

The nomenclature of the Recent Pentastomida (Crustacea), with a list of species and available names

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Abstract The taxonomy of the Recent members of the crustacean subclass Pentastomida is based on nine accepted family names derived from 12 available names, 24 generic names derived from 37 available names (plus two incorrect subsequent spellings and one *nomen nudum*) and 124 accepted species names derived from 183 available names of which six remain *incertae sedis* as to their generic assignment. Compilation of this list has revealed that existing catalogues have included misspellings, wrong attributions and dates of the authors of taxa, and incorrectly nominated type-species. These are corrected here with reference to the original descriptions and diagnoses. Notably, all families except one were erected much earlier and by authors other than Fain (1961), who was credited by Martin & Davis (2001) and other authors before and afterwards with seven of the nine families they recognised. Other significant taxonomic anomalies are revealed. Raillietiellidae Sambon, 1922 is a senior synonym of Cephalobaenidae Heymons, 1922, the name in popular usage for the family including *Cephalobaena* Heymons, 1922 and *Raillietiella* Sambon, in Vaney & Sambon, 1910; here the two genera are placed in separate families following Almeida & Christoffersen (1999). *Heymonsia* Hett, 1934, considered a junior synonym of *Raillietiella*, is a *nomen*

nudum. *Raillietiella geckonis* (Diesing, 1850) is a potential senior synonym of several SE Asian species of this genus. *Raillietiella frenata* Ali, Riley & Self, 1981 is a widely used species name but is a subjective junior synonym of *R. hebitihamata* Self & Kuntz, 1960 according to its own authors. Morphological and molecular evidence suggest that *R. indica* Gedoelst, 1921 is a subjective senior synonym of both species. The priority of Linguatulidae Haldeman, 1851 over Linguatulida Vogt, 1851, erected as a family in the same year, is established by applying the First Reviser rule. *Linguatula serrata* Frölich, 1789 is herein selected as the type-species of *Prionoderma*, making it an objective synonym of *Linguatula* Frölich, 1789. The priority of *L. serrata* over *Taenia rhinaris* Meyer, 1789 and *T. capraea* Abildgaard, 1789, all published in the same year, is established by applying the First Reviser rule. The purported synonymy of *Netrorhynchus* Zenker, 1827, also misspelled *Nettorhynchus*, with *Armillifer* Sambon, 1922 would seem to be ill-founded and without popular support. *Armillifer australis* Heymons, 1935, published as a subspecies of *A. moniliformis* (Diesing, 1836), is both a senior synonym and a homonym of *A. australis* Riley & Self, 1981. Humboldt (1812) is confirmed as the author of *Porocephalus* Humboldt, 1812 and *P. crotali* Humboldt, 1812. Pentastomidae Shipley, 1909 is an older family name than its subjective synonym Porocephalinae Sambon, 1922, but prevailing usage allows the latter to be retained as a family name. *Cayerina mirabilis* Kishida, 1927 is a genus and species from a

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Japanese frog that has not appeared in the more recent pentastome literature. *Sebekia minor* (Wedl, 1861) is an objective senior synonym of the more widely used *S. wedli* Giglioli, in Sambon, 1922. The importance of the many junior synonyms will become evident should refined morphological and molecular evidence reveal cryptic species or greater host-specificity than presently recognised.

Introduction

During the course of preparation of a checklist of the pentastomes of Australia many nomenclatural errors became apparent. These errors included misspellings, wrong attributions and dates of the authors of taxa, and incorrectly nominated type-species, as well as taxonomic irregularities. These errors extend to authoritative revisions and lists, such as Self's (1969) catalogue of species. Martin & Davis' (2001) list of crustacean families and higher taxa, and more recent web-based catalogues (WoRMS, EoL, ZipcodeZoo, Wikipedia, etc) have largely followed Self's taxonomy. Ah Yong et al. (2011) repeated Martin & Davis' taxonomy but omitted two families. While such errors have little impact on our understanding of the biology of these parasites, getting their names right is important for comparing one study with another. This becomes more important as new methods (e.g. Kelehear et al., 2011) demonstrate that our morphological taxonomy is not as reliable as might be believed. The consequences could be the synonymy of accepted species under one name, or the opposite, division of apparently widespread species into several cryptic species if host-specificity is greater than now appreciated. Knowing what names are available and which are the most senior becomes critical in these situations.

Here, a revised classification and species list are presented. The author makes no pretence of having a knowledge of the taxonomy or biology of Pentastomida: this contribution is simply an attempt to correct past nomenclatural errors. The work is not a taxonomic revision and most synonymies have been followed. Every effort has been made to check on the spellings of names, dates and authorities with reference to the original literature, a feat that has been made possible only now with access to old literature through the Biodiversity Heritage Library <http://www.biodiversitylibrary.org/> and similar archives. Much of

the more modern literature is accessible on-line. A bibliography in Endnote[®], including URLs and PDFs, is available on request from the author.

For the Australian fauna these errors have been corrected in the Australian Fauna Directory (Poore & Spratt, 2012), but they have wider implications for the Pentastomida world-wide. This paper draws on the Australian checklist and the several lists of taxa published in regular journals and on the web (e.g. <http://en.wikipedia.org/wiki/Pentastomida> and http://zipcodezoo.com/Key/Animalia/Pentastomida_Subclass.asp).

Much of our understanding of the biology of the Pentastomida can be attributed to the studies of the Berlin zoologist Richard Heymons (1867–1943), whose work was reviewed by Röhlig et al. (2010). An early bibliography of pentastome literature (Hill, 1948) was superseded by another (Self, 1969). Self's publications in the 1960s–1980s and those of John Riley (1970s–2004) also contributed significantly to pentastome systematics and biology. Since these dates, the veterinary and medical literature on pentastome-related diseases in domestic animals and humans has continued to grow.

Pentastomes, also known as tongue worms, are, as adults, obligatory parasites of amphibians, turtles, snakes, lizards, birds and mammals (such as dogs, antelopes, reindeer calves and marsupials). These same host taxa and some fish, plus at least one insect species, may also host the larvae. Adults inhabit the respiratory tracts (lungs, nasal passages and tracheae) of their hosts. Among the mammal species infected by pentastomes are humans, the resultant disease being known as pentastomiasis or porocephalosis (in humans—Drabick, 1987; in pets—Paré, 2008). For this reason, and because they are frequently encountered parasites, the biology and life-cycles are well understood.

The systematic position of pentastomes was for a long time enigmatic (Waloszek et al., 2006; Jenner & Littlewood, 2008; Sanders & Lee, 2010), the group having a mixture of annelid and arthropod features (Nicoli, 1963; Self 1969; Haffner, 1977; Haugerud, 1989). They were long recognised as a separate phylum variously related to platyhelminths, nematodes, onychophorans or arthropods. Among arthropods, pentastomes have been related erroneously to mites or myriapods. Van Beneden (1849) was the first to propose that they are crustaceans, but his views

were not widely accepted until studies of the structure of the spermatozoa provided support, more specifically that they are related to the Branchiura (Wingstrand, 1972; Riley et al., 1978; Storch & Jamieson, 1992; Zrzavý, 2001). This relationship has been supported by ribosomal and mitochondrial DNA molecular analyses (Abele et al., 1989; Spears & Abele, 1998; Lavrov et al., 2004; Møller et al., 2008; Sanders & Lee, 2010) and by larval morphology and cuticular ultrastructure (Karuppaswamy, 1977). The position of the Branchiura-Pentastomida clade (called by some, Ichthyostraca), currently within the Maxillopoda, may be more removed from core Crustacea than the present classification suggests (Giribet et al., 2005; Sanders & Lee, 2010) and the question of their exact position remains open.

Alternative phylogenetic analyses, of morphology, seem to indicate that the Pentastomida is a transitional group between the Arthropoda and groups such as the Nematoda and Nematomorpha, a view supported by some palaeontologists. Upper Cambrian fossils have been discovered that are similar to modern pentastome adults and larvae (Walossek & Müller, 1994; Walossek et al., 1994; Waloszek et al., 2006; Castellani et al., 2011). These authors argued, on the basis of the fossils and modern external morphology, internal anatomy and ontogenetic development, that the evidence does not support a relationship between crustaceans and pentastomes. They have been supported by morphological analyses of modern taxa by Almeida and co-authors (Almeida & Christoffersen, 1999; Almeida et al., 2008a). The value of relying strictly on the morphology of animals that are entirely endoparasitic, and somewhat reduced as a consequence, is limited. The fossils predate the origin of land vertebrates, raising the question of what groups they may have parasitised.

The following list of taxa includes all available names that could be tracked through the extensive literature, but not all genus-species combinations. The classification used and synonymies given may be disputed by some, but seems a workable compromise. In most classifications, two orders are recognised: the Cephalobaenida Heymons, 1935 and the Porocephalida Heymons, 1935. In an alternative treatment, the taxon is divided into four with two additional orders, the Reighardiida Almeida & Christoffersen, 1999 and the Raillietiellida Almeida & Christoffersen, 1999 (see Almeida & Christoffersen, 1999). Neither of these

orders has received wide acceptance, except by Röhlig et al. (2010). Waloszek et al. (2006) proposed the taxon name Eupentastomida Waloszek, Repetski & Maas, 2006 for the ‘crown’ pentastomes, excluding fossil taxa.

The lower taxonomy of the Pentastomida is based on nine accepted family names, which are derived from 12 available family names, 24 generic names derived from 37 available names (plus two incorrect subsequent spellings and one *nomen nudum*), and 124 accepted species names derived from 183 available names, of which six remain *incertae sedis* as to their generic assignment. Their spellings have varied and those used here are justified in cases of ambiguity. Each name is attributed to an authority and year of publication (often corrected from those cited in the recent literature) and the page number where the name first appears. For genera the type-species is given. For species and their recognised synonyms the geographical location and host(s) are given of the type, or types if the number was not determined. Place names have been updated, as have host names with reference to world lists available on the web. Distributions are given for species in general terms. Past taxonomic anomalies are explained in *Remarks* and new combinations and synonymies are proposed only where these are unavoidable if the International Code of Zoological Nomenclature of 1999 (ICZN) is to be followed.

All available species names are accounted for, with the exception of six. Two remain *incertae sedis* as to their generic assignment:

***Pentastomum crocidurae* Parona, 1890**, p. 71 (type: Burma, from Southeast Asian shrew *Crocidura fuliginosa*). Sambon (1922b, p. 418) and Heymons (1935, p. 203) could not assign this species to a genus.

***Porocephalus siamensis* Koch, 1906**, p. 278 (type: Thailand, from ‘Siamese cat’). Heymons (1935, p. 203, 251) could not assign this species to a genus and subsequent authors have largely ignored it.

Junker & Boomker (2006) considered three species with very short diagnoses as doubtful species of *Sebekia*:

***Porocephalus joubini* Vaney & Sambon, 1910**, p. 131 (types: Muséum national d’Histoire naturelle, Paris, from *Crocodylus siamensis*). Erroneously spelled *jubini* by some authors.

***Sebekia acuminata* Travassos, 1924**, p. 240 (types: Amazonas, Brazil, from ‘crocodiles’).

***Sebekia samboni* Travassos, 1924**, p. 240 (types: Amazonas, Brazil, from ‘crocodiles’).

To these could be added from a similar host:

***Pentastomum solaris* Tubangui & Masiluñgan, 1936**, p. 401 (type: Palawan, Philippines, from the saltwater crocodile *Crocodylus porosus*).

Subphylum Crustacea Brünnich, 1772

Class Maxillopoda Dahl, 1956

SUBCLASS PENTASTOMIDA Shipley, 1905

Primary synonym: Pentastomida Shipley, 1905, p. 249.

Junior synonym: Linguatulida Claus, 1872, p. 519.

Remarks: The subclass Pentastomida is commonly wrongly attributed to Diesing (1836). Diesing (1836, and not 1835 as given on the journal title page) discussed the genus *Pentastoma* Rudolphi, 1812, but not a higher taxon based on this name. He included the genus in the Acanthotheca, a group of the Nematoidea. Later, Diesing (1850, p. 609) placed the genus in the ‘Subordo II Proctucha’ and ‘Tribus I Taxobothria’. Later still, Diesing (1863, p. 324) included the genus in the ‘Ordo Cephalocotylea, Sectio I Paramecocotylea, Tribus I Aprocta, Subtribus II Trypanorhyncha’, and ‘Familia Hypobothria’. Leuckart (1860), whose early work is commonly referred to, used, like many others, only the common German plural ‘Pentastomen’. Haldeman (1851), responsible for the family Linguatulidae, included them in the Helminthes. The first record of the name Pentastomida as such is by Shipley (1905), who introduced the name without comment. In a later revisionary chapter on the group, Shipley (1909, p. 488) added a footnote stating ‘The animals included in this group are usually called Linguatulidae or Pentastomidae after the two genera ... The familiar name *Pentastoma* may, however, be preserved by incorporating it in the designation of the group.’ Incidentally, no prior or later mention of ‘Pentastomidae’ as a family name could be traced (see Porocephalidae below).

An older name for the taxon, Linguatulida, has fallen out of use. Claus (1872) treated the Linguatulida as an Order of the Arachnoidea and the term was in common use in the 19th Century and even as late as Hill’s (1948) bibliography. Vogt’s (1851) use of Linguatulida as a family name may be viewed as an earlier mention than that of Claus, in the same year as Haldeman’s family Linguatulidae in the Helminthes. Subclass names are not covered by the ICZN and the later name in common usage can prevail.

The ordinal names are attributed to Heymons alone rather than to Heymons & Vitzhum (1935), as for the family names, although ICZN rules do not apply above the family-group level. The solo paper was published before the joint one.

ORDER CEPHALOBAENIDA Heymons, 1935

Primary synonym: Cephalobaenida Heymons, 1935, p. 203.

Family CEPHALOBAENIDAE Heymons, 1922

Primary synonym: Cephalobaenidae Heymons, 1922, p. 161.

Remarks: The Cephalobaenidae have long included two genera, *Cephalobaena* Heymons, 1922 and *Raillietiella* Sambon, in Vaney & Sambon, 1910, and a third added recently. As such, it has been universally known as the Cephalobaenidae even though the subfamily name Raillietiellinae Sambon, 1922 (published 15 June 1922) predates Heymons’ name (27 October 1922). This failure to apply the ICZN Principle of Priority was pointed out by Stunkard & Gandal (1968), who have been ignored. ICZN Article 35.5 allows, under certain conditions, a family name in prevailing usage not to be displaced by an older subfamily name within that family. These conditions are not met as the realisation of the precedence of Raillietiellinae over Cephalobaenidae was made in 1968, well before 1999 when this rule came into effect. Two options present themselves: (1) to acknowledge the priority of Raillietiellidae over Cephalobaenidae for the family containing all three genera, so disturbing conventional usage; or (2) to follow Almeida & Christoffersen (1999), who avoided the issue and recognised two families, the Cephalobaenidae and the Raillietiellidae, each with only its type-genus. *Yeliarella* Spratt, 2010 would appear to belong to the Raillietiellidae. Whatever choice is made, most species (those belonging to *Raillietiella*) must be removed from Cephalobaenidae. Almeida & Christoffersen’s (1999) taxonomy is followed here to a point; they in fact recognised three separate orders for Cephalobaenidae, Raillietiellidae and Reighardiidae, each with a single genus.

Cephalobaena Heymons, 1922

Primary synonym: *Cephalobaena* Heymons, 1922, p. 159.

Type-species: *Cephalobaena tetrapoda* Heymons, 1922 (by original designation).

***Cephalobaena tetrapoda* Heymons, 1922**

Primary synonym: *Cephalobaena tetrapoda* Heymons, 1922, p. 159 (types: Paraguay, from the pitviper *Bothrops alternatus*).

Junior synonym: *Cephalobaena recurvicauda* Motta, 1963(a), p. 13 (types: Paraguay, type-specimens from Instituto Butantan, São Paulo, Brazil, from the rattlesnake *Crotalus durissus terrificus*). Synonymised by Rego (1983).

Distribution: Paraguay, Argentina.

Family RAILLIETIELLIDAE Sambon, 1922

Primary synonym: Raillietiellinae Sambon, 1922(a), p. 190 (as a subfamily of the Linguatulidae).

Remarks: Almeida & Christoffersen (1999) distinguished the two families, the Cephalobaenidae and the Raillietiellidae, each with only its type-genus. *Yeliarella* Spratt, 2010 would appear to belong to the Raillietiellidae. Treating the two as synonymous, as has been the prevailing usage, creates nomenclatural issues that require *Cephalobaena* to be also included in the Raillietiellidae (see discussion under Cephalobaenidae above).

***Raillietiella* Sambon, in Vaney & Sambon, 1910**

Primary synonym: *Raillietiella* Sambon, in Vaney & Sambon, 1910, p. 140.

Type-species: *Porocephalus boulengeri* Vaney & Sambon, 1910, subsequent designation by Sambon, 1922a, p. 191, chosen from three included species.

Junior synonyms: *Mahafaliella* Gretillat, Brygoo & Domergue, 1962, p. 304 (type-species: *Mahafaliella tetrapoda* Gretillat, Brygoo & Domergue, 1962, by original designation). Synonymised by Ali et al. (1985).

Gretillatia Motta, 1965, p. 8 (type-species: *Raillietiella ampanihyensis* Gretillat, Brygoo & Domergue, 1962, by original designation). Synonymised by Ali et al. (1985).

Travassostulida Motta & Gomes, 1968, p. 7 (type-species: *Travassostulida freitasi* Motta & Gomes, 1968, by monotypy). Synonymised by Ali et al. (1984a).

Remarks: Sambon published a long appendix to joint paper (Vaney & Sambon, 1910) in which he revised some taxa and introduced this genus and several species names. Self (1969) incorrectly mentioned *Pentastomum geckonis* Diesing, 1850 as the type-species. *Heymonsia* Hett, 1934, p. 427, was erected as a subgenus of *Raillietiella* with three included species

but without nominated type-species, thereby making it a *nomen nudum* (ICZN Article 67.4.1). Self (1969) synonymised *Heymonsia*, as a genus, with *Raillietiella*.

***Raillietiella aegypti* Ali, Riley & Self, 1982**

Primary synonym: *Raillietiella aegypti* Ali et al., 1982(b), p. 171 (types: northern Egypt, from lizards of the families Scincidae: *Scincus officinalis*, *Chalcides sepsoides*, *Eumeces schneideriis*; and Agamidae: *Agama stellio*, *A. mutabilis*, *Uromastyx aegyptia*).

Distribution: Egypt.

***Raillietiella affinis* Bovien, 1927**

Primary synonym: *Raillietiella affinis* Bovien, 1927, p. 5 (types: Djombang, Java, Indonesia, from the Tokay gecko *Gekko gekko* [Ali et al., 1982b, p. 171]).

Distribution: Indonesia.

***Raillietiella agcoi* Tubangui & Masiluñgan, 1936**

Primary synonym: *Raillietiella agcoi* Tubangui & Masiluñgan, 1936, p. 400 (types: Cabanatuan, Nueva Ecija, Philippines, from the cobra *Naja naja philippinensis*).

Distribution: Philippines (Ali et al., 1982c).

***Raillietiella ampanihyensis* Gretillat, Brygoo & Domergue, 1962**

Primary synonym: *Raillietiella ampanihyensis* Gretillat et al., 1962, p. 296 (types: Madagascar, from the hognose snake *Leioheterodon madagascariensis* and cat-eyed snake *Madagascarophis colubrina*).

Distribution: Madagascar.

***Raillietiella amphiboluri* Mahon, 1954**

Primary synonym: *Raillietiella amphiboluri* Mahon, 1954, p. 509 (types: Australia, type-specimens from London Zoo, from the bearded dragon *Pogona barbata*).

Distribution: New South Wales, Australia (known only from hosts in zoos: Taronga Zoo, Sydney, and London Zoo, UK; not recorded from the wild).

***Raillietiella belohaensis* McAllister, Riley, Freed & Freed, 1993**

Primary synonym: *Raillietiella belohaensis* McAllister et al., 1993, p. 36 (types: Madagascar, from the big-eyed snake *Mimophis mahfalensis*).

Distribution: Madagascar.

***Raillietiella bicaudata* Heymons & Vitzthum, 1935**

Primary synonym: *Raillietiella bicaudata* Heymons & Vitzthum, 1935(b), p. 157 (types: North America, type-specimens from Berlin Aquarium, from the kingsnake *Lampropeltis getula*).

Distribution: North America.

***Raillietiella boulengeri* (Vaney & Sambon, 1910)**

Primary synonym: *Porocephalus boulengeri* Vaney & Sambon, 1910, p. 132 (types: Africa, type-specimens from the Muséum national d'Histoire naturelle, Paris, from the Gaboon viper *Bitis gabonica*, and London Zoo, from the puff adder *Bitis arietans*).

Distribution: Widespread in West Africa (Ali et al., 1982c).

Remarks: *Raillietiella boulengeri* forma *spiralis* Heymons, 1939 (type: Sobat, Sudan, from the striped sand snake *Psammophis sibilans*; Heymons, 1939b, p. 90) is an available subspecies (ICZN Article 45.6.4), a potential junior homonym of *Raillietiella spiralis* Hett, 1924 at the species level.

***Raillietiella bufonis* Ali, Riley & Self, 1982**

Primary synonym: *Raillietiella bufonis* Ali et al., 1982(a), p. 282 (types: Puerto Rico from the Puerto Rican crested toad *Peltophryne* [as *Bufo*] *lemur*).

Distribution: Puerto Rico.

***Raillietiella cartagenensis* Ali, Riley & Self, 1985**

Primary synonym: *Raillietiella cartagenensis* Ali et al., 1985, p. 113 (types: Colombia, from the skink *Gonatodes* sp. and gecko *Hemidactylus* sp.).

Distribution: Colombia.

***Raillietiella chamaeleonis* Gretillat & Brygoo, 1959**

Primary synonym: *Raillietiella chamaeleonis* Gretillat & Brygoo, 1959, p. 113 (types: Madagascar, from the chameleons *Chamaeleo oustaleti* and *C. verrucosus*).

Distribution: Madagascar.

***Raillietiella colubrilineati* (Leuckart, 1860)**

Primary synonym: *Pentastomum colubri lineati* Leuckart, 1860, p. 157 (type: description and figures by Schubärt, 1853, p. 117, locality not stated, from *Coluber lineatus*).

Junior synonym: *Pentastomum colubri* Diesing, 1863, p. 338 (type: description and figures by Schubärt (1853, p. 117, as above).

Distribution: Uncertain; the host, now *Lygophis lineatus*, is known from northern and central-western South America.

Remarks: Leuckart (1860) listed an imperfect animal with unknown characters as ‘*Pent. colubri lineati* Schub.’ Following ICZN Article 11.9.5, the two specific epithets should be combined as one word. Diesing (1863, p. 338) listed *Pentastomum colubri* under ‘*species indescrita*’, also basing the name on the description of Schubärt (1853) and citing material from *Coluber lineatus*. Neither of these authors provided a description, but the names are available

as they rely on Schubärt’s description of a pentastome he identified as *Pentastoma taeniodes* found under the skin and in the muscles of the snake *Colub[er] lineatus*. *Pentastomum colubrilineati* was listed in the synonymy of *R. orientalis* Hett, 1915 by Heymons (1935, p. 209). If this were accepted, *Pentastomum colubrilineati* Leuckart, 1860 would be a senior synonym of *Porocephalus bifurcatus orientalis*, not the other way around. *Raillietiella colubrilineati* is probably from South America, whereas *R. orientalis* is from Asia.

***Raillietiella congolensis* Fain, 1961**

Primary synonym: *Raillietiella congolensis* Fain, 1961, p. 48 (types: ‘Belgian Congo’, from the vine snake *Thelotornis capensis oatesi*).

Distribution: Democratic Republic of the Congo.

Remarks: In tables, Fain (1961) referred to his own ‘présent travail’ as ‘Fain 1960’, although it was published a year later. This species has been listed as published in 1960.

***Raillietiella crotali* Ali, Riley & Self, 1984**

Primary synonym: *Raillietiella crotali* Ali et al., 1984(b), p. 92 (types: Mexico, from the rattlesnake *Crotalus ruber*).

Distribution: Mexico.

***Raillietiella freitasi* (Motta & Gomes, 1968)**

Primary synonym: *Travassostulida freitasi* Motta & Gomes, 1968, p. 7 (types: Fernando de Noronha, Brazil, from the Noronha skink *Trachylepis atlantica* [as *Mabuya punctata*]). Moved to *Raillietiella* by Ali et al. (1984a).

Junior synonyms: *Travassostulida acutiacanthus* Gomes & Motta, 1968, p. 57 (types: Fernando de Noronha, Brazil, from the Noronha skink *Trachylepis atlantica* [as *Mabuya punctata*] and toad *Rhinella schneideri* [as *Bufo paracnemis*]). Synonymised by Rego (1983) as a species of *Cephalobaena*.

Distribution: Fernando de Noronha, Brazil (Ali et al., 1985).

***Raillietiella furcocercum* (Diesing, 1836)**

Primary synonym: *Pentostoma furcocercum* Diesing, 1836, p. 26 (types: Cuyaba, Brazil, from the Rio tropical racer *Mastigodryas bifossatus* [as *Coluber lichtensteini*], ratsnake *Spilotes* sp. and worm lizard *Amphisbaena flavescens*).

Junior synonyms: *Pentastomum bifurcatum* Diesing, 1850, p. 615 (unnecessary replacement name).

Raillietiella gomesi Motta, 1963(b), p. 9 (types: Brazil, type-specimens from the Instituto Butantan, São Paulo,

Brazil, from Wagler's snake *Waglerophis* [as *Xenodon merremii*]. Synonymised by Rego (1983).

Distribution: Central and South America (Ali et al., 1985).

Remarks: Diesing (1850, 1863) replaced his own species name and the replacement was used by Hett (1915) as the parent of two subspecies, *Porocephalus bifurcatus orientalis* Hett, 1915 (now *Raillietiella orientalis*) and *Porocephalus bifurcatus mediterraneus* Hett, 1915 (now *R. mediterranea*). The adjectival specific epithet *furcocerca* has appeared several times in the literature associated with *Raillietiella* even though Diesing's name would appear a neuter noun in apposition to *Pentostoma* and its ending is not required to change.

***Raillietiella geckonis* (Diesing, 1850)**

Primary synonym: *Pentastomum geckonis* Diesing, 1850, p. 617 (type: bibliographic reference to Dujardin's record (1845, p. 309) of specimens from Thailand, from a 'gecko of Siam').

Distribution: Thailand.

Remarks: The species has often been wrongly attributed to Dujardin (1845), who introduced the species simply as 'pentastome du gecko de Siam.' The name remains doubtfully attributable to any known species (Ali et al., 1982b, p. 178) but is a potential senior synonym of several from SE Asia.

***Raillietiella gehyrae* Bovien, 1927**

Primary synonym: *Raillietiella gehyrae* Bovien, 1927, p. 7 (types: Djombang, Java, Indonesia, from the four-clawed gecko *Gehyra mutilata*).

Distribution: Indonesia, Malaysia (Ali et al., 1985).

***Raillietiella gigliolii* Hett, 1924**

Primary synonym: *Raillietiella gigliolii* Hett, 1924, p. 137 (types: South America, type-specimens from London Zoo, from the red worm lizard *Amphisbaena alba*).

Distribution: South America.

***Raillietiella gowrii* Rajalu & Rajendran, 1970**

Primary synonym: *Raillietiella gowrii* Rajalu & Rajendran, 1970, p. 130 (types: India, from the Asiatic watersnake *Xenochrophis piscator*).

Distribution: India.

Remarks: This is possibly a junior synonym of *R. orientalis* Hett, 1915 (see Ali et al., 1985).

***Raillietiella hebitihamata* Self & Kuntz, 1960**

Primary synonym: *Raillietiella hebitihamata* Self & Kuntz, 1960, p. 885 (types: Lan Yü (Lanyu) Island, Taiwan, from the Asian house gecko *Hemidactylus frenatus*).

Junior synonym: *Raillietiella frenatus* [sic] Ali, Riley & Self, 1981, p. 199 (types: Kuching, Malaysia, from the Asian house gecko *Hemidactylus frenatus*).

Distribution: Southeast Asia; Pacific islands; Christmas Island and Northern Territory, Australia (possibly introduced in several places).

Remarks: The specific name *frenatus* is indubitably an adjective and should be spelled *frenata* in association with the feminine genus *Raillietiella*. This species presents another problem. At the same time as they described *R. frenata*, Ali et al. (1981) explicitly stated 'Other specimens, previously described as *Raillietiella hebitihamata* (= *R. hemidactyli*) by Self & Kuntz (1960) (Table II), from small lizards (including *H. frenatus*), are also included within this taxon'. They included the type-specimens of *R. hebitihamata* in the material of their new species, thereby automatically relegating the latter to a subjective junior synonym of *R. hebitihamata*! *Raillietiella frenata* is a widely used species name in this genus but would appear to be a junior synonym—see discussion under *R. indica* Gedoelst, 1921. It has been recorded from several lizard and amphibian hosts as both *R. frenatus* [sic] and *R. indica* (see Ali et al., 1985; Kelehear et al., 2011; Poore & Spratt, 2012). *Raillietiella hebitihamata* had been previously placed in synonymy with *R. hemidactyli* Hett, 1934 by Self & Garcia-Diaz (1961), but the latter authors' view has been superseded.

***Raillietiella hemidactyli* Hett, 1934**

Primary synonym: *Raillietiella (Heymonsia) hemidactyli* Hett, 1934, p. 428 (types: Burma, from the gecko *Hemidactylus gleadovi* and changeable lizard *Calotes versicolor*).

Distribution: Southeast Asia and Africa (Fain, 1961; Ali et al., 1985).

***Raillietiella indica* Gedoelst, 1921**

Primary synonym: *Raillietiella indica* Gedoelst, 1921, p. 25 (type: ?India, type-specimens from Indian Museum, Calcutta, from the Asian common toad *Duttaphrynus* [as *Bufo*] *melanostictus*).

Distribution: Southeast Asia (Ali et al., 1982a).

Remarks: Kelehear et al. (2011) reported that specimens from Australian cane toads identifiable on the basis of morphology as *R. indica* are allometric variants of what they called *R. frenatus* [sic]. This conclusion was supported by molecular evidence. They reported this species as *R. frenata*, as had all previously published Australian records from the Asian house gecko and the cane toad. However,

R. hebitihamata is a subjective senior synonym of *R. frenata* (see above). Pentastomes from the cane toad in Hawaii have been identified by Barton & Riley (2004) as *R. indica*. If only one species of pentastome is hosted by these two widely-introduced species, the cane toad and the Asian house gecko, and it is the same as the species from the Asian common toad, *Raillietiella indica* would have seniority over both *R. frenata* and *R. hebitihamata*.

***Raillietiella kochi* Heymons, 1926**

Primary synonym: Raillietiella kochi Heymons, 1926(a), p. 45 (type: ‘Abyssinia’, from the lizard *Varanus ocellatus*).

Junior synonym: Raillietiella shipleyi Heymons, 1926(a), p. 46 (type: Africa, from *Varanus ?ocellatus*). Synonymised by Ali et al. (1985).

Distribution: Africa.

***Raillietiella mabuiaie* Heymons, 1922**

Primary synonym: Raillietiella mabuiaie Heymons, 1922, p. 157 (types: Namibia, from the western rock skink *Trachylepis sulcata*).

Distribution: Africa.

***Raillietiella maculilabris* Ali, Riley & Self, 1984**

Primary synonym: Raillietiella maculilabris Ali et al., 1984(a), p. 149 (types: Tanzania, from the speckle-lipped mabuya *Trachylepis maculilabris* and African striped skink *T. striata*).

Distribution: Tanzania.

***Raillietiella maculatus* Rao & Hiregaudar, 1962**

Primary synonym: Raillietiella maculatus Rao & Hiregaudar, 1962, p. 457 (types: Mumbai, India, from the geckos *Hemidactylus maculatus* and *H. leschenaultii*, and keeled Indian mabuya *Eutropis carinata* [as *Maubia carinata*]).

Distribution: India.

***Raillietiella madagascariensis* McAllister, Riley, Freed & Freed, 1993**

Primary synonym: Raillietiella madagascariensis McAllister et al., 1993, p. 40 (types: Madagascar, from the colubrid snake *Lophidium vaillanti*).

Distribution: Madagascar.

***Raillietiella mediterranea* (Hett, 1915)**

Primary synonym: Porocephalus bifurcatus var. *mediterraneus* Hett, 1915, p. 121 (type: Europe, type-specimens from London Zoo, from the Balkan whip-snake *Hierophis gemonensis*).

Distribution: Europe.

***Raillietiella monarchus* Ali, Riley & Self, 1984**

Primary synonym: Raillietiella monarchus Ali et al., 1984(a), p. 154 (types: Malaysia and Taiwan, from the spotted house gecko *Gekko monarchus*).

Distribution: Malaysia and Taiwan.

***Raillietiella morenoi* Abreu-Acosta, Foronda Rodriguez, Valladares & Casanova, 2006**

Primary synonym: Raillietiella morenoi Abreu-Acosta et al., 2006, p. 425 (types: Canary Islands, from the Atlantic lizard *Gallotia atlantica*).

Distribution: Canary Islands.

***Raillietiella mottae* Almeida, Freire & Lopes, 2008**

Primary synonym: Raillietiella mottae Almeida et al., 2008(b), p. 200 (types: Farias Brito, State of Ceará, Brazil, from Peters’ lava lizard *Tropidurus hispidus*).

Distribution: Northeastern Brazil.

***Raillietiella namibiensis* Riley & Heideman, 1998**

Primary synonym: Raillietiella namibiensis Riley & Heideman, 1998, p. 42 (types: Windhoek, Namibia from the agamid lizards *Agama aculeata* and *A. planiceps*).

Distribution: Namibia.

***Raillietiella orientalis* Hett, 1915**

Primary synonym: Porocephalus bifurcatus var. *orientalis* Hett, 1915, p. 120 (types: India, from London Zoo, from the ratsnake *Ptyas mucosa* and Indian cobra *Naja naja*).

Distribution: Widespread on numerous species of snakes in Asia and Northern Territory, Australia (Ali et al., 1982c).

Remarks: *Pentastomum colubrineati* Leuckart, 1860 (see above) was listed in the synonymy of *R. orientalis*, a younger name, by Heymons (1935, p. 209).

***Raillietiella piscator* Nair, 1967**

Primary synonym: Raillietiella piscator Nair, 1967, p. 463 (types: India, from the Asiatic watersnake *Xenochrophis piscator*).

Distribution: India.

Remarks: Ali et al. (1985) believed this to be a possible synonym of *R. orientalis*.

***Raillietiella rileyi* Krishnasamy, Jeffery, Inder Singh & Oothuman, 1995**

Primary synonym: Raillietiella rileyi Krishnasamy et al., 1995, p. 33 (types: Malaysia, from the toad *Duttaphrynus* [as *Bufo*] *melanostictus*).

Distribution: Malaysia.

***Raillietiella schoutedeni* Fain, 1960**

Primary synonym: Raillietiella schoutedeni Fain, 1960, p. 117 (types: Bolobo, ‘Belgian Congo’, from the worm lizard *Monopeltis schoutedeni*).

Distribution: Democratic Republic of the Congo.

***Raillietiella scincoides* Ali, Riley & Self, 1984**

Primary synonym: *Raillietiella scincoides* Ali et al., 1984(a), p. 149 (types: Murray River, South Australia, Australia, from the eastern blue-tongue *Tiliqua scincoides*).

Distribution: South Australia, Western Australia.

***Raillietiella spiralis* Hett, 1924**

Primary synonym: *Raillietiella spiralis* Hett, 1924, p. 139 (types: ‘Palestine’, from the Montpellier snake *Malpolon monspessulanus*).

Distribution: Israel.

***Raillietiella trachea* Riley, Oaks & Gilbert, 2003**

Primary synonym: *Raillietiella trachea* Riley et al., 2003, p. 156 (types: Dholewala, Punjab Province, Pakistan, from the oriental white-backed vulture *Gyps bengalensis*).

Distribution: Pakistan.

***Raillietiella tetrapoda* (Gretillat, Brygoo & Domer-gue, 1962)**

Primary synonym: *Mahafaliella tetrapoda* Gretillat et al., 1962, p. 304 (type: Madagascar, from the Madagascar boa *Acrantophis dumerili*).

Distribution: Madagascar.

***Raillietiella venteli* (Motta, 1965)**

Primary synonym: *Mahafaliella venteli* Motta, 1965, p. 7 (types: Porto Esperança, Matto Grosso, Brazil, from the fer-de-lance *Bothrops atrox*).

Distribution: Brazil.

Remarks: This is a *nomen dubium* according to Rego (1983).

***Yelirella* Spratt, 2010**

Primary synonym: *Rileyella* Spratt, 2003, p. 236.

Type-species: *Rileyella petauri* Spratt, 2003, by original designation.

Replacement name: *Yelirella* Spratt, 2010, p. 319 (necessitated by the senior homonym *Rileyella* Townsend, 1909 (Diptera: Tachinidae)).

***Yelirella petauri* (Spratt, 2003)**

Primary synonym: *Rileyella petauri* Spratt, 2003, p. 236 (types: New South Wales and Queensland, Australia, from the sugar glider *Petaurus breviceps*).

Distribution: New South Wales, Queensland, Australia.

Family REIGHARDIIDAE Heymons, 1926

Primary synonym: Reighardiinae Heymons, 1926(b), p. 128.

Remarks: The Reighardiinae, misspelled, was introduced as a subfamily of the Cephalobaenidae by

Heymons (1926b) and treated as a family by both Heymons (1935) and Heymons & Vitzthum (1935a) and by subsequent authors. The corrected spelling, with the double ‘i’, was introduced in both 1935 papers and has been used since.

***Hispania* Martínez, Criado-Fornelio, Lanzarot, Fernández-García, Rodríguez-Caabeiro & Merino, 2004**

Primary synonym: *Hispania* Martínez et al., 2004, p. 1103.

Type-species: *Hispania vulturis* Martínez et al., 2004, by original designation.

***Hispania vulturis* Martínez, Criado-Fornelio, Lanzarot, Fernández-García, Rodríguez-Caabeiro & Merino, 2004**

Primary synonym: *Hispania vulturis* Martínez et al., 2004, p. 1103 (type: Madrid, Spain, from the black vulture *Aegypius monachus*).

Distribution: Spain.

***Reighardia* Ward, 1899**

Primary synonym: *Reighardia* Ward, 1899, p. 254 (erected without included species).

Type-species: *Pentastomum sterna* Diesing, 1863, subsequent designation by Heymons & Vitzthum, 1935a.

Remarks: Ward (1899) diagnosed his new genus but included no species. He based it on parasites from Bonaparte’s gull collected at Lake Erie, USA. ICZN Article 67.2.2 covers this situation. Shipley (1909) listed only *Reighardia* sp. Sambon (in Vaney & Sambon, 1910, pp. 138–139) appears to be the first to have discussed Ward’s generic name and noted that Ward’s diagnosis had not been ‘published’. Sambon diagnosed the genus and included eight species: ‘*Reighardia sterna*’, *Porocephalus joubini* Vaney & Sambon, 1910, *Pentastoma oxycephalum* Diesing, 1836, *Pentastoma gracile* Diesing, 1836, *Pentastoma platycephalum* Lohrmann, 1889, *Porocephalus indicus* Linstow, 1906 ‘and three new species’, of which only two appeared under this generic name: *Reighardia cincinnalis* Sambon, in Vaney & Sambon, 1910 and *R. lohmanni* Sambon, in Vaney & Sambon, 1910. Only these are available as potential type-species. Sambon (1922a) synonymised ‘*Reighardia* Sambon, 1910’ with both ‘*Sebekia* Sambon, 1922, new genus’ and ‘*Alofia* Giglioli, 1922, new genus.’ These actions would make *Reighardia* [available from Ward] a

senior synonym of both *Sebekia* and *Alofia*, a problem avoided only because each was diagnosed with its own type-species designated. Heymons & Vitzthum (1935a) were the first to explicitly designate a type-species for *Reighardia*, choosing *Pentastomum sterna* Diesing, 1863. An earlier chapter (Heymons, 1926b) listed only one species for the family but did not state that it was the type-species of the genus.

***Reighardia lomviae* Dyck, 1975**

Primary synonym: *Reighardia lomviae* Dyck, 1975, p. 98 (type: Faeroes, Denmark, from the common murre *Uria aagle* [as ‘guillemot’]).

Distribution: Northern Europe.

***Reighardia sterna* (Diesing, 1863)**

Primary synonym: *Pentastomum sterna* *hirundinis* Diesing, 1863, p. 339 (type: Turin, from the tern *Sterna hirundo*).

Junior synonym: *Pentastomum lari* Mégnin, 1883, p. 153 (type: Polar Seas, from the gull *Larus glaucus*).

Distribution: Widespread in the Northern Hemisphere.

Remarks: Authorship has been variously attributed. Leuckart (1860, p. 150) noted a pentastome found by De-Filippi in *Sterna hirudo* without giving it a name. De-Filippi (1861) described the same specimen without naming it. Diesing (1863) named it after its host species, referring back to these authors. Diesing’s specific name ‘*sterna* *hirundinis*’ may be treated as a single word, *sternaehirundinis* (ICZN Article 11.9.5) but has never been so. *Reighardia sterna* is in prevailing usage and is still attributed to the original author and date; it is therefore deemed to be either a justified emendation (Article 33.2.3.1) or a correct original spelling (Article 33.3.1), and *sterna* remains the valid name of the taxon.

ORDER POROCEPHALIDA Heymons, 1935

Primary synonym: Porocephalida Heymons, 1935, p. 214.

Remarks: The Porocephalida is the larger of the two pentastome orders, with six families and 19 genera, depending on whose taxonomy is followed. Ah Yong et al. (2011) listed only four families, omitting the Armilliferidae Kishida, 1928 and Sambonidae Heymons, 1935.

Fain (1961, pp. 24, 35) divided the order into two suborders, ‘Sous-Ordre des Porocephaloidea Sub.-ord. nov.’ and ‘Sous-Ordre des Linguatuloidea Sub.-ord. nov.’, taxa with the superfamily suffix ‘-oidea’. Suborders were not recognised in Heymons’ (1935)

major revision, nor in recent catalogues (e.g. Martin & Davis, 2001; Ah Yong et al., 2011). Instead, the names have been treated, if at all, as superfamilies; for example, by Self (1969) and Almeida & Christoffersen (1999). These authors are followed here; the first did not give authorities and the second wrongly attributed the Linguatuloidea to Leuckart (1860) (see below). The Principal of Coordination (ICZN Article 36) applies and authorship follows those of the nominal families. Incidentally, if these taxa were to be treated as suborders, Fain (1961) is their author.

Superfamily LINGUATULOIDEA Haldeman, 1851

Primary synonym: Linguatuloidea Haldeman, 1851, p. 253.

Remarks: As a superfamily name, Linguatuloidea takes its authority from the oldest family group name (see below).

Family LINGUATULIDAE Haldeman, 1851

Primary synonym: Linguatulidae Haldeman, 1851, p. 49 (also numbered 253).

Junior synonym: Linguatulida Vogt, 1851, p. 499.

Remarks: The use of higher taxon names based on *Linguatula* Frölich, 1789 is a source of confusion. The Linguatulidae is a family well recognised in the modern taxonomy of the group, whereas Linguatulida is an older alternate name for all members of the Pentastomida (see above). Authorship of the family name was rarely acknowledged in the early taxonomic literature. Shipley (1898, 1909), Sambon (1922a), Hett (1924) and Heymons (1935), all of whom reviewed either the Linguatulidae or the Pentastomida as then known, failed to mention an authority. However, some web-based lists and Martin & Davis (2001) attributed the family name to Heymons (1935), and Almeida & Christoffersen (1999) attributed it to Leuckart (1860), but the name appears nowhere in Leuckart’s book.

Haldeman’s (1851) ‘Linguatulidae’ is one of two earliest usages, but his authorship could be contested. While his chapter was based on Heck’s (1849) work, much was ‘entirely rewritten’ and the ‘part on Zoology ... has been compiled entirely anew by its authors and will be found to contain much original matter never before published’. Neither the genus nor family name appear in Heck’s (1849) book (P. Dworschak, pers. comm.). In the same year Vogt (1851) mentioned the ‘Familie der Zungenwürmer (Linguatulida [sic])’,

which could also constitute an available if wrongly spelled family name. Priority of Vogt's name over Haldeman's name cannot be established based on the available evidence, and neither author has been credited with the name in recent literature. In this work, I herewith apply Article 24.2 (Determination by the First Reviser) in selecting Linguatulidae Haldeman, 1851 to have precedence over Linguatulida Vogt, 1851.

Sambon (1922a, p. 405) stated that the family had two subfamilies, the Raillietiellinae Sambon, 1922 and Porocephalinae Sambon, 1922, but did not acknowledge a nominotypical subfamily.

Linguatula Frölich, 1789

Primary synonym: *Linguatula* Frölich, 1789, p. 148.

Type-species: *Linguatula serrata* Frölich, 1789, by monotypy.

Junior synonyms: *Prionoderma* Cuvier, 1817, p. 35 (included species: *Taenia lanceolata* Rudolphi, 1805 [as 'ténia lancéolé, Chabert'], *Polystoma taenioides*, and, in a footnote, *Taenia caprina*, *Polyst[omum] denticulatum*, *Linguatula serrata*; type-species: *Linguatula serrata*, herein selected, making *Prionoderma* an objective synonym of *Linguatula*.

Neolinguatula Haffner, in Haffner et al., 1969, p. 138 (type-species: *Linguatula nuttalli* Sambon, 1922, by original designation). Synonymised by Riley (1986).

Remarks: Cuvier would appear to have credited *Prionoderma* to Rud[olphi] but lists Rudolphi's species in the genus *Polystoma* Zeder, 1800 (now restricted to monogeneans). No type-species ever seems to have been designated from among those initially included by Cuvier, an omission resolved above. All these species are now synonyms of *L. serrata*. The name has sometimes been attributed to Rudolphi but without a date.

Neolinguatula was explicitly attributed to Haffner alone in his joint paper (Haffner et al., 1969).

Linguatula nuttalli Sambon, 1922

Primary synonym: *Linguatula nuttalli* Sambon, 1922(a), p. 414 (types: Kadjiado River, Magade, British East Africa (now Kajiado River, Kenya), from the lion *Panthera leo*).

Distribution: Kenya.

Linguatula recurvata (Diesing, 1850)

Primary synonym: *Pentastomum recurvatum* Diesing, 1850, p. 610 (types: Brazil, from the jaguar *Panthera onca*).

Distribution: South America.

Linguatula serrata Frölich, 1789

Primary synonym: *Linguatula serrata* Frölich, 1789, p. 148 (type: probably Germany, from the European hare *Lepus capensis*).

Junior synonyms: *Taenia capraea* Abildgaard, 1789, p. 52 (types: Denmark or Norway, from the goat *Capra hircus*).

Taenia rhinaris Meyer, 1789 (No types: work is a translation of Chabert's (1787, p. 39) description of 'Ténia lancéolé', according to Heymons (1926b, p. 70, footnote). Synonymised by Diesing (1850).

Taenia caprina Gmelin, 1791, p. 3069 (type: no locality given, from the goat *Capra hircus*).

Tetragulus caviae Bosc, 1811, p. 269 (type: no locality given, from the Guinea pig *Cavia porcellus*).

Linguatula denticulata Rudolphi, 1805, p. 42. Unnecessary replacement name for *Taenia capraea*: see Rudolphi (1809, p. 447).

Linguatula dingophila Johnson, 1910, p. 248 (types: Australia, from the dingo *Canis lupus dingo*). Synonymy suggested by Johnston (1916), Riley et al. (1985) and Poore & Spratt (2012).

Pentastoma emarginatum Rudolphi, 1819, p. 124, 433 (type: no locality given, from the Guinea pig *Cavia porcellus*).

Pentastoma fera Creplin, 1829, p. 76 (type: no locality given, from the cat *Felix silvestris catus*).

Taenia lanceolata Rudolphi, 1805, p. 41 (types: bibliographic reference to a 2-page description of 'Ténia lancéolé,' a French vernacular name (Chabert, 1787, p. 39); material from nose of a horse *Equus caballus* and dog *Canis lupus familiaris*).

Polystoma taenioides Rudolphi, 1809, p. 441 (types: no locality given, from the sinus of a horse *Equus caballus* and dog *Canis lupus familiaris*).

Monostoma settenii Numan, 1840, p. 390 (type: no locality given, from the horse *Equus caballus*).

? *Pentastomum cephalophi pygmaei* Diesing, 1863, p. 328 (type: bibliographic reference to description by Cobbold (1862, p. 357) of material from the Cape guevi *Cephalophus pygmaeus*).

Distribution: Cosmopolitan in many mammals.

Remarks: Several synonyms have been recognised and catalogued with various degrees of accuracy and completeness by, for example, Baird (1853a) and Diesing (1863) under the combination *Pentastoma taenioides* and by Shipley (1898) as *Linguatula taenioides*. Heymons (1926b, 1935) was the first to

propose the seniority of *L. serrata*. Species have been variously placed in original and subsequent combinations in the genera *Cochlus* Zeder, 1803, *Taenia* Linnaeus, 1758, *Halysis* Zeder, 1803, *Echinorhynchus* Blumenbach, 1779, *Polystoma* Zeder, 1800, *Pentastoma* Rudolphi, 1812 or its misspelling *Pentastomum*, *Monostoma* Zeder, 1800 or its misspelling *Monostomum*, *Prionoderma* Rudolphi, 1809, *Lernaea* Linnaeus, 1758 and *Tetragulus* Bosc, 1811. Here, only original combinations are listed. Most of these genera have fallen into disuse; some are even non-pentastome taxa. Only *Prionoderma* (misspelled *Prinoderma*) has reappeared recently in Wikipedia.

Heymons (1926b, p. 70) pointed out that *Taenia rhinaris* Meyer, 1789 might take priority over *Linguatula serrata* Frölich, 1789, if the former were published earlier (see also Stiles, 1927). *Taenia capraea* Abildgaard, 1789 was published in the same year but has never been suggested as a possible senior synonym. The actual dates of publication, in 1789, of these three names have never been determined and the matter of priority has not been tested. However, the likelihood of precedence of one species over the other being objectively determined is low, and ICZN Article 21.3 comes into play. The date to be adopted under this article is 31 December 1789. Stiles (1927, p. 61) applied Article 28 (now Article 24.2. Determination by the First Reviser) in the case of *Taenia rhinaris* and in this work, I herewith apply the same Article in selecting *Linguatula serrata* to have precedence over *Taenia capraea*.

The authority of *Taenia caprina* is not Cuvier, as has sometimes been cited. Diesing (1850), Baird (1853a), Shipley (1898) and others have attributed *Taenia rhinaria* [sic] to Pilger (1803, sometimes cited as 1801). Pilger spelled the name correctly and *rhinaria* is an erroneous subsequent spelling of *rhinaris*. Diesing (1863) listed the name ? *Pentastomum cephalophi pygmaei* among junior synonyms of *Pentastoma* [sic] *taenioides*. Its correct specific name is one word *cephalophipygmaei*. Diesing (1850, p. 616) listed *Monostoma settinii* as a species of *Pentastomum*.

Superfamily POROCEPHALOIDEA Sambon, 1922

Primary synonym: Porocephalinae Sambon, 1922(a), p. 190 (erected as a subfamily of the Linguatulidae).

Junior synonym: Pentastomidae Shipley, 1909, p. 488.
Remark: See comments on priority under Porocephalidae below and on the status of superfamilies under Porocephalida above.

Family ARMILLIFERIDAE Kishida, 1928

Primary synonym: Armilliferinae Kishida, 1928, p. 400.
Junior synonym: Nettorhynchidae Doucet, 1962, p. 117 (*nomen nudum*).

Remarks: The Armilliferidae has often been attributed to Fain (1961) but is preceded by the name at subfamily level in a largely ignored paper by Kishida (1928). The Nettorhynchidae Doucet, 1962 was also preferred for this family without explanation as a ‘*nom. nov.*’ by Nicoli (1963, p. 501). Armilliferidae is the only available name and is more widely used. The second is a *nomen nudum* based on misspelled genus name; See the discussion under *Armillifer* Sambon, 1922. This family name was not listed by Ahyong et al. (2011), who may have considered it synonymous with the Porocephalidae, to which he attributed five genera rather than the four listed here.

Armillifer Sambon, 1922

Primary synonym: *Armillifer* Sambon, 1922(a), p. 200.
Type-species: *Linguatula armillata* Wyman, 1845, as *Armillifer armillatus* (Wyman, 1847), by original designation.

Ligamifer Heymons, 1932(a), p. 416 (Type-species: *Waddycephalus mazzai* Sambon, 1922 [as *Ligamifer mazzai* Sambon, 1922], by monotypy). Subjective synonym.

Remarks: *Armillifer* was erected by Sambon (1922a). In several recent papers the type-species, *Linguatula armillata*, is attributed to Wyman (1847; rightly Wyman, 1848), whereas the species name was first published in 1845 (Nicoli et al., 1965, p. 238, footnote). The species was based on specimens from the intestine of the snake *Python bivittata* collected in West Africa, near Cape Palmas (now Liberia).

Dollfus (1950) argued that *Armillifer* Sambon, 1922 is a junior synonym of *Nettorhynchus* [sic] Zenker, 1827. He believed that *Nettorhynchus* [sic] *blainvillei* is a species of *Armillifer*, apparently *A. armillatus* (Wyman, 1845). The history is complicated, replete with errors, and of interest because of the potential to upset nomenclature.

In 1734 Paisley, a surgeon in Glasgow, described a new worm based on two examples, the first whole but

dead and the second in pieces. According to his detailed story "... a young Man was wounded in a Duel with a small Sword, which entered about four Inches below the right Nipple, and a little towards the back ... After some weeks he become feverish and jaundiced and eventually passed with his faeces and a large amount of blood a large Worm, a Foot and a half long and an Inch and a half in Diameter ..." The term 'nettorhynque' was introduced by Blainville (1824, p. 517), who stated in a footnote: "J'établis ce genre avec un ver intestinal observé par Paisley, et dont it sera parlé plus loin". On page 522 and Appendix Plate I, figures 1 and 2, he described the worm based on Paisley's account and reproduced his illustrations. He found "La tête ... ressemblait beaucoup au bec d'un carnard, ...". The worm was given a Latinised binomen, *Netrorhynchus* [sic] *blainvillei*, by Zenker (1827), so erecting a monotypic genus and its type-species. According to Dollfus (1950), who recounted this history, Zenker explained his etymology, from the Greek, *νητρος* (netros: *fuscus* in Latin, spindle in English) and *ρῦγχος* (*rostrum* in Latin, beak in English). Apparently he misread or confused *νηττα* (*netta* = duck) with *νητρος* (*netros*). As Blainville's name has no standing in nomenclature, *Netrorhynchus* Zenker is the first available for this taxon; I have not been able to see Zenker's work. The name was spelled *Nettorhynchus* by Gervais (1847, p. 630). While one can be sympathetic to his new spelling honouring Blainville's intent, the name has to be interpreted as an incorrect subsequent spelling (ICZN Article 33.3). *Nettorhynchus* is without included species. It has been suggested that *Netrorhynchus*/*Nettorhynchus blainvillei* is in fact a nematode, but neither name appears in modern lists of Nematoda (see the summary by Nicoli et al. (1965)). These authors doubted the synonymy of *Armillifer* and *Nettorhynchus*, believing Blainville's account to be a little exaggerated and nothing in the original suggests a parasite of African snakes. Nevertheless, *Nettorhynchus*, a misspelling of the one-time subjective senior synonym *Netrorhynchus*, has been used as a replacement for *Armillifer*, although rarely. Doucet (1962, 1965) stated that there are three species of *Nettorhynchus* but listed only *N. armillatus*. Gré-tillat & Thiéry (1960, p. 306), who followed Dollfus' (1950) synonymy, stated there were six species, and described the nymph of what they called '*Nettorhynchus* (*Armillifer*) *armillatus* (Wyman, 1835)' from cysts in the body-cavity of a cat from Dakar. Challier

et al. (1967) used the reversed combination *Armillifer* (*Nettorhynchus*) *armillatus* to record cases of porocephalosis from a cow in Mali and a pig from Upper Volta. *Armillifer* is now in common use. It was used in Heymons' (1935) classic review of the Pentastomida; he did not mention *Netrorhynchus*. It is also the generic name used in reviews of the biology and taxonomy of the Pentastomida (Self, 1969; Riley & Self, 1981a; Riley, 1986). Self's (1969) bibliography listed at least 20 papers dealing with *Armillifer*. A search of the Web of Science revealed 16 papers from the 1970s to the present dealing with human health and veterinary issues associated with pentostomiasis linked to species of *Armillifer*. Significant taxonomic (Riley & Self, 1981b) and phylogenetic (Lavrov et al., 2004) reviews refer only to *Armillifer*. Web-based lists of species also use only *Armillifer*. *Nettorhynchus* does not appear to have been used since 1967 and neither spelling of the name is included in the synonymy here.

***Armillifer aborealis* Riley & Self, 1981**

Primary synonym: *Armillifer aborealis* Riley & Self, 1981(b), p. 176 (type: Australia, type-specimens from London Zoo, UK, and from Darwin, Northern Territory, Australia, from the green python *Morelia viridis*).

Distribution: Northern Territory, Western Australia, Australia.

***Armillifer agkistrodontis* Self & Kuntz, 1966**

Primary synonym: *Armillifer agkistrodontis* Self & Kuntz, 1966, p. 259 (types: Ping Tung Hsien (Ping-tung County), Taiwan, from the Chinese moccasin *Deinagkistrodon acutus*).

Distribution: Taiwan.

***Armillifer armillatus* (Wyman, 1845)**

Primary synonym: *Linguatula armillata* Wyman, 1845, p. 295 (types: West Africa, near Cape Palmas, Liberia, from the python *Python bivittata*).

Junior synonyms: *Pentastomum constrictum* Siebold, 1853, p. 65 (types: Cairo, Egypt, from *Homo sapiens*). *Linguatula diesingii* Van Beneden, 1848, p. 189 (types: Africa, type-specimens from Jardin zoologique d'Anvers (Antwerp), Belgium, from the mandrill *Papio mormon*).

Pentastomum tornatum Creplin, 1849, p. 54. Objective synonym (ICZN Article 72.7) and unnecessary replacement name for *Linguatula diesingii*. Creplin argued that intestinal worms should not be named after individuals.

Pentastomum euryzonum Diesing, 1850, p. 611. Objective synonym (ICZN Article 72.7) and unnecessary replacement name for *Linguatula diesingii*.

Pentastoma polyzonum Harley, 1857, pls 46, 47 (type: of unknown provenance). Synonymised by Shipley (1898) but possibly earlier.

Pentastoma leonis Wedl, 1863, p. 415 (types: Africa, type-specimens from Schönbrunner Menagerie, Austria, from the lion *Panthera leonis*).

Pentastomum protelis Hoyle, 1883, p. 188 (type: southern or eastern Africa, type-specimens possibly from a zoo in the UK, from the aardwolf *Proteles cristata*).

Remarks: Wyman published his first description in 1845 and then redescribed the types in a paper published in 1848, but often wrongly cited as 1847, a year that has often been erroneously given as the date of this species. Harley (1857) described an anomalous form of unknown provenance that was named only on the plate legends, not in the text of his article nor in the captions to the plates. *Linguatula diesingii* Van Beneden, 1848 was republished in 1849 (p. 24), a date more commonly cited, and this species name was replaced by *Pentastomum euryzonum* by Diesing (1850) without justification.

***Armillifer australis* Heymons, 1935**

Primary synonym: *Armillifer moniliformis australis* Heymons, 1935, p. 242 (types: Queensland, Australia, from the python *Morelia amethystina*).

Junior synonym: *Armillifer australis* Riley & Self, 1981(b), p. 175 (types: Western Australia and Papua New Guinea, from the amethyst python *Morelia amethystina*). Synonymised by Poore & Spratt (2012).

Distribution: Queensland, Western Australia, Australia; Papua New Guinea; Indonesia.

Remarks: This name presents two issues relating to the date and authorship:

(1) Röhlig et al. (2010) found earlier citations of the subspecies name as *Armillifer moniliformis australis* Heymons, 1932 problematic, as it does not occur in Heymons' (1932) papers but was mentioned by the same author in 1935. Heymons (1935) redescribed this taxon as '*Armillifer moniliformis australis* Heymons 1932' referring to the specimens he had earlier (1932) also described and figured but without naming. The later date is therefore the publication date. Weidner (1959) listed the types as present in the Zoological Museum, Hamburg.

(2) Riley & Self (1981b) stated that their new species *Armillifer australis* was 'clearly the same' as *A. moniliformis australis* Heymons, thereby erecting a subjective synonym and primary homonym. Should their species prove to be different from Heymons', it will require a new name.

***Armillifer grandis* (Hett, 1915)**

Primary synonym: *Porocephalus grandis* Hett, 1915, p. 115 (types: Africa, type-specimens from London Zoo, from the African vipers *Bitis gabonica*, *B. nasicornis* and *Cerastes cornutus*).

Distribution: Africa.

***Armillifer mazzai* (Sambon, 1922)**

Primary synonym: *Waddycephalus mazzai* Sambon, 1922(b), p. 400 (type: bibliographic reference to Mazza's (1892) description of material misidentified by Mazza as *Pentastoma moniliforme* Diesing, 1836, apparently from New Guinea).

Distribution: Queensland, Australia; Papua New Guinea.

***Armillifer moniliformis* (Diesing, 1836)**

Primary synonym: *Pentastoma moniliforme* Diesing, 1836, p. 22 (type: locality not stated, from the Indian python *Python molurus*).

Junior synonyms: *Pentastoma wedlii* Cobbold, 1866, p. 23 (type: Southeastern Asia, type-specimens from the Museum of the Royal College of Surgeons, London, from the flat-headed cat *Felis planiceps*). Synonymised by Sambon (1922a).

Pentastoma aonyxis Macalister, 1875, p. 66 (types: Indus River, Pakistan, from the Asian small-clawed otter *Amblonyx cinereus* [as *Aonyx leptonyx majoi*]). Synonymised by Sambon (1922a).

Armillifer moniliformis heymonsi Sambon, 1922(b), p. 417. (types: locality not specified, from *Broghammerus reticulatus* [as the Malay python *Python reticulatus*]).

Distribution: Southeast Asia.

Remarks: The status of the subspecies has not been investigated.

***Armillifer yoshidai* Kishida, 1928**

Primary synonym: *Armillifer yoshidai* Kishida, 1928, p. 397 (type: Southern and southeast Asia, type-specimen from Ten-noji Zoological Park, Osaka, Japan, from *Python molurus*).

Distribution: Southern and Southeast Asia.

Remarks: This species does not appear on any recent list, which is surprising, since Kishida is the author of the family name.

Family POROCEPHALIDAE Sambon, 1922

Primary synonym: Porocephalinae Sambon, 1922(a), p. 190 (erected as a subfamily of the Linguatulidae).

Junior synonym: Pentastomidae Shipley, 1909, p. 488.

Remarks: Shipley (1909) remarked in a footnote “The animals included in this group [Pentastomida] are usually called Linguatulidae or Pentastomidae ...”. Pentastomatidae, correctly spelled, could be appropriated as a family name for this group, since its type-genus, based on *Polystoma* (*Pentastoma*) Rudolphi, 1812, is a junior synonym of *Porocephalus*. However, ICZN Article 35.5 allows for a family-group name in prevailing usage not to be displaced by an older name within the same subjective family. Pentastomidae seems never to have been adopted as a family name. The family name Porocephalidae was introduced as a ‘*nov. fam.*’ by Kishida (1928, p. 399), despite its earlier proposal at the subfamily level. Martin & Davis (2001) attributed the family name to Fain (1961).

***Cayerina* Kishida, 1927**

Primary synonym: *Cayerina* Kishida, 1927, p. 987, fig. 1901.

Type-species: *Cayerina mirabilis* Kishida, 1927, by monotypy.

Remarks: Kishida (1927) provided a genus and species name in Latin, an illustration and a description in Japanese. He (1928) listed the genus among the Porocephalinae, and it was listed by Neave (1939) as an arachnid, a group to which Pentastomida then belonged. Neither the genus nor its sole species have subsequently appeared in the pentastome literature.

***Cayerina mirabilis* Kishida, 1927**

Primary synonym: *Cayerina mirabilis* Kishida, 1927, p. 987 (type: Japan, from the cricket-frog *Fejervarya limnocharis*).

Remarks: The illustration, description in Japanese and host would seem sufficient to recognise this species, which has been completely ignored in the pentastome literature.

***Cuberia* Kishida, 1928**

Primary synonym: *Cuberia* Kishida, 1928, p. 400.

Type-species: *Pentastoma annulatum* Baird, 1853 by original designation.

Remarks: Kishida said the genus was monotypic but included both of the following species in his key. The genus and its species were not listed by Heymons

(1935) but appeared in Nicoli’s (1963) and Self’s (1969) lists of taxa.

***Cuberia annulata* (Baird, 1853)**

Primary synonym: *Pentastoma annulatum* Baird, 1853(a), p. 113 (type: Egypt, type-specimens from Natural History Museum, London, from the Egyptian cobra *Naja naja*).

Junior synonyms: *Pentastoma multinctum* Harley, 1857, pls 46, 47 (types: Egypt, from the cobra *Naja naja*). Synonymised by Shipley (1898) but possibly earlier.

Pent[astomum] najae Leuckart, 1860, p. 32 ff. (types: none designated).

Pent[astomum] najae sputatricis Leuckart, 1860, p. 157 (types: no locality given, from the cobra *Naja naja*). Doubtfully synonymised with *P. multinctum* by Diesing (1863, p. 335).

Distribution: Egypt.

Remarks: Baird (1853a, b) described this species in two publications in one year. His *Catalogue* is referred to in the other work and is therefore taken to be the prior citation. Harley (1857) described *Pentastoma multinctum* from a cobra; the species name appeared only in the plate legends, not in the text of his article, nor in the captions to the plates. Self (1969) listed this species as *C. armulata*, a misspelling that has been copied elsewhere. Leuckart referred several times to *P. najae* as a new species throughout his discussion of the Pentastomida, but described more formally in the systematic part, as he did other species, only *Pentastomum najae sputatricis*, a name that should be contracted to *najaesputatricis* (ICZN Article 11.9.5). The name was listed as a hyphenated species name, *Porocephalus najae-sputatricis* by Shipley (1898) and, as *Pentastomum naie* (an unjustified emendation), by Sambon (1922b, p. 418). The name was included as a doubtful synonym of *P. multinctum* by Diesing (1863, p. 335) and as an ‘immature forms of doubtful determination’ by Sambon (1922b). The names in all forms have been ignored by later authors.

***Cuberia pomeroyi* (Woodland, 1921)**

Primary synonym: *Porocephalus pomeroyi* Woodland, 1921, p. 337 (types: Ilaro, Nigeria, from the cobra *Naja nigricollis*).

Distribution: Nigeria.

***Giglioella* Chabaud & Choquet, 1954**

Primary synonym: *Giglioella* Chabaud & Choquet, 1954, p. 236.

Type-species: Armillifer brumpti Giglioli, in Sambon, 1922, by monotypy.

***Gigliolella brumpti* (Giglioli, 1922)**

Primary synonym: Armillifer brumpti Giglioli, in Sambon, 1922(a), p. 565 (types: Madagascar, from *Boa madagarensis*).

Distribution: Madagascar.

Kiricephalus Sambon, 1922

Primary synonym: Kiricephalus Sambon, 1922(a), p. 199.

Type-species: Pentastomum proboscideum coarctatum Diesing, 1850, by original designation.

***Kiricephalus clelii* Riley & Self, 1980**

Primary synonym: Kiricephalus clelii Riley & Self, 1980, p. 133 (types: Trinidad, from the pseudoboa *Clelia clelia*).

Distribution: Trinidad.

***Kiricephalus coarctatus* (Diesing, 1850)**

Primary synonym: Pentastomum proboscideum var. coarctatum Diesing, 1850, p. 612 (types: Brazil, from the Rio tropical racer *Mastigodryas bifossatus* [as *Coluber lichensteinii*]; and East Indies, from the ratsnake *Tyas* [as *C.*] *korros*).

Junior synonyms: Porocephalus seurati Neveu-Lemaire, 1900, p. 112 (type: Guatemala, from *Elaps fulvius*).

Porocephalus herpetodryados Shipley, 1905, p. 250 (types: Honduras, from *Herpetodryas carinatus*). Synonymised by Sambon (1922a).

Porocephalus globicephalus Hett, 1915, p. 118 (type: southeastern USA, type-specimen from London Zoo, from *Nerodia fasciata* as the water moccasin *Tropidonotus fasciatus*). Synonymised by Sambon (1922a).

Distribution: Widely viewed as a Central and South American species, but one of the syntypes was said to come from an Asian snake.

***Kiricephalus constrictor* Riley & Self, 1980**

Primary synonym: Kiricephalus constrictor Riley & Self, 1980, p. 133 (types: South America, type-specimens from Chicago Zoo, from *Boa constrictor*).

Distribution: South America.

***Kiricephalus gabonensis* Riley & Self, 1980**

Primary synonym: Kiricephalus gabonensis Riley & Self, 1980, p. 134 (types: Cameroon, from *Miodon gabonensis*).

Distribution: Cameroon.

***Kiricephalus pattoni* (Stephens, 1908)**

Primary synonym: Porocephalus pattoni Stephens, 1908, p. 549 (types: Madagascar, from the ratsnake *Ptyas mucosa*).

Junior synonym: Pentastomum javanicum Bovien, 1927, p. 2 (types: Djombang, Java, Indonesia, from the crab-eating frog *Fejervarya cancrivora*). Synonymised by Hett (1934).

Distribution: Indian, Southeast Asia. The species was said to be found in some Australian snakes but no definitive record exists for Australia (Norval et al., 2009).

***Kiricephalus tortus* (Shiple, 1898)**

Primary synonym: Porocephalus tortus Shipley, 1898, p. 77 (types: New Britain, from the brown tree snake *Boiga irregularis* [as *Dipsamorphus irregularis*]).

Distribution: Papua New Guinea.

Porocephalus Humboldt, 1812

Primary synonym: Porocephalus Humboldt, 1812, p. 300.

Type-species: Porocephalus crotali Humboldt, 1812, by monotypy.

Junior synonym: Polystoma (Pentastoma) Rudolphi, 1812, p. 106 (Type-species: Polystoma proboscideum Rudolphi, 1812 [syn. of Porocephalus crotali Humboldt, 1812], by monotypy). Objective synonym.

Remarks: Humboldt's diagnosis of *Porocephalus*, and his description of its only species, appeared in a section of his *Recueil d'observations de zoologie et d'anatomie comparée ...* published in 1812. Earlier dates have been given for this work, which was published over several years (Sherborn, 1899). Humboldt mentioned the species earlier as a species of '*Echynorynchus*' [sic] in the first (1808) edition of his *Ansichten der Natur ...*. In the third edition of this work, Humboldt (1849, pt. II, p. 75; p. 266 in Mrs Sabine's English translation) added an annotation (no. 6) to page 8 (p. 230 in the translation): 'This animal, which I formerly called an Echinorhynchus, or even a Porocephalus, appears ... to belong to a division of the Pentastomes'. This genus has sometimes been attributed to Rudolphi (1812) (see below).

The genus *Pentastoma* has a convoluted history. It was widely used and gave its name to the subclass but was erected as an unjustified replacement name for *Porocephalus*. The name was introduced by Rudolphi (1812) as a division ("Abtheilung") of the genus *Polystoma* in a discussion of his new species *Polystoma proboscideum*, which he simultaneously equated to *Porocephalus crotali* Humboldt. He mistakenly cited Humboldt's paper as having been published in 1809 rather than 1812. Rudolphi (1819) elaborated,

diagnosing *Pentastoma* (pp. 123, 432) and discussing its species. He again treated *Polystoma proboscideum* and *Porocephalus crotali* as synonyms (pp. 123, 434). With the same type-species, *Polystoma (Pentastoma)* is an objective junior synonym of *Porocephalus*. *Pentastoma* and *Pentastomum* have been used interchangeably. *Pentastomum* appears to have been first introduced by Creplin (1849, p. 54) and was used for all species by Diesing (1850) and several later authors. It is an incorrect subsequent spelling (ICZN Article 33.3) and therefore not an available name.

***Porocephalus basilicus* Riley & Self, 1979**

Primary synonym: *Porocephalus basilicus* Riley & Self, 1979, p. 30 (types: Colima, Mexico, from the rattlesnake *Crotalus basilicus*).

Distribution: Western Mexico.

***Porocephalus benoiti* Fain, 1960**

Primary synonym: *Porocephalus benoiti* Fain, 1960, p. 118 (types: Katanga, ‘Belgian Congo’, from *Naja* sp.).
Distribution: Democratic Republic of the Congo.

***Porocephalus clavatus* (Wyman, 1845)**

Primary synonym: *Linguatula clavata* Wyman 1845, p. 296 (types: from the ‘South American Boa’).

Junior synonyms: *Pentastomum didelphidis virginianae* Leidy, 1850, p. 98 (types: USA, from the possum *Didelphis virginiana*).

Pentastoma imperatoris Macalister, 1875, p. 65 (types: South America, from *Boa imperator*).

Distribution: Americas.

Remarks: Wyman first introduced this name in 1845 but redescribed the species in 1848 in a paper frequently cited as 1847. *Pentastomum didelphidis virginianae* should be treated as *Pentastomum didelphidisvirginianae* (ICZN Article 11.9.5).

***Porocephalus crotali* Humboldt 1812**

Primary synonym: *Porocephalus crotali* Humboldt, 1812, p. 301 (type: Cumana, Central America, from the rattlesnake *Crotalus durissus*).

Junior synonyms: *Polystoma proboscideum* Rudolphi, 1812, p. 106 (unjustified replacement name for *Porocephalus crotali* Humboldt, 1812).

Pentastoma subcylindricum Diesing, 1836, p. 21 (types: Ipanema, Cuyaba, Brazil, from the mammals *Midas chrysopygus*, *Didelphis murina*, *D. philander*, *Procyon carnivorus*, *Dasybus niger*, *Mus pyrrhorhinos*, *M. fuliginous*, *Phyllostoma discolor*).

Remarks: See the comments above on the genus *Porocephalus*. Humboldt mentioned this species in 1808 as a member of *Echinorhynchus* Blumenbach,

1779 but not in a Linnaean combination. Rudolphi (1812) erected *Polystoma proboscideum* as an alternate name for *Porocephalus crotali* without any explanation.

Distribution: Americas.

***Porocephalus dominicana* Riley & Walters, 1980**

Primary synonym: *Porocephalus dominicana* Riley & Walters, 1980, p. 123 (types: Dominica, from *Boa constrictor nebulosus*).

Distribution: Dominica.

***Porocephalus stilesi* Sambon, in Vaney & Sambon, 1910**

Primary synonym: *Porocephalus stilesi* Sambon, in Vaney & Sambon, 1910, p. 137 (types: USA, from the snakes *Lachesis mutus* and *L. lanceolatus*).

Distribution: North America.

***Porocephalus wardi* Sambon, in Vaney & Sambon, 1910**

Primary synonym: *Porocephalus wardi* Sambon, in Vaney & Sambon, 1910, p. 137 (type: bibliographic reference to material figured and misidentified as *Pentastoma proboscideum* by Diesing (1836, pl. 4 figs 1–10), locality not stated, from the lizard ‘Great Teju’ *Tupinambis tequixin*).

Distribution: South America (Sambon, 1922b).

***Porocephalus subuliferum* (Leuckart, 1860)**

Primary synonym: *Pent[astomum] subuliferum* Leuckart, 1860, p. 154 (type: no locality given, from the cobra *Naja naja*).

Junior synonyms: *Porocephalus cercopithecii* Breinl & Hindle, 1909, p. 322 (types: West Africa, type-specimens from Liverpool research lab, UK, from the green monkey *Chlorocebus sabaeus* [as *Cercopithecus callitrichus*]). Synonymised by Heymons (1935, p. 233).

Porocephalus bouvieri Vaney & Sambon, 1910, p. 129 (type: ‘French Congo’, from the Cape filesnake *Gonionotophis capensis*). Synonymised by Heymons (1935, p. 233).

Distribution: Africa.

***Porocephalus tortugensis* Riley & Self, 1979**

Primary synonym: *Porocephalus tortugensis* Riley & Self, 1979, p. 30 (types: Tortuga Island, from the rattlesnake *Crotalus tortugensis*).

Distribution: Tortuga I., Mexico.

Family SAMBONIDAE Heymons, 1935

Primary synonym: Samboninae Heymons, 1935, p. 222 (as a subfamily of the Porocephalidae).

Remarks: Many, but not all, authors have misspelled the family name as Sambonidae instead of the more

correctly derived Samboniidae. ICZN Article 29.5 does not now require this to be corrected if the misspelling is in prevailing usage. The shorter form is used here, largely because that was how it was erected and has been followed by most authors. Almeida & Christoffersen (1999) included all sambonid genera in Sebekidae, a view apparently followed by Ah Yong et al. (2011). Martin & Davis (2001) attributed the family name to Fain (1961).

***Elenia* Heymons, 1932**

Primary synonym: *Elenia* Heymons, 1932(a), p. 413.
Type-species: *Elenia australis* Heymons, 1932, by monotypy.

***Elenia australis* Heymons, 1932**

Primary synonym: *Elenia australis* Heymons, 1932(a), p. 413 (types: Rockhampton, Queensland, Australia, type-host unknown).

Distribution: Queensland, Australia; Papua New Guinea.

***Elenia lialisi* Heymons, 1939**

Primary synonym: *Elenia lialisi* Heymons, 1939(a), p. 686 (type: Papua New Guinea, from the snake lizard *Lialis jicari*).

Distribution: Papua New Guinea.

Remarks: Considered a *nomen dubium* by some.

***Elenia travassosi* Heymons, 1932**

Primary synonym: *Alofia travassosi* Heymons, 1932(b), p. 295 (types: Basey River, Samar Island, Philippines, host unknown).

Distribution: Philippines.

***Parasambonia* Stunkard & Gandal, 1968**

Primary synonym: *Parasambonia* Stunkard & Gandal, 1968, p. 50.

Type-species: *Parasambonia bridgesi* Stunkard & Gandal, 1968, by original designation.

***Parasambonia bridgesi* Stunkard & Gandal, 1968**

Primary synonym: *Parasambonia bridgesi* Stunkard & Gandal, 1968, p. 50 (types: Australia, type-specimens from New York Zoological Park, from the red-bellied black snake *Pseudechis porphyriacus*).

Distribution: New South Wales, Queensland, Australia.

***Parasambonia minor* Riley & Self, 1982**

Primary synonym: *Parasambonia minor* Riley & Self, 1982, p. 128 (type: type-locality unknown, from the lowland copperhead *Austrelaps superbis*).

Distribution: New South Wales, Australia.

***Sambonia* Noc & Giglioli, 1922**

Primary synonym: *Sambonia* Noc & Giglioli, 1922, p. 279.

Type-species: *Reighardia lohrmanni* Sambon, in Vaney & Sambon, 1910 [as *Sambonia lohrmanni*], by monotypy.

Junior synonym: *Megadrepanoides* Self & Kuntz, 1957, p. 196 (type-species: *Megadrepanoides solomonensis* Self & Kuntz, 1957 by original designation). Synonymised by Self & Kuntz (1966).

***Sambonia clavata* (Lohrmann, 1889)**

Primary synonym: *Pentastomum clavatum* Lohrmann, 1889, p. 336 (type: Egypt, from the monitor *Varanus niloticus*).

Junior synonym: *Reighardia lohrmanni* Sambon, in Vaney & Sambon, 1910, p. 138 (unnecessary replacement name for *Pentastomum clavatum* Lohrmann, 1889).

Distribution: Egypt.

Remarks: Sambon (in Vaney & Sambon, 1910) considered *Pentastomum clavatum* Lohrmann, 1889 was preoccupied by *Linguatula clavata* Wyman, 1845 and, quoting from ICZN Article 36, argued that it “cannot be retained because ... a rejected homonym can never be used again, even when the species is placed in another genus”. The names are certainly not primary homonyms and there is no evidence that they were ever secondary homonyms. Sambon himself treated *L. clavata* as a species of *Porocephalus*. Even if they were, ICZN Article 59.3 would seem to apply.

***Sambonia parapodum* Self & Kuntz, 1966**

Primary synonym: *Sambonia parapodum* Self & Kuntz, 1966, p. 257 (types: Palawan, Philippines, from the Asian water monitor *Varanus salvator*).

Distribution: Philippines.

***Sambonia solomonensis* (Self & Kuntz, 1957)**

Primary synonym: *Megadrepanoides solomonensis* Self & Kuntz, 1957, p. 196 (types: Florida I., Solomon Islands, from *Varanus indicus*).

Distribution: Solomon Islands.

***Sambonia varani* (Self & Kuntz, 1957)**

Primary synonym: *Megadrepanoides varani* Self & Kuntz, 1957, p. 197 (types: Florida I., Solomon Islands, from *Varanus indicus*).

Distribution: Solomon Islands.

***Waddycephalus* Sambon, 1922**

Primary synonym: *Waddycephalus* Sambon, 1922(a), p. 203.

Type-species: Pentastoma teretiusculum Baird, 1862 by original designation.

Waddycephalus calligaster Riley & Self, 1981

Primary synonym: Waddycephalus calligaster Riley & Self, 1981(a), p. 250 (types: Australia, from the northern tree snake *Dendrelaphis calligaster*).

Distribution: Queensland, Australia.

Waddycephalus longicauda Riley & Self, 1981

Primary synonym: Waddycephalus longicauda Riley & Self, 1981(a), p. 248 (types: northern Queensland, Australia, from the black-headed python *Aspidites melanocephalus*).

Distribution: Queensland, South Australia, Victoria, Australia.

Waddycephalus porphyriacus Riley & Self, 1981

Primary synonym: Waddycephalus porphyriacus Riley & Self, 1981(a), p. 248 (types: Australia, exact type-locality unknown, from the red-bellied black snake *Pseudechis porphyriacus*).

Distribution: South Australia, Australia.

Waddycephalus punctulatus Riley & Self, 1981

Primary synonym: Waddycephalus punctulatus Riley & Self, 1981(a), p. 250 (types: Queensland, Australia, from the common tree snake *Dendrelaphis punctulatus*).

Distribution: Queensland, Australia.

Waddycephalus scutata Riley & Self, 1981

Primary synonym: Waddycephalus scutata Riley & Self, 1981(a), p. 248 (types: St Francis Island, South Australia, Australia, from the tiger snake *Notechis scutatus*).

Distribution: Northern Territory, South Australia, Australia.

Waddycephalus superbus Riley & Self, 1981

Primary synonym: Waddycephalus superbus Riley & Self, 1981(a), p. 246 (types: Tasmania, Australia, from the lowland copperhead *Austrelaps superbus*).

Distribution: Tasmania, Australia.

Waddycephalus teretiusculus (Baird, 1862)

Primary synonym: Pentastoma teretiusculum Baird, 1862, p. 114 (types: Australia, type-specimens from London Zoo, from the lowland copperhead *Austrelaps superbus*).

Distribution: Queensland, Tasmania, Victoria, Western Australia, Australia.

Family SEBEKIDAE Sambon, 1922

Primary synonym: Sebekini Sambon, 1922(a), p. 192 (erected as a section of the Porocephalinae, subfamily of Linguatulidae).

Junior synonym: Diesingiinae Heymons, 1935, p. 224.

Remarks: Many, but not all, authors have misspelled the family name as Sebekidae instead of the more correctly derived Sebekiidae. ICZN Article 29.5 does not now require this to be corrected if the misspelling is in prevailing usage. The shorter form is used here, largely because that was how it was erected and is followed by most authors. Diesingiinae Heymons, 1935 is given priority here over Diesingiinae in Heymons & Vitzthum (1935a). Martin & Davis (2001) recognised Diesingidae [sic] and Sebekiidae [sic], attributing both to Fain (1961). Junker & Boomker (2006) provided a list of species in crocodiles.

Agema Riley, Hill & Huchzermeyer, 1997

Primary synonym: Agema Riley et al., 1997, p. 211.

Type-species: Agema silvaepalustris Riley, Hill & Huchzermeyer, 1997, by original designation.

Agema silvaepalustris Riley, Hill & Huchzermeyer, 1997

Primary synonym: Agema silvaepalustris Riley et al., 1997, p. 211 (types: Democratic Republic of the Congo, from the dwarf crocodile *Osteolaemus tetraspis*).

Distribution: Democratic Republic of the Congo

Alofia Giglioli, in Sambon, 1922

Primary synonym: Alofia Giglioli, in Sambon, 1922(a), p. 194.

Type-species: Alofia ginae Giglioli, in Sambon, 1922, by original designation.

Remarks: ‘*Alofia* Giglioli, 1922, new genus’ was published as such by Sambon (15 June 1922). Giglioli (1922b) published his own paper in the same journal on 1 December 1922. The same comment applies to *A. ginae*.

In addition to the species listed, there is another that remains problematical. *Alofia adriatica* Hirst, 1922 was described from the Adriatic Sea, where crocodiles, the only known primary hosts of *Alofia* spp., do not occur. The record may be from a secondary host (see *A. ginae* below).

Alofia ginae Giglioli, in Sambon, 1922

Primary synonym: Alofia ginae Giglioli, in Sambon, 1922(a), p. 195 (types: Samoa, “probably from some fish”).

Distribution: Samoa.

Remarks: Junker & Boomker (2006) appear to have assumed that this species was recorded from

Crocodylus porosus and discussed the probability of crocodiles being in Samoa, beyond their known range. However, Sambon's paper did not mention crocodiles. See too *A. merki*.

***Alofia indica* (Linstow, 1906)**

Primary synonym: *Porocephalus indicus* Linstow, 1906, p. 270 (type: India, from the gharial *Gavialis gangeticus*).

Distribution: India.

***Alofia merki* Giglioli, in Sambon, 1922**

Primary synonym: *Alofia* (?) *merki* Giglioli, in Sambon, 1922(a), p. 195 (type: Samoa, "host not known").

Distribution: Northern Territory, Australia; Samoa, Philippines. See remarks under *A. ginae* concerning the probability of this species occurring in Samoa; the types came from the same collector as provided *A. ginae*, probably from fish.

***Alofia nilotici* Riley & Huchzermeyer, 1995**

Primary synonym: *Alofia nilotici* Riley & Huchzermeyer, 1995, p. 232 (types: Okavango swamps, Botswana, from the crocodile *Crocodylus niloticus*).

Distribution: Botswana, South Africa.

***Alofia parva* Riley & Huchzermeyer, 1995**

Primary synonym: *Alofia parva* Riley & Huchzermeyer, 1995, p. 155 (types: Brazzaville, Republic of the Congo, from the West African dwarf crocodile *Osteolaemus tetraspis*).

Distribution: Republic of the Congo.

***Alofia platycephalum* (Lohrmann, 1889)**

Primary synonym: *Pentastomum platycephalum* Lohrmann, 1889, p. 336 (type: locality not given, from an alligator?).

Distribution: Brazil, Paraguay, probably elsewhere in South America.

Remarks: The species name *platycephalum* would appear to be a noun and its ending does not require to be changed to *platycephala*, as appears in the recent literature.

***Alofia simpsoni* Riley, 1994**

Primary synonym: *Alofia simpsoni* Riley, 1994, p. 35 (types: Ghana, host unknown).

Distribution: Ghana, Botswana, South Africa.

***Diesingia* Sambon, 1922**

Primary synonym: *Diesingia* Sambon, 1922(b), p. 397.

Type-species: *Porocephalus kachugensis* Shipley, 1910, by monotypy.

Junior synonym: *Butantanella* Da Fonseca & Ruiz, 1956, p. 471 (type-species: *Pentastoma megastomum* Diesing, 1836, by original designation).

Remarks: Sambon (1922b) definitely included *Porocephalus kachugensis* Shipley, 1910 in his new genus and listed *Pentastomum megastomum* Diesing, 1836 as probably included. Applying ICZN Article 67.2.5 excludes the latter and the former is type-species by monotypy.

***Diesingia kachugensis* (Shipley, 1910)**

Primary synonym: *Porocephalus kachugensis* Shipley, 1910, p. 276 (type: India and Burma, from the terrapin *Kachuga lineata*).

Distribution: India, Burma.

***Diesingia megastomum* (Diesing, 1836)**

Primary synonym: *Pentastoma megastomum* Diesing, 1836, p. 23 (type: no locality given, from the toadhead turtle *Phrynops geoffroana*).

Distribution: Brazil.

Remark: The specific name *megastomum* would appear to be a noun and its ending does not require to be changed to *megastoma*, as appears in the recent literature.

***Leiperia* Sambon, 1922**

Primary synonym: *Leiperia* Sambon, 1922(a), p. 195. *Type-species:* *Reighardia cincinnalis* Sambon, in Vaney & Sambon, 1910, by original designation.

Remarks: Self (1969) erroneously listed '*L. gracilis* (Diesing, 1835)' [sic] as the type-species.

***Leiperia australiensis* Riley & Huchzermeyer, 1996**

Primary synonym: *Leiperia australiensis* Riley & Huchzermeyer, 1996, p. 57, 60 (types: Northern Territory, Australia, from the saltwater crocodile *Crocodylus porosus*).

Distribution: Northern Territory, Queensland, Australia.

***Leiperia cincinnalis* (Sambon, in Vaney & Sambon, 1910)**

Primary synonym: *Reighardia cincinnalis* Sambon, in Vaney & Sambon, 1910, p. 139 (type: Murchison Falls, Nile River, from *Crocodylus niloticus*).

Junior synonym: *Porocephalus nematoides* Beauchamp, 1918, p. 19 (type: Lake Tanganika, Uganda, from the eel fish *Mastacembelus* sp.).

Distribution: Democratic Republic of the Congo, South Africa, Zimbabwe, Uganda.

Remarks: This species has sometimes been attributed to Vaney & Sambon (1910), but Sambon described it alone in an appendix to the joint paper.

***Leiperia gracilis* (Diesing, 1836)**

Primary synonym: *Pentastoma gracile* Diesing, 1836, p. 23 (types: Cuyaba, Caicara, Mato Grosso, Villa Maria, Brazil, from several lizard, snake and fish species: *Tupinambis tequixin*, *Bothrops jararaca*, *Eunectes scytale*, *Tetragonopterus argenteus*, *Salmo auratus*, *S. tamuco*, *Scardinius erythrophthalmus*, *Serrasalmus piranha* and *Erythrinus erythrinus*, plus undescribed species of *Podinema*, *Elaps*, *Pseuderys*, *Tropidonotus*, *Coluber*).

Junior synonyms: *Leiperia neotropica* Heymons & Vitzthum, 1935(b), p. 153 (types: South America, type-specimens from Berlin Museum, from the Peruvian eelgoby *Gobioides peruanus*). Synonymised by Heymons & Vitzthum (1935a).

Porocephalus crocodili Wheeler, 1915, p. 207 (type: Guayas River, Guayaquil, Ecuador, from *Crocodylus americanus*). Synonymised by Heymons & Vitzthum (1935a, p. 45) and in part by Junker & Boomker (2006); also a possible synonym of *Sebekia oxycephalum* (Diesing, 1836).

Distribution: Americas.

Remarks: The types of *Porocephalus crocodili* were considered by Sambon (1922a) to represent two species, which explains Junker & Boomker's (2006) partial synonymy. Self & Rego (1985, p. 40) considered *Pentastoma gracile* the same as *Leiperia cincinnalis*.

***Pelonia* Junker & Boomker, 2002**

Primary synonym: *Pelonia* Junker & Boomker, 2002, p. 53.

Type-species: *Pelonia africana* Junker & Boomker, 2002, by original designation.

***Pelonia africana* Junker & Boomker, 2002**

Primary synonym: *Pelonia africana* Junker & Boomker, 2002, p. 53 (types: Northern Province, South Africa, from the terrapins *Pelomedusa subrufa* and *Pelusios sinuatus*).

Distribution: South Africa.

***Sebekia* Sambon, 1922**

Primary synonym: *Sebekia* Sambon, 1922(a), p. 193.

Type-species: *Sebekia wedli* Giglioli, in Sambon, 1922, by original designation - see comments on this name below.

Junior synonym: *Bdukus* Holl, 1928, p. 64 (type-species: *Bdukus ichthyus* Holl, 1928, by original designation). Synonymised by Junker & Boomker (2006).

Remarks: As explained below under *S. minor*, the type-species is an unjustified replacement name for *Pentastoma oxycephalum minor* Wedl, 1861, now *Sebekia minor* (Wedl, 1861) n. comb. Self (1969) erroneously listed '*S. oxycephala* (Diesing, 1835)' [sic] as the type-species. Other potential species of *Sebekia* are mentioned with other dubious species at the beginning of this catalogue.

***Sebekia cesarisi* Giglioli, in Sambon, 1922**

Primary synonym: *Sebekia cesarisi* Giglioli, in Sambon, 1922(a), p. 193 (types: Africa, from *Crocodylus* sp.).

Distribution: Botswana, South Africa.

***Sebekia divestei* Giglioli, in Sambon, 1922**

Primary synonym: *Sebekia divestei* Giglioli, in Sambon, 1922(a), p. 193 (types: America, from *Crocodylus americanus*).

Distribution: Americas.

Remarks: *Sebekia divestei* was synonymised with *S. oxycephalum* by Self & Rego (1985) but retained by Riley et al. (1990) and Junker & Boomker (2006).

***Sebekia johnstoni* Riley, Spratt & Winch, 1990**

Primary synonym: *Sebekia johnstoni* Riley et al., 1990, p. 15 (types: Northern Territory, Australia, from the freshwater crocodile *Crocodylus johnstoni*).

Distribution: Northern Territory, Australia.

***Sebekia microhamus* Self & Rego, 1985**

Primary synonym: *Sebekia microhamus* Self & Rego, 1985, p. 37 (type: Brazil, from the spectacled caiman *Caiman sclerops*).

Distribution: Brazil.

***Sebekia minor* (Wedl, 1861) n. comb.**

Primary synonym: *Pentastoma oxycephalum minor* Wedl, 1861, p. 225 (type: Egypt, from the crocodile *Crocodylus niloticus*).

Junior synonym: *Sebekia wedli* Giglioli, in Sambon, 1922(a), p. 193 (objective synonym, unnecessary replacement name).

Distribution: Democratic Republic of the Congo, Uganda, South Africa, Botswana.

Remarks: Giglioli, in Sambon (1922a), erected the new species *Sebekia wedli*, listing *Pentastoma oxycephalum minor* Wedl, 1861 as a synonym and no type-specimens. Wedl's name is therefore an objective junior synonym (ICZN Article 72.7). *Sebekia wedli* was synonymised with *S. oxycephalum* by Self & Rego (1985) but is unjustified on biogeographical

grounds (Self et al., 1990); the species was retained by Junker & Boomker (2006) as *S. wedli*.

***Sebekia mississippiensis* Overstreet, Self & Vliet, 1985**

Primary synonym: *Sebekia mississippiensis* Overstreet et al., 1985, p. 266 (types: Louisiana and Mississippi, USA, from the alligator *Alligator mississippiensis*).

Distribution: Southern USA.

***Sebekia multiannulata* Riley, Spratt & Winch, 1990**

Primary synonym: *Sebekia multiannulata* Riley et al., 1990, p. 17 (types: Northern Territory, Australia, from the saltwater crocodile *Crocodylus porosus*).

Distribution: Northern Territory, Australia.

***Sebakia novaeguineae* Riley, Spratt & Winch, 1990**

Primary synonym: *Sebakia novaeguineae* Riley et al., 1990, p. 21 (types: Papua New Guinea, from *Crocodylus novaeguineae*).

Distribution: Papua New Guinea.

***Sebekia okavangoensis* Riley & Huchzermeyer, 1995**

Primary synonym: *Sebekia okavangoensis* Riley & Huchzermeyer, 1995, p. 228 (types: Okavango swamps, Botswana, from *Crocodylus niloticus*).

Distribution: Democratic Republic of the Congo, South Africa, Botswana.

***Sebekia oxycephalum* (Diesing, 1836)**

Primary synonym: *Pentastoma oxycephalum* Diesing, 1836, p. 20 (types: Irisanga, Cuyaba, Rio Cabacal, Brazil, from a caiman as ‘*Crocodylus acutus*’).

Junior synonyms: *Pentastomum heterodontis* Leuckart, 1860, p. 156 (types not stated). Synonymised by Junker & Boomker (2006).

Porocephalus crocodili Wheeler, 1915, p. 207 (type: Guayas River, Guayaquil, Ecuador, from *Crocodylus americanus*). Synonymised in part by Junker & Boomker (2006); also a possible synonym of *Leperia gracilis*.

Bdukus ichthyius Holl, 1929, p. 64 (types: Gibsonville, North Carolina, USA, from the fishes *Ameiurus natalis* and *Eupomotis gibbosus*). Synonymised by Junker & Boomker (2006).

Distribution: Trinidad, South America, North Carolina, USA.

Remarks: The types of *Porocephalus crocodili* were considered by Sambon (1922a) to represent two species, which may explain Junker & Boomker’s (2006) partial synonymy. *Porocephalus heterodontis* was listed by Shipley (1898, p. 69) and, as *Pentastomum heterodontis*, as an ‘immature forms of doubtful

determination’ by Sambon (1922b, p. 418). Junker & Boomker (2006) listed ‘*Pentastoma proboscideum crocodili scleropis* Rudolphi (1819)’ as a synonym, but no combination of parasite and host names exists in Rudolphi’s work. The specific name *oxycephalum* would appear to be a noun and its ending does not require to be changed to *oxycephala* as appears in recent literature.

***Sebekia purdieae* Riley, Spratt & Winch, 1990**

Primary synonym: *Sebekia purdieae* Riley et al., 1990, p. 20 (types: Northern Territory, Australia, from the saltwater crocodile *Crocodylus porosus*).

Distribution: Northern Territory, Australia.

***Sebekia trinitatis* Riley, Spratt & Winch, 1990**

Primary synonym: *Sebekia trinitatis* Riley et al., 1990, p. 4 (types: Trinidad, from the spectacled caiman *Caiman sclerops*).

Distribution: Trinidad, South America.

***Selfia* Riley, 1994**

Primary synonym: *Selfia* Riley, 1994, p. 27.

Type-species: *Selfia porosus* Riley, 1994, by monotypy.

***Selfia porosus* Riley, 1994**

Primary synonym: *Selfia porosus* Riley, 1994, p. 27 (types: Northern Territory, Australia, from the saltwater crocodile *Crocodylus porosus*).

Distribution: Northern Territory, Australia.

Family SUBTRIQUETRIDAE Fain, 1961

Primary synonym: Subtriquetridae Fain, 1961, p. 27.

Remarks: There is a single genus. This is the only family originating from Fain (1961) and the only one to which he appended the phrase ‘fam. nov.’ Self (1969) listed two species in his Table 1, but neither the genus nor its species was in his list of pentastome taxa.

***Subtriquetra* Sambon, 1922**

Primary synonym: *Subtriquetra* Sambon, 1922(a), p. 205.

Type-species: *Pentastoma subtriqueta* Diesing, 1836 by original designation.

***Subtriquetra megacephalum* (Baird, 1853)**

Primary synonym: *Pentastoma megacephalum* Baird, 1853(a), p. 39 (types: India, from *Crocodylus palustris*).

Distribution: India.

Remarks: Baird’s *Catalogue* (1853a) predated his redescription in the same year (Baird, 1853b). The specific name *megacephalum* would appear to be a

noun and its ending does not require to be changed to *megacephala* as appears in recent literature.

***Subtriquetra rileyi* Junker, Boomker & Booyse, 1998**

Primary synonym: Subtriquetra rileyi Junker et al., 1998, p. 162 (types: Phabeni Dam, Kruger National Park, South Africa, from the tilapia fishes *Oreochromis mossambicus* and *Tilapia rendalli*).

Distribution: South Africa.

***Subtriquetra shipleyi* Hett, 1924**

Primary synonym: Subtriquetra shipleyi Hett, 1924, p. 153 (types: ?India, type-specimens from the Indian Museum, Calcutta, from a crocodile).

Distribution: India.

***Subtriquetra subtriquetra* (Diesing, 1836)**

Primary synonym: Pentastoma subtriquetrum Diesing, 1836, p. 17 (type: no locality given, from the spectacled caiman *Caiman sclerops*).

Primary synonym: Pentastomum pusillum Diesing, 1856, p. 31 (type: Augusto, Brazil, from the fish *Cichlasoma bimaculatum* [as *Acarae cuscudo*]).

Distribution: Trinidad, South America.

Summary

Compilation of this list revealed that existing catalogues omit some taxa, and include misspellings, wrong attributions and dates of the authors of taxa, and incorrectly nominated type-species. These have been corrected here with reference to the original descriptions and diagnoses. Some observations with wide-spread implications are:

- All families except one were erected much earlier than Fain (1961), who was credited by Martin & Davis (2001) with seven of the nine families they recognised; their list and authorities have been followed by several web-based lists and other authors. In fact, Fain (1961) used the phrase ‘fam. nov.’ only for the Subtriquetridae but gave no authorities for the others.
- Heymons published two papers in 1935 with similar taxonomies, the first alone on an unspecified date but clearly referring to the second, and the other with H.G. Vitzhum on 5 August 1935. In a short discussion of the literature Heymons & Vitzhum (1935a, p. 103) referred to Heymons’ solo work as ‘jetzt ... veroffentlichten,’ now published. For this reason any names where authorship may be in doubt are credited to Heymons alone.
- Sambon published two papers in the same year (1922a, b). In the first he attributed several new species to ‘Giglioli, 1922’. In a footnote, he stated ‘Dr. G. Giglioli has kindly allowed me to mention in this synopsis some new species which he has not yet published. Their publication here, therefore, should be considered as a preliminary notice by Dr. Giglioli himself.’ These species were published on 15 June 1922 before Giglioli (1922b) published his own paper in the same journal on 1 December 1922. Giglioli is the author of these taxa, published on the earlier date and cited here as ‘Giglioli, in Sambon, 1922.’ Sambon (1922b) published an addendum to his synopsis later (15 December) in the same year.
- Self (1969) listed incorrect type-species for three of the 17 genera in his list of taxa.
- Some papers have been frequently cited without correct dates, but reference to title pages or library catalogues has enabled these to be corrected, e.g. Diesing’s significant review was published in 1836 (according to the library catalogues) not 1835 as commonly cited. He did not introduce the name Pentastomida, as usually stated.

Significant taxonomic anomalies have been revealed that have a bearing on current usage:

- Raillietiellidae Sambon, 1922 is an older name than Cephalobaenidae Heymons, 1922, the name in popular usage for the family including *Cephalobaena* and *Raillietiella*; here the two genera are placed in separate families following Almeida & Christoffersen (1999).
- *Heymonsia* Hett, 1934, considered a junior synonym of *Raillietiella* Sambon, in Vaney & Sambon, 1910, is a *nomen nudum*.
- *Raillietiella geckonis* (Diesing, 1850) is a potential senior synonym of several southeastern Asia species of this genus.
- *Raillietiella frenata* Ali, Riley & Self, 1981 is a widely used but misspelled species name, but is a subjective junior synonym of *R. hebitihamata* Self & Kuntz, 1960. *Raillietiella indica* Gedoelst, 1921 may be a subjective senior synonym of both species.
- The Porocephaloidea and Linguatuloidea are treated as superfamilies as is the prevailing usage despite being erected as suborders.

- The priority of Linguatulidae Haldeman, 1851 over Linguatulida Vogt, 1851, erected as a family in the same year, is established by applying the First Reviser rule.
- *Linguatula serrata* is herein selected as the type-species of *Prionoderma*, making the latter an objective synonym of *Linguatula*.
- The priority of *Linguatula serrata* von Frölich, 1789 over *Taenia rhinaris* Meyer, 1789 and *Taenia capraea* Abildgaard, 1789, all published in the same year, is established by applying the First Reviser rule.
- The synonymy and priority of *Netrorhynchus* Zenker, 1827, also misspelled *Nettorhynchus*, over *Armillifer* Sambon, 1922 would seem to be ill-founded and without popular support.
- *Armillifer australis* Heymons, 1935, published as a subspecies of *A. moniliformis*, is both a senior synonym and homonym of *Armillifer australis* Riley & Self, 1981.
- Humboldt (1812) is confirmed as the author of *Porocephalus* and *P. crotali*.
- Pentastomidae Shipley, 1909 is an older family group name than its subjective synonym Porocephalinae Sambon, 1922. Prevailing usage allows Porocephalinae to be retained as a family name.
- *Cayerina mirabilis* Kishida, 1927 is a genus and species from a Japanese frog that has not appeared in the more recent pentastome literature.
- *Sebekia minor* (Wedl, 1861) is an objective senior synonym of the more widely used *S. wedli* Giglioli, in Sambon, 1922.

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