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Systematics and Distribution of Abraliopsis (Cephalopoda : Enoploteuthidae) in Australian Waters

Kwan Wah Li

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Abstract
Sound taxonomy is the basis for all biological research and fisheries management. However, in some animal groups there are taxonomic uncertainties. This is especially true in the case of non-commercially targeted pelagic marine organisms, which are sometimes poorly known due to the serendipitous nature of their collection and sometimes a lack of well-preserved material. Knowledge of some groups is also limited due to a general lack of taxonomic expertise.

Representatives of one cephalopod genus, Abraliopsis Joubin, 1896, have been recorded from Australian waters; however, there was not much information available regarding the distribution and morphology of representatives of this group prior to the present study. Four species of Abraliopsis have been recorded: A. affinis (Pfeffer, 1912), A. gilchristi (Robson, 1924), A. hoylei (Pfeffer, 1884) and A. tui Riddell, 1985. This work re-examines the morphology and distributions of the Abraliopsis specimens held in two large museum collections (the Australian Museum and Museum Victoria) to assign unidentified specimens to species and determine whether the previous species identifications are correct. Three species were identified: A. gilchristi, A. lineata (Goodrich, 1896) and A. tui. Four female specimens of an unknown species from off the coast of the Queensland (about 254 km offshore) were found among collections. The discovery of A. lineata among specimens from off northeastern Queensland is the first record of this species from Australian waters. This species is fully described in this thesis as a basis for comparison with other specimens elsewhere over its broad geographical range.

At present it is impossible to assign specimens to Abraliopsis hoylei due to the lack of information and loss of the holotype. Until specimens of this species from the type locality in the Western Indian Ocean are examined, and the species redescribed it is not possible to resolve the identity of this species. Based on some very scant descriptions and material available to us it appears that this species may not actually occur in Australian waters, contrary to earlier reports.

This survey of the existing Australian Abraliopsis specimens has enhanced our knowledge of the composition and distribution of species within Australian waters and provides a clearer framework for management and study of these species and some directions for future research.

Prior to this study A. lineata had been recorded from the northern Indian Ocean and elsewhere in the tropical west Pacific. Together with the new north Queensland records the distributions of this taxon is quite disjunct as no specimens have been recorded from in between these three areas. This suggests the need for a more careful study of A. lineata’s distribution and morphological and genetic characters over the full range of the supposed species in case the existing populations may represent more than one, possibly cryptic, species. At this time it is not known whether the apparently disjunct distributions are simply a sampling artefact.

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Systematics and Distribution of *Abraliopsis* (Cephalopoda : Enoploteuthidae) in Australian Waters

Bachelor of Environmental Science (Life Science)

Kwan Wah Li

2015

Supervisors:

Professor David Ayre, Senior Professor, University of Wollongong

Dr Mandy Reid, Collection Manager, Malacology, Australian Museum Research Institute

A thesis submitted in part fulfilment of the requirements of the Bachelor of Environmental Science or Bachelor of Environmental Science Advanced in the School of Earth and Environmental Science, Faculty of Science, Medicine and Health, University of Wollongong 2015
The information in this thesis is entirely the result of investigations conducted by the author, unless otherwise acknowledged, and has not been submitted in part, or otherwise, for any other degree or qualification.
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Finally, I wish to thank my parents for their support and encouragement throughout my study.
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Summary

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Chapter 1 Introduction

1.1 The role of taxonomy

Taxonomy is the discipline of biology that aims to allocate all living organisms to formal classificatory units, or taxa, within a hierarchy of categories in terms of species, genera, families etc. (Dubois, 2003). Accurate and precise identifications are vitally important for conservation and environmental management (Bickford et al., 2006). According to Mayr (1969: 8–9), there are multiple roles of taxonomy in biology: ‘(1) It works out a picture of the existing organic diversity, (2) It provides information and data permitting a reconstruction of the phylogeny of life, (3) It reveals numerous evolutionary phenomena and (4) It is essential in the study of economically or medically important organisms.’ Therefore, more effort and resources need to be put into many areas of taxonomy and taxonomic research so that information and knowledge can be gained to be used in all areas of biology, including conversation and environmental management.

1.1.1 The role of taxonomy in conservation

Species conservation is a practice to protect organisms, either terrestrial or marine, and their habitats. The aim of species conservation is to ensure organisms are able to produce future generations and promote stable populations and biodiversity. Conservation activities need a valid taxonomy and knowledge of organisms such as species habitat, species interaction, ecology, biodiversity etc. in order to provide effective conservation management (Dubois, 2003; Mace, 2004). However, taxonomic studies are often inadequate, with many taxa as yet unknown or poorly understood. Taxonomy and species conservation are completely interdependent activities (Gaston, 2001; Mace, 2004). The Convention on International Trade in Endangered Species (CITES) lists threatened and endangered plants and animals. There are about 35,000 species (approx. 5,600 animals and 30,000 plants) that are CITES listed (CITES, 2015, https://www.cites.org/eng/disc/species.php). It is hoped that organisms listed will be managed or protected according to their threatened status. However, if species are not named and identified formally, they are not able to benefit from targeted conservation planning and legislation (Gaston, 2001; Mace, 2004). Also if species are wrongly identified, their conservation priorities may be decided wrongly (Gaston, 2001).

Consider a European example (Dubois, 2003); two frog species were identified (Rana esculenta and R. ridibunda) in the 1960s; however, after re-examination of the same frog species 40 years later, the number of species had risen from two to twelve. The number of species had been wrongly determined due to careless taxonomic identification. The populations of these frogs species were therefore under-estimated, which in turn can
influence their threatened status under CITES. Correct assignment of taxa should be of paramount importance to the conservation of biodiversity because inappropriate decisions can be made if taxonomic assignments are wrong (Moraes-Barroe et al., 2011).

The level of conservation management concern highly relies on taxonomic precision. Some species that were nearly extinct before being formally named or described and listed as threatened by CITES; have experienced a major improvement in their extinction risk. For example Yarkon Bream (*Aeanthobrama telavivensis*) was once abundant in Israel but decreased sharply in abundance between 1950 and 1970 and was eventually listed as ‘extinct in the wild’. A small number of captive adults were transferred to a special breeding pool at Tel Aviv University. Reintroduction to the wild produced or perhaps enhanced an increase in the population size and its conservation status improved from ‘extinct in the wild’ to ‘vulnerable’ in 2013. CITES can potentially produce greater emphasis on conservation (Goren, 2014). Therefore, more labours, effort and funding should be directed toward taxonomy before making any conservation plans.

**1.1.2 The role of taxonomy in fisheries management**

Fish are a human food source and fishing has a long history of changing the biological diversity of ecosystems (Vecchione et al., 2000). However, some organisms forming bycatch and without commercial value are discarded (about 25% of catches are discarded) and these discarded organisms constitute an important food source for other organism such as large fish and seabirds (Gislason et al., 2000). Proper management should minimise the effect of fishing on marine biodiversity and the goal of fisheries management is to achieve the sustainable use of renewable resources (Vecchione & Collette, 1996). In the past, people focused on single-species management; usually focused on the organisms that they were interested in, such as those that have high commercial value.

Nowadays, there is greater awareness of the interaction between species because species are interdependent (Gislason et al., 2000). Fisheries activities may affect species interactions and activities directly or indirectly and pose negative effects on biodiversity in ways that people never expected (Vecchione & Collette, 1996; Gislason et al., 2000).

Unfortunately, we know little about marine ecology and biodiversity. In order to manage the biological diversity of ecosystems, coordination between fisheries and taxonomy is critical for development of knowledge and the skills necessary for assessment and maintenance of marine biodiversity (Vecchione & Collette, 1996).
1.1.3 Reasons for studying cephalopods

Oceans are extremely productive ecosystems and contain a high level of biomass (Okutani, 1994). However, marine biology is often less understood than terrestrial biology. The cephalopods, which comprise about 800 species worldwide, including octopuses and pelagic species such as squid (Coll et al., 2013) serve to illustrate this point. Cephalopods have recently been considered an important human food source as the demand for cephalopods has increased substantially in last 20 years (Rodhouse, 2001; Coll et al., 2013). This increase in the consumption of cephalopods is attributed to poor management and overfishing of the world’s traditional fish stock.

As the demand for cephalopods is increasing steadily, more study needs to be done to obtain a better understanding of taxonomy to enable conservation biologists to better manage biodiversity. However, most studies focus on cephalopods with commercial value. Deep-sea cephalopods are little studied. Knowledge of some small cephalopods is inadequate; however, small cephalopods such as squids can be a very important food source of fish, particularly in the deep sea (Santo et al., 2001; Guerra et al., 2010; Quetglas et al., 2013). Those small cephalopods with low commercial value play a critical role in the food web or trophic level; hence species are interdependent (Santo et al., 2001; Guerra et al., 2010; Coll et al., 2013; Quetglas et al., 2013; Logan et al., 2013).

Therefore, an understanding of the interactions of cephalopods with other species will be useful in fisheries management and conservation, and can be used to predict the impact of fishing operations on this fisheries resource (Santos et al., 2001; Nottage et al., 2007).
1.2 Difficulties in taxonomic identification

Taxonomy is an important element in conservations and fisheries management. However the identification process can be still very slow due to four main limitations:

First, for some groups, there is insufficient species information. In order to identify organisms at a species level, a good understanding of the organism is needed. However, for some species descriptions done in the distant past are unclear and relatively short. Furthermore, keeping a holotype in good condition is of vital importance in taxonomy. Holotypes are used as a reference which provides objectivity and stability for the species name. Sadly, some holotypes are lost, so researchers are unable to revisit the holotype for comparison.

Second many specimens have already been collected and stored in museums, but remain unstudied. Sometimes collections of particular taxa are scattered in a range of institutions and difficult to access. In some cases it is not possible to borrow specimens for comparative purposes so some groups are tricky to work on.

Third is it takes time and specialist skills to identify species. Sometimes, species identification takes a lot of time, especially for small species and species with similar morphological features. In order to identify species, numerous specimens need to be examined and compared in terms of morphology. However, there is a diminishing pool of taxonomic specialists worldwide, far fewer than the number needed to describe the vast number of species that are as yet unknown to science.

Fourth is the many cases of fragmentary information that has been collected from different sources (Quetglas et al., 2013). This applies especially in the case of organisms of less interest to the majority of people, such as pelagic squid. Quantitative information is usually only available from indirect sources such as commercial fisheries (Botle & Boletzky, 1996). This information is often unclear and incomplete and, it is time consuming to group this fragmented information.

Fortunately, recent technological developments provide alternative methods to identify species so that identification processes can be improved. There are two main approaches that biologists usually use to identify species nowadays: morphological and genetic approaches. More details about these two approaches will be discussed in the following section.
1.3 Methods of identification and their limitations

1.3.1 Morphological approaches

Comparative morphology or the study of internal and external features is the most common and least expensive way to identify and classify species. However, there are some limitations using only a morphological approach. Classical methods of studying anatomy and morphology are sometimes insufficient to distinguish some species especially very small taxa such as fungi, insects etc. (Moraes-Barros et al., 2011; Hind et al., 2014). Therefore, depending on the features of organisms, morphology sometimes can be misleading (Hind et al., 2014).

A second limitation is that morphological methods are not able to identify cryptic species. Therefore, two or more distinct species may be wrongly classified as the same species (Knowlton, 1993; Lajus et al., 2015; Bickford et al., 2006). There are some reasons why morphological change might not be correlated with species differences. For example, cryptic species may either be differentiated by nonvisual mating signals and/or appear to be under selection that promotes morphological stasis (Bickford et al., 2006), therefore, different species have similar external features as morphologies are not the main factors affecting their communication.

A third reason is that many cryptic species are morphologically simple or lack diagnostic characters, such as some sponges and nematodes (Bickford et al., 2006; Diaz-Rodriguez et al., 2015). Misidentification of cryptic species can result in negative consequences such as in attempts at environment management due to over- or under-estimation of economic importance (Bickford et al., 2006).

Cryptic species exist simply because we humans can’t tell them apart. They are cryptic to us if we can’t find differences even if these differences are obvious to the organisms themselves.

In order to avoid misidentification of cryptic species, genetic based approaches are the best way to identify cryptic species.

1.3.2 Genetic approach

The development of new technologies and increasing knowledge with respect to molecular information provides alternative ways to study taxonomy and diversity (Moraes-Barros et al., 2011; Diaz-Rodriguez et al., 2015; Selbach et al., 2015). The use of molecular data and information has brought about a major advancement in taxonomic study because it can be
used both to help to distinguish cryptic species that cannot be identified based on their morphological features alone and re-evaluate or test existing morphological identification criteria (Selbach *et al*., 2015). However, a genetic approach may not necessarily be the best way to identify species based on conventional methods, that is, morphology cannot be completely replaced by genetic approaches. DNA-based approaches are not omnipotent (Lajus *et al*., 2015), they just provide an additional set of characters, however, researchers still need to decide ‘how different is different’ to be a new species, whether using morphological information or sequence data.

### 1.3.3 Integrative approach

No doubt, using both morphological and molecular approaches is the best way to identify species and reduce the chances of misidentification. However, it is sometimes impossible to use both methods for study; for example, the method of tissue preservation may determine the identification methods that can be used. Ideally, fresh, or −80°C frozen material yields the best results in terms of the extraction of a range of genetic material, such as DNA or RNA. Ethanol-preserved tissue is also suitable. However, many of the specimens in museum collections have been fixed in formalin prior to ethanol preservation. While formalin has the effect of making it very difficult to obtain more than tiny fragments of DNA, it is still a favoured fixative to use for subsequent anatomical studies because the tissue is not rendered brittle as is the case with alcohol-preserved specimens. Much research is currently focused on the extraction of DNA from formalin-preserved material, which, if successful, will render museum collections vast repositories of new information. Obviously, no single method can be used to solve all taxonomic problems (Nesis, 1998). However, if they are available, molecular data are important and useful when considered with other types of information (Bickford *et al*., 2006).

In this study, a morphological approach is used to identify *Abraliopsis* species found in Australian waters and their characters and external features will be recorded and compared to look for both similarities and difference between species occurring in Australia with those from elsewhere with the aim to resolve exactly which species occur here and look for new species.
1.4 Background of genus *Abraliopsis*

1.4.1 Genus *Abraliopsis* (Cephalopoda: Enoploteuthidae)

The genus *Abraliopsis* Joubin, 1896 belongs to the family *Enoploteuthidae* which are small to medium sized squids common in tropical and warm temperate oceans; they ascend into epipelagic layers at night and occur in the deeper (mesopelagic) layer during daytime (Riddell, 1985; Arkhipkin, 1996; Laptikhovsky, 1998); females usually are larger than males (Riddell, 1985; Laptikhovsky, 1998). There are four subgenera in the genus *Abraliopsis*: *Boreabraliopsis*, *Abraliopsis*, *Microbralia* and *Pfefferiteuthis*. Species in the genus *Abraliopsis* are without commercial value and therefore they are not widely known to people. Nevertheless they play an important role in the food chain and have been recorded from the stomachs of a variety of large oceanic predators (Riddell, 1985). There are currently eleven named species worldwide.

*Abraliposis* is characterized by having three large spherical black photophores at the tip of arms IV (Fig.1) and five photophores on each eyeball. In Australian waters, some *Abraliopsis* species have been collected and placed in museum without identification to the species level.

Figure 1: Side view of *Abraliopsis* sp. B. A black arrows point to the black photophores at the tip of arms IV. Photograph by R. Young (Sources: Young & Kotaro, 2014)

*Abraliosis* is one of the cephalopod genera that has little known about its biology and distribution in Australian waters. Four species from Australia were recorded prior to this study: *A. affinis*, *A. gilchristi*, *A. hoylei* and *A. tui*. Many *Abraliopsis* species have been collected and placed in museum collections without identification to the species level. This study uses preserved specimens from museums to examine the morphology of the squid genus *Abraliopsis* and its distribution. Distribution maps are used to view their distributions pattern and whether those species have an overlapping habitat (are sympatric) or have unique distributions. As well as examining unidentified material, the aim is also to restudy the species that have been recorded to ensure they are correctly assigned to species and to investigate whether other species are present.
1.4.2 *Abraliopsis* subgeneric designations

There are four subgenera in the genus *Abraliopsis*—*Boreabraliopsis* Tsuchiya & Okutani, 1988, *Abraliopsis* Joubin, 1896, *Micrabralia* Pfeffer, 1900 and *Pfefferiteuthis* Tsuchiya & Okutani, 1988. Features in each subgenus are useful for identifying specimens. Table 1 (Appendix 10) shows the morphological differences between the subgenera. *Pfefferiteuthis* is the most readily identified subgenus. Most of the specimens are assigned to subgenera on the basis of the photophore arrangement on the ventral mantle and head, and also by the morphological features of arms IV in males. However, it is a bit difficult to identify females because the arms are similar in each subgenus (*Pfefferiteuthis* is an exception). In addition, there is some variation among species within subgenera; for example the presence of flaps on the tentacular clubs can be different among species within the same subgenus.

To sum up, subgeneric designation is useful to a certain degree, but the taxonomic validity of subgenera within *Abraliopsis* is uncertain. However, a correct subgeneric designation assists the identification process in an organized way. There are a lot of species in some subgenera and it is hard to start identification at the species level. Because the features among species are slightly different, it is difficult work to examine all the different features at the same time. Therefore, it is a good idea to attempt to designate specimens into subgenera before attempting to identify species.
Chapter 2 Methods and Materials

More than 450 individuals from genus *Abraliopsis* Joubin 1896 were examined; they were collected from Australian waters, which is the area about 200 nautical miles (1 nautical mile = 1853 meters) away from the Australian continent (Appendix 5). Preserved *Abraliopsis* specimens were examined at the Australian Museum (AMS), and some of the specimens were loaned from the National Museum of New Zealand, Te Papa (NMNZ) and the Museum Victoria (MV). No other Australian Museum had *Abraliopsis* holdings. Four hundred and ninety five *Abraliopsis* individuals were studied.

The specimens of all species were collected during forty nine collection trips between 23 March 1971 and 28 August 2003. The collections were mainly made off the coast of New South Wales and Queensland although; some collections were made off the coast of Perth and Tasmania. The collection locations are given in the material examined (Appendix 1-3) and distribution maps (Appendix 4). The collection locations were often recorded as a range corresponding to the start and the end of a trawl. The specimen distributions presented on the maps indicate the midpoints of the ranges. Most of the specimens were collected during the night using trawls nets as part of a survey by CSIRO. The type of collecting gear was not recorded in the museum databases.

Using a light microscope, specimens were assigned to genus and species based on their external features according to the key from ‘Cephalopods of the World’ and species characters listed in TolWeb (Young & Tsuchiya, 2013). The sex of specimens was also recorded since some of the useful diagnostic characters are only restricted to males.

Terminology, measurement, indices and abbreviations for anatomical structures mostly follow Roper & Voss (1983).

The collection location of each individual was recorded and presented in distribution maps (Appendix 4).

Measurements were made using dial callipers, or for small structures through the use of a calibrated graticule fitted to a stereomicroscope eyepiece. Measurements are in millimetres (mm). The range of values for each character is expressed in the description as: minimum-mean-maximum (standard deviation, SD). Some external feature images such as integumental photophores, tentacular clubs, arms and whole body were captured using a microscope camera. Smaller body parts such as the radula were examined after air drying and gold splutter coating using scanning electron microscopy, in a Zeiss Evo LS15 SEM using a Robinson Backscatter detector. Definitions of technical terms and measurements are presented in Appendices 6, 7 and 9.
Chapter 3 Results

Specimens from the Australian Museum and Museum Victoria were examined. Three species were identified: *A. gilchristi* ($n = 68$), *A. lineata* ($n = 16$) and *A. tui* ($n = 381$). The identification of the *A. tui* material was confirmed following examination of the holotype borrowed from the National Museum of Zealand (M89787). Juvenile and immature specimens were not able to be identified due to their small body size and immature features.

Contrary to previous records (Jereb & Roper, 2010; Okutani, 2015) no *A. affinis* or *A. hoylei* were found among the collections.

*Abraliopsis affinis* has been recorded among Museum of Victoria collections, however, I believe that specimens called *A. affinis* have been identified wrongly. *Abraliopsis affinis* has a distinctive feature (a key-hole shaped region devoid of photophores) and none of the MV specimens identified as *A. affinis* have this feature.

The discovery of *Abraliopsis lineata* among the museum material is the first record of this species from Australian waters. It is located off the coast of Queensland (the closest one was found about 57 km away from the coast), off the Great Barrier Reef (Appendix 4 Maps 2a & b). This species was previously only recorded from the north Indian Ocean (Bengal Bay and Arabian Sea) and the tropical west Pacific (Young & Tsuchiya, 2013; Tsuchiya, 2013; Okutani, 2015). A full description of this species is provided below.

In addition, four female specimens of an unknown species in *Abraliopsis* from off the coast of Queensland (collected between -11.052 S, 144.7855 E to -15.2365 S, 149.6295) (Appendix 4 Map 4) were found. They are different from the species mentioned above and cannot be assigned to a named species at present. Below is a table of distinguishing features of the species that have been recorded from Australia showing the main differences between the unknown species and the named species. These four unknown female species are morphologically different from *Abraliopsis lineata*; they are morphologically similar to *A. tui*. These unknown females’ entire ventral mantle is ornamented with scattered photophores; without a bare strip in middle along the ventral mantle. In this they differ from *A. tui*.
<table>
<thead>
<tr>
<th></th>
<th>A. gilchristi</th>
<th>A. hoylei</th>
<th>A. lineata</th>
<th>A. tui</th>
<th>Unknown female species</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Photophore arrangement on ventral mantle</strong></td>
<td>Scattered over entire mantle</td>
<td>Scattered on entire mantle</td>
<td>Six longitudinal rows; a narrow bare strip in middle of mantle along entire ventral mantle midline</td>
<td>Scattered; a distinct bare strip in middle along entire ventral mantle midline</td>
<td>Scattered photophores on entire ventral mantle; no bare strip in middle along entire ventral mantle midline</td>
</tr>
<tr>
<td><strong>Photophores arrangement on ventral head</strong></td>
<td>Four longitudinal series</td>
<td>Uncertain#</td>
<td>Three longitudinal series</td>
<td>Scattered</td>
<td>Scattered</td>
</tr>
<tr>
<td><strong>Keel and carpal flap on tentacular club arm</strong></td>
<td>Present; large</td>
<td>Carpal flap absent; keel present#</td>
<td>Absent</td>
<td>Present; large</td>
<td>Present; large</td>
</tr>
</tbody>
</table>

Table 2: Morphological differences between A. gilchristi, A. hoylei, A. lineata, A. tui and unknown species

# Note, however, that features of A. hoylei are uncertain due to the loss of the holotype and lack of a detailed description. Most of the features described for A. hoylei were discerned from a drawing by Pfeffer (1912).

These four unknown species were unable to be identified to the species level because most of the distinguishing characters are only found on male representatives of this genus. Thus, it is hard to identify a single female precisely.
3.1 Key to *Abraliopsis* species found in Australian waters

1a. Ventral side of head with scattered photophores………. (2)

1b. Ventral side of head with photophores arranged in distinct pattern (i.e. arranged in rows or series) …………… (3)

2a. Ventral mantle with median longitudinal strip that lacks photophores; distinct virtually to anterior mantle margin. Distinctive and large carpal flap and aboral keel on tentacular clubs………… *Abraliopsis tui*

2b. Ventral mantle without median longitudinal strip without photophores. Carpal flap absent; aboral keel present on tentacle club………. *Abraliopsis hoylei*

3a. Four longitudinal series of photophores on ventral side of head. Scattered photophores on entire ventral side of mantle. Tentacular club with large carpal flap and aboral keel. Hectocotylus (right arm IV) with three crests, one on dorsal margin two on ventral margin; modified portion with armature (i.e. the grappling structures of the arms and tentacular clubs, including suckers and/or hooks). Protective membrane present on left arm IV……. *Abraliopsis gilchristi*

3b. Three longitudinal series of photophores on ventral head. Six longitudinal series of photophores on ventral mantle. Narrow, photophore-less strip on middle of ventral mantle. Tentacular club without carpal flap and aboral keel. Hectocotylus (right arm IV) with three crests, one on dorsal margin two on ventral margin; modified portion without armature. Protective membrane absent on arms IV…….. *Abraliopsis lineata*

A diagnosis (the distinctive characterisation of a species) is provided below for each species. As this is the first record of *A. lineata* from Australian waters, this species is described fully below.
3.2 Taxonomy

3.2.1 Abraliopsis (Micrabralia) gilchristi (Robson 1924)

*Abraliopsis gilchristi* belongs to subgenus *Micrabralia* and is probably the most easily identifiable species in this subgenus because of some distinctive morphological features. Males reach at least 39 mm ML; females are a bit larger in size than males. It occupies temperate waters of the southern hemisphere. (Riddell, 1985; Tsuchiya, 2013; Okutani, 2015)

![Figure 2: Ventral view of A. gilchristi. Drawing from Voss, 1967 (Source: Young & Kotaro, 2013)](image)

**Material examined.** Appendix 1

**Diagnosis** (Tsuchiya, 2013; Okutani, 2015):

Four rows of photophores on medio-ventral surface of head that continue to those on aboral side of Arm IV (Fig. 3). Mantle with diffused red photophores and mid-ventral strip devoid of photophores. Arms with 17–28 hooks arranged in two rows and suckers only occur on distal end of arms I to III. Arms IV relatively short with three large black photophores on distal arm tips; distal suckers absent. Males hectocotylized arm IV (right arm IV) with three offset flaps; modified portion with armature. Non- hectocotylized arm IV (left arm) with flattened trabeculae on protective membrane.
Male arms I have dorsal border with lappets and large membrane bearing long and broad trabeculae on ventral border. Male arms II with short trabeculae bearing tubercules on dorsal margin; an enlarged membrane and long, flat trabeculae on ventral margin; both trabeculae and membrane bearing tubercules. Male arms III with lappets only on dorsal side, while on ventral margin, there are trabeculae and membranes without papillae. In females, arms I to III without trabeculate protective membranes on dorsal margins but well developed in ventral margins; trabeculate protective membranes absent from both margins of arms IV; trabeculae and arms without tubercules. Tentacle clubs with eight hooks arranged in two rows and dactylus suckers in four rows; the largest hooks located on ventral side on manus; both carpal flap and aboral keel are present on clubs.

Figure 3: Oral view of tentacular club of *A. gilchristi*. Drawing from Voss, 1967 (Source: Young & Kotaro, 2013)

Figure 4: Oral view of arms of *A. gilchristi*. Drawing from Voss, 1967 (Source: Young & Kotaro, 2013)
**Distribution**

*Abraliopsis gilchristi* is distributed in circum-southern temperate waters between 20°–45° S, including the southern coast of Australia (Appendix 4 Map 1a & b).
3.2.2 Abraliopsis (Abraliopsis) hoylei (Pfeffer 1884)

This species is known from a single female specimen. Unfortunately, the type specimen has been lost. The taxonomic status of *A. hoylei* is unclear, some of the morphological features are only identified from Pfeffer’s drawing (1912).

![Figure 5: Ventral view of A. hoylei. Drawing from Pfeffer (1912) (Source: Young & Kotaro, 2013)](image)

**Diagnosis**

Photophores scattered on ventral mantle and head. Arms with 19–21 hooks in two rows, and minute distal suckers. Tentacle clubs with four pairs of hooks on manus and dactylus suckers arranged in four rows. Aboral keel present judged from drawing.

**Distribution**

Mascarene Islands, western Indian Ocean to the tropical west Pacific (Okutani, 2015). Some juveniles were recorded near Smoky Cape, north coast, New South Wales (Allan, 1945).
Figure 6: Oral view of tentacular club of *A. hoylei*. Drawing from Pfeffer, 1912 (Source: Young & Kotaro, 2013).
3.2.3 Abraliopsis (Micrabralia) lineata (Goodrich 1896)


Figure 7: Dorsal view of mature male Abraliopsis lineata, AM C.495718, 27.3 mm ML, scale bar: 6.8 mm. Figure 8: Ventral view of mature male Abraliopsis lineata, AM C.495718, 27.3 mm ML, Scale bar: 6.8 mm.

Type: Holotype ZSI, 2 syntypes, ZSI Zoological Survey of India, "M" Block, New Alipore, Calcutta 700053, INDIA.

Type locality: Andaman Sea and off Ganjam Coast.

**Material Examined.** Appendix 2

**Diagnosis** (Okutani, 2015; Tsuchiya, 2013; Tsuchiya et al., 1991)

Tentacle club (Fig. 9) without keels and carpal flaps; eight hooks arranged in two rows on manus; three or four large ventral hooks and 3 or 4 small dorsal hooks. Four longitudinal
rows of dactylus suckers. Arms I–III with 14–18 hooks in females or 10–12 hooks in males. Bases of arms II about twice thickness in males than other arms. Males with well developed, spatulated trabeculæ on protective membranes and numerous minute tubercles on oral surfaces on arms I. Six longitudinal series of photophores on ventral mantle, narrow bare longitudinal strip in mid ventrally. Five longitudinal rows of photophores on ventral head.

**Description.** (Based on Australian material)

Counts and indices for individual specimens are given in Appendix 8 Table a & b. Only mature specimens were included: nine males and seven females.

Small species ML mature males 20.08–23.8–27.33 (SD = 2.7). ML mature females 16.33–21.9–28.15 (SD = 4.47) (Fig. 7, 8). Mantle slender, conico-cylindrical; MWI male 30.1–40.5–52.6 (SD = 7.2), female 35.2–43.0–53.9 (SD = 7.1). Fins transversely broad, triangular in shape; fin length about 67% of ML; positioned toward posterior end of body; Flla males 33.8–36.4–40.3 (SD = 2.1), females 31.4–34.1–37.2 (SD = 2.1); fin width approx. 40% ML, FWI males 34.0–39.9–48.8 (SD = 5.1), females 33.8–40.7–46.4 (SD = 4.8).

Head sub-cubic and moderate in size; narrower than opening of mantle. HLI males 31.6–36.4–40.0 (SD = 2.68), females 31.5–34.7–39.9 (SD = 2.84); HWI males 21.6–26.9–33.1 (SD = 3.7), females 21.7–26.5–30.0 (SD = 3.1), shorter than mantle width. Eyes large, EDI males 6.5–10.8–18.7 (SD = 4.0), females 6.05–10.8–14.2 (SD = 2.9) Five orange-yellowish large photophores on eyeballs; photophores in longitudinal row with outer pair largest, three relatively small photophores between these. Eyelids droplet-shaped, numerous photophores around eyelid circumference (Fig. 10). Horn shaped membrane on the aboral side of eyes (Fig. 10). Gills with 19–21 lamellae per demibranch.

Funnel moderate length, conical, broad-based; narrow funnel groove with well-developed posterior rim. Funnel organ V-shaped with rami carrying a prominent fleshy ridge on top. The funnel-locking cartilage is spatulate, expanded posteriorly, with median straight, narrow groove (Fig. 11). Widest part of the cartilage about 30% of its length. Mantle locking-cartilage simple and straight ridge (Fig. 12).

Arms moderately long; order IV, I, II = III in male; female IV, II = III, I. All arms similar in shape. Arm length index of longest arm in male (ALI IV) 52.5–66.2–87.1 (SD = 11.0), female (ALI IV) 57.0–64.3–76.1 (SD = 7.90). Longest arm about 64% of DML in female and 66% in male. Arms I and II with narrow median aboral keel on distal half of their length. Arms III
with broad and large aboral keel along entire length. The arms I to III have protective membranes with trabeculae only along ventral side; arms IV lack protective membrane. Two rows of hooks on all arms (14–21 in male; 14–20 in female on arms 1–3, 10–14 on arms IV). Suckers only present on distal tips of arms of I to III (9–20 in both sexes) (Fig.13, 15); no suckers on arms IV. The inner ring of the arm sucker has about 6–7 rectangular teeth on half of the edge (Fig. 14). The outer rings consist of two rows of oval-shaped pegs and a narrow row of marginal plates (Fig. 14). No teeth on distal suckers of all arms.

The protective membrane of both arms I in the male is well-developed dorsally and ventrally. Trabeculae swollen and flattened. Oral surface of arms I with numerous granular papillae with many minute tubercles. Papillae extend from the basal hooks to distal tip of arms I. Arms II of male with swollen region near the base of the arms; about twice as thick as other arms; protective membrane on ventral side modified with numerous small papillae. Protective membrane modified on arms III with papilla, no tubercules on arms III in both sexes.

Right arm IV of male hectocotylised. Three anterior flaps on right arm IV that vary in size and shape. One rhomboidal flap extends from about middle of proximal ventral flap along dorsal side; two flaps on ventral side of right arm IV. Distal flap crescent-shaped extending from distal to proximal flaps to terminal black photophore (Fig.16); proximal flap wavy and relatively longer than other two flaps; extends from distal-most hooks to start of distal crescent-shaped flap along ventral side. No armature where the flaps present. No flaps or crests on arms IV of females.

Tentacles long with naked stalks. Tentacular club small, not thickened and expanded (Fig. 9). CILI male 17.9–19.5–20.5 (SD = 1.1), female 18.7–24.4–28.6 (SD = 5.1). Largest club suckers approx. 0.15 mm diameter. Most suckers located on dactylus, about 33–50 suckers arranged in approx. four longitudinal, and 12 to 14 transverse rows; and only about 1–3 manus suckers present. Inner ring of carpal suckers smooth without obvious tooth structure; outer ring has dense small and irregularly arranged pegs (Fig. 19). Inner ring of dactylus suckers have three to four rectangular shaped teeth; two rows of pegs on outer rings in oval shape (Fig. 17, 18). No keels on either ventral or dorsal side of clubs. Carpal groups consist of about 3–4 suckers and 4 pads. Manus consists of 2 rows of hooks with 3 or 4 large ventral hooks and relative small dorsal hooks.

Ventral surface of mantle, funnel, head and arms III and IV ornamented with photophores. Photophores vary in size, some with a white centres. Six longitudinal rows of light organs on ventral side of mantle; some scattered photophores between rows; a
narrow strip along midline of mantle without photophores. No light organ on dorsal and ventral sides of fins. Photophores of ventral funnel form four longitudinal rows, of which middle two composed of about eleven and the outer rows of about five light organs.

Ventral side of head with photophores arranged in 5 longitudinal rows, median 3 rows extend to arms IV; photophores on ventral side of arm IV extend to tip of arms while dorsal row is interrupted. Two photophore strips along ventral side of aboral keel of arms III extend distally to arm tip. Tip of arms IV with five black, hemispherical photophores; 2 sub-equal small at distal end; 3 larger proximal photophores, largest one ~ 0.5 mm.

Eight lappets present in buccal membrane. Buccal connectives connected to dorsal side of arms I, II and IV and to ventral side of arm III (DDVD type).

Spermatophoric sac large, relatively long, well developed. Accessory gland relatively short and small. Spermatophoric duct short connected to spermatophoric sac. Spermatophoric organ curvy (Fig. 20). Testis relatively large and long; approx. 50% reproductive tract. Spermatophore (Fig. 21, 22) about 21 mm in length. Sperm mass moderate in length. Cement body simple, conical oral connective complex, and attains about 18% of spermatophore length. Ejaculatory apparatus length about 50% of entire spermatophore length.

Each tooth on radula is sharp and pointed. Rachidian tooth single-cusped with a rectangular base (Figs 23, 24). First lateral tooth with rectangular base and single cusp; slender, longer than radula. Second lateral tooth similar to first lateral in structure and size. Marginal tooth long and slender, slightly longer and thicker than first and second lateral tooth.

**Distribution**

*Abraliopsis lineata* has been recorded from the northern of Indian Ocean (Bengal Bay, off Ganjam coast and Arabian Sea) and the tropical west Pacific. This species also occurs off the coast of northeast coast Queensland and has been collected as far north as New Guinea (Appendix 4 Map 2a & b).

**Remarks**

*Abraliopsis lineata* belongs to the subgenus Micrabralia. It is a relatively small species, which attains 30 mm DML. The holotype is not available for study, therefore it is not possible to compare the Australian Museum specimens with the type and at this time, no
specimens from the type locality (from Andaman Sea and off Ganjam coast (Indian Ocean)) are available for study.

Figures 9: Tentacular club of mature male A. lineata, AM C.495701, 26.1 mm ML, scale bar = 1 mm. Figure 10: Side view of mature A. lineata female, AM C.486601, 24.1 mm ML, scale bar = 1 mm. Figure 11: Funnel locking-cartilage of mature A. lineata, AM C. 495714, 25.5 mm ML, scale bar = 1 mm. Figure 12: Mantle locking-cartilage of mature A. lineata, AM C. 495714, 25.5 mm ML, scale bar = 1 mm. Figure 13: Tip of arm II of female, AM C. 495719, 22.3 mm ML, scale bar = 100 μm. Figures 14: Arm I sucker of male, AM C. 495714, 25.5 mm ML, scale bar = 20 μm.
Figure 15: Tip of arm III of female, AM C.495719, 22.3 mm ML, scale bar = 100 μm. Figure 16: Arm IV of mature male *A. lineata*, AM C.495718, 27.3 mm ML, scale bar = 1 mm. Figure 17-18: Dactylus sucker on female's club, AM C.495719, 22.3 mm ML, scale bar = 20 μm. Figure 19: Carpal suckers on female tentacular club, 22.3 mm ML, AM C.495719, scale bar = 30μm.
Figure 20: Mature male reproductive tract, AM C.495702, 26.3 mm ML, scale bar = 2.25 mm. Abbreviations: appendix of accessory gland (AAG), accessory gland (AG), penis (P), spermatopmic gland (SG), spermatophoric organ (SO), spermatophoric sac (SS), testis (T) and sperm duct (VE).

Figure 21-22: Spermatophore of a mature male, AM C.495718, 27.3 mm ML, scale bar = 1 mm. Figure 23-24: Radula of male, AM C.495703, 21.5 mm ML, scale bar = 40 μm.
3.2.4 Abraliopsis (Abraliopsis) tui (Riddell, 1985)

*Abraliopsis tui* belongs to the subgenus *Abraliopsis*, females reach about 35 mm ML and males are a bit smaller, reaching around 30 mm ML.

![Ventral view of A. tui](source: Tsuchiya, 2013)

**Material examined.** Appendix 3

**Diagnosis**

Photophores on ventral head and mantle scattered; with bare distinct strip extending along length of medio-ventral mantle. Arms I–IV with 17–23 hooks arranged in two rows; arms I–III with about 30 distal suckers. Hectocotylised arm (right arm IV) with single long narrow flap along ventral margin; no membrane on dorsal edge; modified portion with armature (Fig. 26). Large carpal flap and aboral keel present on tentacular clubs; two rows of hooks on manus (Fig. 27).

![Oral view of hectocotylus of A. tui](source: Tsuchiya, 2013)
**Distribution**

*Abraliopsis tui* is found in New Zealand, including Kermadec Island waters (Riddell, 1985). In this study, most of the *A. tui* specimens were found off the coast of NSW and some were collected off the coast of Queensland (Appendix 4 Map 3a-c).

### 3.2.5 Female of unknown species

Among the collections four mature female specimens were found to occur off the coast of Queensland (Appendix 4 Map 4). The collection locations of the unknown female species are similar to *Abraliopsis lineata*. However, these two species have totally different morphological feature (Table 1). Morphological features of the unknown female species are similar to *A. tui* but they lack a bare strip along the centre of the ventral mantle.

**Distribution (Appendix 4 Map 4)**

These unknown female species were collected off the Great Barrier Reef (Queensland).
Chapter 4 Discussion

4.1 Summary and implications of results

Four species of *Abraliopsis* were recorded from Australian waters prior to this study: *A. affinis*, *A. hoylei*, *A. gilchristi* and *A. tui* (Jereb & Roper, 2010). *Abraliopsis* specimens from collections of the Australian Museum and Museum Victoria (Australia’s two largest repositories of cephalopods) were examined, and three species were identified; *A. gilchristi*, *A. lineata* and *A. tui*. Most of the specimens were *A. tui* and *A. gilchristi*; a small number of specimens were designated as *A. lineata* which is the first record of this species from Australian waters. *Abraliopsis affinis* and *A. hoylei* were previously thought to occur in Australian waters. No *A. affinis* or *A. hoylei* (as far as the latter species can be determined) were found among the material examined.

*Abraliopsis gilchristi* and *A. tui* appear to have a sympatric distribution off south-eastern of Australia (Appendix 4, Map 1 & 4). Whether there is habitat partitioning between these two species cannot be determined from the collection data. They may occur together; they may occupy different depths, or perhaps have differing ecological requirements. According to the specimen information, *A. gilchristi* was collected at depth between 0 and 823 m, while *A. tui* was found at depth ranging from 0 to 960 m. However, the data available for each specimen does not provide a clear indication of the depth of capture and a variety of different trawl methods were used. Where opening-closing nets were used, the capture depth is a real collection depth, but if nets are kept open for the duration of a trawl until the surface is reached, animals may have been collected at any depth throughout the time of the trawl. Also, according to the study by Roper and Young (1975), enoploleuthids, including genus *Abraliopsis*, migrate from 300 to 700 m by day to the upper 100 m or so by night; therefore, the time of capture will reflect differences in depths occupied by the animals. Unfortunately, information on each specimen about capture time and time of the trawl is not clear enough, therefore, it is not possible to compare *A. gilchristi* and *A. tui* habitat in terms of depth.

*Abraliopsis hoylei* is apparently distributed over a wide geographic range (Indian Ocean, Mascarene Islands, tropical and subtropical Indo-West Pacific Ocean from Hokkaido to the Tasman Sea and from eastern Africa to Hawaii) (Jereb & Roper, 2010; Young & Tsuchiya, 2013; Okutani, 2015). This species was thought to occur widely in Australian waters (Allan, 1945) however, no specimens of this species were found among the *Abraliopsis* specimens from the Australian Museum and the Museum Victoria.

The specimens from the Australian Museum collection identified as *Abraliopsis hoylei* in Allan’s (1945) paper were examined. However, the specimens were too small (all juvenile)
and all specimens have turned dark brown perhaps due to the long period of preservation or fixation method; it is therefore impossible to study the photophore arrangement on the specimens’ body surface. Also their bodies were so brittle; specimens are damaged easily in the examination process. It is not possible to obtain any extra information from those specimens and, therefore, it is uncertain whether those specimens identified by Allan (1945) were named correctly. Unfortunately, despite this dubious identification the species name and its supposed occurrence in Australian waters has persisted in the literature for seven decades.

_Abraliopsis hoylei_ is hard to identify for two reasons. First, there is a lack of information; the information on Tolweb and in the literature relies on the drawing and brief description by Pfeffer, as a result there are a lot of uncertainties about the features of _A. hoylei_. Second because the holotype has been lost, it is not possible to compare specimens to the holotype to ensure that all features are matched. We were unable to borrow any _A. hoylei_ from anywhere near the type locality (Mascarene Island in the Indian Ocean). However, referring to the brief description in Tolweb (2013) and Jereb & Roper (2010) in this study I believe that no specimens in the available collection are referrable to _A. hoylei_. A full redescription of _A. hoylei_ based on specimens from the type locality is very much needed.

_Abraliopsis lineata_ is a new record from Australian waters; it occurs in the north-eastern region (off the GBR) (Appendix 4 Map 2a & b) at depths of between 0 and 200 meters. The species is also found in the Andaman Sea (Pfeffer, 1900) and the Seychelles (Nesis, 1986). This species was originally placed in the genus _Abralia_ based on a single male collected from the Andaman Sea, and a single female from off the Gamjam coast, Bay of Bengal (Goodrich, 1896). The discovery of the species in Australian waters is a considerable range extension for the species. The recent complete, and well-illustrated description of _A. lineata_ published by Tsuchiya _et al._, 1991, and also details published on TolWeb (Tsuchiya, 2013) has enabled a detailed comparison to be made between the north-eastern Australian specimens and _A. lineata_ found from the regions off Pakistan and north-western Indian Ocean, confirming and its identify with near certainty. The Australian _A. lineata_ conforms in most respects with the species described by Tsuchiya _et al._, 1991 except the order of the arm length. Photophore patterns on the ventral mantle vary among specimens; the median longitudinal strips on ventral mantle are sometimes hard to see under a microscope. Ideally, it would be useful to compare the Australian specimens with type material, however, unfortunately this held in the Zoological Survey of India, New Alipore, Calcutta, India, and is unavailable for loan. A comparison with animals from the general type locality from Andaman Sea and off Ganjam coast (Indian Ocean) would be useful also. _Abraliopsis lineata_ mentioned by Tsuchiya _et al._, 1991 was found in the regions off Pakistan and the north-
western Indian Ocean, so not close to the type locality. The three regions where *A. lineata* occur are disjunct; no *A. lineata* has been recorded between those regions. Additional support for these identifications will follow when specimens from across the full species range are compared. So to confirm this finding, specimens need to be compared with type specimens, or from the type locality.

*Abraliopsis lineata* is now known to be distributed over a wide geographical range, however, its apparent distribution is disjunct with specimens collected from three regions and no reported between these areas. There are three possibilities that might explain this: (1) The disjunct distribution is real with populations separated as a result of historical events, for example the populations were separated because of past geological events; (2) *A. lineata* does occur in the regions in between the known populations but has not yet been collected or identified, or (3) The populations of *A. lineata* are indeed genetically distinct but cannot be distinguished on the basis of morphology alone; perhaps cryptic species are present. To test these competing hypotheses, representatives of the three populations need to be examined in detail using both morphological and (if possible) molecular characters. Cryptic species are species that are difficult to distinguish using morphological features and therefore two or more distinct species may be classified as the same species incorrectly (Bickford et al., 2006). In order to make sure they are not cryptic species, genetic information is vitally important.

To avoid the misclassification of species due to the presence of cryptic species, an integrative approach is suggested to identify organisms. An integrative approach uses both morphological and molecular approaches to identify species to reduce the chances of misidentification (Selbach et al., 2015). Such an approach is not always possible, as was the case in this study. The specimens that were available for this project were fixed in formalin after capture. Formalin has been commonly used as a fixative for museum material and remains to be the most suitable fixative for long-term preservation. While DNA can be more readily extracted from ethanol preserved specimens, ethanol tends to make the tissue quite brittle and not so useful for anatomical investigations. At this time it is not easy to extract DNA from formalin preserved specimens; the DNA is generally highly degraded or fragmented. Current collection methods ensure that some specimens or parts of specimens are preserved so that they are useful for molecular study (either ethanol fixed, or (preferably) tissue is stored in a minus 80 degree freezer). However, if new methods are developed that ensure a greater success in working with formalin fixed material; vast museum collections worldwide will be able to be tapped for molecular data. An integrative approach is usually the best way to ensure that specimens are not misidentified and can provide a greater amount of
information regarding population structure and species boundaries. Such an approach could be usefully applied to future studies of A. *lineata* collected across its range.

### 4.2 Problems of sampling

The samples available for this study did not cover all Australian waters due to limited collecting effort expended and consequently limited geographic spread of collections held by museums. *Abraliopsis* species are not targeted and available collections were bycatch from other studies with the majority of surveys and specimens obtained from sites off the coast of New South Wales and Queensland, although some were collected around Tasmania and off the coast of southwestern Western Australia. In consequence the distribution of *Abraliopsis* within large areas of Australia’s waters is unknown particularly in the northern regions. In order to find out whether *Abraliopsis* does occur in those regions, more collections in those areas are needed and additional effort should be directed at restudying the collections in different museums to ensure no *Abraliopsis* specimens have missed. Many of the Australian Museum specimens were found among unidentified material. However, it is a difficult work because a lot of labour efforts and resources such as money are needed. As I mentioned before, people are not interested in *Abraliopsis* due to their low commercial value.

### 4.3 Importance of species identification

Accurate species identification is essential information with significant conservation implications. Animals cannot be list as vulnerable or endangered in CITES (the Convention on International Trade in Endangered Species) list unless they are formally named; species only benefit from the sets of legislative and planning tools if they are named and identified formally (Mace, 2004). Therefore, assigning animals to the correct conservation status in CITES is important to biodiversity management and conservation. If organisms are designated to incorrect categories they may be treated inappropriately in terms of management and this may result in a negative effect on biodiversity conservation. For instance, if cryptic species are wrongly considered as the same species, the population sizes of those species maybe under- or overestimated. Taxonomy and species conservation are assumed to be interdependent activities; taxonomy will influence the conversation decision and therefore should be regarded as high priority field of research (Gaston, 2001; Dubois, 2003; Mace, 2004). While there is no available evidence as yet to determine the conservation status of any *Abraliopsis* species; they are not targeted by commercial fishers (therefore requiring management) and are unlikely threatened at this time, the studies such as this one provide a basis for future monitoring.
More research effort is needed if we are ever to fully manage marine ecosystems but expense prevents extensive targeted surveys for most species and in reality those available via museums have often been simply only bycatch from other studies (Gislason et al., 2000). The exceptions most often are organisms with high commercial importance that are collected over broad distributional ranges or studies that seek to determine biodiversity within particular geographical areas. In the case of Abraliopsis lineata in this study existing collections resulted from a CSIRO sampling survey to examine planktonic animals in the Coral Sea. The Abraliopsis specimens were not target of the survey and collections are clearly incomplete. The existing specimens were placed in museums without study more than ten years.

Taxonomy is important in biodiversity management and conservation, however, the identification process is very slow. Sometimes there is a shortage of information on particular animals. The taxonomy of a group must be based on the reliable taxonomic information or literature from extensive examination of specimens (Vecchione et al., 2000). For example, A. hoylei is difficult to identify because the lack of a detailed description and loss of the holotype to compare morphological features. Reliable and thorough information is useful in identification. Specimen collections are also scattered around the world, time is needed to study the specimens from different museums. Also, some of the specimens are unavailable to loan, for example the holotype of A. lineata in this study. Good communication between museums assists the identification process, but worldwide museums suffer from staff and funding limitations and this is an increasing problem. Another limitation is the condition of specimens. Some animals may be damaged during the capture process; damage of specimens can influence the accuracy of identification due to the loss of distinctive features. Also because it is not always possible to identify specimens immediately, some pigments in body tissue can fade out after long periods of preservation. In addition, particularly in cephalopods with few soft parts, the contraction of body tissues may also make the identification difficult.

**Conclusion**

To conclude, through this study, we found that more taxonomic investigation needs to be done; there are a lot of specimens amassed over centuries in many museum collections worldwide that are yet to be studied. Also the shortage of information and taxonomic expertise in some cases can become a barrier to species identification. Naming species correctly is an important starting point in species conservation and management. Therefore, taxonomy should be highly considered in order to improve species conservation and management.
References


Hind KR, Gabrielson PW, Lindstrom SC and Martone PT, 2014, ‘Misleading morphologies and the importance of sequencing type specimens for resolving coralline taxonomy


Appendix 1: *Abraliopsis gilchristi* (Robson, 1924) material examined

1 male, 34.92 mm ML (mature), Australia, NSW, East of Cape Howe, 37° 24' 00" S, 150° 30' 00" E to 37° 28' 00" S, 150° 33' 00" E, 485m, 1 Nov 1977, KJ Graham (AM C. 131809); 1 male, 36.94 mm ML (mature), Australia, NSW, Off Brush Is, 35° 36' 00" S, 150° 55' 00" E to 35° 39' 00" S, 150° 56' 00" E, 549m, 27 Oct 1977, TB Gorman & KJ Graham (AM C. 495723); 1 male, 36.62 mm ML (mature), Australia, NSW, Off Shoalhaven Heads, 34° 54' 00" S, 151° 10' 00" E to 34° 58' 00" S, 151° 09' 00" E, 494-585m, 10 Sep 1986, KJ Graham (C. 399141); 1 male, 26.69 mm ML (immature), Australia, NSW, 72km E of Broken Bay, 33° 19' 00" S, 152° 25' 00" E to 33° 23' 00" S, 152° 28' 00" E, 0-640m, 13 Dec 1977, JP Paxton (AM C. 495706); 2 males, 22.25-24.28 mm ML (immature), Australia, NSW, 97km E of Broken Bay, 33° 28' 00" S, 152° 34' 00" E to 33° 36' 00" S, 152° 35' 00" E, 630m, 14 Dec 1977, JP Paxton (AM C. 495727); 2 males, 35.10 mm ML (mature), 23.36 mm ML (immature), Australia, NSW, 64km E of Sydney Heads, 33° 53' 00" S, 152° 02' 00" E, 0-800m, 14 Dec 1977, JP Paxton (AM C. 495724); 1 male, 18.68 mm ML (immature), Australia, NSW, Off Sydney, 33° 30' 00" S, 152° 05' 00" E to 33° 27' 00" S, 152° 07' 00" E, 823m, 21 Dec 1976, KJ Graham & PH Colman (AM C. 495726); 1 male, 36.03 mm ML (mature), 1 female, 41.89 mm ML (mature), Australia, Western Australia, Perth, Canyon, 31° 51' 40" S, 114° 47' 35" E, 0-200m, 28 Aug 2003, JA Koslow (AM C. 486598); 1 male, 36.02 mm ML (mature), 1 female, 43.42 mm ML, Australia, NSW, Off Batemans Bay, 36° 03' 00" S, 150° 27' 00" E to 35° 59' 00" S, 150° 28' 00" E, 247m, 7 Aug 1979, KJ Graham (AM C. 486597); 1 male, 36.30 mm ML (mature), 1 female, 36.45 mm ML (mature), Australia, NSW, East of Ulladulla, 35° 01' 00" S, 152° 47' 00" E to 35° 02' 00" S, 152° 48' 00" E, 190m, 25 Oct 1979, CSIRO (AM C. 137007); 1 male, 35.78 mm ML (mature), 2 females, 35.98-39.35 mm ML (mature), Australia, NSW, Off Port Kembla, 34° 28' 00" S, 151° 29' 00" E, 0-229m, 22 Jul 1974-24 Jul 1974, JP Paxton & KJ Graham (AM C. 495705); 1 female, 41.96 mm ML (mature), Australia, NSW, Off Kiama, 34° 40' 00" S, 151° 15' 00" E to 34° 35' 00" S, 151° 17' 00" E, 604-686m, 3 Nov 1977, KJ Graham (AM C. 495725); 1 female, 42.16 mm ML (mature), Australia, NSW, Off Sydney, 33° 43' 00" S, 151° 55' 00" E, 686m, 19 Oct 1972, KJ Graham (AM C. 391664); 1 female, 42.72 mm ML (mature), Australia, NSW, Off Port Kembla, 34° 28' 00" S, 151° 29' 00" E, 0-229m, 22 Jul 1974-24 Jul 1974, JP Paxton & KJ Graham (AM C. 119661); 2 males, 20.69-22.63 mm ML (immature), Pedra Branca vicinity, SW of TAS, 147° 0' 54", 44° 14' 7", 100m, 17 Feb 1992 (MV F 80462)
Appendix 2: *Abraliopsis lineata* (Goodrich, 1896) material examined

1 male, 24.10 mm ML (mature), 2 females, 19.83-27.62 mm ML (mature), Australia, Queensland, 12° 33' 22" S, 144° 32' 20" E to 12° 35' 06" S, 144° 26' 13" E, 0-12m, 26 May 1997, CSIRO (AM C. 486601); 1 male, 24.91 mm ML (mature), 1 female, 25.36 mm ML (mature), Australia, Queensland, 14° 19' 41" S, 145° 30' 36" E to 14° 13' 01" S, 145° 26' 13" E, 0-12m, 28 May 1997, CSIRO (AM C.495714); 1 male, 25.87 mm ML (mature), 1 female, 24.29 mm ML (mature), Coral Sea, 10° 45' 11" S, 147° 09' 47" E to 10° 39' 11" S, 147° 10' 55" E, 0-12m, 21 May 1997, CSIRO (AM C.495702); 1 male, 21.50 mm ML (mature), 2 females, 22.31 mm ML (mature), 16.80 mm ML (immature), Australia, Queensland, 10° 58' 30" S, 144° 32' 40" E to 10° 59' 38" S, 144° 41' 02" E, 25-50m, 25 May 1997, CSIRO (AM C.495719); 1 male, 21.74 mm ML (mature), Australia, Coral Sea, 14° 52' 16" S, 148° 59' 28" E to 14° 53' 31" S, 149° 04' 26" E, 50-100m, 10 May 1997, CSIRO (AM C. 495703); 1 male, 26.66 mm ML (mature), Australia, Queensland, 16° 12' 32" S, 146° 15' 43" E to 16° 17' 38" S, 146° 17' 06" E, 50-100m, 30 May 1997, CSIRO (AM C.495701); 1 male, 20.08 mm ML (mature), Australia, Coral Sea, 12° 38' 53" S, 146° 41' 10" E to 12° 36' 04" S, 146° 40' 52" E, 0-12m, 20 May 1997, CSIRO (AM C.495716); 1 male, 27.51 mm ML (mature), Australia, Coral Sea, 12° 45' 36" S, 146° 35' 20" E to 12° 42' 04" S, 146° 38' 53" E, 50-100m, 19 May 1997, CSIRO (AM C.495718); 1 male, 22.84 mm ML (mature), Coral Sea, 09° 19' 30" S, 145° 20' 28" E to 09° 19' 55" S, 145° 14' 17" E, 0-12m, 24 May 1997, CSIRO (AM C.495717); 1 male, 14.89 mm ML (immature), Australia, Queensland, 13° 52' 59" S, 144° 58' 41" E to 13° 55' 44" S, 145° 02' 31" E, 25-50m, 28 May 1997, CSIRO (AM C.495715); 1 female, 31.37 mm ML (mature), Australia, Queensland, 12° 33' 22" S, 144° 32' 20" E to 12° 35' 6" S, 144° 26' 13" E, 0-200m, 26 May 1997, CSIRO (AM. C. 495741); 1 female, 13.27 mm ML (immature), Coral Sea, 12° 3' S, 153° 37' 59" E to 11° 59' 20" S, 153° 30' 36" E, 0-12m 14 May 1997, CSIRO (AM. C. 495733); 1 female, 13.38 mm ML (immature), Australia, Coral Sea, 15° 3' 58" S, 149° 20' 56" E to 15° 7' 30" S, 149° 26' 56" E, 0-12m, 10 May 1997, CSIRO (AM. A. 495744); 2 juveniles, 10.19-14.95 mm ML, Australia, Coral Sea, 9° 19' 30" S, 145° 20' 28" E to 9° 19' 55" S, 145° 14' 17" E, 0-12m 24 May 1997, CSIRO (AM. A. 495729); 1 female, 20.36 mm ML (mature), Australia, Queensland, 12° 38' 28" S, 144° 22' 5" E to 12° 41' 28" S, 144° 17' 42" E, 0-200m 26 May 1997, CSIRO (AM. C. 495728)
Appendix 3: *Abraliopsis tui* (Riddell, 1985) material examined

1 male (holotype), 28.7 mm ML (mature), New Zealand, Kermadec Island, NE of Raoul Island, 28°18'00"S, 174°56'00"W to 28°20'20"S, 174°56'00", 94m, 14 Dec 1976, FRV *James Cook* (M.98797); 1 male, 25.28 mm ML (mature), Australia, NSW, Off Sydney, 33° 57' 00" S, 152° 20' 00" E to 33° 28' 00" S, 151° 17' 00" E, 0-800m, 14-15 Dec 1977, JP Paxton (AM C.391693); 2 males, 23.55-24.99 mm ML (mature), 1 female, 27.96 mm ML (mature), Australia, NSW, Off Sydney, 32° 42' 00" S, 152° 02' 00" E to 32° 36' 00" S, 152° 05' 00" E, 0-960m, 24 Mar 1971, J. Paxton (AM C.495712); 1 male, 23.23 (mature), 1 female, 22.60 mm ML (mature), Australia, NSW, Off Botany Bay, 34° 27' 00" S, 151° 38' 00" E to 34° 20' 00" S, 151° 40' 00" E, 0-550m, 23 May 1978, K. J Graham (AM C. 495709); 1 male, 25.23 mm ML (mature), 1 female, 29.49 mm ML (mature), Australia, NSW, East of Newcastle, 33° 05' 00" S, 151° 50' 00" E to 33° 06' 00" S, 151° 51' 00" E, 0-91m, 29 Nov 1979, KJ Graham (AM C.486599); 2 males, 25.76 mm ML (mature), 22.59 mm ML (immature), 2 females, 23.00-23.32 mm ML (mature), Australia, NSW, Off Sydney, 33° 59' 27" S, 151° 16' 48" E, 0-64m, 17 Apr 1973, KJ Graham (AM C.495707); 2 males, 26.70 mm ML (mature), 23.43 mm ML (mature), 3 females, 15.09-22.09 mm ML (mature), Australia, NSW, Southeast of Newcastle, 33° 20' 00" S, 153° 04' 00" E to 33° 12' 00" S, 153° 13' 00" E, 0-640m, 28 Nov 1979, KJ Graham (AM C.495711); 6 males, 20.94-25.26 mm ML (mature), 20.83 mm ML (1 immature), 10 females, 22.77-29.46 mm ML (mature), Australia, NSW, 97km East of Broken Bay, 33° 28' 00" S, 152° 32' 00" E to 33° 36' 00" S, 152° 35' 00" E, 630m, 14 Dec 1977, JP Paxton (AM C.391582); 9 males, 25.59-16.02 mm ML (8 mature), 17.59 mm ML (1 immature), 6 females, 23.32-28.23 mm ML (5 mature), 20.40 mm ML (1 immature), Australia, NSW, 80km East of Tuggerah Lakes, 33° 20' 00" S, 152° 32' 00" E, 0-300m, 14 Dec 1977, JP Paxton (AM C.495713); 29 males, 20.42-26.51 mm ML (27 mature), 17.79-23.88 mm ML (5 immature), 27 females, 30.30-21.00 mm ML (25 mature), 17.67-20.90 mm ML (2 immature), Australia, NSW, 80km East of Tuggerah Lakes, 33° 20' 00" S, 152° 32' 00" E, 0-300m, 14 Dec 1977, JP Paxton (AM C.391709); 73 males, 19.19-29.10 mm ML (30 mature), 15.35-22.50 mm ML (43 immature), 54 females, 18.73-28.81 mm ML (25 mature), 14.76-21.78 mm ML (29 immature), Australia, NSW, Off Sydney, 33° 59' 27" S, 151° 16' 48" E, 0-64m, 17 Apr 1973, KJ Graham (AM C. 391584); 2 males, 22.75 mm ML (1 mature), 14.65 mm ML (1 immature), 2 females, 25.88-28.48 mm ML (mature), Australia, NSW, Southeast of Newcastle, 33° 15' 00" S, 153° 06' 00" E to 33° 20' 00" S, 153° 04' 00" E, 366m, 27 Nov 1979, KJ Graham (AM C.486660); 3 males, 22.54-25.66 mm ML (2 mature), 19.98 mm ML (immature), 6 juveniles, 12.35-15.51 mm ML, Australia, NSW, East of Newcastle, 33° 05' 00" S, 153° 05' 00" E to 33° 13' 00" S , 153° 05' 00" E, 0-640m, 28 Nov 1979, KJ Graham (AM C 495708); 5 males, 20.16-26.50 mm ML (mature), 2 females, 26.33-29.81 mm ML (mature), 2 Juveniles, 9.47-18.16 mm ML, Australia, NSW, Off Sydney, 34°
09' 00" S, 152° 07' 00" E to 34° 20' 00" S, 152° 02' 00" E, 0-550m, 23 Mar 1971, JP Paxton
(AM.C.131807); 3 males, 19.20-23.87 mm ML (mature), 2 females, 21.44-28.98 mm ML
(mature), 2 juveniles, 17.36-18.18 mm ML, Australia, NSW, Off Broken Bay, 33° 27' 00" S,
152° 30' 00" E to 33° 23' 00" S, 152° 32' 00" E, 0-220m 13 Dec 1977, JP Paxton & KJ
Graham (AM.C.391532); 10 males, 18.45-24.70 mm ML (6 mature), 17.93-19.31 mm ML (4
immature), 15 females, 23.68-39.43 mm ML (13 mature), 19.14-19.89 mm ML (2 immature),
2 juveniles. 13.11-15.74 mm ML, Australia, NSW, 72km East of Broken Bay, 33° 19' 00" S,
152° 25' 00" E to 33° 23' 00" S, 152° 28' 00" E, 0-640m, 13 Dec 1977, JP Paxton (AM.
C.391552); 1 male, 18.70 mm ML (immature), 4 juveniles, 12.84-16.00 mm ML, Australia,
NSW, East of Newcastle, 33° 05' 00" S, 153° 05' 00" E to 33° 13' 00" S, 153° 05' 00" E, 0-
640m, 28 Nov 1979, KJ Graham (AM.C.495721); 1 juvenile, 20.00 mm ML, Australia, NSW,
97km East of Broken Bay, 33° 28' 00" S, 152° 34' 00" E to 33° 36' 00" S, 152° 35' 00" E,
630m, 14 Dec 1977, JP Paxton (AM.C.119567); 4 males, 20.98-24.04 mm ML (mature),
20.47 mm ML (immature), 3 females. 25.01-29.92 mm ML (mature), 23.02 mm ML
(immature), 1 juvenile, 19.61 mm ML, Australia, NSW, 64km East of Sydney Heads, 33° 53'
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mm ML (mature), Australia, NSW, East of Newcastle, 33° 05' 00" S, 153° 05' 00" E to 33° 13'
00" S, 153° 05' 00" E, 0-640m, 28 Nov 1979, KJ Graham (AM.C.133441); 1 female, 34.27
mm ML (mature), Australia, Queensland, 14° 19' 41" S, 145° 30' 36" E to 14° 13' 01" S, 145°
26' 13" E, 0-12m 28 May 1997, CSIRO (AM.C.495720); 1 female, 18.04 mm ML (mature),
Australia, Coral Sea, 12° 45' 36" S, 146° 35' 20" E to 12° 42' 04" S, 146° 38' 53" E, 50-100m,
19 May 1997, CSIRO (AM.C.495722); 1 female, 27.13 mm ML (mature), Australia, NSW, Off
Newcastle, 33° 19' 60" S, 152° 16' 60" E to 33° 25' 60" S, 152° 13' E, 0-650m, 18 Dec 1969,
JP Paxton (AM.C.495735); 3 juvenile, 10.87-17.56 mm ML, Australia, NSW, E of Broken
Bay, 33° 31' S, 152° 19' 60" E to 33° 28' S, 152° 22' E, 549m, 12 Dec 1977, KJ Graham
(AM.C.391541); 1 male, 15.45 mm ML (immature), 3 female, 23.65-29.71 mm ML (mature),
Australia, NSW, Off Norah Head, 33° 16' 60" S, 152° 31' E to 33° 19'S, 152° 31'E, 0-91m, 13
Dec 1977, J Paxton & KJ Graham (AM.C.391523); 1 female, 21.88 mm ML (immature),
Australia, NSW, Off Brush Is, 35° 36' S, 150° 55' 60" E to 35° 39' S, 150° 55' 60" E, 549m 27
Oct 1977, TB Gorman & KJ Graham (AM.C.495740); 1 juvenile, 10.41 mm ML, Australia,
NSW SE of Newcastle, 33° 15' S, 153° 6' E to 33° 19' 60" S, 153° 4' E, 366m, 27 Nov 1979,
KJ Graham (AM.C.495737); 1 female, 28.05 mm ML (mature), Australia, NSW, Off Port
Kembla, 34° 28' S, 151° 28' 60" E, 0-229m, 22-24 Jul 1974, J Paxton & KJ Graham (AM.C.
269841); 1 female, 26.61 mm ML (mature), Australia NSW NE of Newcastle, 32° 51' S, 153°
1' E to 32° 58' 60" S, 152° 54'E, 0-1472m, 29 Nov 1979, KJ Graham (AM.C.398578)
Appendix 4: Species distributions

Map 1a and b: *Abraliopsis gilchristi* specimen distributions indicated in orange. Grey lines indicate the boundary of Australian waters (Areas of marine jurisdiction within 200 nautical miles). Map 1a scale bar: 200 km, map 1b scale bar: 100 km.
Map 2a and b: *Abraliopsis lineata* specimen distributions indicated in brown. Grey lines indicate the boundary of Australian waters (Areas of marine jurisdiction within 200 nautical miles). Map 2a scale bar: 200 km, map 2b scale bar: 100 km.
Map 3a-c: *Abraliopsis tui* specimen distributions in purple. Grey lines indicate the boundary of Australian waters (Areas of marine jurisdiction within 200 nautical miles). Map 3a scale bar: 200 km, map 3b & c scale bar: 100 km.

Map 4: Unknown female specimen distribution in green. Grey lines indicate the boundary of Australian waters (Areas of marine jurisdiction within 200 nautical miles). Scale bar: 100 km.
Map 5: Unidentified species (immature or juveniles) indicate in blue. Grey lines indicate the boundary of Australian waters (Areas of marine jurisdiction within 200 nautical miles). Scale bar: 200 km.

Map 6: Specimen distributions. Scale bar: 200 km
Appendix 5: Australian continental shelf confirmed by the Commission on the Limits of the Continental Shelf

Australian continental shelf confirmed by the Commission on the Limits of the Continental Shelf. **Blue** indicates territorial sea and internal waters. **Purple** indicates area of Australian continental shelf beyond 200 nautical miles as confirmed by the Commission on the Limits of the Continental Shelf. **Green** indicates areas of marine jurisdiction within 200 nautical miles of Australia and its external territories. **Yellow** indicates Joint Petroleum Development Area under Timor Sea Treaty 2002 (Source: Commonwealth of Australia, Geoscience Australia, 2008).
Appendix 6: Table of terminology, measurement, indices and abbreviations

1. AF Arm Formula (arm numbers ordered from longest to shortest)
2. AL: Arm Length, length measured from the basal sucker or hooks to the tip of arm
3. ALI Arm Length Index: Arm length as percentage of mantle length
4. AS: Arm sucker diameter
5. ASCn Arm sucker count: number of suckers on normal arms
6. ASCh Arm sucker count on hectocotylised arm of male
7. CSC: Club suckers count
8. CIL: Club length measured from the base of carpus to the end of tentacle
9. CIRC: Club row count
10. CIS: Club suckers diameter
11. DSc: Dactylus suckers count
12. ED: Eye diameter
13. EGL: The diameter of the egg from mature female
14. FW: Fin width
15. Fla: Measured from the bottom end of mantle to the fin
16. FL: Length of fin
17. FuL: Length of funnel from attachment to the opening
18. FFuL: Dorsal length of the funnel from attachment to the mantle to funnel opening.
19. GilL: The length of gill
20. GilC Gill Count: Number of gill lamellae per demibranch
21. HL Length of head: measured from anterior point of dorsal nuchal cartilage to junction of dorsal arms
22. HcL: Length of hectocotylus arm
23. HW: Width of head across eyes
24. HWI Head Mantle Width Index: Head width as percentage of mantle length
25. MaSC Manus Sucker Count: number of suckers on manus of club
26. MaHC Manus Hook Count: number of hooks on manus of club
27. ML Mantle length: Dorsal mantle length measured from anterior most point of mantle to posterior apex of mantle or tip of united fins
28. MW Mantle width: Width across ventral surface of mantle
29. MWI Mantle Width Index: Greatest straight-line width across ventral surface of mantle as a percentage of mantle length.
30. STC: for largest suckers on manus, dactylus, arm 3 and arm 4, especially
31. TCIRc: Transverse row sucker count
32. VML: Ventral mantle length
Appendix 7: Illustration of technical terms and measurements

Figure a and b: Illustration of technical terms (Source: Memoirs of the National Museum of Victoria, pp60-61).
Appendix 8: Tables of *Abraliopsis lineata* (Goodrich 1896) measurements (mm), indices and counts of mature specimens of both sexes (a: male, b: female). The index gives a direct proportional relationship to the mantle length. All abbreviation and indices follow the guidelines of Roper and Voss, 1983. * indicates damaged features, -- indicates features that were not able to be counted or measured.

Table a: Males *A. lineata*.

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Appendix 9: Glossary (Jereb & Roper, 2010)

Arm formula—Comparative length of the 4 pairs of arms expressed in descending order

Buccal—Pertaining to the mouth

Buccal membrane—Muscular membrane the surround the mouth like an umbrella that form the buccal crown

Cement body—Structure of spermatophore that allows adhesion of the discharged spermatophore to a female

Dactylus—The distal, terminal section of the tentacular club

Distal—Away from the central region of the body

Ejaculatory apparatus—Portion of the spermatophore involved in the vigorous extrusion of the sperm mass

Funnel-locking cartilage—Cartilaginous groove or depression on each ventrolateral side of the posterior part of the funnel that joins with the mantle component to lock the funnel and mantle together.

Gill lamella—Leaf-like convoluted individual components of the gills

Hectocotylus—Modified arm(s) in male squids used to transfer spermatophores to the female

Holotype—A single specimen designated by the original author of a species to represent the new species name. It is a reference provides objectivity and stability for the species name

Protective membrane—Thin web-like integument along the lateral angles of the oral surface of the arms and clubs lateral to the suckers

Proximal—Opposite to distal; near to the centre of the body

Radula—Chitinous, ribbon-like band in the mouth of cephalopods that aid in transport of food

Spermatophore—A tubular structure manufactured by male cephalopods for packing sperm

Sperm cord—Coiled rope of sperm that lies within the spermatophore

Sperm duct (VE)—The tube of male reproductive system through which the spermatophores

Spermatophoric organ (SO)—Male organ where the spermatophores are formed

Spermatophoric sac (SS)—as known as Needham’s sac, the elongate, membraneous organ of males where spermatophores are stored

Tentacle—Modified fourth pair of appendages in squids

Tentacle club—Distal, terminal, expanded part of the tentacle

Trabeculae—Muscular rods that support the protective membrane on the arms and club of squid
# Appendix 10: Distinguishing features of each subgenus

<table>
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<tr>
<th>Subgenus</th>
<th>Abraliopsis</th>
<th>Micrabalia</th>
<th>Pfefferiteuthis</th>
<th>Boreabraliopsis</th>
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<tr>
<td>Left arm IV (male)</td>
<td>Flaps absent</td>
<td>Flaps absent</td>
<td>Large, ventral, round-trapezoidal flap present</td>
<td>Flaps absent</td>
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<td>Ventral flap</td>
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<td>Tentacular club</td>
<td>Club keel</td>
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<td>Carpal flap</td>
<td>Large</td>
<td>Absent or present</td>
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<tr>
<td>Photophore pattern on the ventral head</td>
<td>Scattered</td>
<td>Three or four longitudinal series</td>
<td>Three longitudinal series</td>
<td>Scattered</td>
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</table>

Table 1: Taxonomic features of each subgenus. * indicates that features are uncertain due to the and lack of a detailed description. (Source: Young & Kotaro, 2014)