# Descriptions of Nautilus pompilius Linnaeus, 1758 from the type area, Ambon

*by* Z G

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# Descriptions of *Nautilus pompilius* Linnaeus, 1758 from the type area, Ambon, Molucca Islands, and from Sumbawa - Lombok Islands, Indonesia

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**Abstract:** The taxonomic history of *Nautilus pompilius* Linnaeus, 1758, the most widely distributed species of *Nautilus* Linnaeus, 1758, is complex, mostly owing to the antiquity of the earliest description by the naturalist Rumphius (Rumpf) in 1705. His account of its habits and illustrations of soft anatomy of specimens from Ambon, Molucca Islands, Indonesia were cited by Linnaeus in his description of *N. pompilius*. Nevertheless, there is almost no information on *Nautilus* in Indonesia. Live-caught animals ($n$ = 44) from 150–400m depth off Ambon provide the first morphologic and genetic details on *Nautilus pompilius* from the type region, including a recently proposed neotype for the type species. An additional sample ($n$ = 62) obtained from the Sumbawa-Lombok Islands area, Indonesia, 1,500km to the southeast appears identical to those from Ambon. These populations have the largest known mature shells (mean ~198mm diameter, ~1,160g shell plus body weight) of any of the numerous Indo-Pacific occurrences of *Nautilus pompilius s.l.* presently assigned to this species. Aside from size, few major phenotypic aspects differ from other populations of the species throughout its broad Indo-Pacific range. Data from two mitochondrial DNA gene regions identified a strongly supported clade comprising Ambon, Sumbawa, and Philippines *N. pompilius s.s.* These new data provide a baseline for evaluating genetic, phenotypic and geographic variation in the broadly distributed species *N. pompilius s.l.*, as well as for establishing taxonomic relationships in populations of living *Nautilus*, including *N. pompilius pompilius* Linnaeus, 1758.

**Key words:** proposed neotype population, Indonesian *Nautilus*, chambered nautilus, Cephalopoda, Nautiloidea

The earliest illustration and description of the soft anatomy of *Nautilus pompilius* Linnaeus, 1758 was published in *D'Amboinsche rariteitkamer* (The Ambonese Curiosity Cabinet) in 1705 by Georgius Everhardus Rumphius (Rumpf; 1627-1702). The publication includes one illustration of *Nautilus* soft parts and two of shells (Rumphius 1705, book 2, Plate XVII; see Davis 1987, Beekman 1999). This account contains remarkably accurate descriptions of the *Nautilus* shell as well as soft anatomy, with details of the eye, siphon, siphuncle, jaws, and tentacles. There were descriptions of the use of *Nautilus* for food, the shell for artifacts, and the habits of the animal. Rumphius' comments on the distribution of *Nautilus* follow:

> "One will find them in all the seas of the Moluccan Islands, as well as around the thousand Islands before *Batavia* (Jakarta) and *Java*, but usually as only the empty shell, because the animal is seldom found, unless it crawls into the weels (traps)." (1705, *in* Beekman 1999 transl., p. 89).

Linnaeus (1758) cited Rumphius' 1705 illustrations of *Nautilus* in the binomial naming and diagnosis of the type species, *N. pompilius*, but there is uncertainty regarding the whereabouts of the actual specimens. This has left the exact typology of this iconic taxon clouded. Nikolaeva (2015) recently published a detailed account of the "type series" of specimens of *Nautilus pompilius* according to ICZN (1999) rules. These would include: "…all the specimens included by the author (Linnaeus) in the new nominal taxon at the time of description…" including, "All specimens figured by pre-Linnaean authors indicated by reference by Linnaeus (1758)…" She concluded that, "…none of the surviving specimens has been formally designated as a lectotype…" (Nikolaeva 2015, pp. 55-56.)

The first post-Rumphius anatomy of *Nautilus* was the classic account by Richard Owen (1832), based on a single specimen identified as *N. pompilius*, obtained from the New Hebrides (Vanuatu). The shell had been broken and lost during recovery, except for a small fragment clearly shown adhering to the "shell-muscle" (Owen 1832, Pl. 1, Fig. h), but not enough to clearly ascertain the shell's current species affinity. Unquestionably, the most important effort to study *Nautilus* was the five-year expedition of Arthur Willey at the turn of the 20th century (Willey 1902), which spanned parts of New Guinea as well as the New Britain, New Ireland, Solomon and Loyalty archipelagoes. He provided excellent details of the soft parts of *N. pompilius*, *N. macromphalus* Sowerby 1849, and even of a surface-stranded necrotic specimen of *Allonautilus scrobiculatus* (Lightfoot 1786). At about the same time, an exhaustive anatomy of *N. pompilius* from the south central Philippines was published by Griffin (1900). Notably, no one has attempted to match the three excellent anatomical accounts cited above. The primary source of *Nautilus* shells for at least the past century has been the Philippines, from whence tens of thousands of shells of *N. pompilius s.l.* have been exported annually, to the point that conservation alarm has been sounded over the effects of overfishing in the region (Del Norte-Campos 2005, Dunstan *et al.* 2010, 2011, De Angelis 2012).

The long history of *Nautilus* investigations has involved multiple accounts of distantly isolated regional populations and as many as six to eleven species. While uncertainty persists over the exact definition of the most widely distributed type species, it seems clear that the taxonomic concept should be anchored to populations in the Molucca Islands, Indonesia; more specifically, the region around Ambon, from whence Rumphius first described the living animal. However, almost nothing has been added to knowledge of the animal in any Indonesian waters since Rumpf's account more than three centuries ago. In order to fill in the Indonesian gap in the natural history of *Nautilus,* an effort was undertaken in 1987 (W.B. Saunders, L.C. Hastie) to trap living *N. pompilius* in the Ambon, Molucca Is. (Moluku) area in conjunction with Operation Raleigh (U.K.) activities (http://operationraleighseram.com/about-2/operationraleigh10f/). This resulted in obtaining the first documented living *N. pompilius* Linnaeus, 1758 in the area from whence the animal had first been described almost three centuries earlier (Figs. 1A, 2A-2E, 3A-3F). In 2011, a second population of *Nautilus pompilius* was trapped in the southern Indonesian area in the vicinity of Sumbawa Island (Fig. 1B) led by R.H. Mapes. Here, we present phenotypic details along with genetic data from these two populations. Our goal is to establish a baseline of characteristics of *N. pompilius s.s.* from the region of its original description, with comparisons to a second population, separated by ~1,500km map distance. It should be noted that a proposal has recently been published by the ICZN (Nikolaeva *et al.* 2015), formally requesting designation of a neotype for *Nautilus pompilius*, based on some of the material obtained in Ambon, which is being described here for the first time.

## MATERIALS AND METHODS

### Trapping methods and yields

Rectangular traps were constructed of rebar frames covered with wire mesh. The traps contained funnel entrances with bait (fish or chicken) placed at the center of the trap. The trap site (Fig. 1A) is located ~6 km southwest of Ambon City, Ambon Island (Maluku Province), just off the small coastal village of Eri. Traps were set overnight on the bottom at depths of ~150 - 400 m, attached to surface buoys, before being pulled to the surface by hand. Forty-four *Nautilus pompilius* were obtained from five traps (Table 1), and their yields included the following:

1. ~150 m depth, 13 *Nautilus pompilius*, 12 caridean shrimps (*Plesionika longirostris?*, one moray eel (*Gymnothorax* sp.), one conger eel (*Conger* sp.), along with three small teleosts (*Polymixia* sp.?), one unidentified opisthobranch, one lobster, and one hermit crab.
2. ~150 m depth, 12 *N. pompilius*, 2 *Conger* sp., 3 *Gymnothorax* sp., 3 *Polymixia* sp.?, 3 caridean shrimps.
3. ~175 m depth, 16 *N. pompilius*, 3 *Conger* sp., 11 caridean shrimps.
4. ~300 m depth, 3 *N. pompilius*, 150 caridean shrimps (*Heterocarpus ensifer* and *H. gibbosus*), one shark (*Squalus* sp.), one *Conger* sp., one unidentified eel.
5. ~400 m depth, 2 *Squalus* sp., 41 *H. ensifer* and *H. gibbosus*.

Following trap retrieval, specimens were weighed, measured, sexed, judged as to maturity, and photographed. Samples of adductor muscle, mantle, or tentacle were obtained from each specimen and frozen. Shells and/or soft-parts were deposited with the Indonesian Institute of Sciences (LIPI), Institute of Oceanography, Ambon, and at the Biology Laboratory, University of Pattimura, Poka Campus, Ambon. In the U.S.A., shells and tissue samples from Ambon are deposited in the Smithsonian National Museum of Natural History (USNM) collections, Washington DC, and at the American Museum of Natural History (AMNH), New York City.

The Sumbawa–Lombok Indonesia locations that yielded *Nautilus* (Fig. 1B) are near Saleh Bay on Sumbawa Island, west side of Moyo Island, and near the Lombok–Sumbawa pass. A total of 62 *Nautilus pompilius* were recovered over 16 days in traps set at 200-250m depth (Table 2). Samples of material from the Sumbawa region, Indonesia were deposited at Hasanuddin University, Department of Fisheries in Makassar, South Sulawesi Island. The Indonesian shells cannot leave the country because *Nautilus* is protected. Samples of tissue were preserved in 95% ethanol and vouchered in the Ohio University Zoology Collections (OUZC).

DNA was purified from either mantle or tentacle tissue using a DNeasy Kit (Qiagen, Inc.). A fragment of the Cytochrome Oxidase subunit I (COI) was amplified by the polymerase chain reaction (PCR) using the HCO and LCO

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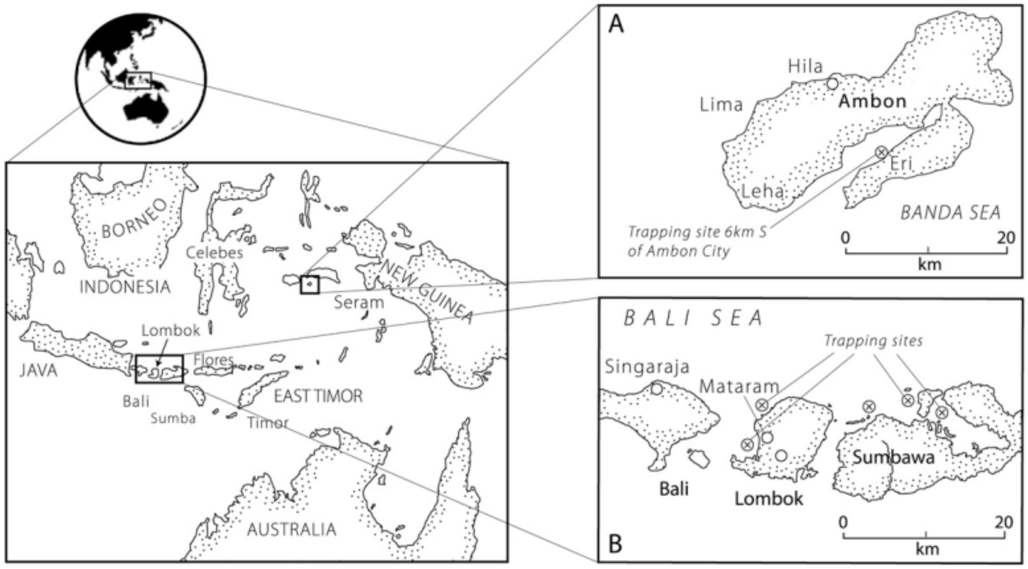


**Figure 1.** Map showing locations where *Nautilus pompilius pompilius* was live-caught in 1987 and 2011. A, illustrated specimens were trapped at ~150–300m depth off village of Eri, 6km S of Ambon City, Ambon (WBS, LCH; 1987). Ambon, (Molucca Islands), should be regarded as the type area for the genus, species and subspecies (See Beekman 1999 and Nikolaeva *et al.* 2015 for historical accounts.). B, a second population of Indonesian *Nautilus pompilius* was live-caught in 2011 in the Sumbawa - Lombok regions at ~200-250m depth (RHM).

primers (Folmer *et al.* 1994). A fragment of the 16S rDNA gene was amplified using the 16sa and 16sb primers (Palumbi 1996). Twenty µl reaction contained 2.0 µl of DNA, 1X PCR buffer (GenScript, Inc.), 0.2 mM each dNTP, 0.5 mM each primer, and 1.0 U Taq polymerase (Genscript, Inc.). PCR conditions were as follows: 5 min at 94°C followed by 40 cycles of 94°C for 30 sec, 50°C for 30 sec and 72°C for 30 sec, with a final extension step of 7 min at 72°C in an MJ Research PTC-200 thermal cycler. Amplified products were purified using a QuickClean 2M PCR Purification kit (Genscript, Inc.). Approximately 10-30ng of each purified product was sequenced with a 3730 DNA Analyzer (Applied Biosystems). Additional sequences of *Nautilus pompilius* (Ambon, Vanuatu, Carter Reef [GBR], Philippines) and *N. belauensis* Saunders, 1981 (Palau) were obtained from Genbank (Table 3, Fig. 4). DNA sequences were aligned using CLUSTALX v1.81 (Jeanmougin *et al.* 1998).

The DNA data were evaluated for fit to 24 evolutionary models in MEGA5 (Tamura *et al.* 2011). Based on Bayesian Information Criteria the best fit model of nucleotide substitution for both gene regions was the Tamura 3-parameter model (T92+G; Tamura 1992). Data from the two gene regions were combined. Phylogenetic relationships among haplotypes were estimated using Maximum-Likelihood (ML). The inferred phylogeny was tested for robustness using 1000 bootstrap replicates. Trees were rooted to COI and 16S sequences for *Nautilus macromphalus* (GQ280226, GQ280160), and *Allonautilus scrobiculatus* (GQ 280250, GQ280184).

## RESULTS AND DISCUSSION

### Shell size, maturity and sex ratios

The Ambon *Nautilus pompilius* population provides valuable data on the demographic characteristics in its type area. Mature shell sizes ($n$ = 44) range from 183.2 to 207.0 mm in diameter, with a mean = 194.6 mm (SD = 5.7) (Table 1). Total weight (shell plus body) range from 990 g (a mature female) to 1,330 g with a mean = 1,160 g (SD = 99.6). The Sumbawa specimens ($n$ = 60 [for comparison, two immature specimens [<132.5 mm] are excluded) range from 150.5 to 218.2 mm in diameter with a mean = 199.8 mm (SD = 11.5) (Table 2).

Both of the Indonesian population samples described here are highly skewed in the proportion of mature animals and sex ratios: 97.6% male, 95% mature (Ambon) and 95% male and 90% mature (Sumbawa). Sexual dimorphism in mature shells is prominent. The average shell size of the combined Ambon and Sumbawa specimens ($n$ = 104), is 197.6 mm

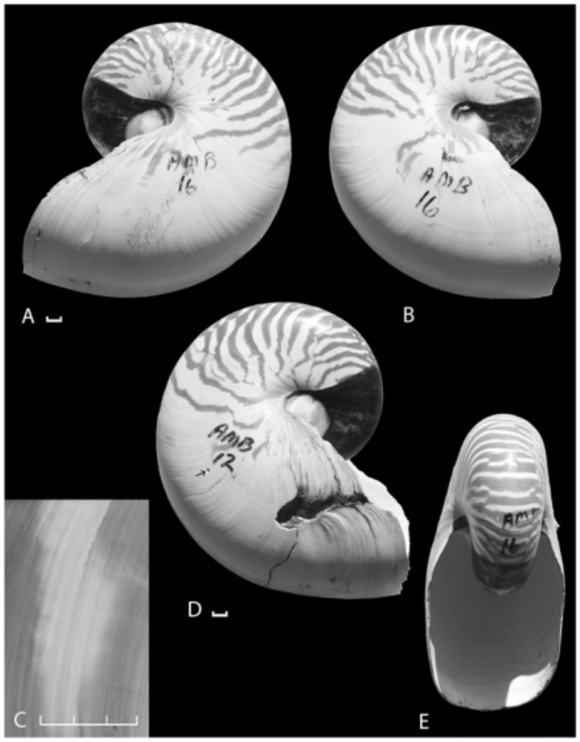


**Figure 2.** *Nautilus pompilius pompilius* from Ambon, Molucca Islands Indonesia. (For data on individuals see Table 1). A, B, E, proposed neotype (USNM 816877); (See Nikolaeva *et al.* 2015) left, right and apertural views of shell of mature male (soft parts preserved in alcohol). Inked field number AMB 16 refers to number in Table 1. Scale bar = 10.0 mm. C, magnified view of topotype, (AMNH 79686, AMB 5) showing faint, finely-developed, longitudinal lirae crossing the coarser growth lines in front of the edge of the black layer on the ventrolateral part of the shell; scale bar = 3.0 mm. D, right lateral view of topotype AMNH 79685 (AMB 12) showing major repaired injury on the shell flank, with distorted post-trauma growth lines and associated black material indicating that the animal survived injury to the mantle. Arrow points to *Octopus* boring shown in Fig. 3D. Scale bar = 10.0 mm.

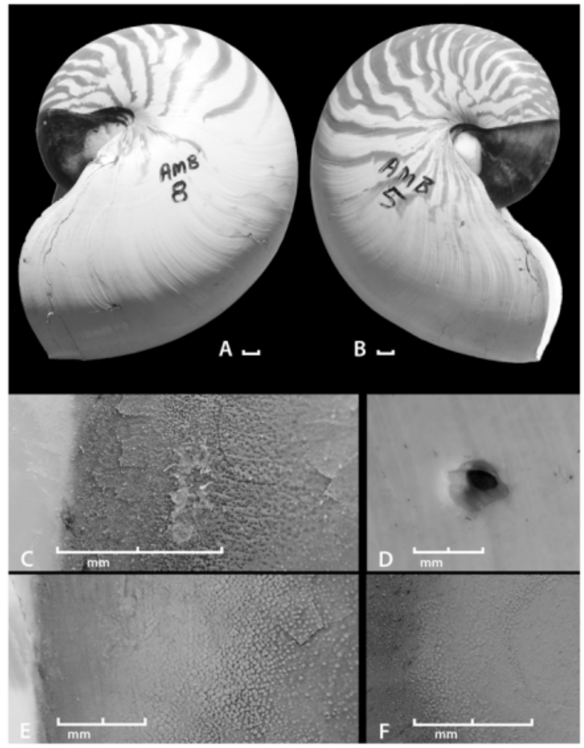


**Figure 3.** *Nautilus pompilius pompilius* topotypes from Ambon, Molucca Islands, Indonesia. (For data on individuals see Table 1). A, B, left and right lateral views of topotypes AMNH 79696 (AMB 8) and AMNH 79686 (AMB 5) showing variation in density of color striping. C, E, close up views of topotypes AMNH 79686 (AMB 5), D, octopod boring (indicated by arrow in Fig. 2D; topotype, AMNH 79685 (AMB 12). and F, 79685 (AMB 12) showing variation in the terminal edge of the black layer of the wrinkle layer. Note that these pustular structures only develop on mature shells after terminal shell growth is completed. Shells in C, E, F are lightly coated with ammonium chloride. Scale bars for. A, B = 10.0 mm.

in diameter; Tables 1, 2). Although this is the largest mean population size recorded for *Nautilus pompilius s.l.*, even larger specimens (~220 mm dia.) have been reported from Western Australia, (Saunders 1987b, Figs. 3A, 4), but their species identification is uncertain, as some seem referable to a questionable species *N. repertus* Iredale, 1944). The Indonesian *Nautilus* are closest in size to *N. belauensis*, known only from Palau, which average 204 mm and average weight of 1,308g ($n$ = 375; Saunders and Spinosa 1978). By comparison, *N. pompilius* from Tañon Strait, Philippines average 165mm in diameter, with an average shell plus body weight ~850g ($n$ = 234; 1979 *Alpha Helix* data; Saunders, *in litt.*). Isolated populations in Papua New Guinea average 144 mm (Lae) to 169 mm in diameter (New Ireland; Saunders 1987a, Fig. 4). By far the smallest mature shells (~114mm dia.) are those from Tubbataha Reef, Sulu Sea, Palawan, named *N. pompilius suluensis* by Habe and Okutani (1988). (These are enigmatic forms, about which little is known, and they appear to be endemic to one locality within the geographic range of Philippine *N. pompilius*.)

All *Nautilus* and *Allonautilus* populations studied to date show well-differentiated sexual dimorphism (with some overlap) in late growth stages. Mature females tend to be smaller, with a more compressed shell aperture (Willey 1902,

**Table 1.** Morphologic data from specimens of *Nautilus pompilius pompilius* Linnaeus, 1758, trapped at 150-400 m depth, adjacent to the village of Eri, Ambon Island, Indonesia, July, 1987. $D_m$, maximum shell diameter; $W_m$, maximum aperture width; $W_s$, aperture width beneath ocular sinus; Mature, maturity, judged as fully mature (blackened, thickened aperture with full growth achieved); MBI, barely mature (with almost full growth, final aperture contour present, but shell aperture not fully thickened or blackened); I, immature (growth incomplete); Borings, number of *Octopus* borings; Epizoans including barnacles *Balanus* (Bal), *Lepas* (Lep), bryozoans (Bry) and serpulids (Serp). All measurements are in millimeters.

| Specimen # | $D_m$ | $W_m$ | $W_s$ | $W_t$ | Sex | Mature | Borings | Epizoans |
|---|---|---|---|---|---|---|---|---|
| 1 | 192.8 | 92.3 | 88.4 | 1150 | M | M | - | None |
| 2 | 196.2 | 97.0 | 91.2 | 1295 | M | M | - | Serp, Lep, Bal, Bry |
| 3 | 189.1 | 89.4 | 86.8 | 1075 | M | M | - | Bry |
| 4 | 203.7 | 98.9 | 94.9 | 1295 | M | M | - | None |
| 5 | 192.5 | 90.3 | 85.0 | 1090 | M | M | - | Bry |
| 6 | 193.5 | 93.7 | 89.5 | 1190 | M | M | - | 1 Lep |
| 7 | 197.2 | 98.9 | 95.5 | 1230 | M | M | - | Bry |
| 8 | 201.2 | 100.0 | 92.3 | 1340 | M | M | - | Bry, Serp,Lep |
| 9 | 190.0 | 91.8 | 88.2 | 1120 | M | M | - | Lep |
| 10 | 196.9 | 93.2 | 89.5 | 1225 | M | M | - | Lep |
| 11 | 190.5 | 86.7 | 76.3 | 990 | F | M | - | Lep |
| 12 | 200.0 | 99.2 | 95.2 | 1330 | M | MBI | 3 | Bry |
| 13 | 186.9 | 94.7 | 88.7 | 1110 | M | M | - | Bal, Lep |
| 14 | 198.2 | 95.5 | 92.6 | 1250 | M | M | 1 | Lep |
| 15 | 193.9 | 89.6 | 84.7 | 1290 | M | M | - | None |
| 16 | 199.2 | 92.8 | 88.5 | 1275 | M | M | - | Lep |
| 17 | 196.6 | 94.0 | 88.9 | 1140 | M | M | - | None |
| 18 | 191.9 | 90.3 | 88.7 | 1100 | M | M | - | None |
| 19 | 197.5 | 92.2 | 88.2 | 1200 | M | M | - | None |
| 20 | 207.0 | 90.7 | 89.9 | 1185 | M | M | - | Serp |
| 21 | 184.8 | 95.0 | 94.4 | 975 | M | MBI | - | None |
| 22 | 201.6 | 99.6 | 93.8 | 1290 | M | M | - | None |
| 23 | 202.0 | 98.0 | 93.0 | 1210 | M | M | - | Lep |
| 24 | 199.2 | 95.8 | 90.9 | 1145 | M | M | - | None |
| 25 | 195.0 | 89.8 | 84.0 | 1100 | M | M | - | None |
| 26 | 197.5 | 94.8 | 92.9 | 1210 | M | M | - | Lep |
| 27 | 191.6 | 96.2 | 92.6 | 1170 | M | M | - | Lep |
| 28 | 198.8 | 92.8 | 90.0 | 1200 | M | MBI | - | Serps |
| 29 | 196.8 | 98.2 | 93.6 | 1185 | M | M | - | None |
| 30 | 183.2 | 96.2 | 91.3 | 1025 | M | M | - | None |
| 31 | 193.2 | 92.2 | 87.2 | 1120 | M | M | - | Leps |
| 32 | 187.5 | 90.8 | 89.6 | 1075 | M | M | - | None |
| 33 | 193.6 | 92.0 | 88.0 | 1050 | M | M | - | None |
| 34 | 196.3 | 92.3 | 86.2 | 1130 | M | M | - | None |
| 35 | 187.8 | 89.6 | 82.2 | 950 | M | M | - | Serp. Lep |
| 36 | 201.8 | 92.9 | 89.4 | 1190 | M | M | - | Serp |
| 37 | 192.0 | 93.2 | 91.6 | 1190 | M | M | - | Serp |
| 38 | 197.4 | 98.0 | 92.6 | 1195 | M | M | - | Lep, Bry |
| 39 | 191.7 | 91.7 | 88.4 | 1115 | M | M | - | None |
| 40 | 189.2 | 92.0 | 86.0 | 1190 | M | M | - | Leps |
| 41 | 183.2 | 92.0 | 88.6 | 1016 | M | M | - | Serp |
| 42. | 184.5 | 91.4 | 86.8 | 1000 | M | M | - | Lep |
| 43 | 193.9 | 94.7 | 89.9 | 1100 | M | M | - | Serp |
| 44 | 202.8 | 97.3 | 92.4 | 1325 | M | M | - | None |

Saunders and Spinosa 1978). *Nautilus* and *Allonautilus* demographics are dominated by males and by mature animals (Willey 1902, Haven 1977, Saunders and Spinosa 1978, Saunders and Ward 1987a, Collins and Ward 1987). More specifically, recent trapping data compilations have shown that previously undisturbed (*i.e.*, unfished) *Nautilus* populations

**Table 2.** Morphologic data from specimens of *Nautilus pompilius pompilius* Linnaeus, 1758, trapped at 200–225 m depth on the west side of Salah Bay, the west side of Moro Island and at the northwest corner of Sumbawa Island, Indonesia during July - August, 2010. Data format and abbreviations are the same as in Table 1. (Note: Sumbawa animal weights and counts of shell injuries are not available.)

| Specimen # | $D_m$ | $W_m$ | $W_s$ | $W_t$ | Sex | Mature | Borings | Epizoans |
|---|---|---|---|---|---|---|---|---|
| 1 | 199.5 | 99.0 | 91.8 | NT | male | M | - | None |
| 2 | 194.5 | 96.0 | 93.0 | NT | male | M | - | None |
| 3 | 210.2 | 107.8 | 95.4 | NT | male | M | - | None |
| 4 | 214.6 | 101.0 | 99.1 | NT | male | M | - | Bry |
| 5 | 210.0 | 97.5 | 97.0 | NT | male | M | - | None |
| 6 | 201.8 | 98.1 | 96.9 | NT | male | M | - | Serp |
| 7 | 203.5 | 98.1 | 95.5 | NT | male | M | - | None |
| 8 | 206.9 | 99.9 | 97.0 | NT | male | M | - | None |
| 9 | 188.0 | 88.2 | 88.2 | NT | female | M | - | Bry, Serp |
| 10 | 208.8 | 100.0 | 99.1 | NT | male | M | - | None |
| 11 | 212.5 | 100.9 | 96.2 | NT | male | M | - | Serp |
| 12 | 193.1 | 96.8 | 95.0 | NT | male | I | - | None |
| 13 | 199.2 | 94.2 | 88.9 | NT | male | M | - | None |
| 14 | 215.8 | 100.2 | 99.2 | NT | male | M | - | None |
| 15 | 188.2 | 95.1 | 91.2 | NT | male | M | - | None |
| 16 | 188.4 | 90.1 | 90.1 | NT | male | M | - | None |
| 17 | 211.9 | 98.7 | 95.8 | NT | male | M | - | Bry, Serp |
| 18 | 197.5 | 95.1 | 92.4 | NT | male | M | - | |
| 19 | 206.7 | 97.1 | 96.1 | NT | male | M | - | Bry, Serp |
| 20 | 197.5 | 95.2 | 93.0 | NT | male | M | - | None |
| 21 | 197.5 | 94.9 | 91.0 | NT | female | M | - | None |
| 22 | 194.1 | 96.2 | 94.1 | NT | male | M | - | None |
| 23 | 150.5 | 75.6 | 75.6 | NT | female | I | - | None |
| 24 | 202.0 | 90.1 | 81.0 | NT | female | M | - | Serp |
| 25 | 188.0 | 83.2 | 83.2 | NT | I | I | - | None |
| 26 | 132.5 | 66.6 | 66.6 | NT | I | I | - | None |
| 27 | 195.9 | 95.9 | 90.9 | NT | male | M | - | None |
| 28 | 185.8 | 90.2 | 90.2 | NT | male | M | - | Serp |
| 29 | 202.1 | 92 | 87.1 | NT | male | M | 2 | |
| 30 | 201.2 | 90.6 | 89.6 | NT | male | M | - | Serp |
| 31 | 198.5 | 95.8 | 94 | NT | male | M | 1 | |
| 32 | 196.5 | 95 | 93.7 | NT | male | M | - | None |
| 33 | 206.2 | 98.9 | 93.4 | NT | male | M | - | None |
| 34 | 210.0 | 97.5 | 99.4 | NT | male | M | - | Bry & Serp |
| 35 | 208.8 | 91.3 | 88.1 | NT | male | M | 1 | None |
| 36 | 202.1 | 94.5 | 92.8 | NT | male | M | 2 | Serp |
| 37 | 192.7 | 97.9 | 94.1 | NT | male | M | 1 | Bry & Serp |
| 38 | 197.3 | 91.5 | 89.7 | NT | male | M | - | None |
| 39 | 197.8 | 97.8 | 82.1 | NT | male | M | - | None |
| 40 | 205.3 | 95.8 | 94.0 | NT | male | M | - | None |
| 41 | 200.7 | 94.8 | 92.3 | NT | male | M | - | Serp |
| 42 | 98.2 | 93.6 | 91.0 | NT | male | M | - | Serp |
| 43 | 204.2 | 95.6 | 94.3 | NT | male | M | - | Serp |
| 44 | 216.9 | 104.2 | 100.1 | NT | male | M | - | None |
| 45 | 209.3 | 99.8 | 97.0 | NT | male | M | - | None |
| 46 | 186.0 | 97.7 | 93.9 | NT | male | M | - | None |
| 47 | 197.5 | 99.6 | 95.6 | NT | male | M | - | Bry & Serp |
| 48 | 211.1 | 160.2 | 96.8 | NT | male | M | - | Serp |
| 49 | 207.2 | 96.1 | broken | NT | male | M | - | Bry & Serp |
| 50 | 203.9 | 95.5 | 91.8 | NT | male | M | 1 | None |
| 51 | 210.3 | 105.3 | 101.5 | NT | male | M | - | Serp & Bry |

**Table 2.** (Continued)

| Specimen # | $D_m$ | $W_m$ | $W_s$ | $W_t$ | Sex | Mature | Borings | Epizoans |
|---|---|---|---|---|---|---|---|---|
| 52 | 218.2 | 106.8 | 103.5 | NT | male | I | - | None |
| 53 | 200.5 | 97.2 | 94.8 | NT | male | M | - | Serp |
| 54 | 204.8 | 94.1 | 90.7 | NT | male | M | - | Serp |
| 55 | 186.9 | 94.1 | 90.3 | NT | female | M | - | None |
| 56 | 202.1 | 94.0 | 92.2 | NT | male | M | 2 | Serp |
| 57 | 212.2 | 101.8 | 99.5 | NT | male | M | - | None |
| 58 | 175.6 | 92.6 | 92.6 | NT | male | IM | - | None |
| 59 | 201.0 | 87.9 | 84.0 | NT | male | M | - | None |
| 60 | 187.3 | 91.9 | 90.2 | NT | female | M | - | Serp |
| 61 | 193.3 | 90.5 | 88.7 | NT | male | M | - | None |
| 62 | 177.1 | 90.2 | 84.7 | NT | male | M | - | None |

typically comprise ~75% males and ~74% mature animals (data from16 different isolated populations, total $n$ = 2,669; Saunders and Ward in review). The large combined proportions of males (~96%) and mature animals (~93%) in the two isolated Indonesian populations of Ambon and Sumbwa strongly indicate that the populations have not been disturbed by fishing efforts. (Although *N. pompilius* was added to Indonesia's protected species list in 1987, widespread trade in the shells has been reported in Java and Bali by Nijman *et al.* 2015). By contrast, heavily fished populations in the central Philippines in 1979 averaged ~28% males and ~31% mature animals ($n$ = 453; Saunders and Ward in review). This, along with crashes in regional *Nautilus* fisheries elsewhere in the region, has raised the issue of whether *Nautilus* and *Allonautilus* should be protected as threatened or endangered, through listing by CITES (Convention on International Trade in Endangered Species (Dunstan 2011, De Angelis 2012, Barord *et al.* 2014). These concerns give added significance to protecting the Ambon population from commercial exploitation.

**Injuries and predation**

All shells from Ambon and Sumbawa-Lombok have repaired minor shell damage, and 17 (39%) of the Ambon specimens showed significant repaired shell or mantle injuries (*e.g.*, Fig. 2D). Less obvious evidence of predation is present as octopod drill holes in the body chambers (Figs. 2D, 3D), which were present in 11% of the Sumbawa and 4.5% of the Ambon shells (Tables 1, 2). Repaired injuries reflect unsuccessful, or sub-lethal, predatory efforts, and they have been recorded in all live-caught *Nautilus* populations. Most of the major repaired injuries were probably due to predation by sharks and teleosts and by intraspecific conflicts (Saunders *et al.* 1987, Mapes and Chaffin 2003). Boreholes representing unsuccessful *Octopus* predation were present in two (4.5%) of the live-caught Ambon specimens and in seven (11.3%) of those from Sumbawa (= 9/106 [8.5%]). These figures are similar to the largest comparable data base available, from Palau (1977–1982), where 211 of 2,720 (7.8%) of live caught shells had been bored (Saunders *et al.* 1987). No data are available for drifted shells from either Palau or Indonesia, but figures from drift shells obtained in Manus, PNG, indicated ~50% mortality ($n$ = 1,532) from *Octopus* predation in shells of *Nautilus pompilius* and *Allonautilus scrobiculatus* (Saunders *et al.* 1987, 1991). Tucker and Mapes (1978) reported that 28.7 % of 150 purchased *Nautilus* shells, probably from the Philippines, had *Octopus* borings. (Many of these shells were probably live-caught, which might explain the lower frequency of *Octopus* borings than in the Manus population).

**Shell Sculpture**

A delicate, almost imperceptible pattern of closely spaced scallops, or crenulations developed along the course of the growth lines is restricted to the ventral-ventrolateral and umbilical portions of the Indonesian shells (Fig. 2C). A pattern of longitudinal, or lirate, shell sculpture has long been known to occur to varying degrees in some living nautiloid populations; indeed, this feature is reflected in the specific name of *Allonautilus scrobiculatus* (Lightfoot, 1786) where it is most strongly developed. It is so strongly expressed in *Nautilus belauensis* that it was cited as a hallmark of that taxon (Saunders, 1981, Fig. 5). Though the overall impression of this type of sculpture is one of concentric lirae, when examined closely it is seen to actually consist of delicate scallops of the growth lines. This sculptural pattern is variously developed in isolated populations, ranging from being absent in some (*e.g., N. stenomphalus* [GBR], and in most Philippine shells).

**Shell Coloration**

Shell coloration consists of irregular yellowish brown radiating stripes that typically extend from venter to near the umbilicus. These stripes typically end at about the position of the final septum in mature shells, and the density of their

**Table 3.** Species, sample locations, voucher[1] numbers, and Genbank accession numbers for samples of *Nautilus* and *Allonautilus*.

| Species | Sample | Voucher # | Location | COI | 16S |
|---|---|---|---|---|---|
| *N. pompilius* | 1 | OUZC5976 | Saleh Bay, Sumbawa, Indonesia | KU550735 | KU550709 |
| | 2 | OUZC5977 | “ | KU550736 | KU550710 |
| | 4 | OUZC5978 | “ | KU550737 | KU550711 |
| | 6 | OUZC5980 | “ | KU550738 | KU550712 |
| | 8 | OUZC5981 | “ | KU550743 | KU550717 |
| | 9 | OUZC5982 | “ | KU550744 | KU550718 |
| | 10 | OUZC5983 | “ | KU550745 | KU550719 |
| | 11 | OUZC5984 | Moyo Island, Sumbawa, Indonesia | KU550753 | KU550727 |
| | 12 | OUZC5985 | “ | KU550754 | KU550728 |
| | 13 | OUZC5986 | “ | KU550755 | KU550729 |
| | 14 | OUZC5987 | “ | KU550756 | KU550730 |
| | 17 | OUZC5988 | “ | KU550746 | KU550720 |
| | 20 | OUZC5989 | “ | KU550747 | KU550721 |
| | 21 | OUZC5990 | “ | KU550757 | KU550731 |
| | 24 | OUZC5991 | “ | KU550740 | KU550714 |
| | 27 | OUZC5992 | “ | KU550739 | KU550713 |
| | 29 | OUZC5994 | Sumbawa-Lombok pass, Indonesia | KU550741 | KU550715 |
| | 44 | OUZC5995 | “ | KU550742 | KU550716 |
| | 49 | OUZC5997 | “ | KU550757 | KU550732 |
| | 55 | OUZC5998 | “ | KU550759 | KU550733 |
| | 61 | OUZC5999 | “ | KU550749 | KU550723 |
| | 62 | OUZC6000 | “ | KU550760 | KU550734 |
| | | USNM816877 | Ambon, Indonesia | KU550748 | KU550722 |
| | | UIS400 | Ambon, Indonesia | GQ280190 | GQ280125 |
| | | UIS401 | Ambon, Indonesia | GQ280191 | GQ280126 |
| | | UIS409 | Carter Reef, Australia | GQ280197 | GQ280131 |
| | | UIS426 | Philippines | GQ280192 | U11626 |
| | | UIS701 | Philippines | GQ280193 | GQ280127 |
| | | UIS702 | Philippines | GQ280194 | GQ280128 |
| | | AMNH129530 | Vanuatu | GQ280249 | GQ280183 |
| *N. belauensis* | | USNM730544 | Palau | KU550752 | KU550726 |
| | | USNM730633 | Palau | KU550750 | KU550724 |
| | | USNM730634 | Palau | KU550751 | KU550725 |
| *N. macromphalus* | | AMNH185275 | Noumea, New Caledonia | GQ280217 | GQ280151 |
| *A. scrobiculatus* | | UIS427 | Little Ndrova Is., PNG | GQ280250 | GQ280184 |

[1] OUZC – Ohio University Zoology Collection, USNM – Smithsonian National Museum of Natural History, UIS – University of Illinois Springfield.

shell coverage varies from ~40% to 70% of the shell (Figs. 2A, 2B). The two isolated Indonesian samples at hand seem indistinguishable in terms of degree and patterns of shell coloration. Like shell sculpture, shell coloration is variable both within and between various populations and species of *Nautilus* and *Allonautilus* and includes degree of coloration (*e.g.*, total percent of coloration of the entire mature shell, how far striping extends over the flanks of the shell, patterns of striping, and even pigment color. Swan and Saunders (1987) showed that shell coloration patterns can be quantified and used to distinguish isolated populations of *N. pompilius* in Papua New Guinea. Patterns could be correlated to both distance between populations sampled and to separation by deep water (>500m). However, as noted above, coloration does not appear to differ between the Ambon and Sumbawa shells.

**Genetic Analysis.**

Here, 412 bases of the COI gene, corresponding to bases 160–572 in the *Nautilus macromphalus* mitochondrial genome (Boore 2006; Genbank NC007980) and 399 bases of the 16S gene (bases 2836–3235 in the *N. macromphalus* genome) were resolved for specimens from Sumbawa, Ambon, and Palau (Table 3). Sequence variation ranged from 0.1–0.6% among *N. pompilius* samples from Sumbawa, Ambon, and the Philippines to 5.4-5.9% between this clade and Vanuatu *N. pompilius*. The ML analysis (Fig. 4) identified a strongly supported group (bootstrap value = 91) that

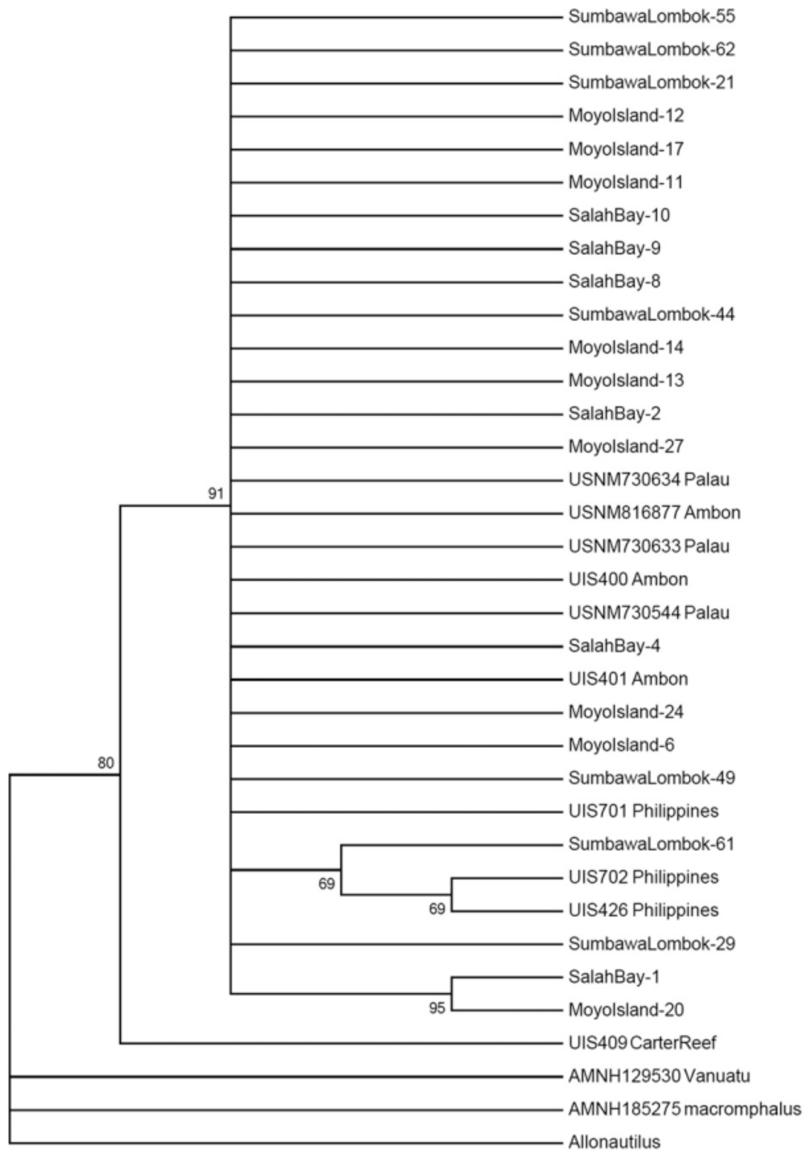


**Figure 4.** The 50% condensed tree of the Maximum Likelihood analysis of the combined COI and 16SrRNA sequence data for haplotypes of *Allonautilus scrobiculatus* (Manus, PNG); *Nautilus macromphalus* (New Caledonia – Loyalty Is.); *Nautilus pompilius s.l.* (Vanuatu); *N. pompilius s.l.* (Carter Reef, GBR, Australia) *N. belauensis* (all specimens labeled Palau); and *N. pompilius s.s.* (Ambon, Molucca Is.; Moyo Island, Salah Bay, Sumbawa-Lombok (southcentral Indonesia). All individuals labeled "Ambon" are topotypes of *N. pompilius pompilius* and USNM 816877 is the proposed neotype. (Nikolaeva *et al.* 2015).

includes all of the Sumbawa, Ambon, and Philippines *N. pompilius* samples and the Palau *N. belauensis* samples. The sequences from this region are part of a monophyletic group that demonstrates little intra-clade sequence variation. Our data are consistent with Bonacum *et al.* (2011, Fig. 3), who recognized three highly divergent clades among *Nautilus pompilius* including a Western Australia/Indonesia clade containing samples from Palau, Ambon, Rowley Shoals (Western Australia), and the Philippines. The data suggest a widespread and closely related group of populations within which the type specimen described by Rumphius almost certainly occurred. The selection of a neotype specimen from Ambon (Figs. 2A,B,E; Table 1 [USNM 816877 = AMB 16]) is consistent with these observations.

## SYSTEMATICS

Phylum Mollusca
Class Cephalopoda Cuvier, 1798
Order Ectocochlia Schwartz, 1894
Subclass Nautiloidea Hyatt, in Zittel 1900
Family Nautilidae de Blainville, 1835
Genus *Nautilus* Linnaeus, 1758

### Diagnosis

(Emended from Saunders 1987b.) Shell compressed and involute, mature shell size variable between geographically isolated populations (~100–240mm in diameter, most ~175 mm); umbilical callus present in some species. Sexual dimorphism prominent in mature animals, with males being larger, with a broader aperture than females. Growth lines sinuous, with ocular and hyponomic sinuses well developed in mature shells. Shell surface details range from smooth to finely reticulate, as a result of minute parallel, serial scallops on growth lines in some isolated populations and species. Shell coloration variable, with brown, reddish- to purple-brown, irregular single and bifurcating stripes that are lacking on the body chamber at maturity in most, but cover much or all of the body chamber in juvenile and sub-mature forms. Shell periostracum thin and transparent. Internally, ~32 septa at maturity, with a central orthochoanitic siphuncle; suture moderately sinuous, with lateral, umbilical and dorsal lobes. In live animals the cartilaginous hood is mottled brown and white, and may be covered with elevated papillae in some species. Radula includes 13 elements; anterior portions of the jaws possess distinctive calcareous deposits.

The number of species in the genus *Nautilus* is uncertain. At least two fossil forms are known (Saunders *et al.* 1996, Wani *et al.* 2008) and eleven living species, one subspecies and seven variants have been named, of which Saunders (1987) regarded five or six species as valid. Two species (*Nautilus scrobiculatus* Lightfoot, 1786 and *N. perforatus* Conrad, 1849) were assigned to a new genus *Allonautilus* (type species *N. scrobiculatus*), by Ward and Saunders (1997) based on shell morphology and soft-part differences. The validity of the new genus was challenged by (Harvey *et al.* 1999), and the challenge rebutted (Ward 1999), and there has been strong subsequent support for *Allonautilus* as a separate genus (*e.g.*, Bonnaud *et al.* 2004, Bonacum *et al.* 2011, Greenfest-Allen *et al.* 2009).

Based on DNA, others have suggested that there is only one phylogenetic species of *Nautilus* (*N. macromphalus*), and that *N. pompilius* is a paraphyletic assemblage of populations and does not represent a true phylogenetic species (Bonacum *et al.* 2011). However, if phylogenetic justification is required to validate species, does this leave the genus *Nautilus* without a valid type species? To shift the type species to the only phylogenetically recognized species, *N. macromphalus* Sowerby, 1849 would be taxonomic folly. Establishment of a neotype of *Nautilus pompilius*, the type species of *Nautilus* Linnaeus, 1758, including molecular data from the type locality, should allow resolution of this issue.

*Geographic Distribution*

The distribution of *Nautilus* is generally described as Indo-Pacific, with living populations ranging from ~30°S - 30°N and 90°W - 185°W (see Saunders 1987a p. xxv). This broad geographic range largely reflects occurrences of *Nautilus pompilius* Linnaeus, 1758 s.*l.* Indeed, all other known species of *Nautilus* thought to be valid comprise endemic species within the range of *N. pompilius*; *e.g.*, *N. belauensis* (Palau), *N. stenomphalus* (GBR), *N. macromphalus* (New Caledonia - Loyalty Is.). However, within this range, comprising hundreds of archipelagoes and thousands of islands, there have been few efforts to systematically document the presence of living populations. Historically, most data on living populations were derived from indigenous artisanal fisheries information (*e.g.*, Willey 1899, Griffin 1900), with only a few quantitative accounts of these efforts (*e.g.*, Haven 1972, Hayasaka *et al.* 1982, 1987, Tanabe *et al.* 1990, Del Norte-Campos 2005, Dunstan *et al.* 2010, 2011). There are relatively few published accounts documenting new occurrences of living populations (*e.g.*, Saunders and Davis 1985, Saunders and Ward 1987b, Saunders *et al.*1989). Even fewer studies have reported fruitless trapping efforts indicating that *Nautilus* is *not* present at specific locales. Confounding the issue is the potential for postmortem distribution of drifted shells (Saunders and Spinosa, 1979, House 1987). Geographic variation in both phenotypic and genetic characters in isolated *N. pompilius* populations have been documented (*e.g.*, Woodruff *et al.* 1983, 1987, Swan and Saunders 1987, Wray *et al.* 1995, Sinclair *et al.* 2007, Bonacum *et al.* 2011).

*Nautilus pompilius* Linnaeus, 1758

**Diagnosis**

(Emended from Saunders 1987b.) Small umbilicus (~5% of shell diameter), with most closed by a callus in post-juveniles. Shell color bands form irregular radiating stripes that typically extend from venter to near the umbilicus and end at the approximate position of the last septum; typically 11–14 color bands on the last whorl with a wide range of variation in stripe density and shell coverage (Figs. 6, 7); color stripes may coalesce across the venter and most have some brown coloration in the umbilical region. Fine, parallel scalloping may be superimposed on growth lines in some isolated populations, giving the impression of delicate concentric lirae in the umbilical, ventrolateral, or ventral portions of the shell; dorsal black layer (which underlies the leading edge of the hood in live animals) may show a net-like pattern with isolated pustules. Mature shell size typically ~165mm diameter, but may vary in isolated populations (Saunders 1987b, Fig. 4).

Thanks are owed S. V. Nikolaeva (Nikolaeva 2015) for having reconstructed the history of the type series in detailed fashion (Nikolaeva 2015), and also for proposing the following to the International Commission on Zoological Nomenclature (ICZN):

> "…to designate as a neotype specimen USNM 816877 (AMB 16) …" and "…to place on the Official List of Species Names in Zoology the name *pompilius* Linnaeus 1758, as published in the binomen *Nautilus pompilius* Linnaeus, 1758 and as defined by the neotype…" (Nikolaeva *et al.* 2015 p. 281).

This recommendation would have the effect of anchoring the morphologic and genetic characters of the type species of *Nautilus* to a live-caught, preserved shell and soft parts belonging to a neotype, plus topotypes, along with ecological parameters, from Ambon, Molucca Is., Indonesia. The specimen chosen as the neotype is part of the population sample described here, obtained in 1987, and is supplemented by additional information from a second, allopatric population from the Sumbawa and Lombok Islands regions ~1,500km to the southeast.

If Rumphius was based in Ambon and if the specimens he described and illustrated came from waters near Ambon, it is logical to use a specimen from Ambon for a neotype. However, even if the original specimen was not from the immediate vicinity of Ambon, the genetic data suggests that individuals from as far away as Sumbawa and the Philippines are part of the same genetic population and that any of these locations would be a genetically appropriate source for a neotype (see discussion below).

**Description of the neotype**

Inasmuch as the recommendation to designate a neotype (Nikolaeva *et al.* 2015) did not include details of the type specimens, these are presented here as follows:

The shell of the neotype, a mature male (Figs. 1A, B, E; Table 1 [USNM 816877 = AMB 16]), has a well-developed black band around the thickened aperture, which displays well-developed ocular and hyponomic sinuses. Measurements are 199.2 mm in diameter, 92.8 mm maximum width, live weight (shell + body) 1,275 g. The umbilicus is covered by a well-developed callus. Brown color banding ends at ~136.0 mm diameter, coincident with the last septum. On the midlateral part of the shell there are 18-21 moderately wide, brown stripes that extend most of the way to the umbilicus; some bands bifurcate on the ventrolateral flanks (in other shells the stripes extend into the umbilicus; Figs. 6, 7). There is a faintly expressed concentric or longitudinal component of shell sculpture, consisting of almost imperceptible corrugations of the growth lines (~5-7 lirae per mm), which are seen across the ventral and ventrolateral parts of the phragmocone, but they do not extend to the flanks or the body chamber in most shells.

The edge of the dorsal black area (the region covered by the hood in the live animal) has a surface texture similar to the wrinkle layer, or *runzelschict,* such as is seen in analogous areas in some ammonoids. On the neotype, this texture begins on the edge of the black layer near the umbilicus, as simple depressions or pits that may be connected, forming a maze-like pattern that varies in relief, forming a pustulose texture (Figs. 3C, E, F).

The mitochondrial DNA sequence data places the proposed neotype specimen (USNM 816877) from Ambon within a clade of similar sequences from Sumbawa, Philippines, Ambon, and Palau (Fig. 4).

*Nautilus pompilius pompilius* Linnaeus, 1758

**Diagnosis**

As for *Nautilus pompilius* Linnaeus, 1758. This subspecies has a much larger mature shell (~160 - 200mm diameter) compared to that of the only other named subspecies, *Nautilus pompilius suluensis* Habe and Okutani, 1988 (~114mm diameter). The latter also has different coloration (see below). It is notable that the geographic range of *N. pompilius pompilius* Linnaeus, 1758 spans that of *N. pompilius suluensis* Habe and Okutani, 1988, which is known from only one locality in the Philippines (see below).

According to Article 46.1, Principle of Coordination (ICZN 1999), "A name established for a taxon at either rank in the species group is deemed to have been simultaneously established by the same author for a taxon at the other rank in the group; both nominal taxa have the same name-bearing type, whether that type was originally fixed or subsequently."

Thus, with the naming of a new subspecies of *Nautilus pompilius* (*Nautilus pompilius suluensis* Habe and Okutani, 1988; see below), Linnaeus is considered to have automatically established the subspecies *N. pompilius pompilius* Linnaeus, 1758. Additionally, the newly recommended neotype for *Nautilus pompilius* by Nikolaeva *et al.* (2015) serves for both specific and subspecific taxa.

**Geographic distribution**

With definition of the type locality of *Nautilus pompilius s.s.* as the Molucca Is., clarification of distribution of the species and subspecies will require direct comparisons to other known populations of *N. pompilius s.l.* Presently, the Ambon and Sumbawa-Lombok populations appear morphologically and genetically homogeneous based on combined COI and 16SRNA sequence data for haplotypes (Fig. 4), and are currently regarded as the only documented occurrences of *N. pompilius pompilius s.s.* However, the species is widely distributed across the Indonesian and adjacent archipelagoes and is likely connected through the geographic ranges of overlapping populations, such as was documented for *N. pompilius* in Papua New Guinea (Swan and Saunders 1987, Woodruff *et al.* 1987). In addition, chance dispersals from isolated, non-adjacent and even distant populations may have occurred (*e.g.*, see notes on atypical specimen in Lorengau, Manus, PNG population (Wray *et al.* 1995, p. 225; Bonacum *et al.* 2011, pp. 6, 7, and Fig. 3).

*Nautilus pompilius suluensis* Habe and Okutani, 1988

(see Saunders 1987b, Figs. 3C,D)

**Diagnosis**

As for *Nautilus pompilius pompilius* Linnaeus, except as noted here. The shell of *Nautilus pompilius suluensis* Habe and Okutani, 1988 averages ~60 -70% smaller than that of *N. pompilius pompilius*; the shell coloration has a purplish hue, with fewer and markedly coarser stripes.

A new subspecies was proposed for a diminutive shell of *Nautilus pompilius* with purplish-brown stripes that occurs on Tubbataha Reef, in the Sulu Sea, Philippines (which is well within the geographic range of *Nautilus pompilius pompilius* Linnaeus, 1758):

Proof Only

*Nautilus pompilius suluensis* Habe and Okutani, 1988 (holotype in the National Science Museum Tokyo, NSMT Mo-64608 [*fide* Nikolaeva 2015]; see also topotypes figured by Saunders 1987b figs. 3C,D [USNM 816893, 816894]). This distinctive, apparently endemic form differs from *N. pompilius pompilius* Linnaeus, 1758 in having the smallest mature shell of any known extant nautilid (~114 mm diameter, range 103-126 mm; based on a collection of shells ($n$ = 29) made available to WBS in 1986 by Donald Dan). The shell coloration also differs in having a purplish hue, and the color stripes tend to be fewer and coarser. Available shells of *N. p. suluensis* appear to be fresh and live-caught rather than drift shells, but details of their soft parts are currently unknown, as is any knowledge of their ecology or genetic relationships with other populations. Tubbataha Reef National Marine Park, Palawan, the first such reserve in the Philippines, is protected as a UNESCO World Heritage Site, which augers well for possible protection of this unusual taxon.

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Descriptions of Nautilus pompilius Linnaeus, 1758 from the type area, Ambon

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