THE PELAGIC OCTOPOD OCYTHOE TUBERCULATA RAFINESQUE, 1814

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A large octopod from southern Australia was sent to the National Museum of Natural History (NMNH) by Brian Smith, National Museum of Victoria, Melbourne, Australia, for identification. The specimen was a large female of the pelagic octopod Ocythoe tuberculata Rafinesque, 1814. Because this species is uncommon in collections, this fine specimen stimulated a search of the literature to determine the previously reported specimens and their distribution. The South Australian specimen is the first recorded capture of O. tuberculata from the waters of Australia. Furthermore, the species previously has not been reported from the entire central Pacific or the Indian Oceans. This paper records major extentions in range that verify a world-wide distribution, and it adds new information concerning certain aspects of the biology of O. tuberculata.

HISTORICAL REVIEW

The original description of Ocythoe tuberculata by Rafinesque (1814) was very short and carried no illustrations. The translation from the French follows:

"XVII G. Ocythoe Eight arms, the upper two winged towards the inside, with inner suckers pedunculate, joined by the lateral wings, no membrane at the base of the arms.

73. Ocythoe tuberculata. Ventral side tuberculate, dorsum smooth, arms [as] long as the body, keeled on the outer side, with two rows of suckers, eight suckers around the mouth."

Rafinesque's only other mention of the species appeared in 1840 in an obscure paper that comprised the first number in a proposed series of ten booklets entitled "Amenities of Nature"; each number was to be extensively illustrated. Unfortunately, Rafinesque died in 1840, and neither the remaining nine numbers nor any of the 10 supplements of illustrations was published. The article added valuable information to the initial meager description of O. tuberculata, and it clarified the misconception of contemporary biologists that O. tuberculata (or Todarus) was the animal that lived

in the Argonauta shell. Rafinesque's comments on Ocythoe are quoted here because the 1840 work is not readily available and largely has been overlooked resulting in misinterpretations by some subsequent workers who had not seen it. (See also Binney & Tryon, 1864).

"12. On the 3 Genera of Cephalopodes, Ocythoe, Todarus and Anisoctus.

"My G. Ocythoe altho' adopted by Leach and others, is yet a problematical animal for many, and I find even in late Journals discussions on its being or not the animal of the Argonauta shell it would be wiser to ask me (the original discoverer) for my opinion or experience. I once wrote to Leach about it, but it was during his sickness, and I believe he omitted to publish my remarks, which were at variance with his. It is time therefore to settle this question, or rather throw new doubts on it perhaps; my recollections of my Ocythoe are quite vivid as a very remarkable animal.

"I omitted in my short account of the Genus (in my precis of 1814) to state the size of this animal, and thence have originated many wrong surmises. I did not state that it was the animal of the Argonauta since I never dreamt of such a thing, knowing the Todarus as the animal often found in it, (in Sicily,) while the Ocythoe never could dwell in it, being larger than a man's head, and weighing 15 pounds.

"Such was my Ocythoe tuberculata type of the genus and certainly not the same as that of Leach: this animal was brought to me alive in 1811 as a rare kind of Octopus, it was ferocious endeavoring to bite and wound the holder, although out of water for one hour: it changed color like a Chameleon from white to red in its angry and dying moments. It was killed as usual with the Octopus by turning its head [= mantle], a process well known to the Fishermen of the Mediterranean: else they will live long out of the water and are

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dangerous till dead. I did eat this Ocythoe which afforded a meal for many, and it was as good as usual with the Octopus. The Fishermen never told me that it dwelt in the Argonauta, while all deemed their Todaru the animal of it, calling the shell and animal by the same name, while the Ocythoe was called Pulpu.

"I do therefore aver that my Ocythoe is not the animal of the Argonauta, and could never be, by its size and thick spherical body, unfit even to enter it."

Rafinesque leaves little doubt that he ate the type-specimen! Robson (1932), citing Isnard (1922), erroneously stated that the type-specimen originally was in Orbigny's collection, but Isnard actually referred to the deposition of Verany's types. We can deduce that the type was a female

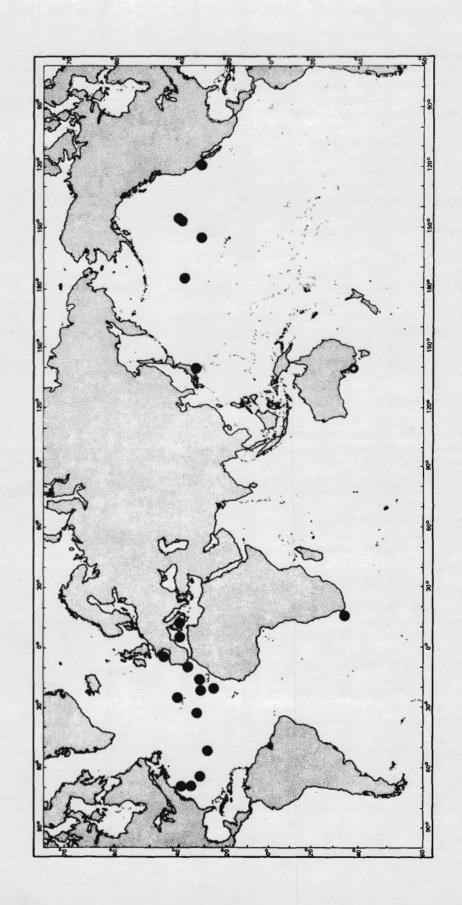
because it was "...larger than a man's head and (weighed) 15 pounds." Males of Ocythoe are known to be small, and probably do not exceed about 30 mm in mantle length (ML).

A summary of the verifiable records of specimens of O. tuberculata is presented in Table 1. Jatta (1896) and Naef (1923 a) gave extensive synonymies, although both omitted reference to Rafinesque's obscure 1840 paper. A great deal of nomenclatorial turmoil, only partly reflected in Table 1, accompanied O. tuberculata for three-quarters of a century, until Jatta (1896) was able to stabilize the uncertainty. Robson (1932) reviewed the literature but gave little specific data about the specimens he had, so their sizes and localities cannot be verified. The measurements of length listed in Table 1 are those given by the original authors or deduced from the discussions or from illustrations.

Table 1. A summary of the records of Ocythoe tuberculata.

Author, date: page	Species Name	No:	Se	x Size*(mm)	Location	Remarks	
Rafinesque, 1814:29	Ocythoe tuberculata	1	Q		Med.	Type; no longer extant	
Verany, 1851:37	Octopus catenulatus	1	9	280 ML	Med.	Plate 12	
Verany, 1851:34	Octopus carena	1	o*	30 DML	Med.	Plate 14, figures 2,3	
Verany, 1851:126	Hectocotylus octopodis	1	of	-	Med.	Plate 41	
Verrill, 1880:293	Parasira catenulata	1	9	51 ML	NW Atl.	Also, Verrill, 1882:362, Plate 33	
Ortmann, 1888:642	Tremoctopus doderleini	1	Q	200 VML	NW Pac.	Tokyo Bay, Japan, Plate 20	
Jatta, 1896:198	Ocythoe tuberculata	1	♂*	30 ML	Med.	Gulf of Naples, Plates 6,7,19	
Jatta, 1896:198	Ocythoe tuberculata	1	9	100 ML	Med.	Gulf of Naples.	
Joubin, 1900:26	Ocythoe tuberculata	3	Q	?-200 ML	Med.	Plates 6,7,19 Stomach of Grampas griseus	
Wulker, 1910:4	Ocythoe tuberculata	3	9	?-60 ML	NW Pac.	Sagami, Japan. Plate 1	
Berry, 1916:3	Ocythoe tuberculata	1	Q	160 DML	NE Pac.	Southern California	
Degner, 1925:81	Ocythoe tuberculata	1	ď	20 ML	Med.	R/V THOR	
Sasaki, 1929:26	Ocythoe tuberculata	2	ď	18-21 VML	NW Pac.	Sagami, Japan. Plates 3,8	
Sasaki, 1929:26	Ocythoe tuberculata	5	Q	70-160 VML	NW Pac.	Sagami, Japan.	
Bouxin & Legendre, 1936:30	Ocythoe tuberculata	1		35 BL	NE Atl.	Plates 3,8 Bay of Biscay	
Joubin, 1937:38	Ocythoe tuberculata	7	3 *	8-30 TL	N Atl.	R/V DANA. Figures 36,3	
Joubin, 1937:38	Ocythoe tuberculata	7	9	8-120 TL	N Atl.	R/V DANA, Figures 36,3	
Berry, 1955:177	Ocythoe tuberculata	9	Ф	16-163 ML		Southern California, Figur	
Rees & Maul,	Ocythoe tuberculata	6	ę	12-190 DML	N Pac.	omach of Alepisaurus bored Madeira Islands. Stomach	
1956:274 Torchio, 1965:270	Ocythoe tuberculata	2	Q	155-175 DML	Med.	Alepisaurus ferox Figure 4	
Voss, 1967:86	Ocythoe tuberculata	1	9	21 ML	SE Atl.	South Africa	
Hardwich, 1969:68	Ocythoe tuberculata	1	ਾ	16 DML	NE Pac.	Southern California. In s	
Young, 1972:92	Ocythoe tuberculata	1	o*	14 ML	NE Pac.	Southern California	
Young, 1972:92	Ocythoe tuberculata	3	Q .	12-80 ML	NE Pac.	Southern California	
Roper & Sweeney	Ocythoe tuberculata	1	P :	310 DML		Southern Australia	

^{*}DML - Dorsal Mantle Length; VML - Ventral Mantle Length; ML - Mantle Length (Aspect unknown); BL - Body Length (Mantle & Head); TL - Total Length.



The anatomy of Ocythoe tuberculata has been described and illustrated by several authors, and the references are cited because they represent specimens not necessarily referred to in Table 1. Illustrations of the whole female and male animals are given by Jatta (1896), Naef (1923), and Young (1972). The internal anatomy was described by Jatta (1896), Marchand (1907), and Naef (1923). The radula was illustrated by Brock (1880) and Young (1972). Verany & Vogt (1852) and Naef (1923) described the spermatophore. The beak was figured by Jatta (1896) and Iverson & Pinkas (1971). Naef (1928) described the embryology.

AUSTRALIAN SPECIMEN

The specimen was given to the South Australian Fisheries Department after it was discovered stranded on the beach at Port Macdonnell, South Australia, during a storm on 9 August 1973. The body was strongly compressed, probably because the animal had lain on the beach for some time. The mantle length is 310 mm dorsally and 270 mm ventrally, although both values may have been slightly affected by the flattening of the mantle. Even so, this specimen represents the largest recorded to date, the maximum previously reported was the 280 mm (presumed mantle length) specimen of Verany (1851). The specimen is a mature female with approximately 104,000 eggs (volumetric determination) in the ovarian sac and oviducts. The eggs measure 1.75 mm in length and 1.00 mm in width (average of a number of measurements). No embryos were found in the narrow, unexpanded oviducts, and the eggs, all nearly identical in size, appeared to be unfertilized. There are 19 and 20 lamellae on the outer and inner demibranchs, respectively, of both gills. Measurements and counts of the specimen are presented in Table 2.

Table 2. Measurements (in mm) and counts of female specimen of Ocythoe tuberculata from South Australia.

Dorsal Mantle	Length*	.310
Ventral Mantle	Length	.270
Arms -	LeftR	ight
I	Broken	500
II	360Brol	ken

III	335	340				
IV	410	400				
Number of Gill Lamellae - Left (outer demibranch)19						
Left (inner demibranch)20						
Right (outer demibranch)19						
Right (inner demibranch)20						
Number of Eggs (volumetric measure)104,000						
Size of Eggs (average) Length1.75						
Width1.0						

* Measured from posterior tip of the mantle to midpoint between the center of the eyes.

DISTRIBUTION

The occurrence of O. tuberculata in the waters of South Australia represents a considerable extension in the range of this species. The majority of records of O. tuberculata have been concentrated in the northern hemisphere, primarily in the western Mediterranean Sea and the eastern North Atlantic (Canaries, Azores, and Madeira) and less frequently in the western North Atlantic (Sargasso Sea, Gulf Stream) (Figure 1).

We include an additional record of O. tuberculata from the Mediterranean Sea, a female, 62 mm ML, captured at the surface (USNM 727831), as well as specimens from off Bermuda: 1 male, 9 mm ML, at 200 m (USNM 728669) and 1 male, 6 mm ML, at 96-102 m (USNM 728670).

Other records come from the eastern North Pacific off southern California and the western North Pacific off Japan (Figure 1). It has not been recorded previously from the Indian Ocean or from the entire central Pacific Ocean. Only a single record exists for the entire southern hemisphere, that from the South Atlantic off South Africa (Voss, 1967).

Since the sole South Australian specimen was found washed ashore after a storm, little can be stated about its probable natural location. Knox (1963) stated that warm surface currents run eastward from the Indian Ocean during April through November, north of the cold West Wind Drift, with an apparent reversal in direction

during the austral summer. If currents during the period around 9 August 1973 conformed to this pattern, it seems possible that the specimen could have come as a stray from the west and indicates that the species may indeed occur in the Indian Ocean. It is interesting to note that the extensive ENDEAVOUR investigations in the great Australian Bight did not capture the species (Berry, 1918).

The occurrence of O. tuberculata off South Africa also may indicate its presence in the Indian Ocean as the Agulhas Current is a strong, persistant outflow capable of dispersing animals from that ocean towards the Atlantic. On the other hand, the Agulhas Current can act as a cool, forceful barrier to the eastward extention of a warm water species from the Atlantic. Until specimens are captured in the Indian Ocean proper, the occurrence of O tuberculata there will remain somewhat problematical.

The question of the existence of O. tuberculata in the broad expanse of the Pacific Ocean is answered in an unpublished report on the cephalopods collected by National Marine Fisheries Service vessels from the Fisheries Center in Hawaii (Burgess, unpublished). That report lists the following eleven specimens (sex not given) from the central North Pacific:

1 specimen, 15 mm ML, 32°12'N 154° 48'W

1 specimen, 55 mm ML, 37°54'N 174°46'W

2 specimens, 20,35 mm ML, 38°32'N 147°16'W 5 specimens, 18-80 mm ML, 39°49'N 146°25'W 2 specimens, 15,23 mm ML, 40°00'N 145°00'W

R. E. Young (pers. comm.) reports no specimens of O. tuberculata in the waters around Hawaii, in spite of intensive sampling effort during recent years. All specimens listed above are concentrated well north of Hawaii, although NMFS surveys have extended throughout the central North

Pacific and southward to the Equator.

Therefore, Ocythoe tuberculata appears to be a cosmopolitan epipelagic species in warm waters of the world, but some intriguing gaps remain in its currently recorded distribution, particularly in the Indian Ocean and the southern hemisphere. One other pattern appears to emerge from the records. Captures of O. tuberculata occur primarily in the vicinity of land masses and islands, although oceanic captures do occur. The absence of O. tuberculata from intensively surveyed areas of the Atlantic, Pacific, and Indian Oceans where oceanographic conditions appear conducive to its occurrence remains to be explained by a more intensive study.

The depth distribution of O. tuberculata appears to be limited to the near-surface waters.

The closing-net captures recorded above from the Sargasso Sea and the Mediterranean occurred at the surface, 100 m, and 200 m. Other captures are presumed to be from near the surface, and some were taken right at the surface or by divers. Joubin (1937) records open-net captures from 50 m to 1000 m, but undoubtedly the deeper records are incorrect and the specimens were captured at shallower depths when the open net was retrieved.

BIOLOGICAL NOTES

A marked sexual dimorphism occurs that results in an extreme disparity of size at maturity. Females attain a dorsal mantle length (DML) in excess of 300 mm, the largest recorded to date being the South Australian specimen at 310 mm. Unfortunately, Rafinesque did not give the size of the holotype, but it must have approached that of the Australian specimen, as he said it was as large as a man's head and weighed 15 pounds. Males, on the other hand, remain small and apparently do not exceed a DML of about 30 mm (Table 1). Males have an extraordinarily well-developed hectocotylus on the third right arm, the structure of which is described in detail by Naef (1923). The hectocotylus, containing the spermatophores, is detached during mating and remains in the mantle cavity of the female during an extended period of fertilization.

The count of 104,000 eggs from the South Australian specimen indicates the high fecundity in Ocythoe. Naef (1923) had estimated 100,000 eggs in one of his specimens. Size of the eggs is very small, 1.75 mm in length and 1.00 mm in width. A large number of smal eggs apparently is the rule in epipelagic octopods, as Tremoctopus violaceus, for instance, has been known to carry 139,000 eggs, the smallest of which were 3.6 mm long and 2.1 mm wide and presumably were fertilized (Hamabe, 1973).

Ocythoe tuberculata is reported to be viviparous, several authors having observed embryos in various stages of development in broadly expanded oviducts. While Jatta (1896) found embryos ready to hatch, Naef's (1923) specimens were in earlier stages of development. Sasaki (1929) claimed that the embryos developed in the 'renal sacs,' but this seems a curious and unhospitable site for embryonic development. We suggest that the renal sacs of Sasaki's specimen may have been damaged or poorly preserved to the extent that embryos were washed in from the oviducts or ruptured ovarian sac. The oviducts of the South Australian specimen were narrow and unexpanded and the

eggs contained therein showed no indication of development. No hectocotyli were present in the mantle cavity. so even though this specimen is very large and fully mature, it apparently had not mated.

Jatta (1896) observed that the male Ocythoe resides in the empty pallial chamber of the pelagic salp, Salpa tilesii. Apparently this interesting association is a universal trait, as Hardwich (1970) while SCUBA diving observed a male Octuberculata in the test of the salp, Tethys vagina. The octopod deserted the test when first disturbed, then re-entered it and was captured. While Naef (1923) commented on the possible phylogenetic significance of this behavior in relation to the evolution of the shell in the related Argonauta (females only), additional observations are required before any behavioral or phylogenetic conclusions can be made.

A considerable number of epipelagic predators reportedly prey on O. tuberculata including the lancetfishes, Alepisaurus borealis (by Berry, 1955) and A. ferox (by Rees & Maul, 1956); the tunas, Thunnus alalunga (by Iverson, 1971), Thunnus (by Pinkas, 1971), and Germon germon (by Bouxin & Legendre, 1936); and Risso's dolphin, Grampus griseus (by Joubin, 1900). The vertical ranges of these predators, where known, are fairly extensive, so we are unable to precisely relate this predation to the vertical distribution of O. tuberculata, although indications are that it encompasses the upper 100-200 m.

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