

Shell Morphology of *Nautilus pompilius* and *N. macromphalus**

By

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Introduction

It appears that *Nautilus* was for the first time observed scientifically by HOOK (1696) and was given taxonomic status by LINNAEUS (1758). Subsequently, mainly behavior (e.g., WILLEY, 1897a-h) and anatomy (e.g., MACDONALD, 1855, 1857) of *N. pompilius* and *N. macromphalus* were reported, a trend which continued to 1900s (e.g., GRIFFIN, 1900). Recently modern methods have been employed on living *Nautilus* such as the morphogenetic studies of isotopes (EICHLER and RISTEDT, 1966a, b) and of shell-structure with the electron microscope (e.g., GREGOIRE, 1962, 1967; BLIND, 1976).

Knowledge of ontogeny, autecology, distribution and variation of *Nautilus* which lives in a deep sea of the south-west Pacific, however, is still incomplete so that the systematics has not improved. Five species are currently distinguished: *N. pompilius* LINNE, 1758, *N. repertus* IREDALE, 1944, *N. stenomphalus* SOWERBY, 1849, *N. macromphalus* SOWERBY, 1849 and *N. scrobiculatus* SOLANDER, 1786, but a significant number of conchologists believe in the validity of only *N. pompilius*, *N. macromphalus* and *N. scrobiculatus* (e.g., HABE, 1977).

Recently, the Yomiuri Land Marine Aquarium and JECOLN (Japanese Expert Consultation on Living *Nautilus*) have succeeded in the long-time rearing of *Nautilus macromphalus* (e.g., HAMADA, 1977a; MIKAMI *et al.*, 1976; MIKAMI and OKUTANI, 1977; KAWAMOTO, 1978) and they are now in the third stage of rearing. The rearing of *N. macromphalus* and the work of JECOLN promote the study of the shell morphology as well as of the behavior, physiology and anatomy.

The purpose of this paper is to describe biometrically the shell morphology of *N. pompilius* and *N. macromphalus*, both easy to procure, to compare the shell morphology of the two species and of the somewhat isolated populations to assume the life history

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of the animals.

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Material and Method

The material studied is: sample (N=15) of *N. pompilius* collected off Puerto Princesa, Philippines, in February, 1972; sample (N=32) of *N. pompilius* collected off Zamboanga, Philippines, in February, 1974; and sample (N=2) of *N. macromphalus* collected off Noumea, New Caledonia, in 1976. The *N. pompilius* samples were purchased from dealers in Japan and the *N. macromphalus* sample was collected by the Noumea Aquarium and donated to Yomiuri Land Marine Aquarium. The specimens seem to be sexually mature according to their size (Table 1) and the volution angle of the white colouration on the venter. Some specimens, however, do not show approximation of the ultimate septum.

Table 1. Measurements (cm) of the studied samples of *N. macromphalus* and *N. pompilius*.

	Max. diameter			Max. width		Max. umb. d.		Number of chambers	
	N	Mean	S. d.	Mean	S. d.	Mean	S. d.	Mean	S. d.
P. P.	10	16.353	5.459	8.071	4.382	—	—	33.9	1.4
Za.	32	17.469	0.826	8.300	0.470	—	—	34.0*	1.2*
N. C.	2	14.598	0.491	7.545	0.191	1.215	0.078	28.0	1.4

* Seven specimens are studied.

After the specimens were cut in the median plane, we measured the radius, shell thickness, septal thickness and the inside diameter of the siphuncular neck at each 90° of the spiral (Fig. 1). To set the base line for measurements, we first inscribe a circle in the umbilical perforation (Fig. 1). This circle has its center O where the line CD is longest. The base line AB is obtained by drawing a line from O perpendicular to the line CD. The base line forms an angle of approximately 25° with line EO, between the apex and the center O of the inscribed circle. Since line EO cuts the first camera, line AOB is preferred to line EO as the base line. Some specimens were cut vertically to the median plane, and half breadth, whorl height and umbilical radius were measured (Fig. 2). The measurements were made with Nikon Profile Projector V-16 (scale 1 μ) and the calculation with SEIKO Personal Computer 5500 MII.

It has been known empirically that the growth of parts of the body relative to the whole body shows a certain functional relation, represented by the equation $y = \beta x^\alpha$ (NOMURA, 1926; HUXLEY, 1932). The growth of cephalopods is not exception since the

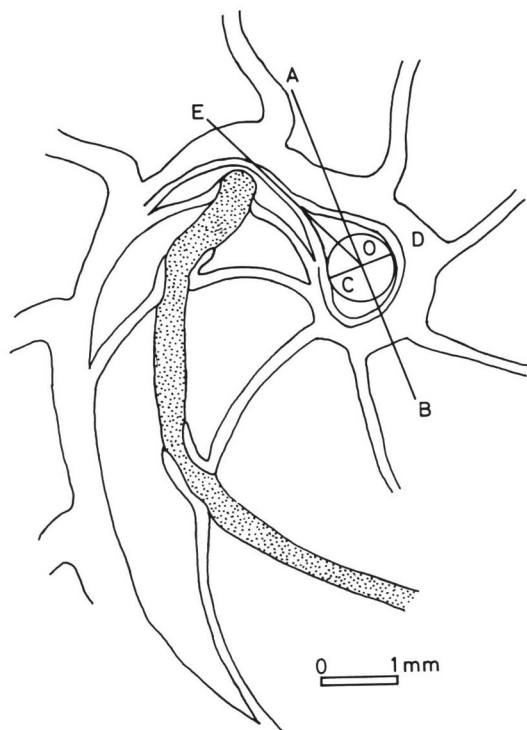


Fig. 1. Schematic diagram of *Nautilus* showing the base line (AB) used for measurements. O is the center of the inscribed circle in the umbilical perforation, and at C and D this circle inscribed the margin of the perforation. $AOB \perp COD$, EO is the line drawn between the apex and the center O. The angle $\angle AOE$ usually approximates 25° .

relative growth patterns of character pairs show high linear correlation on logarithmic or semi-logarithmic coordinates (e.g., OBATA, 1959, 1960, 1961, 1964, 1965; HIRANO, 1975, 1977a, b, 1978). The analyses of these plots were done by the reduced major axis (independent two characters) or the least squares method (one character versus spiral).

N. pompilius

A. Results

The growth pattern of radius versus spiral of *N. pompilius* was described previously (HIRANO, 1977b; Fig. 3 in this paper). This growth pattern is very stable in each local population like some Cretaceous ammonites (e.g., HIRANO, 1975, 1977a, 1978). A critical point exists at the 1.0π volution, where the growth index (α) of radius versus spiral changes. The pattern shows a high linear correlation in the stages

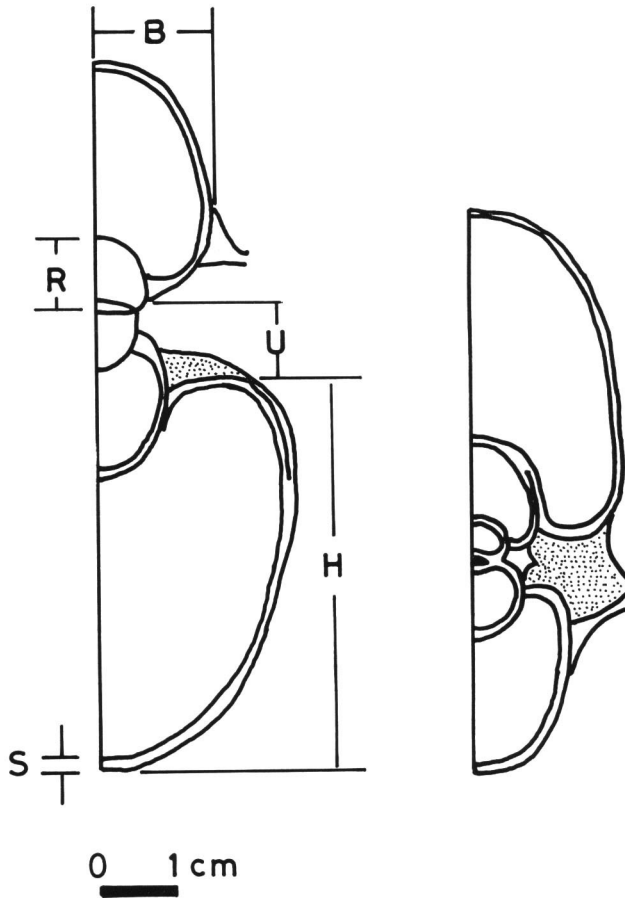


Fig. 2. Schematic diagram of *Nautilus* showing the measured portion of the cross section. Left: *N. macromphalus*, Right: *N. pompilius*. B: 1/2 breadth of whorl, R: radius, U: umbilical radius, H: height of whorl, S: shell thickness. Dotted portion: umbilical plug (callus), the secondary deposits of calcium carbonates.

before and beyond the point. The interpopulational variation, however, represented by the samples of Puerto Princesa and Zamboanga, which are about 570 km apart, is fairly large (HIRANO, 1977b, See also Table 9 in this paper).

The growth pattern of the whorl-breadth in relation to the spiral has a critical point at 3.0π revolution as illustrated (Fig. 4). This critical point is not so obvious in appearance, but the linear correlation is increased when the pattern is divided at 3.0π into two stages. The growth index becomes higher beyond this point. The variation of the growth index is higher before than after the critical point. The growth pattern of whorl-breadth versus radius also has a critical point at 3.0π (Fig. 5). This derives from the change of the growth index for breadth versus spiral because the

growth pattern of radius versus spiral does not show a critical point beyond 1.0π .

The growth pattern of whorl-height versus spiral shows very high linear correlation and no critical points appear between 1π and 5π (Fig. 6). The growth index is very constant and the variation very small.

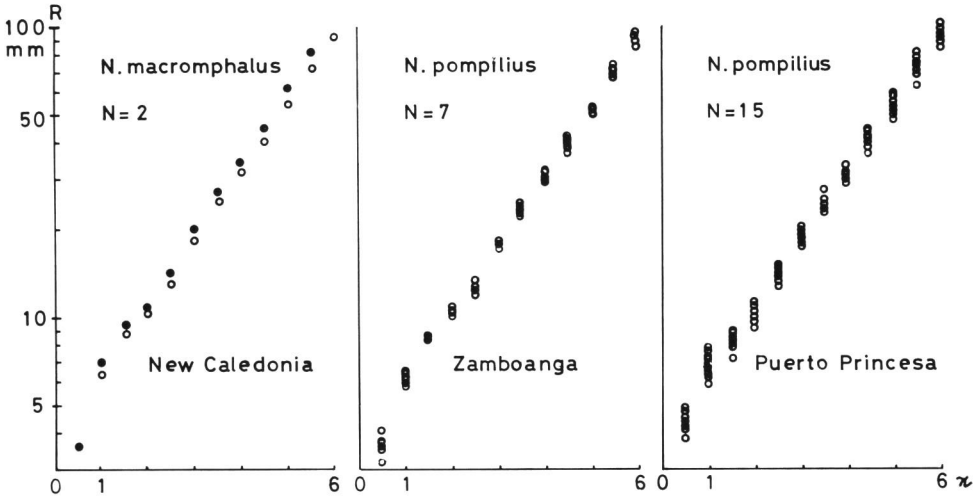


Fig. 3. Growth pattern of radius (R) versus spiral of the New Caledonia sample of *N. macromphalus* and of the Puerto Princesa and Zamboanga samples of *N. pompilius*. *N. macromphalus*—black dot: specimen A, circle: specimen B.

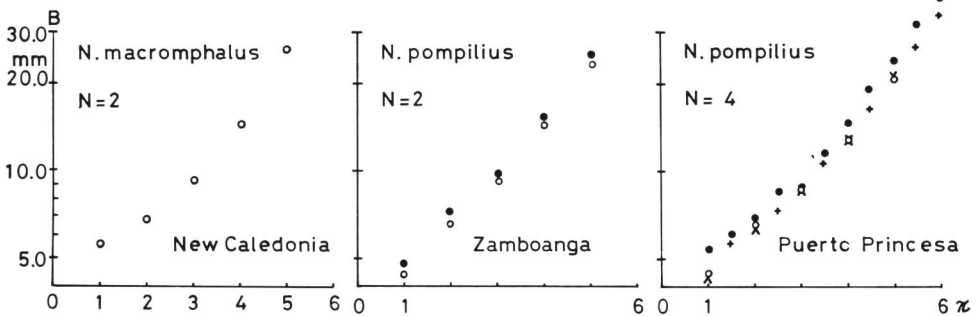


Fig. 4. Growth pattern of $1/2$ breadth (B) in relation to the spiral.

The cross section of the whorl which is expressed by S ($=B/H$) as defined by RAUP (1967), develops in general from depressed via circular to compressed. Beyond 3π , however, change decelerates so that the ratio becomes only slightly less than 1 (a circle), *i.e.* the whorl is somewhat compressed (Table 2).

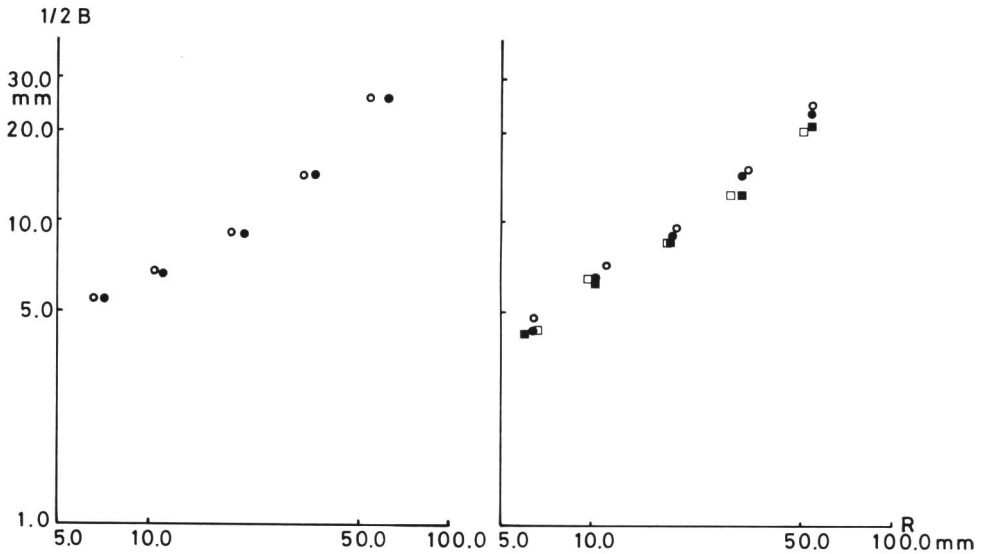


Fig. 5. Growth pattern of 1/2 breadth (B) versus radius. Left: *N. macromphalus* (dot: specimen A, circle: specimen B). Right: *N. pompilius* (dot: specimen No. 4 from Zamboanga, circle: No. 5 from Zamboanga, black square: No. 7 from Puerto Princesa, square: No. 15 from Puerto Princesa).

Table 2. Ontogenetic change of cross-section ($S=B/H$) value in *N. pompilius* off Zamboanga and Puerto Princesa.

Stage	Mean	Zamboanga		N	Mean	Puerto Princesa		N
		S. d.	C. v.			S. d.	C. v.	
1 π	1.542	0.190	12.339	2	1.542	0.019	1.239	2
2	1.319	0.025	1.877	2	1.330	0.059	4.414	2
3	1.116	0.021	1.838	2	1.146	0.057	4.936	2
4	1.033	0.027	2.601	2	0.998	0.030	2.976	2
5	0.979	0.005	0.506	2	0.932	0.021	2.276	2

The growth pattern of shell-thickness versus spiral is somewhat more variable than other characters and the linear correlation lower in each individual, although the correlation is significant (Fig. 7). The shell-thickness changes irregularly because of repair of breakage and the formation of constriction. In most of the studied specimens, however, a critical point is detected between 2.5π and 3.0π and the growth index becomes much larger beyond this point.

The growth pattern of septal thickness versus spiral shows a critical point with a gap between 1.5π and 2.0π . The correlation coefficients are high before and after this point (Fig. 8). This gap is derived from the large difference in thickness between the 7th and 8th septa. The variation of the growth index is small. Septal thickness

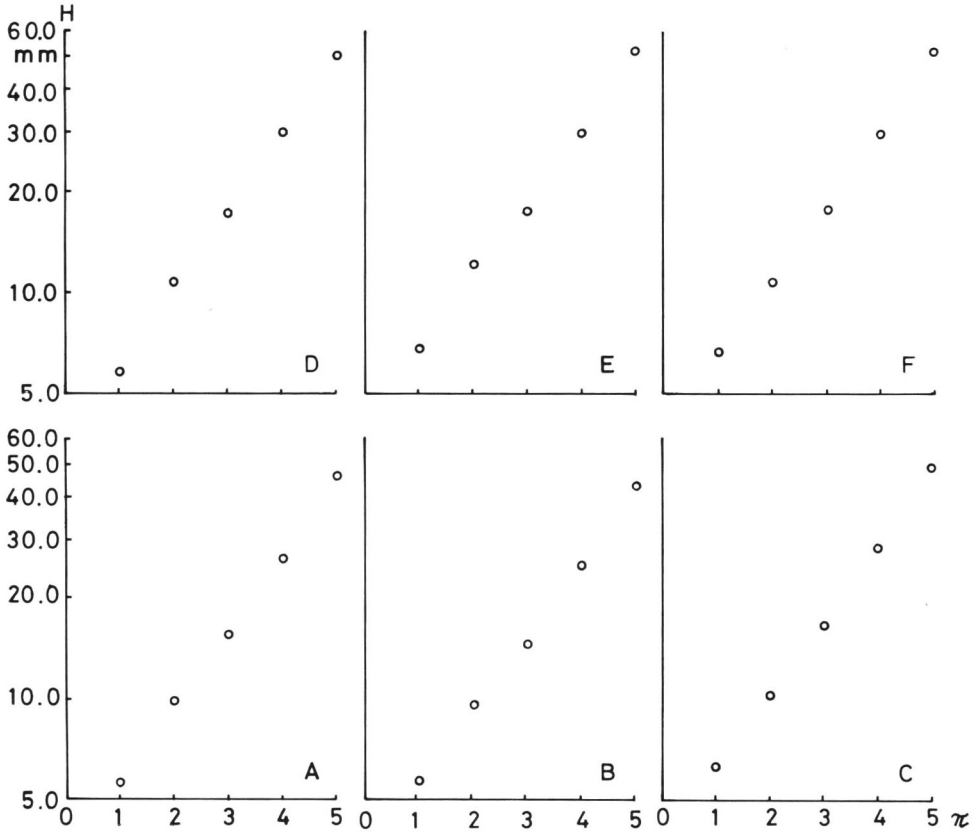


Fig. 6. Growth pattern of whorl-height (H) versus spiral. A–D: *N. pompilius*, A–No. 7 from Puerto Princesa, $H=3.381 \theta^{0.226}$, $r=0.999$; B–No. 15 from P. P., $H=3.428 \theta^{0.215}$, $r=0.999$; C–No. 4 from Zamboanga, $H=3.733 \theta^{0.221}$, $r=0.999$; D–No. 5 from Zamboanga, $H=3.532 \theta^{0.233}$, $r=0.999$; E–F: *N. macromphalus*, E–Specimen A from New Caledonia, $H=4.266 \theta^{0.216}$, $r=0.998$; F–Specimen B from New Caledonia, $H=3.882 \theta^{0.224}$, $r=0.999$.

and shell-thickness are very important in respect to the pressure resistance and were studied in detail by some palaeontologists (*e.g.*, WESTERMANN, 1977). We intend to discuss the buoyancy system after we have analysed its control system with data on the pressure and condition of the liquid in the phragmocone when *Nautilus* dives. JECOLN has been rearing the animals and we want to avoid the mechanical analogy of *Nautilus* with a submarine.

The characteristic disruptive colouration appears at about 3π of the spiral. The shell is ivory coloured and lattice-like sculptured with spiral and radial subcostae from the first camera to 1π . The spiral subcostae of the lattice-like sculpture become weak beyond 1π and almost disappear before 2π . The colouration changes in the stage just before 2π from pale orange to brown. This change in colouration correlates

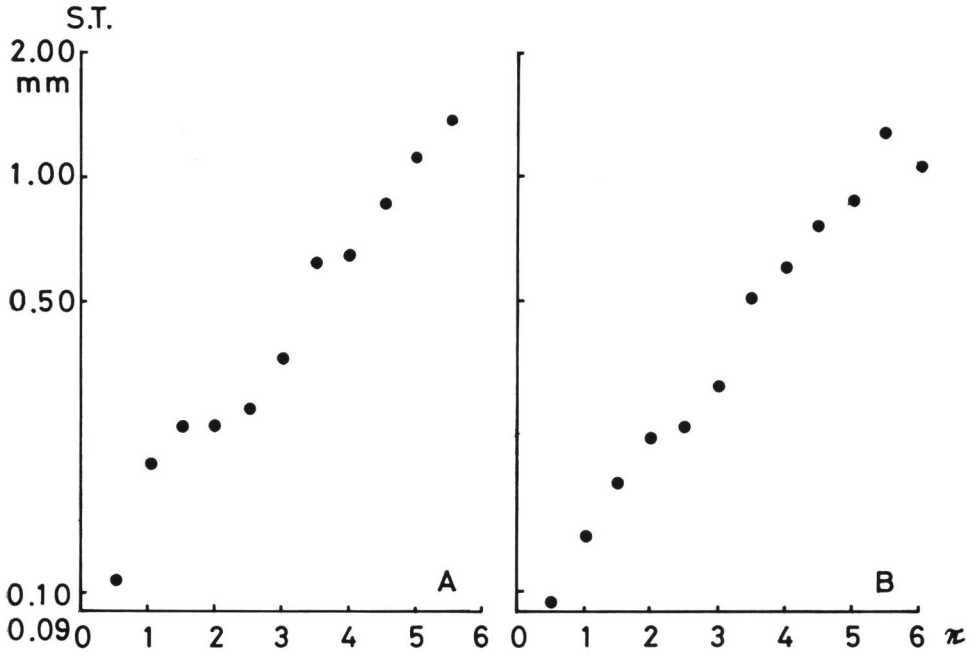


Fig. 7. Growth pattern of shell thickness (S. T.) versus spiral of *N. macromphalus*. A-0.5-3.0π: S. T.=0.114 $\theta^{0.174}$, $r=0.906$; 3.5-5.5π: S. T.=0.130 $\theta^{0.185}$, $r=0.982$; B-0.5-3.0π: S. T.=0.200 $\theta^{0.084}$, $r=0.976$; 3.5-6.0π: S. T.=0.154 $\theta^{0.151}$, $r=0.941$.

with that in surface sculpture. At about 3π the disruptive colouration appears, continuing to about 6.6π , and the shell is white in the final stage. The disruptive colouration is interpreted as camouflage by COWEN *et al.* (1973).

In the adult, the body chamber occupies about 150° and the muscle scar about $70-80^\circ$ on its side. However the soft part is easily removed from the shell by an impact, in the live and dead animal. In the removed soft parts the muscle shows no tear, and the attachment surface of the muscle is covered by connective tissue (being studied by members of JECOLN). This demonstrates that spiral length and area of the muscle scar are not related to strength of adherence of the soft part to the shell and to the activity of the animal. This conclusion may be extended to the ammonites. Furthermore, it is confirmed that soft part kept in fixative changed in proportion and shape owing to contraction and rigidity.

The nepionic constriction seems to be of high significance. The following statistics was obtained on the position of the nepionic constriction in the Puerto Princesa sample (N=11). Volution angle from the base line, $\bar{\theta}=535^\circ 27'$; Standard deviation, S. d.= $42^\circ 55'$; Coefficient of variability, C. v.=8.016. Some constrictions occur also later in mature specimens.

The number of septa in the specimen with septal approximation ranges from 32

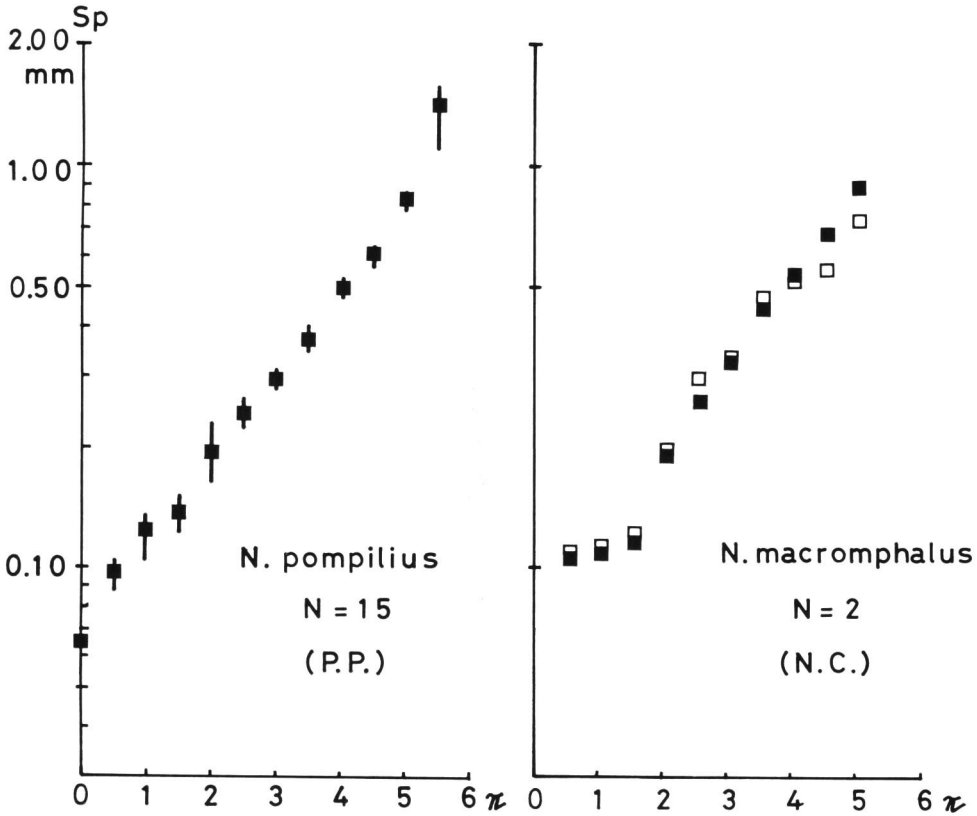


Fig. 8. Growth pattern of septal thickness (Sp) versus spiral of *N. pompilius* (Puerto Princesa) and *N. macromphalus* (New Caledonia). 95% confidence limit ($\text{mean} \pm t_{0.05} \text{S.d.}/\sqrt{N}$) is shown in the Puerto Princesa sample of *N. pompilius*. *N. pompilius*—2.5~5.0 π : $\bar{\alpha}$ =0.216, S.d.=0.032, C.v.=14.65; *N. macromphalus*—2.5~5.0 π : $\bar{\alpha}$ =0.199, S.d.=0.026, C.v.=13.02.

to 35 with mean of 34 in the Puerto Princesa sample and from 33 to 36 with mean of 34 in the Zamboanga sample. The diameter of these shells range from 156.70 mm to 166.55 mm with the mean of 160.57 mm in the Puerto Princesa sample and from 163.00 mm to 178.00 mm with the mean of 172.86 mm in the Zamboanga sample. The septa are more numerous and the size is larger in these two samples than in the Fiji sample described by WARD *et al.* (1977). The diameter of the shell where the disruptive colouration disappears on the venter ranges from 108.20 mm to 129.90 mm with the mean of 119.05 mm in the Zamboanga sample. The coefficient of variability is 4.91.

WARD *et al.* (1977) reported the dimorphism of the disruptive colouration of the Fiji sample and referred them as variants A and B. They concluded that variant B is absent in the Philippine population, and that the dimorphism in the Fiji population

Table 3. Numerical ratios of varieties A to B in the samples off Puerto Princesa and Zamboanga, and χ^2 (2×2 contingency table) test on the ratios.

	Variety A	Variety B	test
P. P.	10	2	0.807
Za.	7	5	

$$\chi^2_{0.05(\nu=1)} = 3.84$$

is due to the deeper habitat. As will be mentioned later this dimorphism has been known by conchologists for a long time and the presence of the dimorphism in the Philippine population is also well known. The same dimorphism is present in our samples from Puerto Princesa and Zamboanga, Philippines. The proportion of variety A to variety B is 7:5 in the Zamboanga sample and 10:2 in the Puerto Princesa sample (Table 3). Although there are two intermediate forms in each sample, varieties A and B are in general distinct in our samples. According to Dr. T. HABA, an authority of conchology, it is difficult to distinguish the dimorphs when the sample is sufficiently large (personal comm.). This dimorphism is not related to sex according to WARD *et al.* (1977). Preliminary analysis of our small sample shows that the dimorph frequencies between the samples from Puerto Princesa and Zamboanga are not significantly different (Table 3). More than half of the Fiji sample is said to consist of variety A (WARD *et al.*, 1977). But exact ratio is not given, so that we cannot compare the ratios between their and our samples. We also examined the correlation of this dimorphism with other characters. The means of the growth indices of the radius between the varieties A and B of the Puerto Princesa sample do not differ significantly (Table 4). The same test is carried out on the growth indices of septal thickness and shell-thickness in relation to the spiral of the same sample, without detecting significant difference, in both characters (Table 5). These results lead us to the conclusion that the cause of the dimorphism in the disruptive colouration does not genetically correlate with these characters.

We mentioned the significant difference in the means of the growth indices of radii versus spirals between the Puerto Princesa and Zamboanga samples, and we

Table 4. Growth index of radius versus spiral and *t*-test for the difference between the samples of varieties A and B of *N. pompilius* off Zamboanga and Puerto Princesa.

Sample	Variety	N*	Growth index		<i>t</i> **
			Mean	S. d.	
P. P.	A	10	0.229	0.005	0.896 \ll $t_{0.05(\nu=10)}$
	B	2	0.232	0.002	
Za.	A	2	0.236	0.002	1.458 \ll $t_{0.05(\nu=3)}$
	B	2	0.231	0.006	

* Not all the specimens of each sample are analysed for this study.

** There is not a significant difference between variances (F).

Table 5. Growth indices of the shell-thickness and the septal thickness versus the spiral and *t*-test for the differences between the samples of varieties A and B off Puerto Princesa.

	Mean	Variety A S. d.	N	Mean	Variety B S. d.	N	<i>t</i> *
Shell	0.158	0.052	10	0.169	0.013	2	0.292
Septum	0.211	0.038	10	0.221	0.008	2	0.356

* There is not a significant difference between variances (F). $t_{0.05(\nu=10)}=2.228$

made the same test on the varieties A and B. A significant difference exists in the variety A between the Puerto Princesa and Zamboanga samples but not in the variety B (Table 6).

Table 6. F-test for the variance and *t*-test for the difference of the growth index of radius versus spiral of varieties A and B between the Puerto Princesa and Zamboanga samples (Data as in Table 4).

Variety	F	<i>t</i>
A	$9.807 \ll F_{0.025(\nu=9/2)}$	$t_{0.01(\nu=11)} > 2.418 > t_{0.05(\nu=11)}$
B	$9.000 \ll F_{0.025(\nu=1/1)}$	$0.295 \ll t_{0.05(\nu=2)}$

B. Discussion

The morphology of *N. pompilius* was biometrically described above based on the Puerto Princesa and Zamboanga samples. The basic growth patterns of some characters were clarified, although other morphological attributes of the species need to be studied.

The means of the growth indices of radius versus spiral differ markedly between the samples from Puerto Princesa and Zamboanga. In the Sulu Sea between Puerto Princesa and Zamboanga, a depth barrier is absent but the distance is great (570 km). In the rearing experiment of JECOLN we determined the swimming velocity of *N. macromphalus* (OKUTANI *et al.*, in press); it would take the animal about 150 days from Puerto Princesa to Zamboanga without rest. This may markedly restrict gene exchange between the two populations. This and the biostatistical results support partly the hypothesis of HAMADA (1977b). Recently an individual of *N. pompilius* traveled from Philippines to Kagoshima of southwest Japan but this is an exceptional and ineffective travel for the gene flow. Because no population of *N. pompilius* exists around Japan.

The intrapopulation variation of the growth patterns of some characters in relation to the spiral is generally low and the growth patterns are fairly consistent with respect to the critical points as well as the growth indices. Most of the critical points of the characters studied concentrate at 1π and/or 3π whorl, as preliminarily mentioned in the previous paper (HIRANO, 1977b). At about 1π , the growth patterns of shell-thickness and whorl-breadth in relation to the spiral change, the lattice sculpture

becomes weak and the colouration changes from ivory to pale orange. On the other hand, at about 3π , the growth patterns of shell-thickness, whorl-breadth, septal thickness and inside-diameter of the siphuncular neck in relation to the spiral change, a nepionic constriction is formed and disruptive colouration appears. Thus the growth points where many growth patterns change seem to represent important developmental changes.

As mentioned above the dimorphism of the disruptive colouration has been known in connection with *N. repertus* (IREDALE, 1944), but only a few conchologists approve of the specific independence of *N. repertus*. The supposition that this dimorphism exists only in the Fiji population (WARD *et al.*, 1977) is mistake since the Philippine population shows the same dimorphism. The locality of their Philippine sample should be described in detail and the geographic variation of the frequencies should be studied throughout the distribution of *N. pompilius*. Ontogenetically this dimorphism seems to appear at 3π , together with the disruptive colouration. It is necessary to clarify if this dimorphism is caused by differences in the environmental or feeding habit, or if it is genetic etc. Since *Nautilus* can now be reared in an aquarium, breeding experiments should be carried out. If this dimorphism is genetical, we may grasp the conditions of the gene flow and more clearly recognize the barriers for the living *Nautilus*.

N. macromphalus

A. Results

Biometrical studies of *N. macromphalus* are as rare as those of *N. pompilius*. The growth pattern of radius versus spiral as seen in the median section was preliminarily reported by HIRANO *et al.* (in press). The linear correlation is high; there is a critical point at 1.0π ; the growth index decreases beyond this point (Fig. 3); and the intrapopulation variation is small.

The growth pattern of breadth versus spiral shows one critical point near 3.0π , the high linear correlation before and beyond this point (Fig. 4) and an increase of the growth index beyond this point. The growth pattern of breadth versus radius also shows a critical point at 3.0π (Fig. 5), at which the growth index increases as predicted.

The value *S* of the cross-section clearly decreases with growth and the pattern is from depressed via circular to compressed (Table 7, Fig. 9). The rate of decrease, however, diminishes near 3.0π and the value is not so far from 1. This change reflects the needs of the soft part with developing organ and the economy of pressure resistance, and the change of the shape seems to relate with the presumed change of the habitat (EICHLER and RISTEDT, 1966; HIRANO, 1977b) near the 3.0π point.

In the growth pattern of whorl-height versus spiral, the linear correlation is high and there is no critical point between 1.0π and 5.0π (Fig. 6). The variation of the growth index is low.

Table 7. Ontogenetic change of cross-section ($S=B/H$) in *N. macromphalus* off New Caledonia and *N. pompilius* off Puerto Princesa and Zamboanga.

Stage	<i>N. macromphalus</i>				<i>N. pompilius</i>				t*
	Mean	S. d.	C. v.	N	Mean	S. d.	C. v.	N	
1 π	1.656	0.054	3.245	2	1.542	0.110	7.160	4	1.329
2	1.216	0.128	10.53	2	1.324	0.037	2.819	4	1.742
3	1.045	0.003	0.271	2	1.131	0.039	3.444	4	2.937
4	0.987	0.006	0.645	2	1.016	0.031	3.024	4	1.240
5	0.998	0.007	0.709	2	0.955	0.030	3.103	4	1.894

* Student's *t*-test for the difference of means in the two species. If there is a significant difference between the variances, Welch's method was applied. $t_{0.05(\nu=4)} = 2.776$ The *t*-test at 3 π shows a significant difference ($0.05 > P > 0.01$).

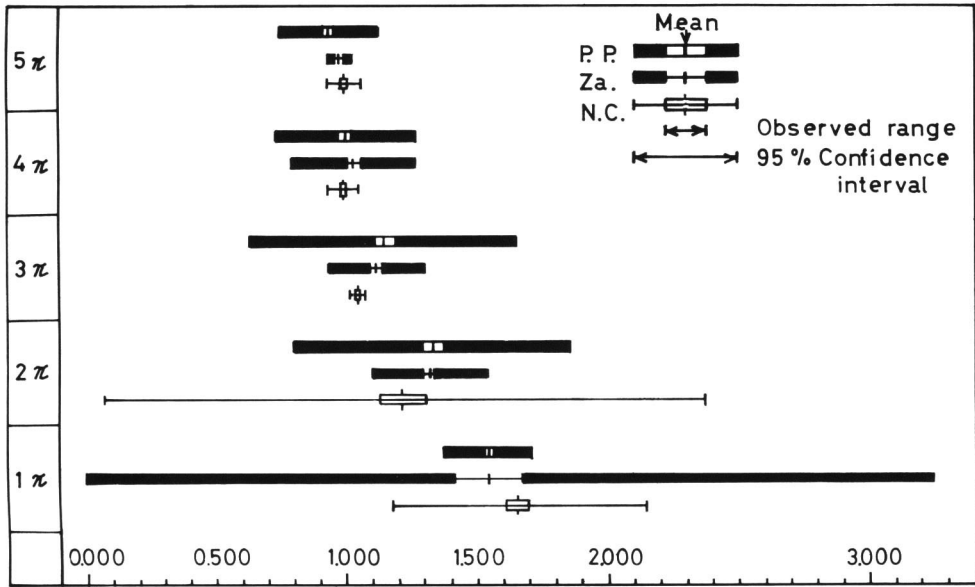


Fig. 9. Ontogenetic change of the cross section ($S=B/H$) of *N. pompilius* and *N. macromphalus*. P. P.: Sample off Puerto Princesa (N=2), Za.: Sample off Zamboanga (N=2), N. C.: Sample off Noumea, New Caledonia (N=2).

The growth pattern of the shell-thickness in relation to the spiral has a critical point between 3.0 π and 3.5 π (Fig. 7). The linear correlation, however, is not high (although significant) and therefore the critical point is not obvious. Thus the shell-thickness varies during the ontogeny. This can also be observed on the secreted shell of living *N. macromphalus* in the rearing tank. That is, repaired shell after injury and shell developed under different condition often very in thickness and are discordant with the previous or surrounding shell.

The growth pattern of septal thickness versus the spiral shows high linear correlation and has a critical point with a gap between 1.5π and 2.0π (Fig. 8). This gap is due to the large difference of the septal thickness between the 7th and 8th septa as in *N. pompilius*, and the growth index increases after the critical point.

N. macromphalus has an open umbilicus like *N. stenomphalus*. The ontogenetic change of the umbilical radius is shown in Table 8.

Table 8. Comparison of the umbilical radius (mm) at the three defined growth points of *N. pompilius* and *N. macromphalus*.

Sample	3π		4π		5π		N	Growth index		t^*
	Mean	S. d.	Mean	S. d.	Mean	S. d.		Mean	S. d.	
P. P.	1.728	0.123	2.991	0.391	3.665	0.387	2	0.163	0.038	0.531
Za.	1.896	0.547	2.764	0.517	4.649	0.523	2	0.199	0.088	
Average	1.812	0.338	2.877	0.396	4.157	0.681	4	0.181	0.059	
N. C.	2.787	0.467	4.958	0.243	8.406	2.240	2	0.237	0.022	1.237

* If there is a significant difference between the variances, Welch's method was applied. The umbilical radii at the three growth points are not significantly different between the Puerto Princesa (P. P.) and Zamboanga (Za.) samples of *N. pompilius*, but are significantly different between the samples of *N. pompilius* (P. P.+Za.) and *N. macromphalus* (N. C.).

The measurements of the studied sample are shown in Table 1. No specimen shows approximation of the final septum.

The surface sculpture and the colouration will be mentioned in detail in a forthcoming paper although they were already illustrated in colour by HABE (in press).

The statistical analysis on the position of the nepionic constriction has not yet been carried out but one specimen has a nepionic constriction at 2.97π .

B. Discussion

As *N. pompilius*, the growth pattern of *N. macromphalus* is also characterized by stable mode, but the study is preliminary. The critical points of some characters concentrate also around 1π and 3π ; *i.e.*, around 1π the growth indices of radius and septal thickness versus the spiral change; while around 3π the growth indices of breadth, shell-thickness and S versus the spiral change at the nepionic constriction. The simultaneous changes of these characters suggest important changes in the life history.

Comparison

We studied the similarity and difference of some principal characters between *N. pompilius* and *N. macromphalus* using biometrics.

The growth pattern of radius versus spiral is similar in both. The critical point occurs at the same stage, and the mean values of the growth indices are not significantly different (Table 9).

Table 9. Growth index of radius versus spiral of *N. pompilius* and *N. macromphalus*, and Student's *t*-test for the difference of means between two samples of *N. pompilius* and between two species.

Sample	Mean	S. d.	C. v.	Mean $\pm t_{0.05}$ S.d./ \sqrt{N}	N	t*
P. P.	0.230	0.005	2.041	0.227-0.232	15)	2.227
Za.	0.234	0.004	1.598	0.231-0.238	7)	
P. P.+Za.	0.231	0.005	2.120	0.229-0.233	22)	1.365
N. C.	0.236	0.004	1.834	0.197-0.274	2)	

* Significant difference ($0.05 > P > 0.01$) is indicated by gothic numerals. There is no significant difference between the variances.

Table 10. Growth index of 1/2 breadth (B) versus spiral of *N. pompilius* and *N. macromphalus*. The growth stage $0\pi-3\pi$ is shown above and the stage $3\pi-6\pi$ below.

	Mean	S. d.	C. v.	Mean $\pm t_{0.05}$ S.d./ \sqrt{N}	N	t*
P. P.	0.198	0.059	29.790	0.104-0.292	4)	0.948
Za.	0.156	0.006	4.000	0.100-0.212	2)	
P. P.+Za.	0.184	0.051	27.616	0.131-0.237	6)	3.554
N. C.	0.110	0.0004	0.348	0.106-0.113	2)	
P. P.	0.201	0.010	5.045	0.185-0.217	4)	0.187
Za.	0.205	0.0003	0.159	0.202-0.208	2)	
P. P.+Za.	0.202	0.008	4.034	0.194-0.211	6)	3.833
N. C.	0.225	0.002	1.063	0.203-0.246	2)	

* Student's *t*-test for the difference of means between two samples and between two species. Significant ($0.05 > P > 0.01$) and very significant ($0.01 > P$) differences are indicated by gothic and italic numerals, respectively. If there is a significant difference between the variances, Welch's method was applied.

Concerning the growth pattern of breadth versus spiral, both species have a critical point at 3.0π after which the growth indices increases. The means of the growth indices are significantly larger in *N. pompilius* than in *N. macromphalus* up to 3.0π but not significantly different beyond this point in both species (Table 10).

In the growth pattern of radius versus breadth, the mean of the growth index differs significantly before 3.0π but not beyond this point (Table 11).

The ratio B/H (cross-section of the whorl) is significantly different at 3π of the two species, but not at the other growth points (Table 7). In both species the whorl section changes from moderately depressed via subcircular at around 4π to slightly compressed ($1.5\pm \rightarrow 1.0 \rightarrow 0.8\pm$).

The growth patterns of shell thickness and septal thickness versus spiral are not significantly different between the two species. The thickness of the shell and that of the septum also are not significantly different at some measured points between the two species.

The umbilicus of *N. pompilius*, which has a plug (callus) of calcium carbonate (Fig. 2), is measured in the cross section. The umbilical radius is larger in *N. macrom-*

Table 11. Growth index of 1/2 breadth (B) versus radius. The upper line is the statistics for the growth stage $1\pi-3\pi$ and the lower for $3\pi-5\pi$ in each sample.

Sample	Mean	S. d.	C. v.	Mean \pm $t_{0.05}$ S.d./ \sqrt{N}	N	t^*
P. P.	0.648	0.020	3.044	0.471-0.825	2	(0.004) (10.193)
	0.835	0.005	0.564	0.792-0.877		
Za.	0.666	0.039	5.925	0.312-1.021	2	
	0.897	0.007	0.798	0.833-0.961		
P. P.+Za.	0.657	0.028	4.210	0.613-0.701	4	(8.242) (2.962)
	0.866	0.036	4.206	0.808-0.924		
N. C.	0.483	0.005	1.029	0.439-0.528	2	
	0.947	0.010	1.103	0.853-1.041		

* Student's t -test for the difference of means between two samples and between two species. Significant ($0.05 > P > 0.01$) and very significant ($0.01 > P$) differences are indicated by gothic and italic numerals respectively. There is not a significant difference between the variances.

phalus than in *N. pompilius* in the growth stage from 3π to 5π (Table 8).

It follows from these comparisons that these two species resemble each other closely in most of the principal characters, although they differ throughout ontogeny in the presence or absence of the umbilical callus and in umbilical size (excluding the callus).

It is interesting that simultaneous changes of some principal shell characters, indicating important ontogenetical changes, occur around the 1.0π and 3.0π points in the both species. The similarities of morphology, habitat (not clear in detail) and behavior suggest that these two growth points have similar significance. The animal is too large at the 3.0π stage (Figs. 3, 4, 6) to fit in the egg capsul as measured at the Yomiuri Land Marine Aquarium (MIKAMI and OKUTANI, 1977; Table 12 in this paper).

Table 12. Size (mm) and weight (g) of egg capsul of *N. macromphalus*.

	Mean	S. d.	C. v.	Mean \pm $t_{0.05}$ S.d./ \sqrt{N}	O. r.	N
Height	36.8	3.3	9.0	31.5-42.1	32.0-39.0	4
Diameter	24.8	6.9	28.1	13.8-35.8	20.0-35.0	4
Weight	3.7	0.2	4.9	3.4- 4.0	3.5- 3.9	4

Data from MIKAMI *et al.* (1977).

From the preceding discussion, the isotopic study of EICHLER and RISTEDT (1966a, b), and the observation at Fiji by DAVIS and MOHORTER (1973), we conclude that the animal hatches at approximately the 1.0π stage and migrates to deeper sea at about the 3.0π stage.

Conclusion

1. The mean of the growth index of radius versus spiral is markedly different

between the samples of *N. pompilius* from Puerto Princesa and Zamboanga. Based on the swimming velocity of *N. macromphalus*, and the distance between these two habitats we draw preliminarily conclusion that the distance of 500 km is an effective barrier for *Nautilus*.

2. The changes in some characters and the changes in growth patterns of some others concentrate at approximately 1π and 3π spiral. We preliminarily interpret these points as the stages of hatch and migration to the deeper sea, respectively.

3. Dimorphism of disruptive colouration is present in the samples of *N. pompilius* from Puerto Princesa and Zamboanga. This dimorphism does not correlate with the measured principal characters and the relative frequencies of the dimorphs are not significantly different between the Puerto Princesa and Zamboanga samples. Breeding experiments and field research is necessary to clarify the mechanism of this dimorphism and for the study of population dynamics (if the dimorphism is genetical).

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