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THE CURRENT STATE OF OCTOPUS TAXONOMY

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ABSTRACT: Much has changed since the 1988 CIAC sponsored workshop on octopus systematics in Washington DC and the decisions reported in the resulting workshop publications. This paper provides an update on the status of octopus taxonomy 17 years on and reports revisions, omissions, corrections and additions (new species). Information on 374 nominal species is presented, of which we consider around half (186) to represent valid names. This tally is considered a significant underestimate of the total number of extant species. More than 150 undescribed species have been recognised in the past 17 years through examination of museum collections, primary field surveys and discovery of many cryptic species. The rate at which new species are being discovered is significantly higher than the rate at which new species are being formally described. This is largely due to a small, aging and diminishing cohort of octopod taxonomists. As these animals receive a higher profile in fisheries, biodiversity and behavioural studies, the need for thorough and detailed taxonomy is higher than ever before. The authors call for higher moral and financial support for this critical alpha taxonomy.

INTRODUCTION

In July 1988, the "International Workshop on Systematics and Biogeography of Cephalopods" was held in Washington DC. The workshop was sponsored by the Cephalopod International Advisory Council (CIAC). The primary objectives of this workshop were to address the numerous taxonomic problems associated with many cephalopod groups, particularly the cuttlefishes and octopuses, and several speciose, commercially important families of squids. The results of this workshop were published in two volumes (Voss *et al*. 1998), with these works making a considerable contribution to the field.

For the benthic octopuses (Family Octopodidae), much has changed in the intervening 15 years. Considerable research activity has been focused on octopus systematics, particularly in the Indo-West Pacific and Australian regions (Stranks, 1988a–b, 1990; Gleadall, 1991a–b, 1993a–b, 1997, Gleadall and Naggs, 1991; Lu and Stranks, 1992; Norman, 1992a–c, 1993a–c, 1998, 2000, 2001; Stranks and Norman, 1993; Norman and Hochberg, 1994; Allcock, 1997; Norman and Sweeney, 1997; Norman *et al.* 1997; Lu, 1998; Gonzalez *et al.*, 1998; Hochberg, 1998; Nateewathana, 1997; Nateewathana and Norman, 1999; O'Shea, 1999; Guerra *et al.*, 2000; Guerrero Kommritz, 2000; Norman and Lu, 2000; Norman and Finn, 2001; Allcock and Piertney, 2002; Muus, 2002; Allcock *et al.*, 2003).

The aim of this paper is to revise the species-level taxonomy of the family Octopodidae, updating the earlier works that resulted from the Washington workshop. Through both primary field surveys and studies of museum collections, many taxonomic problems have been addressed and clarified. A number of nominal species of octopuses have been revised and numerous new species have been recognised. Revisions, omissions, corrections and a list of new taxa are presented. A generic level revision and updates on phylogenetic studies on this group are currently in progress.

The past 17 years have been a productive period for discovery of new species. More than 150 new species are currently recognised from the Indo-West Pacific region alone (see cited references above, and Norman and Hochberg, unpubl. data). This more than doubles the estimated total number of octopus species in the world. These new discoveries have resulted from

increased fieldwork, improved sampling techniques and critical review of previously unexamined preserved specimens in museum collections. Major surveys have been undertaken in tropical, temperate and polar regions, in all habitats from intertidal areas to the deep sea.

As the value and profile of octopuses increases as fisheries targets, the need for rigorous taxonomic knowledge is greater than ever before. Current impediments to progress on octopus taxonomy are discussed along with recognition of future priorities.

Revision of taxonomic decisions

As a result of this recent research activity, many of the decisions made by the octopus working group in 1988 now require updating. Table 1 presents revised designations for a number of species treated in Toll and Voss (1998) and Toll (1998).

Two key species groups previously treated within the genus *Octopus* have been sources of considerable taxonomic confusion. Norman and Finn (2001) revised the "*horridus* species-group" *sensu* Norman (1992c), coining the subgeneric name *Abdopus* to define these small long-armed octopuses. Recent molecular studies of the phylogeny of octopuses of the family Octopodidae (Hudelot, 2000) have demonstrated that the genus *Octopus* is polyphyletic and that a major generic revision of the family is required. We consider that the characters defining *Abdopus* are sufficient to warrant generic status and, as such, it is here raised to generic level.

In Norman and Finn (2001) the status of many historical names were reviewed. The main taxonomic decisions were:

· *Abdopus aculeatus* d'Orbigny, 1834 is resurrected as a valid species (removed from synonymy of *filamentosus* Blainville, 1826 on the basis of gill lamellae counts).

· The type series of *Octopus aranea* d'Orbigny, 1834 consists of two species, the poorest condition specimen also being the holotype of *filamentosus*. At present, *aranea* is considered unrecognisable and unresolved.

· *Octopus argus* Krauss, 1848 is resurrected as a valid species (removed from the synonymy of *A. horridus* d'Orbigny, 1826 on the basis of spermatophore characters and the presence of enlarged suckers).

· *Octopus filamentosus* Blainville, 1826 is considered unrecognisable (and invalid) as the single type specimen is in such poor condition. Until well-preserved material from the type locality (Mauritius) is obtained, the status of this species remains unresolved.

· *Abdopus harmandi* Rochebrune, 1882 is placed in the synonymy of *aculeatus* (removed from synonymy of the unrecognisable *filamentosus*, differing in gill lamellae counts).

· Toll and Voss (1998) placed *Octopus niveus* Lesson, 1830 in the synonymy of *O. filamentosus* at the same time as designating the type of *A. aculeatus* as the neotype for *O. niveus*. In the absence of a type specimen, any additional material from the type locality and any valid diagnostic characters, *niveus* is considered as unrecognisable and unresolved. We do not consider Toll and Voss's designated neotype as valid.

Similar confusion surrounds members of the "*aegina* species-group" *sensu* Robson (1929) and Norman (1992c) (= the genus *Amphioctopus* Fischer, 1882). A detailed discussion of key non-ocellate member taxa is provided in the Appendix. The primary taxonomic decisions are:

· *Amphioctopus aegina* Gray, 1849, *A. kagoshimensis* Ortmann, 1888 and *A. marginatus* Taki, 1964 are considered distinct and valid species.

· *A. dollfusi* Robson, 1928 and *A. hardwickei* Gray, 1849 are junior synonyms of *A. aegina*.

· *A. striolatus* Dong, 1976 is a junior synonym of *A. marginatus*.

In addition, it should be reinforced that *A. areolatus* de Haan in d'Orbigny, 1839–41, *A. ocellatus* Gray, 1849 and *A. brocki* Ortmann, 1888 are all junior synonyms of *A. fangsiao* d'Orbigny, 1839–41 (see Gleadall and Naggs, 1991).

Several taxa treated in O'Shea's (1999) revision of New Zealand octopods require comment. Following examination of reference material from eastern Australia and New Zealand, we propose that *Octopus gibbsi* O'Shea, 1999 is a synonym of *O. tetricus* Gould, 1852, a common

Table 1. Revised designations to nominal species of the family Octopodidae.

Species	1988 Workshop decision	Revised status	Comments
INDIAN OCEAN			
Octopus aranea Orbigny, 1834	junior synonym of *Octopus filamentosus* Blainville, 1826	unresolved	see Norman and Finn, 2001
Octopus argus Krauss, 1848	junior synonym of *Octopus horridus* Orbigny, 1826	valid species	see Norman and Finn, 2001
Octopus filamentosus Blainville, 1826	valid	unresolved	see Norman and Finn, 2001
WEST PACIFIC			
Octopus aculeatus Orbigny, 1834	junior synonym of *Octopus filamentosus* Blainville, 1826 as well as being designated neotype of another proposed synonym, *O. niveus* Lesson, 1830	valid species	see Norman and Finn, 2001 = *Abdopus aculeatus*
Octopus aegina Gray, 1849	*nomen dubium*	valid species in Appendix	= *Amphioctopus aegina* see discussion on *Amphioctopus*
Callistoctopus arakawai Taki, 1964	uncertain junior synonym of *Callistoctopus ornatus* Gould, 1848	junior synonym of *Callistoctopus ornatus* Gould, 1848	see Norman 1993c
Octopus areolatus de Haan in Orbigny, 1839–41	valid	junior synonym of *Amphioctopus fangsiao* d'Orbigny, 1839–41	see Gleadall, 1991
Octopus berenice Gray, 1849	*nomen dubium*	valid species, based on additional material linked to the type in the British Museum	Hochberg, unpubl. data
Octopus brocki Ortmann, 1888	valid	junior synonym of *Amphioctopus fangsiao* d'Orbigny, 1839–41	see Gleadall, 1991
Octopus dollfusi Robson, 1928	junior synonym of *Octopus hardwickei* Gray, 1849	junior synonym of *Amphioctopus aegina* Gray, 1849	see discussion on *Amphioctopus* in Appendix
Octopus hardwickei Gray, 1849	valid	junior synonym of *Amphioctopus aegina* Gray, 1849	see discussion on *Amphioctopus* in Appendix
Octopus harmandi Rochebrune, 1882 Blainville, 1826	junior synonym of *Octopus filamentosus* d'Orbigny, 1834	junior synonym of *Abdopus aculeatus*	see Norman and Finn, 2001
Octopus hawiiensis Eydoux and Souleyet, 1852	*nomen dubium*	valid species, missing type found in MNHN, Paris	Hochberg, unpubl. data
Octopus marginatus Taki, 1964	*nomen dubium*	valid species	=*Amphioctopus marginatus* see discussion on *Amphioctopus* in Appendix
Octopus niveus Lesson, 1830	junior synonym of *Octopus filamentosus* Blainville, 1826	unresolved	see Norman and Finn, 2001
Octopus striolatus Dong, 1976	valid	junior synonym of *Amphioctopus marginatus* Taki, 1964	see discussion on *Amphioctopus* in Appendix

species in New South Wales. In the absence of type material, O'Shea resurrects *Pinnoctopus cordiformis* (Quoy and Gaimard, 1832) as the senior synonym of *Macroctopus maorum* Hutton, 1880. Quoy and Gaimard's original description of *cordiformis* refers to a large animal with arms of almost equal length, the lateral pairs being slightly shorter. This arm formula does not match with that of the species previously treated under the name *maorum*, which has an arm formula of 1>2>3>4, the dorsal arms being obviously longer and more robust than the subsequent arm pairs. Quoy and Gaimard's description more closely matches *Enteroctopus zealandicus*, another large octopus found in the same general region. The genus *Pinnoctopus* was coined by Orbigny (1845) with the diagnostic character of a fin-like flap around the margin of the mantle. We believe that this structure is an artefact of poor preservation, where loose skin settles in a flange around the lateral mantle border. We have observed such a structure while preserving specimens of *Enteroctopus dofleini* (Wülker, 1910) from the northern Pacific Ocean. This has not been observed while preserving specimens of *maorum*. This preservation artefact further supports the suggestion that Quoy and Gaimard's species is in fact a member of the genus *Enteroctopus* (namely *zealandicus*). In the light of this confusion, the limited original description and the absence of a type specimen for *cordiformis*, we choose at this stage to leave the name *Pinnoctopus cordiformis* as unresolved, making *Macroctopus maorum* the available name for the distinctive species found in New Zealand and temperate Australian waters.

Table 2 presents the details and proposed status of an additional eight historical species names omitted from the 1988 workshop publications.

Table 2. Nominal species omitted from Toll and Voss (1998) and Toll (1998).

Old species omitted	Type locality	Status	Comments
Octopus appendiculatus De. de Montford (date?)	(Indian Ocean)	*nomen nudum*	unsourced reference in Blainville, 1826
Octopus cuvieri Orbigny, 1826	Pondicherry, India	junior synonym of *Callistoctopus lechenaulti* Orbigny, 1840	-
Octopus cyanea var. *gracilis* Robson, 1929	Madras, India	junior synonym of *Octopus cyanea* Gray, 1849	see Norman, 1992a
Octopus dubius Souleyet, 1852	Bourbon Is. (= Reunion Is.), Indian Ocean	*nomen dubium*	by Thomas, 1977
Eledonenta filholiana Rochebrune, 1884	Fiji	unresolved	member of *Callistoctopus*
Octopus hoylei var. *annae* Robson, 1929	Persian Gulf	junior synonym of *Pteroctopus hoylei* (Hoyle, 1909)	potential mixed lot: paratypes from shallow water
Octopus lechenaulti Orbigny, 1826	Pondicherry, India	unresolved	member of *Callistoctopus*
Callistoctopus magnocellatus Taki, 1964	Iyeno-Kushi, Japan	junior synonym of *Octopus cyanea* Gray, 1849	see Norman, 1992a (not *Callistoctopus*)

Revisions to the "Classification of Recent Cephalopoda" (Sweeney and Roper, 1998)

The following octopus taxa have been described since the 1988 workshop and should be added to Sweeney and Roper's (1998) Classification of Recent Cephalopoda:

· *Abdopus abaculus* Norman and Sweeney, 1997
· *Abdopus capricornicus* Norman and Finn, 2001
· *Adelieledone piatkowski* Allcock *et al.*, (2003)
· *Amphioctopus neglectus* Nateewathana and Norman, 1999
· *A. rex* Nateewathana and Norman, 1999
· *A. siamensis* Nateewathana and Norman, 1999
· *Callistoctopus nocturnus* Norman and Sweeney, 1997
· *Bathypolypus pugniger* Muus, 2002
· *Benthoctopus clyderoperi* O'Shea, 1999
· *B. karubar* Norman, Hochberg and Lu, 1997
· *B. tangaroa* O'Shea, 1999
· *B. tegginmathae* O'Shea, 1999
· *Galeoctopus lateralis* Norman, Boucher and Hochberg, 2004
· *Graneledone gonzalezi* Guerra, Gonzales and Cherel, 2000
· *G. taniwha taniwha* O'Shea, 1999
· *G. taniwha kubodera* O'Shea, 1999
· *G. yamana* Guerrero Kommritz, 2000
· *Microeledone mangoldi* Norman, Hochberg and Boucher-Rodoni, 2004
· *Octopus bulbus* Norman, 2001
· *O. harpedon* Norman, 2001
· *O. kaharoa* O'Shea, 1999
· *O. mernoo* O'Shea, 1999
· *O. micros* Norman, 2001
· *O. pumilus* Norman and Sweeney, 1997
· *O. pyrum* Norman, Hochberg and Lu, 1997
· *Thaumeledone marshalli* O'Shea, 1999
· *T. zeiss* O'Shea, 1999
· *Vulcanoctopus hydrothermalis* Gonzalez *et al.*, 1998

Table 3 is an alphabetical list of nominal species in the family Octopodidae. Generic placements and taxonomic status for each name are presented. A number of species previously placed in the genus *Octopus* are treated here under recently resurrected generic names. These include: *Amphioctopus* Fischer, 1882; *Callistoctopus* Taki, 1964; *Enteroctopus* Rochebrune and Mabille, 1889; *Macroctopus* Robson, 1928; *Macrotritopus* Grimpe, 1922 and *Paroctopus* Naef, 1923. Taxa designated as "unplaced" are currently treated under the genus Octopus until a major generic-level revision of the family Octopodidae is undertakenjects of a major generic revision in progress by the authors.

Potential species names are also identified for a number of regional populations of octopuses currently treated under the catchall names "*vulgaris*", "*macropus*" and "*defillipi*". These names are available should current studies demonstrate that any of these populations warrant distinct species status.

A total of 374 species names are listed for this family (Table 3) of which 186 we consider to be valid. A total of 102 names are considered synonyms of other species. Five names are considered to lack any form of description or type material (*nomina nuda*), while 23 names are considered dubious (*nomina dubia*) due to problems with type material (poor, lost or none designated), type locality (ill-defined, indecipherable or none designated) and/or insufficient original descriptions to allow species recognition. Four names were pre-occupied of which three were assigned replacement names. The remaining 55 names are considered unresolved and await further investigation.

We consider the tally of valid species to be a considerable underestimate of the total number of extant species in this family. We have amassed observations, museum records, data and descriptions in progress for more than 150 additional unnamed species within this family. It is clear that there is a considerably higher diversity of octopuses than previously suspected. Currently the rate at which new species are being discovered greatly exceeds the rate at which species are being formally described.

Hidden diversity

Regional surveys

The bulk of new species discoveries are coming from recent regional reviews of octopod faunas. Nateewathana (1997) reported 11 species of benthic octopuses from the waters surrounding Thailand of which five were new to science. Lu (1998) reported 22 species from Taiwanese waters

Table 3. Alphabetical listing of nominal species of the Family Octopodidae

Valid species in bold. * = type species of recognised genera.
Authorities for genera: *Abdopus* Norman and Finn, 2001; *Adelieledone* Allcock *et al.* (2003); *Ameloctopus* Norman, 1992; *Amphioctopus* Fischer, 1882; *Bathypolypus* Grimpe, 1921a; *Bentheledone* Robson, 1932; *Benthoctopus* Grimpe, 1921; *Callistoctopus* Taki, 1964; *Cistopus* Gray, 1849; *Eledone* Leach, 1817; *Enteroctopus* Rochebrune and Mabille, 1889; *Euaxoctopus* Voss, 1971; *Galeoctopus* Norman, Boucher and Hochberg., 2004; *Graneledone* Joubin, 1918; *Grimpella* Robson, 1928; *Hapalochlaena* Robson, 1929; *Macrochlaena* Robson, 1929; *Macroctopus* Robson, 1928; *Macrotritopus* Grimpe, 1922; *Megaleledone* Taki, 1961; *Octopus* Cuvier, 1797; *Microeledone* Norman, Hochberg and Boucher-Rodoni, 2004; *Pareledone* Robson, 1932; *Paroctopus* Naef, 1923; *Pteroctopus* Fischer, 1882; *Robsonella* Adam, 1938; *Scaeurgus* Troschel, 1857; *Teretoctopus* Robson, 1929; *Tetracheledone* Voss, 1955; *Thaumeledone* Robson, 1930; *Velodona* Chun, 1915; *Vosseledone* Palacio, 1978; *Vulcanoctopus* Gonzalez *et al.*, 1998.

Taxa	Generic placement	Status
abaculus (Norman and Sweeney, 1997: 109)	*Abdopus*	valid
abruptus (Sasaki, 1920: 173)	*Benthoctopus*	valid
aculeatus (d'Orbigny, 1834: pls 7, 8)	*Abdopus*	valid
		synonym: *harmandi* Rochebrune, 1882: 73
adamsi Benham, 1944: 259	unplaced	synonym of *huttoni*
***adelieana** (Berry, 1917: 17)	***Adelieledone***	valid
aegina (Gray, 1849: 7)	*Amphioctopus*	valid
		synonyms: *dollfusi* Robson, 1928: 43
		hardwickei Gray, 1849: 8
		smedleyi Robson, 1932: 24
alatus Sasaki, 1920: 180	unplaced	unresolved
alberti Joubin, 1895: 18	unplaced	juvenile: *nomen dubium*
albida (Berry, 1917: 15)	*Bentheledone*	valid
albidus (Taki, 1962: 397)	*Pteroctopus*	synonym of *hoylei*
albus Rafinesque, 1814: 29	*Octopus*	synonym of *vulgaris*
alcocki Robson, 1932: 251	*Teretoctopus*	valid
alderi (Verany, 1851: 32)	*Callistoctopus*	synonym of *macropus*
aldrovandi (Montfort, 1802: 55)	*Eledone*	synonym of *cirrhosa*
alecto Berry, 1953: 56	unplaced	valid
alpheus (Norman, 1993: 270)	*Callistoctopus*	valid
amboinensis Brock, 1887: 598	unplaced	*nomen dubium*
americanus Baker in Denys de Montfort, 1802: 38	*Octopus*	unresolved
		potential name for West Atlantic "vulgaris"
		synonyms: *bakerii* d'Orbigny, 1826: 144
		eudora Gray, 1849: 9
		geryonea Gray, 1849: 7
annae (Robson, 1929: 220)	*Pteroctopus*	synonym of *hoylei*
antarctica (Thiele, 1920: 434)	*Pareledone*	valid
antarctica Voss, 1976: 448	*Graneledone*	valid

Table 3. (continued)

Taxa	Generic placement	Status
antillarum "d'Orbigny ??" in Dall, 1896: 27	unplaced	*nomen nudum*
apollyoni (Berry, 1912: 284)	*Enteroctopus*	synonym of *dofleini*
appendiculatus Blainville, 1826: 185	unplaced	*nomen nudum*
**arakawai* Taki, 1964: 292	*Callistoctopus*	synonym of *ornatus*
aranea d'Orbigny, 1834: pl. 5	unplaced	unresolved
araneoides Taki, 1964: 307	unplaced	unresolved
arborescens Hoyle, 1904: 189	unplaced	unresolved
arcticus (Prosch, 1847: 59)	*Bathypolypus*	valid synonyms: *faeroensis* Russell, 1909: 446 *grönlandicus* Dewhurst in Steenstrup, 1856: 17 *sasakii* Robson, 1927: 257
areolatus (de Haan, 1839–1841: 65)	*Amphioctopus*	synonym of *fangsiao*
argus Krauss, 1848: 132	unplaced	valid
asper (Akimushkin, 1963: 138)	*Enteroctopus*	synonym of *dofleini*
aspilosomatis (Norman, 1993a: 279)	*Callistoctopus*	valid
australis Hoyle, 1885: 224	unplaced	valid
bairdii (Verrill, 1873: 5)	*Bathypolypus*	valid synonyms: *lentus* Verrill, 1880: 138 *obesus* Verrill, 1880: 137 *proschi* Muus, 1962: 13
bakerii d'Orbigny, 1826: 144	*Octopus*	synonym of *americanus* (if latter is valid name for W. Atlantic "vulgaris")
balboai Voss, 1971: 16	unplaced	valid
bandensis Hoyle, 1885: 227	unplaced	juvenile: *nomen dubium*
berenice Gray, 1849: 11	unplaced	valid
bermudensis (Hoyle, 1885: 228)	*Callistoctopus*	synonym of *furvus* (if latter is valid name for W. Atlantic "macropus")
berrima Stranks and Norman, 1993: 355	unplaced	valid
berryi Robson, 1924: 658	*Benthoctopus*	valid
bimaculatus Verrill, 1883b: 121	*Octopus*	valid
bimaculoides Pickford and McConnaughey, 1949: 14	*Octopus*	valid
bitentaculatus Risso, 1854: 61	*Octopus*	synonym of *vulgaris*
bocki Adam, 1941: 1	unplaced	valid
boreopacifica Nesis, 1982:322	*Graneledone*	valid synonym: *pacifica* Voss and Pearcy, 1990
boscii Lesueur, 1821: 110	unplaced	*nomen nudum*

Table 3. (continued)

Taxa	Generic placement	Status
brevipes d'Orbigny, 1835: 22	unplaced	juvenile: *nomen dubium*
***brevis** (Hoyle, 1885: 230)	*Thaumeledone*	valid
brevitentaculatus Blainville, 1826: 187	*Octopus*	synonym of *vulgaris*
briareus Robson, 1929: 612	unplaced	valid
brocki (Ortmann, 1888: 645)	*Amphioctopus*	synonym of *fangsiao*
bulbus Norman, 2001: 680	unplaced	valid
bunurong (Stranks, 1990: 462)	*Callistoctopus*	valid
burryi (Voss, 1950: 76)	*Amphioctopus*	valid synonyms: *vincenti* Pickford, 1955: 159
bursarius Steenstrup in Hoyle, 1886: 14	*Cistopus*	synonym of *indicus*
caerulescens Blainville, 1826: 189	unplaced	*nomen dubium*
californicus Berry, 1911: 590	unplaced	valid
campbelli Smith, 1902: 201	unplaced	valid
canthylus Voss and Pearcy, 1990: 69	*Benthoctopus*	valid
caparti Adam, 1950: 7	*Eledone*	valid
capensis Eydoux and Souleyet, 1852: 11	unplaced	juvenile: *nomen dubium*
capricornicus Norman and Finn, 2001: 24	*Abdopus*	valid
carlgreni Thore 1945: 52	*Eledone*	synonym of *schultzei*
carolinensis (Verrill, 1884: 235)	*Amphioctopus*	unresolved
cassiopeia Gray, 1849: 9	*Octopus*	synonym of *vulgaris*
cephea Gray, 1849: 15	unplaced	unresolved
challengeri (Berry, 1916: 49)	*Graneledone*	valid
***charcoti** (Joubin, 1905: 22)	*Pareledone*	valid
***charrua** Palacio, 1978: 282	*Vosseledone*	valid
chierchiae Jatta, 1889: 64	unplaced	valid
chromatus (Heilprin, 1888: 324)	*Callistoctopus*	synonym of *furvus* (if latter is valid name for W. Atlantic "macropus")
chuni Grimpe, 1922	unplaced	unresolved
ciliatus Rang, 1837: 65	unplaced	unresolved
cirrhosa (Lamarck, 1798: 130)	*Eledone*	valid synonyms: *aldrovandi* Montfort, 1802: 55 *octopodia* Linne, 1758: 658 (as *Sepia*) *pennanti* author unknown, in Hoyle, 1909: 296 *sepioidea* Rochebrune, 1884: 156
clyderoperi O'Shea, 1999: 209	*Benthoctopus*	valid
cocco (Verany, 1846: 109)	*Pteroctopus*	synonym of *tetracirrhus*
coerulescentes Fra Piero, 1895: 267	*Octopus*	synonym of *vulgaris*

Table 3. (continued)

Taxa	Generic placement	Status
colossus Gray, 1849: 19	unplaced	apocryphal: *nomen nudum*
communis (Park, 1885: 198)	*Macroctopus*	synonym of *maorum*
conispadiceus Sasaki, 1917: 367	unplaced	valid
cordiformis Quoy and Gaimard, 1832: 87	unplaced	unresolvedsee discussion
cornutus Owen, 1881: 131	unplaced	*nomen dubium*
cuvieri (d'Orbigny, 1826: 18)	*Callistoctopus*	synonym of *lechenaultii*
cyanea Gray, 1849: 15	*Octopus*	valid
		synonyms: *glaber* Rüppell in Wülker, 1920: 51
		gracilis Robson, 1929: 98
		herdmani Hoyle, 1904: 187
		horsti Joubin, 1898: 23
		magnocellatus Taki, 1964: 298
		marmoratus Hoyle 1885: 227
dana Robson, 1929: 140	*Macrotritopus*	synonym of *defillipi*
defilippi (Verany, 1851: 30)	*Macrotritopus*	valid
		synonyms: *dana* Robson, 1929: 140
		kempi Robson, 1929: 312
		Unresolved West Atlantic form:
		Available name: *scorpio*, Berry, 1920: 299
didynamus (Rafinesque, 1814: 28)	*Callistoctopus*	synonym of *macropus*
dierythraeus (Norman, 1993: 284)	*Callistoctopus*	valid
****digueti*** Perrier and Rochebrune, 1894: 770	*Paroctopus*	valid
dofleini (Wulker, 1910: 7)	*Enteroctopus*	valid
		synonyms: *apollyoni* Berry, 1912: 284
		asper Akimushkin, 1963: 138
		gilbertianus Berry, 1912: 284
		punctatus Gabb, 1862: 170
dollfusi (Robson, 1928: 43)	*Amphioctopus*	synonym of *aegina*
duplex Hoyle, 1885: 226	unplaced	synonym of *superciliosus*
elegans Brock, 1887: 597	unplaced	*nomen dubium*
**equivocus* (Robson, 1929: 169)	*Macrotritopus*	juvenile: unresolved
		synonym: *gracilis* Verrill, 1884: 236
ergasticus (Fischer and Fischer, 1892: 298)	*Bathypolypus*	valid
		synonyms: *lothei* (Chun, 1913: 18)
		profundicola (Massy, 1907: 377)
eudora Gray, 1849: 9	*Octopus*	synonym of *americanus*
		(if latter is valid name for W. Atlantic "vulgaris")

Table 3. (continued)

Taxa	Generic placement	Status
eureka (Robson, 1929: 179)	*Benthoctopus*	synonym of *hyadesi*
eurycephala (Taki, 1964: 313)	*Pteroctopus*	unresolved
exannulatus (Norman, 1993: 321)	*Amphioctopus*	valid
faeroensis (Russell, 1909: 446)	*Bathypolypus*	synonym of *arcticus*
fangsiao (d'Orbigny, 1839–1841: 70)	*Amphioctopus*	valid
		synonyms: *areolatus* de Haan, 1839–1841: 65
		brocki Ortmann, 1888: 645
		fangsiao etchuanus Sasaki, 1929: 53
		fangsiao typicus d'Orbigny, 1839–1841: 70
		ocellatus Gray, 1849: 15
fangsiao etchuanus (Sasaki, 1929: 53)	*Amphioctopus*	synonym of *fangsiao*
fangsiao typicus (d'Orbigny, 1839–1841: 70)	*Amphioctopus*	synonym of *fangsiao*
fasciata (Hoyle, 1886: 94)	*Hapalochlaena*	valid
		synonym: *pictus* Brock, 1882: 603
		robustus Brock, 1887: 317
favonius Gray, 1849: 9	unplaced	valid
filamentosus Blainville, 1826: 188	unplaced	unresolved
filholiana Rochebrune, 1884: 157	unplaced	unresolved
filosus Howell, 1867: 240	unplaced	valid
		synonym: *hummelincki* Adam, 1936: 1
fimbriatus (Rüppell in d'Orbigny, 1841: 64)	*Abdopus*	synonym of *horridus*
fitchi Berry, 1953: 54	unplaced	valid
flindersi (Cotton, 1932: 543)	*Macroctopus*	synonym of *maorum*
fontaniana africana Robson, 1929: 189	unplaced	unresolved
fontanianus (d'Orbigny, 1834: 28)	*Robsonella*	valid
framensis Lu and Stranks, 1994: 227	*Pareledone*	valid
frayedus (Rafinesque, 1814: 28)	*Callistoctopus*	synonym of *macropus*
fujitai Sasaki, 1929: 70	unplaced	unresolved
furvus (Gould, 1852: 475)	*Callistoctopus*	unresolved
		potential name for West Atlantic "macropus"
		synonyms: *bermudensis* Hoyle, 1885: 228
		chromatus Heilprin, 1888: 324
fuscus Taki, 1964: 316	*Benthoctopus*	valid
fusiformis Brock, 1887: 601	unplaced	*nomen dubium*
gardineri Hoyle, 1905: 976	unplaced	valid
gaucha Haimovici, 1988: 82	*Eledone*	valid
geryonea Gray, 1849: 7	*Octopus*	synonym of *americanus*
		(if latter is valid name for W. Atlantic "vulgaris")

Table 3. (continued)

Taxa	Generic placement	Status
gibbsi O'Shea, 1999: 120	*Octopus*	synonym of *tetricus*
gigas Oken, 1835: 345	unplaced	apocryphal: *nomen nudum*
gilbertianus (Berry, 1912: 284)	*Enteroctopus*	synonym of *dofleini*
glaber (Sasaki, 1920: 172)	*Benthoctopus*	synonym of *hokkaidensis*
glaber Rüppell in Wülker, 1920: 51	*Octopus*	synonym of *cyanea*
globosus Appellöf, 1886: 7	unplaced	unresolved
gonzalezi Guerra, Gonzales and Cherel, 2000	*Graneledone*	valid
gracilis (Verrill, 1884: 236)	*Macrotritopus*	pre-occupied name replaced by *equivocus*
gracilis Robson, 1929: 98	*Octopus*	synonym of *cyanea*
granulatus (Lamarck, 1799: 130)	*Amphioctopus*	unresolved
graptus (Norman, 1993: 296)	*Callistoctopus*	valid
grimpei Robson, 1924: 208	*Bathypolypus*	synonym of *valdiviae*
grönlandicus (Dewhurst in Steenstrup, 1856: 17)	*Bathypolypus*	synonym of *arcticus*
gronosus (Blainville, 1826: 186)	*Callistoctopus*	synonym of *macropus*
guangdongensis (Dong, 1976: 213)	*Abdopus*	unresolved
gunteri Robson, 1930:392	*Thaumeledone*	valid
hardwickei (Gray, 1849: 8)	*Amphioctopus*	synonym of *aegina*
harmandi (Rochebrune, 1882: 73)	*Abdopus*	synonym of *aculeatus*
harpedon Norman, 2001: 677	unplaced	valid
harrissoni (Berry, 1917: 24)	*Pareledone*	valid
hattai Sasaki, 1929: 87	unplaced	valid
hawiiensis Eydoux and Souleyet, 1852: 9	unplaced	valid
herdmani Hoyle, 1904: 187	*Octopus*	synonym of *cyanea*
heteropus Rafinesque, 1814: 28	*Octopus*	synonym of *vulgaris*
hoeki Joubin, 1898	unplaced	unresolved
hokkaidensis (Berry, 1921: 352)	*Benthoctopus*	valid synonym: *glaber* Sasaki, 1920: 172
hongkongensis Hoyle, 1885: 224	unplaced	unresolved synonym: *tenuicirrus* Sasaki, 1929: 78
horridus (d'Orbigny,1826: 144)	*Abdopus*	valid synonyms: *fimbriatus* Rüppell in d'Orbigny, 1841: 64
horsti Joubin, 1898: 23	*Octopus*	synonym of *cyanea*
hoylei (Berry, 1909: 407)	*Pteroctopus*	valid synonyms: *albidus* Taki, 1962: 397 *annae* Robson, 1929: 220
hubbsorum Berry, 1953: 53	*Octopus*	valid

Table 3. (continued)

Taxa	Generic placement	Status
hummelincki Adam, 1936: 1	unplaced	synonym of *filosus*
huttoni Benham, 1943: 53	unplaced	valid
		synonym: *adamsi* Benham, 1944: 259
hyadesi Rochebrune and Mabille, 1889: H6	unplaced	valid
		synonyms: *eureka* Robson, 1929: 179
		magellanicus Robson, 1930a: 333
hyalinus Rang, 1837: 66	unplaced	juvenile: unresolved
****hydrothermalis*** Gonzalez *et al.*, 1998: 172	*Vulcanoctopus*	valid
incertus Targioni-Tozzetti, 1869: 589	unplaced	*nomen dubium*
inconspicuous Brock, 1887: 603	unplaced	unresolved
****indicus*** (Rapp, 1835: 24)	*Cistopus*	valid
		synonym: *bursarius* Steenstrup in Hoyle, 1886: 14
****indicus*** Robson, 1929: 608	*Teretoctopus*	valid
januarii (Hoyle, 1885: 229)	*Benthoctopus*	valid
joubini Robson, 1929: 161	unplaced	valid
kagoshimensis (Ortmann, 1888: 664)	*Amphioctopus*	valid
kaharoa O'Shea, 1999: 174	unplaced	valid
karubar Norman, Hochberg and Lu, 1997: 360	*Benthoctopus*	valid
kaurna Stranks, 1990: 460	unplaced	valid
kempi Robson, 1929: 312	*Macrotritopus*	synonym of *defillipi*
keralensis (Oommen, 1966: 56)	*Pteroctopus*	unresolved
****lateralis*** Norman, Boucher and Hochberg, 2004	Galeoctopus	valid
kermadecensis (Berry, 1914: 138)	*Callistoctopus*	valid
lechenaultii (d'Orbigny, 1826: 18)	*Callistoctopus*	valid
		synonym: *cuvieri* d'Orbigny, 1826: 18
leioderma (Berry, 1911: 590)	*Benthoctopus*	valid
lentus (Verrill, 1880: 138)	*Bathypolypus*	synonym of *bairdii*
leucoderma Sangiovanni, 1829: 317	*Eledone*	unresolved
levis (Hoyle, 1885: 229)	*Benthoctopus*	valid
****litoralis*** Norman, 1992: 569	*Ameloctopus*	valid
lobensis Castellanos and Menni, 1969: 92	*Octopus*	synonym of *tehuelchus*
longimanus (d'Orbigny, 1840: 18)	*Callistoctopus*	synonym of *macropus*
longipes Leach, 1817: 139	unplaced	*nomen dubium*
longispadiceus Sasaki, 1917: 366	unplaced	unresolved
lothei (Chun, 1913: 18)	*Bathypolypus*	synonym of *ergasticus*
****lunulata*** (Quoy and Gaimard, 1832: 86)	*Hapalochlaena*	valid
luteus (Sasaki, 1929: 45)	*Callistoctopus*	valid
machikii Brock, 1887: 599	unplaced	*nomen dubium*

Table 3. (continued)

Taxa	Generic placement	Status
macrophallus Voss and Pearcy, 1990: 82	*Benthoctopus*	valid
macropodus (San Giovanni, 1829: 319)	*Callistoctopus*	synonym of *macropus*
macropus (Risso, 1826: 3)	*Callistoctopus*	valid
		synonyms: *alderi* Verany, 1851: 32
		didynamus Rafinesque, 1814: 28
		frayedus Rafinesque, 1814: 28
		gronosus Blainville, 1826: 186
		longimanus d'Orbigny, 1840: 18
		macropodus San Giovanni, 1829: 319
		ruber Cantraine, 1841: 18
		Unresolved West Atlantic form:
		Available name: *furvus* Gould, 1852: 475
		synonyms: *bermudensis* Hoyle, 1885: 228
		chromatus Heilprin, 1888: 324
macrotyla Voss, 1976: 454	*Graneledone*	valid
maculatus Rafinesque, 1814: 29	*Octopus*	synonym of *vulgaris*
maculosa (Hoyle, 1883: 319)	*Hapalochlaena*	valid
madokai Berry, 1921: 352	unplaced	unresolved
		replacement name for preoccupied *pustulosus* Sasaki, 1920: 176
magellanicus Robson, 1930: 333	*Benthoctopus*	synonym of *hyadesi*
magnificus (Villanueva, Sanchez and Compagno, 1992: 39)	*Enteroctopus*	valid
magnocellatus Taki, 1964: 298	*Octopus*	synonym of *cyanea*
****mangoldi*** Norman, Hochberg and Boucher-Rodoni, 2004		
****maorum*** (Hutton, 1880: 1)	*Macroctopus*	valid
		synonyms: *communis* Park, 1885: 198
		flindersi Cotton, 1932: 543
marginatus (Taki, 1964: 304)	*Amphioctopus*	valid
		synonym: *striolatus* Dong, 1976: 212
marinum Koelreut (date unknown)	*Octopus*	synonym of *vulgaris*
marmoratus Hoyle 1885: 227	*Octopus*	synonym of *cyanea*
marshalli O'Shea, 1999: 249	*Thaumeledone*	valid
massyae Voss, 1964: 511	*Eledone*	valid
maya Voss and Solis, 1966: 617	*Octopus*	valid
medoria Gray, 1849: 14	unplaced	unresolved
megalocyathus (Gould, 1852: 471)	*Enteroctopus*	valid
		synonyms: *brucei* Hoyle, 1912: 276
		juttingi Robson, 1929b: 616
		membranaceus Rochebrune and Mabille,1889:H7

Table 3. (continued)

Taxa	Generic placement	Status
		patagonicus Lönnberg, 1907: 50
		pentherinus Rochebrune and Mabille, 1889: H7
megalops Taki, 1964: 310	unplaced	unresolved
**membranaceus* (Quoy and Gaimard, 1832: 89)	*Amphioctopus*	*nomen dubium*
**membranaceus* Rochebrune and Mabille,1889:H7	*Enteroctopus*	synonym of *megalocyathus*
mercatoris Adam, 1937: 76	unplaced	valid
mernoo O'Shea, 1999: 165	unplaced	valid
microphthalmus Goodrich, 1896: 20	unplaced	valid
micropyrsus Berry, 1953: 52	unplaced	valid
micros Norman, 2001: 683	unplaced	valid
microsicya (Rochebrune, 1884: 158)	*Eledone*	synonym of *moschata*
mimus Gould, 1852: 473	*Octopus*	valid
minor minor Sasaki, 1920: 181	unplaced	unresolved
minor pardalis Sasaki, 1929: 94	unplaced	unresolved
minor typicus Sasaki, 1929: 90	unplaced	unresolved
mollis Gould, 1852	unplaced	*nomen dubium*
monterosatoi Fra Piero, 1895: 268	unplaced	unresolved
montevideo Rang, 1837: 62	unplaced	*nomen dubium*
moschata (Lamarck, 1798: 130)	*Eledone*	valid
		synonyms: *microsicya* Rochebrune, 1884c: 158
moschatus Rafinesque, 1814: 28	*Octopus*	synonym of *vulgaris*
moschites Carus, 1824: 319	*Eledone*	unresolved
mototi (Norman, 1993: 329)	*Amphioctopus*	valid
mutilans Taki, 1942: 71	unplaced	valid
nanhaiensis Dong, 1976: 211	unplaced	unresolved
nanus Adam, 1973: 42	unplaced	valid
neglectus (Nateewathana and Norman, 1999: 452)	*Amphioctopus*	valid
nierstraszi (Adam, 1938: 14)	*Hapalochlaena*	valid
niger Rafinesque, 1814: 29	*Octopus*	synonym of *vulgaris*
nigra (Hoyle, 1910: 262)	*Eledone*	synonym of *schultzei*
niveus Lesson, 1830: 239	unplaced	unresolved
nocturnus (Norman and Sweeney, 1997: 117)	*Callistoctopus*	valid
normani (Massy, 1907: 379)	*Benthoctopus*	valid
obesus (Verrill, 1880: 137)	*Bathypolypus*	synonym of *bairdii*
occidentalis Steenstrup in Hoyle, 1885: 77	*Octopus*	valid
ocellatus (Gray, 1849: 15)	*Amphioctopus*	synonym of *fangsiao*
ochotensis Sasaki, 1920: 174	unplaced	unresolved

Table 3. (continued)

Taxa	Generic placement	Status
octopodia Linne, 1758: 658 (as *Sepia octopodia*)	*Eledone*	synonym of *cirrhosa*
octopodia Tryon, 1879: 113	*Octopus*	synonym of *vulgaris*
oculifer Hoyle, 1904: 14	*Octopus*	valid synonym: *roosevelti* Stuart, 1941: 1
oliveri Berry, 1914: 136	unplaced	valid
oregonae Toll, 1981: 88	*Benthoctopus*	valid
oregonensis Voss and Pearcy, 1990: 73	*Benthoctopus*	valid
ornatus (Gould, 1852: 476)	*Callistoctopus*	valid synonym: *arakawai* Taki, 1964: 292
oshimai Sasaki, 1929: 44	unplaced	unresolved
ovulum (Sasaki, 1917: 364)	*Amphioctopus*	valid
pacifica Voss and Pearcy, 1990: 85	*Graneledone*	synonym of *boreopacifica*
palari Lu and Stranks, 1992: 73	unplaced	valid
pallidus Hoyle, 1885: 223	unplaced	valid
**panamensis* Voss, 1971: 25	*Euaxoctopus*	valid
parvus Sasaki, 1917: 365	unplaced	valid
patagiatus Berry, 1913: 564	*Scaeurgus*	valid
penicillifer Berry, 1954: 66	unplaced	valid
pennanti author unknown, in Hoyle, 1909: 296	*Eledone*	synonym of *cirrhosa*
peronii Lesueur, 1821: 101	unplaced	unresolved
piatkowski Allcock, Hochberg, Rodhouse and Thorpe (2003)	*Adelieledone*	valid
pictus (Brock, 1882: 603)	*Hapalochlaena*	name pre-occupied synonym of *fasciata*
pictus Blainville, 1826: 8	unplaced	*nomen dubium*
pictus Verrill, 1883: 112	unplaced	name pre-occupied replaced by *verrilli verrilli*
pillsburyae Voss, 1975: 346	*Euaxoctopus*	valid
pilosus Risso, 1826: 4	*Octopus*	synonym of *vulgaris*
**piscatorum* (Verrill, 1879: 470)	*Benthoctopus*	synonym of *Bathypolypus bairdii* (see Muus, 2002) As a consequence, genus *Benthoctopus* requires revision
polymorpha (Robson, 1930: 390)	***Adelieledone***	valid
		polyzenia (Gray, 1849: 13) *Amphioctopus* valid
prashadi Adam, 1939: 103	unplaced	unresolved
pricei Berry, 1913: 73	unplaced	unresolved
profundicola (Massy, 1907: 377)	*Bathypolypus*	synonym of *ergasticus*

Table 3. (continued)

Taxa	Generic placement	Status
profundorum Robson, 1932: 237	*Benthoctopus*	valid
proschi Muus, 1962: 13	*Bathypolypus*	synonym of *bairdii*
pryzdensis Lu and Stranks, 1994: 232	*Pareledone*	valid
pseudonymus (Grimpe, 1922: 41)	*Benthoctopus*	valid
pugniger Muus, 2002: 195	*Bathypolypus*	valid
pulcher (Brock, 1887: 607)	*Amphioctopus*	juvenile: *nomen dubium*
pumilus Norman and Sweeney, 1997: 127	unplaced	valid
punctatus (Gabb, 1862: 170)	*Enteroctopus*	synonym of *dofleini*
pusillus Gould, 1852: 478	unplaced	*nomen dubium*
pustulosus Blainville, 1826: 186	unplaced	*nomen dubium*
pustulosus Sasaki, 1920: 176	unplaced	pre-occupied name, replaced by *madokai*
pyrum Norman et al., 1997: 365	unplaced	valid
rabassin Risso, 1854: 67	*Octopus*	synonym of *vulgaris*
rapanui (Voss, 1979: 360)	*Callistoctopus*	valid
rex (Nateewathana and Norman, 1999: 447)	*Amphioctopus*	valid
robsoni (Adam, 1941: 1)	*Amphioctopus*	valid
robustus (Brock, 1887: 317)	*Hapalochlaena*	synonym of *fasciata*
robustus Voss and Pearcy, 1990: 67	*Benthoctopus*	valid
roosevelti Stuart, 1941: 1	*Octopus*	synonym of *oculifer*
****rotunda*** (Hoyle, 1885: 230)	*Bentheledone*	valid
ruber (Cantraine, 1841: 18)	*Callistoctopus*	synonym of *macropus*
ruber Rafinesque, 1814: 28	*Octopus*	synonym of *vulgaris*
rubescens Berry, 1953: 51	unplaced	valid
rugosus Bosc 1792: 24	unplaced	unresolved
salebrosus Sasaki, 1920: 182	unplaced	valid
salutii Verany, 1839: 93	unplaced	valid synonym: *saluzzii* Naef, 1923: 699
saluzzii Naef, 1923: 699	unplaced	synonym of *salutii*
sanctaehelenae Robson, 1929: 74	*Octopus*	valid
saphenia Gray, 1849: 11	unplaced	unresolved
sasakii Robson, 1927: 257	*Bathypolypus*	synonym of *arcticus*
sasakii Taki, 1942: 75	unplaced	unresolved
scalenus (Hoyle, 1904: 13)	*Euaxoctopus*	valid
schmidti (Joubin, 1933: 4)	*Pteroctopus*	valid
schultzei (Hoyle, 1910: 261)	*Eledone*	valid

Table 3. (continued)

Taxa	Generic placement	Status
		synonym: *carlgreni* Thore 1945: 52
		nigra Hoyle, 1910: 262
		thysanophora Voss, 1962d: 265
scorpio (Berry, 1920: 299)	*Macrotritopus*	unresolved
		potential name for West Atlantic “defillipi”
selene Voss, 1971: 11	unplaced	valid
**senoi* Taki, 1961: 297	*Megaleledone*	synonym of *setebos*
sepioidea Rochebrune, 1884: 156	*Eledone*	synonym of *cirrhosa*
setebos Robson, 1932: 313	*Megaleledone*	valid
		synonym: *senoi* Taki, 1961: 297
siamensis (Nateewathana and Norman, 1999: 456)	*Amphioctopus*	valid
sibiricus Loyning, 1930: 1	*Benthoctopus*	valid
sinensis d’Orbigny, 1834: pl. 9	*Octopus*	unresolved
		potential name for Japanese “vulgaris”
smedleyi (Robson, 1932: 24)	*Amphioctopus*	synonym of *aegina*
***spinicirrus** Voss, 1955: 107	*Tetracheledone*	valid
spinosus Sasaki, 1920: 177	unplaced	unresolved
sponsalis (Fischer and Fischer, 1892: 297)	*Bathypolypus*	valid
striolatus (Dong, 1976: 212)	*Amphioctopus*	synonym of *marginatus*
superciliosus Quoy and Gaimard, 1832: 88	unplaced	valid
		synonyms: *duplex* Hoyle, 1885: 226
		westerniensis d’Orbigny, 1834: pl. 10
tangaroa O’Shea, 1999: 202	*Benthoctopus*	valid
taniwha kubodera O’Shea, 1999: 233	*Graneledone*	valid
taniwha taniwha O’Shea, 1999: 222	*Graneledone*	valid
taprobanensis (Robson, 1926: 165)	*Callistoctopus*	*nomen dubium*
tegginmathae O’Shea, 1999: 200	*Benthoctopus*	valid
tehuelchus d’Orbigny, 1834: 27 [in 1834–1847]	*Octopus*	valid
		synonym: *lobensis* Castellanos and Menni, 1969: 92
tenebricus Smith, 1884: 35	unplaced	valid
tenuicirrus Sasaki, 1929: 78	unplaced	synonym of *hongkongensis*
tenuipulvinus Sasaki, 1920: 182	unplaced	unresolved
***tetracirrhus** (Chiaie, 1830: pl. 72)	*Pteroctopus*	valid
		synonym: *cocco* Verany, 1846: 109
		titanotus Troschel, 1857: 51
tetradynamus Rafinesque, 1814: 28	*Octopus*	synonym of *vulgaris*
tetricus Gould, 1852: 474	*Octopus*	valid

Table 3. (continued)

Taxa	Generic placement	Status
		synonym: *gibbsi* O'Shea, 1999: 120
teuthoides Robson, 1929: 133	unplaced	juvenile: *nomen dubium*
***thaumastocheir** Robson, 1928: 110	*Grimpella*	valid
thielei Robson, 1932: 233	*Benthoctopus*	valid
thysanophora Voss, 1962: 265	*Eledone*	synonym of *schultzei*
titanotus (Troschel, 1857: 51)	*Pteroctopus*	synonym of *tetracirrhus*
***togata** Chun, 1915: 479	*Velodona*	valid
		synonym: *togata capensis* Robson, 1924: 206
togata capensis Robson, 1924: 206	*Velodona*	synonym of *togata*
tonganus (Hoyle, 1885: 225)	*Abdopus*	valid
tritentaculatus Risso, 1854: 63	*Octopus*	synonym of *vulgaris*
troscheli Targioni-Tozzetti, 1869: 113	*Octopus*	synonym of *vulgaris*
tsugarensis Sasaki, 1920: 175	unplaced	unresolved
tuberculatus Targioni-Tozzetti, 1869: 156	*Octopus*	synonym of *vulgaris*
turqueti (Joubin, 1905: 29)	*Pareledone*	valid
***unicirrhus** (Chiaie, 1839–1841: 70)	*Scaeurgus*	valid
valdiviae (Thiele, in Chun, 1915: 485)	*Bathypolypus*	valid
		synonym: *grimpei* Robson, 1924: 208
validus Sasaki, 1920: 183	unplaced	unresolved
variabilis Sasaki, 1929	unplaced	unresolved
variolatus Blainville, 1826: 186	unplaced	*nomen dubium*
varunae (Oommen, 1971: 69)	*Amphioctopus*	valid
veligero Berry, 1953: 57	unplaced	valid
venustus Rang, 1837: 66	unplaced	juvenile: unresolved
ventricosus Grant, 1827: 309	unplaced	unresolved
verrilli palliata Robson, 1929: 163	unplaced	juvenile: *nomen dubium*
verrilli verrilli Hoyle, 1886: 93	unplaced	juvenile: *nomen dubium*
***verrucosa** (Verrill, 1881: 105)	*Graneledone*	valid
		synonyms: *verrucosa media* Joubin, 1918a: 5
verrucosa media Joubin, 1918: 5	*Graneledone*	synonym of *verrucosa*
verrucosus Hoyle, 1885: 222	*Octopus*	valid
vincenti (Pickford, 1955: 159)	*Amphioctopus*	synonym of *burryi*
violescens Taki, 1964: 320	*Benthoctopus*	valid
vitiensis Hoyle, 1885: 226	unplaced	valid
***vulgaris** Cuvier, 1797: 380	*Octopus*	valid
		synonyms: *albus* Rafinesque, 1814: 29
		bitentaculatus Risso, 1854: 61

Table 3. (continued)

Taxa	Generic placement	Status
		brevitentaculatus Blainville, 1826: 187
		cassiopeia Gray, 1849: 9
		coerulescentes Fra Piero, 1895: 267
		heteropus Rafinesque, 1814: 28
		maculatus Rafinesque, 1814: 29
		marinum Koelreut ??
		moschatus Rafinesque, 1814: 28
		niger Rafinesque, 1814: 29
		octopodia Tryon, 1879: 113
		pilosus Risso, 1826: 4
		rabassin Risso, 1854: 67
		ruber Rafinesque, 1814: 28
		tetradynamus Rafinesque, 1814: 28
		tritentaculatus Risso, 1854: 63
		troscheli Targioni-Tozzetti, 1869: 113
		tuberculatus Targioni-Tozzetti, 1869: 156
		Unresolved West Atlantic form:
		Available name:
		americanus Baker in Denys de Montfort, 1802: 38
		synonyms: *bakerii* d'Orbigny, 1826: 144
		eudora Gray, 1849: 9
		geryonea Gray, 1849: 7
		Unresolved Japanese form:
		Available name:
		sinensis d'Orbigny, 1834: pl. 9
warringa Stranks, 1990: 457	unplaced	valid
westerniensis d'Orbigny, 1834: pl. 10	unplaced	synonym of *superciliosus*
winckworthi (Robson, 1926: 161)	*Macrochlaena*	valid
witjazi Akimushkin, 1963: 145	*Pteroctopus*	unresolved
wolfi Wülker, 1913: 458	unplaced	valid
yamana Guerrero Kommritz, 2000	*Graneledone*	valid
yaquinae Voss and Pearcy, 1990: 76	*Benthoctopus*	valid
yendoi Sasaki, 1920: 179	unplaced	unresolved
zealandicus (Benham, 1944: 256)	*Enteroctopus*	valid
zeiss O'Shea, 1999: 246	*Thaumeledone*	valid
zonatus Voss, 1968: 647	unplaced	valid

of which 13 were new to science. O'Shea (1999) reported 30 shallow and deep-water species from New Zealand waters of which 11 were new to science. Australia has received more attention than most regions. In 1985, Lu and Phillips were the first to generate a list of octopus species from Australian waters. A total of 31 species were recorded of which 12 proved to be valid species records or names. Stranks (1998) listed 26 shallow-water octopus species names of which he proposed 15 to be valid. Through Australia-wide field collection over the past six years, the tally has now reached 76 valid species of which 55 have been recognised in the past decade (works of Norman, Stranks, Lu, Finn and Hochberg, see literature cited above).

Works in progress in other regions of the world are uncovering similar numbers of new species. New Caledonian waters (Norman, Hochberg and Boucher, unpublished data) contain at least 20 shallow-water species (of which 14 are new to science) and 13 deep-water species (all of which are new to science, including three new genera) Norman *et al*., 2004a, 2004b. A preliminary census of the benthic octopuses of South Africa by Norman, Hochberg, Allcock and colleagues at the CIAC conference in South Africa in 1997 recognised 27 species of which 16 are new to science. Hochberg (unpublished data, see also Young *et. al*., 1989) found 16 species of octopodid paralarvae in Hawaiian waters while only 8 species had been recognised in the adult fauna. The total tally for this region is likely to be even higher as the planktonic paralarvae only represent small-egg species. Additional large-egg species with benthic young also occur around Hawaii. Elsewhere in the Pacific Ocean, many new species are coming to light including in Tonga (Huffard, unpubl. data), Indonesia (Norman, unpubl. data; Huffard, unpubl. data), Marquesas (Hochberg, Boucher and Norman, unpubl. data), Fiji (Herb and Roper, unpubl. data), Peru (Hochberg and Cardoso, unpubl. data), and Mexico to Panama (Hochberg and Sweeney, unpubl. data).

Recent studies on Antarctic benthic octopuses have found a high diversity of new species in (and related to) the genus *Pareledone* (Allcock *et al.*, 2003). Allcock (pers. comm.) suggests more than 20 new species from the genus *Pareledone* alone may be present in southern polar waters.

Cryptic species

Cryptic species are also coming to light amongst the better-known faunas. Pygmy species are being discovered in all regions of the world from tropical shallow waters (Norman, 2000, 2001; Hochberg, unpubl. data) to the deep sea (Norman, Hochberg and Boucher, 2004 and unpubl. data, Vecchione, this volume). Molecular studies are uncovering sympatric cryptic species, as found recently for *Amphioctopus marginatus* in Taiwan (Ho *et al.*, 2000). Purported anti-tropical distributions are also being questioned for sibling subtropical taxa split on the periphery of the tropical Pacific Ocean (Norman, 2000), namely *Amphioctopus kagoshimensis* Ortmann, 1888 (Japan) and *A.* cf *kagoshimensis* Norman, 2000 (eastern Australia); *Hapalochlaena fasciata* Hoyle, 1886 (eastern Australia) and *Hapalochlaena* sp. 2 Norman, 2000 (Japan/China). An *Octopus "vulgaris"*-like species in Japan and *O. tetricus* and *O.* cf *tetricus* in Australia appear to be similar sibling species.

It is clear that there is much higher diversity of octopuses than previously considered. Voss (1977) calculated the rate at which new species of cephalopods were being described each decade since 1835, in order to assess the rate of discovery over the previous 140 years. He suggested an average rate of 6.7 species being described annually. As there was no obvious decline of this rate with time, he suggested that "one is forced to the belief that we have nowhere near exhausted the number of undescribed species either on our museum shelves or in the sea". Voss went on to state that "it seems clear that we are indeed still in the descriptive or *alpha* stage of systematics and that we are far from knowing the total number of species of cephalopods". These statements are still valid 28years later, particularly for benthic octopuses. The total tally for octopus species and genera is likely to rise dramatically should an in-depth, global census be undertaken. There are many species yet to be discovered, studied and described. Efforts to date may just be skimming the surface of the real diversity that is present in the world's oceans.

Impediments to taxonomic progress

Voss (1977) also discussed the problems impeding better taxonomic knowledge, listing them as:

· lack of detailed morphometric studies
· lack of adequate study material
· failure to analyse character variations
· need to examine type material
· prevalence of uncritical reviews of literature, perpetuating historical errors.

Today many of these taxonomic problems are still evident. Some factors have shown improvement. Historically there has been little consistency in approach to species recognition and description. This is slowly changing. In the past five years in particular, more detailed and consistent diagnoses and descriptions have been produced in describing new species of octopuses (see list of recent taxonomic works in Introduction). Other improvements include better international links, faster electronic communication and easier travel than ever before. There is also better technology for detection, sampling, photography and video documentation of taxa and the visual attributes of live animals.

Other factors have deteriorated. There continues to be problems with poor retention of material, few replicates from a paucity of localities, poor curation and a lack of defined characters. There is disturbingly little support for alpha taxonomy research, with the few extant cephalopod taxonomists being an aging and diminishing cohort. The changing nature of research institutions and available funding means few of these researchers have younger understudies on to which the mantle (!) can be passed. Diminishing support for the traditional curation roles of museums has also taken its toll. As museum curators retire, they are not being replaced. Many of the major research collections of cephalopods around the world are neither actively worked nor growing. At best they are maintained by collection managers responsible for multiple and diverse collections of invertebrates and other biological resources. As a consequence of reduced science funding (and priority) worldwide, there are fewer primary field surveys being undertaken, compared with the many peaks of activity over the past century.

Despite the decline of support for this primary taxonomic research, the demands for information are greater than ever. As many finfish harvests collapse around the world, commercial fisheries attention is shifting to exploitation of cephalopod resources. Octopuses, squids and cuttlefishes are fast growing, fecund marine animals which make them favoured and profitable fishery targets. The capacity of fisheries authorities to effectively manage octopus fisheries is severely hampered by many problems, most of which stem from poor taxonomy. These include species lumping, lack of detailed diagnostic tools (regional keys), inadequate fisheries catch statistics (including lack of catch per unit effort data), dearth of biological information for target species, lack of detailed regional censuses (or even comprehensive fish market surveys) and a lack of well-preserved and well-managed reference and voucher collections.

Sound taxonomy underpins all other fields of biological research. At this stage, octopod taxonomy is still in need of major revision and stabilization. An immediate priority is production of detailed and accurate descriptions for all species (including redescriptions of named species supplemented by fresh reference material collected from type localities). Support should be sought for alpha taxonomy on a scale sufficient to clarify the extant fauna, and should include encouragement of students to enter and become active in this field. Regional revisions should also be instigated and supported, particularly in regions where our knowledge is poorest or where fisheries are developing fastest.

Only this approach will enable production of appropriate identification tools, particularly guides and keys for field and fisheries identification. Armed with such information and tools it will be possible to develop appropriate monitoring and management systems for octopuses of current and potential fisheries value, as well as identifying species potentially vulnerable to such exploitation. Addition of molecular studies in such studies will also provide valuable insights into the population genetics and origins of these creatures. Without even basic information on the composition, distribution and biology of these animals, sound management is unlikely.

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APPENDIX

Clarification of the non-ocellate members of *Amphioctopus* Fischer, 1882

Considerable confusion surrounds the group of small to moderate-sized octopuses historically known as the *Octopus aegina* species-group (Robson, 1929; Norman, 1992c, 1993b). Members of this genus are characterised by arms approximately 2–3 times mantle length, deep lateral webs (approximately 20% of arm length) and a very shallow dorsal web. The oral surface of the shallow dorsal web has the same sculpture and colour pattern as the dorsal surfaces of body and arms. Species included in the genus may be either ocellate or non-ocellate. Norman (1993b) and Nateewathana and Norman (1999) have treated the ocellate members of this species-group.

Member species are found throughout the Indo-Pacific region (*A. aegina* Gray, 1849, *A. exannulatus* Norman, 1993b, *A. fangsiao* d'Orbigny, 1839–41, *A. kagoshimensis* Ortmann, 1888, *A. marginatus* Taki, 1964, *A. mototi* Norman, 1993b, *A. neglectus* Nateewathana and Norman, 1999, *A. polyzenia* Gray, 1849, *A. rex* Nateewathana and Norman, 1999, *A. robsoni* Adam, 1941, *A. siamensis* Nateewathana and Norman, 1999, *A. varunae* Oommen, 1971 and at least six undescribed species).

Fewer non-ocellate species are represented in the Atlantic Ocean (*A. burryi* Voss, 1950 and at least one undescribed species). The status or validity of several old names variously applied to members of this group in the Atlantic still need to be resolved (*rugosus* Bosc 1792; g*ranulatus* Lamarck 1799; *carolinensis* Verrill 1884; and *vincenti* Pickford 1955).

There has been considerable confusion over the non-ocellate members of the "*aegina* species-group", primarily due to inadequate original descriptions, type material that is in very poor condition or not extant, and historical lumping of distinct species (see review in Adam, 1960). A failure to formally describe type and other material in detail for members of this group has meant this confusion continues today.

The species pivotal in creating most of the confusion is *Amphioctopus aegina* Gray, 1849. The species was treated as dubious by Toll and Voss (1998). The type of *A. aegina* exists (BM 1928.2.14.1) and has been examined by the authors. It is a mature female, which clearly shows the colour pattern diagnostic of this species; namely a pale longitudinal stripe along the dorsal mantle, a narrow transverse head bar and numerous distinctive circular reticulations over the mantle, arm crown and arms. We believe that this recognisable species is valid. Examination of the type of *A. hardwickei* Gray, 1849 from the Indian Ocean (presumed Singapore) found it to be identical in form and colour pattern with the type and other material attributed by us to *A. aegina*. Toll and Voss (1998) recognised that the taxon they treated under the name *A. hardwickei* has "armed" spermatophores. This type of spermatophore is characterized by the presence of sharp teeth in the ejaculatory apparatus that may aid penetration of the sperm bulb as the spermatophore everts within the oviduct of the female or may prevent removal by a competing male. All males attributed by us to the genuine *A. aegina* possess such armed spermatophores. No other octopuses of similar morphology throughout the region possess such armature. Remains of spermatophores in the type of *A. dollfusi* Robson, 1928 from Vietnam clearly show this armature. As a consequence, both *A. hardwickei* and *A. dollfusi* are placed in the synonymy of *A. aegina*, the former on the basis of page priority by *A. aegina* in Gray's (1849) original descriptions.

Subsequent confusion has arisen in this species-group through the use of the name *Amphioctopus aegina* for two related but distinct octopus species, namely *A. kagoshimensis* and *A. marginatus*. The former species is easily distinguished from *A. aegina* based on characters of the patch and groove skin sculpture which has regular polygonal patches (versus round patches). The ligula is of moderate length (4–7% of arm length) and the terminal organ ("penis") is greatly elongated and recurved to accommodate the very long, unarmed spermatophores of this species

(1.5–2 times mantle length versus 0.6–1.2 in *aegina*). *Amphioctopus marginatus* Taki, 1964 is recognised by its dark purple colour pattern in sharp contrast to the white to blue suckers along the dorsal faces of arms 1–3. The skin is sculptured in rounded elongate patches that form irregular longitudinal rows, displayed as branched veins on the lateral arm crown. In this species, the ligula is small (1.5–3.5% of arm length) and the spermatophores are unarmed and only moderately long (approximately 0.75 to 1.2 times mantle length).

Robson (1929) initiated much of the confusion surrounding this group by lumping records of all three distinct species under the name *aegina*. In the same publication, Robson also treated members of this species group under the name *Octopus rugosus* (Bosc, 1792), due to the nature of the "rugose" skin found in well-preserved material.

Bosc (1792) coined the name *rugosus* on the basis of an animal from Senegal, west Africa that had granular skin. There is no type material. The name often has been treated in a long list of synonyms for *Octopus vulgaris*. A non-ocellate member of *Amphioctopus* has been reported off the coast of Senegal under the name *O. burryi* Voss, 1952 (Roper *et al*., 1984) and a further species, *O. vincenti* Pickford, 1955 was described from a nearby locality.

Re-examination of the original material listed by Robson (1929) under the name *rugosus* turned up a number of Indo-Pacific members of *Amphioctopus*, including three ocellate species (*e.g., A. polyzenia* Gray, 1849 from Torres Strait, Australia: Robson, 1929: 65 and an undescribed species from Amirante Atoll, Indian Ocean, Robson, 1929: 64) plus two non-ocellate species (*A. aegina* Gray, 1849 from Gulf of Martaban, Indian Ocean: Robson, 1929: 64 and an undescribed species from Madras, India: Robson, 1929: 64).

The other name associated with the non-ocellate members of *Amphioctopus* is *granulatus* Lamarck, 1798. Sasaki (1929) used this name for his treatment of *A. kagoshimensis*. Although Lamarck (1798) did not provide a type locality for his species and no type material has been traced we have determined that the material he examined came from Martinique in the Caribbean. Other than having granular skin, there are no characters enabling recognition of this species from the brief original description. Robson (1929) placed this taxon in the synonymy of *rugosus* whereas many other authors treat it as a synonym of *Octopus vulgaris*. At this stage, the name *granulatus* remains unresolved.

In order to help clarify the named Indo-Pacific non-ocellate members of *Amphioctopus*, table 4 presents the primary diagnostic characters for the named member species considered here to be valid: *A. aegina, A. kagoshimensis* and *A. marginatus*. Data for *A. aegina* and *A. marginatus* are based on multiple reference specimens. Data for *A. kagoshimensis* are based on limited available material and treatments of this species in historical literature (including Sasaki's [1929] treatment of this octopus under the name *Octopus granulatus*).

In an attempt to clarify past literature records of these three member species, we also present the following annotated synonymies:

Amphioctopus aegina Gray, 1849
(treated and illustrated in Norman and Sweeney, 1997, Norman, 1998, 2000)

Octopus rugosus (non Bosc, 1792). Robson, 1929.

O. hardwickei Gray, 1849. Toll and Voss, 1998.

O. dollfusi Robson, 1928. Voss and Williamson, 1972, Li, 1983, Roper *et al*., 1984, Chikuni, 1987, Dong, 1988, Chaitiamvong, 1993, Chotiyaputta, 1993.

A. kagoshimensis Ortmann, 1888
(treated and illustrated in Norman, 2000; under *O. granulatus* in Sasaki, 1929)

O. granulatus (non Lamarck, 1798). Sasaki, 1929.

O. aegina (non Gray, 1849). Robson, 1929 (in part), Taki, 1965, Dong, 1988, Okutani *et al*., 1987 (in part).

O. dollfusi (non Robson, 1928). Roper *et al*., 1984 (in part).

A. marginatus Taki, 1964
(treated and illustrated in Norman, 1993c, 1998, 2000; Norman and Hochberg, 1994)

O. aegina (non Gray, 1849). Voss and Williamson, 1972, Chaitiamvong, 1993.

O. dollfusi (non Robson, 1928). Roper *et al*., 1984 (in part).

O. striolatus Dong, 1976. Dong, 1979, 1988.

Table 4. Comparison of Indo-Pacific non-ocellate members of the genus *Amphioctopus*. [m = male, f = female, AL = arm length, HAL = hectocotylised arm length, LL = ligula length, ML = mantle length (eye to posterior tip)].

	kagoshimensis	***marginatus***	***aegina***
Synonyms:	-	*striolatus*	*dollfusi* *hardwickei*
Misidentifications:	*granulatus* *aegina, dollfusi*	*aegina* *dollfusi*	*rugosus*
Distribution:	NW Pacific Ocean (southern Japan to Taiwan)	Indian and W Pacific oceans	Indian and W Pacific oceans
Affinity:	subtropical	tropical	tropical
Mantle length:	to 86 mm	to 80 mm	to 90 mm
Total length:	to 295 mm	to 280 mm	to 300 mm
Arm length:	2.4, 2.6 x ML	2.0–2.8 x ML	2–3 x ML
Web depth:	25.6, 21.4% AL	26.3–33.3% AL	20.0–32.8% AL
Normal arm sucker count:	157, 164 (m), 169 (f)	127–152 (both)	96–130 (both)
Hectocotylised arm sucker count:	68–88	61–84	55–70
Ligula length:	5, 6.7% HAL	1.6–3.6% HAL	4–6% HAL
Calamus length:	17% LL	37.9–65.0% LL	19–25% LL
Enlarged suckers:	none	4–5 slightly enlarged	2–3 enlarged
Male sucker diameter:	to 9.0% ML	to 14.5% ML	to 16.6% ML
Spermatophores:	no internal teeth (unarmed)	no internal teeth (unarmed)	internal teeth (armed)
Spermatophore length:	117–160 mm	37–68 mm	25–51 mm
Spermatophore length versus ML:	160, 186% ML	73–116% ML	58–115% ML
Colour pattern:	Cross around eye, reticulate markings produced by dark grooves.	White triangle under eye, dark purple leading edges of arms in contrast to white-blue suckers.	Longitudinal pale stripe on dorsal mantle. Dark circular reticulations.
Skin sculpture:	Polygonal patches over all surfaces with distinct grooves.	Oval to elongate patches in irregular longitudinal rows.	Circular raised patches with indistinct grooves.