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Morphological Analysis of Living *Nautilus* from Palau

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Abstract

Morphological features of living *Nautilus* in Palau (*Nautilus belauensis* Saunders), are described on the basis of 94 live specimens captured from Mutremdiu Bay in 1988 and 1989. Except for its larger mature size, this species is closely similar in overall shell morphology and radular and jaw structure to the wide spread species *N. pompilius* Linnaeus in the Southwest Pacific. This fact and available genetic data suggest a possibility that *N. belauensis* merely represent s a geographic variant on *N. pompilius* with high levels of morphological and genetic differentiation.

Introduction

Sampling of *Nautilus belauensis* and other marine fauna using a baited trap was carried out on two occasions, between August 22 to September 17, 1988 and between January 6- 13, 1989, in Mutremdiu Bay, Palau. This paper documents the morphological characteristics of this species, with remarks on its taxonomy.

Trapping Records

Methods of trapping

Trapping experiments were made using the R/V Mesekiu of the Bureau of Resources and Development, Palau at 20 locations in the eastern margin of Mutremdiu Bay, near Augulpelu Reef (Fig. 1). A double entry wire- framed trap of 110cm x 80cm x 81cm size (6mm mesh) with bait (small tuna) was used for trapping (Fig. 2). It was set in the morning on the bottom with a line and was attached to a surface buoy with a floating line, and drawn up in the next morning. Trapping locations and their depths were determined by a triangular net on navigational markers and by echo-sounding profiles, respectively.

We could not recover a trap at two locations (T6 and T22), but the other trials were successful. The study area is the main habitat of *Nautilus belauensis*, from which a large number of specimens of this species have been collected by W. B. Saunders and his co-workers.

Basic data on Nautilus

As a result of trapping experiments, a total of 94 specimens of *N. belauensis* (57 male, 36 female and one juvenile) were captured from 14 locations ranging from 140m to 450m in depth (Table 1). All of the sampling points are located on the abruptly dropping scarp of the outer reef margin.

Key words: Palau, *Nautilus belauensis*, *N. pompilius*, morphology, taxonomy

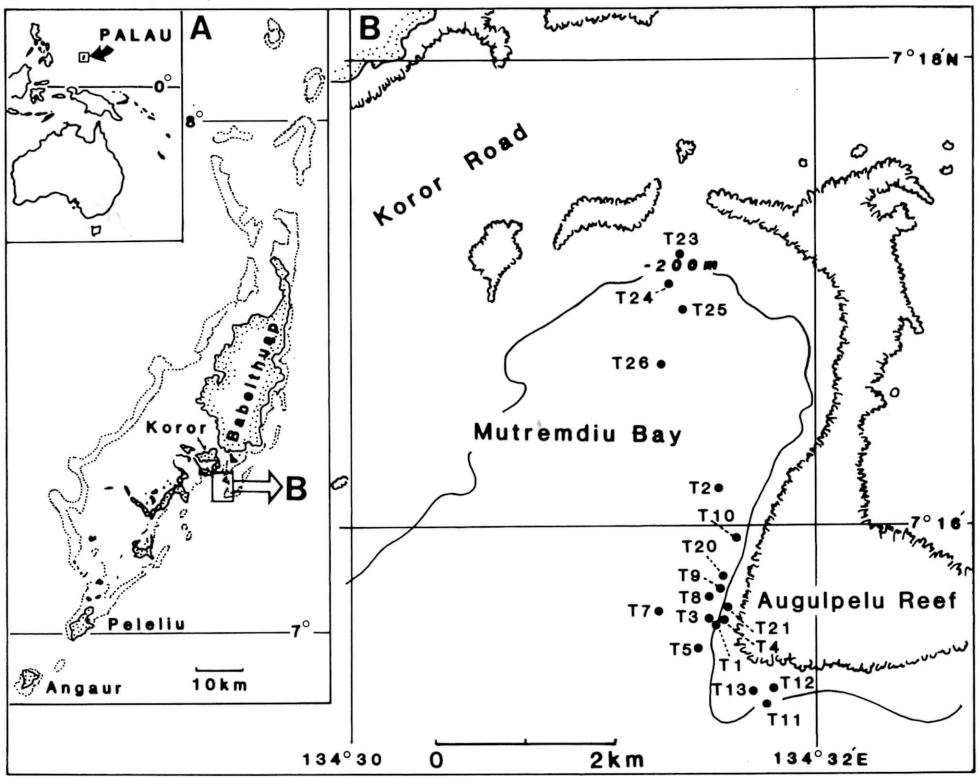


Fig.1. Map of Palau, Western Caroline Islands, showing the trapping locations of living *Nautilus*.

After capture, each specimen was labeled, weighed, sexed and measured following the methods described in previous reports (Tanabe, 1985, 1988). Of 94 specimens captured, 39 were kept alive in water tanks at Micronesian Mariculture Demonstration Center in Koror for several days, then they were tagged and released near the trapping locations. Nine specimens were transferred to Kagoshima by air for further laboratory work (two of them are still alive as of November, 1989). Soft and shell parts of the remaining specimens were removed separately, and weighed. Fresh gonad was also removed from the soft tissue of 36 specimens, and was weighed with a dial scale (accuracy ± 0.01g). Basic biological data on captured *Nautilus* are summarized in Table 2.

Although we did trapping experiments during limited intervals of different seasons (August - September and January), the male -female ratio of the total catch in summer (28:21) is slightly larger than that of winter (29:15). Similar seasonal differences in sex ratios have been recognized in other species of *Nautilus* (e.g. *N. pompilius*) from the Philippines and Fiji (Haven, 1977, table 3; Tanabe, 1988, table 2).

Fig.2. Double entry wire-framed trap used for capturing *Nautilus* and other animals (110 X 80 X 81 cm in size).

Table 1. Capture records of *Nautilus belauensis* from Mutremdiu Bay, Palau during August 22-September 17, 1988 (T1-T13), and during January 8-13, 1989 (T20-T26).

Locality no.	Water depth(m)	No.of traps	No. of *Nautilus* Male	Female	Total
T 1	210	1	4	3	7
T 2	210	1	10	6	16
T 3	400	1	2	0	2
T 4	132	1	0	0	0
T 5	270	1	2	2	4
T 6	50	1		trap missing	
T 7	560	1	0	0	0
T 8	192	1	1	1	2
T 9	228	1	5	2	7
T 10	180	1	0	0	0
T 11	190	1	0	1	1
T 12	200	1	2	2	4
T 13	200	1	2	4	6
T 20	260	1	3	5	8
T 21	180-190	1	4	1	5
T 22	200	1		trap missing	
T 23	140	1	8	0	8
T 24	270	1	0	0	0
T 25	350	1	6	4	10
T 26	450	1	8	5	14*

* One specimen is a juvenile whose sex is unknown.

Table 2. Biological data for *Nautilus belauensis* captured from Mutremdiu Bay, Palau in 1988-89.

Date of collection	Specimen	Sex	Weight(g)			Shell size(mm)			From ratios			Remarks
			Total	Tissue	Shell	D	B	H	B/D	H/D	B/H	
Aug. 22-23,'88	T1-1	M	1240+	— — —	— — —	220.0	102.9	155.0	.468	.705	.664	Released(Aug.23)
	T1-2	F	848	— — —	— — —	193.0	82.4	134.2	.427	.695	.614	ditto
	T1-3	M	1095	— — —	— — —	206.0	96.0	141.1	.466	.685	.681	ditto
	T1-4	M	1240+	— — —	— — —	218.5	97.6	147.0	.447	.673	.664	ditto
	T1-5	F	910	— — —	— — —	192.5	88.5	138.6	.460	.720	.639	ditto
	T1-6	F	868	— — —	— — —	192.5	86.0	135.6	.447	.704	.634	ditto
	T1-7	M	1078	— — —	— — —	200.5	93.7	141.4	.467	.705	.663	ditto
Aug. 29-30,'88	T2-1	M	1309+	915.0	393.7	214.3	100.3	132.7	.468	.619	.756	Dissected(Sep.8)
	T2-2	M	(1120)	— — —	— — —	200.0	94.8	129.4	.474	.647	.733	Released(Aug.30)
	T2-3	M	(1200)	— — —	— — —	198.7	92.9	125.5	.468	.632	.740	ditto
	T2-4	F	832+	563.4	268.8	188.9	85.2	117.0	.484	.619	.728	Died(Sept.3)
	T2-5	M	(1100)	— — —	— — —	201.7	97.7	127.8	.484	.634	.764	Released(Aug.30)
	T2-6	M	(1030)	— — —	— — —	195.9	95.9	127.7	.490	.652	.751	ditto
	T2-7	F	(1140)	— — —	— — —	207.2	93.6	135.3	.452	.653	.692	ditto
	T2-8	M	(1210)	— — —	— — —	216.1	98.6	141.2	.456	.653	.698	ditto
	T2-9	M	(840)	— — —	— — —	185.5	93.7	118.4	.505	.638	.791	ditto
	T2-10	F	977+	652.1	324.9	201.0	89.3	129.3	.444	.643	.691	Died(Sept.3)
	T2-11	M	(1160)	— — —	— — —	210.4	101.0	136.7	.480	.651	.739	Released(Aug.30)
	T2-12	F	(950)	— — —	— — —	198.3	92.3	129.2	.465	.652	.714	ditto
	T2-13	F	(840)	— — —	— — —	192.8	90.9	119.3	.471	.619	.762	ditto
	T2-14	M	471+	304.9	166.4	148.2	75.4	97.2	.509	.656	.776	Died(Sept.3)
	T2-15	F	(910)	— — —	— — —	197.5	90.9	123.0	.460	.623	.739	Released(Aug.30)
	T2-16	M	(990)	— — —	— — —	199.3	92.7	123.7	.465	.621	.749	ditto
Sept. 6-7,'88	T3-1	M	1267+	887.2	379.9	206.5	99.2	132.8	.480	.643	.747	Dissected(Sept.14)
	T3-2	M	1251+	877.0	373.7	205.9	100.3	129.1	.487	.627	.777	Dissected(Sept.16)
Sept. 7-8,'88	T5-1	M	1194+	845.3	348.7	206.0	98.0	127.7	.476	.620	.767	Dissected(Sept.8)
	T5-2	M	1326+	372.7	953.0	210.9	100.8	142.1	.478	.674	.709	Died(Sept.12)
	T5-3	F	880+	598.5	281.1	187.1	87.0	115.8	.465	.619	.751	Died(Sept.12)
	T5-4	F	1040+	656.0	384.0	205.5	90.5	130.0	.440	.633	.696	Dissected(Sept.8)
Sept.11-12,'88	T8-1	F	866+	550.9	315.2	192.4	88.5	120.0	.460	.624	.738	Dissected(Sept.17)
	T8-2	M	1349+	946.9	401.6	215.4	99.5	139.5	.462	.648	.713	Dissected(Sept.16)
Sept.13-14,'88	T9-1	M	1283+	925.2	357.6	205.3	96.9	133.0	.472	.648	.729	Dissected(Sept.14)
	T9-2	M	1226+	859.7	366.0	206.0	94.0	132.0	.456	.641	.712	ditto
	T9-3	F	995+	685.4	309.9	192.1	93.7	127.8	.488	.665	.733	ditto
	T9-4	M	1022+	700.4	321.4	197.4	98.2	127.5	.497	.646	.770	Dissected(Sept.16)
	T9-5	F	854+	581.3	272.8	187.6	83.6	117.9	.446	.628	.709	Dissected(Sept.17)
	T9-6	M	1545+	1059.7	485.7	220.8	101.7	142.9	.461	.647	.712	Died(Sept.15)
	T9-7	M	1032+	729.8	302.6	194.0	98.0	127.4	.505	.657	.769	ditto
Sept.14-15,'88	T11-1	F	924+	752.1	311.3	195.3	88.2	112.7	.452	.577	.783	Dissected(Sept.17)
Sept.15-16,'88	T12-1	F	1063+	752.1	311.3	196.0	86.8	122.1	.443	.623	.711	ditto
	T12-2	M	1364+	985.6	378.5	209.5	103.2	131.8	.493	.629	.783	ditto
	T12-3	M	1118+	817.6	300.7	195.2	90.6	127.7	.464	.654	.709	ditto
	T12-4	F	1121+	782.9	337.7	197.9	92.5	126.3	.467	.638	.732	ditto
Sept.16-17,'88	T13-1	F	(1241)	— — —	— — —	197.3	90.0	144.8	.456	.734	.622	Bring to Japan
	T13-2	M	(1386)	— — —	— — —	200.4	94.3	144.2	.471	.720	.654	ditto
	T13-3	F	931+	633.4	287.3	185.7	82.5	132.6	.444	.714	.622	Dissected(Sept.17)
	T13-4	F	1062+	698.2	364.0	199.4	88.4	141.7	.443	.711	.624	ditto
	T13-5	M	(1418)	— — —	— — —	193.6	100.1	141.7	.517	.732	.706	Bring to Japan
	T13-6	F	(1166)	— — —	— — —	191.6	87.0	142.4	.454	.743	.611	ditto
Jan. 6-7,'89	T20-1	M	1180.6	756.2	312.5	195.1	95.8	123.5	.491	.646	.776	Dissected(Jan.7)
	T20-2	F	1175.5	707.1	346.4	197.1	91.2	127.3	.463	.646	.716	ditto
	T20-3	F	1080.2	713.3	305.6	190.0	91.3	117.4	.481	.618	.778	ditto
	T20-4	M	1272.6	875.9	365.9	206.2	95.7	131.0	.464	.635	.731	ditto
	T20-5	F	964.0	661.6	299.3	188.8	85.4	119.0	.452	.630	.718	ditto
	T20-6	M	1342.8	935.4	335.0	204.4	97.1	130.7	.475	.639	.743	ditto
	T20-7	F	1130.2	714.7	330.2	194.7	89.0	123.3	.457	.633	.722	ditto
	T20-8	F	1057.1	659.1	309.6	197.2	93.2	126.8	.473	.643	.735	ditto
Jan. 7-8,'89	T21-1	M	1247.1	900.2	305.4	201.5	98.3	128.6	.488	.638	.764	Dissected(Jan.8)
	T21-2	M	1399.8	— — —	— — —	203.7	107.6	136.8	.528	.672	.787	Released(Jan.8)
	T21-3	M	1319.0	955.9	326.2	203.3	96.7	128.8	.476	.634	.751	Dissected(Jan.8)
	T21-4	M	1394.3	991.9	361.3	207.4	101.6	133.5	.490	.644	.761	ditto
	T21-5	F	664.7	408.5	232.9	159.0	85.0	104.9	.535	.660	.810	ditto

Table 2 (continued).

Date of collection	Specimen	Sex	Weight(g)			Shell size(mm)			From ratios			Remarks
			Total	Tissue	Shell	D	B	H	B/D	H/D	B/H	
Jan. 9-10,'89	T23-1	M	1373.0	962.6	400.3	193.6	94.7	129.2	.489	.667	.733	ditto
	T23-2	M	1413.6	981.5	355.3	206.1	101.9	131.8	.494	.639	.773	ditto
	T23-3	M	1227.3	828.0	345.9	197.2	90.7	128.0	.460	.649	.709	ditto
	T23-4	M	1478.6	— — —	— — —	208.9	98.5	134.0	.472	.641	.735	Released(Jan.10)
	T23-5	M	1294.8	— — —	— — —	197.4	94.5	129.9	.479	.658	.727	ditto
	T23-6	M	1361.3	— — —	— — —	204.3	97.8	135.4	.479	.663	.722	ditto
	T23-7	M	1176.5	— — —	— — —	194.6	91.2	126.2	.469	.649	.723	ditto
	T23-8	M	1333.6	— — —	— — —	203.8	100.5	136.3	.493	.669	.737	ditto
Jan.10-11,'89	T25-1	F	836.8	502.3	303.0	165.8	87.7	111.4	.529	.672	.787	Dissected(Jan.11)
	T25-2	F	1090.3	668.1	294.2	189.2	90.5	121.9	.478	.644	.742	ditto
	T25-3	M	1012.3	— — —	— — —	185.0	94.4	115.1	.510	.622	.820	Released(Jan.11)
	T25-4	F	916.8	568.6	322.2	178.3	89.0	113.7	.499	.638	.783	Dissected(Jan.11)
	T25-5	M	1562.9	— — —	— — —	205.9	101.8	136.9	.494	.665	.744	Released(Jan.11)
	T25-6	M	1458.2	1057.1	325.4	198.5	105.0	136.2	.529	.686	.771	Dissected(Jan.11)
	T25-7	F	1172.1	— — —	— — —	193.6	93.1	129.8	.481	.670	.717	Released(Jan.11)
	T25-8	M	1560.7	— — —	— — —	188.0	87.4	122.5	.465	.652	.713	ditto
	T25-9	M	1188.3	— — —	— — —	189.2	99.6	122.1	.526	.645	.816	ditto
	T25-10	M	1338.6	— — —	— — —	203.9	97.0	131.2	.476	.643	.739	ditto
Jan.12-13,'89	T26-1	M	1317.1	— — —	— — —	201.4	98.1	128.3	.487	.637	.765	Bring to Japan
	T26-2	F	1080.7	— — —	— — —	188.0	87.4	122.5	.465	.652	.713	ditto
	T26-3	M	1425.2	— — —	— — —	203.0	98.9	129.6	.487	.638	.763	ditto
	T26-4	F	1037.2	— — —	— — —	189.1	88.9	122.5	.470	.648	.726	Released(Jan.13)
	T26-5	F	1045.2	667.2	294.2	183.9	90.8	120.4	.494	.655	.754	Dissected(Jan.13)
	T26-6	M	1239.3	— — —	— — —	187.1	92.5	126.6	.494	.677	.731	Released(Jan.13)
	T26-7	M	1517.5	— — —	— — —	203.3	100.8	134.2	.496	.660	.751	ditto
	T26-8	M	1035.8	— — —	— — —	182.4	97.1	114.9	.532	.630	.845	ditto
	T26-9	M	1296.1	— — —	— — —	197.2	97.1	125.2	.492	.635	.776	ditto
	T26-10	F	958.7	— — —	— — —	184.2	86.4	128.2	.470	.697	.674	ditto
	T26-11	M	1630.0	— — —	— — —	210.9	102.2	137.7	.485	.653	.742	ditto
	T26-12	F	1139.7	— — —	— — —	190.5	90.9	124.7	.477	.655	.729	Bring to Japan
	T26-13	M	1503.4	— — —	— — —	210.9	101.3	134.8	.480	.639	.751	Released(Jan.13)
	T26-14	?	320.3	— — —	— — —	122.9	64.0	79.4	.521	.646	.806	Bring to Japan

Remarks. The weight data with parentheses were obtained by means of a spring balance, and cross-checked with the data by a dial balance (accuracy ±0.01g).

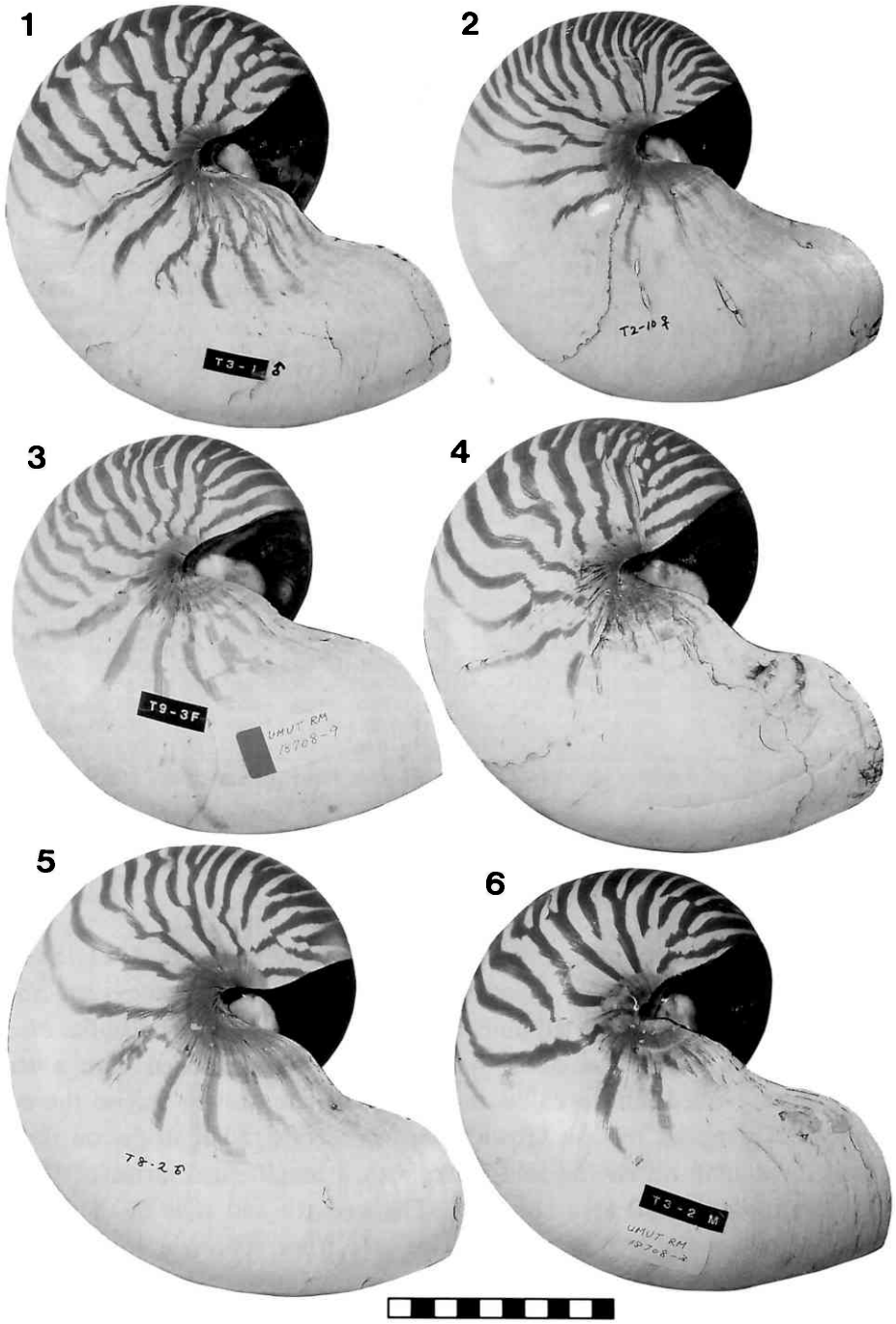
Morphological Observations

Shell

The Palauan *Nautilus*, named *Nautilus belauensis* by Saunders, 1981 (Saunders, 1981a,b, 1987) is very closely allied in overall shell morphology to *Nautilus pompilus*, which has a wide geographic range in the Southwestern Pacific. Namely, as in *N. pompilius*, the whorls of *N. belauensis* are tightly coiled with a narrow umbilicus, mostly filled with a callus in the middle-late growth stages; the coloration consists of irregular reddish brown to brown serrate radial stripes on the flank and venter branching across the mid-flank, with a longitudinal stripe of the same color around the umbilical area (Plate 1). The strength and style of the branching pattern of serrate radial stripes are quite variable from specimen to specimen. In addition to the above features, well marked, longitudinally crenulated ridges running across the sinuous growth lines are developed on the whorl surface (Saunders, 1981a; Tanabe *et al.*, 1990).

Radula

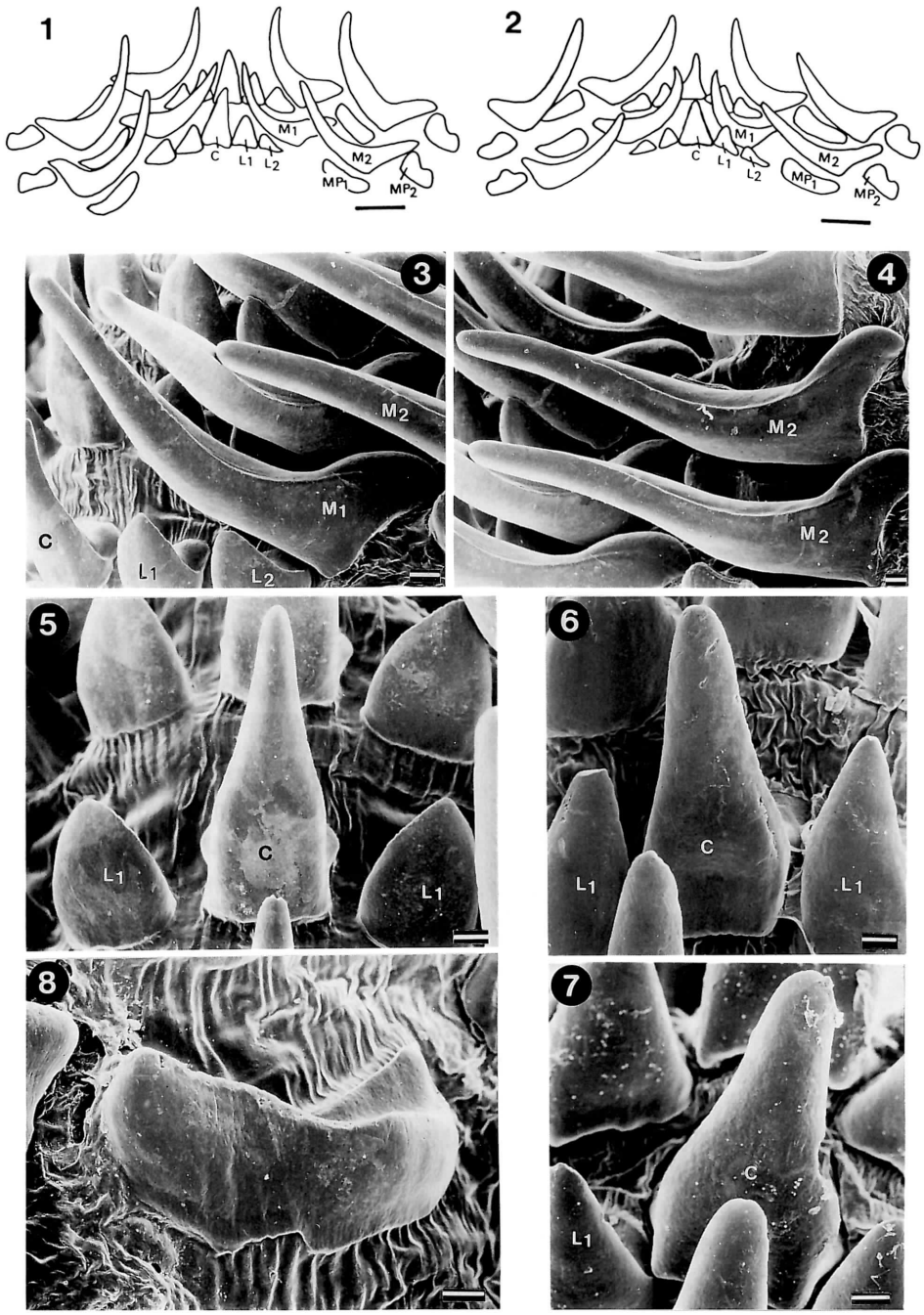
The radula of *N. belauensis* consists of nine chitinous primary teeth (one



Explanation of Plate 1

Nautilus belauensis from Palau. Lateral views. Scale bar represents 10cm.

Fig.1. Specimen T 3-1 (mature male).
Fig.2. Specimen T 2-10 (mature female).
Fig.3. Specimen T 9-3 (mature female).
Fig.4. Specimen T 9-6 (mature male).
Fig.5. Specimen T 8-2 (mature male).
Fig.6. Specimen T 3-2 (mature male).



Explanation of Plate 2

Drawings (1-2) and scanning electron micrographs (3-8) of radula in *Nautilus belauensis* from Palau. Abbreviations. c: central rachidian tooth; L_1 and L_2: inner and outer lateral teeth; M_1 and M_2: inner and outer marginal teeth; MP_1 and MP_2: inner and outer marginal support plates. Scale bars indicate 0.5mm for 1-2 and 10μm for 3-8.

Fig.1. Radular arrangement. Specimen T 9-2 (mature male).
Fig.2. Radular arrangement. Specimen T 5-4 (mature female).
Figs.3-5. Inner (3) and outer (4) lateral teeth, and central tooth (5). Specimen T 5-4.
Fig.6. Central tooth. Specimen T 9-2.
Fig.7. Central tooth. Specimen T 2-14 (immature male).
Fig.8. Inner marginal plate. Specimen T 5-4.

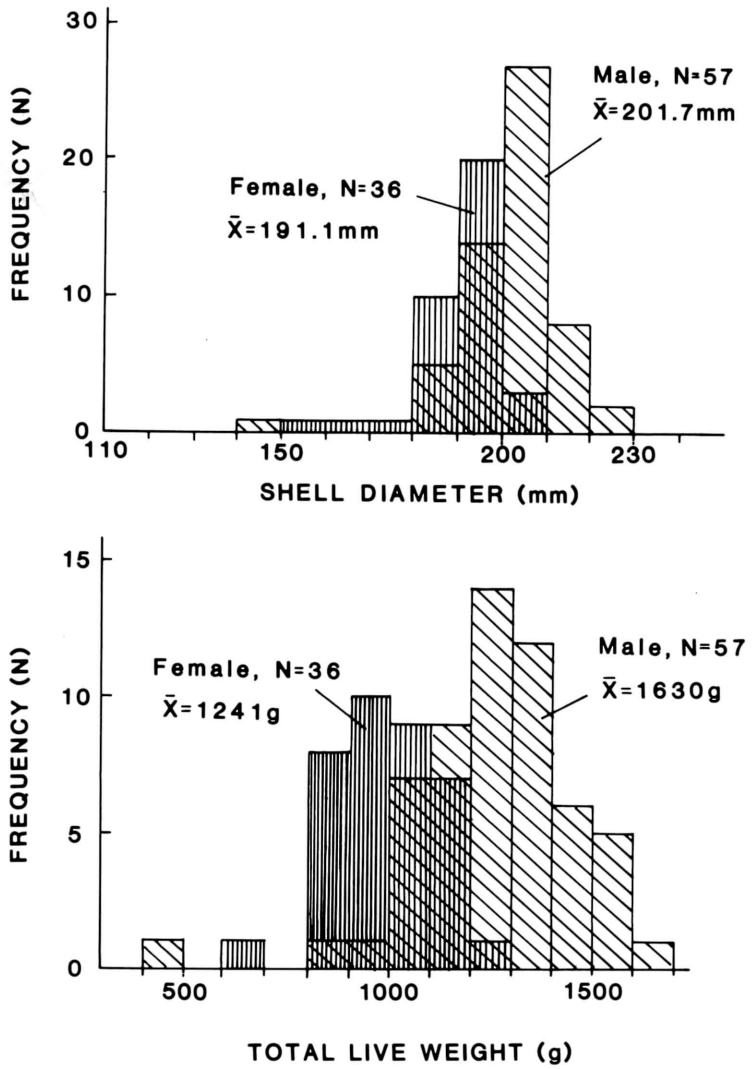


Fig.3. Size and weight frequency distributions of captured *N. belauensis*.

central rachidian, two pairs of laterals and marginal on each side) and two pairs of marginal support plates (Plate 2). This arrangement is common to all modern *Nautilus* species (Thiele, 1983; Vayssiere, 1896; Griffin, 1990; Naef, 1923; Solem and Richardson, 1975; Mikami *et al.*, 1980., Saunders, 1981a, 1987; Tanabe and Fukuda, 1987; Tanabe *et al.*, 1990), and is clearly distinguished from that of coleoids with seven primary teeth and a pair of marginal plates.

The central rachidian tooth is triangular in shape, and is more than two times as high as the two laterals (Plate 2, Figs. 5-6). The two marginal teeth are similar in overall morphology to each other. They are gently curved and acutely projected anteriorly, with a strong ridge along their longitudinal axis. In the anterior position the teeth are subcircular in cross section with a round top, but they tend to

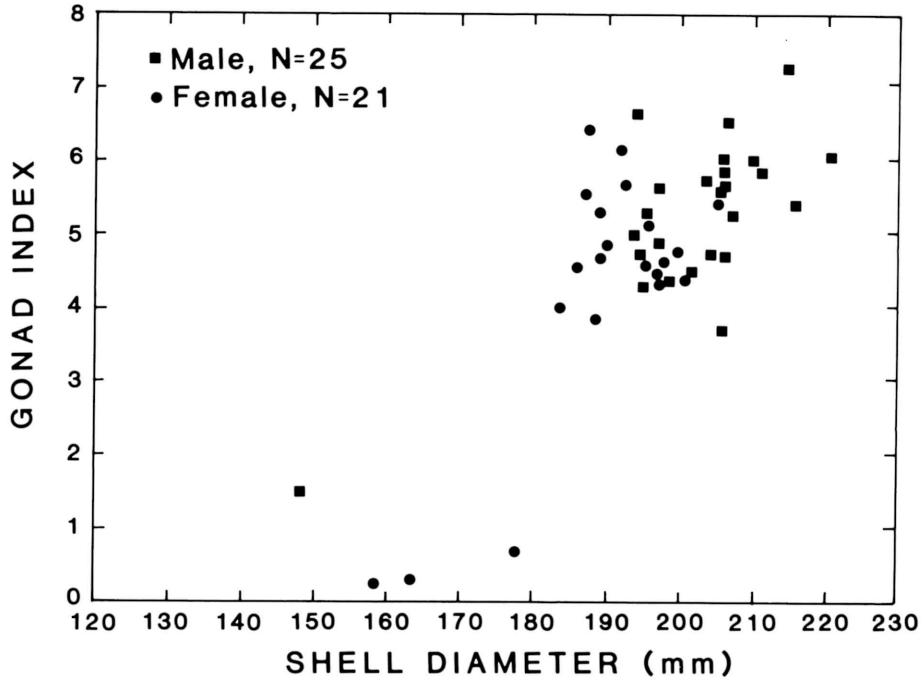


Fig.4. Scatter plot of gonad index [= weight percent of ovary or testis to soft tissue] versus shell diameter for captured *N. belauensis*.

broaden and become more compressed towards the base. The base of the teeth is characterized by a spatular-like anterior expansion (Plate 2, Figs. 3-4). The marginal support plates are rectangular in frontal view, with a marked anterior depression in the outer one (Plate 2, Fig. 8). The shape of each radular element does not differ between males and females, but the height/width ratio of the central tooth is markedly variable from specimen to specimen (Plate 2, Figs. 5-7).

Sexual Dimorphism

Sexual dimorphism in *N. belauensis* is expressed by differences in the soft anatomy, and by the size and proportion of the shell (Saunders and Spinosa, 1978). This evidence was confirmed in the specimens captured; namely, mature males are generally larger and heavier than mature females (Fig. 3). Sexual dimorphism in dimensions at maturity is clearly expressed by comparing gonad development in relation to shell size between males and females. A scatter plot of gonad index (weight percent or ovary or testis to soft tissue) versus shell diameter (Fig. 4) shows that the gonads are poorly developed in specimens of less than 180 mm in shell diameter for both sexes . The gonad index is large (>4) in all specimens exceeding 185 mm in diameter. If we set a provisional standard of sexual maturity of 3.0 on the gonad index, the mean shell diameter of males (204.3mm: N=23) is slightly larger than that of mature females (193.2mm: N=19), through the range of variation for both sexes partly overlaps each other (males: 193.6 - 220.8

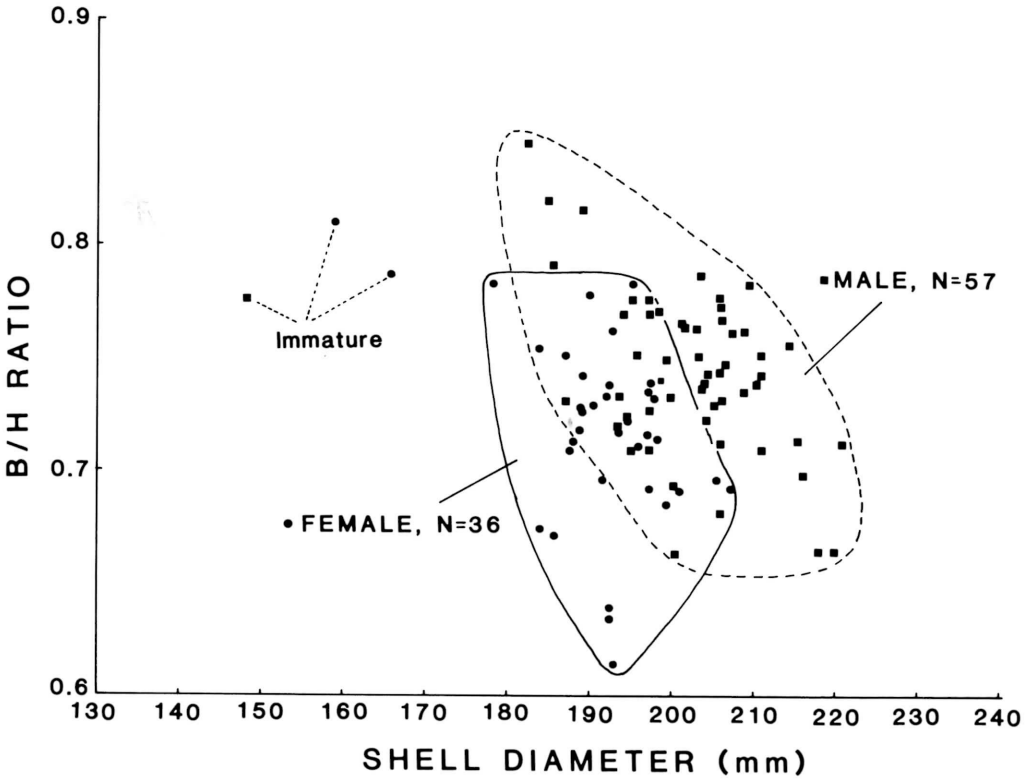


Fig.5. Scatter plot of whorl breadth (B)/whorl height ratio (H) versus shell diameter for captured *N. belauensis*.

mm, females: 183.9 - 205.5mm). The above data correlate well with the measurements on many live-caught specimens by Saunders and Spinosa (1978, fig. 5), who defined sexual maturity on the basis of a blackened and constricted aperture.

This species also exhibits a conspicuous sexual difference in apertural shape; *i.e.* mature males generally have a broader and rounder aperture than mature females (Figs. 5-6). This fact was already recognized by Saunders and Spinosa (1978, figures 8 & 10). As stated by Saunders and Spinosa (1978), the larger aperture breadth/height ratios of mature males compared to females are apparently accompanied by the development of the spadix.

Although we have not examined sufficient material, mature males generally have relatively longer upper and lower jaws than mature females (Fig. 7).

Notes on Taxonomy

The presence of living *Nautilus* in Palauan waters was first documented by Dugale and Faulkner (1976). It was subsequently identified as *N. pompilius* (Faulkner, 1976; Saunders and Ward, 1979; Carlson, 1979), or *N.* cf. *pompilius* (Saunders *et al.*, 1978; Saunders and Spinosa, 1978, 1979). More recently, Saunders (1981a) proposed a new species, *N. belauensis* for the Palauan population, on the

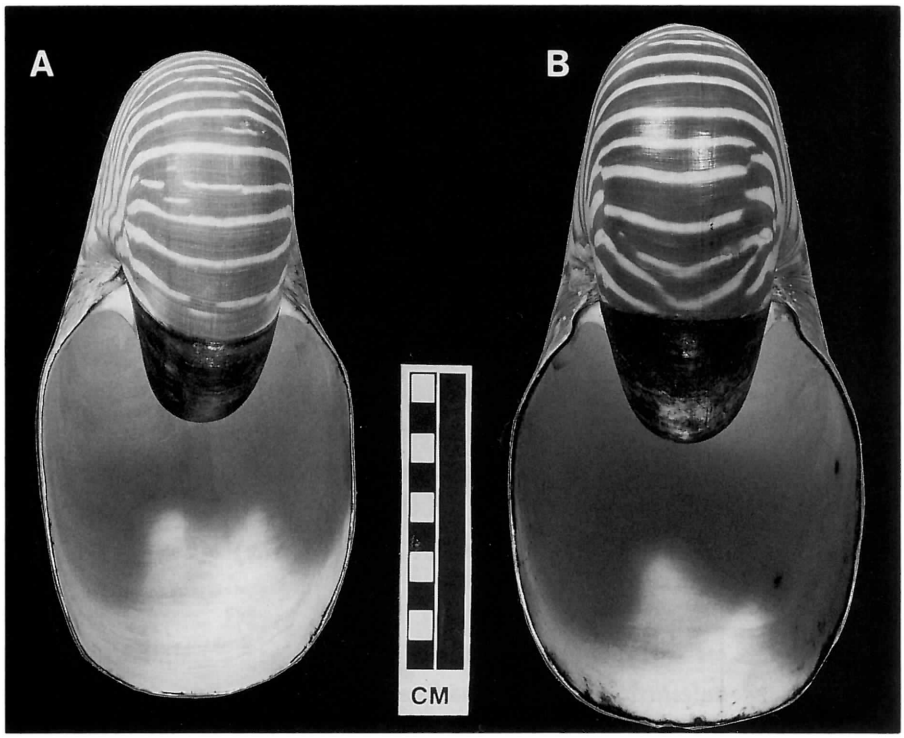


Fig.6. Sexual dimorphism of *N. belauensis* expressed by the difference in apertural shape (frontal views). A. Specimen T 9-3 (mature female). B. T 3-2 (mature male). Scale bar indicates 10cm.

basis of the examination of more than 1000 live-caught specimens. According to Saunders (1981a, b, 1987), *N. belauensis* is indigenous to Palau, and is distinguished from the very closely allied *N. pompilius* by its much larger mature size and wider central rachidian radular tooth, and by the presence of longitudinal crenulated ridges on the shell. Tanabe *et al.* (1990) examined the comparative morphology of *N. belauensis* from Palau and *N. pompilius* from Fiji and the Philippines on the basis of live-caught specimens. These authors confirmed the longitudinal crenulated shell ornamentation in many specimens from Fiji and the Philippines. They also suggested that the shape of the central radular tooth appears to be of little significance for species-level systematics because of the marked variability in the width/height ratio of the central radular tooth among and within populations.

As stated above, the Palauan *Nautilus* has unusually large mature size (ca. 185 - 220 mm in shell diameter) as compared with *N. pompilius* from other regions (ca. 140 - 175 mm in diameter) (Saunders, 1981a, b, 1987; Tanabe *et al.*, 1990). The widespread species *N. pompilius*, however, displays remarkable geographic variations in morphology (dimensions of adult animals and proportion and coloration of the shells) (Ward *et al.*, 1977; Hayasaka *et al.*, 1982; Tanabe and Tsukahara, 1987; Saunders, 1987; Tanabe *et al.*, 1990) and genetics (Masuda and Shinomiya, 1983; Woodruff *et al.*, 1987).

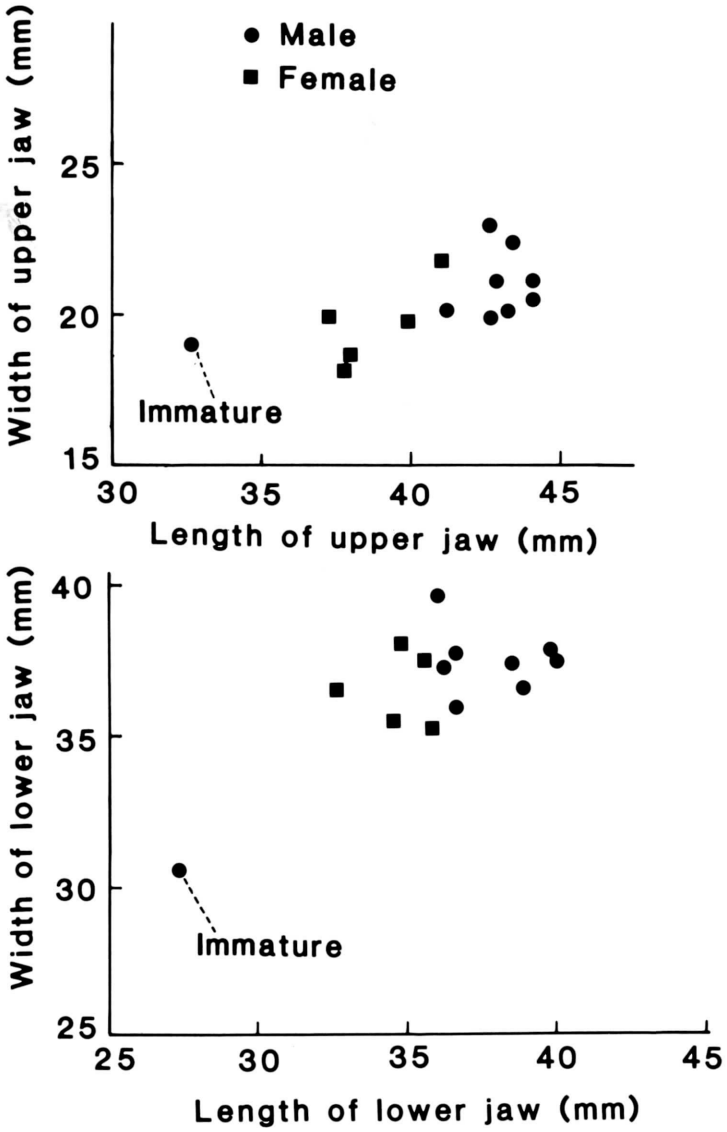


Fig.7. Width/length ratios of upper and lower jaws for selected specimens of *N. belauensis*.

Based on the genetic distance coefficients calculated, Woodruff *et al.* (1987) suggested that the Palauan population (*N. belauensis*) and possibly the Fijian population (*N. pompilius*) are closely related to, but well differentiated at the species level from the population around New Guinea and Queensland (*N. pompilius*). The genetic distance coefficients between the samples of *N. belauensis* and *N. pompilius* from New Guinea, Queensland and Fiji are, however, much smaller than those between sample pairs of *N. pompiliuss, N. scrobiculatus* and *N. macromphalus*, all of which can be easily distinguished from one another by differences in overall shell morphology. Furthermore, genetic differentiation detected by electrophoretic

analyses of enzymes is especially conspicuous between geographically separated populations (Matsuda and Shinomiya, 1983; Woodruff *et al.*, 1987).

In view of the available morphological and genetic data, we can not simply accept the opinion of Woodruff *et al.* (1987) that the Palauan population is reproductively isolated from other populations of *N. pompilius*. In relation to this problem, Tanabe *et al.* (1990) recently presented two possibilities about the taxonomic relationship of the Palauan population; one is that the population merely represents a geographic form of *N. pompilius* with high level of genetic and morphological differentiation, and the other is that it is a distinct species (*N. belauensis*) that branched off from its sister species, *N. pompilius*, by peripheral isolation.

Further biometric and genetic analyses at intra- and inter- populational levels including breeding tests of allopatric animals are required to solve the above problem.

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