FIRST OCCURRENCE, SYSTEMATICS, AND FUNCTIONAL MORPHOLOGY OF *NIPPONITES* (CRETACEOUS LYTOCERATINA) FROM THE AMERICAS

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ABSTRACT—*Nipponites occidentalis* n. sp. from the Turonian of southern Oregon marks the first record of *Nipponites* in the Western Hemisphere. Volume and density estimates indicate a neutral to slightly positive buoyancy for the complete animal without cameral fluid. Together with the interpretation of apertural orientation, they suggest a planktonic existence for the adult.

INTRODUCTION

THE aberrantly coiled Upper Cretaceous ammonite *Nipponites* Yabe has often been cited as the single known example of an ectocochliate cephalopod adapted to a sessile, benthonic habitat. Diener (1912, p. 78) regarded the *Nipponites* conch as a convergence with the irregular conch of the sessile Vermetid gastropods. This view was reiterated by Berry (1928), Moore, Lalicker & Fischer (1952), and Tasch (1973). Trueman (1941) also considered *Nipponites* as benthonic, but not necessarily sessile.

A single concretion from the Hornbrook Formation of southern Oregon has yielded two ammonites which we propose as a new species of *Nipponites*. This marks the first known occurrence of the genus in the Western Hemisphere. The extraordinarily complete preservation of these specimens allows inference of their mode of life through estimates of conch volume and buoyancy, based on the methods of Trueman (1941), Raup & Chamberlain (1967), and Heptonstall (1970). These estimates indicate a buoyancy regulatory ability.

SYSTEMATIC PALEONTOLOGY

Suborder LYTOCERATINA Hyatt, 1889
Family NOSTOCERATIDAE Hyatt, 1894
Genus NIPPONITES Yabe, 1904

Remarks.—Matsumoto & Muramoto (1967, p. 364) redefined the genus as follows: "A few whorls in the early growth stage form a loose helical coiling and are followed by whorls of later growth-stages which form several U-turns in different orientations around every side of the early helix. In some atypical species

the last whorl may descend downward with a slight sigmoidal twisting and then form a retroversal U-turn. The whorl is ornamented with numerous, simple ribs. The last whorl typically has flared ribs. The suture is florid and of modified lytoceratid type, with a narrowed stem of saddles."

Although more openly coiled than the previously known species of *Nipponites*, the new species is assigned to this genus because of its resemblance in coiling geometry, ornamentation, and septal nature.

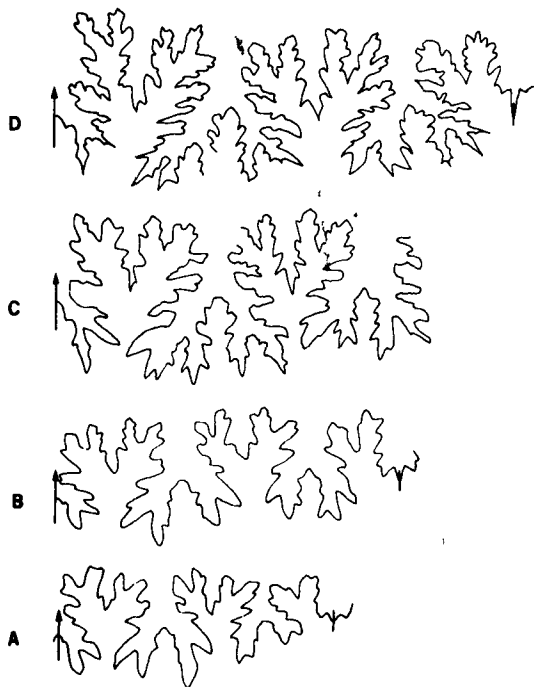### NIPPONITES OCCIDENTALIS n. sp.
Pl. 1, figs. 1–5, Text-figs. 1–3

Material.—Holotype UCLA 38180, and Paratype UCLA 38181; locality UCLA 6235 (=CIT1622):road cut on old highway 99 about two miles south of Southern Oregon College Campus, near midpoint of west boundary, sec. 24, T39S, R1E, Medford Quadrangle, Jackson County.

Diagnosis.—Shallow helicoid followed by primary gyrocone with secondary curvatures of increasing amplitude orthogonal to the plane of gyroconic coiling; ornamentation of very sharp, nonturberculate floored ribs separated by concave interspaces. Aperture marked by collared constriction. Whorl section circular throughout.

Measurements.—See Table 1.

Description.—The holotype consists of two and one-half sinusoidal secondary curvatures following the early helicoid; the earliest phragmocone less than 3 mm in diameter is missing. The aperture appears unbroken and complete. Because it is smaller in size than the
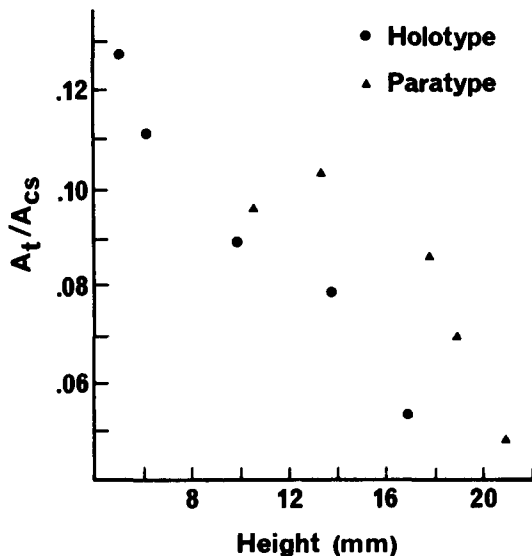
TEXT-FIG. *1*—Septal sutures of *Nipponites occidentalis*, holotype. *A*, at whorl height H = 3.1 mm; *B*, H = 4.2 mm; *C*, H = 7.1 mm; *D*, H = 10.5 mm. Bar scale represents 2 mm.

TEXT-FIG. *2*—Ratio of test area (At) to cross sectional area (A_{cs}), plotted against whorl height (H).

paratype, and shows no collared constriction or sutural approximation, the holotype is judged to have been immature. The phragmocone consists of the helocoid. Septal sutures are illustrated in Text-figure 1.

The paratype was preserved as two parts closely associated in the same concretion. One consists of the collared, apertural end of the body chamber attached to an external mold (impression) of the remainder of the body chamber and a portion of the phragmocone; the other part consists of the majority of the phragmocone, exclusive of that part below 5 mm whorl diameter. The final sinusoidal curvature is deeper than the others, and effectively describes a U-shape, with the aperture facing the phragmocone.

The shape and dimensions of the primary and secondary curvatures are similar in the two specimens, suggesting a low degree of intraspecific variability. Similarly, low variability has been observed in *N. bacchus*, Matsumoto & Muramoto and *N. mirabilis* Yabe (Matsumoto & Muramoto, 1967).

*Comparisons*.—In mode of coiling, *N. oc-*

cidentalis resembles *N. bacchus* more closely than *N. mirabilis*, the type species. *N. bacchus* has whorls which ". . . form a peculiar coiling of the *Nipponites mirabilis* type, but their U-turns are more opened than in that species. The body whorl at first descends down from the septate whorls with a sigmoidal twisting and then makes another, gentle U-turn, forming a hook-like shape for the entire shell"

TABLE *1*—Summary of data for *Nipponites occidentalis* n. sp. (All measurements in cm, all weights in g).

	Holotype	Paratype
Diameter of initial helicoid	5.86	5.90
Maximum diameter of conch	8.31	8.95
Diameter aperture	1.79	2.00
Diameter at phragmocone terminus	1.20	1.31
Total cone length	29.70	40.50
Phragmocone length	17.0	20.50
Test area/whorl area average phragmocone	0.10	0.10
body chamber	0.08	0.08
V_c	27.40	46.65
V_b/V_p	2.9	3.6
V_s	2.47	4.17
Weight test	6.47	10.94
Weight body (ρ_t 1.07 & 1.05)	19.83(19.49)	35.93(35.22)
Total weight	26.30(25.96)	46.86(46.16)
Density entire animal	0.96 (0.95)	1.00 (0.99)
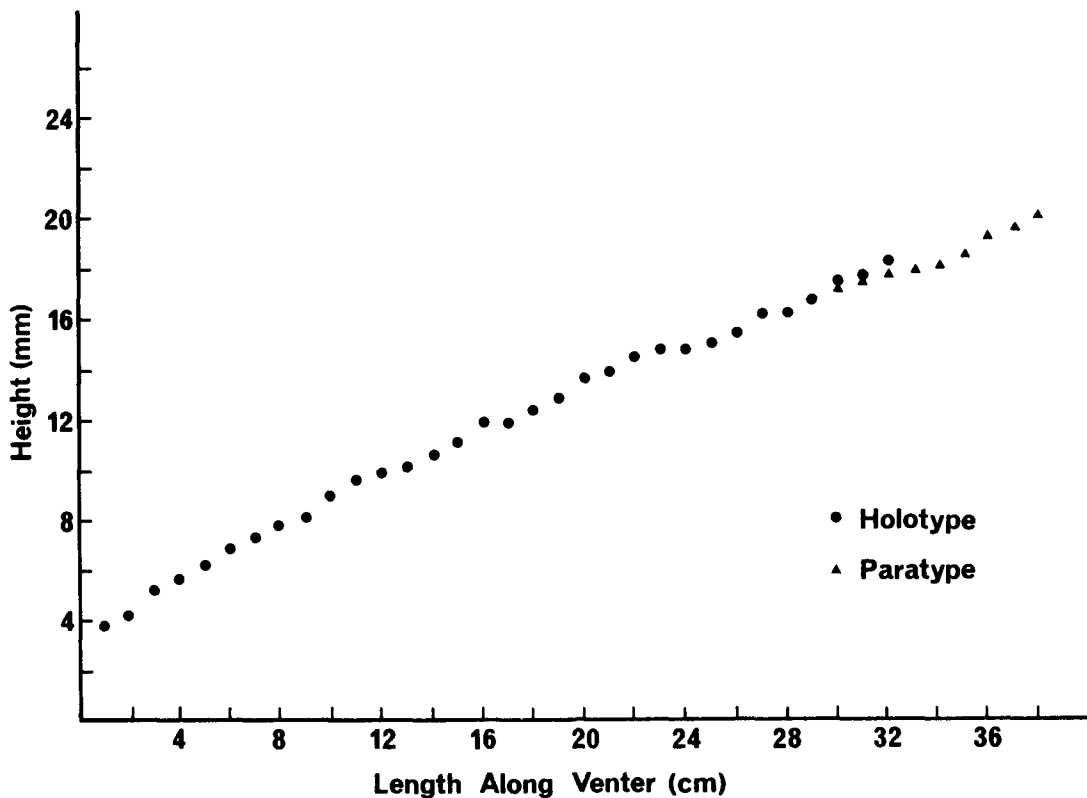
TEXT-FIG. *3*—Whorl height (H) plotted against length along venter.

(Matsumoto & Muramoto, 1967, p. 365). The initial helix, mode of coiling around that helix, and type of ribbing are features common to both species. *N. occidentalis* differs from *N. bacchus* in the presence of an apertural collar, the lack of a long, sigmoidal body chamber, and having three as opposed to four sinusoidal curvatures.

N. mirabilis differs from *N. bacchus* and *N. occidentalis* in the more closed, compact coiling of the phragmocone, and the greater number of secondary curvatures (six in the holotype).

Two other species described from the Upper Turonian of southern Oregon seem close to *N. occidentalis*. "*Bostrychoceras(?) serpiens*" Anderson shows an initial helicoid which is similar to the initial two whorls of *Nipponites*; unfortunately the only collected specimen has been lost, and no plastotypes are known. *Hyphantoceras(?) irregulare* Anderson is known from fragments of less than one whorl which, with their nontuberculate ribbing and

irregular coiling, seem more characteristic of *Nipponites* than *Hyphantoceras*. Typical *Hyphantoceras* has tuberculation, size differentiation in ribbing, and helicoid coiling in all stages except the terminal living chamber.

Age.—Turonian (upper?).

FUNCTIONAL MORPHOLOGY

Heteromorph ammonites with a U-shaped body chamber have been considered planktonic by Schmidt (1925), Berry (1928), Donovan (1964), and Packard (1972). The shape and position of the aperture in relation to the phragmocone in *N. occidentalis* and *N. bacchus* resemble the upward curving body chambers characteristic of the ancylocerids, turreted nostoceratids, and some scaphitids. The life orientation of these latter forms was inferred by Trueman (1941) to be floating so that both the shell apex and the aperture pointed upward; however, life orientation could perhaps have been altered by positioning fluid in different stages of the phrag-

mocone (Westermann, 1975). It seems likely that the aperture in *Nipponites* also pointed upward.

Although all previous writers have considered the *Nipponites* conch as a benthonic adaptation, it seems to show none of the traits which Wiedmann (1973) has correlated with bottom dwelling ammonites: degeneration and simplification of the hydrostatic apparatus (and concurrent shell thickening?), and increase in coiling variability. *Nipponites* spp. show no reduction in sutural complexity, and an apparently low degree of coiling variability.

Further information on the mode of life of *N. occidentalis* can be inferred from the results of volume and density studies following Trueman (1941), Raup & Chamberlain (1967), and Heptonstall (1970). The problem is simpler than for planispiral ammonites, because the conch approaches a cone due to its circular whorl section, mode of coiling; and constant expansion rate (Text-fig. 4). Volume and density were computed for the holotype and paratype using the following equations.

1) Volume of conch $(V_c) = \frac{1}{3}\pi\ r^2\ l\ K_1$

where l is the length and $K_1 = 1.1$ the rib correction factor. V_c = volume phragmocone (V_p) + volume body chamber (V_b).

2) Volume of test $(V_s) = V_c\ \dfrac{A_s}{A_{cs}}\ K_2$

A_s and A_{cs} are the areas of test and total in cross section; and $K_2 = 1.06$ is the correction factor for septa + siphuncle.

3) Weight of test $= V_s\rho_s$

where $\rho_s = 2.62$ in the density of test.

4) Weight of body $= \dfrac{b}{b + 1}\ (1 - a)V_c\rho_t$

where $b = V_b/V_p$, $a = V_s/V_c$, and $\rho_t = (1.05$ to) 1.07 is tissue density.

5) Density of animal $= \dfrac{\text{weight test + body}}{V_c}$

The value for the rib correction factor is based on camera lucida drawings of longitudinal sec-

tions showing the additional area above that of the interspace to be approximately 10 percent. The length value for the conch is the mean of length measurements along the venter, dorsum, and right and left sides of the conch. Test volume is approximated by the product of total conch volume and the average ratios of test to total area in cross section (Trueman, 1941). For greater accuracy these ratios were separately derived from shell thickness data for the phragmocone and body chamber, because this value markedly decreases with ontogeny (Trueman, 1941; Westermann, 1971; and Text-fig. 2). The values used here represent upper limits, and take into account the thickened rib crests. The length of missing phragmocone was estimated at 30 mm for the holotype, and 50 mm for the paratype; both estimates were based on extrapolations from Text-figure 3. Because of the small volume of the initial phragmocone relative to the remainder of the conch, *i.e.*, 0.6 percent and 1.5 percent respectively, the possible error is negligible.

Although the positions of septal sutures were marked on fragments of shell material at several positions in the mold of the paratype, the exact length of the phragmocone in this specimen is not known. In the calculations the terminus of the phragmocone was considered to be marked by the last visible septum within the mold. Because it is possible that the phragmocone was slightly longer, the buoyancy estimate will be conservative.

The conservative estimates (Table 1) result in density values of 0.96 and 1.0, respectively, for holotype and paratype, *i.e.*, slightly less than the density of seawater (1.026). Assuming a lower value for tissue density (1.05 instead of 1.07) lowers the estimates only slightly (0.95 and 0.99). Major assumptions underlying these calculations are that the density of the ammonite tissue and test were close to that of recent *Nautilus* (1.05–1.07 and 2.62, respectively, and that the tissues completely filled the body chamber when withdrawn. Although

only approximations, the results suggest a buoyancy regulatory capability by inference with density values for *Nautilus* which, without cameral liquid, are also slightly lower than seawater (≈ 0.99; cf. Denton & Gilpin-Brown, 1973). The difference of our estimates is almost certainly within the operating error.

The depth limits of recent and ancient cephalopods have been discussed by Westermann (1971) and Denton & Gilpin-Brown (1973). Westermann used a measure of siphuncular strength for estimating implosion depths. The siphuncular radius (r) and thickness (h) of ammonites were used to derive an estimator of siphuncular strength with the expression ($^h/_r \times 100$); larger values indicate stronger siphuncles, and hence the ability to withstand greater ambient pressure with depth. The *Nautilus* siphuncle has a strength value of about 12 and withstands internal pressure equivalent to a depth of about 700 m. Westermann showed Ammonitina to have values ranging from 2–9, and most Phylloceratina and Lytoceratina from 12–19. By comparison, r and h for *N. occidentalis* are 300μ (r) and 30μ (h) at 7.5 mm whorl height and 450μ and 40μ at 12.7 mm whorl height. The corresponding ($^h/_r \times 100$) values of 10 and 9 are between those for *Nautilus* and Ammonitina. A depth limit of around 500–600 m is indicated

In summary, because *Nipponites occidentalis* appeared to be about neutrally buoyant, and because the shell shows no sign of either adaptation to a benthonic mode of life (shell thickening, reductions in sutural complexity) or adaptation to a vagile mode of life (*i.e.*, conch streamlining), we infer it to have been adapted to a passive planktonic mode of life. Packard (1972) viewed the heteromorph lytoceratine ammonites as forms which radiated into the mesopelagic regions from the shallow shelf in response to active competition from the rapidly expanding Cretaceous teleost stocks. He further suggested that the heteromorphs occupied the same niche as the living cranchid squids. These forms are passive, balloon-like floaters; many feed on copepods and euphasids, and some come to the surface at night (Clarke, 1966). In such a niche selective pressure for conch streamlining and swimming ability would probably be low. During the Turonian, inhabitants may have been the world-wide scaphitids and *Hyphan-*

toceras, and Indo-pacific *Madagascarites* and *Nipponites*.

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