

PAST, PRESENT AND FUTURE STUDIES ON CEPHALOPOD DIVERSITY IN TROPICAL WEST PACIFIC

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Abstract: The history and present status of studies on Tropical West Pacific cephalopods have been reviewed. The loliginids in this region contain multiple species-complexes or exhibit remarkable polymorphism. Some 34 species of shallow-water octopuses have hitherto been identified from the Tropical West Pacific, but many more unsolved species are existing there. The future intensive and rapid promotion of alpha-taxonomy of the Tropical West Pacific cephalopods is recommended.

INTRODUCTION

Of the world's oceans, the Tropical West Pacific is richest in animal diversity. The cephalopod fauna in this region is likewise rich, but the taxonomic/faunistic inventory of the cephalopods inhabiting this area seems to be still insufficient or fragmentary. The present paper reviews the contributions of the early authors, and the current status of knowledge on Tropical West Pacific cephalopod diversity, comprising mainly neritic species (*i.e.* Sepiidae, Loliginidae and shallow water Octopodidae), and suggests directions for future research. The Tropical West Pacific termed here is tentatively delineated as ranging from Hong Kong and the South China Sea south to the Arafura Sea, covering the main part of Indonesian waters. This area is a part of the vast Indo-West Pacific Region (Ekman, 1953; Briggs, 1973). This is also part of the Indo-Malaysia, Sino-Japan and Polynesia described by Khromov (1998) (Figure 1).

The cephalopod diversity in the subtropical regions in the north, such as Taiwan and southwestern Japan, has been recently inventoried by Lu (1998a) and Kubodera and Lu (2002). Those in the south, such as subtropical Australian waters, have been consolidated by contributions of Roper (1983), Lu (1998b), and Norman (1992a, b, c) among others. Some but not all species in these adjoining seas are in common with the fauna occupying the region under discussion.

HISTORICAL STUDIES

Except for several fragmentary works in the past, the earliest systematic study on Tropical West Pacific cephalopods may be that based on the *Astrolabe* collection. Quoy and Gaimard (1832) reported five species from New Guinea or Celebes: *Sepia latimanus*, *Sepioteuthis guinensis*, *S. lunulata*, *Onychoteuthis (=Abralia) armatus*, and *Octopus membranaceus*.

Among 17 "zoogeographical regions" of Hoyle (1886) based on the cephalopod collection by the HMS *Challenger*, the Area IX (The Indo-Malayan Region) covers most of the Tropical West Pacific related here. Hoyle enumerated 40 neritic species plus 7 pelagic (offshore) species. Those 40 neritic species consisted of 19 sepiids, four sepiolids, eight loliginids and nine octopodids. About 57% (22 spp.) of them are still valid species. Most of the commercially important species, which are large in both body and stock sizes, were already named at that date.

The Dutch *Siboga* Expedition yielded a quite rich cephalopod collection from Indonesian waters. Adam (1939a, b, 1954) made thorough studies on this collection. He (1939a) lumped the 12 names of *Sepioteuthis* in use at that time into a single species *S. lessoniana* Lesson, 1930, describing it as the sole species living in this region.

Adam (1939b) also reviewed the Tropical West Pacific Sepiidae; he recognized 17 species of the genus *Sepia* and two species of the genus *Sepiella* in this area. Strangely enough, one of the

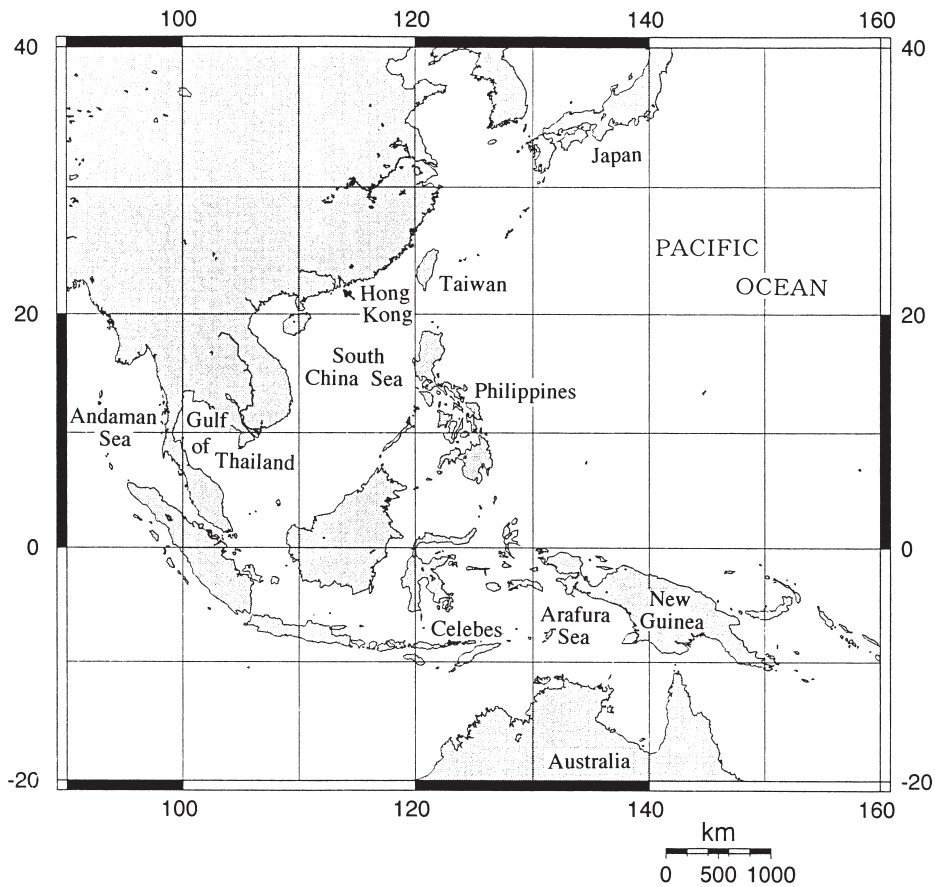


Figure 1. Map of Tropical West Pacific and adjacent waters.

commonest commercial species, *Sepia recurvirostra* was not in Adam's material. In the later revision by Adam and Rees (1966) *Sepia* species living in the region were reduced to ten in number. Adam (1954) also studied the Loligininae finding seven, including two new, species. The genera he used were *Loliolus*, *Loligo*, *Doryteuthis* and *Uroteuthis*.

In a later study, besides 11 oegopsids, three bathypelagic and four epipelagic octopods, Adam (1954) also identified ten species of *Octopus* and two species of *Hapalochlaena*, but four deep-water *Benthoctopus* species in the *Siboga* collection remained unidentified.

Voss (1963) published the monograph of the Philippine cephalopods, treating 54 species (one Nautilidae, 30 neritic and 23 oceanic species) mostly taken by the U.S. Fisheries Steamer

Albatross between 1907 and 1909. For this monograph, he (1962) established eight new species/subspecies that were thought to be endemic to the Philippines. However, two oegopsid taxa therein were later discovered elsewhere. Particularly noteworthy were discoveries of four new bobtail cuttlefish (three sepiolids and a single sepiadariid). Voss (1963) enumerated 17 taxa (among which 9 are neritic species) as the Indo-Pacific elements, eight as the Indo-Malayan elements, and five being common with the Japanese fauna.

RECENT STUDIES

The recent critical morphological studies and exploration of new localities revised the systematics of many cephalopod taxa.

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Since the world-wide revision of the Sepiidae by Adam and Rees (1966), more species have been added from South Africa (Roeleveld, 1972), the Indian Ocean (Khromov, 1982, 1988a ; Homenko and Khromov, 1984), Japan (Okutani *et al.*, 1987) and elsewhere. But, only a few additions to the Tropical West Pacific sepiid fauna have been made public (Khromov, 1987).

According to the recent reviews of this family by Lu (1998b), Khromov *et al.* (1998), Khromov (1998b), and Norman and Lu (2000), the Tropical West Pacific yields the following 24 species:

Sepia aculeata Orbigny, 1848; *S. andreana* Steenstrup, 1875; *S. bandensis* Adam, 1939; *S. brevimana* Steenstrup, 1875; *S. carinata* Sasaki, 1929; *S. elliptica* Hoyle, 1885 (?= *S. madokai* Adam, 1939); *S. esculenta* Hoyle, 1885; *S. kubiensis* Hoyle, 1885; *S. latimanus* Quoy and Gaimard, 1832; *S. lorigera* Wülker, 1910; *S. lycidas* Gray, 1849; *S. nanshiensis* Li and Chen, 1898; *S. papuensis* Hoyle, 1885; *S. pharaonis* Ehrenberg, 1831; *S. recurvirostra* Steenstrup, 1875; *S. smithi* Hoyle, 1885; *S. stellifera* Homenko and Khromov, 1984; *S. vietnamica* Khromov, 1987; *S. vossi* Khromov, 1896; *Metasepia pfefferi* Hoyle, 1885; *M. tullbergi* Appellöf, 1886; *Sepiella inermis* Orbigny, 1848; *S. japonica* Sasaki, 1929; and *S. weberi* Adam, 1939.

The existence of four more species need to be confirmed by future investigations: *S. mestus* Gray, 1849; *S. prashadi* Winckworth, 1939; *S. sulcata* Hoyle, 1885; and *Sepiella ocellata* Pfeffer, 1884. Among these 24 species, 46% (11 species) are common with subtropical Taiwanese fauna studied by Lu (1998). The other four species occurring in Taiwan have not been reported from the Tropical West Pacific: *Sepia foliopeza* Okutani and Tagawa, 1987, *S. perdex* Sasaki, 1913, *S. cf. mestus* Gray, 1849 and *S. sp. TW1*.

Natsukari and Okutani (1975) reduced *Loligo etheridgei* Berry, 1918, *L. formosana* Sasaki, 1929 and *L. indica* sensu Hoyle, 1886 to be synonyms of *L. chinensis* Gray, 1849. Yeatman and Benzie (1993) recognized the existence of cryptic "species" in *Loligo* in northern Australia. This suggests that the *L. chinensis* (now *Uroteuthis photololigo*) by Vecchione *et al.*, 1998) population in the vast Tropical West Pacific is a species-

complex comprising multiple morphologically/genetically segregated populations.

This is the same in *Loligo edulis* (now *Uroteuthis photololigo*) by Vecchione *et al.*, 1998). Natsukari *et al.* (1986) clarified that two morphologically different forms, that had been treated as either species/subspecies or local variants by the early authors (Wakiya and Ishikawa, 1921; Ishikawa, 1933; Sasaki, 1929; Okutani, 1967 *etc.*), are geographical/seasonal broods within a species. The *U. edulis* population in the Japanese waters exhibits remarkable variability, especially body proportion and size at maturity (Okutani, 1979), therefore, local fishermen name them differently (Figure 2). The existence of small-mature populations near Australia (Lu, personal communication) and in the Gulf of Thailand (*Loligo* n. sp. of Chotiyaputta, 1993), as well as *Loligo* sp. A of Voss, 1963 (= *L. vossi* Nesis, 1987) may represent polymorphism or possible species-complex within the vast distributional range of *U. edulis*.

Another polymorphism/species-complex is observed in *Loligo duvauceli* (now *Uroteuthis photololigo*) by Vecchione *et al.*, 1998) as well. It is well known that there is a very slender type and a chubby type within the commercial catch.

The taxonomic status of *Loligo singhalensis* Ortmann 1888 (now *Uroteuthis photololigo*) by Vecchione *et al.*, 1998) was reviewed by Korzun and Alexyev (1991) on the basis of gladius morphology. It is most probable that specimens hitherto identified as *Loligo singhalensis* (e.g. Adam, 1954; Okutani, 1970; Voss, 1963; Voss and Williamson, 1972 *etc.*) may contain slender specimens of *U. edulis*, otherwise either *U. bengalensis* (Jothinayagam, 1987) or *U. robsoni* (Alexyev, 1992).

Among the critical revision of small-sized loliginids by Natsukari (1983, 1984) the establishment of a new subgenus *Nipponololigo* of *Loligo* (now a subgenus of *Liololus* by Vecchione *et al.*, 1998) may be noteworthy. This revision lumped about ten names into four species (*L. japonica*, *L. uyii*, *L. sumatrensis* and *L. beka*) that are clearly diagnosed and characteristically confined to the temperate to Tropical West Pacific. The cephalopod fauna in southern China reported by Dong (1988) contained three out of four taxa (excluding *L. japonica*), but he still used "old"

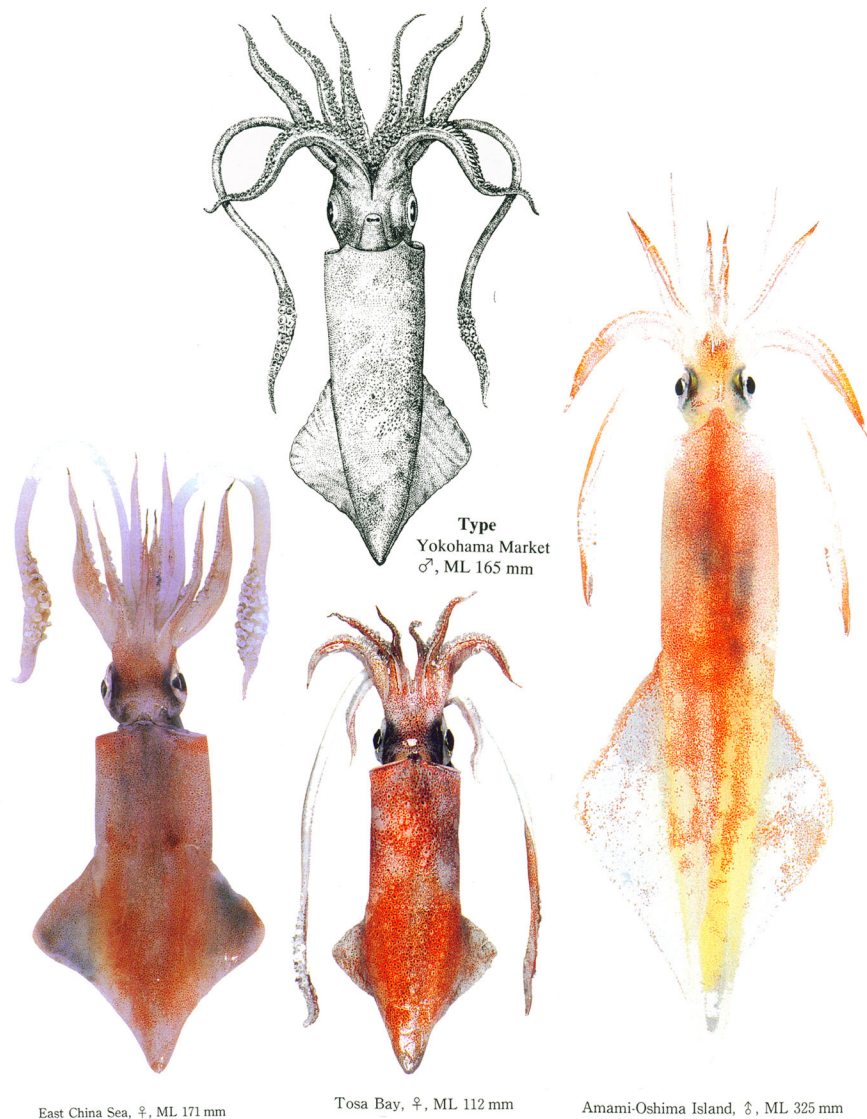


Figure 2. Three phenotypic specimens of *Loligo* (= *Uroteuthis* (*Photololigo*)) *edulis* with illustration of the type specimen in *Challenger Report* (Hoyle, 1886).

names. Nateewanthana (1992) also confirmed that *L. beka* extends to the Andaman Sea. Norman and Lu (2000) admitted that the above-mentioned four taxa all extend down to the Tropical West Pacific, such as the Gulf of Thailand. Two species of *Loliolus* (s.s.), namely, *L. hardwickei* (Gray, 1849) and *L. affinis* Steenstrup, 1856 are confined to

the Indo-Malayan region including Indonesian waters. Both of them never extend to the subtropical zones in both north and south.

The diversity of shallow-water octopodids in the Tropical West Pacific has still been only partially solved at present (see Norman and Lu, 2000). According to the recent revision of the family

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Octopodinae in the West Pacific by Toll and Voss (1998), out of 82 names 20 are *nomen dubia* and only several valid species were from the Tropical West Pacific. According to them, the names commonly applied to Tropical West Pacific octopuses, such as *Octopus dollfusi* Robson, 1928, and *O. membranaceus* Quoy and Gaimard, 1832 are included under the category of *nomen dubia*.

The effort of the recent taxonomic revision and review of Tropical West Pacific octopodids by Norman (1991, 1992a, b, c, 1993), Norman and Hochberg (1994), Norman and Sweeney (1997), Nateewathana (1997), Nateewathana and Norman (1999), Norman and Lu (2000), Kubodera and Lu (2002) and others resulted in determining the existence of some 34 shallow-water species in this region (Table 1). The number of identified species (34) is far larger than octopodine diversity in Australian waters (15 species by Stranks, 1998: three are common with the Tropical West Pacific fauna), the western Atlantic Ocean (15 species by Voss and Toll, 1998), Indian Ocean and Red Sea (12 species by Toll, 1998: two are common herewith), and the eastern Atlantic and the Mediterranean Sea (eight by Mangold, 1998). The achievement hitherto obtained by the effort of recent taxonomists clarified that the Tropical West Pacific yields the most diversified littoral (shallow-water) octopodid fauna. This may be also the same for deep-sea species, although they have not yet been worked out (Norman *et al.*, 1997). Kubodera and Lu (2002) reported that the Chinese-Japanese Subtropical Region yielded 52 species of Octopodidae, about 1.5 times as many species as those listed in Table 1 showing the latest literature review on identified shallow-water octopodids in the Tropical West Pacific. Such a high diversity is because the fauna that they reported partially overlap those reported here and their list also contained some cool-temperate elements.

The taxonomy of the Tropical West Pacific octopuses is progressing, but there are many more species still unsolved with only tentative species numbers (such as 1, 2, 3 or A, B, C by author). Five species among 11 shallow-water octopodids from the Hong Kong's territorial waters examined by Norman and Hochberg (1994), *Octopus* sp.1 to sp.5 remain unidentified. They re-identified

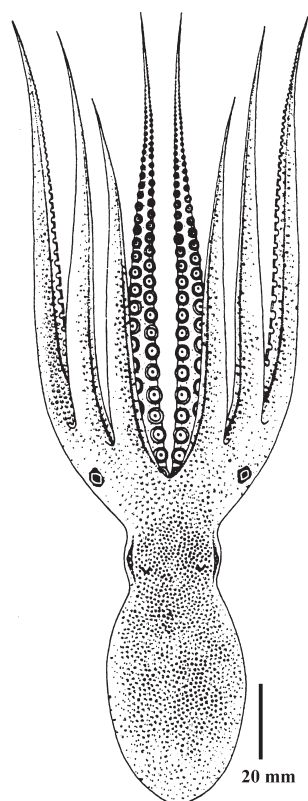
Octopus spp. in Voss and Williamson (1972) showing that *O. "aegina"* sensu Voss and Williamson was *O. marginatus*, *O. "dollfusi"* was *O. aegina*, *O. "macropus"* was *O. luteus*, *O. "membranaceus"* was *O. areolatus* (in part) and *Octopus* sp. 5 (in part) of Norman and Hochberg, 1994. The latter has now been described as *O. rex* Nateewathana and Norman, 1999. They also clarified that *Octopus* A of Voss and Williamson (1972) was *Cistopus indicus*. However, *Octopus* B, C, and D still remain unsolved.

Norman and Sweeney (1997) likewise re-identified octopodids recorded from the Philippines by previous authors including Voss (1963). They found that among six species reported by him, *O. "macropus"* sensu Voss was *O. nocturnus*, *O. "membranaceus"* was *O. exannulatus*, and *O. "horridus"* was mixture of *O. aculeatus*, *O. cyanea* and *O. sp. 2* of Norman and Sweeney, 1997. Five species (sp. 1 to sp. 5) out of 20 Philippine shallow-water octopodids by Norman and Sweeney (1997) remain unidentified, except *Octopus* sp. 1 which has been subsequently identified as *O. rex*. In the comprehensive treatment of world-wide octopuses by Norman (2000), several unidentified octopodids in the Tropical West Pacific are included such as *Hapalochlaena* sp. 1 and sp.4, and *Octopus* sp. 6, sp. 16, sp. 18, sp. 19, and sp. 20 among others.

Such an insufficient taxonomic status is common to the octopod fauna of the adjacent waters: Nateewathana (1997) studied ten species of the genus *Octopus* in the Andaman Sea, but 3 species (ocellate A B, and C) remained unidentified. (Later, they were described as *O. rex*, *O. neglectus* and *O. siamensis*, respectively, by Nateewathana and Norman in 1999) (Figure 3). Lu (1998) investigated Taiwanese cephalopod diversity in which he listed 22 species of the family Octopodidae. Among them, 10 species (45%) were unidentified (*Octopus* sp. 1, sp. 5, and sp. 6 to sp. 13). Kubodera and Lu (2002) published a check list of cephalopods hitherto recorded from Japan, Taiwan, the East China Sea and the South China Sea. In their list there are 52 species of the Octopodidae. In here, 13 unidentified species (*Octopus* TW1 to TW13) from Taiwan are included. In addition are several more unidentified taxa, such as Voss and Williamson's sp. B and C, and studies of them are

Table 1. Latest literature review on identified shallow-water octopdids in the Tropical West Pacific

Species	Occurrence (Reference)
<i>Ameloctopus litoralis</i> Norman, 1992	Arafura Sea (Norman, 1992)
<i>Cistopus indicus</i> (Rapp in Orbigny, 1835)	South China Sea (Norman and Lu, 2000); Hong Kong (Norman and Hochberg, 1994); Philippines (Norman and Sweeney, 1997); Thai (Nateewathana, 1997); Celebes (Toll and Voss, 1998)
<i>Hapalaochlaena lunulata</i> (Q. and G., 1832)	South China Sea (Norman and Lu, 2000); Philippines (Norman and Sweeney, 1997); Papua New Guinea (Toll and Voss, 1998)
<i>H. nierstrazi</i> (Adam, 1938)	Singapore to Burma (Norman and Lu, 2000)
<i>H. cf. fasciata</i> (Hoyle, 1885)	South China Sea (Norman and Lu, 2000); Hong Kong (Norman and Hochberg, 1994)
<i>H. cf. maculosa</i> (Hoyle, 1883)	South China Sea (Norman and Lu, 2000)
<i>Octopus abaculus</i> Norman and Sweeney, 1997	Philippines (Norman and Sweeney, 1997)
<i>O. aculeatus</i> Orbigny, 1834	Philippines (Norman and Sweeney, 1997); South China Sea (Norman and Lu, 2000); Hong Kong (Norman and Hochberg, 1994); Philippines (Norman and Sweeney, 1997); Thai (Nateewathana, 1997)
<i>O. aegina</i> Gray, 1849	South China Sea (Norman and Lu, 2000); Hong Kong (Norman and Hochberg, 1994); Philippines (Norman and Sweeney, 1997); Thai (Nateewathana, 1997)
<i>O. areolatus</i> Orbigny, 1839	Hong Kong (Norman and Hochberg, 1994)
<i>O. bocki</i> Adam, 1941	Western Pacific (Norman and Lu, 2000)
<i>O. cyanea</i> Gray, 1849	Tropical Pacific (Norman, 1991)
<i>O. dierythraeus</i> Norman, 1992	Northern Australia (Norman, 1992b)
<i>O. exannulatus</i> Norman, 1993	Northern Australia (Norman, 1992b); Philippines (Norman and Sweeney, 1997); Thai (Nateewathana, 1997)
<i>O. fangsiao</i> d'Orbigny, 1939-41	Hong Kong (Norman and Lu, 2000)
<i>O. favonius</i> Gray, 1849	Singapore (Toll and Voss, 1998)
<i>O. graptus</i> Norman, 1992	Northern Australia (Norman, 1992b)
<i>O. harmandi</i> Rochebrune, 1882	South Vietnam (Toll and Voss, 1998); South China Sea (Norman and Lu, 2000)
<i>O. luteus</i> (Sasaki, 1929)	Hong Kong (Norman and Hochberg, 1994); Philippines (Norman and Sweeney); Thai (Nateewathana, 1997)
<i>O. marginatus</i> Taki, 1964	Hong Kong (Norman and Hochberg, 1994); Thai (Nateewathana, 1997)
<i>O. microphthalmus</i> Goodrich, 1886	Singapore to Malaysia, South China Sea (Norman and Lu, 2000)
<i>O. mototi</i> Norman, 1993	Western Pacific (Norman and Lu, 2000)
<i>O. nocturnus</i> Norman and Sweeney, 1997	Philippines (Norman and Sweeney, 1997)
<i>O. negletus</i> Nateewathana and Norman, 1999	Thai (Nateewathana and Norman, 1999)
<i>O. cf. niveus</i> Lesson, 1830	Thai (Nateewathana, 1997)
<i>O. ornatus</i> Gould, 1852	Tropical West Pacific (Norman, 1993)
<i>O. polyzenia</i> Gray, 1849	Northern Australia (Norman, 1992)
<i>O. pumilus</i> Norman and Sweeney, 1997	Philippines (Norman and Sweeney, 1997)
<i>O. rex</i> Nateewathana and Norman, 1999	Hong Kong (Norman and Hochberg, 1994); Philippines (Norman and Sweeney, 1997); Thai (Nateewathana and Norman, 1999)
<i>O. siamensis</i> Nateewathana and Norman, 1999	Thai (Nateewathana and Norman, 1999)
<i>O. teuthoides</i> Robson, 1929	Philippines (Norman and Sweeney, 1997)
<i>O. cf. vitiensis</i> Hoyle, 1885	Philippines (Norman and Sweeney, 1997); South China Sea (Norman and Lu, 2000)
<i>O. cf. vulgaris</i> Cuvier, 1797	Thai (Nateewathana, 1997)
<i>O. wolfi</i> Wülker, 1913	Philippines (Norman and Sweeney, 1997); Tropical West Pacific (Norman and Lu, 2000)



Octopus rex Nateewathana and Norman, 1999

- = *Octopus* sp. 5 of Norman and Hochberg, 1994
- = *Octopus* sp. 1 of Norman and Sweency, 1997
- = *Octopus* sp. A of Nateewathana, 1997
- = *Octopus* sp. A of Norman, 1998

Figure 3. *Octopus rex* Nateewathana and Norman ever called by 4 code names.

still underway by either of two authors (Lu and Kubodera) or others. Lu (2000) also investigated the cephalopod fauna around Tong-Sha Island (Pratas Islands) where he found six unidentified octopodids (sp. A to F). Lu and Norman (2000) published an abridged list of synonyms and unsolved species of South China Sea cephalopods. Among 29 names listed by them, 12 were misidentifications and 5 were synonyms, and remaining names are still in an unsolved status. Lu and Boucher-Rodoni (2001) treated the genus *Octopus* from the Wallis and Futuna Islands (central South Pacific). But, all four species were unsolved (sp. 1 to sp. 4).

It is axiomatic that the status of some octopuses that are still unsolved from adjacent seas mentioned above are included in the common elements to the Tropical West Pacific fauna. The promotion of taxonomic studies on them are indispensable in obtaining the whole picture of Tropical West Pacific octopodid diversity.

FUTURE STUDIES

As was mentioned above, *Sepioteuthis lessoniana* in the Indo-Pacific had once been lumped into a single species by Adam (1939). However, the critical comparisons of reproductive biology (spawning season, egg-laying substratum, and number of eggs per capsule), behavior (habitat depth and schooling) and morphology (size and chromatophore pattern) on the populations of Okinawa revealed that *S. "lessoniana"* consisted of three taxa (Segawa *et al.*, 1993a, b; Izuka *et al.* 1994). This was corroborated by biochemical analyses (Izuka *et al.*, 1996). The investigation has thus far been restricted to the populations of the Japanese Archipelago, therefore, studies on more extensive areas of Tropical West Pacific are needed to clarify the true status of the *S. "lessoniana"*-complex. The next step will be the settlement of scientific names for each taxon.

Thus the recognition of separate species needs the observation in life history besides the morphological examination on the fixed/preserved specimens.

Similar approaches may be required to elucidate the true picture of species complexes of the three *Uroteuthis (Photololigo)* species: *edulis*, *chinensis*, and *duvauceli*. For instance, it is already clear that the *U. edulis*-complex may contain variable phenotypes. The taxonomic status of *U.(P.) singhalensis* may need more scrutiny. Molecular approaches may help to elucidate the relationships, particularly those of cryptic species, but the morphological re-evaluation on voucher specimens is most indispensable.

Some modern students are apt to rely on biochemical/molecular approaches without having sufficient acquaintance with the morphological recognition of taxa. In response to this demand, the precise alpha-taxonomical description for

stability of the names should be more intensively promoted by the well-trained teuthologists. Alpha-taxonomists are sometimes too cautious in establishing new species, resulting in delay of publication.

Such a too prudent attitude of taxonomists may be caused by: (1) The existence of too many ambiguous names in early times. It is not known if the type materials are still extant or not. (2) The severe demands of modern referees who often require more detailed anatomy and biological data in new species description.

The early unsolved names, of which the type material is proved to be no longer extant by the extensive survey, such as by Sweeney and Roper (1989), should be treated as *nomen dubium* (as in Toll and Voss, 1989). Otherwise the selection of a neotype is needed (as for *Octopus vulgaris*, now in progress) to settle the old names. When the discovery of the type specimens fails after serious searches, taxonomists should make the quick decisions to discard the old dubious names. The neotype should be designated, if the old description was clear enough.

The description of new species, from an operational point of view, may not need to be accompanied by too much detailed anatomy, fine structure, and details of ecology and life history data. The precise diagnostic morphological description with clear characters that are usable for separating it from the related species will be enough, and will provide the minimum requirement

to promote a faunal inventory (as in Nateewathana and Norman, 1999, a good example). The detailed, intensive biological research on the new species can be published in subsequent separate papers.

Without such a steady and rapid promotion of sound taxonomy of the Tropical West Pacific cephalopods, particularly neritic octopuses, many vernacular names are created by amateur photographers and television media. Such a confusion of names has already happened in the field of opisthobranchs. The grim resolution of taxonomists is now required for settlement of the names of every taxon.

The future taxonomic resolution in respect to cephalopod diversity has been repeatedly proposed by Roper (1983), Lu (1998), Norman and Lu (2000) among others. As they pointed out, it might well be left unsaid that the future study on cephalopod diversity in the Tropical West Pacific needs the financial supports and international collaborations of taxonomists for exchanging expertise, developing the collections, and research as well as training the students.

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