian, Hainan, Guangxi, Sichuan, Guizhou, Yunnan, Xizang), India, Japan, Nepal, Malaysia.

Remarks. Li & Ren (2008) reported this species in Henan; however, the genitalia are quite different from those of *L. haraldusalis* (Walker, 1859) provided by Marumo (1942). Meanwhile, their figure of the adult matches the original figure of *L. insulsalis* (Lederer, 1863). Thus, their description actually refers to *L. insulsalis* (Lederer, 1863) rather than *L. haraldusalis* (Walker, 1859). In addition, the species was wrongly recognized as *L. ficki* by Yamanaka (2000). We correct their identification here.

Lista insulsalis **(Lederer, 1863)**

Figs 5, 17, 27

Paracme insulsalis Lederer, 1863: 339, pl. 6. f. 11.
Stericta rubiginetincta Caradja, 1925: 58; Lu and Guan 1953: 109.
Lista insulsalis (Lederer): Solis 1992: 283.
Lista haraldusalis (nec. Walker): Li and Ren, 2008: 35 (misidentified).

Diagnosis. The species differs from other species by rustier colored scales on the wings, the uncus with two extremely elongated arms laterally located, and the slender processes of the sacculus about twice as long as in other species.

Material examined. Hunan: Nanyue, 2♂♂8♀♀, 29.V.1974, Song Shimei (gen. slide no. Ep13, Ep22); Hengshan, 1♂7♀♀, 29.V.1974, Song Shimei; Hengshan, 2♂♂1♀, 16.VIII.1979, Zhang Baolin. Fujian: Wuyishan, 2♀♀, 12–17.VIII.1979, Song Shimei; Yezhou, 1♀, 13.V.1980; Jiangle, 2♀, 16.IX.1990; Wuyishan, 8♂♂2♀♀, 520–1260m, 24–30.VII.2000, Song Shimei & Wang Jiashe. Zhejiang: Huangyan, 1♀, 26.IX.1962, Zhang Baolin; Tianmushan, 3♂♂2♀♀, 1–2.IX.1981, Song Shimei (gen. slide no. Ep71); Lin'an, 8♂♂6♀♀, 1350m, 28–29.VII.2003, Xue Dayong & Han Hongxiang (gen. slide no. Ep510, Ep511, Ep512); Anji, 1♂1♀, 13.VII.1995, Wu Hong & Wang Zhengru; 1♀, 23.VII.1996; Shaanxi: Luonan, 1♀, 8.IX.1980; Liuba, 2♂♂3♀♀, 1350m, 19–24.VII.1998, Yao Jian & Zhang Xuezhong (gen. slide no. Ep513); Foping, 2♀♀, 950m, 23–24.VII.1998, Yao Jian & Yuan Decheng; Ningshan, 1♂, 1580m, 27.VII.1998, Yuan Decheng. Henan: Xinyang, 1♂, 250m, 20–21.VII.2002, Han Hongxiang. Guangdong: Dinghushan, 1♂, 29.VII.2005, Chen Fuqiang (gen. slide no. Ep541); Ruyuan, Nanling, 2♂♂, 865m, 15.VII.2005, Chen Fuqiang;

Lianping, 1♀, 13.V.1973, Zhang Baolin. Jiangxi: Guling, 2♀♀, 30.VII–VIII.1935; Jiulianshan, 1♀, 11.VI.1975, Song Shimei; Lushan, 4♀♀, 16–30.VII.1980, Song Shimei; Luzhi, 1♂2♀♀, 30.VI–9.VII.1980, Shanxi: Zhongtiaoshan, 4♀♀, VIII.1978, Zhu Huiqian. Jiangsu: 2♀♀, 21–26.VIII.1933. Anhui: Huangshan, 1♂, 29.VII.1976. Yunnan: Xishuangbanna, 1♂, 1200–1600m, 18.VII.1958, Wang Shuyong; Luxi, 2♂♂1♀, 7–8.V.1980, Song Shimei; Yiliang, 8♂♂1♀, 19–20.VII.1982, Song Shimei; Lufeng, 2♂♂, 22.VI.1982, Song Shimei; Yongsheng, 1♂, 2250m, 10.VII.1984, Liu Dajun; Shiping, 1♂, 1650m, Liu Yongjie. Xinjiang: Urumqi, 1♀, 5.VI.1984; Guangxi: Xing'an, 2♀♀, 5.VI.1984; Miaoershan, 1♂, 8.VII.1985; Shangsi, 3♂♂4♀♀, 250–300m, 27–29.V.1999, Yuan Decheng et al.; Jinxiu, 1♂2♀♀, 200–900m, 20–29.V.1999, Li Wenzhu et al.; Shangsi, 1♀, 250–300m, 9.VI.2000, Zhu Chaodong.

Distribution. China (Hebei, Shanxi, Henan, Shaanxi, Gansu, Xinjiang, Jiangsu, Anhui, Zhejiang, Hubei, Jiangxi, Hunan, Fujian, Taiwan, Guangdong, Hainan, Guangxi, Sichuan, Guizhou, Yunnan), Russia, Korea, India, Sri Lanka, Myanmar, Indonesia.

Remarks. The species was wrongly recognized as *L. haraldusalis* (Walker, 1859) by Li and Ren (2008). We correct their identification here.

Lista longifundamena sp. n.

http://zoobank.org/B225247C-D569-44A9-A60D-A7D5054B6AD0

Figs 6, 18, 28

Diagnosis. This new species is larger in body than other species of the genus. The species is similar to *L. gilvasa* sp. n. Their differences are described under *L. gilvasa* sp. n.

Description. Adult. Forewing length 11.5–13.0mm ($n = 6$). Head pale brown, mixed with fuscous scales; labial palpus upturned, mixed with fuscous scales; maxillary palpus pale yellow; antenna brown, scape extension fuscous, mixed with golden scales in male. Thorax mixed with pale brown and black scales. Forewing covered with pale brown, yellow and pink scales; postmedial fascia straight, yellow with brown edges, outer area covered with fuscous and dark pink scales; cilia brown. Hindwing with similar pattern as forewing, but basal area mixed with black scales and outer area covered with pink scales.

Male genitalia (Fig. 18). Uncus broad, suffused with dense setae, two spine-like processes at base. Gnathos incurved apically, with four small spines at apex. Valva slightly constricted from middle to apex, terminal margin truncated; costa slightly sclerotized, sacculus with two processes in middle, the inner one spine-like, slender, the outer one with mini spines at apex, a thin sclerotized plate from sacculus to centre of valva. Juxta bifurcated at apex and with two strongly sclerotized slender arms at both sides. Phallus slender, curved in middle, with a sclerotized plate-like cornutus.

Female genitalia (Fig. 28). Ovipositor broad, suffused with setae. Apophysis anterioris 1/3 longer than apophysis posterioris. Ductus bursae slender, membranous. Corpus bursae elliptic, with two slightly sclerotized of rounded signa.

Holotype. ♂, Hainan: Jianfengling, 18–20.IV.1982, Chen Zhiqin (gen. slide. no. Ep531).

Paratypes. Hainan: 1♀, 16.III.1982, Zhang Baolin (gen. slide. no. Ep555); Jianfengling, 2♂♂2♀♀, 4.XI.1981, Liu Yuanfu (gen. slide. no. Ep122, Ep561); Jianfengling, 1♀, 18–20.IV.1982, Chen Zhiqin; Jianfengling, 1♂, 4.XI.1981 (gen. slide. no. Ep122).

Distribution. China (Hainan).

Etymology. The name is derived from Latin *longus* (= long) and *fundamen* (= base), in accordance with the juxta and two long spines at base.

Lista menghaiensis **sp. n.**

http://zoobank.org/76C7A60E-5A2F-46D8-9542-0492D1A76518
Figs 7, 19, 29

Diagnosis. This new species is very similar to *L. haraldusalis*, but the basal area on the forewing is slightly paler than the latter. In the male genitalia, the gnathos has three spines at the apex in the new species while the gnathos has a serrated apex in *L. haraldusalis*. Furthermore, the sclerotized plate on the valva strongly extends toward the outer margin in the new species.

Description. Adults. Forewing length 9.0–10.5mm (n = 2). Head yellow, mixed with blackish-brown; labial palpus upturned, mixed with pale yellow and black scales; maxillary palpus pale yellow; antenna brown; scape extension black, mixed with yellow scales in male. Thorax mixed with brown and fuscous scales. Forewing covered with brown, yellow or pink scales; basal area mixed with yellow and pale brown scales; costal margin with two black spots at middle and terminal trisection; postmedial fascia yellow with brown edges, outer area covered with dark pink scales; cilia brown. Hindwing with same pattern as forewing.

Male genitalia (Fig. 19). Uncus broad, suffused with dense setae totally. Gnathos with three spines at apex and two long spines 1/3 of gnathos at base medially. Valva broad, with terminal smoothly incurved; sacculus with two processes in middle, the inner one strong with apex serrated, the outer one thorn-like; a well-developed sclerotized plate from sacculus to center of valva, strongly extended toward outer manrgin. Juxta bifurcated, blunt. Phallus slightly curved.

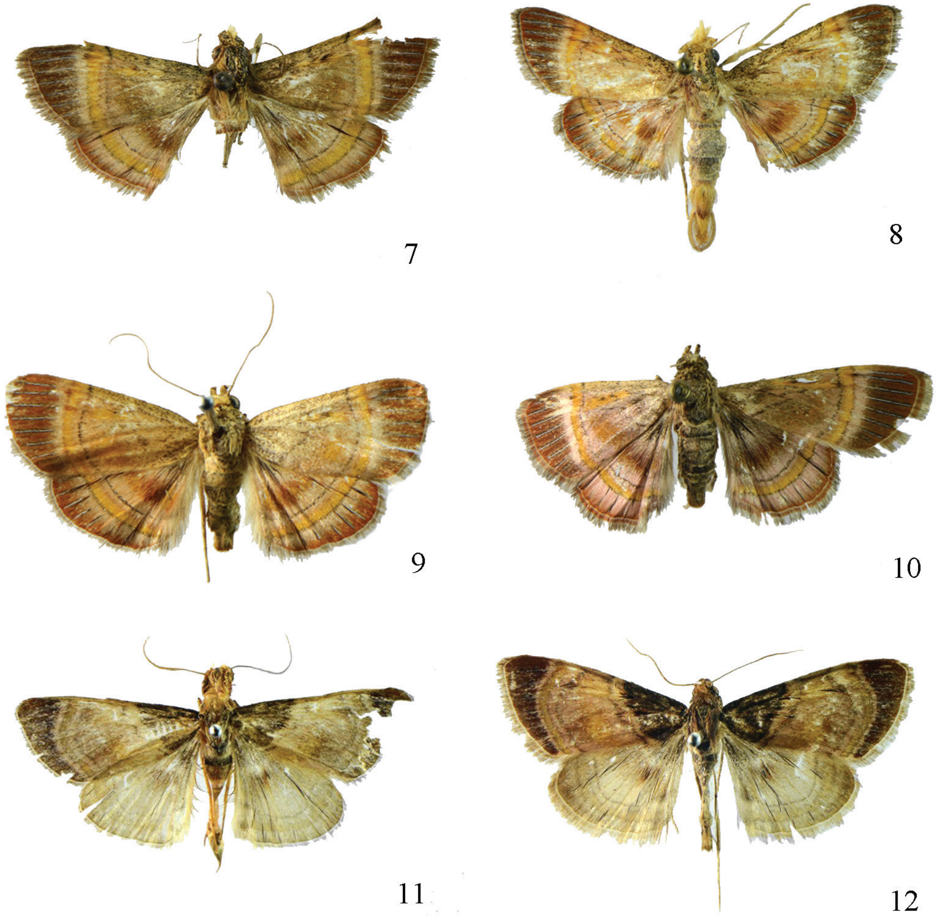
Female genitalia (Fig. 29). Ovipositor broad, suffused with setae. Apophysis anterioris 1/4 longer than apophysis posterioris. Antrum incurved at apex. Ductus bursae slender, membranous. Corpus bursae elliptic, with two signa, slightly rounded sclerotized.

Holotype. ♂, Yunnan: Xishuangbanna, Menghai, 18.VII.1958, Wang Shuyong (gen. slide. no. Ep539).

Paratype. 1♀, same data as holotype (gen. slide no. Ep558).

Distribution. China (Yunnan).

Etymology. The species is named after the type locality, Menghai in Yunnan province.



Figures 7–12. Adults. **7** *Lista menghaiensis* sp. n., male, holotype **8** *L. plinthochroa* (West, 1931), male **9** *L. plinthochroa* (West, 1931), female **10** *L. sichuanensis* sp. n., female, paratype **11** *L. variegata* (Moore, 1888), male **12** *L. variegata* (Moore, 1888), female.

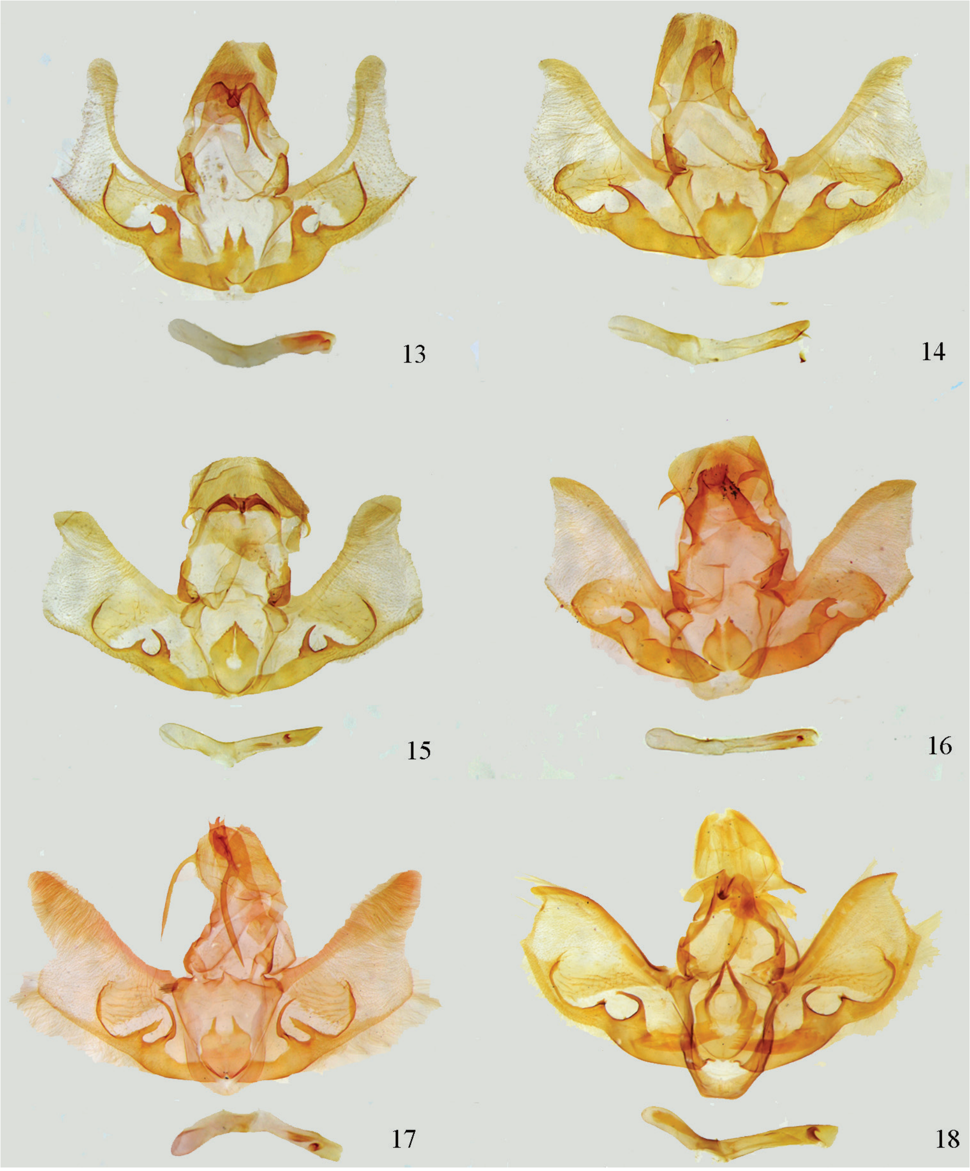
Lista plinthochroa (West, 1931)

Figs 8–9, 20, 30

Stericta plinthochroa West, 1931: 210.
Lista plinthochroa (West): Solis 1992: 283.

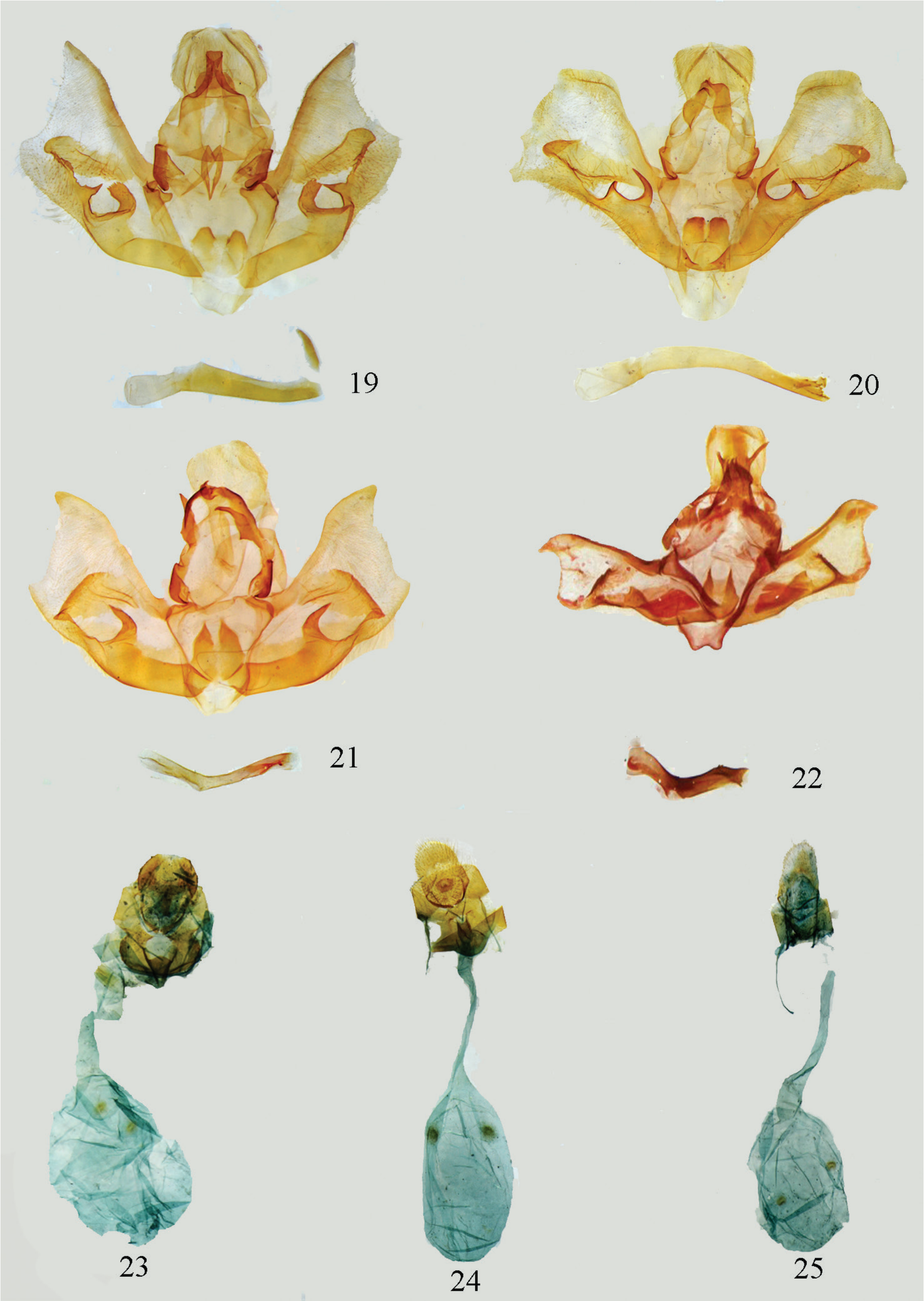
Diagnosis. This species is significantly different from others by the end of the abdomen with long hair-like scales. In the male genitalia, the valva broadens from the base to the outer margin and the sclerotized plate on the valva extends toward outer margin.

Material examined. Sichuan: Emeishan, 3♂♂16♀♀, 800–1000m, 6.V–30.VI.1957, Zhu Fuxing & Huang Keren (gen. slide no. Ep11, Ep518, Ep525, Ep6–1, Ep572); Emeishan, 1♀, 9.VI.1979, Gao Ping; Qinchengshan, 1♂, 700–1600m, 30.V.1979 (gen.

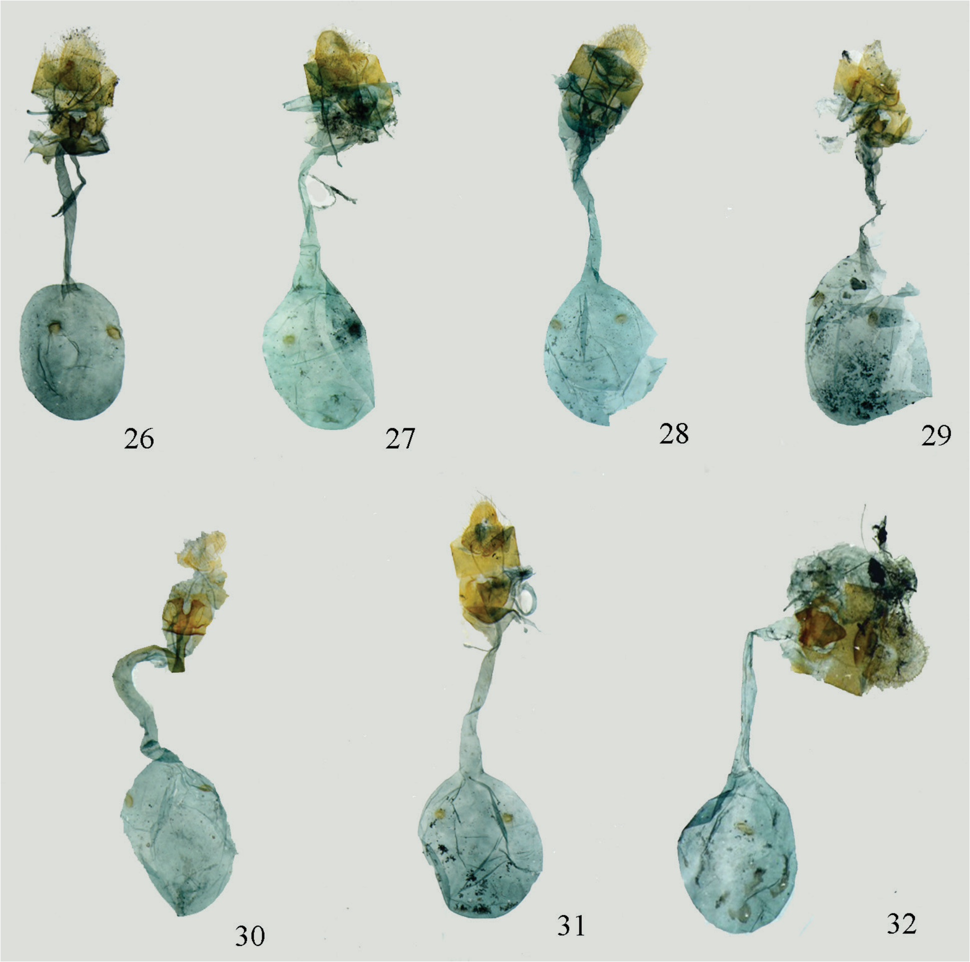


Figures 13–18. Male genitalia. **13** *Lista angustusa* sp. n., holotype, gen. slide no. Ep549 **14** *L. ficki* (Christoph, 1881), gen. slide no. Ep523 **15** *L. gilvasa* sp. n., holotype, gen. slide no. Ep524 **16** *L. haraldusalis* (Walker, 1859), gen. slide no. Ep527 **17** *L. insulsalis* (Lederer, 1863), gen. slide no. Ep511 **18** *L. longifundamena* sp. n., holotype, gen. slide no. Ep122.

slide no. Ep520); Fujian: Sangang, Wuyishan, 1♂, 1.VI.1983, Mai Guoqing; Sangang, 2♀♀, 740m, 6–17.VII.1980, Zhang Yiran; Sangang, 1♀, 740m, 26.IV.2000, Wang Jiashe. Yunnan: Pingbian, 1♀, 1500m, 8.VI.1956, Huang Keren. Gansu: Chengxian, 1♂, 1020m, 4.VII.1999, Yaojian; Kangxian, 1♂, 1400m, 8.VII.1999, Zhu Chaodong



Figures 19–22. Male genitalia. **19** *Lista menghaiensis* sp. n., holotype, gen. slide no. Ep539 **20** *L. plinthochroa* (West, 1931), gen. slide no. Ep543 **21** *L .sichuanensis* sp. n., paratype, gen. slide no. Ep521 **22** *L. variegata* (Moore, 1888), gen. slide no. Ep123.



Figures 23–32. Female genitalia. **23** *Lista angustusa* sp. n., paratype, gen. slide no. Ep562 **24** *L. ficki* (Christoph, 1881), gen. slide no. Ep552 **25** *L. gilvasa* sp. n., paratype, gen. slide no. Ep563 **26** *L. haraldusalis* (Walker, 1859), gen. slide no. Ep557 **27** *L. insulsalis* (Lederer, 1863), gen. slide no. Ep512 **28** *L. longifundamena* sp. n., paratype, gen. slide no. Ep555 **29** *L. menghaiensis* sp. n., paratype, gen. slide no. Ep558 **30** *L. plinthochroa* (West, 1931), gen. slide no. Ep553 **31** *L. sichuanensis* sp. n., paratype, gen. slide no. Ep554 **32** *L. variegata* (Moore, 1888), gen. slide no. Ep603.

(gen. slide no. Ep528). Taiwan: Pinglin, 1♀, 1000m, 13.IV.1984; Lianhuachi, 1♀, 11.VIII.1984, Wang Xiaoyue. Guangdong: Nanling, 1♂1♀, 865m, 9–15.VII.2005, Chen Fuqiang. Jiangxi: Jiulianshan, 1♂6♀♀, 21.VI–30.VII.1975, Song Shimei; Dayu, 13♂♂7♀♀, 14.VI–16.VIII.1975 (gen. slide no. Ep519, Ep553). Hainan: Jianfengling, 3♂♂, 26.III.1984, Song Shimei (gen. slide no. Ep543, Ep574, Ep576).

Distribution. China (Gansu, Jiangxi, Fujian, Taiwan, Guangdong, Hainan, Sichuan, Yunnan), Philippines.

Remarks. The species is reported in China for the first time.

***Lista sichuanensis* sp. n.**

http://zoobank.org/E3FB5DA9-91CA-4A47-BA7C-88D8702B513E
Figs 10, 21, 31

Diagnosis. This species is hard to distinguish by its external characters. It differs from other species by the sacculus with a single process in the middle, while the sacculus usually has two processes in other species. Furthermore, the sclerotized plate on the valva is twice or three times as broad as others.

Description. Adults. Forewing length 11.0–12.5mm (*n* = 6). Head blackish-brown; labial palpus upturned, mixed with fuscous and black scales, stronger in male; maxillary palpus pale yellow; antenna brown, scape extension black, mixed with fuscous scales in male. Thorax mixed with brown and fuscous scales. Forewing covered with brown, black and pink scales; base mixed with yellow and black scales; costal margin yellow; postmedial fascia orange with brown edges, outer area covered with pink and fuscous scales; cilia grey. Hindwing with same pattern as forewing.

Male genitalia (Fig. 21). Uncus broad, suffused with dense setae. Gnathos broad, base extended to two strongly sclerotized spine-like processes laterally located, apex with three spines. Valva nearly the same width from base to apex; costa extruded the apex of valva; sacculus with a single spine-like process in middle; a well-developed sclerotized broad plate from sacculus to centre of valva. Juxta bifurcated with two pointed plates at apex. Phallus slender, slightly curved.

Female genitalia (Fig. 31). Ovipositor broad, densely suffused with setae. Apophysis anterioris longer than apophysis posterioris. Ductus bursae slender, membranous. Corpus bursae round, with two rounded signa, slightly sclerotized.

Holotype. ♂, Sichuan: Dukou, 14.VI.1981 (gen. slide. no. Ep521).

Parataypes. Sichuan: Qingchenshan, 1♂, 5.VI.1979, Shang Jinwen; same data as holotype, 2♂♂2♀♀ (gen. slide. no. Ep554).

Distribution. China (Sichuan).

Etymology. The species is named after the type locality, Sichuan Province.

***Lista variegata* (Moore, 1888)**

Figs 11–12, 22, 32

Scopocera variegata Moore, 1888: 203, pl. 7. f. 4.
Lista variegata (Moore): Solis 1992: 283.

Diagnosis. The species differs from others by the hindwing with pale yellow scales. In the male genitalia, the center of the uncus has two spines, and the phallus is about half as long as others.

Material examined. Xizang: Nielamu, Zhangmu, 1♂, 2232m, 12.V.1974, Zhang Xuezhong; Motuo, Gedang, 1♀, 4.IX.1982, Lin Zai; Bomi, 1♂, 2700m, 5.IX.1983, Han Yinheng (gen. slido no. Ep123); Linzhi, Niyanghe, 2♂♂, 3000m, 2.VIII.2006, Chen Fuqiang; Milin, Paixiang, 2♀♀, 2910m, 5.VIII.2006, Chen Fuqiang; Bomi, Zhamuzhen, 2♀♀, 2840m, 28.VIII.2006, Chen Fuqiang (gen. slide no. Ep603).

Distribution. China (Xizang), India.

Remarks. The species is reported in China for the first time.

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References

Bulter AG (1889) Illustrations of Lepidoptera Heterocera of the British Museum (Part VII). Trustees of the BM, London, 124 pp.

Caradja A (1925) Ueber Chinas Pyraliden, Tortriciden, Tineiden nebst kurze Betrachtungen, zu denen das Studium dieser Fauna Veranlassung giebt. Memoriile Sectiunii Stiintifice Academia Româna 7: 1–127.

Christoph H (1881) Neue Lepidopteren des Amurgebietes. Bulletin de la Société impériale des naturalistes de Moscou 56: 1–80.

Hampson GF (1896) The Fauna of British India, including Ceylon and Burma – Fauna Br. India (Moths) 4. Taylor & Francis, London, 594 pp.

Hampson GF (1916) Descriptions of new Pyralidae of the subfamilies Epipaschiinae, Chrysauginae, Endotrichinae, and Pyralinae. The Annals and Magazine of Natural History (8) 18: 126–160. https://doi.org/10.1080/00222931608693833

Heppner JB, Inoue H (1992) Lepidoptera of Taiwan. Association for Tropical Lepidoptera Scientific Publishers, Taipei 1(2): 91–92.

Inoue H (1982) Pyralidae. Moths of Japan. 307–404 [vol. 1]; 223–254 [vol. 2].

Janse AJT (1931) A contribution towards the study of the genera of the Epipaschiinae (Family Pyralidae). Transactions of the Entomological Society of London 79: 439–492. https://doi.org/10.1111/j.1365-2311.1931.tb00712.x

Lederer J (1863) Beitrag zur Kenntnis der Pyralidinen. Wiener Entomologische Monatschrift 7: 241–504.

Li HH, Ren YD (2008) Insect Fauna of Henan (Lepidoptera: Pyraloidea). Science Press, Beijing, 440 pp.

Lu JR, Guan ZH (1953) Recorded species of Pyralidae from China, a supplement to Wu's Catalogus, Insectorum Sinensium. Acta Entomologica Sinica 1(1): 92–118.

Marumo N (1942) Studies on Rice Borers VI: Classification of the subfamily Pococerinae in Japan. Department of Agriculture, Ministry of Agriculture and Forestry, Tokyo, 29 pp.

Moore F (1888) Descriptions of Indian Lepidoptera Heterocera from the collection of the late Mr. W. S. Atkinson. Taylor & Francis, London, 199–204.

Slamka F (2006) Pyraloidea of Europe – Volume 1: Pyralinae, Galleriinae, Epipaschiinae, Cathariinae & Odontiinae. Bratislava, 138 pp.

Solis MA (1992) Check list of the old world Epipaschiinae and the related new world genera *Macalla* and *Epipaschia* (Pyralidae). Journal of the Lepidopterists' Society 46 (4): 280–297.

Wang JS, Song SM, Chen TM (2003) Fauna of Pyralidae of Wuyishan Nature Reserve in China. China Science and Technology Press, Beijing, 328 pp.

Walker F (1859) List of specimens of Lepidopterous insects in the collection of the British Museum, Part. 19, Pyralides. British Museum (Natural History), London, 799–1036.

West RJ (1931) Descriptions of new species of Japanese, Formosan and Philippine Pyralidae. Novitates Zoologicae Tring 36: 206–219. https://doi.org/10.5962/bhl.part.10112

Yamanaka H (2000) Pyralidae of Nepal (III). Tinea 16: 63–69.

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RESEARCH ARTICLE

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The first species of *Aplastodiscus* endemic to the Brazilian Cerrado (Anura, Hylidae)

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Abstract

The genus *Aplastodiscus* includes 14 nominal species in four monophyletic groups with occurrence in the Atlantic Forest and Brazilian Cerrado (Brazilian Savanna) of South America. A recent study reviewed the taxonomy and phylogenetic relationships of the genus and suggested a third species for the *A. perviridis* Group. Herein, on the basis of morphology and advertisement call, we describe this species and test its monophyly. The new species is the only *Aplastodiscus* with endemic occurrence in the Cerrado Biome. In addition, its geographical distribution and conservation status are discussed.

Keywords

Aplastodiscus lutzorum sp. n., Cophomantinae, new species, integrative taxonomy

Introduction

The genus *Aplastodiscus* includes 14 nominal species in four monophyletic groups (Berneck et al. 2016) with occurrence mainly in Atlantic Forest in Brazil and Argentina (Frost, 2016). The species are stream-breeding treefrogs, usually of green color and medium size. The *A. perviridis* species Group includes *A. perviridis* Lutz 1950 and *A. cochranae* (Mertens 1952), which share, among other characters, bicolored irises, no webbing between toes I and II, and reduced webbing among their remaining toes (Garcia et al. 2001).

Berneck et al. (2016) recently reviewed the taxonomy and phylogenetic relationships of all *Aplastodiscus* species and suggested a third species for the *A. perviridis* Group, the "*Aplastodiscus* sp. 3". This species was previously called *A. perviridis* by the previous authors (Garcia et al. 2001; Bastos et al. 2003; Morais et al. 2012; Valdujo et al. 2012). Herein, on the basis of morphology and advertisement call, this species is described as new, and its monophyly tested. In addition, its geographical distribution and conservation status are discussed.

Materials and methods

Descriptions of adults and their calls

The following measurements follow Duellman (1970):

SVL	snout-vent length,
HL	head length,
HW	head width,
ED	eye diameter,
TD	tympanum diameter,
END	eye-nostril distance,
IOD	interocular distance,
THL	thigh length,
FL	foot length; including tarsus.

However, the tibia length (**TBL**) follows Heyer et al. (1990). Measurements are in millimeters and were taken with a digital caliper and, except for SVL, HL, HD, THL, and TBL, under a stereomicroscope. The webbing formula follows Savage and Heyer (1967) and Myers and Duellman (1982). Adult males were collected while calling and/or recognized by the presence of vocal slits.

The adult specimens are housed in the following Brazilian collections: Célio F. B. Haddad collection (**CFBH**) at the Universidade Estadual Paulista, Rio Claro, SP; Coleção Herpetológica da Universidade de Brasília (**CHUNB**) at the Universidade de Brasília, Brasília, DF; Museu de Ciências Naturais da Pontifícia Universidade Católica de Minas Gerais (**MCN-AM**), Belo Horizonte, MG; and Coleção de Anuros da Universidade Federal de Uberlândia (**AAG-UFU**), Uberlândia, MG.

Males of the new species were recorded in the Municipality of Alto Paraíso de Goiás, Goiás State (N = 6) and Brasília, Distrito Federal. For comparative purposes, males of *A. perviridis* were recorded at the type-locality (N = 5), in Serra da Bocaina, São José do Barreiro, São Paulo State. Calls were recorded with a Marantz PMD 671, a Boss BR-864 (both with a Sennheiser ME67/K6 microphone) or a MicroTrack (ME66/K6 microphone), all set at 44.1 kHz and 16-bit resolution. Calls were recorded from 50 to 150 cm from calling males, and 10 to 15 calls were analyzed for each male. Acoustic variables were analyzed with RAVEN PRO 1.5, 64-bit version (Bioacoustics Research Program 2014); terminology used for call features were according to Raven's manual (Charif et al. 2010). A 500 Hz high pass filter was applied prior to call analyses and figuring to reduce wind noise interference. Sound figures were obtained with the SEEWAVE 1.6.4 (Sueur et al. 2008) R package (R Development Core Team, 2012, v. 2.15.1), settings used were the Hanning window, 85% overlap, and 256 points resolution. Measured call parameters were: 1) call duration (CD), 2) peak of dominant frequency (PDF), 3) lower dominant frequency (LDF), 4) higher dominant frequency (HDF), 5) time to frequency peak (TFP) (expressed as % of call duration). All calls used in descriptions are housed at the AAG-UFU collection (Suppl. material 1, Table 1).

Laboratory protocols and genetic distance calculation

The extraction of DNA was carried out using ethanol-preserved tissues and the DNeasy isolation kit (Qiagen, Valencia, CA, USA). We carried out DNA amplification in a 25 µL volume reaction using master mix Fermentas Taq Polymerase and reagents. The Polymerase chain reactions (PCR) included an initial denaturing step of 30s at 94 °C, followed by 35 cycles of amplification with a final extension step at 72 °C for 6 min. The products of PCR were sent for sequencing to Macrogen, South Korea. We sequenced DNA fragments in both directions to minimize potential errors. The chromatograms were read and edited using SEQUENCHER 3.0 (Gene Codes, Ann Arbor, MI, USA) and complete sequences were edited with MEGA 6.06 (Tamura et al. 2013). The distance estimations of genetic p-distances were calculated in MEGA 6.06 for the regions delimited by the primers 16sAR (Palumbi et al. 1991), Wilk2 (Wilkinson et al. 1996), and COI (Jungfer et al. 2013), considering d:transitions + transversions, uniform rates among sites, and gaps/missing data as complete deletion. A list of vouchers, GenBank accession numbers, and locality data is available in Suppl. material 2.

Phylogenetic analysis and taxon sampling

Berneck et al. (2016) studied *Aplastodiscus* in a wider context and consequently included only one specimen of the species described here. Therefore, we carried out a reduced phylogenetic analysis that included all terminals of the *A. perviridis* Group analyzed by Berneck et al. (2016) and four specimens of the species described here. As outgroups, we included two terminals of the *A. albosignatus* Group and two of the *A. albofrenatus* Group, rooting the tree in the *A. sibilatus* Group (see Berneck et al. 2016). The dataset used for the analysis were the fragments delimited by the primers 16sAR, Wilk2, and COI forward and reverse.

Sequence alignments were performed in Clustawl (Thompson et al. 1994) under MEGA 6.06. For the phylogenetic analysis T.N.T Willi Hennig Society Edition was employed (Goloboff et al. 2008) with searches by "new technology", search level 50, sectorial searches included, tree drift, and tree fusing (Goloboff 1999), hitting the best length 100 times. Parsimony Jackknife absolute frequencies (Farris et al. 1996) were also estimated using "new technology" and requesting 10 hits, driven searches, and 1000 replicates. Edition of trees were made with FIGTREE (Rambaut 2014).

Results

Aplastodiscus lutzorum **sp. n.**

http://zoobank.org/C506C42B-20FF-41B6-9E5F-177E50C3415F
Figs 1, 2

Aplastodiscus perviridis Garcia et al. (2001)
Aplastodiscus perviridis Bastos et al. (2003)
Aplastodiscus perviridis Morais et al. (2012)
Aplastodiscus perviridis Valdujo et al. (2012)
Aplastodiscus sp. Santoro and Brandão (2014)
Aplastodiscus sp. 3 Berneck et al. (2016)

Holotype. (Figs 1 and 2) AAG-UFU 864. Adult male collected at Fazenda São Bento (14°09'39"S, 47°34'55"W; 1150 meters above sea level), Municipality of Alto Paraíso de Goiás, Goiás State, Brazil, on 12 December 2011, by A. A. Giaretta and K. G. Facure.

Paratypes. CFBH 22777–80, four adult males collected at Fazenda Água Limpa, Brasília, Distrito Federal (15°56'55.45"S; 47°56'17.83"W) on 18 February 2009. AAG-UFU 863, 865-867 and AAG-UFU 1639 collected on December 2012, AAG-UFU 3343 on 29 November 2013, AAG-UFU 3350–51, 5073–76, 5091, AAG-UFU 0867, adult female, all collected with the holotype. CHUNB 17015–17016 adult males collected on 31 December 1995 at Alexânia, Goiás (16°5'42.00"S; 48°31'20.60"W), CHUNB 17018, adult male collected on 12 December 1985 at Alexânia, Goiás, and CHUNB 74504–74508 adult males from Fazenda Água Limpa, Brasília, Distrito Federal, collected on March 2013. All localities are in Brazil.

Referred specimens. All males. MCN-AM 8809–12 and 8767–72 from AHE Queimado, Unaí, Minas Gerais (16°20'55.51"S; 46°52'48.93"W), collected on February–March 2007.

Figure 1. Holotype of *Aplastodiscus lutzorum* sp. n. (AAG-UFU 864). **A** Lateral view of head **B** dorsal view of head **C** plantar view **D** palmar view. Scale bar 12 mm.

Figure 2. Dorsal and ventral views of the Holotype of *Aplastodiscus lutzorum* sp. n. (AAG-UFU 864).

Diagnosis. *Aplastodiscus lutzorum* sp. n. belongs to the *A. perviridis* Group and thus bears bicolored irises, lacks webbing between toes I and II, has reduced webbing among the remaining toes, and lacks peri-cloacal ornamentation. The new species is diagnosed by its small SVL for the *A. perviridis* Group (30–36 mm) and by the advertisement call 2.5 times longer.

Description of holotype. Adult male: head 20% wider than long; snout rounded in profile, nearly rounded in dorsal view; *canthus rostralis* curved; loreal region concave; nostrils ovoid; internarial region grooved. Supratympanic fold distinct, from posterior corner of orbit to insertion of forearm; tympanum distinct, almost circular; tympanum diameter 48.5% of eye diameter. Upper eyelid smooth as the dorsum. Thoracic fold just discernible. External vocal sac single, subgular, and expanded. Fingers long, slender, no lateral fringe, bearing discret round terminal discs; relative lengths of fingers I, II, IV, III; similar sized discs on fingers II, III and IV, larger than disc of Finger I. Diameter of disc of Finger III equals to diameter of Toe IV, about 42% eye diameter. Subarticular tubercles well defined, rounded; supernumerary tubercles poorly defined on palm, rounded; inner metacarpal tubercle large, rounded, about four times the size of subarticular tubercles; other metacarpal tubercle barely defined; spine of prepollex absent; no nuptial pads; ulnar crest barely defined. Hand webbing formulae: I-II 2^{-}-3^{-} III 2^{+}-2 IV. Tarsal texture smooth; tarsal fold discrete, extending to the entire length of tarsus; heel smooth; inner metatarsal tubercles large, elongate, three times the size of foot subarticular tubercles; outer metatarsal tubercle absent; subarticular tubercles distinct, large, and rounded, diameter about 3/4 width of terminal disc on the same toe; supernumerary tubercles absent; toes long, slender, without lateral fringe; toes bearing rounded discs, smaller in diameter to those of fingers II-IV. Foot webbing formula: I 2^{+} - 3^{-} II 2^{+} - $3^{1/2}$ III 2^{+} - 4^{-} IV 3^{+} - 2V. Supra cloacal fold absent. Skin on dorsum smooth; skin on throat, belly, ventral surface of

Table 1. Acoustic variables of the advertisement call of topotypes *Aplastodiscus perviridis* and *A. lutzorum* sp. n. n = number of recorded males.

Call Features	***A. lutzorum* sp. n. (n = 12)** **Range**	**Mean (SD)**	***A. perviridis* (n = 5)** **Range**	**Mean (SD)**
Call Duration (seconds)	0.26–0.40	0.32 (0.05)	0.12–0.15	0.13 (0.01)
Higher Frequency (kHz)	2334–2647	2468 (97)	2419–2750	2519 (135)
Lower Frequency (kHz)	1494–1732	1595 (76)	1587–1806	1690 (82)
Dominant Peak (kHz)	1884–2156	2027 (79)	1981–2153	2078 (66)
Time to Frequency Peak (%)	49–70	61 (7)	23–38	34 (6)
Air temperature range	19–22 °C		16–19 °C	
Record hour	20:00–22:00 h		20:30–21:00 h	

Table 2. Measurements (in millimeters) of the type-series of *Aplastodiscus lutzorum* sp. n. Abbreviations are: SVL (snout-vent length), HL (head length), HW (head width), ED (eye diameter), TD (tympanum diameter), END (eye-nostril distance), IOD (interocular distance), THL (thigh length), TBL (tibia length), and FL (foot length).

Measurement	Holotype	Female paratype	Males paratypes N = 25 (Mean)
SVL	34.6	33.7	30.7–36 (33.5)
HL	10.6	11.4	8.8–11.4 (10.5)
HW	11.4	11.1	10.5–12.4 (11.4)
ED	3.3	3.4	3–3.7 (3.4)
TD	2.1	2.4	1.5–2.4 (2)
END	3.2	3.1	1.6–3.3 (2.7)
IOD	5.3	5.7	4.5–5.9 (5.4)
THL	18.1	16.2	12–18.7 (17)
TBL	15.8	16.4	14.2–18.5 (16)
FL	18.3	18.8	14.9–19.6 (17)

thigh, and arm granular. Dorsal and dorsolateral surfaces almost entirely pale yellow with small dark spots or mottles on dorsal surfaces. Belly pale yellow. Measurements of the holotype (mm): SVL 34.6, HL 10.6, HW 11.4, ED 3.3, TD 2.1, END 3.2, IOD 5.3, THL 18.1, TBL 15.8, and FL 18.4 (Table 2).

Color in life of the type-series: Dorsal head surface dark green, almost olive. Dorsal body surface and flanks yellowish green with small and scattered melanophores. The superior third of eye is golden, whereas the inferior 2/3 is red copper. Eye surrounded by a black ring. Vocal sac bluish green. In preservative, colors fade to pale beige and the dorsum shows several dark brown dots, making it darker than other parts of the body. The belly is uniformly pale yellow.

Variation in the type series. The main variation in type series is the body size (Table 2). Small brown chromatophores are along the dorsal skin; but the amount of these chromatophores is variable, ranging from sparse to dense.

Calls. Advertisement calls of *A. lutzorum* sp. n. (Figure 3 and 4, Table 1) are long regularly-spaced single notes released at a mean rate of 39 calls/minute (SD = 8; n = 12

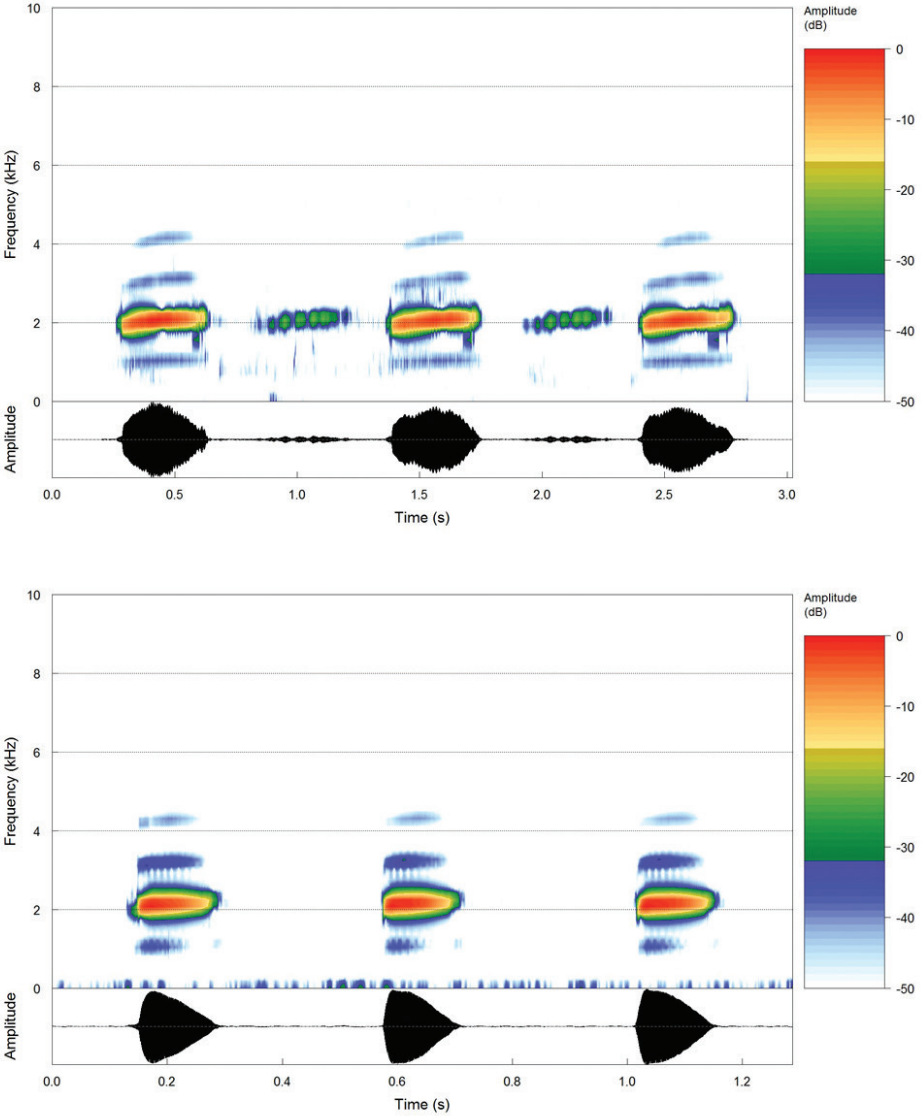

Figure 3. Above, audiospectrogram and oscillogram of three advertisement calls of the holotype of *Aplastodiscus lutzorum* sp. n. (Chapada dos Veadeiros, 12 December 2011, air temperature 20 °C); the background calls are from another male calling in antiphony. Bellow, audiospectrogram and oscillogram of three advertisement call of *A. perviridis* (Serra da Bocaina, 10, January 2012, air temperature 16 °C).

males). Calls resemble a whistle lasting around 0.26–0.40s. Most of the energy is between 1,494–1,732 Hz and 2,334–2,647 Hz, peaking between 1,884–2,156 Hz. Call exhibits an ascending frequency modulation, reaching its maximum between 49–70% of the call duration.

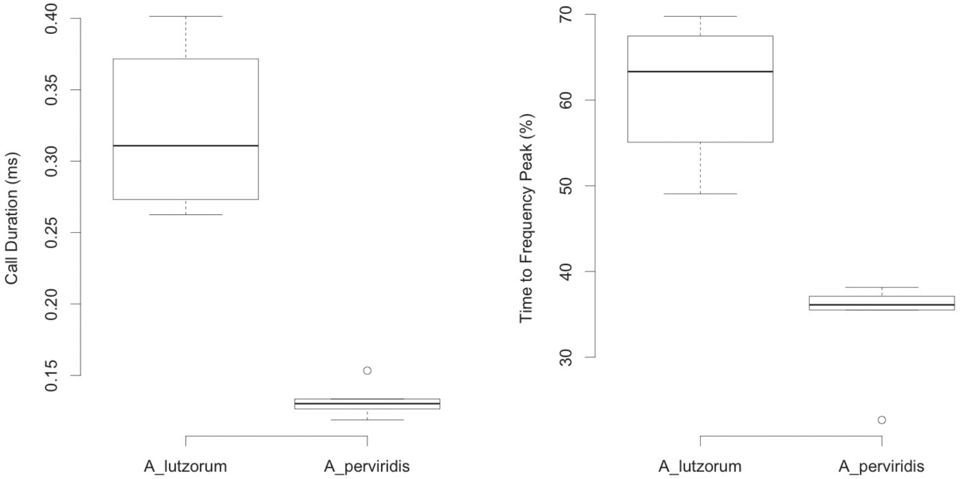

Figure 4. A comparison between duration and frequency peak time of *Aplastodiscus lutzorum* (N = 12 males) and *A. perviridis* (N = 5 males). In both samples, calls are of topotypes.

Aplastodiscus perviridis' advertisement call (Figure 3 and 4, Table 1) is released in groups of 1–11 (mode = 5–7); within groups, call released at a rate of 140/min. Calls resemble a short whistle lasting around 0.12–0.15 s. Most of the energy is between 1,587–1,806 Hz and 2,419–2,750 Hz, peaking between 1,981–2,153 Hz. Call with an ascending frequency modulation, reaching its maximum between 23–38% of the call duration. The advertisement call of *A. cochranae* is described by Garcia et al. (2001) as being barely indistinguishable from the call of *A. perviridis*.

Natural history and geographic distribution. All specimens of *Aplastodiscus lutzorum* sp. n. were collected along gallery forests with scattered buriti (*Mauritia flexuosa*) palm trees within the Cerrado Biome (see also Brandão and Araujo, 2002; Morais et al. 2012; Santoro and Brandão, 2014) (Figure 5). A female bearing large oocytes seen by the transparency of the body walls was found in mid-December and calling males were found from December to March. Males call during the night in proximity of riverine forests (< 2m), perched on leaves or branches from the water level to 5 m high (Figure 6). *Aplastodiscus perviridis* males call during the night along swamps in open areas, perched on grass leaves or bushes bordering streamlets, from 0.5 m to 3 m high. Tadpoles are unknown. Sometimes, the species also uses places with wet and soft mud soil, covered by a layer of dense bush, in places where the forest was removed, but is under secondary growth. Sympatric frog species were *Hypsiboas ericae* (Caramaschi and Cruz, 2000) and *H. albopunctatus* (Spix, 1824). All localities where *A. lutzorum* sp. n. was found are 1000 m above sea level or more.

Etymology. The new species is named after the Brazilian scientists Adolfo and Bertha Lutz, who were pioneers in discovering and studying *Aplastodiscus* and some species of *Hyla* now included in the genus *Aplastodiscus*.

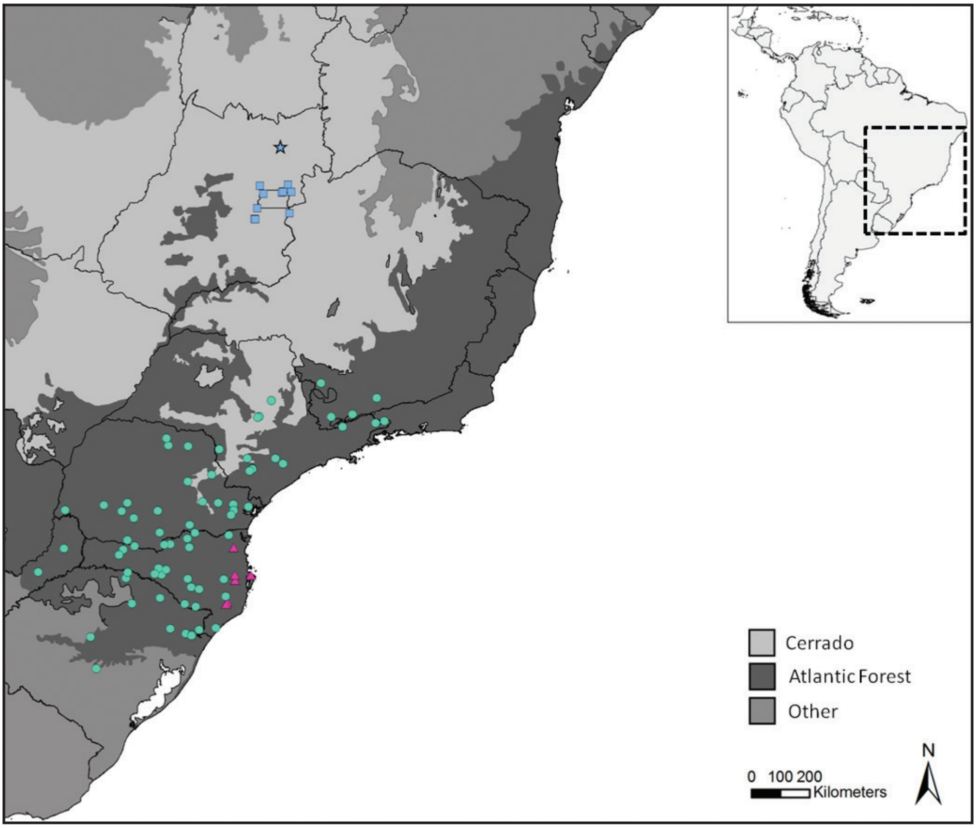

Figure 5. Geographic distribution of *Aplastodiscus cochranae* (pink triangles), *A. perviridis* (green circle), and *A. lutzorum* sp. n. (blue squares, blue star indicates its type-locality). Note that *A. lutzorum* shows a disjunctive distribution regarding the other *Aplastodiscus* species, occurring deep within Cerrado Biome.

Comparison with congeneric species. *Aplastodiscus lutzorum* sp. n. can be distinguished from the species of other groups of *Aplastodiscus* (*A. albosignatus*, *A. albofrenatus,* and *A. sibilatus* groups) by the presence of bicolored irises, the lack of the webbing between toes I and II, the webbing among the remaining toes reduced, and the absence of peri-cloacal ornamentation. The new species is diagnosed from *A. perviridis* and *A. cochranae* by having smaller SVL (30–36 mm SVL in the new species, 38–44.7 mm in *A. perviridis*, and 41–46.4 mm in *A. cochranae*) and longer advertisement calls (0.38–0.42 in new species, 0.14–0.17 in *A. perviridis* and 0.10–0.18 in *A. cochranae*). From *A. cochranae* it can be also distinguished by the green dorsal color in life (*A. cochranae* is brown) and by the absence of a brown line on the loreal region and a white line in the cloacal region (both present in *A. cochranae*). (Figures 1–4; Tables 1 and 2).

Phylogenetic relationships and genetic p-distances. The two DNA fragments aligned and concatenated resulted in a matrix of 1,227pb. Our analysis recovered four most parsimonious trees with 808 steps each (Figure 7). The differences in topology among these trees are the position of *A. lutzorum* sp. n. specimens from different locali-

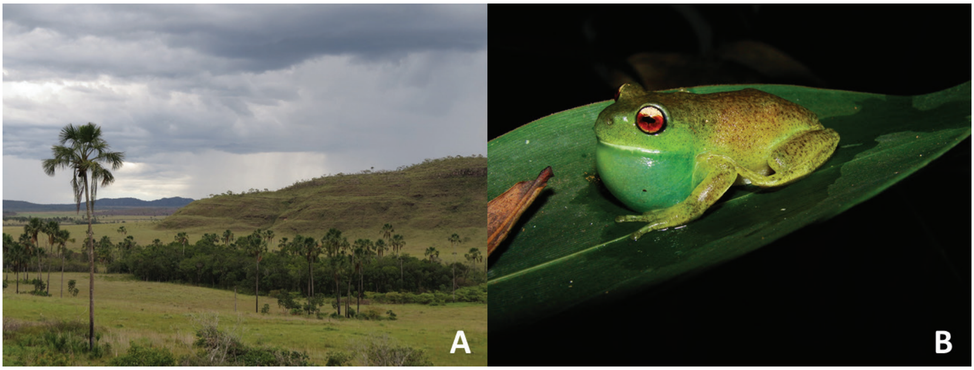

Figure 6. A The habitat of *A. lutzorum* sp. n.: flooded gallery forests **B** A male in calling activity at Fazenda Água Limpa, Brasília, Distrito Federal, Brazil.

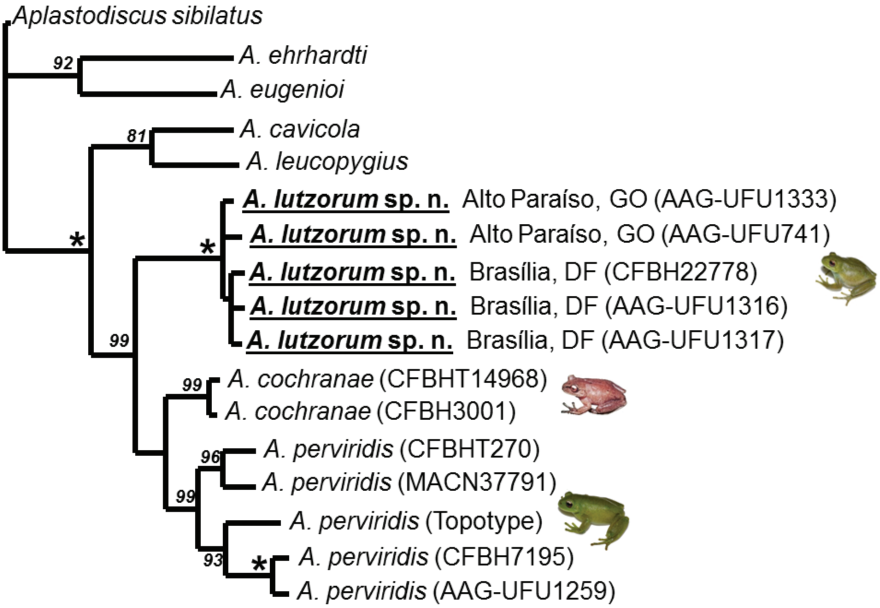

Figure 7. One of the four most parsimonious trees recovered. Asterisks indicate 100% Parsimony Jackknife absolute frequency; only values above 75% are shown. See Suppl. material 2 for details and complete locality names.

ties. *Aplastodiscus lutzorum* sp. n. were recovered as a monophyletic group with 100% Parsimony Jackknife Support (hereafter PJS) being the sister species of *A. perviridis* plus *A. cochranae*. The *A. perviridis* plus *A. cochranae* clade is low supported (54% PJS) and both species are supported by 99% of PJS each. The p-distances calculated for 16s of species in the *A. perviridis* Group range from zero to 5.9% (for all distances see Table 3). The internal distances among specimens of the new species range from zero to 0.93%. The p-distance in 16s between the new species and *A. perviridis* is 4.4–5.8% and between the new species and *A. cochranae* is 4.0–4.5%.

Table 3. Uncorrected pairwise sequence distances (p-distances) of the Cytochrome c oxidase subunit 1 (above the diagonal) and 16s fragments (below the diagonal) for the species of the *Aplastodiscus perviridis* species Group. See the Material and methods section for the primers that delimitate each fragment. Values are in percentage.

		1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
1	*A. cochranae* CFBH3001 Rancho Queimado, SC	—	1.06	9.13	–	–	9.55	8.92	9.77	9.98	9.77	8.92	10.19
2	*A. cochranae* CFBHT14968 Lauro Muller, SC	–	—	9.34	–	–	9.77	9.34	9.98	10.19	9.98	9.13	10.4
3	*A. lutzorum* sp. n. CFBH22778 Brasília, DF	4.28	–	—	–	–	0.42	0.42	10.4	9.34	9.98	9.13	9.55
4	*A. lutzorum* sp. n. AAG1316 Brasília, DF	4.28	–	0.56	—	–	–	–	–	–	–	–	–
5	*A. lutzorum* sp. n. AAG1317 Brasília, DF	4.09	–	0.37	0.19	—	–	–	–	–	–	–	–
6	*A. lutzorum* sp. n. AAG1333 Alto Paraíso, GO	4.09	–	0.37	0.19	0	—	0.85	10.19	9.13	9.77	8.92	9.55
7	*A. lutzorum* sp. n. AAG741 Alto Paraíso, GO	4.46	–	0.93	0.19	0.56	0.56	—	10.4	9.34	9.98	9.13	9.55
8	*A. perviridis* CFBH18119 Topotype	3.35	–	5.2	5.2	5.02	5.02	5.58	—	5.3	6.37	4.03	5.1
9	*A. perviridis* CFBH7195 Santo Antônio do Pinhal, SP	3.16	–	5.39	5.39	5.2	5.2	5.76	2.23	—	6.16	4.25	0.64
10	*A. perviridis* CFBHT270 São Bento do Sul, SC	2.23	–	4.83	4.83	4.65	4.65	5.02	2.79	2.42	—	2.76	5.94
11	*A. perviridis* MACN37791 Misiones, Argentina	3.16	–	5.76	5.76	5.58	5.58	5.95	3.35	3.16	0.93	—	4.03
12	*A. perviridis* AAG1259 Atibaia, SP	2.97	–	5.39	5.39	5.2	5.2	5.76	2.23	0.37	2.42	2.97	—

Discussion

The *A. perviridis* Group now includes a third species, *Aplastodiscus lutzorum*, a species diagnosed mainly by its advertisement call, small size, and genetic differentiation. Genetic p-distances and phylogenetic topology support our hypothesis of the new species. Garcia et al. (2001), when re-describing *A. perviridis*, included six specimens that here we recognize as *Aplastodiscus lutzorum* (CHUNB 404; 268–70; 1378; 1704) the minimum snout-vent lengths values of *A. pervirids* in that work overlaps the SVL of the new species. Garcia et al. (2001) also discuss an unusual condition for any anuran species, observed in *A. perviridis* and *A. cochranae*: identical advertisement calls with clearly distinct coloration (*A. cochranae* is the only brown species of the genus). The description of the advertisement calls of *A. perviridis* in Garcia et al. (2001) were based on specimens from Ribeirão Branco (São Paulo State) and so, do not belong to *A. lutzorum*. The identical advertisement call shared by *A. perviridis* and *A. cochranae* highlight the taxonomic importance of the differences we found in *A. lutzorum*.

Berneck et al. (2016) included only one specimen of the *A. lutzorum* (as *Aplastodiscus* sp. 3), therefore the monophyly of the new species was tested for the first time by our analysis. Berneck et al. (2016) recovered *Aplastodiscus lutzorum* as a sister species of *A. cochranae*, a topology not corroborated by the present work, where the new species is a sister species of *A. cochranae* plus *A. perviridis*. In the present work, the node of *A. perviridis* plus *A. cochranae* is supported by less than 70% of PJS while in Berneck et al. (2016) the node of *A. lutzorum* plus *A. cochrane* was poorly supported (also less than 70%). Those are possibly the reason of the instability in the internal relationships of members of the *A. perviridis* Group. However, our dataset and taxon sampling is very reduced in relation to that of Berneck et al. (2016) and so the analysis of these authors is preferable for relationships of *Aplastodiscus* species.

The scope of this paper was not to test biogeographic hypotheses. However, *Aplastodiscus lutzorum* is the only species of *Aplastodiscus* that occurs deep in the Cerrado Biome (see Silva et al. 2006) with a disjunctive distribution from its sister species of the Atlantic Forest (Valdujo et al. 2012). Therefore, it seems interesting to point out some remarks on its geographic distribution pattern (Figure 5). The new species has been reported in several localities in the Brazilian Central Plateau and our topology suggests an origin of the *A. perviridis* Group in the Brazilian Central Plateau (Figure 7). However, the low PJF support of the clade *A. perviridis* + *A. cochranae* and the incongruence between our topology and that of Berneck et al. (2016) make any further inference premature.

A population from the dam of Queimado in the municipality of Unaí, in the state of Minas Gerais, Brazil (an area flooded by the construction of a hydroelectric station) was included as "referred specimens" for *A. lutzorum* The conservation status of this population is unknown. We consider the new species to be listed as a "Least Concern", due to the fact that most of its area of occurrence is in protected places, such as the Parque Nacional da Chapada dos Veadeiros, Área de Relevante Interesse Ecológico (ARIE) do Capetinga/Taquara (Fazenda Água Limpa), Estação Ecológica de Águas Emendadas, and Floresta Nacional de Silvânia.

Goin (1961) suggested that *Chorophilus cuzcanus* Cope, 1878 should be an *Aplastodiscus*, but had not stated that it was *Aplastodiscus perviridis* (as pointed out by Frost, 2016). Lutz (1968) suggested that *C. cuzcanus* was possibly a second species of *Aplastodiscus* at that time. According to Frost (2016), the combination *Chorophilus cuzcanus* is a junior synonym to both *A. perviridis* and *Gastrotheca marsupiata* (Duméril and Bibron 1841). We recognize only the synonym of Duellman and Fritts (1972) for *G. marsupiata* as valid; therefore *A. perviridis* has no junior synonyms.

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References

Bastos RP, Motta JAO, Lima LP, Guimarães LDA (2003) Anfíbios da Floresta Nacional de Silvânia, Estado de Goiás. Goiânia, Brazil, 29 pp.

Berneck BVM, Haddad CFB, Lyra ML, Cruz CAG, Faivovich J (2016) The Green Clade Grows: a phylogenetic analysis of *Aplastodiscus* (Anura; Hylidae). Molecular Phylogenetics and Evolution 97: 213–223. https://doi.org/10.1016/j.ympev.2015.11.014

Bioacoustics Research Program (2014) Raven Pro: Interactive Sound Analysis Software (Version 1.5) [Computer software]. The Cornell Lab of Ornithology, Ithaca, NY. http://www.birds.cornell.edu/raven

Brandão RA, Araujo AFB (2002) A herpetofauna da Estação Ecológica de Águas Emendadas. In: Marinho-Filho JS, Rodrigues FC, Guimarães MM (Eds) Vertebrados da Estação Ecológica de Águas Emendadas, História Natural e Ecologia em um Fragmento de Cerrado do Brasil Central. Brasília, 92 pp.

Charif RA, Strickman LM, Waack AM (2010) Raven Pro 1.4 User's Manual. The Cornell Lab of Ornithology, Ithaca, NY. http://www.birds.cornell.edu/raven

Duellman WE (1970) The hylid frogs of Middle America. Monograph of the Museum of Natural History, University of Kansas 1–2: 1–753.

Duellman WE, Fritts TH (1972) A taxonomic review of the southern Andean marsupial frogs (Hylidae: *Gastrotheca*). Occasional Papers of the Museum of Natural History 9: 1–37.

Farris JS, Albert VA, Källersjö M, Lipscomb D, Kluge AG (1996) Parsimony jackknifing outperforms neighbor-joining. Cladistics 12: 99–124. https://doi.org/10.1111/j.1096-0031.1996.tb00196.x

Frost DR (2016) Amphibian Species of the World: An Online Reference. Version 6.0 (September, 4, 2016). American Museum of Natural History, New York. Electronic Database accessible at http://research.amnh.org/herpetology/amphibia/index.html

Garcia PCA, Caramaschi U, Kwet A (2001) O status taxonômico de *Hyla cochranae* e recaracterização de *Aplastodiscus* A. Lutz (Anura, Hylidae) Revista Brasileira de Zoologia 18: 1197–1218. http://dx.doi.org/10.1590/S0101-81752001000400015

Goin CJ (1961) Synopsis of the genera of hylid frogs. Annals of the Carnegie Museum 36: 5–18.

Goloboff PA (1999) Analyzing large datasets in reasonable times: solutions for composite optima. Cladistics 15: 415–428. https://doi.org/10.1111/j.1096-0031.1999.tb00278.x

Goloboff PA, Farris JS, Nixon KC (2008) TNT, a free program for phylogenetic analysis. Cladistics 24: 1–13. https://doi.org/10.1111/j.1096-0031.2008.00217.x

Heyer WR, Rand AS, Cruz CAG, Peixoto OL, Nelson CE (1990) Frogs of Boracéia. Arquivos de Zoologia 31: 231–410. http://dx.doi.org/10.2307/1446606

Jungfer KH, Faivovich J, Padial JM, Castroviejo-Fisher S, Lyra ML, Berneck BVM, Iglesias PP, Kok PJR, MacCulloch RD, Rodrigues MT, Verdade VK, Torres-Gastello CP, Chaparro JC, Valdujo PH, Reichle SM, Gvoždík V, Gagliardi-Urrutia G, Ernst R, De la Riva I, Means DB, Lima AP, Señaris JC, Wheeler WC, Haddad CFB (2013) Systematics of spiny-backed treefrogs (Hylidae: *Osteocephalus*): an Amazonian puzzle. Zoologica Scripta 42: 351–380. https://doi.org/10.1111/zsc.12015

Lutz B (1950) Anfíbios anuros da coleção Adolpho Lutz do Instituto Oswaldo Cruz. V. Frogs in the Adolpho Lutz collection of the Instituto Oswaldo Cruz. V. Memórias do Instituto Oswaldo Cruz 48: 599–637. https://doi.org/10.1590/S0074-02761950000100022

Lutz B (1968) Taxonomy of the Neotropical Hylidae Pearce-Sellards Series Texas Memorial Museum 11: 3–26.

Morais AR, Bastos RP, Vieira R, Signorelli L (2012) Herpetofauna da Floresta Nacional de Silvânia, um remanescente de Cerrado no Brasil Central. Neotropical Biology and Conservation 7: 114–121. https://doi.org/10.4013/nbc.2012.72.05

Myers CW, Duellman WE (1982) A new species of *Hyla* from Cerro Colorado, and other tree-frog records and geographical notes from Western Panama. American Museum Novitates 2752: 1–32.

Palumbi SR, Martin A, McMillan WO, Stice L, Grabowski G (1991) The simple fool's guide to PCR, Version 2.0. http://palumbi.stanford.edu/SimpleFoolsMaster.pdf

Rambaut A (2014) FigTree, ver. 1.4.2. (Online 2016, May 29). http://tree.bio.ed.ac.uk/software/figtree/

Santoro GRCC, Brandão RA (2014) Reproductive modes, habitat use, and richness of anurans from Chapada dos Veadeiros, central Brazil. North-Western Journal of Zoology 10: 365–373. http://biozoojournals.ro/nwjz/content/v10n2.html

Savage JM, Heyer, WR (1967) Variation and distribution in the tree-frog genus *Phyllomedusa* in Costa Rica, Central America. Beiträge zur Neotropischen Fauna 5: 111–131. http://dx.doi.org/10.1080/01650526709360400

Silva JF, Fariñas MR, Felfili JM, Klink CA. (2006) Spatial heterogeneity, land use and conservation in the Cerrado region of Brazil. Journal of Biogeography 33: 536–548. doi:10.1111/j.1365-2699.2005.01422.x

Sueur J, Aubin T, Simonis C (2008) Seewave: a free modular tool for sound analysis and synthesis. Bioacoustics 18: 213–226. https://doi.org/10.1080/09524622.2008.9753600

Tamura K, Stecher G, Peterson D, Filipski A, Kumar S (2013) MEGA6: Molecular Evolutionary Genetics Analysis Version 6.0. Molecular Biology and Evolution 30: 2725–2729. https://doi.org/10.1093/molbev/mst197

Thompson JD, Higgins DG, Gibson TJ (1994) CLUSTAL W: Improving the sensitivity of progressive multiple sequence alignment through sequence weighting. position-specific gap penalties and weight matrix choice Nucleic Acids Research 22: 4673–80. https://doi.org/10.1093/nar/22.22.4673

Valdujo PH, Silvano DL, Colli G, Martins M (2012) Anuran species composition and distribution patterns in Brazilian Cerrado, a Neotropical hotspot. South American Journal of Herpetology 7: 63–78. http://dx.doi.org/10.2994/057.007.0209

Wilkinson JA, Matsui M, Terachi T (1996) Geographic variation in a Japanese tree frog (*Rhacophorus arboreus*) revealed by PCR-aided restriction site analysis of mtDNA. Journal of Herpetology 30: 418–423. https://doi.org/10.2307/1565184

Supplementary material 1

Analyzed sound files; from Ariovaldo A. Giaretta collection

Authors: Bianca V. M. Berneck, Ariovaldo A. Giaretta, Reuber A. Brandão, Carlos A. G. Cruz, Célio F. B. Haddad

Data type: species data

Supplementary material 2

List of voucher specimens, GenBank accession numbers, and locality data

Authors: Bianca V. M. Berneck, Ariovaldo A. Giaretta, Reuber A. Brandão, Carlos A. G. Cruz, Célio F. B. Haddad

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RESEARCH ARTICLE

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A reassessment on the state of knowledge of Chilean Falconidae in the last hundred years

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Abstract

Eight species of falcons (Falconidae) have been recorded in Chile. To date, all relevant studies considered birds of prey in general, with no specific focus on this family. Based on a comprehensive review of the literature, an updated report is presented on the state of knowledge of falcons in Chile. This data set comprises a total of 165 studies published from 1915 to 2015. Scientific productivity was lowest in 1945-1955 and highest in 2005-2015, with a steady increase since 1985. However, the focus of research in Chile is biased towards two species: *Milvago chimango* and *Falco sparverius*. Two administrative regions, Santiago Metropolitan Region and Araucanía, were the most studied whereas Arica, Tarapacá, and Antofagasta regions accounted for fewer than 1% of the studies. Faunistic studies (including abundance) were the most common research topic. It is suggested that the lack of knowledge regarding species in the genus *Phalcoboenus* may negatively affect the conservation status of these species, and believed that the lack of preference for certain research topics, such as systematics and natural history, are the result of historical factors including the decrease of field biology and perhaps a biased interest of the researchers. Finally, this review highlights the paucity of information on falcons and provides a framework for directing future research.

Keywords

Birds of prey, Falconidae, Knowledge, Diversity, Chile, Natural history

Introduction

Falcons (family Falconidae) are small to medium sized, exclusively diurnal birds of prey, which are top predators inhabiting a broad range of habitats (Yáñez et al. 1982, Biondi et al. 2005). Falcons are considered good indicators of ecological and environmental health (Rau and Jaksic 2004), as are other birds of prey (Pfeiffer and Meyburg 2015). They fulfil an important role maintaining control over plague species and regulating the ecosystem (Rau 2014). The 64 species are grouped in 11 genera and 2 subfamilies: Polyborinae (caracaras and forest falcons) and Falconinae (true falcons and falconets) (White et al. 1994). Eight species of falcons inhabit Chile: five species of caracaras (*Caracara plancus* (Miller 1777), *Milvago chimango* (Vieillot 1816), *Phalcoboenus albogularis* (Gould 1837), *P. australis* (Gmelin 1788), and *P. megalopterus* (Meyen 1834)), and three Falconinae (*Falco femoralis* (Temmnick 1822), *F. peregrinus* (Tunstall 1771), and *F. sparverius* (Linnaeus 1758)).

Research and reviews in Chile have mostly focused on birds of prey in general. A review was carried out by Muñoz-Pedreros and Norambuena (2011), who covered a period of 200 years, and focused on publication type, temporal trends, and research topics. Although only covering 30 years of scientific research, Raimilla et al. (2012) identified a marked bias towards nocturnal species, centering on diet and reproductive aspects. Two other reviews focused on one type of bird of prey. Figueroa et al. (2015) focused on the biology of owls in Chile and relevant conservation strategies. Figueroa (2015) documented a lack of research on the natural history of *Milvago chimango*. All these investigations are significant as they expose a deficiency in information, and thus, indicate where more research is warranted, regardless of possible limitations typical to this type of studies as indicated by Bimrose et al. (2005). Limitations may include a limited temporal scope, insufficient access to information, and the selection and classification of studies.

Our aim is to describe the current state of knowledge regarding falcons in Chile based on a comprehensive review of the literature. We identify deficiencies in temporal, thematic, geographic, and species-specific knowledge, discuss the possible causes and suggest directions for future research.

Methods

The bibliographical review consisted of an exhaustive search of the ornithological literature on falcons in Chile, published between 1915 and 2015, and presented in scientific publications, national and international journals (both indexed and non-indexed), books, book chapters, and undergraduate and graduate theses (only those with online free access). Relative productivity was measured and compared across time (10 year intervals beginning in 1915), space (administrative regions), subject (research topic), and species.

We classified research topics into 13 categories identified by Muñoz-Pedreros and Norambuena (2011). However, due to the lack of literature for some topics, only 11 applied to our data set: Natural History (NH): studies that cover descriptions of morphology, distribution, identification, ecology, and systematics. Field manuals and monographs also fall into this category; Systematics and Taxonomy (ST): studies on classification, description of new species, species reviews, and phylogenetic analyses; Distribution and Biogeography (DB): studies focusing on distribution patterns, updates in distribution ranges, and the study of processes which originate and modify said distribution; Faunistics, Biodiversity, and Abundance (FBA): studies with observation data, new registries, sightings, species diversity, and abundance data. Studies that present abundance data are considered in this category, as ecologic studies contemplate gathering said data along with visual observations and registries, which coincide with the most common methodologies (see: Bibby et al. 1993); Diet and Trophic Ecology (DTE): these studies exclusively observe the feeding preferences of the species, stomach content, pellets, trophic position, trophic chains, and feeding activity; Reproduction and Development (RD): studies related to reproductive characteristics, courting, fertilization, nesting, hatching, number of hatchlings, waiting period in the nest, embryo development, and yearly development period; Ethology, Migration, and Home range (EMH): studies on migratory behavior, patterns, and habits, and home range according to the definition by Burt (1943) as the area occupied by an individual during feeding, mating, and nestling care; Parasitology and Medicine (PM): studies related to the internal or external parasitic flora of the species, new parasite species registries, clinical data, medical reports, and veterinary procedures; Conservation and Legislation (CL): studies regarding conservation plans, conservation state, anthropogenic effects, environmental legislation, hunting manuals, and hunting and closed-season reports; Study Methods and Techniques (SMT): studies on sample recollection and manipulation, notes on observation and data registry, and comparisons between study methods; and "Environmental Education and Science Outreach" (ESO): studies that focus on teaching environmental sciences by using birds of prey to a non-specialists audience.

Publications which did not explicitly mention the scientific or common name(s) of the study species were omitted from our data set.

Results

A total of 165 studies between 1915 and 2015 included scientific data on falcons in Chile. The most studied research topics were "Faunistics, Biodiversity, and Abundance" and "Diet and Trophic Ecology" with 63 and 34 studies, respectively. "Study Methods and Techniques" and "Environmental Education and Science Outreach" were the least studied topics, with 5 and 1 publications, respectively (Figure 1). The

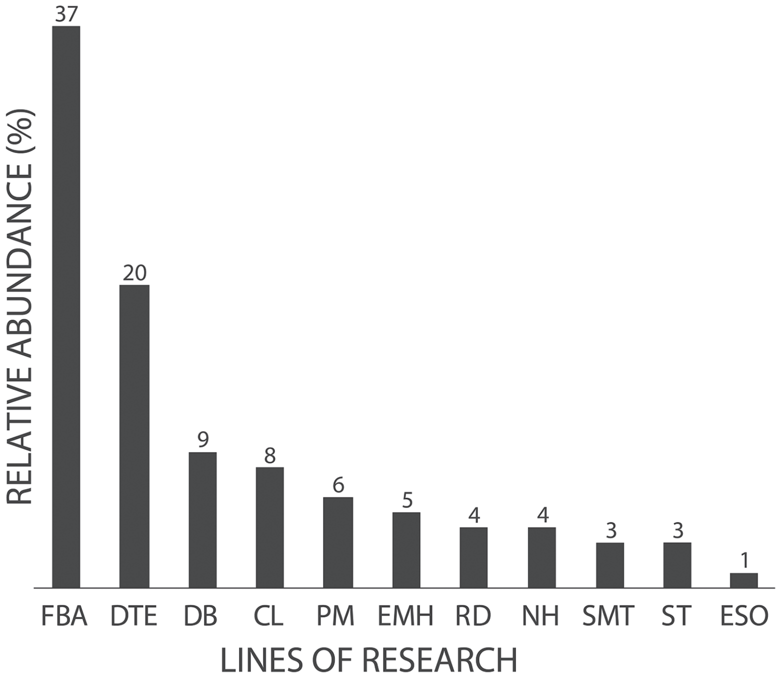

Figure 1. Relationship between different lines of investigation: (FBA) Faunistics, Biodiversity, and Abundance, (DTE) Diet and Trophic Ecology, (DB) Distribution and Biogeography, (CL) Conservation and Legislation, (PM) Parasitology and Medicine, (EMH) Ethology, Migration, and Home environment, (RD) Reproduction and Development, (NH) Natural History, (SMT) Study Methods and Techniques, (ST) Systematics and Taxonomy, and (ESO) Environmental Education and Science Outreach.

highest productivity was observed during the last 10 years (2005–2015) with 52 publications, in contrast with the decade between 1945 and 1955 which only presented one study (Figure 2). Of the administrative regions (Figure 3), Metropolitan Santiago was best represented with 15% of contributions, followed by Araucanía with 14% and Los Lagos and Magallanes with 13% each. The O'Higgins region contributed no studies. Most (78%) studies were scientific papers, followed by books (11%), and books chapters (10%). Only 1% of publications were theses. Across species, *M. chimango, F. sparverius,* and *F. pererinus* were most often mentioned, with 23, 23, and 20% of contributions, respectively. The remaining species contributed fewer than 11% of citations (Figure 4).

In the following section, results are summarized for each one of the research topics:

Natural history. The natural history of falcons in Chile is poorly documented. Studies by Quijada (1917), Housse (1934; 1937), and Barros (1960) regarding *M. chimango*, by Housse (1935) regarding *F. sparverius*, and Housse (1936a) regarding *C. plancus* discuss aspects of morphology, behaviour, reproduction, development, foraging, and as well as anecdotal observations of daily activity. Particularly, the complete reproductive cycle of *P. megalopterus* was described by Housse (1937), whereas data

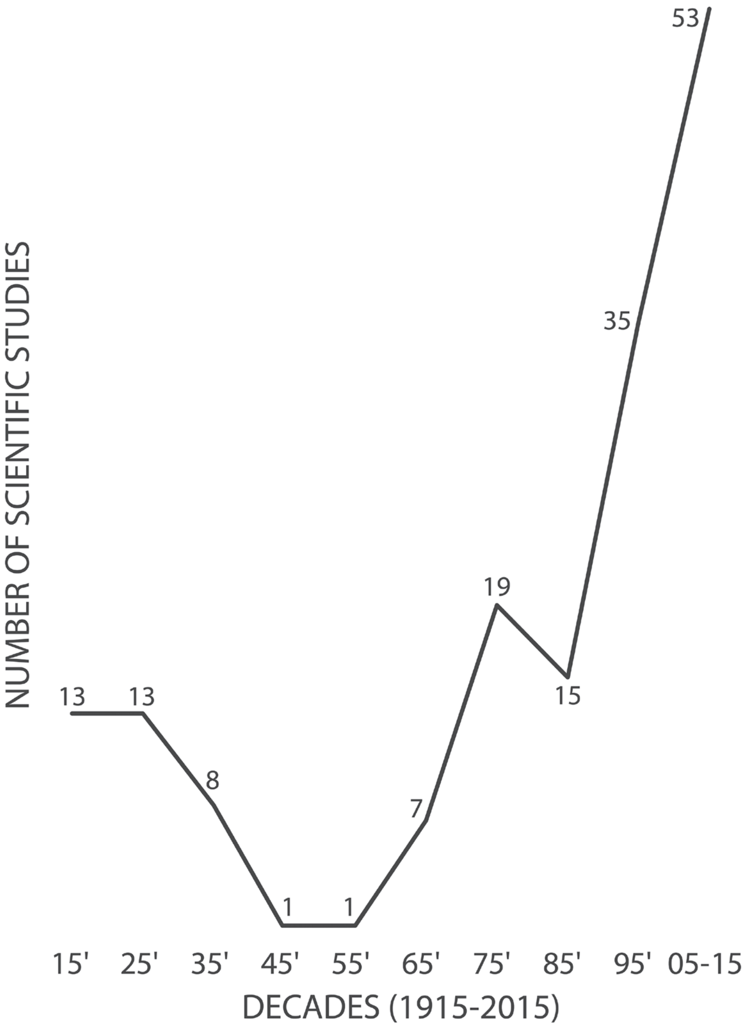

Figure 2. Number of studies regarding the Falconidae family published in the last century (from 1915 to 2015).

are missing for the remaining species. Figueroa (2015) analyzed the scarce literature regarding the natural history of *M. chimango*.

Systematics and taxonomy. The systematics and taxonomy of falcons have been clarified by Fuchs et al. (2012, 2015). They reported polyphyly of the genus *Milvago*, and found that *M. chimango* is part of the *Phalcoboenus* clade and should be transferred to this genus (Fuchs et al. 2012). The genus *Falco* was found to be monophyletic (Fuchs et al. 2015). There is little information regarding intraspecific variation and evolution of falcons in Chile. *Falco sparverius fernandensis* was described by Chapman (1915). Two subspecies of *M. chimanago* are known: *M. chimango temucoensis* (Sclater 1918) is found is most of Chile (Housse 1934) and *M. chimango fuegiensis* (Johnson

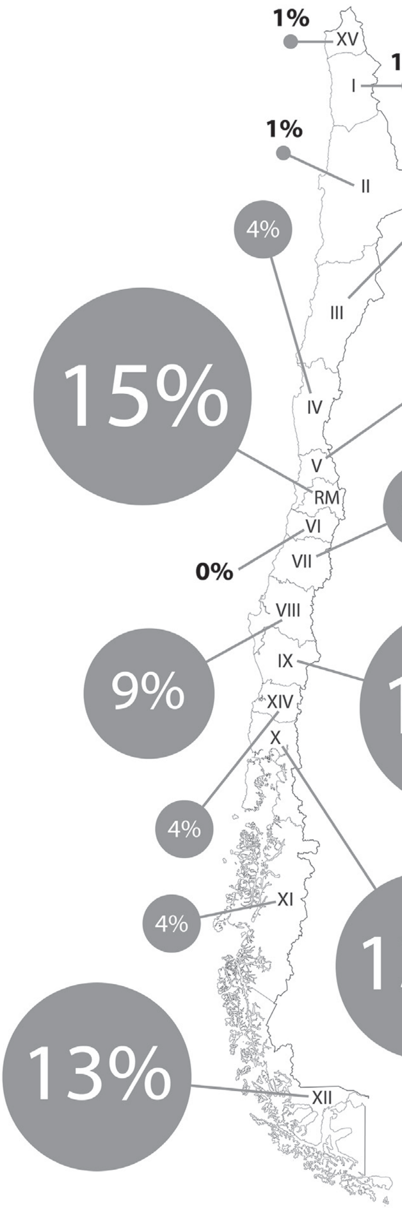

Figure 3. Relative abundance of studies published for each administrative region of Chile.

and Behn 1957), which is endemic in Tierra del Fuego. The latter subspecies is no longer recognized as a valid taxon by most taxonomists (e.g. Dickinson & Remsen 2013). Drouilly's (1968) identification key provides accurate diagnostic recognition characteristics for species classification. McNutt (1984) established that the pale coloration in *F. peregrinus* is recessive in the genotype of the species.

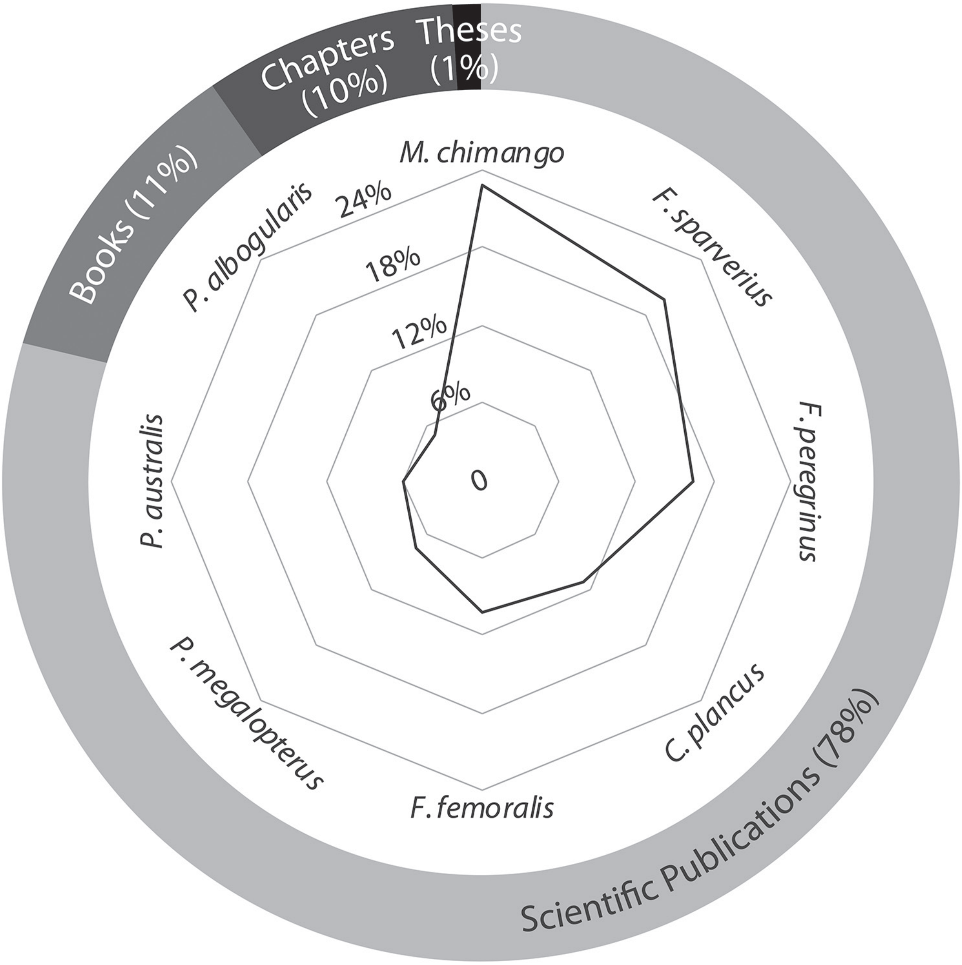

Figure 4. Relative bibliographic importance according to circulation medium and researched species.

Distribution and biogeography. The genera *Falco* (Kleinschmidt 1929; Reynolds 1934; Bullock 1949; Torres 1970; Araya et al. 1974; Schlatter 1976; Araya and Millie 1998), *Caracara* (Reynolds 1934), and *Milvago* (Jaksic et al. 2002) can be found from Arica to Magallanes regions. Among *Phalcoboenus*, *P. megalopterus* is the most widely distributed species occurring from the extreme north (Hellimayr 1932) south to Magallanes (Jaksic et al. 2002); *P. albogularis* (Vuilleumier 1985, Cursach et al. 2009) has been sighted once in the central area of Chile, and *P. australis* is limited to the extreme south (Reynolds 1934, Drouilly 1968, Collar 1986, Marín et al. 2006).

Faunistics, biodiversity, and abundance. During an extended period, only the presence or absence of species was documented without attention for abundance (e. g. Jaffuel Pirion 1927, Gigoux 1928, Bullock 1929a, Bullock 1929b, Reynolds 1934, Housse 1936b, Philippi 1937, Barros 1937, Bullock 1938, Millie 1938, Larraín 1939, Araya et al. 1974, Cody 1970, Keith 1970). Population estimates began with general ornithofaunal observations at some locations, albeit in a non-systematic manner, which resulted in low estimates (with the exception of *M. chimango*) (e. g: Cody 1970, Markham 1970, Araya et al. 1974, Schlatter 1976, Ellis and Glinski 1980, Venegas 1981, Figueroa et al. 2000a, Simeone et al. 2008, Imberti 2005). The greatest abundance and number of species were registered in national parks and reserves (e.g. *F. femoralis, F. peregrinus,* and *M. chimango* in the National Ñuble Reserve, Estades 1997; *C. plancus, F. femoralis,* and *M. chimango* in the Huemules de Niblinto Nature Sanctuary, Figueroa et al. 2000b; and *C. plancus*, *F. peregrinus*, *F. sparverius*, *M. chimango,* and *P. albogularis* in the National Futaleufú Reserve Elgueta et al. 2006).

Diet and Trophic Ecology. The feeding preferences and habits of *C. plancus*, *F. femoralis*, *F. sparverius* and *M. chimango* have been described (Barros 1925). *Falco femoralis* exclusively feeds on birds and insects (Jiménez 1993, Jaksic et al. 1993, 1996), depending on the food supply (Figueroa and Corales 2005). *Falco peregrinus* is considered an opportunist (McNutt 1981) and is a top predator of granivore birds (Marquet et al. 1998), as well as an avid insect eater, again depending on supply (Simeone et al. 1997). The feeding habits of *F. sparverius* are known in detail; it is classified as a predator of insects, reptiles (Goodall et al. 1951, Jaksic et al. 1982, Jaksic and Ostfeld 1983, Marquet et al. 1998, Jaksic and Feinsinger 1991, Simeone et al. 1997), and small mammals (Jaksic 1986), and the supply of the latter increases species abundance (Jaksic et al. 1992, Jaksic et al. 1993, 1996). *F. sparverius* is capable of changing its diet following the seasons (Figueroa and Corales 2002, Mella 2002, 2005) and geographic location (Ellis et al. 2002). No trophic superposition between *F. femoralis* and *F. sparverius* has been documented in Chile (Torres-Mura 2004, Rau and Jaksic 2004). The feeding habits and preferences of *M. chimango* are described in detail through stomach content and pellets (Yáñez et al. 1980): it is an omnivore and a scavenger (Núñez and Yáñez 1981, Núñez et al. 1982, Yáñez et al. 1982, Cabezas Schlatter 1987, Jaksic and Simonetti 1987, Sazima and Olmos 2009). Observations by Figueroa et al. (2004) reveal *P. megalopterus* as an insectivore and carnivore of small birds and mammals. Finally, *P. australis* has been described as the most important predator of *Eudyptes chrysocome* (Forster 1781) eggs (Sphenisciformes) (Cursach et al. 2014).

Reproduction and Development. Information on reproductive cycle and development is available for *F. sparverius*, *C. plancus*, *M. chimango*, and *P. australis*. Nesting data on *P. megalopterus* in Chile are limited to a monograph by Housse (1937), who presumed the species would nest in the rich vegetation areas of the mountains. In general, falcons begin nesting in early spring, laying between 2 and 4 eggs, with an incubation period of 15 to 20 days (Housse 1934, Housse 1935, Housse 1936a, Morrison and Phillips 2000, Díaz and Armesto 2003, Marín et al. 2006). Raimilla et al. (2014) described cooperation in care and nursing in *P. australis*.

Ethology, migration, and home environment. Information for this topic is fragmented across a number of brief publications and reviews. *M. chimango* is a resident species associated with highly urbanized areas (Lobos et al. 2011). *F. sparverius* and *F. peregrinus* are classified as semi-residents (Teneb et al. 2013, Cursach and Rau 2008). The only migrant species of falcon recorded in Chile is *F. femoralis* (Jaksic and Simonetti 1987). For instance, the species is considered only a summer visitor to Las Chinchillas National Reserve, North of Santiago (Jaksic and Lazo 1999).

Parasitology and medicine. Intestinal endoparasite fauna has been described for *M. chimango* (San Martín et al. 2006), and included bacteria (*Haemoproteus tinnunculi* (Wasielewski and Wilker 1918), *Leucocytozoon toddi* (Sambon 1908) (Protozoa: Haemosporine) (Forrester et al. 2001)), and ectoparasites (new Ischnocera species (Insecta: Phthiraptera) (Mey and González-Acuña 2000), and *Argas* (*persicargas*) *keiransi* (Acari: Argasidae)) sampled from the neck (Estrada-Peña et al. 2003). *Escherichia coli* (Migula 1985) has been identified as a cause of fatal meningoencephalitis in *Milvago chimango* (Seguel et al. 2012). The parasites described and registered in other species of falcons include *Degeeriella rufa* (Phthiraptera: Philopteridae) in *F. femoralis* and *F. peregrinus*; *Acutifrons megalopterus* (Carriker, 1956) (Phthiraptera: Ischnocera) and *Colpocephalum megalopteri* (Price 1967) (Phthiraptera: Menoponidae) in *P. megalopterus;* and *Laemobothrion tinnunculi* (Phthiraptera: Laemobothriidae) (González-Acuña et al. 2008) and nematodes, cestodes, and trematodes (Gonzáles-Acuña et al. 2011) in *F. sparverius*.

Conservation and legislation. The only species of falcons in Chile which are considered to warrant conservation priority are *P. albogularis* and *P. australis* (Pavéz 2004, Trejo 2007). However, the mechanisms and processes that affect their population have not been identified. Population size of *F. sparverius* and *M. chimango* in San Carlos de Apoquindo in the Andean foothills of Santiago has decreased over time (Pavéz et al. 2010). These species, along with *F. peregrinus*, are at risk for population decrease due to anthropogenic factors (Díaz and Armesto 2003), including accidents such as electrocution on high-voltage lines (González et al. 2014). Tala and Iriarte (2004) provide important data regarding legislation and potential threats to falcons.

Study methods and techniques. Studies focusing on study methods and techniques are few. Nevertheless, much information is available on capture and monitoring (Pavéz 2004), diet (Yáñez et al. 1980; Muñoz-Pedreros and Rau 2004), observation and counting techniques (Márquez et al. 2004), and use of baits (Contreras and González 2007).

Environmental education and science outreach. The single paper on this subject (Figueroa 1995) provides a plan for teaching ecology and environmental biology through the use of birds of prey, including *M. chimango* and *F. sparverius* species.

Discussion

The results presented here show that knowledge on falcons in Chile is uneven across species, research topics and administrative regions. Despite the limitations of this type of study, our data have the advantage of directly visualizing gaps in knowledge of specific topics (Bimrose et al. 2005). Previous reviews (e. g. Muñoz-Pedreros and Norambuena 2011, Raimilla et al. 2012) have demonstrated a recent increase in productivity, mostly resulting from the work of dedicated researchers (Bierregaard 1995).

Given that the classification of research topics used were those of Muñoz-Pedreros and Norambuena (2011), it is not surprising that our review finds similar trends in productivity and circulation medium. Comparison to the study by Raimilla et al. (2012) is hampered by the fact that their findings were not reported separately by species and administrative region. Nevertheless, two clear patterns emerge from these two reviews and the present study: productivity has increased considerably during the last 30 years for birds of prey in general and for Falconidae in particular, and peer-reviewed publications are the most frequently-used circulation medium to report study results. These patterns are not exclusive to these groups but represent a general trend in all sciences (Bornmann and Mutz 2015).

Our review shows that the most common research topic in studies of falcons is "Faunistics, Diversity, and Abundance" and that *M. chimango* is the most frequent study species. In contrast, Raimilla et al. (2012) found that, studies focusing on "diet" were the most common study subject and *F. sparverius* was the most commonly studied species of falcon. Population trends in time are hampered by the fact that older studies typically represented reports of the presence of species and provided no data on abundance. In contrast to Raimilla et al. (2012), we found that studies of *M. chimango* outnumbered those of *F. sparverius*. However, in agreement with Raimilla et al. (2012) we found that members of the genus *Phalcoboenus* are poorly covered in the literature, as underscored by the absence of studies on four of the ten study topics.

The concentration of publications on falcons in a small number of regions (Metropolitan Santiago, Araucanía, Los Lagos, and Magallanes) reflects the location of research centers (Raimilla et al. 2012). The same pattern was observed in works that focus on community structure (Jaksic 1985) and continental water birds (Victoriano et al. 2006). There were no studies which report on falcons in the O'Higgins region (central Chile) despite its proximity to the Metropolitan region. The lack of studies may be due to changes in regional administration throughout time (Errázuriz 1998) that may lead to incorrect registry of avifauna near the political-geographic limits. Future studies should focus on poorly studied areas, especially those within a biodiversity hotspot such as Los Ríos and Aysén regions (Arroyo et al. 2008). Our review indicates that some topics remain little studied. Publications on "Study Techniques and Methods" were rare (five citations). We suggest these topics warrant further study because current studies are carried out based on protocols developed for falcons in the northern hemisphere (e.g. Bird and Bildstein 2007) which may not be optimal for research in Chile. The lack of knowledge on the biology of species native to Chile may hamper the application of techniques developed elsewhere for other species. The use of non-suitable techniques may produce biases or errors and perhaps even harm captured individuals (Ford 2003).

Only a single study dealt with "environmental education and divulgation" of falcons (Figueroa 1995). Other works have presented a complete bird of prey education program, but mainly focused on birds of prey in general (e.g. Möler and Muñoz and Pedreros 2004). Nevertheless, both studies illustrate how birds of prey (including falcons) may be used to increase awareness of various environmental problems to a non-specialized audience.

Knowledge on “natural History” is deficient for most species of falcons in Chile. Figueroa (2015) suggested that the lack of knowledge on natural history of *M. chimango* results from historical factors, a shift from field biology to other types of study, difficulties in studying diet, and perhaps changing interests of researchers. These factors may also apply to the study of other species of falcons in Chile.

Conclusions

This review of the state of knowledge on falcons in Chile indicates bias in all assessed categories: research topics are biased towards faunistic data; geographically, with many subsampled or unsampled regions; and in preferred species, with two major researched species. Due to the increase in scientific productivity for Falconidae and birds of prey, especially in recent years, reporting where information is lacking and which regions and species have not been studied is essential to continue the study of this group optimally. Much remains to be done and further research is needed. We hope this work may provide an impetus to fill the historical, ecological, and geographical gaps in knowledge.

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References

Araya B, Millie G (1998) Guía de campo de las aves de Chile. 8va Edición. Editorial Universitaria, Santiago, 406 pp.

Araya B, Millie G, Magnere O (1974) Aves del Parque Nacion al “Vicente Pérez Rosales”. Anales del Museo de Historia Natural de Valparaíso Chile 7: 311–316.

Arroyo M, Marquet P, Marticorena C, Simonetti J, Cavieres L, Squeo F, Rozzi R, Massardo F (2008) El hotspot chileno, prioridad mundial para la conservación. In: Conama (Ed.) Biodiversidad de Chile, Patrimonios y Desafíos. 1ra Edición. Ocho Libros Editores, Santiago, Chile, 90–95.

Barros R (1920) Aves del valle de Nilahue (Segunda parte). Revista Chilena de Historia Natural 24: 43–49.

Barros R (1925) Observaciones ornitológicas relacionadas con la agricultura y la caza. Revista Chilena de Historia Natural 29: 238–279.

Barros R (1937) Aves observadas en Maullín. Revista Chilena de Historia Natural 41: 182–186.

Barros R (1960) El tiuque *Milvago chimango chimango* (Vieillot). Revista Universitaria 44/45: 31–37.

Bibby C, Burgess N, Hill D (1993) Bird Census Techniques. Academic Press, Cambridge, 257 pp.

Bierregaard R (1995) The biology and conservation status of Central and South American Falconiformes: a survey of current knowledge. Bird Conservation International 5: 325–340. https://doi.org/10.1017/S0959270900001076

Biondi L, Bó M (2008) Experimental assessment of problem solving by *Milvago chimango* (Aves: Falconiformes). Journal of Ethology 26: 113–118. https://doi.org/10.1007/s10164-007-0035-2

Bimrose J, Barnes S, Brown J (2005) A systematic literature review of research into carreer Interventions for Higher Education. Institute for Employment Research University of Warwick, Warwick, 77 pp.

Bird D, Bildstein K (2007) Raptor research and management techniques. Institute for Wildlife Research, National Wildlife Federation, Washington DC, 464 pp.

Bornmann L, Mutz R (2015) Growth rates of modern science: A bibliometric analysis based on the number of publications and cited references. Journal of the Association for Information Science and Technology 66(1): 2215–2222. https://doi.org/10.1002/asi.23329

Brooke de L, Hanley S, Laughlin B (1999) The scaling of eye size with body mass in birds. Proceedings of the Royal Society 266: 405–412. https://doi.org/10.1098/rspb.1999.0652

Bullock D (1929a) Aves observadas en los alrededores de Angol. Revista Chilena de Historia Natural 33: 171–211.

Bullock D (1929b) Aves de los pinares de Nahuelbuta. Revista Chilena de Historia Natural 33: 121–127.

Bullock D (1932) Los nombres científicos de Molina. Revista Chilena de Historia Natural 36: 113–117

Bullock D (1938) Aves observadas en la Región de Toltén. Revista Chilena de Historia Natural 42: 105–114.

Bullock D (1949) Sobre algunas aves norteamericanas en Chile. Boletín de la Sociedad de Biología de Concepción 24: 7–14.

Burt W (1943) Territoriality and home range concepts as applied to mammals. Journal Mammal 24: 346–352. https://doi.org/10.2307/1374834

Cabezas V, Schlatter R (1987) Hábitos y comportamientos alimentarios de *Milvago chimango* Vieillot Aves: Falconidae. Anales del Museo de Historia Natural de Valparaíso Chile 18: 131–141.

Chapman F (1915) Descriptions of New Birds from Colombia, Ecuador, Peru, and Argentina. American Museum Novitates 80: 515–516.

Cody M (1970) Chilean bird distribution. Ecology 51: 455–464. https://doi.org/10.2307/1935380

Collar N (1986) Threatened Raptors of Americas: Work in Progress from the ICBP/IUCN Red Data Book. Bird of Prey Bulletin 3: 13–25.

Contreras P, González M (2007) Respuestas en aves rapaces frente al uso de señuelos acústicos en censos diurnos y nocturnos en el sur de Chile. Gestión Ambiental 14: 79–87.

Cory B (1915) Notes on South American birds, with descriptions of new subespecies. Field Museum of Natural History, Chicago, 48 pp. https://doi.org/10.5962/bhl.title.2570

Cursach J, Rau J (2008) Avifauna presente en dos parques urbanos de la ciudad de Osorno, sur de Chile. Boletín Chileno de Ornitología Chile 14: 98–103.

Cursach J, Suazo C, Rau J, Niklitschek E, Vilugrón J (2014) Observaciones sobre el pingüino de penacho amarillo *Eudyptes c. chrysocome* en isla Gonzalo, Archipiélago Diego Ramírez, Chile. Revista de Biología Marina y Oceanografía 49: 361–366.

Díaz I, Armesto J (2003) La conservación de las aves silvestres en los ambientes urbanos de Santiago. Ambiente y Desarrollo 19: 31–38.

Dickinson EC, Remsen JV Jr (2013) The Howard and Moore complete checklist of the birds of the world. Fourth edition, vol 1: Non-passerines. Aves Press, London, 461 pp.

Drouilly P (1968) Clave de identificación de los Falconiformes de Chile. Noticiario Mensual Museo de Historia Natural 12: 3–10.

Elgueta E, Reid S, Pliscoff P, Méndez M, Núnez J, Smith-Ramírez C (2006) Catastro de vertebrados terrestres y análisis en seis hábitats presentes en la Reserva Nacional Futaleufú, Provincia de Palena, X Región, Chile. Gayana 70: 195–205. https://doi.org/10.4067/s0717-65382006000200006

Ellis D, Glinski R (1980) Some unusual records for the Peregrine and Pallid falcons in South America. Condor 82: 350–351. https://doi.org/10.2307/1367410

Ellis D, Sabo B, Fackler J, Millsap B (2002) Prey of the peregrine falcon (*Falco peregrinus cassini*) in southern Argentina and Chile. Journal of Raptor Research 36: 315–320.

Estades C (1997) Bird habitat relationships in a vegetational gradient in the Andes of central Chile. Cóndor 99: 719–727. https://doi.org/10.2307/1370483

Errázuriz A (1998) Manual de Geografía de Chile. Editorial Andrés Bello, Santiago.

Estrada-Peña A, Venzal J, González-Acuña D, Guglielmone A (2003) *Argas (Persicargas) keiransi* n. sp. (Acari: Argasidae), a parasite of the Chimango, *Milvago c. chimango* (Aves: Falconiformes) in Chile. Morphology Systematics and Evolution 40: 766–769.

Figueroa R (2015) El rapaz olvidado – ¿Por qué hay tan pocos estudios sobre la historia natural y ecología básica del tiuque (*Milvago chimango*) en Chile? Boletin Chileno de Ornitología 21(1–2): 103–118.

Figueroa R, Alvarado S, Corales E, González-Acuña D, Schlatter R, Martínez D (2015) Los Búhos de Chile. In: Enríquez P (Ed.) Los búhos Neotropicales, Diversidad y Conservación. El Colegio de la Frontera Sur (ECOSUR), San Cristóbal de las Casas, Chiapas, México. Primera Edición, 173–273.

Figueroa R, Corales E (2002) Winter diet of the American Kestrel (*Falco sparverius*) in the forested Chilean Patagonia, and its relation to the availability of prey. International Hawkwatcher 5: 7–14.

Figueroa R, Corales E (2005) Aplomado Falcon (*Falco femoralis*) in an agricultural area of araucanía, southern Chile. Journal of Raptor Research 39: 55–60.

Figueroa R, Orellana A, Corales E (2004) Notes on a range expansion and summer diet of the mountain Caracara in the Andes of South-Central Chile. Journal of Raptor Research 28(3): 290–292.

Figueroa R, Corales E, Cerda J, Saldivia H (2000a) Roedores, rapaces y carnívoros de Aysén. Servicio Agrícola y Ganadero, Gobierno Regional de Aysén, 195 pp.

Figueroa R, Bravo C, Corales E, López R, Alvarado S (2000b) Avifauna del Santuario de la Naturaleza Los Huemules del Niblinto, Región del Bío Bío, Chile. Boletín Chileno de Ornitología 7: 2–12.

Ford S (2003) Avian Care and Handling at the Alaska Raptor Center. Reference materials for volunteers in the performance of husbandry, bird training, and basic medical care. Alaska Raptor Center, 132 pp.

Forrester D, Foster G, Morrison J (2001) *Leucocytozoon toddi* and *Haemoproteus tinnunculi* (Protozoa: Haemosporina) in the chimango caracara (*Milvago chimango*) in southern Chile. Memorias do Instituto Oswaldo Cruz 96: 1023–1024.

Fuchs J, Johnson J, Mindell D (2012) Molecular systematic of the caracaras and allies (Falconidae: Polyborinae) inferred from mitochondrial and nuclear sequence data. Ibis 154: 520–532. https://doi.org/10.1111/j.1474-919X.2012.01222.x

Fuchs J, Johnson JA, Mindell DP (2015) Rapid diversification of falcons (Aves: Falconidae) due to expansion of open habitats in the Late Miocene. Molecular Phylogenetics and Evolution 82: 166–182. https://doi.org/10.1016/j.ympev.2014.08.010

Gigoux E (1928) Aves de la quebrada del León y alrededores. Revista Chilena de Historia Natural 32: 144–148.

González G, Ossa G, Sánchez L, Silva R (2014) Medidas de mitigación de impactos en aves silvestres y murciélagos. Análisis de Información encargado por el SAG (Servicio Agrícola y Ganadero), Ministerio del Medio Ambiente, Santiago, 984 pp.

González-Acuña D, Ardiles K, Figueroa R, Barrientos C, González P, Moreno L, Cicchin A (2008) Lice of Chilean diurnal raptors. Journal of Raptor Research 42: 281–286. https://doi.org/10.3356/JRR-07-69.1

González-Acuña D, Lohse E, Cicchino A, Mironov S, Figueroa R, Ardiles K, Kinsella M (2011) Parasites of the American Kestrel *Falco sparverius* in south-Central Chile. Journal of Raptor Research 45: 188–193. https://doi.org/10.3356/JRR-10-68.1

Goodall J, Johnson A, Philippi R (1951) Las aves de Chile, su conocimiento y sus costumbres. Vol. 2. Platt Establecimientos Gráficos S. A, Buenos Aires, Argentina, 445 pp.

Hellmayr C (1932) Birds of Chile. Field Museum of Natural History. Publications 308 (Zoological Series) 19: 1–472.

Housse R (1934) Monografía del tiuque. Revista Chilena de Historia Natural 38: 49–53.

Housse R (1935) Monografía del cernícalo *Cerchneis sparveria cinnamemina* (Swainson). Revista Chilena de Historia Natural 39: 59–63.

Housse R (1936a) Monografía del traro *Polyborus plancus plancus* (Miller). Revista Chilena de Historia Natural 40: 19–26.

Housse R (1936b) Avifauna de la Isla Santa María. Revista Chilena de Historia Natural 40: 63–69.

Housse R (1937) El tiuque Cordillerano, *Phalcoboenus megalopterus*. Revista Chilena de Historia Natural 41: 131–134.

Imberti S (2005) Distribución otoñal de aves marinas y terrestres en los canales Chilenos. Anales del Instituto de la Patagonia 33: 21–30.

Jaffuel F, Pirion A (1927) Aves observadas en el valle de Marga-Marga. Revista Chilena de Historia Natural 31: 102–115.

Jaksic F (1986) Predation upon small mammals in shrublands and grasslands of southern South America: ecological correlates and presumable consequences. Revista Chilena de Historia Natural 59: 209–221.

Jaksic F, Feinsinger P (1991) Bird assemblages in temperate forests of North and South America: a comparison of diversity, dynamics, guild structure and resource use. Revista Chilena de Historia Natural 64: 491–510.

Jaksic FM, Lazo I (1999) Response of a bird assemblage in semiarid Chile to the 1997–1998 El Niño. Wilson Bulletin 111: 527–535.

Jaksic F, Simonetti J (1987) Predator/prey relationships among terrestrial vertebrates: an exhaustive review of studies conducted in southern South America. Revista Chilena de Historia Natural 60: 221–244.

Jaksic F, Ostfeld R (1983) Numerical and behavioral estimates of predation upon rabbits in Mediterranean type shrublands: a paradoxical case. Revista Chilena de Historia Natural 56: 39–49.

Jaksic F, Greene H, Schwenk K, Seib R (1982) Predation upon reptiles in Mediterranean habitats of Chile, Spain and California: a comparative analysis. Oecologia 53: 152–159. https://doi.org/10.1007/BF00545658

Jaksic F, Iriarte J, Jiménez J (2002) The raptors of Torres del Paine National Park: species accounts, diversity, and niche relationships. Revista Chilena de Historia Natural 75: 449–461. https://doi.org/10.4067/S0716-078X2002000200014

Jaksic F, Jiménez J, Castro S, Feinsinger P (1992) Numerical and functional response of predators to a long-term decline in mammalian prey at a semiarid Neotropical site. Oecologia 89: 90–101. https://doi.org/10.1007/BF00319020

Jaksic F, Feinsinger P, Jiménez J (1993) A long-term study of the dynamics of guild structure among predatory vertebrates at a semi-arid Neotropical site. Oikos 67: 87–96. https://doi.org/10.2307/3545099

Jaksic F, Feinsinger P, Jiménez J (1996) Ecological redundancy and long-term dynamics of vertebrate predators in semiarid Chile. Conservation Biology 10: 252–262. https://doi.org/10.1046/j.1523-1739.1996.10010252.x

Jaksic F, Pavéz E, Jiménez J, Torres-Mura J (2001) The conservation status of raptor in the Metropolitan Region, Chile. Journal of Raptor Research 35: 151–158.

Jiménez J (1993) Notes of the diet of the Aplomado falcon (*Falco femoralis*) in northcentral Chile. Journal of Raptor Research 27: 161–163.

Keith A (1970) Bird Observation from Tierra del Fuego. The Condor 72(3): 361–363. https://doi.org/10.2307/1366015

Kleinschmidt O (1929) *Falco kreyenborgi*. Falco 3: 33–35.

Larraín T (1939) Sobre las aves de rapiña observadas en la hacienda "San Jerónimo", zona de Casablanca, vecina la mar, provincia de Valparaíso. Revista Chilena de Historia Natural, 43: 116–123.

Lobos G, Bobdilla P, Alzamora A, Thomson R (2011) Patrón de actividad y abundancia de aves en un relleno sanitario de Chile central. Revista Chilena de Historia Natural 84: 107–113. https://doi.org/10.4067/S0716-078X2011000100008

Marín M, Kusch A, Oehler D, Drieschman S (2006) Distribution, breeding and status of the striated Caracara *Phalcoboenus australis* (Gmelin, 1788) in southern Chile. Anales del Instituto de la Patagonia (Chile) 34: 65–74.

Markham B (1970) Reconocimiento faunístico del área de los fiordos Toro y Cóndor, Isla Riesco, Magallanes. Anales del Instituto de la Patagonia Chile 11: 41–59.

Márquez C, Sánchez I, Rau J (2004) Técnicas de observación y estimación de abundancia de aves rapaces. In: Muñoz-Pedreros A, Rau, Yáñez J (Eds) Aves Rapaces de Chile. CEA Ediciones, Valdivia, 253–264.

Marquet P, Bozinovic F, Bradshaw G, Cornelius C, Gonzalez H, Gutiérrez J, Hajek E, Lagos J, Lopez-Cortez F, Núñez L, Rosello E, Santoro C, Samaniego H, Standen V, Torres-Mura J, Jaksic F (1998) Los ecosistemas del desierto de Atacama y área andina adyacente en el norte de Chile. Revista Chilena de Historia Natural 71: 593–617.

McNutt J (1981) Selección de presa y comportamiento de caza del Halcón peregrino (*Falco peregrinus*) en Magallanes y Tierra del Fuego. Anales del Instituto de la Patagonia 12: 221–228.

McNutt J (1984) A Peregrine falcon polymorph: observation of the reproductive behavior of *Falco kreyenborgi*. The Condor 86: 378–382. https://doi.org/10.2307/1366810

Mella J (2002) Dieta del Cernícalo *Falco sparverius* y del Tucúquere *Bubo magellanicus* en un ambiente cordillerano de Chile central. Boletín Chileno de Ornitología 9: 34–37.

Mella J (2005) Cambios estacionales en la avifauna del Monumento Natural El Morado, cordillera de Santiago. Boletín Chileno de Ornitología 11: 2–10.

Méndez P, Curti M, Herrera de Montuto K, Benedetti A (2006) Las aves Rapaces. Guía Didáctica de Educación Ambiental. The Peregrine Fund Editorial, Panamá, 124 pp.

Mey E, González-Acuña D (2000) A new genus and species of Ichnocera (Insecta, Phthiraptera) of Chimango Caracara, *Milvago chimango* from Chile with annotated checklist off chewing lice parasitizing caracaras (Aves, Falconiformes, Falconidae). Rudolstäter Naturhistoriche Schriftent 10: 59–73.

Millie W (1938) Las aves del valle del Huasco y sus alrededores (Prov. de Atacama). Revista Chilena de Historia Natural 42: 181–205.

Moore E (1916) Excursión a la Península de Taitao. Boletín del Museo Nacional de Chile 9: 143–171.

Morrison J, Phillips L (2000) Nesting habitat and success of the *Chimango Caracara* in southern Chile. Wilson Bulletin 112: 225–232. https://doi.org/10.1676/0043-5643(2000)112[0225:NHASOT]2.0.CO;2

Muñoz-Pedreros A, Norambuena H (2011) Dos siglos de conocimiento de las aves rapaces de Chile (1810–2010). Gestión Ambiental 21: 69–93.

Muñoz-Pedreros A, Rau J (2004) Estudio de egagrópilas en aves rapaces. In: Muñoz-Pedreros A, Rau J, Yáñez J (Eds) Aves Rapaces de Chile. CEA Ediciones, Valdivia.

Muñoz-Pedreros A, Rau J, Yáñez J (2004) Aves Rapaces de Chile. CEA Ediciones. Valdivia.

Núñez H, Yáñez J (1981) Alimentación del Tiuque *Milvago chimango* (Vieillot) (Aves: Falconiformes). Noticiario Mensual del Museo Nacional de Historia Natural Chile 25: 5–9.

Núñez H, Sallaberry M, Vergara R, Yáñez J (1982) Alimentación anual de *Milvago chimango* (Vieillot) (Aves: Falconiformes). Boletín Museo Nacional de Historia Natural Chile 39: 125–130.

Pavéz E (2004) Descripción de las aves rapaces chilenas. In: Muñoz-Pedreros A, Rau J, Yáñez J (Eds) Aves Rapaces de Chile. CEA Ediciones, Valdivia, 29–104.

Pavéz E, Lobos G, Jaksic F (2010) Cambios de largo plazo en el paisaje y los ensambles de micromamíferos y rapaces en Chile central. Revista Chilena de Historia Natural 83: 99–111.

Philippi R (1937) Aves de la región de Zapallar. Revista Chilena de Historia Natural 41: 28–38.

Raimilla V, Rau J, Muñoz-Pedreros A (2012) Estado de arte del conocimiento de las aves rapaces de Chile: Situación actual y proyecciones futuras. Revista Chilena de Historia Natural 85: 469–480. https://doi.org/10.4067/S0716-078X2012000400009

Quijada B (1917) La ornitología chilena en el diccionario de la lengua castellana. Boletín del Museo Nacional de Chile 10: 5–27.

Raimilla V, Suazo C, Robertson G, Rau J (2014) Observations suggesting cooperative breeding by Striated Caracaras (*Phalcoboenus australis*). Journal Raptor Research 48: 189–191. https://doi.org/10.3356/JRR-12-49.1

Rau J, Jaksic F (2004) Diversidad de las aves rapaces de Chile. In: Muñoz-Pedreros A, Rau J, Yáñez J (Eds) Aves Rapaces de Chile. CEA Ediciones, Valdivia, 121–128.

Reynolds P (1934) Apuntes sobre aves de Tierra del Fuego. El Hornero 5: 339–353.

Rottmann J (1972) Algunas aves silvestres de los valles agrícolas inferiores a 1.000 m de altitud en el Departamento de Arica. IDESIA Chile 2: 59–63.

San Martín J, Brevis I, Rubilar C, Krone O, Gonzalez-Acuña D (2006) Parasitismo gastrointestinal en tiuque común *Milvago chimango chimango* (Vieillot, 1816) (Aves, Falconidae) en la zona de Ñuble, Chile. Parasitología Latinoamericana 61: 63–68. https://doi.org/10.4067/S0717-77122006000100009

Sazima I, Olmos F (2009) The Chimango Caracara (*Milvago chimango*), an additional fisher among Caracarini falcons. Biota Neotropica Brasil 9: 403–405. https://doi.org/10.1590/S1676-06032009000300036

Schlatter R (1976) Aves observadas en el sector del Lago Riñihue, provincia de Valdivia, con alcances sobre su ecología. Boletín de la Sociedad de Biología de Concepción Chile 50: 133–143.

Seguel M, Moroni M, Gómez M, Hernández C, Paredes E (2012) Bacterial meningoencephalitis in a free Chimango Caracara (*Milvago chimango temucoensis*). Brazilian Journal of Veterinary Pathology 5: 16–19.

Simeone A, Oviedo E, Bernal M, Flores M (2008) Las aves del Humedal de Mantagua: Riqueza de especies, amenazas y necesidades de conservación. Boletín Chileno de Ornitología 14: 22–35.

Simeone A, Valencia J, Schlatter R, Lanfranco D, Ide S (1997) Depredación de aves sobre larvas de *Rhyacionia buoliana* en plantaciones jóvenes de *Pinus radiata*. Bosque 182: 67–75. https://doi.org/10.4206/bosque.1997.v18n2-07

Tala C, Iriarte A (2004) Conservación y Legislación. In: Muñoz-Pedreros A, Rau J, Yáñez J (Eds) Aves Rapaces de Chile. CEA Ediciones. Valdivia, 281–294.

Teneb E, Gomez H, Cárcamo J (2013) Cronotipos en aves del Humedal de tres Puentes, Punta Arenas, Magallanes, Chile. Anales del Instituto de la Patagonia (Chile) 41: 61–69. https://doi.org/10.4067/S0718-686X2013000100005

Torres D (1970) Cernícalo *Falco sparverius fernandensis* (Chapman 1915) en Isla Alejandro Selkirk. Noticiario Mensual del Museo Nacional de Historia Natural Chile 14: 10.

Torres-Mura J (2004) Lista de aves rapaces de Chile. In: Muñoz-Pedreros A, Rau J, Yáñez J (Eds) Aves Rapaces de Chile. CEA Ediciones. Valdivia, 11–14.

Trejo A (2007) Identificación de especies y áreas prioritarias para el estudio de la reproducción de aves rapaces de Argentina. Hornero 22: 85–96.

Venegas C (1981) Aves de las Islas Wollaston y Bayly, Archipiélago del Cabo de Hornos. Anales del Instituto de la Patagonia Chile 12: 213–219.

Vázquez A, Romero H (2007) Efectos ambientales de la Expansión Urbana de Alta y Baja Densidad en el Gran Santiago Durante las últimas tres Décadas. Anales de la Sociedad Chilena de Ciencias Geográficas 2007: 232–236.

Victoriano P, González A, Schlatter R (2006) Estado de conocimiento de las aves de aguas continentales de Chile. Gayana 70: 140–162. https://doi.org/10.4067/s0717-65382006000100019

Vuilleumier F (1985) Forest birds of Patagonia: ecological geography, speciation, endemism and faunal history. In: Buckley P, Foster M, Morton E, Riedely R, Buckley F (Eds) Neotropical Ornithology. Ornithological Monographs 36: 255–304. https://doi.org/10.2307/40168287

White C, Olsen P, Kiff L (1994) Family Falconidae (Falcons and Caracaras). In: del Hoyo J, Elliott A, Sargatal J (Eds) Handbook of the Birds of the World, Vol. 2. Lynx Ediciones, Barcelona, 216–275.

Yáñez JL, Núñez H, Jaksic FM (1980) Diet and weight of American Kestrels in central Chile. Auk 97: 629–631.

Yáñez JL, Núñez H, Jaksic FM (1982) Food habits and weight of Chimango Caracara in central Chile. Auk 99: 170–171. https://doi.org/10.2307/4086036