Anatomy of living *Nautilus*: Reevaluation of primitiveness and comparison with Coleoidea

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Abstract. The anatomy of *Nautilus pompilius* was reinvestigated on the basis of material from the Philippines to evaluate the "primitiveness" of the living fossil cephalopod. All organ systems were dissected at the gross level, photographed, and described. The results of dissection were compared with the knowledge of other living cephalopods (Coleoidea) and noncephalopod conchiferan molluscs. As a result, 16 characters were identified as synapomorphies of the Recent cephalopods, and there are more possible characters in the buccal musculature and various types of cartilage. Further comparison revealed clear differences in 52 characters between *Nautilus* and the Coleoidea. These differences include *Nautilus* autapomorphies and/or coleoidean synapomorphies. By outgroup comparison within the Conchifera, especially with basal gastropods and scaphopods, the polarity and "primitiveness" were evaluated for each character. Sixteen characters were inferred to be obviously plesiomorphic in *Nautilus*, but others are apomorphic or ambiguous. The large number of arms and ctenidia in *Nautilus* are possibly derived characters rather than primitiveness. The two-paired renopericardial organs might also be apomorphic, but this hypothesis should be tested in further ontogenetic studies.

Key words: Cephalopoda, *Nautilus pompilius*, Coleoidea, body plan, synapomorphy, plesiomorphy

Introduction

The Recent *Nautilus* is a typical example of a living fossil (e.g., Ward, 1984) and also a key taxon in understanding the origin of cephalopods. The morphologic character states of *Nautilus* are, therefore, essential in considering the evolution and phylogeny of cephalopods (House, 1988; Teichert, 1988; Lindgren et al., 2004; Nishiguchi & Mapes, 2008) or Coleoidea (Engeser & Bandel, 1988; Vecchione et al., 2000) and of the basal gastropods (Ponder & Lindberg, 1997; Sasaki, 1998; Aktipis et al., 2008) as a sister group.

The body plan of *Nautilus* has drawn much attention from both zoologists and paleontologists, with numerous publications since the 19th century or even earlier (see Davis, 1987, for historical review). In 1987, previous knowledge of living *Nautilus* was extensively summarized by Saunders and Landman (1987). Since then, the morphology of *Nautilus* has been further examined in terms of various characters including the embryonic shell and shell ultrastructure (Arnold, 1988; Blind, 1988; Landman et al., 1989; Arnold et al., 1990; Mutvei & Doguzhaeva, 1997; Tanabe & Uchiyama, 1997), mantle (Westermann et al., 2005), body musculature (Bizikov, 2002), muscle attachments (Mutvei et al., 1993; Isaji et al., 2002), buccal organs and musculature (Young, 1991; Tanabe & Fukuda, 1999; Messenger & Young, 1999), digestive tract and glands (Ruth et al., 1988; Westermann & Schipp, 1998; Westermann et al., 2002), siphuncular cord (Tanabe et al., 2000), nervous system (Young, 1965; 1987), sensory tentacles (Munz & Wentworth, 1995; Ruth et al., 2002), statocysts (Neumeister & Budelmann, 1997), and development (Arnold, 1987a, b; Tanabe and Uchiyama, 1997; Shigeno et al., 2008). Taxonomic studies based on morphology have also been performed at generic and species levels (Tanabe et al., 1990; Ward & Saunders, 1997). All anatomic data published before 1997 were reviewed together with those on the Coleoidea by Budelmann et al. (1997).

In spite of numerous earlier publications, there are still some gaps in our knowledge of the character states in *Nautilus*. For example, data on the reproductive system were mostly based on older descriptions by Griffin (1900) and Willey (1902), and the structure of the buccal organs was relatively unclear. In addition, comparisons between *Nautilus* and noncephalopod conchiferan molluscs (Monoplacophora, Bivalvia, Scaphopoda, and Gastropoda) were insufficient.

This study was thus undertaken to present new results on four topics: (1) the description of gross-level anatomy for all organ systems; (2) reinvestigation of cephalopod synapomorphies; (3) an updated list of characters distinguishing *Nautilus* and the Coleoidea; and (4) a reevaluation of the "primitiveness" of living-fossil *Nautilus*. The discussion of some characters was also reinforced by the results of our recent developmental study (Shigeno *et al.*, 2008). The uncertainties pointed out in this paper will be the main target of future work on molluscan histology, molecular phylogeny, and evolution.

Materials and methods

Dissection was performed manually with forceps, scissors, and steel knives. Every step of dissection was sequentially photographed to record anatomic structures. Some dissected parts were freeze-dried and observed with a scanning electron microscope, as described previously (Sasaki, 1998). Dissected specimens were registered and deposited in the Department of Historical Geology and Paleontology, The University Museum, The University of Tokyo (UMUT).

Descriptions in this study are based on specimens from four different sources, all from the Philippine coastal waters: (1) three complete specimens of two adult females and one adult male (see Tanabe *et al.*, 1990, for sampling data) (registration number: UMUT RM30005-30007); (2) isolated buccal masses from seven adults (UMUT RM30008-30014); (3) five immature specimens purchased from an aquarium company (UMUT RM30015-30019); and (4) two embryos obtained from the Toba Aquarium (UMUT RM30020-30021). All of the adult samples were originally fixed in 10% formalin and preserved in 70% ethanol. The embryos were fixed in 4% paraformaldehyde/phosphate-buffered saline solution and preserved in 75% ethanol as described in Shigeno *et al.* (2008).

Results

External anatomy.—The animal is symmetrical in outline, laterally compressed, and slightly curved (Figure 1) according to the shape of the body chamber of the exogastric shell (with forwardly curving viscera). The body surface consists of several distinct parts, *viz.*, the head, pallial cavity with the mantle, visceral mass, and cephalic retractor muscles.

The head is highly muscular and stiffened. The exterior is divided into the hood, digital tentacles, and eyes. The hood (hd: Figure 1A–C) is on the anterodorsal surface of the animal, rigid, and brown with many white spots. Along the anterolateral margins, a pair of oblique lines are visible (hfl: Figure 1B, C) representing the line of fusion between part of the arms and hood anlage in ontology (see Shigeno *et al.*, 2008, for details).

The digital tentacles surround the mouth and anterior outer surface of the animal (see sense organs below). Each tentacle has a double-structured outer sheath (dts: Figures 1A and B, 2A) and inner cirri (dtc: Figure 1A, B). The sheaths are stiffened, arranged in parallel along the anteroposterior axis, and completely fused with the body wall. The cirri are flexible and retractile. There are 19 tentacle pairs, as shown in the cross section of the head (Figure 3A).

The eyes (e: Figure 1A) are located on the sides of the head at the posterior boundary between the hood and the digital tentacles (see sense organs for inner structures).

The mouth (mo: Figure 3A) is in the center of a circle of digital tentacles and invisible in fixed specimens. The labial tentacles (lt: Figure 3A, E) originate from the laterally paired lobes, are flexible and retractile into the sheaths, and are smaller than the digital tentacles.

The ventral side of the body has a funnel (also termed hyponome) (fR, fL: Figures 1D, E, 2A, 3A–C). It forms a seemingly tubular structure, but the left and right lobes are separate and unfused. In all specimens except for one deformed one (Figure 3B), the right lobe (fR) is located more ventrally than the left (fL: Figures 1D, E, 2A, 3A). In cross section, both lobes are enrolled clockwise when seen from the anterior (Figure 3A). The base of the funnel is stiffened by funnel cartilage (fc: Figure 3C), which can be recognized by its white color. The funnel valve (fv: Figure 3C) projects from the dorsal wall of the funnel.

The surface of the visceral mass is covered with a thin epithelium. Externally, several organs such as the digestive glands (dgR, dgL: Figure 1A, C) and intestine (i: Figure 1A) are seen through the epithelium.

The siphuncular cord (sc: Figure 1A, C) arises from the posterodorsal side of the visceral mass. It contains
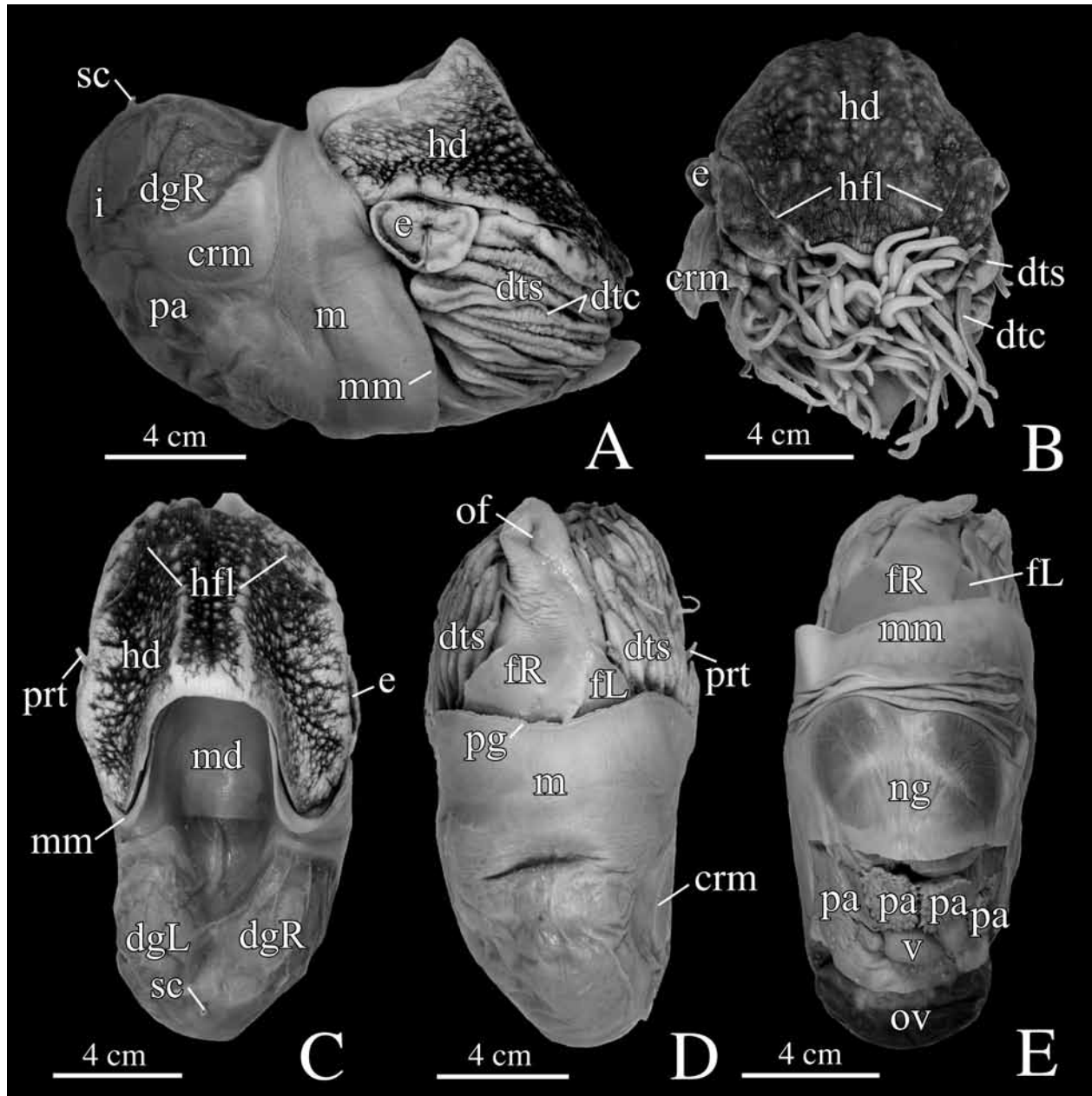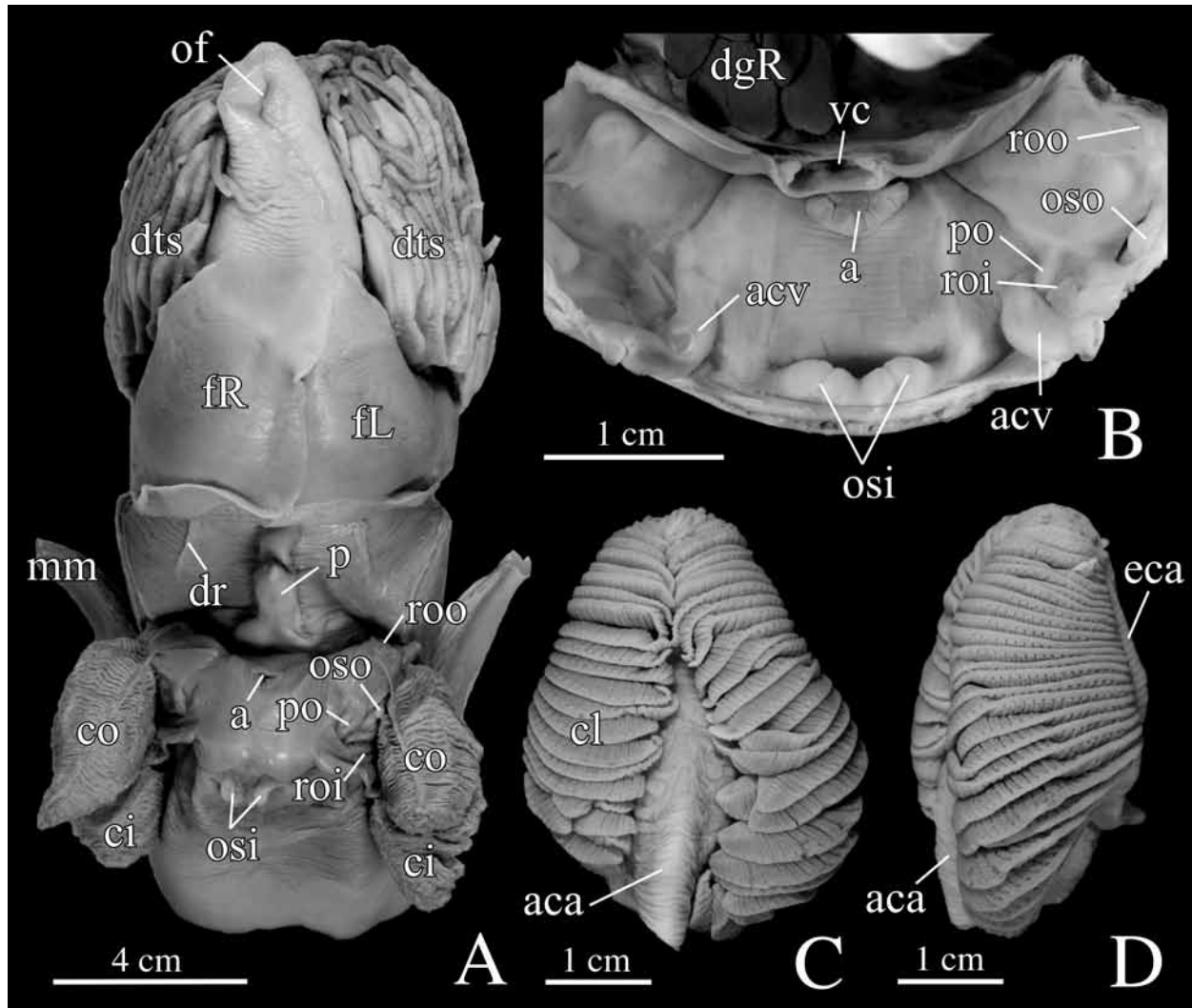
Figure 1. *Nautilus pompilius* Linnaeus. External anatomy. **A**. Right lateral view of female. **B**. Frontal view. **C**. Dorsal view. **D.** Ventral view of male. **E**. Ventral view of female with epithelium of visceral mass removed. Abbreviations: co, outer ctenidium; crm, cephalic retractor muscle; dgL, left lobe of digestive gland; dgR, right lobe of digestive gland; dtc, cirrius of digital tentacle; dts, sheath of digital tentacle; e, eye; fL, left lobe of funnel; fR, right lobe of funnel; hd, hood; hfl, fusion line of hood; i, intestine; m, mantle; md, dorsal extension of mantle; mm, mantle margin; ng, nidamental gland; of, opening of funnel; ov, ovary; pa, pericardial appendage; pg, periostracal groove; prt, preocular tentacle; sc, siphuncular cord; v, ventricle. A–C, E. UMUT RM30005. D. UMUT RM30006.

a thick vein in the center, four arteries that are smaller in diameter than the vein, and a network of connective tissue (see Tanabe *et al*., 2000: figures 2–4, for details).

The middle part of the animal is covered with the mantle (m: Figure 1A) which is thin for cephalopods and becomes thicker toward the mantle margin (mm:

Figure 1A). The periostracal groove (pg: Figure 1D) is conspicuous along the mantle margin. The mantle is distributed circularly around the animal but narrows markedly along the cephalic retractor muscles (crm: Figure 1A). The dorsally depressed part of the animal is covered with an extended part of the mantle (md: Figure

Figure 2. *Nautilus pompilius* Linnaeus. Pallial organs. **A**. Ventral view of animal with mantle removed. **B**. Frontal view of posterior wall of pallial cavity. **C**. Dorsal view of inner right ctenidium. **D**. Outer lateral view of same ctenidium. Abbreviations: a, anus; aca, afferent ctenidial axis; acv, afferent ctenidial vessel; ci, inner ctenidium; cl, ctenidial lamella; co, outer ctenidium; dgR, right lobe of digestive gland; dr, dorsal ridge of pallial cavity; dts, sheath of digital tentacle; eca, efferent ctenidial axis; fL, left lobe of funnel; fR, right lobe of funnel; mm, mantle margin; of, funnel opening; osi, inner osphradium; oso, outer osphradium; p, penis; po, pericardial opening; roi, opening of outer renal sac; roo, opening of inner renal sac; vc, vena cava. A. UMUT RM30006, B. UMUT RM30019, C, D. UMUT RM30005.

1C) in contact with the inner whorl of the shell.

Pallial cavity.—The pallial cavity is located mainly on the ventral side of the animal and contains two pairs of ctenidia (gills) (ci, co: Figure 2A), the anus (a: Figure 2A, B), two pairs of openings of the renal cavities (roi, roo: Figure 2A, B), a pair of openings of the pericardial cavity (opc), two pairs of osphradia (osi, oso), the openings of reproductive system, and the nidamental glands in females (ng: Figure 1E).

The inner and outer pairs of ctenidia are almost the same size. The ctenidia are not suspended from the pallial roof but attached to the posterior pallial wall. The dorsal and ventral rims are supported by afferent and efferent axes (aca, eca: Figure 2C, D), respectively. The surface of the ctenidia is divided into many vertically aligned lamellae (cl: Figure 2C, D) which are corrugated with fine horizontal ridges. The afferent axis is thicker than the efferent axis. The inner structure of the ctenidium was not examined in this study.

There are three pairs of slit-like openings on the posterior pallial wall (Figure 2A, B). The openings of the inner renal cavities (roi) and the pericardial cavity (po) are located near the bases of the inner afferent branchial vessels (acv: Figure 2B). The openings of the outer renal cavities (roi) are near the bases of the outer afferent branchial vessels.
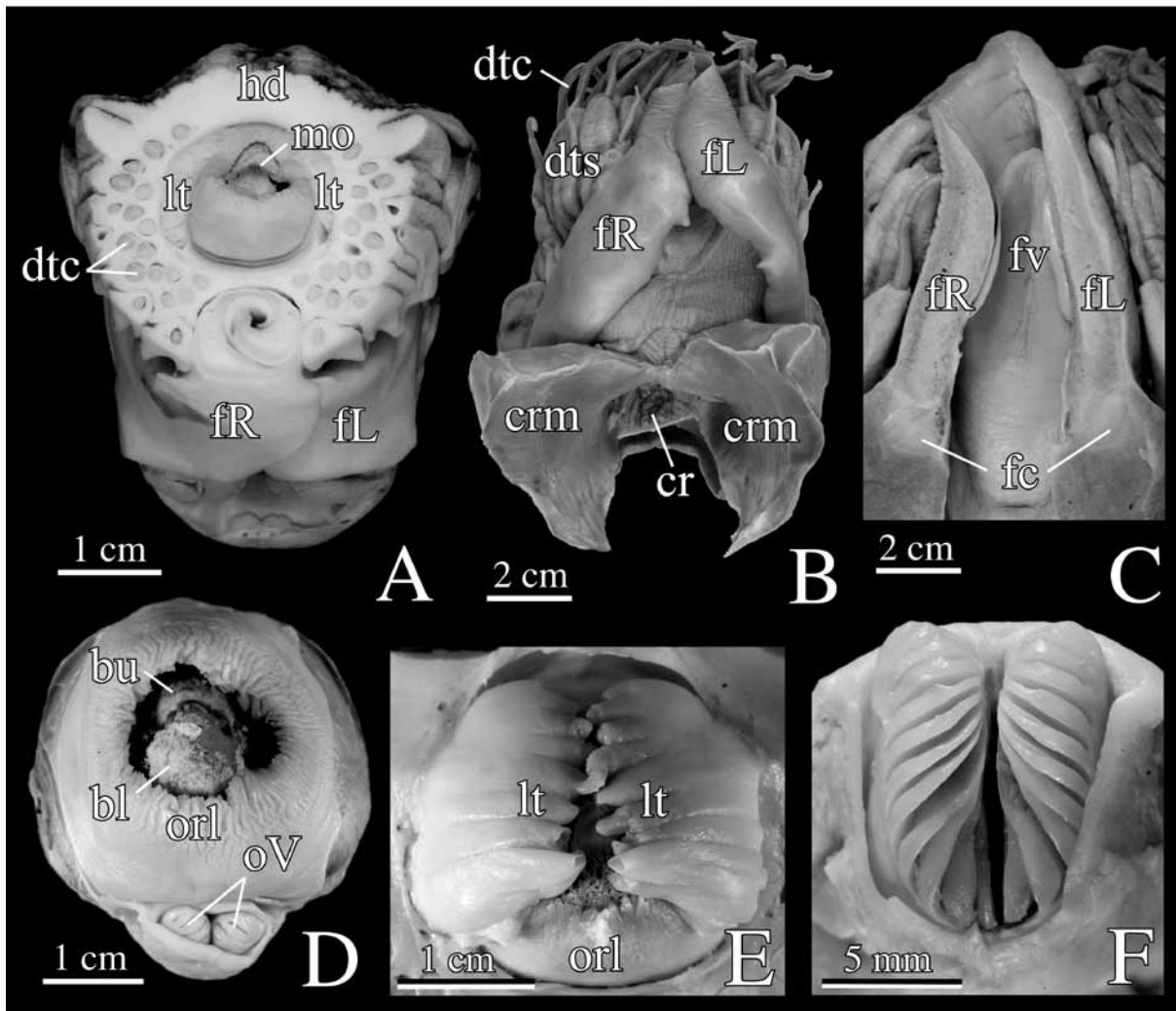
Figure 3. *Nautilus pompilius* Linnaeus. **A**. Frontal view of animal with dissected head. **B**. Ventral view of head and cephalic retractor muscles with visceral mass removed. **C**. Funnel valve inside funnel. Right and left lobes of funnel dissected and removed. **D**. Frontal view of mouth part. **E**. Labial tentacles. **F**. Organ of Valenciennes. Abbreviations: bl, lower beak; bu, upper beak; cr, crop; crm, cephalic retractor muscle; dtc, cirrius of digital tentacle; dts, sheath of digital tentacle; fc, funnel cartilage; fL, left lobe of funnel; fR, right lobe of funnel; fv, funnel valve; hd, hood; lt, labial tentacle; mo, mouth; orl, oral lip; oV, organ of Valenciennes. A, E. UMUT RM30019, B. UMUT RM30005, C. UMUT RM30006, D, F. UMUT RM30008.

Musculature.—The cephalic retractor muscles (crm: Figure 1A) originate from the inner part of the head and funnel and are inserted on the shell laterally. They are a distinct single pair, as obvious from the posterior view after removal of the visceral mass (Figure 3B). The funnel also contains retractor muscles, but they are part of branches of the cephalic retractor muscles and not independent elements. See the digestive system section below for muscles associated with the buccal mass, radula, and beaks.

Digestive system.—The digestive system is composed of the mouth, buccal mass, radula, beaks, esophagus, stomach, caecum, digestive glands, intestine, and anus.

The mouth opens in the center of the labial tentacles and is fringed with a circular oral lip (orl, Figure 3A, D) with a densely fimbriate margin. The buccal mass and buccal cavity are posterior to the mouth.

The buccal mass is a highly muscular structure attached to the body wall circularly at the base of the oral lip. A pair of dorsal retractor muscles of the buccal mass (rbd: Figure 4A) is well developed and widely covers the buccal mass. A pair of ventral retractor muscles of the buccal mass (rbv: Figure 4B) originates from narrower areas on the posteroventral side.

The buccal mass contains dorsoventrally paired beaks (jaws). Both upper and lower beaks are mostly organic
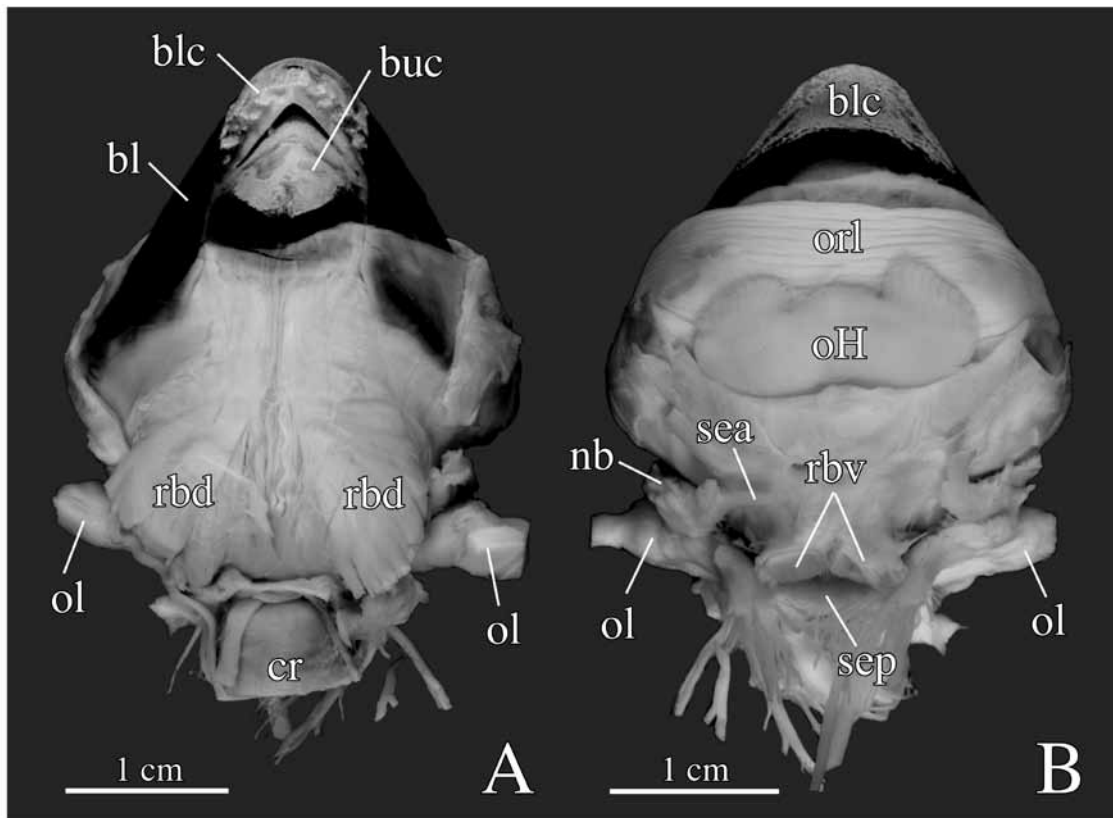
Figure 4. *Nautilus pompilius* Linnaeus. Buccal mass with central nervous system. **A**. Dorsal view. **B**. Ventral view. Abbreviations: bl, lower beak; blc, calcified part of lower beak; buc, calcified part of upper beak; cr, crop; nb, brachial nerve; oH, organ of van der Hoeven; ol, optic lobe; orl, oral lip; rbd, dorsal retractor muscle of buccal mass; rbv, ventral retractor muscle of buccal mass; sea, anterior subesophageal commissure (artificially cut); sep, posterior subesophageal commissure. UMUT RM30019.

and black, but the anterior tips are heavily calcified and white (blc, buc: Figure 5A–C). The lower beak (bl: Figure 5C) is larger than the upper one, and the margin of the calcified tip (blc: Figure 4A) is serrated with small denticles. Both beaks consist of inner and outer lamellae that join on the anterior side. In the upper beak, the inner lamella is much longer than the outer one and is posteriorly elongated, whereas in the lower beak, the inner lamella is reduced and entirely covered by the well-developed outer lamella, so that it cannot be seen from the lateral side (see Saunders *et al.*, 1978; Tanabe *et al.*, 1990).

Both jaws are tied with thick muscles (bm: Figure 5A–C) connecting the inner surface of the lower jaw (bma: Figure 5A, B) and outer surface of the upper jaw.

The floor of the buccal cavity in front of the radula has a subradular organ (so: Figure 5A). Its base is visible from the ventral view of the buccal mass (Figure 5C) and attached by thin muscles (msr: Figure 5C).

The radula is straight and symmetrical, but strongly folded dorsoventrally in the buccal mass. The radular teeth (rdt: Figures 5A, 6) are enclosed in the radular sac (rds: Figure 5C), except for the part exposed in the buccal cavity. The radular teeth consist of 13 elements (rachidian, two laterals, two marginals, and two marginal plates) in each row (see Tanabe *et al.*, 1990: figure 9C, D). The radula is fixed to the retractor muscles inserted on the subradular membrane (srm: Figure 6B, D) on both sides. The protrusion of the radula is controlled by a pair of thin muscles (pr: Figure 5C). The end of the radular sac is enlarged laterally as the radular caecum (rdc: Figure 5C). The radular sac is fixed by a tensor muscle (trd: Figure 5C) on the ventral surface.

The floor of the buccal cavity posterior to the radular teeth is covered by tripartite radular appendages (cf. Messenger & Young, 1999, for terminology). The middle lobe (raM: Figure 6C, D) has a longitudinal sharp ridge. The right and left lobes (raR, raL: Figure 6B, C) arise laterally and overlie the middle lobe. The
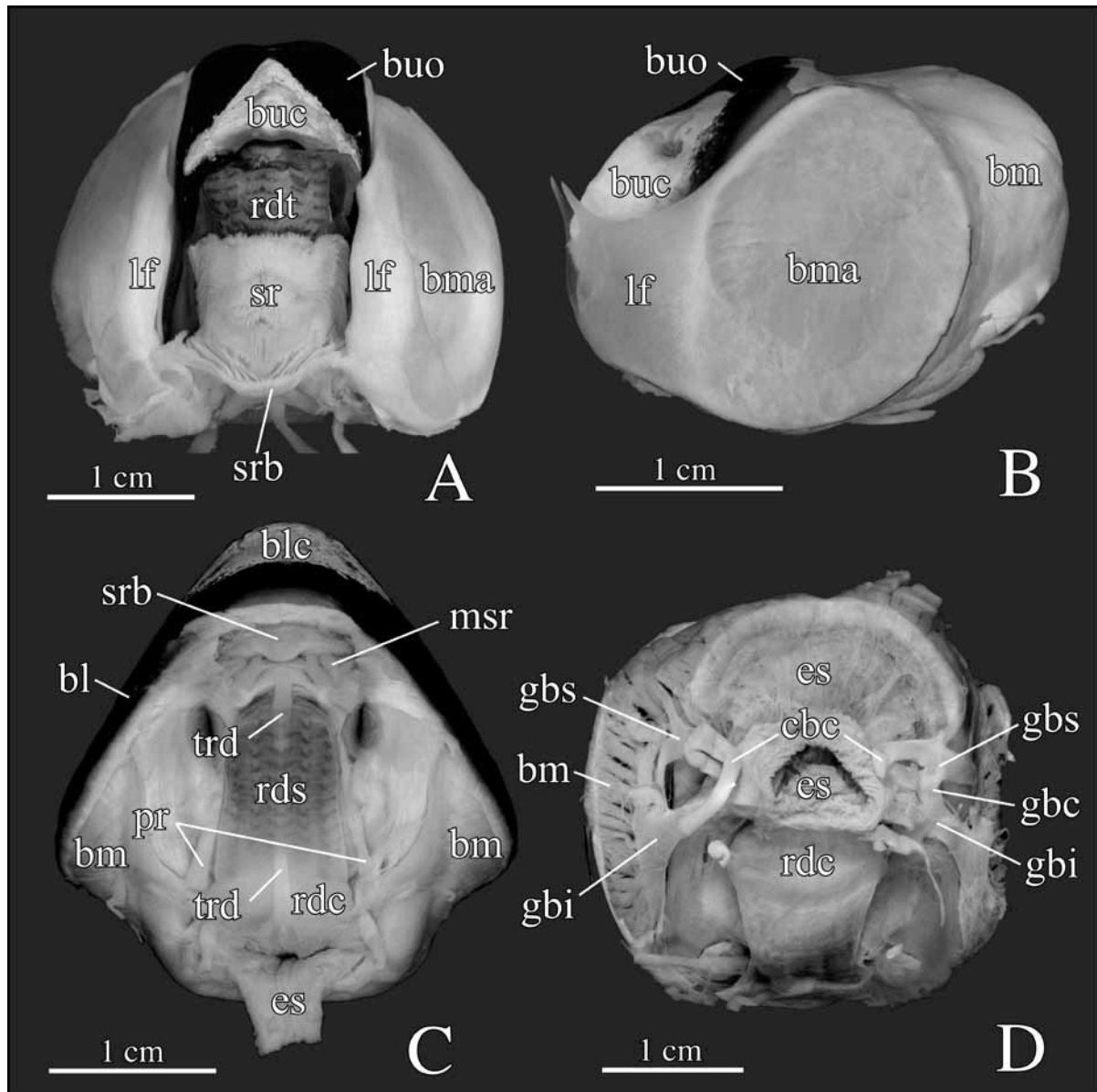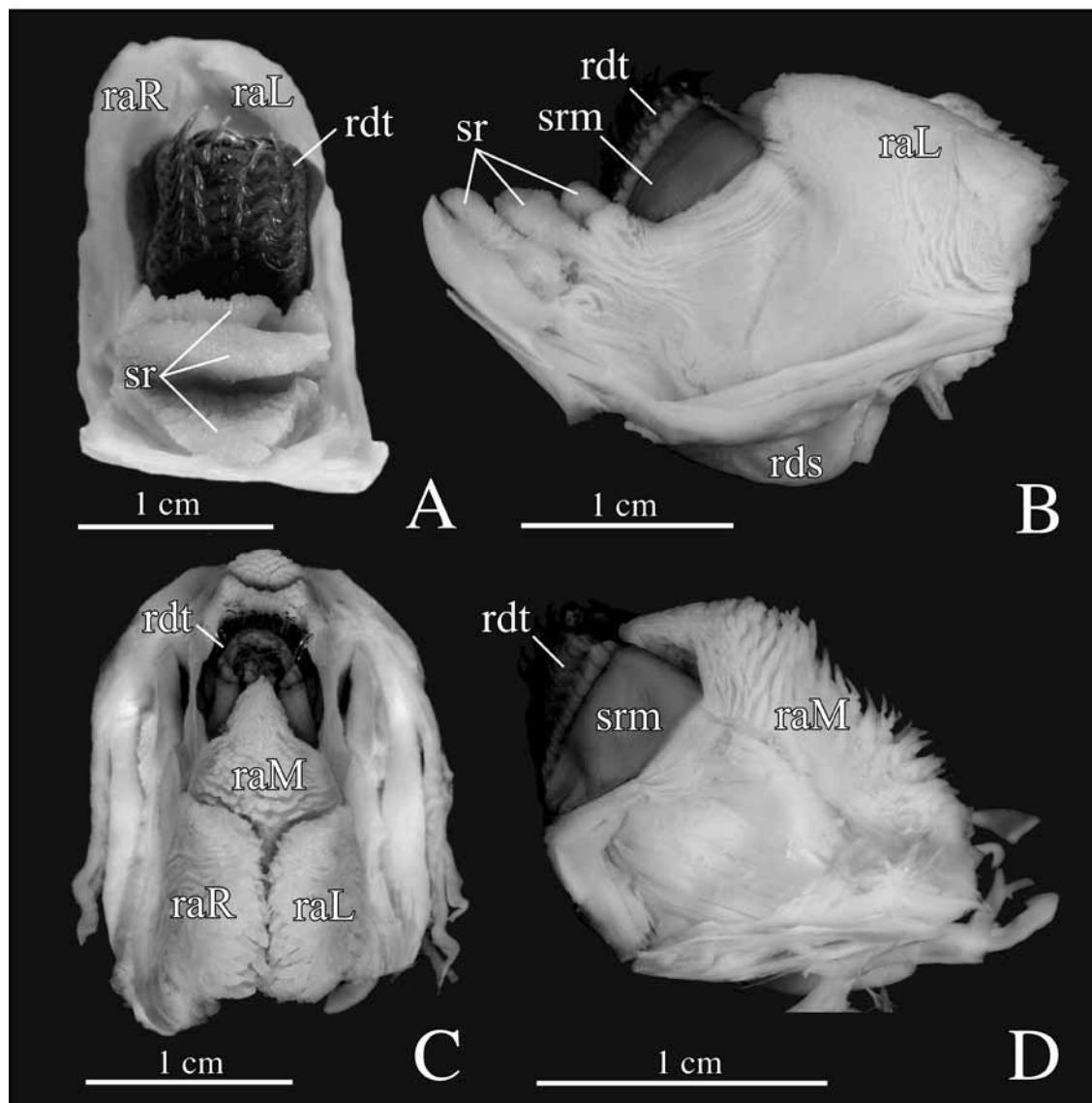
Figure 5. *Nautilus pompilius* Linnaeus. Buccal mass with lower beak removed (A, B) or intact (C, D). **A**. Frontal view. **B**. Left lateral view. **C**. Ventral view. **D**. Dorsal view. Abbreviations: bl, lower beak; blc, calcified part of lower beak; bm, muscle connecting lower and upper beaks; bma, attachment of beak muscle; buc, calcified part of upper beak; buo, outer lamella of upper beak; cbc, cerebrobuccal connective; es, esophagus; gbc, connective between superior and inferior buccal ganglia; gbi, inferior buccal ganglion; gbs, superior buccal ganglion; lf, lateral flap; msr, protractor muscle of subradular organ; pr, protractor muscle of radula; rdc, radular caecum (= end of radular sac); rds, radular sac; rdt, radular teeth; sr, subradular organ; srb, base of subradular organ; trd, tensor muscle of radular sac. A, B. UMUT RM30013, C. UMUT RM30019. D. UMUT RM30012.

edges of all three lobes are finely indented. There are no posterior salivary glands behind the buccal mass.

The radula is supported by a pair of muscular bodies containing membrane-enclosed rods. This part corresponds to the odontophoral bolsters of other molluscs but lacks true cartilage (cf. Katsuno & Sasaki, 2008, for the structure of the molluscan odontophore).

The digestive tract posterior to the buccal mass forms the esophagus (es: Figures 5C, D, 7), which is markedly narrowed in the ring of the brain, enlarged posteriorly to form the crop (cr: Figure 7), and attenuated posteriorly. The inner wall is longitudinally wrinkled in the fixed specimens, but there are no ridged structures comparable to the dorsal and ventral folds in other

Figure 6. *Nautilus pompilius* Linnaeus. Radula and associated structures. **A**. Frontal view. **B**. Left lateral view. **C**. Dorsal view. **D**. Left lateral view with subradular sacs and lateral lobes of radular appendages removed. Abbreviations: raL, left lobe of radular appendage; raM, middle lobe of radular appendage; raR, right lobe of radular appendage; rds, radular sac; rdt, radular teeth; sr, subradular organ; srm, subradular membrane. A, B. UMUT RM30014, C, D. UMUT RM30008.

molluscs (Figure 8A).

The stomach (st: Figure 7) is globular in outline and in fixed specimens it is slightly constricted into two globular parts (Figure 7). Its wall is double-layered, and the inner layer (sti: Figure 8A, B) is much thicker than the outer layer (sto: Figure 8B, C). The inner surface is finely striated in parallel. The esophagus enters into the stomach from the right anteroventral side (Figure 7C).

The digestive gland is large, dark brown in color, and separated into left and right lobes (dgL, dgR: Figure 9A–C). Each lobe is enclosed separately in a thin membrane (Figure 9B). The glands are further divided

into several groups of small lobes but they are regarded as a single pair because their ducts are connected at their bases (ddg: Figure 7B). The digestive gland opens into the caecum via a paired duct (Westermann & Schipp, 1998; ca: Figure 7).

The caecum is half-coiled, smaller than the stomach, and attached to the initial part of the intestine posterior to the stomach (Figure 7C). The surface of the inner wall of the caecum is enlarged by numerous lamellae and they can be seen through the exterior as parallel lines.
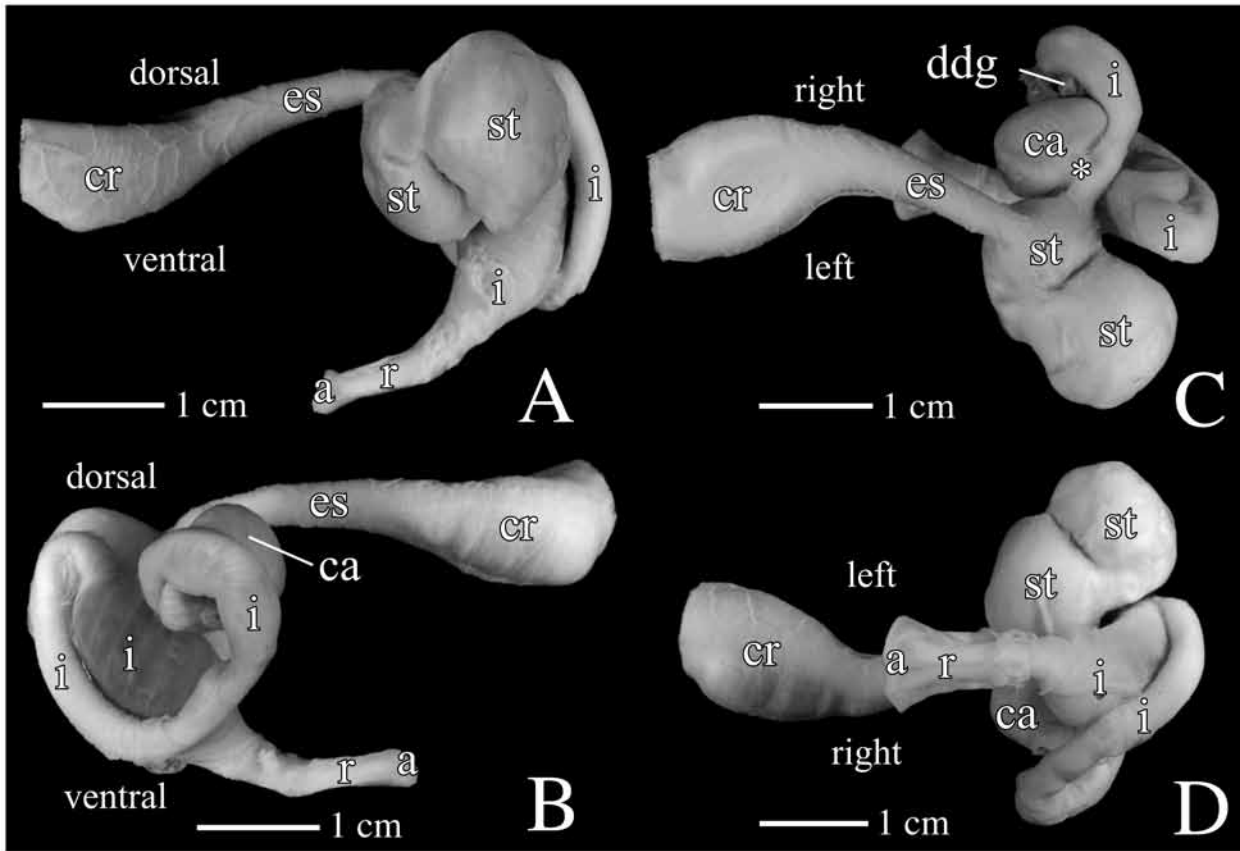
Figure 7. *Nautilus pompilius* Linnaeus. Digestive tract from crop to anus. **A**. Left lateral view. **B**. Right lateral view. **C**. Dorsal view. Asterisk indicates connection to caecum. **D**. Ventral view. Abbreviations: a, anus; ca, caecum; cr, crop; ddg, duct of digestive gland; es, esophagus; i, intestine; r, rectum; st, stomach. UMUT RM30019.

The intestine (i: Figure 7) begins posterior to the connection between the esophagus and stomach (Figure 7C) and turns twice. The proximal loop from the stomach extends ventrally, and the distal loop ascends dorsally, is tightly folded ventrally, and ends on the ventral center of the pallial cavity. The inside of the proximal loop is conspicuously sectioned by longitudinal and transverse ridges. The distal loop is also striated by a pair of longitudinal typhlosoles (ty: Figure 8D) and transverse ridges (tr: Figure 8D), but the ridges in this region are weaker than those in the proximal loop. The rectum (r: Figure 8D) is thicker than other regions of the intestine, and its inner wall is longitudinally grooved. The anus (Figure 8D) opens as a distinct papilla. The ink gland complex is absent.

Circulatory system.—The heart is located in the pericardial cavity behind the renal cavities and consists of two pairs of auricles (au: Figure 9A, D, E) and the ventricle (v: Figure 9A, D, E). The auricles are thin walled, elongated, and located posterolateral to each pericardial appendage. The ventricle is transversely elongate, very thick, connected to the auricles laterally, and attached to the membrane (ligament) that separates the pericardial and digestive organs in the visceral mass.

The arteries extend both forward and backward from the heart. The thickest element of the artery is the cephalic aorta (ac: Figure 9C) that extends forward on the dorsal left side of the esophagus. The aorta gives off several lateral branches of arteries to the pallial cavity (apd: Figure 9C).

The siphuncular artery (as: Figure 9A, D) arises from the anterior side of the ventricle, crosses the ventricle, extends to the base of the siphucular cord, and connects to smaller arteries of the visceral mass.

The primary element of the venous blood system is the vena cava, which runs ventral to the esophagus and just above the pallial cavity and is divided into the right and left branches in front of the heart to connect to the afferent ctenidial vessels (acv: Figure 9D, E). The blood returned from the efferent ctenidial vessels enters the heart through the auricles.

Excretory system.—The excretory organ consists of
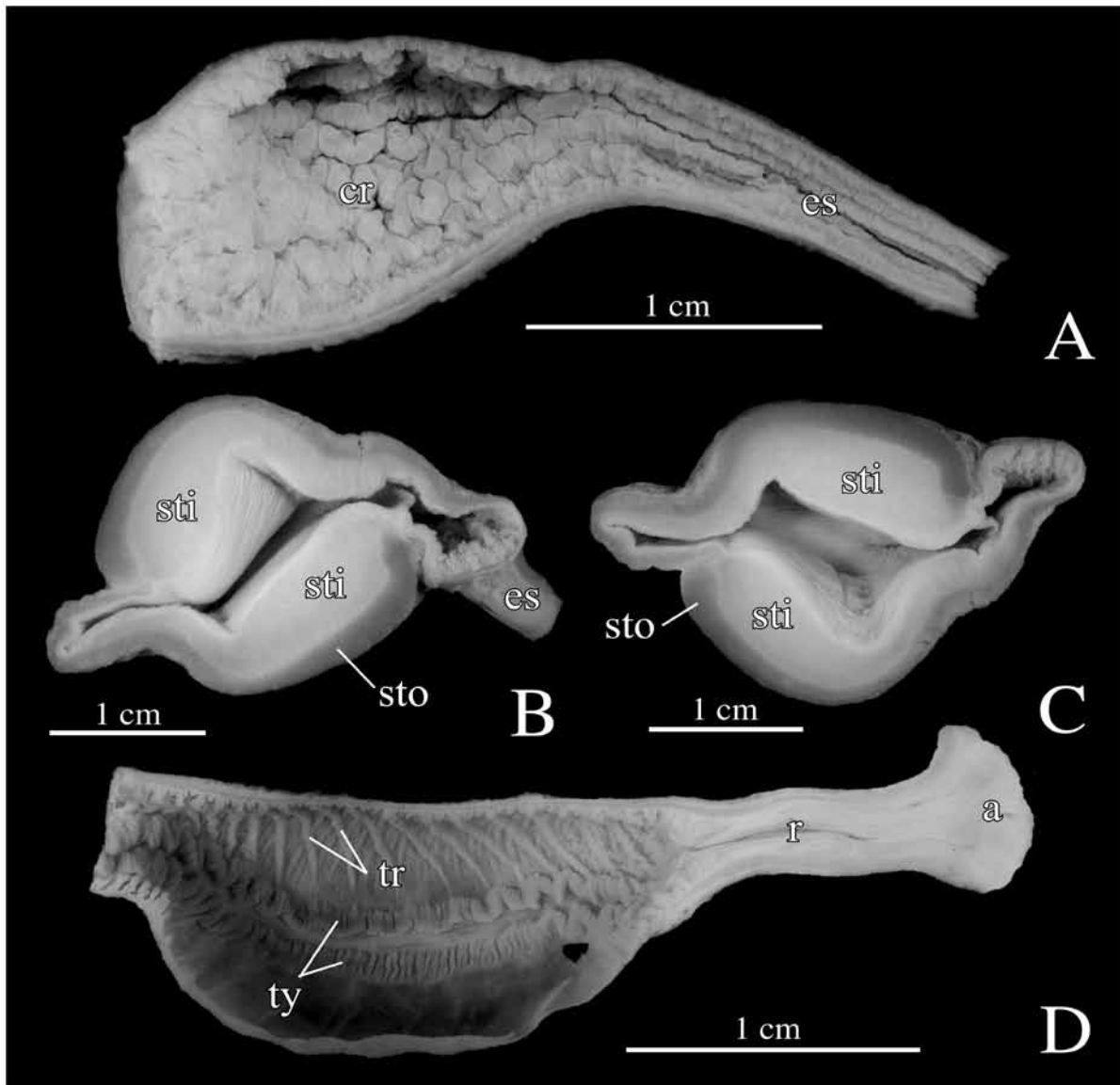
Figure 8. *Nautilus pompilius* Linnaeus. Inner structure of digestive tract. **A**. Longitudinal section of crop and posterior part of esophagus. **B**, **C**. Stomach cut into half. **D**. Longitudinal section of distal intestine, rectum, and anus. Abbreviations: a, anus; cr, crop; es, esophagus; r, rectum; sti, inner layer of stomach; sto, outer layer of stomach; tr, transverse ridge of intestine; ty, typhlosole. A, D. UMUT RM30019, B, C. UMUT RM30006.

renal and pericardial appendages and cavities. These structures are located on the anteroventral part of the visceral mass (Figure 9A, D, E).

The pericardial appendages (pa: Figure 9A, D) are two-paired in the pericardial cavity and develop on the dorsal side of the veins to the afferent branchial vessels. The surface of the appendages is conspicuously divided into many papilla. The pericardial cavity opens into the pallial cavity through a pair of openings (see pallial cavity section above).

The renal appendages (ra: Figures 9D, E, 10) are also two-paired in the renal cavities and on the dorsal side of the pericardial appendages. Their surface is smoother than that of the pericardial appendages. In magnified view, there are many small pores on the surface (rao: Figure 10B) that connect to nearly vertically extended thinner tubules (rat: Figure 10C, D). Each renal cavity has a single opening in the pallial cavity (see pallial
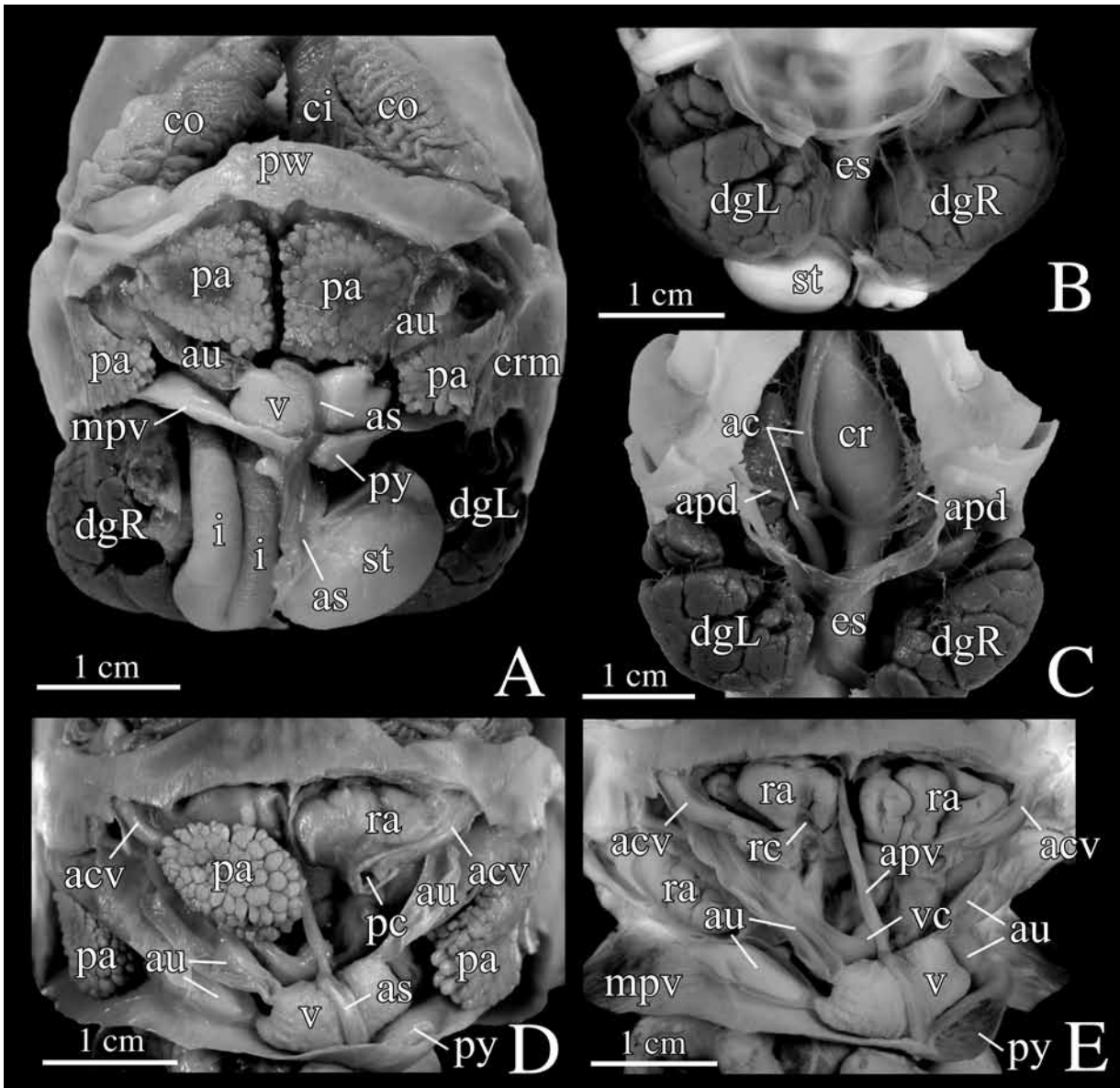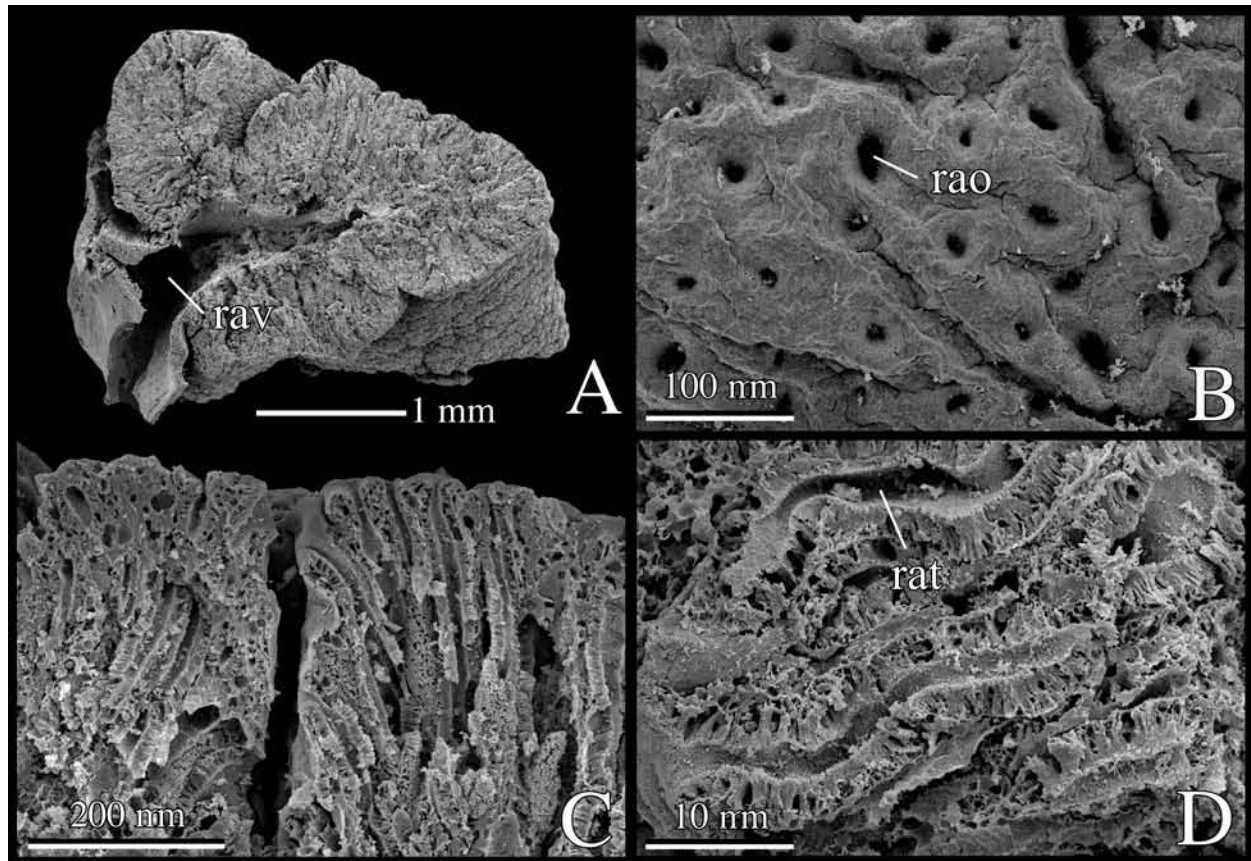
Figure 9. *Nautilus pompilius* Linnaeus. Digestive glands and pericardial and renal cavities. **A**. Ventral view of visceral mass after epithelium removed. **B**. Dorsal view of visceral mass showing paired lobes of digestive glands enclosed in a thin membrane. **C**. Same view after dorsal epithelium was removed. **D**. Organs in pericardial and renal cavities. Left inner pericardial appendage removed to show connection with afferent branchial vessel. **E**. Same view after all pericardial appendages removed. Dorsal half of pyriform gland (pg) is dissected to show the interior. Abbreviations: ac, cephalic artery; acv, afferent ctenidial vessel; apd, dorsal pallial artery; apv, ventral pallial artery; as, siphuncular artery; au, auricle; ci, inner ctenidium; co, outer ctenidium; cr, crop; crm, cephalic retractor muscle; dgL, left lobe of digestive gland; dgR, right lobe of digestive gland; es, esophagus; i, intestine; mpv, membrane between pericardial and visceral cavities; pa, pericardial appendage; pc, connection from afferent branchial vessel to pericardial appendage; pw, posterior pallial wall; py, pyriform sac; ra, renal appendage; rc, connection from branchial vessel to renal appendage; st, stomach; v, ventricle; vc, vena cava. A–C. UMUT RM30015, D. UMUT RM30019.

cavity section above).

Reproductive system.—The sexes are separate. The male and females can be distinguished externally based on four main criteria: (1) the presence or absence of nidamental glands; (2) the position and morphology of openings of the reproductive duct (right in females and central in males); (3) the presence or absence of the spadix; and (4) the sexually dimorphic organ below the mouth (see below for details).

The female reproductive system can be divided into four parts: the ovary; oviduct; nidamental glands; and organ of Valenciennes.

Figure 10. *Nautilus pompilius* Linnaeus. Scanning electron micrographs of renal appendage. **A**. Vertical section of renal appendage with connection to afferent branchial vessel. **B**. Pores on exterior surface. **C**. Marginal part of vertical section. **D**. Enlarged view of tubules. Abbreviations: rao, opening of tubule of renal appendage; rat, tubule of renal appendage; rav, connection of blood vessel to renal appendage. UMUT RM30019.

The ovary (o: Figure 11A, B) is located on the dorsal left of the visceral mass, enclosed in a thin membrane, and tied to the epithelium of the visceral mass with a thick membrane (cm: Figure 11B). The ovary contains eggs of different developmental stages and variable size.

The ovary has an opening (ovo: Figure 11A) on the anteroventral side. This opening is located at the posterior end of the oviduct, but they are not directly connected. The oviduct is markedly short and consists of two parts. The posterior section (odp: Figure 11C–F) is thin and membranous. The anterior section (oda: Figure 11C–F) is thickened and rugose on both the exterior and interior surfaces. The oviduct is depressed dorsoventrally, as is seen in the lateral view (Figure 11E). Its opening is a transverse slit (odo: Figure 11E).

The nidamental glands are attached to the ventral interior of the mantle and divided into three parts. The median part (ngM: Figure 11H) is completely exposed in the pallial cavity and striated with transverse lines

(Figure 11G). The anterolateral parts (ngR, ngL: Figure 11G) are mostly covered with a membrane and exposed in the pallial cavity only in the posterior area.

A distinct projection below the buccal mass is considered to be a reproductive organ because its morphology differs between males and females. In females, the organ is divided into two ridged and grooved structures and called the organ of Valenciennes (Figure 3F; terminology from Haven, 1977: p. 235; Arnold, 1987b: p. 355). In males, the organ in the corresponding position is a undivided flap termed the organ of van der Hoeven (oH: Figure 4B; terminology from Haven, 1977: p. 232; Arnold, 1987: p. 355).

The male reproductive system consists of the testis, spermatophoric gland, vas deferens, spermatophore sacs, penis, organs of van der Hoeven, and spadix.

The testis (t: Figure 12A, B) is on the dorsal left, as is the ovary in females. The surface of the testis is finely glandular and enclosed in a thin membrane.

The testis and spermatophoric gland (Figure 12B–
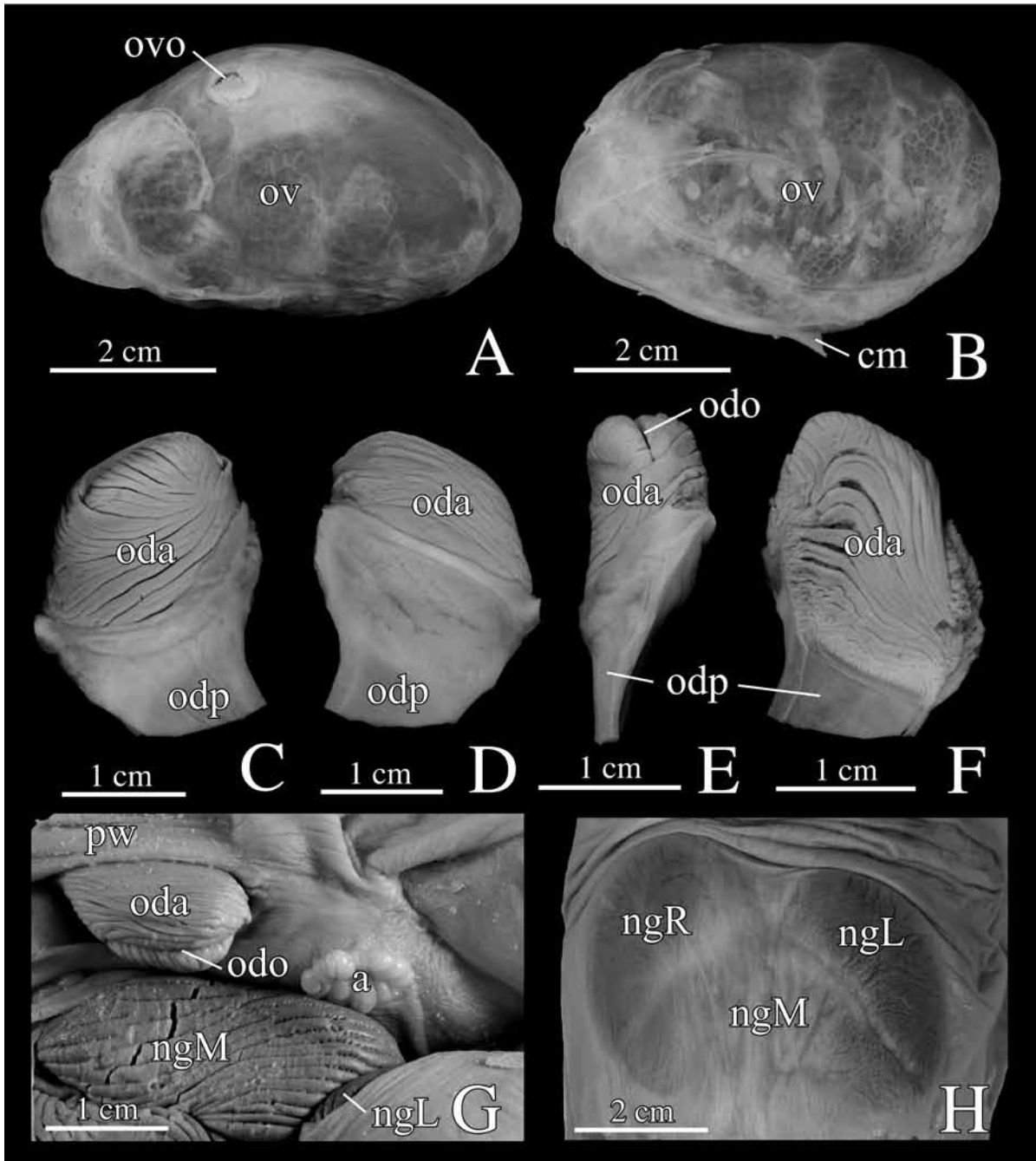
Figure 11. *Nautilus pompilius* Linnaeus. Female reproductive system. **A**, **B**. Ovary. A. Ventral view. B. Posterior view. **C-F**. Oviduct. C. Dorsal view. D. Ventral view. E. Left lateral view. F. Interior of oviduct cut into half. **G**. Frontal view of posterior pallial cavity. **H**. Ventral view of nidamental glands. Abbreviations: a, anus; cm, connecting membrane of ovary; ngL, left nidamental gland; ngR, right nidamental gland; ngM, middle nidamental gland; oda, anterior part of oviduct; odo, opening of oviduct; odp, posterior part of oviduct; ov, ovary; ovo, opening of ovary; pw, posterior pallial wall. UMUT RM30005.

E) are tied dorsally with an epithelium on the surface, but internally they are not directly connected to each other as a duct, as in the female system. The testis has a short constricted tube (to: Figure 12B), and its opening

projects into a larger opening of the spermatophoric gland (spo: Figure 12B).

The vas deferens winds complexly in the spermatophoric gland and opens into the posterior
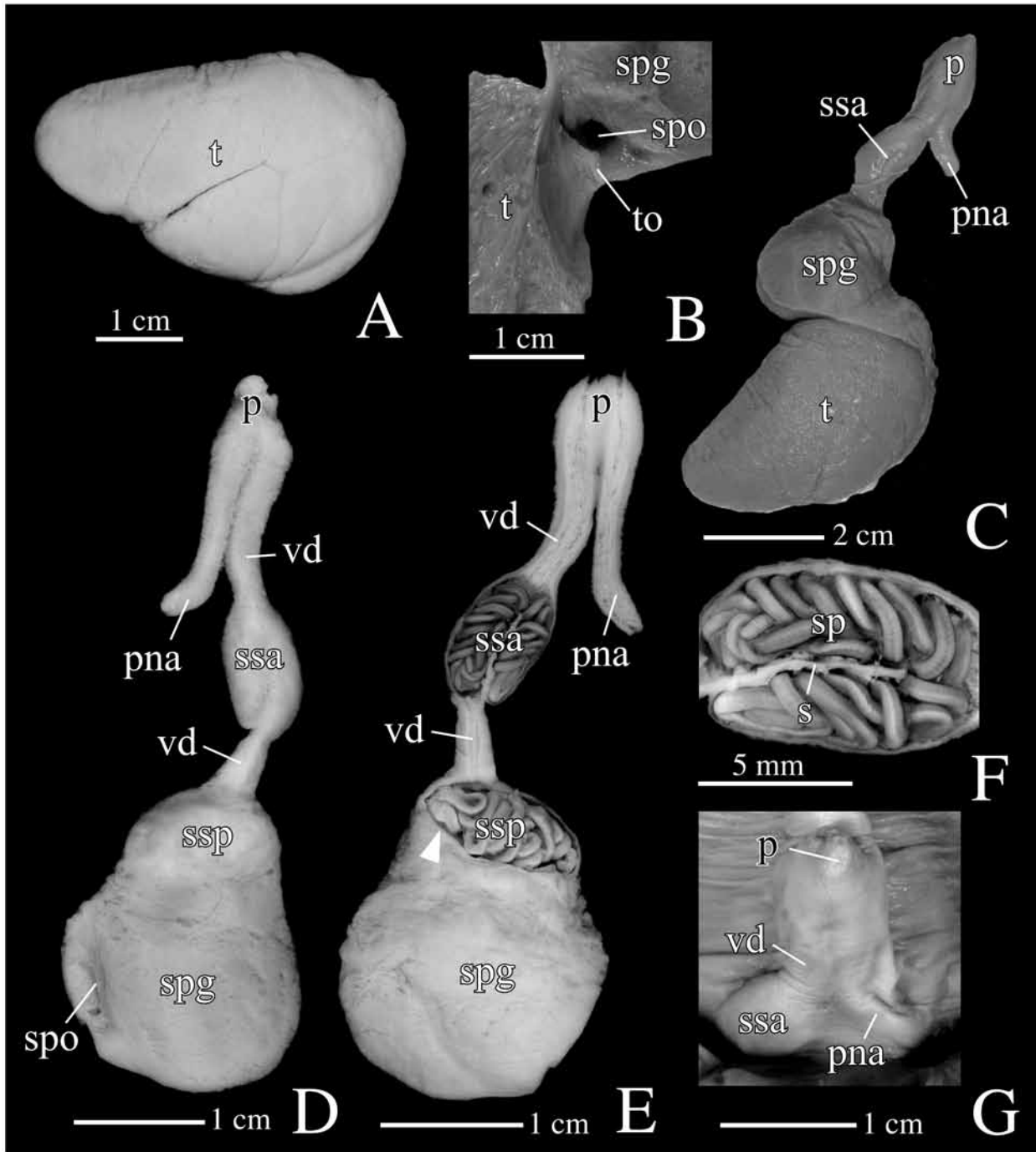
Figure 12. *Nautilus pompilius* Linnaeus. Male reproductive system. **A**. Testis. **B**. Connection between testis (t) and spermatophoric gland (spg). **C**. Entire ventral view of male reproductive system. **D**. Dorsal view of spermatophoric gland to penis. **E**. Ventral view of the same part with epithelium of spermatophore sacs (ssa, ssp), penis (p), and associated structures removed. Arrowhead indicates opening of vas deferens into posterior spermatophore sac. **F**. Enlarged view of spermatophore (sp) in anterior spermatophore sac. **G**. Penis and associated structures of posterior pallial wall. Frontal view. Abbreviations: p, penis; pna, penial appendage; s, septum of anterior spermatophore sac; sp, spermatophore; spg, spermatophoric gland; spo, opening of spermatophoric gland; ssa, anterior spermatophore sac; ssp, posterior spermatophore sac; t, testis; to, opening of testis; vd, vas deferens. UMUT RM30006.

spermatophore sac on the left side (arrowhead in Figure 12E). The spermatophore with a bright brownish hue is

coiled and stored in the sac (Figure 12E).

From the anterior border of the posterior
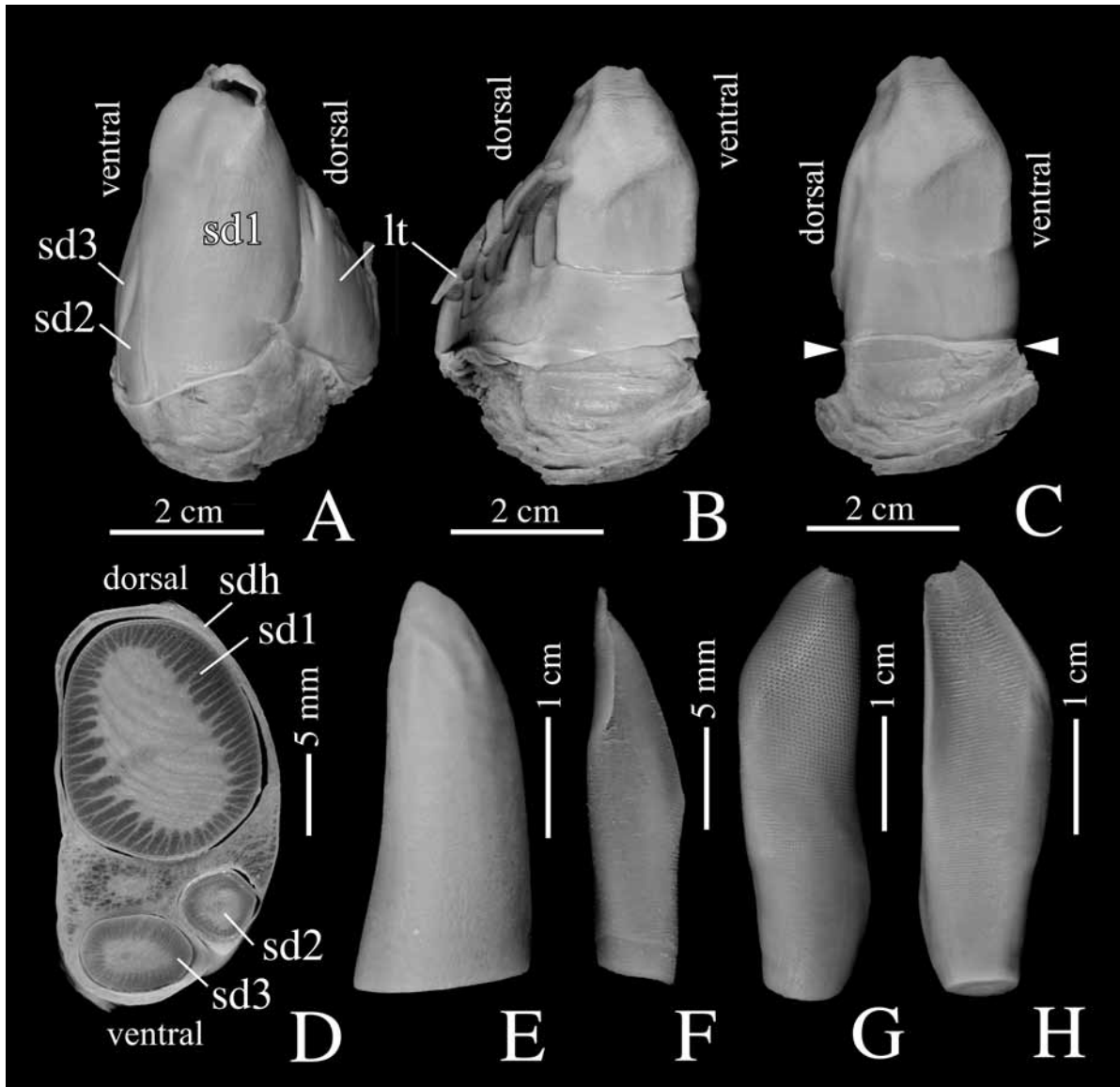
Figure 13. *Nautilus pompilius* Linnaeus. Spadix of male. **A**, **B**. Spadix with adjacent labial tentacles. **C**. Entire view of spadix. Arrowhead indicates cut position in D. **D**. Cross section of spadix. **E**. Spadix tentacle 1. **F**. Spadix tentacle 2. **G**, **H**. Spadix tentacle 3. A, E–G. Outer lateral view. B, C, H. Inner lateral view. D. Frontal view. Abbreviations: lt, labial tentacle; sd1–3, spadix tentacle 1–3; sdh, sheath of spadix tentacle. UMUT RM30006.

spermatophore sac, the vas deferens (vd: Figure 12D, E) thickens and extends forward to the penis. In the middle part, the duct is enlarged to form the anterior spermatophoric sac (ssa: Figure 12D, E) which contains a complete spermatophore (sp: Figure 12F) with a dark brownish color. The inside of the sac is sectioned by a longitudinal septum (ss: Figure 12F) except for the anterior one-fifth, and the coiled spermatophore is folded into a U-shape (Figure 12F). This part is embedded below the epithelium of the posterior wall of the pallial cavity, and its presence is discernible from

the outside (Figure 12G).

The pallial vas deferens further extends to the midline of the body and ends as the penis (p: Figure 12D, E, G) in the pallial cavity. Slightly behind the penis, there is a short appendage (pna: Figure 12C–E, G) on the right side.

In males, the labial tentacles are modified as the spadix (Figure 13) on the right ventral side. The spadix is a complex of three tentacles (sd1–3: Figure 13A, D) enclosed by a sheath (sdh: Figure 13D).

The spadix tentacle 1 (ad1: Figure 13A, D, E) is
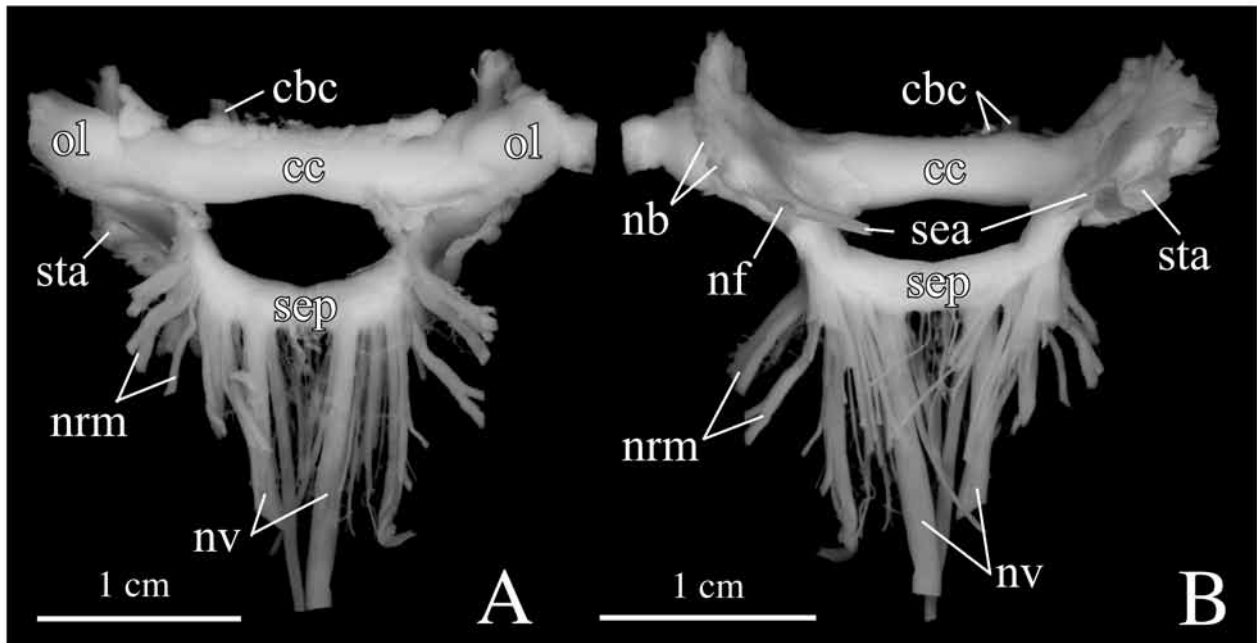
Figure 14. *Nautilus pompilius* Linnaeus. Central nervous system. **A**. Dorsal view. **B**. Ventral view. Abbreviations: cbc, cerebro-buccal connective; cc, cerebral cord; nb, brachial nerve; nf, funnel nerve; nrm, nerve to retractor muscle; nv, visceral nerve; ol, optic lobe; sea, anterior subesophageal cord; sep, posterior subesophageal cord; sta, statocyst. UMUT RM30019.

located on the dorsal-most side, prominently thick, and oval in cross section. Its surface is completely smooth on both the inner and outer sides. Numerous bundles of longitudinal muscles are distributed along the outer surface, as seen in cross section (Figure 13D). A thick nerve is also visible in the center of the tentacle.

The spadix tentacle 2 (sd2: Figure 13A, D, F) is the smallest in diameter among the three tentacles and located on the outer ventral side. Its cross-sectional form is circular at its base but concave on the inner side and convex on the outer side near the terminal part. Its surface is also smooth.

The spadix tentacle 3 (sd3: Figure 13A, D, G, H) is on the ventral side and of moderate thickness. Its cross-sectional form is depressed and ventrally convex near the distal end. The surface is smooth at the proximal one-fifth, but rough to the touch with a shagreen-like surface on the distal four-fifths on both the dorsal and ventral sides.

The spadix sheath completely surrounds the three tentacles and opens at the distal ends. In cross section, the sheath is thin near the surface of the tentacles, but there is a thickened part between spadix tentacles 1 and 2 to 3. This part contains a nerve fiber and distinct muscle fibers possibly used to contract the sheath.

Nervous system.—The central nervous system is concentrated posterior to the buccal mass (Figure 4) and consists of three major parts, the cerebral, anterior

subesophageal, and posterior subesophageal cords (Figure 14).

The cerebral cord (cc: Figure 14; also termed the supraesophageal cord) overlies the esophagus and sends nerves to the buccal structures. Some small nerves from the cord directly innervate the dorsal side of the buccal mass. The lateroventral sides of the buccal mass are innervated by the buccal ganglia (see below). Laterally, the cerebral cord is connected to the eyes through the optic lobes (ol: Figure 14).

The ventral side of the central nervous system is connected by two cords. The anterior subesophageal cord (sea: Figure 14) is anteroventral to the esophagus. The lateral part of the cord is swollen and innervates the tentacles (digital, labial, pre- and postocular tentacles), the hood, and the funnel. Because the bases of brachial and infundibular nerves are somewhat separated, they can be called the "brachial" and "infundibular" lobes, respectively. The cord on the ventral side is very thin compared with the lobes on the lateral side.

The posterior subesophageal cord (sep: Figure 14; also termed the palliovisceral cord) is very thick and posterior to the anterior subesophageal cord. The cord sends numerous nerves to the posterior part of the body. Most nerves radiating from the cord innervate the cephalic retractor muscles. A pair of thick nerves (nv: Figure 14A) extends along both sides of the vena cava and sends nerves to the organs of the visceral mass and
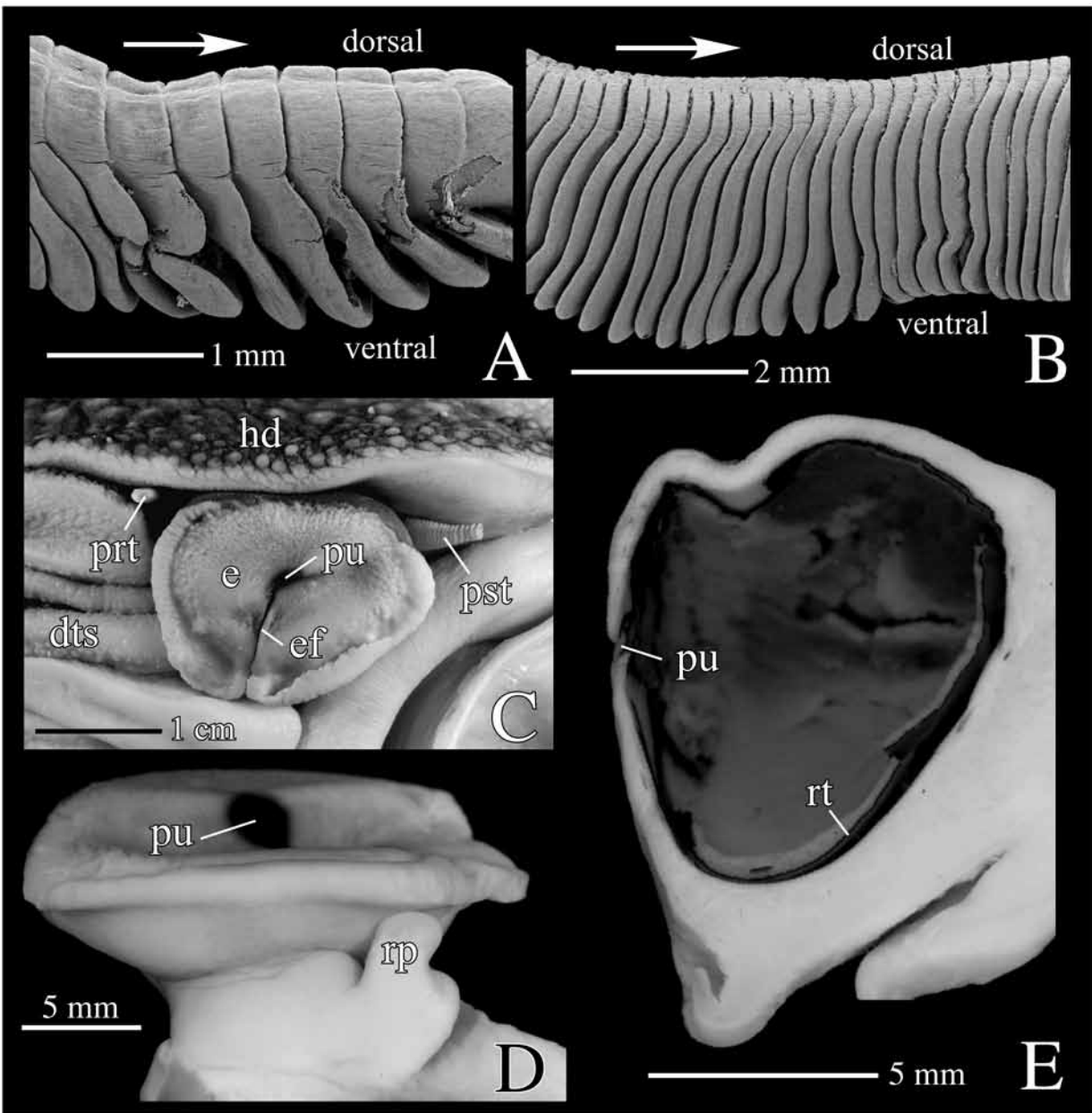
Figure 15. *Nautilus pompilius* Linnaeus. Sense organs. **A**. Scanning electron micrographs of preocular tentacle. Arrow indicates anterior. **B**. Scanning electron micrographs of postocular tentacle. Arrow indicates anterior. **C**. Left eye (e) and associated structures. **D**. Ventral view of left eye with rhinophore (rp). **E**. Vertical section of eye. Abbreviations: dts, sheath of digital tentacle; e, eye; ef, fissure of eye; hd, hood; prt, preocular tentacle; pst, postocular tentacle; pu, pupil; rp, rhinophore; rt, retina. A, B. UMUT RM30019, C. UMUT RM30015, D, E. UMUT RM30019.

pallial cavity.

The buccal mass contains a complex network of nerves. There are two small ganglia, the superior and inferior buccal ganglia (gbs, gbi: Figure 5D), both of which are visible on the surface of the buccal mass from the posterior view (Figure 5D).

The superior buccal ganglia (gbs: Figure 5D) are located on the dorsolateral side of the buccal mass, receive connectives from the cerebral cord, and extend nerves to the lateral walls of the buccal cavity.

The inferior buccal ganglia (gbi: Figure 5D) are at the mid-level of the buccal mass, connected to the superior buccal ganliga via a pair of connectives (gbc: Figure 5D), and innervate the ventral side of the buccal structures as well as the esophagus.

The optic lobes (ol: Figure 14) form a distinct mass
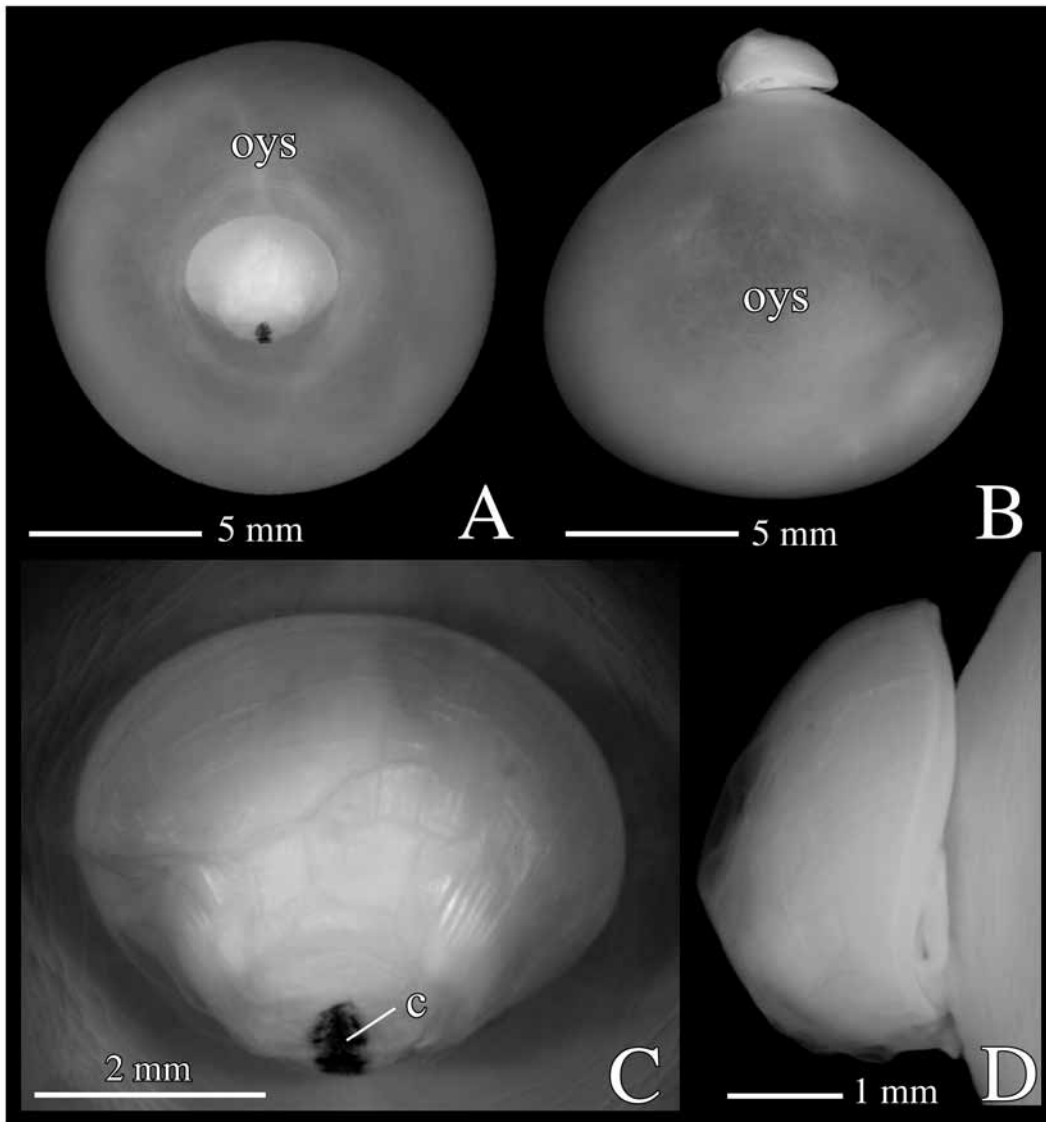
Figure 16. *Nautilus pompilius* Linnaeus. Embryo of 4-month-old. **A**, **B**. Embryo with outer yolk sac. **C**, **D**. Enlarged view of embryonic shell. A, C. Dorsal view. B, D. Right lateral view. Abbreviations: c, cicatrix; oys, outer yolk sac. UMUT RM30021.

on the lateral side of the central nervous system and are connected to the eyes.

Sensory organs.—The sensory organs are composed of digital tentacles, eyes, pre- and postocular tentacles, rhinophore, and statocysts.

The cirri of the digital tentacles are flexible and surrounded by an inflexible sheath. The surface is markedly indented by numerous annular ridges that are continuously formed from the proximal base to the distal tip.

The eyes (e: Figures 1A, 15C) are on the lateral wall of the head. The outline on the surface is oval, and the margin is distinctly edged. The pupil (pu: Figure 15C–E) opens in the center as a small pore, and from there to the ventral midpoint a vertical fissure (ef: Figure 15C, D) is clearly visible on the surface. There is no cornea or lens inside (Figure 15E). The interior is lined with a black layer of the retina (rt: Figure 15E). The distribution of extraocular muscles was not observed in this study.

The pre- and postocular tentacles (prt, pst: Figure 15C) are on the anterior and posterior sides of the eyes, respectively. The preocular tentacles are more prominently ridged ventrally than dorsally (Figure 15A). The postocular tentacles are similarly annulated dorsally and ventrally (Figure 15B).

The rhinophore (rp: Figure 15D) is located below the posteroventral part of the eyes and invisible when contracted in fixed specimens. The inside of the
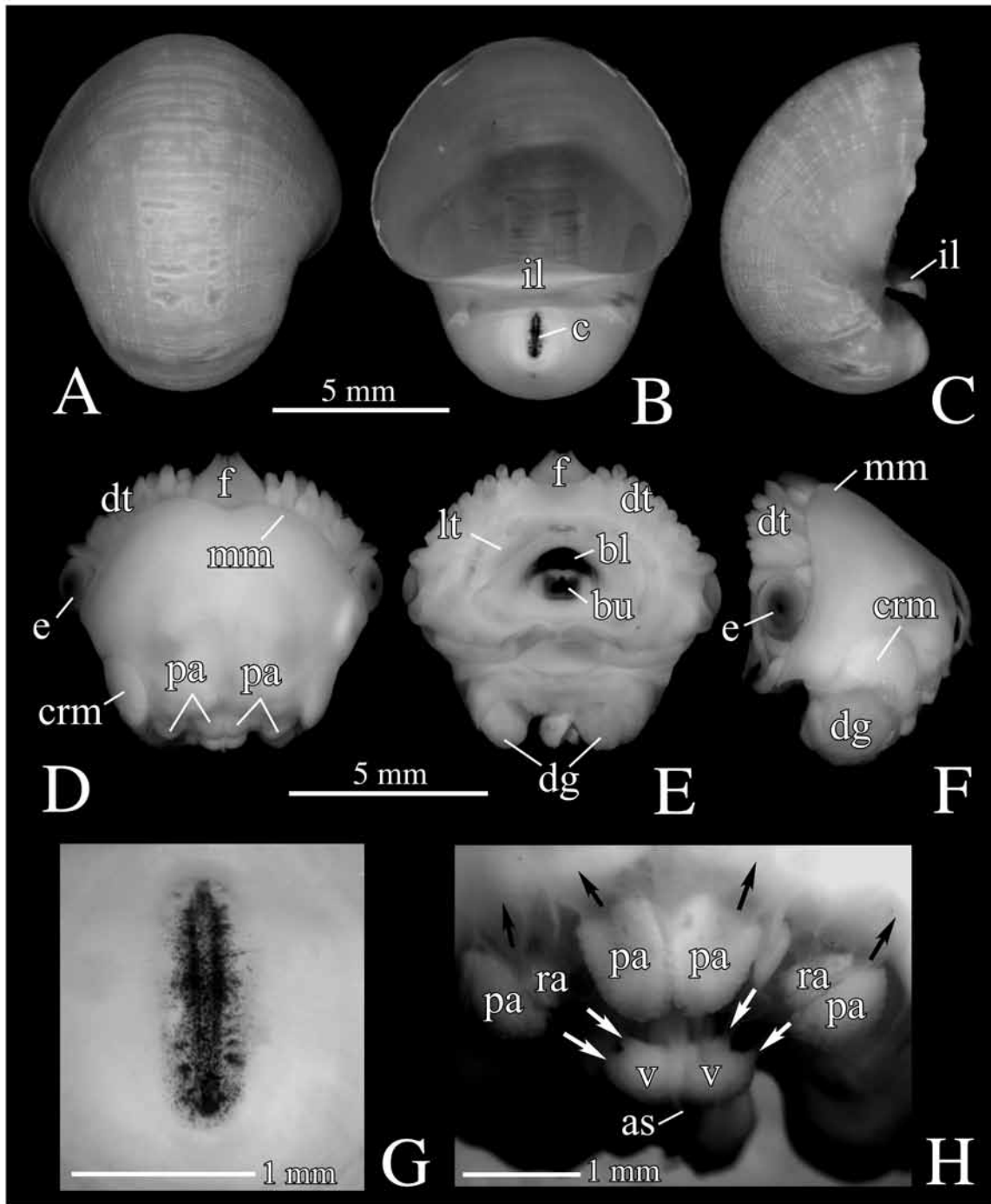
Figure 17. *Nautilus pompilius* Linnaeus. Embryo of 6-month-old. **A–C**. Embryonic shell. **D–F**. Animal. **G**. Enlarged view of cicatrix. **H**. Heart and pericardial and renal organs. Black and white arrows indicate auricles and afferent ctenidial vessels, respectively. A, D, G, H. Dorsal view. B, E. Ventral view. C. Right lateral view. F. Left lateral view. Abbreviations: as, siphuncular artery; bl, lower beak; bu, upper beak; c, cicatrix; crm, cephalic retractor muscle; dg, digestive glands; dt, digital tentacle; e, eye; f, funnel; il, inner lip; lt, labial tentacle; mm, mantle margin; pa, pericardial appendage; ra, renal appendage; v, ventricle. UMUT RM30020.

rhinophore is equipped with a thin hollow tube.

The statocysts (sta: Figure 14) are on the outer lateral side of the central nervous system. The outline of the statocysts is oval, and the inside is hollow and smooth at the gross anatomic level.

Development.—The embryonic shell is initially limpet-like (Figure 16) and later coiled spirally with an extended inner lip (il: Figure 17B, C). The midline

of the early shell is marked by a cicatrix (c: Figures 16C, 17B, G) that consists of a longitudinal groove and lateral undulations in black (see also Tanabe & Uchiyama, 1997: Figures 1B, 2B).

The embryo is attached to a large outer yolk sac (oys: Figure 16A, B) that contains a large amount of yolk. The digital tentacles originate from the lateral side, increase in number with growth, and are partially fused to form the hood in the head. The details of ontogenetic changes in external structures and their neural progenitor patterns were described by Shigeno *et al.* (2008).

The two pairs of the ctenidia do not appear simultaneously at the embryonic stage. The outer pair are formed first and the inner pair appears considerably later (cf. Shigeno *et al.*, 2008: figures 3, 4). At the 6-month stage, the latter are still small and bud-like.

The developmental process of the heart-kidney complex was not observed, but at the 6-month stage it is already well developed like that in adults (Figure 17H). The pericardial appendages (pa: Figure 17D, H), renal appendages (ra: Figure 17H), and two pairs of associated blood vessels are connected to the ventricle (v: Figure 17H) and the ctenidia. Therefore, the renopericardial system is already complete by at least the 6-month stage.

Discussion

Cephalopod synapomorphies

The synapomorphies of cephalopods are revealed by searching for the homologous similarities shared by all cephalopods but lacking in other molluscs. By comparison among *Nautilus*, coleoideans, and various conchiferan molluscs of other classes, the following characters are inferred to be obvious synapomorphies of cephalopods.

1. Arms: The arms/tentacles encircling the mouth are one of most obvious cephalopod synapomorphies. Recent ontogenetic studies of *Nautilus* have revealed a conserved five-pair pattern of *Nautilus* tentacles and coleoidean arms/tentacles (Shigeno *et al.*, 2008; cf. Boletzky, 1993, for the Coleoidea). Some authors assumed that the cerebrally innervated appendages of Scaphopoda (captacula) are homologues of cephalopod arms (e.g., Steiner & Dreyer, 2003), but ontogeny does not support this hypothesis. In the *Nautilus* embryo, the arms are derived from a pedally innervated region and merge with the head at a later stage (Shigeno *et al.*, 2008).

2. Funnel: The funnel is shared by all cephalopods and used to control movement through water by jet propulsion (Wells & O'Dor, 1991). It should be noted that the funnel valve is not a general cephalopod character. The valve is present in *Nautilus* (Figure 3C) and the decapods Coleoidea and Vampyroteuthis but absent in octopods (Vecchione *et al.*, 2000: character 28).

3. Branchial cartilage on afferent side: The ctenidial lamellae of cephalopods are supported at the afferent side by branchial cartilage in *Nautilus* (Saure *et al.*, 1987) and the Coleoidea (e.g., *Sepia*: Schipp *et al.*, 1979: figure 1). In other molluscs, the skeletal rods have a similar supportive function, but they are always on the efferent side of the lamellae if present (Yonge, 1947; Ponder & Lindberg, 1997: p. 113; Sasaki, 1998).

4. Dorsoventral paired beaks: The cephalopod beaks have been regarded as homologues of the jaws of other conchiferan molluscs (e.g., Wingstrand, 1985; Salvini-Plawen, 1988; Ponder & Lindberg, 1997; Haszprunar, 2000). The jaw is single, laterally paired, or lost in other molluscs, but dorsoventrally paired in cephalopods.

5. Simplified stomach inner structure: Generally in conchiferan molluscs, the inside of the stomach is differentiated into functionally and morphologically different regions. The common elements include the ciliated sorting area, a pair of typholosoles (major and minor typholosoles), the gastric shield, and the style sac containing the protostyle or crystalline style (see Salvini-Plawen, 1988, for the molluscan stomach in general; Purchon, 1987, 1990, for bivalves; Graham, 1949; Fretter & Graham, 1962; Sasaki, 1998; Strong, 2003, for gastropods). However, in cephalopods, all of the above structures are missing, and the inner epithelium is entirely homogeneous (Figure 8C; see also Westermann & Schipp, 1998, for *Nautilus*).

6. Caecum posterior to stomach: The large caecum separated posteriorly from the stomach is a unique character of cephalopods. In other caecum-bearing molluscs, it generally opens into the stomach near the sorting area of the proximal part of the stomach, as is found in vetigastropods (Sasaki, 1998) and heterodont bivalves (type 5 stomach of Purchon, 1987, 1990). In cephalopods, the caecum arises from the junction between the stomach and intestine (termed the vestibule), not directly from the stomach (Boucaud-Camou & Boucher-Rodoni, 1983; Mangold & Young, 1998).

7. Connection to digestive gland ducts: The digestive gland is connected to the caecum via the digestive gland ducts in *Nautilus* (Figure 7C) and the Coleoidea (Mangold & Young, 1998). In other conchiferan molluscs, the ducts open into the anterior part of the stomach, not into the caecum (e.g., Sasaki *et al.*, 2006a,

b; Sasaki & Haga, 2007: figure 6D; see also Graham, 1949; Fretter & Graham, 1962; Salvini-Plawen, 1988).

8. Renal appendages: The renal appendages are specialized outgrowths from the blood vessel between the vena cava and the afferent ctenidial vessel. No homologous structure is known in other molluscs.

9. Pericardial appendages: The pericardial appendages have an excretory function to filter waste from the afferent ctenidial vessel to the pericardial cavity (Schipp *et al.*, 1985). The pericardial glands in other molluscs are functionally analogous, but their position is different. The glands are attached to the wall of the auricles in vetigastropods (Andrews, 1985; see also Andrews, 1988; Voltzow, 1994: p. 189, for review) and basal bivalves (Andrews & Jennings, 1993; Morse & Zardus, 1997) or in the wall of the pericardial cavity in certain heterodont bivalves (Morse & Zardus, 1997).

10. Circulatory system: A "closed" circulatory system is a general character of cephalopods except for the terminal part consisting of peripheral sinuses. The vascular system is less well developed in *Nautilus* than in coleoids, especially in the venous system (Bourne, 1987; Schipp, 1987; Wells, 1983).

11. Brain: The central nervous system is more prominently concentrated in cephalopods than in other molluscs and forms a completely continuous ring or tight mass of nerve cords (Young, 1988; Budelmann, 1995; Nixon & Young, 2003). In other molluscan classes, various ganglia may aggregate around the head area (e.g., Shigeno *et al.*, 2007), but the nerve cords do not densely concentrate as in cephalopods.

12. Optic lobes: The eyes of cephalopods are controlled by the well-developed optic lobes of the brain. In gastropods, the eyes are innervated from the cerebral ganglia via a pair of thin optic nerves.

13. Extraocular muscles: The presence of specific muscles controlling the movement of the eyes are unique to cephalopods. In eye-bearing gastropods, the direction of vision is adjusted by changing the position of the head and/or eye stalks. In other molluscs, there are no homologous cephalic eyes innervated by the cerebral ganglia (Haszprunar, 2000: character 54).

14. Direct development without larval stage: The lack of true larval stages (trochophore, veliger, or other modified forms such as pericalymma and glochidium) is the character separating the cephalopods from other molluscs.

15. Meroblastic, nonspiral cleavage: The eggs of cephalopods contain a large amount of yolk which hinders total cleavage. The process of cleavage has not been observed in *Nautilus*, but partial cleavage can be assumed from the discoidal embryo much smaller than the yolk (Arnold & Carlson, 1986: figure 16).

16. Outer yolk sac: The presence of an enlarged epithelium containing a huge mass of yolk (Figure 16 in *Nautilus*) is an obvious synapomorphy of cephalopods. It is formed by epibolic gastrulation in ontogeny (e.g., Boletzky, 1988a, b). In other molluscs, the yolk is generally contained only inside embryos.

In addition to the above characters, there are additional features that may be truly synapomorphic for all cephalopod groups. The states of these characters are still ambiguous and should be studied extensively among various groups of cephalopods.

The buccal musculature in cephalopods differs markedly from that of other molluscs. The entire musculature is voluminous (cf. Boyle *et al.*, 1979; Young, 1991; Kear, 1994), but the division of muscles is more simplified compared with that in other molluscs, especially Poly- and Monoplacophora (Lemche & Wingstrand, 1959; Graham, 1973; Wingstrand, 1985). In Gastropoda, a pair of retractor muscles is present only on the ventral side in most groups of Caenogastropoda, and there is no odontophoral retractor in any group of basal gastropods (Sasaki, 1998). In Scaphopoda, the buccal musculature has not been described in detail. The buccal musculature probably encompasses several synapomorphies confined to cephalopods and must be compared more widely among cephalopods in future studies.

Various forms of cartilage are generated in different parts of the cephalopod body (Budelmann *et al.*, 1997: p. 161). Their presence is a common cephalopod character, but they are probably a complex of different characters. Therefore, more detailed comparisons of cartilage forms are necessary throughout the cephalopods. In *Nautilus*, cartilage is distributed at the base of the funnel (the funnel cartilage), as shown by Bizikov (2002) and in this study (Figure 3C). Histologically the cartilage is not uniform among various groups of cephalopods (Nixon, 1998a).

The acquisition of the siphuncle and septa in the shell is the most obvious hallmark of ancestral cephalopods (Yochelson *et al.*, 1973). However, these are not present throughout living cephalopods but considered to be secondarily lost in shelless groups. Therefore, these characters are recognized as putative synapomorphies of ancestral cephalopods.

Other characters listed in past studies are not synapomorphic for cephalopods but diagnostic for the Coleoidea. For example, the cranial cartilage was listed as a cephalopod synapomorphy by Waller (1998: p. 15), but the brain is not encased in a thick cartilage in *Nautilus* as in all other molluscan classes. Characters

lacking in *Nautilus* should no longer be considered as cephalopod synapomorphies.

The presence of the nidamental glands has been listed as one of the cephalopod synapomorphies by some authors (e.g., Engeser, 1996). The glands are present in *Nautilus* and decapods, but there is no homologous gland in octopods or *Vampyroteuthis* (Vecchione *et al.,* 2000: character 23). In the latter groups, the function of the nidamental glands is compensated for by the oviductal gland formed in the oviduct (e.g., Froesch & Marthy, 1975; Villanueva, 1992).

Endothelial blood vessels seem to be a shared cephalopod-specific character, but this may not be entirely true. In the Coleoidea, the blood vessels, especially large ones in arteries, are obviously three-layered with a tunica adventitia, tunica intima, and tunica media (Budelmann *et al.*, 1997: p. 247). Meanwhile, the corresponding innermost layer is absent in the aorta of *Nautilus macromphalus* (Budelmann *et al.*, 1997: figure 112).

Nautilus versus Coleoidea

Major differences are recognized between *Nautilus* and the remainder of living cephalopods (Coleoidea) and also noncephalopod conchiferan molluscs. A list of their clear differences is revised below based on our own observations and a literature search (Table 1). In the literature, most data for the Nautilidae were derived from *Nautilus pompilius* and *N. macromphalus* (see Budelmann *et al.*, 1997). The anatomy of *"Allonautilus"* (Ward & Saunders, 1997) has not been clearly described, but there are no striking differences in anatomic characters according to the character matrix of Lindgren *et al.* (2004: as *Nautilus scrobiculatus*).

1. Shell: Cephalopods possibly originated from a monoplacophoran-like ectocochleate ancestor (Yochelson *et al.*, 1973) and subsequently underwent the internalization and loss of the shell. The shell is primitively external in *Nautilus*.

2. Embryonic shell: The cup-shaped early embryonic shell of *Nautilus* may be comparable to the protoconch of Monoplacophora (Warén, 1988; Warén & Hain, 1992). The shells of other conchiferan molluscs also start from a shield-like form in the initial stage of their formation, and thus the flattened form is inferred to be primitive among conchiferan molluscs. In this view, the bulbous embryonic shells in *Spirula* and Ammonoidea (Landman *et al.*, 1996) are more derived.

3. Cicatrix: The embryonic shell possesses a grooved structure called the cicatrix in *Nautilus* (Arnold, 1987a; Landman *et al.*, 1989; Tanabe & Uchiyama, 1997) but does not in other coleoidean cephalopods. The presence

of this character is apomorphic, since no comparable structure is found in the protoconch of noncephalopod molluscs. The *Nautilus*-type cicatrix is also known in *"Orthoceras"* sp. (Tanabe & Uchiyama, 1997: figure 9).

4. Arms: The number of arms/tentacles is much greater in *Nautilus* than in the Coleoidea (four to five pairs). The total number in *Nautilus* is 38 outer arms (digital tentacles) and 24 (male) or 48–52 (female) inner arms (labial tentacles) (Budelmann *et al.*, 1997: p. 127). Ontogenetically, the numerous pairs of *Nautilus* arms arise from the five-pair condition (Shigeno *et al.*, 2008). This suggests that the greater number of *Nautilus* arm is apomorphic, or the lower number of coleoidean arms is paedomorphic.

5. Digital tentacles: In *Nautilus*, the digital and labial tentacles are composed of an outer sheath and inner cirri (see Fukuda, 1987; Kier, 1987, for tentacle inner structure), but the arms of the Coleoidea lack the outer sheath. The polarity of this character is ambiguous.

6. Suckers: The arms/tentacles are equipped with suckers in all cephalopods except for *Nautilus*. The polarity is also indeterminate.

7. Funnel: The funnel is unfused and enrolled in *Nautilus* (Figure 3A), but closed as a complete tube in the Coleoidea. Because the closed funnel of the Coleoidea is derived from paired primordia ontogenetically (Naef, 1928), the state in *Nautilus* may represent a primitive condition.

8. Hood: The muscular hood is a character confined to *Nautilus*. Functionally, it is used to seal the shell aperture for protection and analogous to the gastropod opercula. The presence of this character is an autapomorphy of *Nautilus*.

9. Mantle thickness: The mantle of *Nautilus* is primitively thin as in other conchiferan molluscs. In the Coleoidea, the mantle is substantially thickened with layers of muscles and connective tissue (see Kier, 1988; Kier & Thompson, 2003, for review). Functionally, this difference is correlated with the mode of ventilation in the pallial cavity: the water current into the pallial cavity is generated by the muscle contraction of the mantle in the Coleoidea but by contraction of the cephalic retractor muscle and undulating contractions of the funnel wings in *Nautilus* (Wells, 1988; Wells & O'Dor, 1991; Bizikov, 2002).

10. Periostracal groove: The periostracal groove (Figure 1D) is primitively distinct in the mantle margin in *Nautilus* (see Westermann *et al.*, 2005, for histologic evidence) but lacking in the Coleoidea. The groove is located between the thinner outer lobe and thicker inner lobe (but further divided marginally: Westermann *et al.*, 2005) in *Nautilus*, Gastropoda, and Scaphopoda (Stasek

& McWilliams, 1973). In the Bivalvia, the groove is between the outer and middle folds, but this condition is possibly derived from the bipartite mantle margin (Morton & Peharda, 2008). Therefore, the double-folded mantle margin is possibly primitive among conchiferan molluscs except for specialized Monoplacophora (Schaefer & Haszprunar, 1997, with correction by Lemche & Wingstrand, 1959).

11. Fins: Fins are absent in all noncephalopod molluscs, *Nautilus*, and incirrate octopods. Their absence in *Nautilus* is plesiomorphic, and the state in incirrate octopods is presumably a consequence of secondary loss.

12. Chromatophores: Various forms of chromatic elements (the chromatophore organs, iridophores, reflector cells, and leukophores) develop in the skin of most groups of Coleoidea (Herring, 1977: table 1, 1988; Budelmann *et al.*, 1997: p. 137–144) and are used for inter-/intraspecific communication and protection (Hanlon & Messenger, 1996). All of these elements are lacking in *Nautilus*, possibly because it is not necessary for an animal with a complete outer shell and weak vision to change body color. Their absence, as in other molluscs, is plesiomorphic.

13. Photophores: Luminescent organs are commonly observed in many species of Coleoidea (Herring, 1988; Budelmann *et al.*, 1997: p. 144–153) but undeveloped on the body surface of *Nautilus* and other molluscs. The absence of photophores is a plesiomorphy for cephalopods.

14. Ctenidia: Ontogeny suggests that the tetrabranchiate condition in *Nautilus* has been secondarily multiplied from an original single pair, or that the single-paired condition in the Coleoidea arose by paedomorphosis. In the early embryonic stage of *Nautilus*, the two pairs are not equal: the outer pair appears first and grows more rapidly than the inner pair (Arnold, 1987b: figure 3; Shigeno *et al.*, 2008: figures 3, 4). This means that the ctenidia increase toward the posterior with development. In the adult stage of other molluscs, the number of the ctenidium(a) is none, unpaired, or a single pair in the possible sister classes Gastropoda and Scaphopoda. Therefore, fewer ctenidia seem to be primitive for cephalopods.

15. Afferent ctenidial membrane: The ctenidia are suspended from the afferent ctenidial membrane (gill ligament) in the Coleoidea (e.g., Wells & Wells, 1982) but hang freely from the posterior pallial wall in *Nautilus* (Figure 2A; see also Saure *et al.*, 1987) and basal gastropods (Patellogastropoda). In other conchiferan classes, the ctenidia is suspended vertically from the pallial roof in Bivalvia (except septibranchs) and Monoplacophora (Haszprunar & Schaefer, 1997)

or entirely lost in Scaphopoda (Shimek & Steiner, 1997). Thus, the absence of a long membrane along the ctenidial axis is a primitive character.

16. Cephalic retractor muscle: The cephalic/funnel retractors are attached to the shell laterally in *Nautilus*, but inserted dorsally into the shell, gladius, or mantle in the Coleoidea (Wells, 1988). In other conchiferan molluscs, the head retractor muscles are inserted dorsally on the shell, if present (see Haszprunar & Wanninger, 2000, for details). Therefore, the lateral shift of the muscle in *Nautilus* is autapomorphic.

17. Extraocular muscles: The extraocular muscles number four in *Nautilus*, seven in octopods, and 13 or 14 in decapod coleoids (Young, 1965; Budelmann & Young, 1993; Budelmann *et al.*, 1997: p. 353). Since the homologous muscle is absent in other molluscs, the polarity of this character is equivalent.

18. Radular appendages: The radular appendages are an autapomorphy of *Nautilus* (Messenger & Young, 1999: figure 40; this study: Figure 6A, B) but absent in coleoid cephalopods and other conchiferan molluscs.

19. Posterior salivary glands: There are no posterior salivary glands in *Nautilus*, unlike the Coleoidea (Mangold & Young, 1998: Table 1; see Budelmann *et al.*, 1997: p. 193–196 for a review of the three types of cephalopod salivary glands). The duct of the posterior salivary glands opens into the salivary papilla used for shell drilling in *Octopus* (Nixon, 1980). In noncephalopod molluscs, various forms of gland associated with the buccal structure are called salivary glands, and their homology is not always clear. Therefore, the polarity of this character is uncertain.

20. Radular teeth: The radula comprises 13 elements in *Nautilus* (rachidian, four lateral, four marginal teeth, and four marginal plates) (Tanabe *et al.*, 1990) rather than nine (rachidian, four lateral, two marginal teeth, and two marginal plates) as in the Coleoidea (Nixon, 1998b) and Ammonoidea (Tanabe & Fukuda, 1999) except for the radulaless *Spirula*. The polarity of this character is indeterminable, because the number of radular teeth varies extremely widely among mollsucs (see Salvini-Plawen, 1988).

21. Beak calcification: The beaks are strengthened by calcareous tips with denticles in *Nautilus* but are noncalcified in the Coleoidea (Tanabe & Fukuda, 1987, 1999; Clarke & Maddock, 1988a; Nixon, 1988). The beak calcification is an obvious apomorphy found only in some cephalopods among molluscs. A *Nautilus*-like lower beak with a calcareous tip is also known in lytoceratid and phylloceratid ammonoids (Tanabe & Fukuda, 1999).

22. Lower beak: In Recent species, the inner lamella

Table 1. Differences between *Nautilus* and the Coleoidea and their polarity inferred by outgroup comparison. Abbreviations: a, apomorphic; e, equivalent; p, plesiomorphic. *States in *Nautilus* are apomorphic, or those of the Coleoidea are paedomorphic under the ontogenetic critera. **Scaphopod captacula may be homologized with cephalopod arms (Steiner & Dreyer, 2003), but ontogeny does not support this view (Shigeno *et al.,* 2008).

#	Character	*Nautilus*	Coleoidea	Other conchiferan molluscs
1	Shell	external (p)	internal/lost (a)	external (mostly), internal or absent
2	Embryonic shell	cup-shaped (p)	bulbous or unmineralized (a)	initially shield-like
3	Cicatrix	present (a)	absent (p)	absent
4	Number of arms/tentacles	62–90 (e)*	8–10 (e)*	Absent**
5	Digital tentacles	present (e)	absent (e)	absent
6	Suckers	absent (e)	present (e)	absent
7	Funnel	unfused (e)	fused (e)	absent
8	Hood	present (a)	absent (p)	absent
9	Mantle thickness	thin (p)	thick (a)	thin
10	Periostracal groove	present (p)	absent (or internal?) (a)	present
11	Fins	absent (p)	present (a) or absent	absent
12	Chromatophores	absent (p)	present (a) or absent	absent
13	Photophores	absent (p)	present (a) or absent	absent
14	Ctenidia	2 pairs (a)*	1 pair (p)*	absent, single, 1 pair, or 3–6 pairs
15	Afferent ctenidial membrane	absent (p)	present (a)	absent (mostly) or weakly developed
16	Cephalic/funnel retractor muscles	laterally inserted (a)	dorsally inserted (p)	dorsoventral muscles dorsally inserted
17	Number of extraocular muscles	4 (e)	7, 13 or14 (e)	absent
18	Radular appendages	present (a)	absent (p)	absent
19	Posterior salivary glands	absent (e)	present (e)	present or absent
20	Radular teeth	13 (e)	9 (mostly), 5, or 0 (rare) (e)	numerous to absent
21	Beak calcification	present (a)	absent (p)	absent
22	Inner lamella of lower beak	reduced (e)	developed (e)	absent
23	Caecum	small (e)	large (e)	small, large, or absent
24	Ink gland complex	absent (p)	present (a)	absent
25	Pericardial appendages, position	from veins to afferent ctenidial vessels (e)	posterior to branchial heart (e)	absent

26	Pericardial and renal appendages	2 pairs (e)	1 pair (e)	absent
27	Digestive gland appendages	absent (p)	present (a)	absent
28	Openings of renal cavities	2 pairs (a)	1 pair (p)	1 pair or single
29	Openings of pericardial cavity	1 pair (a)	absent (p)	absent
30	Male gonoduct	right (e)	left (e)	paired, right or left
31	Spadix	present (a)	absent (p)	absent
32	Spermatophore	simple (p)	with ejaculatory apparatus (a)	absent or simple
33	Organ of van der Hoeven	present (a)	absent (p)	absent
34	Female gonoduct	right (e)	left or paired (e)	paired, right or left
35	Nidamental glands	ventral (e)	dorsal or absent (e)	absent
36	Organ of Valenciennes	present (a)	absent (p)	absent
37	Pyriform sac	present (a)	absent (p)	absent
38	Branchial heart	absent (p)	present (a)	absent
39	Number of auricle(s)	2 pairs (a)	1 pair (p)	1 pair, single or absent
40	Valves between auricle and ventricle	unpaired (e)	paired (e)	absent
41	Cephalic aorta	left (e)	right (e)	center, left, or right
42	Site of hemocyanin synthesis	digestive glands (e)	branchial glands (e)	uncertain (rhogocytes)
43	Brain	less concentrated (p)	highly concentrated (a)	circumesophageal nerve loop
44	Cranial cartilage	absent (p)	present (a)	absent
45	Stellate ganglia	absent (p)	present (a)	absent
46	Eyes	open without lens (p)	closed with lens (a)	open, closed, or absent
47	Pre- and postocular tentacles	present (a)	absent (p)	absent
48	Rhinophore	present (a)	absent (p)	absent
49	Osphradia	present (p)	absent (a)	present or absent
50	Position of statocysts relative to central nervous system	lateral (p)	ventral (a)	lateral, anterior, or posterior to pedal ganglia
51	Statoconia/statoliths	statoconia (e)	statolith (e)	statoconia or statolith
52	Inner wall of statocysts	simple (p)	complex (a)	simple

is short in *Nautilus* (Okutani & Mikami, 1977; Tanabe & Fukuda, 1987, 1999) but projected posteroventrally in the Coleoidea (see Tanabe & Fukuda, 1999 for details). The polarity is uncertain for this character, because the lower jaw is absent in all classes of noncephalopod molluscs.

23. Caecum: The caecum associated with the stomach is small and consists only of a half coil in *Nautilus* (Westermann & Schipp, 1998; this study: Figure 7), but is larger with one or two coils in the Coleoidea (e.g., Mangold & Young, 1998). In other molluscs, the caecum is small, multispiral (some Vetigastropoda), or absent. The polarity is also unclear in this character.

24. Ink gland: The ink gland complex (ink gland, ink sac, and ink sac duct) is connected to the rectum in the Coleoidea (Budelmann *et al.*, 1997: figure 75) but primitively absent in *Nautilus* and noncephalopod molluscs. The ink is used for antipredatory defense and probably developed in relation to the internalization of the shell in cephalopods.

25. Position of pericardial appendages: The pericardial appendages (= the branchial heart appendages in the Coleoidea) arise from the posterior wall of the branchial heart in the Coleoidea but directly from the vessels to the ctenidia in *Nautilus* (Schipp *et al.*, 1985; Budelmann *et al.*, 1997: figure 119; this study: Figure 9). No homologous structure develops in the afferent ctenidial vessels of other molluscs. The polarity of this character is indeterminable.

26. Renal appendages: There are two pairs of renal appendages in *Nautilus* (Figure 9), but a single pair in the Coleoidea. See also Schipp & Martin (1981, 1987) and Budelmann *et al.* (1997: figures 128, 130) for details of this character. The polarity is also uncertain.

27. Digestive gland appendages: The digestive gland duct appendages (= pancreatic appendages) have excretory and reabsorptive functions from the duct of digestive glands in the Coleoidea (Schipp & Boletzky, 1976; Budelmann *et al.*, 1997: pp. 200, 261–264) but are absent in *Nautilus* (Mangold & Young, 1998) and other noncephalopod molluscs. Their absence is obviously plesiomorphic.

28. Opening of renal cavity: There are two pairs of openings of the renal cavities in *Nautilus* (Figure 2A, B), but a single pair of openings in the renal sacs of the Coleoidea. In other molluscs, the number of opening(s) is one or two based on the number of renal organs. The two pairs of openings are an autapomorphy of *Nautilus*.

29. Opening of pericardial cavity: A pair of pericardial openings is located close to the inner renal openings in *Nautilus* (Figure 2A, B), but the pericardial cavity opens only into the renal sacs via a pair of renopericardial

ducts in the Coleoidea (Martin, 1983; Schipp *et al.*, 1985; Budelmann *et al.*, 1997). The latter condition is common among conchiferan molluscs and considered to be primitive for cephalopods.

30. Male gonoduct: The male gonoduct is on the right side in *Nautilus* (Figure 12) but on the left side in the Coleoidea (Budelmann *et al.*, 1997: p. 281). In outgroups, the gonoduct is on the right side and connected to the right nephridium in Scaphopoda (Shimek & Steiner, 1997: p. 771). In Gastropoda, the gonoduct is also unpaired and occurs on the right side in most species but on the left side in sinistrally coiled species. In other mollucsan classes, the ducts are always paired. The right gonoduct may be primitive, but this is not decisive.

31. Spadix: The spadix on the ventral left side is used for spermatophore transfer from males to females in *Nautilus* (Haven, 1977; Mikami & Okutani, 1977, 1981; Arnold, 1984, 1987b). The hectocotylus (see Nesis, 1995, for review) is a functionally analogous organ on various arms in the Coleoidea. This character is an autapomorphy of *Nautilus*.

32. Spermatophore: The spermatophore of *Nautilus* is simple and filamentous but equipped with accessory structures for ejection in the Coleoidea (see Budelmann *et al.*, 1997: figure 147). The specialized form of coleoidean spermatophore is apomorphic among molluscs.

33. Organ of van der Hoeven: The organ of van der Hoeven (Figure 3D, F) below the buccal mass is known only in *Nautilus* males among molluscs.

34. Female gonoduct: The female gonoduct is on the right side in *Nautilus* (Figure 12) but either paired as in most oegopsid squids (e.g., Nigmatullin *et al.*, 1991) and incirrate octopods or on the left side as in sepioids, myopid squids, and cirrate octopods (Budelmann *et al.*, 1997: p. 281). The polarity of this character is difficult to determine clearly.

35. Nidamental glands: A pair of nidamental glands is attached dorsally to the visceral mass in decapods or absent in octopods but develops ventrally on the mantle in *Nautilus* (Figures 1E, 11G, H). Since homologous glands are unknown in outgroups, the polarity of this character is uncertain.

36. Organ of Valenciennes: The organ of Valenciennes (Figure 3D, F) is known only in *Nautilus* females among molluscs.

37. Pyriform sac: The pyriform sac (py: Figure 9) is present in *Nautilus* but absent in the Coleoidea and other molluscs. Griffin (1900) and Arnold (1987b: p. 358) assumed that it is a reduced part of originally paired gonoducts, but this hypothesis should be confirmed in

future studies. Although this organ has been called the pyriform "gland" by some authors (e.g., Willey, 1902; Arnold, 1987b), the actual function of this organ has not yet been confirmed.

38. Branchial heart: The branchial heart at the base of the afferent ctenidial vessels is one of the synapomorphies of the Coleoidea. In *Nautilus*, this character is absent, although a contractile part of the afferent ctenidial vessels may be homologized with coleoidean branchial hearts (Schipp & Martin, 1987). There is no homologous organ in other molluscs.

39. Auricles: There are two pairs of auricles in *Nautilus* but a single pair in the Coleoidea in accordance with the number of ctenidia. The increased number in *Nautilus* compared with the Coleoidea and other molluscs is regarded as an apomorphy.

40. Valves of heart: The valves separating the ventricle and auricles are paired in the Coleoidea but unpaired in *Nautilus* (Budelmann *et al.*, 1997: p. 236). In other molluscs, there is no specialized valve in the heart. Thus, the polarity of this character is equivalent.

41. Cephalic aorta: The cephalic aorta is on the left side in *Nautilus* (Figure 9C; also Bizikov, 2002: figures 2–4 as dorsal aorta) but on the opposite side in the Coleoidea (Budelmann *et al.*, 1997: p. 236). In other molluscs, the aorta is along the midline in symmetrical forms. In many gastropods, its position shifts to the left side in dextral forms but is on the right side in sinistral forms. The polarity of this character is difficult to interpret. This asymmetry might be correlated with the inversion of male/female gonoducts between *Nautilus* and the Coleoidea.

42. Site of hemocyanin synthesis: Hemocyanin is synthesized in the digestive gland (= mid-gut gland) in *Nautilus* (Ruth *et al.*, 1988, 1999) but in the branchial glands located between the ctenidial membrane (gill ligament) and ctenidial lamellae in the Coleoidea (Budelmann *et al.*, 1997: p. 228, 233; see Wells & Wells, 1982, for position). In other molluscs, the cite of hemocyanin synthesis has not been generally identified, but thogocytes have been inferred to have a function in hemocyanin synthesis (Haszprunar, 1996; Albrecht *et al.*, 2001).

43. Brain: The central nervous system in *Nautilus* consists of three large loops around the esophagus and is less concentrated than in the Coleoidea (Young, 1965, 1987; Nixon & Young, 2003: figure 14). The number of brain lobes (excluding optic lobes) is 12 in *Nautilus* and 24 in octopods and decapods, but the latter can be subdivided into 36 to37 (Budelmann *et al.*, 1997: p. 312). This simple morphology of the *Nautilus* brain is functionally explained by the lower learning

ability, slow movement, and absence of fins and chromatophores.

The more diffused brain of *Nautilus* can be viewed as a plesiomorphy by outgroup comparison. Based on the relative position and innervation pattern, the cerebral, anterior subesophageal, and posterior subesophageal cords of *Nautilus* correspond to the cerebral, ventral (pedal) cord, and lateral (visceral) cords of other molluscs, respectively.

44. Cranial cartilage: The brain is enclosed in cartilage in the Coleoidea but it is free of cartilage in *Nautilus* and noncephalopod molluscs. The latter state is undoubtedly plesiomorphic.

45. Stellate ganglia: Stellate ganglia are present in the mantle in the Coleoidea but absent in *Nautilus* and other molluscs. This is also a plesiomorphy of *Nautilus*.

46. Eyes: The eyes are hollow without lens in *Nautilus* (Nixon & Young, 2003: figure 3.8; this study: Figure 15), but have lens in the Coleoidea except for *Cirrothauma* (Aldred *et al.*, 1983). Hollow eyes are also found in the most basal group of gastropods (Patellogastropoda: see Sasaki, 1998: figure 92). Therefore, it is likely that primitively open eyes are retained in basal groups of both gastropods and cephalopods. Cerebrally innervated eyes are one of the unambiguous synapomorphies supporting the clade Gastropoda + Cephalopoda (Visceroconcha) (Salvini-Plawen & Steiner, 1996; Haszprunar, 2000).

47. Pre- and postocular tentacles: A pair of short tentacles on the anterior and posterior sides is present only in *Nautilus* (Figure 15C) among molluscs (autapomorphy).

48. Rhinophores: A pair of rhinophores is present below the eyes in *Nautilus* (rp: Figure 15D) but absent in the Coleoidea and all other molluscs. This organ may be homologous to the olfactory organs of the Coleoidea (see Nixon & Young, 2003: figure 3.7, for microstructure) which appear as a pair of small bulges on the head (see Shigeno *et al.*, 2008: figure 1). The histology of receptor cells is similar between the *Nautilus* rhinophore and coleoid olfactory organ (Barber & Wright, 1969; Barber, 1987: figure 2; Ruth *et al.*, 2002).

49. Osphradia: Two pairs of osphradia (interbranchial and postanal papillae) are present in *Nautilus* (Figure 2A, B), but absent in other cephalopods. Because osphradia are widely known in various molluscs except for Monoplacophora and Scaphopoda, their presence represents plesiomorphy. See Haszprunar (1987: p. 53) for a discussion of homology to the osphradia of other molluscs.

50. Statocyst position: The statocysts are located

lateral to the brain in *Nautilus* (Young, 1965, 1987: figures 2, 4; this study: Figure 14) but more ventrally positioned in the Coleoidea. In other molluscs, the statocysts are located lateral to the pedal ganglia in Monoplacophora (Lemche & Wingstrand, 1959: figures 136, 165; Wingstrand, 1985: figures 3, 4; Haszprunar & Schaefer, 1996: figures 10, 11; Schaefer & Haszprunar, 1996: figures 2d, 10; Haszprunar & Schaefer, 1997: figure 12), Bivalvia (Morse & Zardus, 1997: p. 77), and Patellogastropoda (Sasaki *et al.*, 2006a). In some Gastropoda (e.g., Sasaki, 1998; Sasaki *et al.*, 2006b) and Scaphopoda (Shimek & Steiner, 1997: figure 57), the statocysts are attached to the pedal ganglia and slightly shifted to an anterior or posterior position, but they are not in a ventral position, unlike in the Coleoidea. Therefore, the lateral position is plesiomorphic, and the ventral position is apomorphic.

51. Statoconia/statoliths: The statocysts contain many statoconia in *Nautilus* (Neumeister & Budelmann, 1997) but large statoliths occur in the Coleoidea (e.g., Clarke & Maddock, 1988b; Budelmann, 1990; Clarke, 1998, 2003). In other molluscs, statoconia are also found in Monoplacophora (see above for reference), protobranch bivalves, Scaphopoda, and many gastropods including the most basal group, Patellogastropoda (Sasaki *et al.*, 2006a). Based on outgroup comparison, the presence of statoconia is viewed as plesiomorphic, as was discussed for gastropods (Ponder & Lindberg, 1997: p. 169). Ontogenetically, however, the number of statoconia increases with growth, starting from a single statolith. Therefore, the polarity of this character is not conclusive.

52. Inner wall of statosysts: The wall of statocysts is oval and simply ciliated inside in *Nautilus* (e.g., Neumeister & Budelmann, 1997) as in other conchiferan molluscs (e.g., Sasaki *et al.*, 2006a, b, 2007 for gastropods), but more complicated with gravity receptor systems and an angular acceleration receptor system in the Coleoidea (Budelmann *et al.*, 1997: pp. 362–375, figures 220–223). Accordingly, the former is judged as the original conchiferan condition.

Nautilus is well known as a notable example of "living fossils" that typically belong to a clade with an old, rich fossil record, exhibit morphologic stasis over long geologic time, and have low diversity in modern fauna. Therefore, a large number of characters could be expected to remain primitive. In our morphologic analysis, at least 16 characters in *Nautilus* are regarded as primitive for cephalopods: the external shell (see above, character #1), cup-shaped embryonic shell (#2), thin mantle (#9), periostracal groove (#10), absence of fins (#11), absence of chromatophores (#12), absence of photophores (#13), absence of the afferent ctenidial membrane (#15), absence of digestive gland appendages (#27), less concentrated brain (#43), absence of cranial cartilage (#44), absence of stellate ganglia (#45), open eyes (#46), osphradia (#49), lateral position of statocysts (#50), and simple inner wall of statocysts (#52). However, others are equivocal or rather derived (autapomorphies), as discussed above (cf. also Ponder & Lindberg, 1997; Sasaki, 1998; Haszprunar, 2000, for discussion among Conchifera).

Acknowledgments

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