Original article

Palaeobiogeographical provenance, taphonomy, and mode of life of *Aturia cubaensis* (Cephalopoda, Nautiloidea) from Cainozoic deposits of Chile[☆]

Provenance paléobiogéographique, taphonomie et mode de vie d'*Aturia cubaensis* (Cephalopoda, Nautiloidea) dans les sédiments Cénozoïques du Chili

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Abstract

The presence of *Aturia cubaensis* (Lea) is reported from several Cainozoic localities along the central and southern Chilean coast. The shells are very well preserved and the ultrastructure of the shell, especially of the siphuncular tube, of *A. cubaensis* is described and the function of the siphuncular tube discussed. *A. cubaensis* shows an interesting distributional pattern in Chile, becoming more frequent towards higher latitudes. It occurs in the Navidad, Ranquil, and Lacui formations of central and southern Chile and the Cameronian Stage of Tierra del Fuego, spanning a time of Eocene-Oligocene to latest Miocene, possibly even earliest Pliocene. Tierra del Fuego is the southernmost record of this species. The preservation of *Aturia* in all these localities is exceptionally good, no incrustation and microboring is observed in the shells. Post-mortem shell breakage is present, but usually the phramocone is not destroyed. These records contradict either the subtropical to tropical nature of the genus *Aturia* or existing climatic reconstructions for the southeastern Pacific during the middle to late Cainozoic. A number of southern South American names for nautiloids are synonymized with *A. cubaensis*: *Nautilus maldonadi* Philippi, *Nautilus caroliameghinoi* Ihering, *Aturia* (*Sphenaturia*) *brueggeni* Ihering, *Aturia* (*Sphenaturia*) *felschi* Ihering. *Nautilus araucanus* Philippi and *Nautilus magellanicus* Philippi are *nomina nuda* but presumably also synonyms of *A. cubaensis*.

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Résumé

La présence d'*Aturia cubaensis* (Lea) est signalée dans plusieurs sites Cénozoïques de la côte du Chili central et méridional. Les coquilles sont très bien conservées, et l'ultrastructure de la coquille, en particulier celle du tube siphonculaire, est décrite pour cette espèce, avec une discussion sur le fonctionnement du tube siphonculaire. *A. cubaensis* présente un schéma de répartition intéressant au Chili, avec une fréquence qui augmente avec la latitude. Elle se trouve dans les formations de Navidad, Ranquil et Lacui du Chili central et méridional et dans l'étage Caméronien en Terre de Feu, allant de l'Eocène-Oligocène au Miocène terminal, peut-être même au Pliocène basal. La Terre de Feu est le site le plus méridional de cette espèce. L'état de conservation d'*Aturia* dans tous ces sites est excellent, et on n'observe ni incrustations ni micro-perforations des coquilles. Des cassures post-mortem sont fréquemment trouvées au niveau des coquilles, mais en règle générale le phragmocône est resté intact. Ces observations contredisent le caractère sub-tropical à tropical du genre *Aturia* ainsi que les reconstitutions du climat proposées pour le Sud-Est du Pacifique au cours du Cénozoïque moyen et tardif. Plusieurs noms de nautiloïdés de l'Amérique du Sud sont mis en synonymie

avec *A. cubaensis* : *Nautilus maldonadi* Philippi, *Nautilus caroliameghinoi* Ihering, *Aturia* (*Sphenaturia*) *brueggeni* Ihering, *Aturia* (*Sphenaturia*) *felschi* Ihering. *Nautilus araucanus* Philippi et *Nautilus magellanicus* Philippi sont des *nomina nuda* mais peut-être aussi des synonymes de *A. cubaensis*.

1. Introduction

The nautiloid genus *Aturia* Bronn, 1838, is generally interpreted to have lived in tropical to subtropical regions (e.g., Beu and Maxwell, 1990; Ozawa and Tomida, 1996) based on comparison with modern *Nautilus*. The known stratigraphical range is Palaeocene to Miocene (Kummel, 1956; Casadío et al., 1999), but only *Aturia cubaensis* (Lea, 1841) and *Aturia coxi* Miller, 1947 survived to the end of the Miocene (Beu, 1973). *A. cubaensis* is reported from Ibaraki Prefecture (Noda et al., 1995) and Northeast Honshu (Masayuki et al., 2001) in Japan to Te Waewae Bay in southernmost New Zealand (Beu, 1973; Beu and Maxwell, 1990), spanning an exceptionally wide latitudinal range. However, this extraordinary geographical distribution has been identified for some regions as produced by transport of dead shells through ocean currents (Chirat, 2000). Accordingly, the palaeogeographical distribution of the once living species was questioned.

South American occurrences of this species include reports from Colombia, Venezuela and Peru (Miller and Thompson, 1937; Miller and Furnish, 1938; Jung, 1966; Casadío et al., 1999). From southern South America, *Nautilus maldonadi* Philippi (1897) was the first species treated systematically, apart from the report of two species named earlier by Philippi, 1897, who did neither describe nor illustrate the material. However, *Aturia caroliameghinoi* (Ihering, 1902) represents the first published record of South American nautiloids that has been recognized in subsequent literature. *A. caroliameghinoi* is known from the San Julián Formation from the Golfo San Jorge, Argentina (Casadío et al., 1999), which has been assigned an Eocene-Oligocene (Bertels, 1975) or late Oligocene (Barreda, 1997) age. In his monograph on the 'Tertiary nautiloids of the Americas', Miller (1947) included the three species of *Aturia* from Argentina and Chile reported by Ihering (1902, 1921, 1922) while other reports of nautiloids from Chile (Philippi, 1897; Tavera, 1942, 1979) were missed by subsequent workers. In the current investigation we try to clarify aspects of the mode of life and of the taphonomy of *A. cubaensis* that can help to evaluate its palaeobiogeographical distribution.

The investigation of the functional morphology of the siphuncle is central within the argumentation of the mode of life of cephalopods (Kröger, 2003). The siphuncular tube of *Aturia* is unique within the entire Nautilida in exhibiting extraordinarily long septal necks, which are nested into each other. It is therefore not surprising that a causal connection between the extraordinary siphuncular morphology and its extraordinary wide palaeobiogeographical occurrence has been proposed (e.g., Chirat, 2000). The unique structure of the siphuncle in *Aturia* was first recognized by Spath (1933), who noted the multi-layered nature of the siphuncular tube. Miller and Thompson (1937) and Miller (1947) described the structure of the siphuncle as consisting of long septal necks and connecting rings with a 'continuous thin lamellar deposit' on the inside, which they obviously identified as the innermost layer of the siphuncular tube (Miller and Thompson, 1937, p. 66). Sturani (1959) described the shell and especially the siphuncular tube of *Aturia aturi*, based on shells from the Miocene near Torino in Italy. According to his observations, the siphuncular tube consists of several layers with a nacreous outer layer, an intermediate layer with small channels and an internal lining. Sturani (1959) also described the beginning of the siphuncular tube in the first chamber of the phragmocone as being attached to the apical inner wall with a prismatic layer. According to his observations, the tube consists of the extended collar of the septum that crossed the whole chamber, a spiculous layer ('strato a spicule') in the middle of the tube, and an internal lining as the inner layer of the tube. In his reconstruction of the siphuncular tube, Sturani (1959, Fig. 2) basically followed Miller (Miller and Thompson, 1937, Fig. 3; Miller, 1947, Fig. 21) and connected all inner layers with each other. However, a detailed investigation of the ultrastructure of the siphuncular-septal neck complex that proves and illustrates these reconstructions was lacking until the current investigation. Such a detailed investigation is a precondition in order to compare the mode of life of *Aturia* with that of other cephalopods.

2. Fossil bearing localities

Fossil nautiloids belonging to the genus *Aturia* have been found at several localities along the coast of central and southern Chile (Figs. 1 and 2). The sedimentology of the Navidad Formation has been treated in detail by Tavera (1979) and Encinas et al. (2006) but only very short sedimentological descriptions are available for the Ranquil Formation (García, 1968) and the Lacui Formation (Antinao et al., 2000). The localities described here, except that in Tierra del Fuego, have been dated as latest Miocene to earliest Pliocene by Finger et al. (2007). Since reworking of older sediments and subsequent displacement into greater depths have been recognized for many localities (Finger et al., 2007), Miocene specimens of *Aturia* may occur together with early Pliocene foraminifera.

2.1. Navidad Formation

The fauna at Matanzas (MAP, Navidad Formation) is currently the best known marine Miocene invertebrate fauna
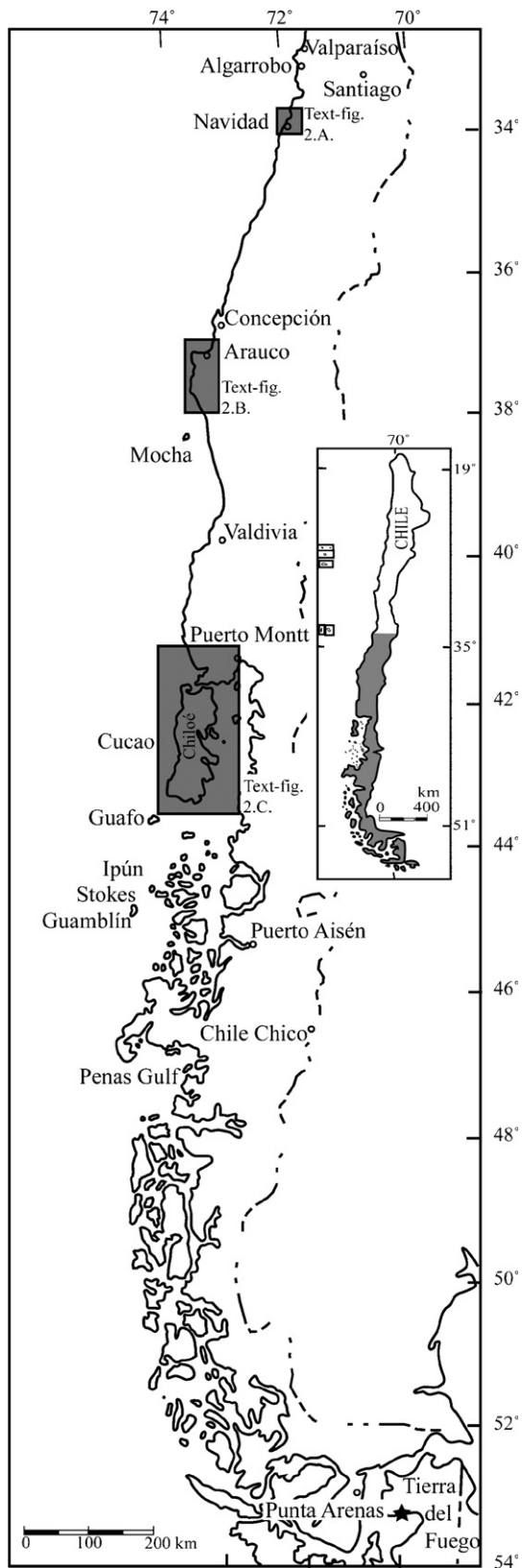
Fig. 1. Overview of central and southern Chile indicating areas shown in Fig. 2 and the locality containing *Aturia cubaensis* (Lea) at Bahía Inútil (POR), Tierra del Fuego, type locality of *Aturia brueggeni* Ihering.
Vue d'ensemble du Chili central et méridional, indiquant les zones montrées dans la Fig. 2 et le site contenant Aturia cubaensis *(Lea) à Bahia Inutil (POR), Tierra del Fuego, localité type d'*Aturia brueggeni *Ihering.*

from Chile. It includes mainly bivalves (Frassinetti and Covacevich, 1993) and gastropods like *Tegula chilena*, *Tegula matanzensis*, *Diloma miocenica*, *Nerita chilensis*, *Cirsotrema* sp., *Strombus medinae*, *Perissodonta chilensis*, *Neverita pachystoma*, *Sinum subglobosum*, *Echinophoria monilifera*, *Distorsio thersites*, *Ficus gayana*, *Lamprodomina dimidiata*, *Olivancillaria claneophila*, *Testallium cepa*, *Terebra undulifera*, and several species of cancellariids and architectonicids (Frassinetti and Covacevich, 1981, 1982; Covacevich and Frassinetti, 1986; Nielsen and Frassinetti, 2003; Nielsen et al., 2004; Nielsen, 2004, 2005), but also an abundant and diverse microfauna (Finger et al., 2007), scaphopods and shark teeth.

2.2. Ranquil Formation (Arauco Peninsula)

The fauna of the grey deepwater mudstone at Punta El Fraile (FRM, Ranquil Formation) is less well known. It includes *Imbricaria chiloensis*, *Struthiochenopus bandeli* and a new species of *Dalium*, several turrids, some echinoids and *Palaega*-like isopods (Nielsen, 2005; Finger et al., 2007).

The fauna at Ranquil (RAN, Ranquil Formation) is very similar to that of the sandy Navidad sediments. Common gastropod species are *S. subglobosum*, *D. thersites*, *L. dimidiata*, *O. claneophila*, and *T. cepa*. A coarse sand at Ranquil (RQS, Ranquil Formation) yielded a low-diversity, rather coastal fauna, including some corals and the gastropods *D. miocenica*, *S. subglobosum*, and *O. claneophila*. However, it seems that part of the fauna is reworked, as apparently younger species of *Nacella* and *Acanthina* have been found which do not occur at other localities.

2.3. Lacui Formation

The cliffs at Cucao (CUC, Lacui Formation) yielded a rich fauna that is still under study. It contains species in common with Navidad and Arauco but differs notably in general composition from that of those areas. Typical gastropod species are *Natica chiloensis*, *N. pachystoma*, 'Natica' *striolata*, *S. subglobosum*, *E. monilifera*, *L. dimidiata*, *O. claneophila*, *T. cepa*, *I. chiloensis* and *Cancellaria medinae*.

The fauna at Punta Chocoi (CHO, Lacui Formation) is basically the same as in Cucao, including species like 'N.' *striolata*, *S. subglobosum*, *O. claneophila*, *T. cepa*, and *T. undulifera*.

2.4. Cameronian Stage

The locality at Bahía Inútil (POR) is the type section of the Late Eocene-Early Oligocene Cameronian Stage of Natland and Gonzalez (1974). This stage consists of *ca.* 500 m of predominantly 'light-grey silty claystone and fine-grained silty sandstone with some locally developed thick lenticular fine to medium sandstones' (Natland and Gonzalez, 1974, p. 28). The specimens of *Aturia* come from calcareous concretions, otherwise preservation of aragonitic molluscs is of internal moulds. No additional fauna has been determined.
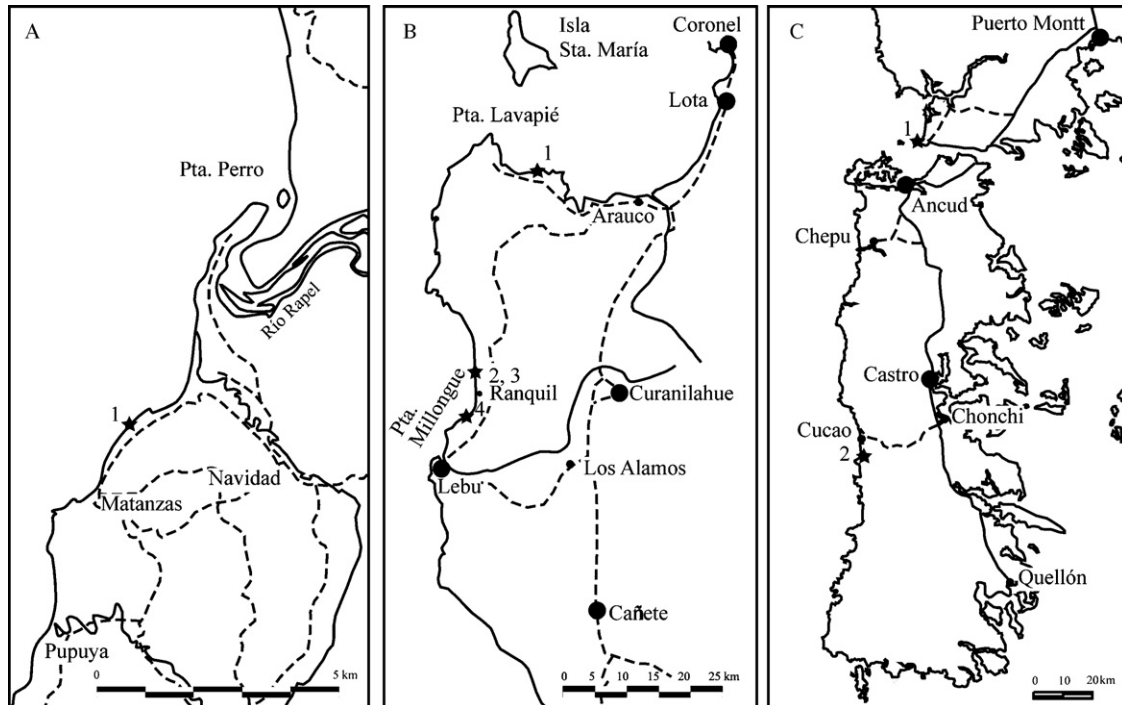
Fig. 2. Localities containing *Aturia cubaensis* (Lea) along the Chilean coast. **A**. Navidad Formation: Locality Matanzas (MAP) (1). **B**. Ranquil Formation: Punta El Fraile (FRM) (1), Caleta Ranquil (2–4), locality RAN (2), locality RQS (3), locality MIB (4). **C**. Lacui Formation: Punta Chocoi (CHO) (1), type locality of *Aturia felschi* Ihering, Cucao (CUC) (2).
Sites contenant Aturia cubaensis *(Lea) sur les côtes chiliennes.* **A**. *Formation de Navidad : Site Matanzas (MAP) (1).* **B**. *Formation de Ranquil : Punta El Fraile (FRM) (1), Caleta Ranquil (2–4), site RAN (2), site RQS (3), site MIB (4).* **C**. *Formation de Lacui : Punta Chocoi (CHO) (1), localité type d'*Aturia felschi *Ihering, Cucao (CUC) (2).*

3. Material and methods

Material used or mentioned in this study is housed in the following institutions: Museo Argentino de Ciencias Naturales ''Bernardino Rivadavia'' (MACN), Buenos Aires, Argentina; SGO.PI, Museo Nacional de Historia Natural, Santiago, Chile; Senckenberg Museum (SMF), Frankfurt am Main, Germany. Parts of specimen SGO.PI.6422, which broke during extraction, were newly broken to obtain fresh edges, mounted on stubs, coated with gold and examined by scanning electron microscopy using a LEO1455VP. Heights given are maximum diameters.

4. Systematic palaeontology

Class CEPHALOPODA Cuvier, 1797
Superfamily NAUTILOIDEA de Blainville, 1825
Family ATURIIDAE Chapman, 1857
Genus *Aturia* Bronn, 1838
Type species: *Nautilus aturi* Basterot, 1825, from the Miocene of southwestern France.

Aturia cubaensis (Lea, 1841)
Figs. 3 and 4
1841. *Nautilus cubaensis* Lea: 259, Pl. 10, Fig. 15.
1887. ?*Nautilus araucanus* Philippi: 33 [*nomen nudum*].
1887. ?*Nautilus magellanicus* Philippi: 33 [*nomen nudum*].
1896. *Aturia* cf. *aturi* Möricke: 553.

1897. *Nautilus maldonadi* Philippi: 365–366, Pl. 1, 2.
1902. *Nautilus caroli-ameghinoi* Ihering: 134, Pl. 19, Figs. 1, 2.
1931. *Nautilus caroli-ameghinoi* Windhausen: Pl. 45, Fig. 2.
1903. *Aturia caroli-ameghinoi* Ihering: 197.
1907. *Aturia caroli-ameghinoi* Ihering: 96.
1947. *Aturia caroli-ameghinoi* Miller: 91, Pl. 74, Figs. 8, 9.
1921. *Aturia* (*Sphenaturia*) *Brüggeni* Ihering: 76.
1922. *Aturia* (*Sphenaturia*) *Brüggeni* Ihering: 472, Figs. 2, 5.
1921. *Aturia* (*Sphenaturia*) *Felschi* Ihering: 76.
1922. *Aturia* (*Sphenaturia*) *Felschi* Ihering: 473, Figs. 3, 4.
1927. *Aturia*? *brüggeri* [*sic*] Spath: 22.
1931. *Aturia brüggeni* Schenck: 450.
1947. *Aturia brüggeni* Miller: 90, Text-Fig. 24, Pl. 74, Fig. 5.
1937. *Aturia curvilineata* Miller and Thompson: 69, Pl. 9, Figs. 1–4, Pl. 10, Figs. 1, 2.
1942. *Aturia* cf. *zigzag* Tavera: 600, foto 8.
1942. *Aturia* sp. Tavera: 603.
1979. *Aturia* sp. Tavera: 14.
1947. *Aturia felschi* Miller: 95, Text-Fig. 27, Pl. 74, Fig. 4.
1966. *Aturia cubaensis* Jung: 489, Pl. 1, Figs. 2–7, Pl. 2, Figs. 2–6 [synonymy].
1973. *Aturia cubaensis* Beu: 298, Pl. 32, Figs. 1–7 [synonymy].
1990. *Aturia cubaensis* Beu and Maxwell: 239, Pl. 26, Fig. Q [synonymy].
1974. *Aturia* (*Sphenaturia*) *felschi* Erben and Flajs: Pl. 5, Figs. 3, 4 [cicatrix].
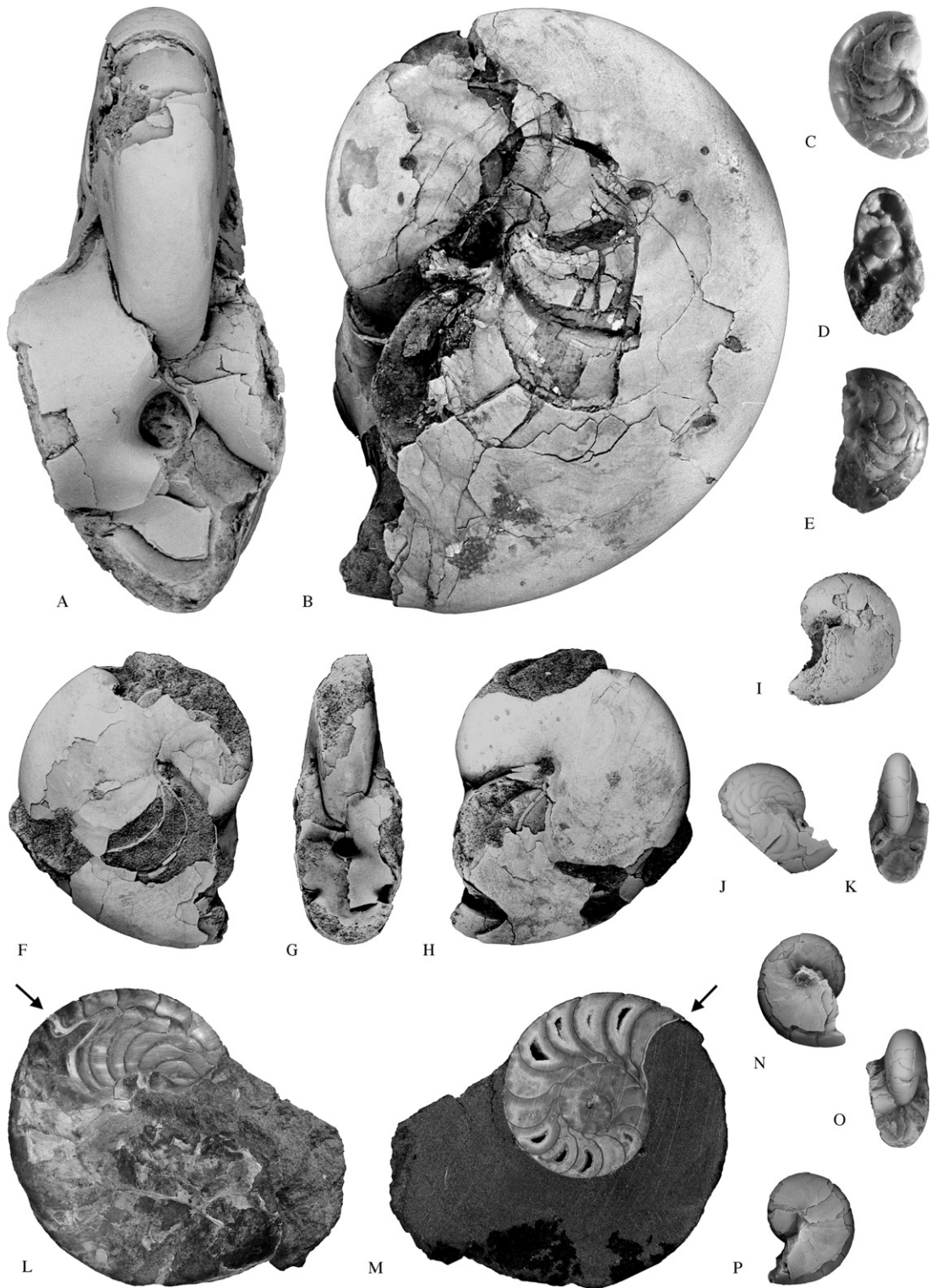
Fig. 3. **A–P**. *Aturia cubaensis* (Lea). **A, B**. Neotype of *Nautilus maldonadi* Philippi, SGO.PI.6421, height 102 mm, Cucao (CUC), Chiloé, Lacui Formation. **C–E**. Holotype of *Aturia brueggeni* Ihering, MACN-pi 2491, height 25 mm, Punta Boquerón, Bahía Inútil, Tierra del Fuego. **F–H**. Neotype of *Aturia felschi* Ihering, SGO.PI.6419, height 50 mm, Punta Chocoi (CHO), Lacui Formation. **I**. SGO.PI.4973, height 22.6 mm, Matanzas (MAP), Navidad Formation. **J, K**. SGO.PI.6423-2, height 22 mm, Bahía Inútil near Porvenir (POR), Cameronian Stage. **L, M**. SGO.PI.6423-4, height 57 mm, Bahía Inútil near Porvenir (POR), Cameronian Stage. Arrow indicates last septum. **N–P**. SGO.PI.6423-1, height 20 mm, Bahía Inútil near Porvenir (POR), Cameronian Stage. All specimens × 1.

A–P. Aturia cubaensis *(Lea)*. A, B. Néotype de *Nautilus maldonadi* Philippi, SGO.PI.6421, hauteur 102 mm, Cucao (CUC), Chiloé, formation Lacui. *C–E. Holotype de* Aturia brueggeni *Ihering, MACN-pi 2491, hauteur 25 mm, Punta Boquerón, Bahía Inútil, Terre de Feu. F–H. Néotype de* Aturia felschi *Ihering, SGO.PI.6419, hauteur 50 mm, Punta Chocoi (CHO), formation Lacui. I. SGO.PI.4973, hauteur 22,6 mm, Matanzas (MAP), formation Navidad. J, K. SGO.PI.6423-2, hauteur 22 mm, Bahía Inútil près de Porvenir (POR), Caméronien. L, M. SGO.PI.6423-4, hauteur 57 mm, Bahía Inútil près de Porvenir (POR), Caméronien. La flèche indique le dernier septum. N–P. SGO.PI.6423-1, hauteur 20 mm, Bahía Inútil près de Porvenir (POR), Caméronien. Tous les specimens × 1.*
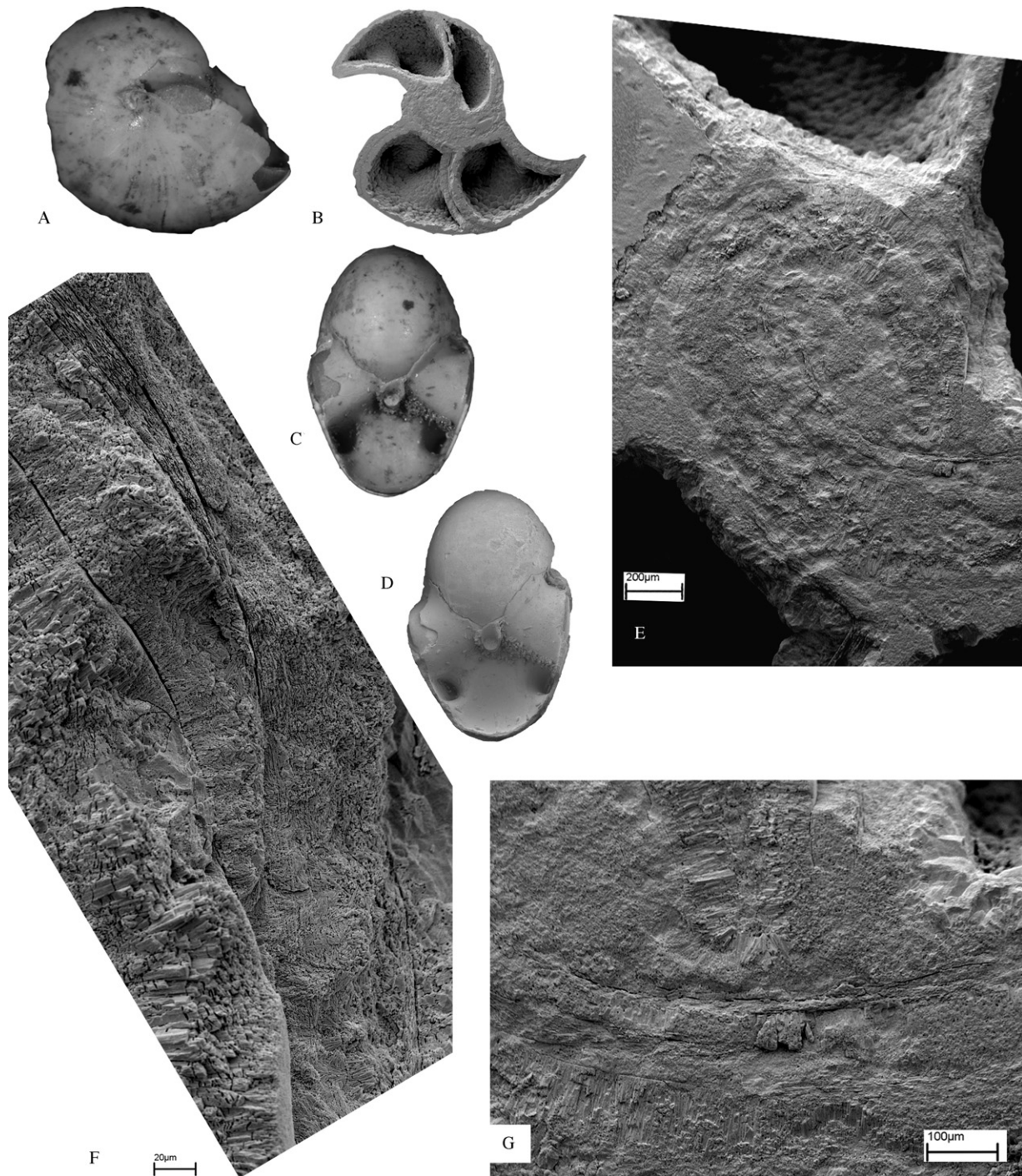
Fig. 4. **A–G**. Embryonic shell of *Aturia cubaensis* (Lea), SGO.PI.6422 from Cucao, Chiloé, preserving the five adapical chambers. **A**. Lateral view. **B**. Median section; note that septal spacing is wide in comparison with *Nautilus* (compare Mutvei and Doguzhaeva, 1997); note also the broadly elliptical cross section of the shell. **C**. Adoral view. **D**. Adoral view, scanning electron microscopy (SEM) picture. **E**. Overview of the median section of the umbilicus. Note the heavy diagenetic cement within the umbilicus; note also the long septal necks of the initial septum. **F**. Adapical end of the second septal neck, dorsal side to the right. Note the thick wedge of the spherulitic porous layer at left, the thin wedge of the nacreous layer of the second septal neck, and the thick layer of the initial septal neck at right. **G**. Detail of the initial part of the shell showing the distance between apical shell wall (horizontal structure) and adapical end of the initial septal neck (vertical structure). **A–D**: × 9.

*A–G. Coquille embryonnaire d'*Aturia cubaensis *(Lea), SGO.PI.6422 provenant de Cucao, Chiloé, avec conservation des cinq loges adapicales. A. Aspect latéral. B. Coupe médiane ; notez l'espacement des cloisons qui est large par rapport à* Nautilus *(Mutvei et Doguzhaeva, 1997) ; notez également la coupe transversale de la coquille qui forme une ellipse large. C. Aspect adoral. D. Aspect adoral, vue au microscope à balayage. E. Vue d'ensemble de la coupe médiane de l'ombilic. Notez l'épais ciment diagénétique dans l'ombilic ; notez également les trompes septales longues au niveau des loges initiales. F. Extrémité adapicale de la deuxième trompe septale, face dorsale à droite. Notez le coin épais formé par la couche sphérulitique poreuse à gauche, le coin mince de la couche nacrée de la deuxième trompe septale et l'épaisse couche de la trompe septale initiale à droite. G. Vue de détail de la partie initiale de la coquille montrant la distance entre la paroi apicale de la coquille (structure horizontale) et l'extrémité adapicale de la trompe septale initiale (structure verticale). A–D : × 9.*

1979. *Aturia* (*Sphenaturia*) *felschi* Tavera: 14, 100.
1996. *Aturia* (*Sphenaturia*) *felschi* Parodiz: 224, 225, 285.
1996. *Aturia* (*Sphenaturia*) *brueggeni* Parodiz: 205, 285.
1996. *Aturia* (*Sphenaturia*) *caroliameghinoi* Parodiz: 211, 285.
1999. *Aturia caroliameghinoi* Casadío, Rodriguez, Reichler and Camacho: 197, Figs. 3.F, 6.C, D.

Type material: The holotype of *N. maldonadi* is not present in the Philippi collection in the SGO.PI and must be considered lost. To justify the synonymy of *N. maldonadi* with *A. cubaensis*, designation of a neotype according to International Commision on Zoological Nomenclature (ICZN) Article 75 (ICZN, 1999) is required. SGO.PI.6421 (CUC, height 102 mm, Fig. 3(A, B)) comes from Chiloé and agrees basically with the description and figure given by Philippi (1897, p. 365–366, Pl. 1, 2) even if it is much more complete; it is here designated as the neotype of *N. maldonadi*. The holotype of *N. caroliameghinoi* is present under MACN 544 (see Casadío et al., 1999, Figs. 6.C, 6.D). Of the two specimens of *A. brueggeni* mentioned by Ihering (1922), only one is present under MACN-pi 2491 (Fig. 3(C–E)), coming from Punta Boquerón, Bahía Inútil, Tierra del Fuego. It is the specimen figured by Ihering (1922, Fig. 5) and the only one he mentioned when introducing this species (Ihering, 1921). Ihering (1921) called it 'ejemplar típico' so it is therefore regarded as holotype of *A. brueggeni*. The holotype of *A. felschi* could not be located in the MACN and must be considered as lost. To justify the synonymy of *A. felschi* with *A. cubaensis*, designation of a neotype according to ICZN Article 75 is required. SGO.PI.6419 (CHO, height 50 mm, Fig. 3(F–H)) comes from the type locality, Punta Chocoi, and agrees well with description and figure given by Ihering (1922, p. 473, Figs. 3, 4); it is here designated as the neotype of *A. felschi*.

Other material examined: SGO.PI.4973 (one specimen, MAP, height 22.6 mm, Fig. 3(I)), SGO.PI.6416 (FRM, about half a whorl, height *ca*. 300 mm), SGO.PI.6417 (RAN, one specimen), SGO.PI.6418 (RQS, one specimen), SGO.PI.6420 (CHO, one specimen), SGO.PI.6422 (CUC, one strongly fragmented specimen, Figs. 4(A–G), 5(A–G) and 6(A–G)), SGO.PI.6423 (POR, 16 specimens, Fig. 3(J–P)), SMF 327967 (FRM, two quarter whorls and fragments), SMF 327968 (RAN, one specimen), SMF 327969 (CHO, five fragments), SMF 327970 (POR, eight specimens), SGO.PI.4243 (Ipún Island, one specimen), SGO.PI.4251 (Ipún Island, one specimen), SGO.PI.unnumbered (Crosslet Island, one fragment).

SE Pacific occurrences: MAP, FRM, RAN, RQS, MIB, CHO, CUC, Ipún Island, Crosslet Island, POR; Eocene-Oligocene to Miocene, central to southernmost Chile. *A. cubaensis* is very rare in the Navidad Formation (MAP). Philippi (1887) and Tavera (1979) reported a few specimens that could not be located in their collections. In spite of good sampling coverage, only a single small nucleus is present in the collection of Covacevich and Frassinetti (SGO.PI.4973, Fig. 3(I)). From Arauco (FRM, RAN, RQS, MIB), a few specimens have been collected by the authors. These include nuclei and specimens with body chamber. Nuclei of *Aturia* are frequent in Miocene strata on Chiloé (CHO, CUC) and abundant in concretionary blocks on the northern coast of Bahía Inútil, Tierra del Fuego (POR). At this latter locality, *Aturia* is even more frequent than the 'mass occurrence' of *Aturia* in the lower-middle Eocene La Meseta Formation of Seymour Island, Antarctica (Zinsmeister, 1987; Dzik and Gaździcki, 2001) as concretionary blocks at Bahía Inútil yielded more than 20 specimens near the surface of a 1 m^3 block (i.e., about 5 m^2). Therefore, in contradiction to the general pattern where *Aturia* is most frequent at lower latitudes (e.g., Chirat, 2000), in Chile *Aturia* is more frequent towards the south.

Description

Siphuncular tube: the septa consist of a nacreous layer and the septal necks merge continuously and without any marked morphological break, so that it is not possible to define at which point the individual septal neck inserts. Each septal neck forms a funnel-like tube near the dorsal part of the outer shell that reaches back through the entire preceding chamber and touches the preceding septal neck (Fig. 7). The median layer of the septal neck is composed like the septum of nacre stacks as is characteristic for *Nautilus* (e.g., Mutvei, 1972). Between the nacreous layer of a septal neck and the nacreous layer of the preceding septal neck a porous aragonitic ring is present. This ring consists of two layers that are attached at the inner surface of the nacreous layer and at the outer surface, respectively. Both porous layers are thickest at the adapical end of the nacreous septal neck and wedge out in the direction of the following septum (adorally). The inner layer consists of coarse aragonitic needles that are arranged perpendicular to the shell surface, forming pillar-like bundles that are encircled by empty interspaces. The outer chalky layer is much more porous than the inner pillar layer. It is built of rather uniform but quite unordered aragonitic crystallites with only a few calcitic crystals among them that formed during diagenesis. The chalky outer layer covers large parts of the median nacreous layer of the septal neck and extends toward the adapical tip of the preceding septal neck, thus covering the entire siphuncular tube (connecting ring) and parts of the septal neck.

Embryonic shell: Spath (1933) already noted that the first three septa of the phragmocone are thinner than later ones, and probably represent chambers with which the young animal changed its life from planktonic to benthic, while Naef (1923) suggested that it hatched from its egg with three septa completed. Miller (1947, p. 78) described the extreme adapical portion of the early ontogenetic shell as not pointed but rather truncated, bearing a circular scar interpreted as possible 'cicatrix of attachment of a chitinous protoconch'. Stenzel (1957) brought all these observations together.

According to Landman (1988), the shell shape of the early whorls of *Aturia morrissi* Michelotti, 1847 from Italy is compressed and the first septa are all equally spaced. A four-fold increase in thickness occurs between septa 3 and 4, which may indicate the point of hatching. Thus, the embryonic shell of *A. cubaensis* (Fig. 4(A–D)) measures *ca*. 4 mm across. A nepionic constriction as present in some other post-Triassic nautiloids (Chirat, 2001) was not observed. The septal spacing of the initial 360° of growth is significantly wider in *Aturia* than
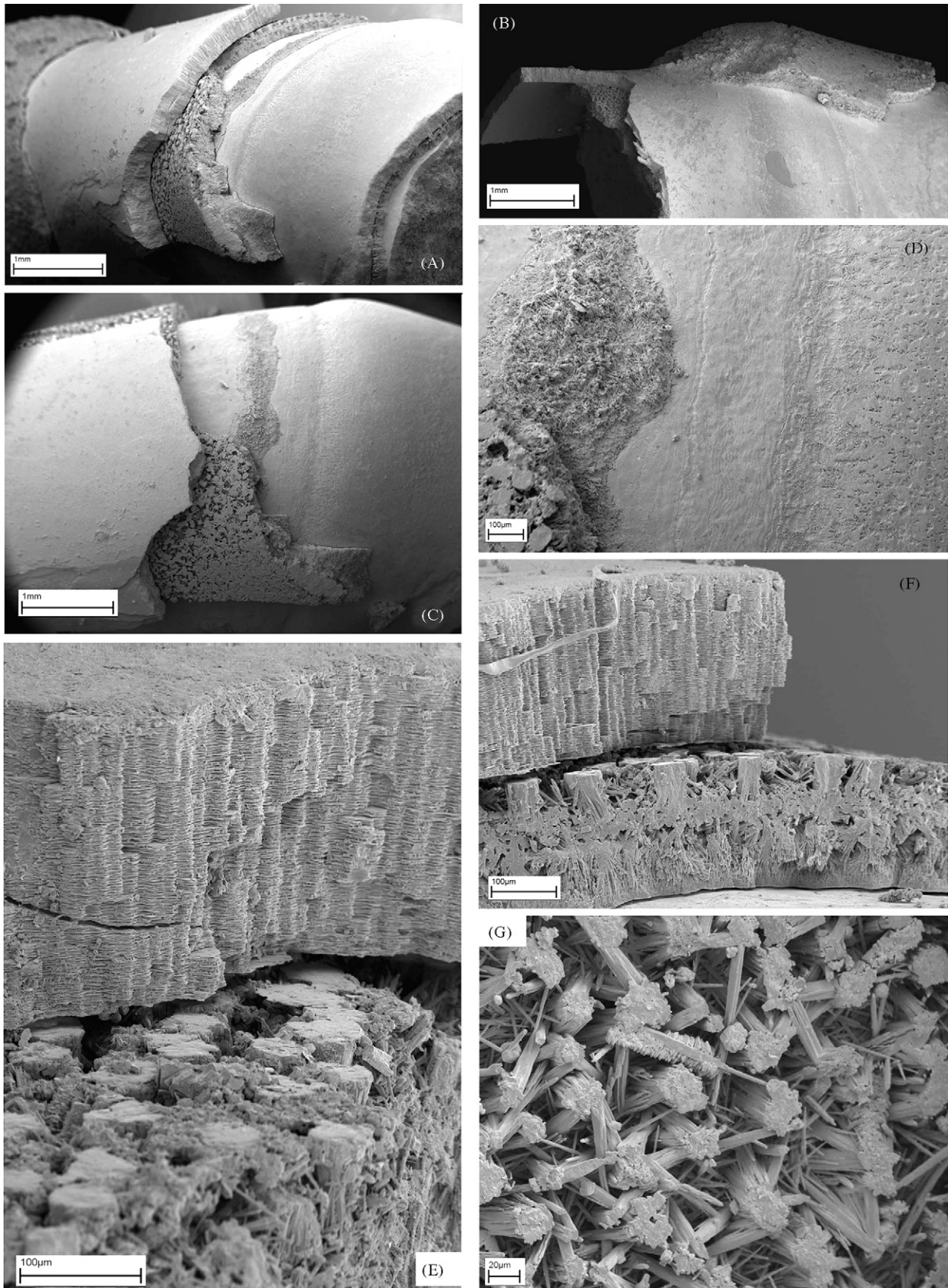
Fig. 5. **A–G**. Ultrastructure of the siphuncular tube of *Aturia cubaensis* (Lea). Specimen SGO.PI.6422, Cucao, Chiloé, Lacui Formation. **A**. Fragment of two nested siphuncular segments, each consisting of a chalky layer (equal to the spherulitic-prismatic layer, spl), a nacreous layer (equal to the nacreous part of the septal neck, n), and a pillar layer (equal to the inner prismatic layer, ipl). The oldest (outermost) nacreous layer of the septal neck shows only at the very left end of the picture remnants of the belonging chalky layer (see B for detail). At the base of the outer nacreous layer, a thick pillar layer is attached. The second (innermost) siphuncular

in *Nautilus*. In *Aturia*, five septa occur in the initial whorl, in *Nautilus* occur 10 to 11 (compare Mutvei and Doguzhaeva, 1997).

The nacreous continuation of the septal neck of the first septum of *Aturia* reaches far down into the chamber forming much of the outer wall of the siphuncle (Fig. 4(B, E)). Connected to it is the organic continuation of the tube arising from the second septum. The transition from nacre to organic tube is well preserved in specimen SGO.PI.6422 (Fig. 4(E, F)), while the organic material has disappeared leaving a sheet-like opening. Between the organic inner tube and nacreous outer tube, the porous layer is found as in all following chambers. In reconstruction, only the crystalline layers formed during early diagenesis have to be recognized and subtracted. These layers have actually formed very early within the diagenetic history of the shell, probably replacing much of the mucus layer that lined the interior walls of the chambers, as is the case within the chambers of living *Nautilus*. The reason for assuming this rapid post-mortem crystal growth is that fungal borings are found within them, with the fungi having exploited the organic material of the mucus layer contained within the aragonitic growth (Fig. 4(E–G)). Also the cement is aragonitic, which indicates its growth within the marine environment, as present when the shell had just become covered up by the mud of the sea bottom.

Remarks: From central Chile, Philippi (1887) named *Nautilus araucanus* from Navidad, Lebu and Llanchahue (close to Valdivia), Ihering (1922) described *A. felschi* from 'Punta Chocroi [*sic*], Carelmapu, Chile' (equal to CHO) and Tavera (1979) reported this species from Navidad (close to PPN), Punta El Fraile (FRM), Isla Mocha, and Chocoi (CHO). In a

little known article, Philippi (1897) described *N. maldonadi* from Punta Zorra, Chiloé. From Tierra del Fuego, Philippi (1887) named *N. magellanicus* from eastern Tierra del Fuego and Ihering (1922) described *A. brueggeni* from 'Punta Boquerón, Bahía Inútil, Tierra del Fuego', presumably the same locality as POR as the rock-type and preservation are the same. At Philippi's localities Lebu and Tierra del Fuego occur specimens of *Aturia* and *Eutrephoceras*, so it cannot be excluded that Philippi (1887) referred to a specimen of the latter genus. However, *Aturia* is more common at both localities and Philippi's names are without figure or description and are therefore *nomina nuda*.

5. Discussion

5.1. Taphonomy

Nautiloids are usually not abundant in Cainozoic strata (Ward, 1987). Accordingly, occurrences of several to many shells are often attributed to post-mortem drift because nautiloid shells, especially of the genus *Aturia*, float well (Chirat, 2000). Oceanic currents between the Eocene and the Miocene are supposed to come from the Antarctic region and, finally, New Zealand where those shells occur widely but are uncommon (Beu and Maxwell, 1990). They are also relatively common and beautifully preserved in southern Australia (Beu, 1973). Chirat (2000) suggested that Central America (and adjacent regions) is the most likely area in which *Aturia* has actually lived. From this area, shells should have drifted easily across the Atlantic and through the Pacific Ocean, which we agree may be possible. To reach Tierra del Fuego and central

segment preserves parts of a thin chalky layer at the left part of the picture that wedges out at the ring-like depression at the surface of the nacreous layer of the inner (younger) septal neck. Underneath this inner nacreous layer, the corresponding pillar layer is attached. The central part of the siphuncular tube is filled by an aragonitic-calcitic matrix. **B**. Detail of the outer siphuncular segment near the adapical end of the siphuncular neck; at the ring-like depression, remnants of a thin chalky layer are preserved that wedges out toward the left. The layer attached to the surface of the nacreous layer left of the depression represents sedimentary matrix. **C**. Detail of A, showing the ring-like depression at the surface of the nacreous septal neck near the adoral end of the fragment. **D**. Detail of the ring like depression with remains of the chalky layer at the left. Note the wrinkled surface of the nacreous layer of the corresponding septal neck. **E**. Detail of A, showing stacked nacre plates of the outer septal neck and parts of the pillar layer. The surface of attachment of the pillar layer is slightly broken off, leaving an interspace between nacreous layer and pillow layer. Note the individual bases of the individual pillars that are composed of several aragonitic needles. **F**. Detail of a sequence of the outer nacreous layer of the outer septal neck and its corresponding pillar layer at the basal surface. The lower part of the sequence is composed of fine aragonitic crystallites that form spherulitic sectors, representing the chalky layer of the succeeding siphuncular segment. The denser median layer in between the pillar layer and the chalky layer is composed of calcite crystals that have begun to fill the empty spaces much later in diagenesis. At the base of the picture, the sedimentary infill of the tube is visible. **G**. View on the surface of the pillar layer that was attached to the nacreous layer, showing pillars composed of aragonitic crystals.

*A–G. Ultrastructure du tube siphonculaire d'*Aturia cubaensis *(Lea). Spécimen SGO.PI.6422, Cucao, Chiloé, formation Lacui. A. Fragment de deux segments siphonculaires emboîtés, chacun consistant en une couche crayeuse (*chalky layer *égale couche sphérulitique-prismatique, spl), une couche nacrée (égale partie nacrée de la trompe septale, n) et une couche à piliers (égale couche prismatique interne, ipl). La couche nacrée la plus ancienne (la plus extérieure) de la trompe septale montre uniquement à l'extrême gauche de l'image des résidus la couche crayeuse (voir B pour le détail). À la base de la couche nacrée externe, une couche épaisse à piliers est attachée. Le deuxième (le plus intérieur) segment siphonculaire conserve des parties d'une mince couche crayeuse dans la partie gauche de l'image, s'amincissant à la dépression annulaire de la surface de la couche nacrée de la trompe septale interne (plus jeune). Sous cette couche nacrée interne, la couche à piliers correspondante est attachée. La partie centrale du tube siphonculaire est remplie d'une matrice aragonitique calcitique. B. Détail du segment siphonculaire externe, près de l'extrémité adapicale de la trompe siphonculaire, au niveau de la dépression annulaire ; des résidus d'une mince couche crayeuse sont conservés qui s'amincissent et disparaissent vers la gauche. La couche attachée à la surface de la couche nacrée, à gauche de la dépression, représente une matrice de sédiment. C. Détail de A, qui montre la dépression annulaire à la surface de la trompe septale nacrée, près de l'extrémité adorale du fragment. D. Détail de la dépression annulaire, avec des résidus de la couche crayeuse à gauche. Notez la surface ridée de la couche nacrée de la trompe septale correspondante. E. Détail de A, montrant des plaques de nacre empilées au niveau de la trompe septale extérieure et des parties de la couche à piliers. La surface de fixation de la couche à piliers est légèrement érodée, laissant un espace entre la couche nacrée et la couche à piliers. Notez les bases individuelles des différents piliers qui sont composées d'aiguilles aragonitiques. F. Détail de la séquence de la couche nacrée externe de la trompe septale externe et sa couche à piliers correspondante à la surface basale. La partie inférieure de la séquence est composée de fins cristaux d'aragonite qui forment des secteurs sphérulitiques, représentant la couche crayeuse du segment siphonculaire suivant. La couche médiane plus dense entre la couche à piliers et la couche crayeuse est composée de cristaux de calcite qui ont commencé à remplir les espaces vides pendant la diagénèse ultérieure. À la base de l'image, le remplissage sédimentaire du tube est visible. G. Aspect de la surface de la couche à piliers qui était fixée sur la couche nacrée, montrant des piliers composés de cristaux d'aragonite.*
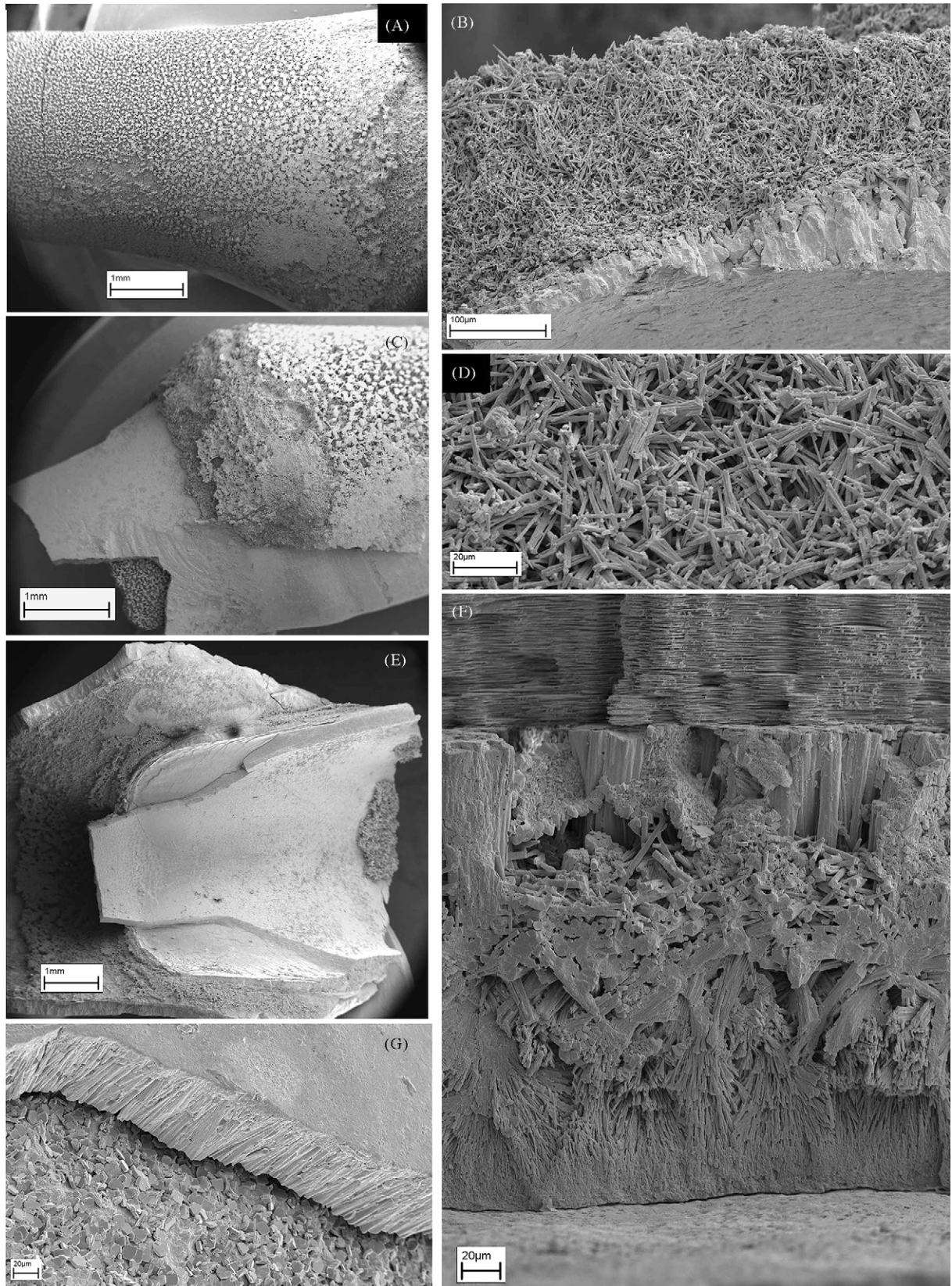
Fig. 6. **A–G**. Ultrastructure of the siphuncular tube of *Aturia cubaensis* (Lea). Specimen SGO.PI.6422, Cucao, Chiloé, Lacui Formation. **A**. Fragment showing the pillar layer (ipl) at the attachment surface between pillar layer and nacreous layer of the corresponding septal neck. The nacreous layer is completely chopped off. **B**. Detail of the chalky layer (spl); note the irregularly spaced felt-like aragonitic needles and the high porosity of this layer. **C**. Detail of the adapical end of the fragment of A, showing the ring-like depression at the nacreous layer of the corresponding septal neck at the position where the chalky layer wedges out (toward left). Note the remains of the chalky layer in the middle of the picture. The pillar layer which is on top of the chalky layer belongs to the next older siphuncular segment.
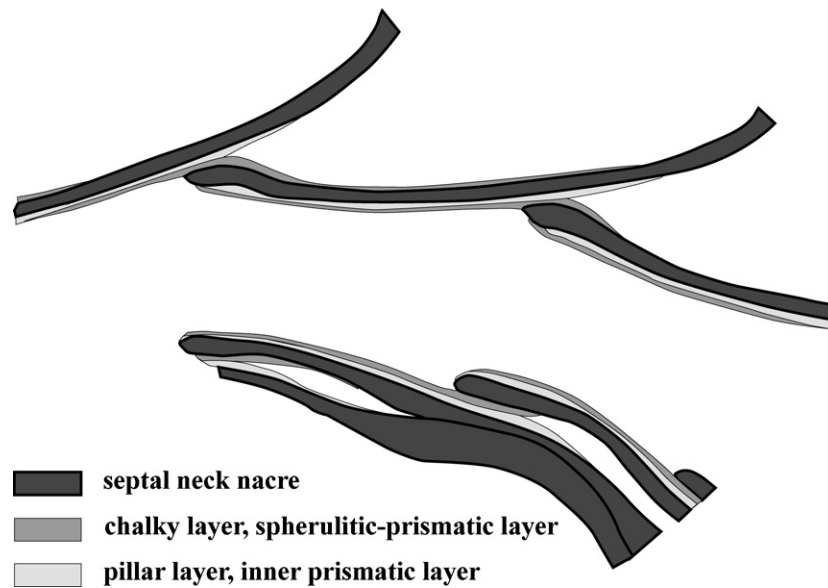
Fig. 7. Camera lucida drawing of the siphuncular tube of *Aturia cubaensis* (Lea) from the Miocene Gatun Formation at Sabanita, Panama (SMF 331870), adapical direction to the top (× 1.5).
*Dessins faits à la chambre claire, montrant le tube siphonculaire d'*Aturia cubaensis *(Lea) de la formation du Miocène de Gatun, à Sabanita, Panama (SMF 331870), direction adapicale vers le haut (× 1,5).*

Chile, however, they must have drifted across the Pacific in equatorial regions, passed New Zealand on the way back and, finally, reached Tierra del Fuego still in large numbers. From there, some specimens must have drifted further north and reached central Chile, largely undamaged and without any trace of settled organisms, i.e. epizoans. This seems very unlikely. Post-mortem epizoans are known since the early Palaeozoic (Davis et al., 1999) but are not present on most beached Recent *Nautilus* and *Allonautilus* shells because the outer prismatic layer is usually eroded (Landman et al., 1987). However, the prismatic layer is still present on our material, although it is partly broken away in some specimens (see e.g. Fig. 3(A, B)).

Indeed most specimens, especially from Tierra del Fuego, are relatively small nuclei, as those correctly noted by Chirat (2000) to represent the remains of once larger shells, but in some specimens the body chamber is preserved (Fig. 3(L, M)). Excellent preservation of original aragonite, as is the case in the specimens from Chiloé, can be seen in many specimens of

Aturia worldwide. Those specimens do not show evidence of microboring or settled organisms as can be expected on floated shells and are here interpreted as being parautochthonous, which means that they may have drifted a short time after death or were possibly displaced after deposition together with the surrounding sediment. Since most chambers of the shell remained unfilled by sediment, the phragmocone was largely intact when covered by marine muds. This preservation therefore does not support an interpretation as shells that have been floating for a long time, nor does it suggest heavy reworking after original deposition. Therefore, a quasi autochthonous origin of *Aturia* is assumed for the Chilean locations.

5.2. Interpretation of the siphuncular tube

The siphuncular tube of Recent *Nautilus* is well known (Erben et al., 1969; Bandel and Boletzky, 1979; Mutvei and

D. Detail of the chalky layer; note the small pyritic rhomboid in the upper right of the picture. **E**. Fragment of the contact between siphuncular tube and outer shell wall. **F**. Nacreous layer of the septal neck at top and the porous layers at the base: the pillar layer, belonging to same siphuncular segment like the nacreous layer, and the chalky layer, that is built by spherulitically arranged crystallites, belonging to the subsequent siphuncular segment. The interspace in between the two porous layers is built by diagenetically grown crystals of calcite. **G**. A layer of cement coats all former surfaces as usually toward the interior of the chambers and siphuncular tubes attached to the nacreous plate of the septum.
*A–G. Ultrastructure du tube siphonculaire d'*Aturia cubaensis *(Lea). Spécimen SGO.PI.6422, Cucao, Chiloé, formation Lacui. A. Fragment montrant la couche à piliers (ipl) à la surface de fixation entre la couche à piliers et la couche nacrée de la trompe septale correspondante. La couche nacrée est complètement érodée. B. Vue de détail de la couche crayeuse (spl) ; notez les aiguilles d'aragonite disposées de manière irrégulière, formant une sorte de feutre, et la grande porosité de cette couche. C. Vue de détail de l'extrémité adapicale du fragment illustré en A, avec la dépression annulaire de la couche de la trompe septale correspondante, située à l'endroit où la couche crayeuse s'amincit pour disparaître (vers la gauche). Notez les résidus de la couche crayeuse dans le centre de l'image. La couche à piliers qui est superposée à la couche crayeuse appartient au segment précédent, plus ancien. D. Vue de détail de la couche crayeuse ; notez le petit losange de pyrite en haut à droite. E. Fragment de la zone de contact entre le tube siphonculaire et la paroi externe de la coquille. F. La couche nacrée de la trompe septale en haut et les couches poreuses en bas : la couche à piliers appartenant au même segment siphonculaire que la couche nacrée et la couche crayeuse qui est faite de petits cristaux disposés en sphérulite, appartenant au segment siphonculaire suivant. L'espace entre les deux couches poreuses est occupé par des cristaux de calcite due à la diagenèse. G. Une couche de ciment enrobe, comme toujours, toutes les surfaces anciennes vers l'intérieur des loges et des tubes siphonculaires attachés à la plaque nacrée du septum.*

Doguzhaeva, 1997). It begins in the first chamber with a blind end that lies in contact with the primary septum and is of the same construction as the succeeding tube. The tube has an inner organic layer and an outer spherulitic chalky layer composed of crystallites of aragonite with open spaces between them. The chalky layer functions like blotting paper, sucking up liquid and holding it ready to be pumped from the chamber (Ward, 1987). It lies around the organic siphuncular tube and the septal neck, where it wedges out. This layer has been called the spherulitic-prismatic layer (spl) since Mutvei (1964) (equal to the spicule-bearing layer of Stenzel, 1964). The inner organic tube represents a continuation of the nacreous septum closing a chamber. Where the septum passes into the siphuncular tube it turns into a conchiolinic collar (inner conchiolin layer of Mutvei, 1964, icl). At the inner surface of the septal neck, a prismatic layer (ipl) is present that wedges out adorally at the septal surface. According to Bandel and Boletzky (1979), the final portion of the organic tube is laminar with organic sheets held distinct from each other by aragonitic crystallites.

As in Recent *Nautilus,* the outer shell wall, the septa and the septal necks of the observed *Aturia* specimens consists principally of an inner prismatic (ipl), an inner nacreous (nl), and an outer prismatic layer (opl) (e.g., Bandel and Boletzky, 1979; Mutvei and Doguzhaeva, 1997 and references therein; Fig. 7). The nacreous septal necks of *Aturia* are covered on the adapical surface by a chalky layer that represents the spherulitic-prismatic layer. At the inner, adoral surface of the septal neck, a wedge of a pillar layer is present in *Aturia* that represents the inner prismatic layer. The inner conchiolinic layer is not preserved but visible at a cavity between the aragonitic surrounding of the shell (Fig. 5(E, F)).

However, there are some important differences (Miller, 1947) between *Aturia* and *Nautilus*:

- the shell of *Aturia* is less globular and therefore more discoidal than in *Nautilus*;
- the sutures are farther advanced in *Aturia* and represent the most advanced in Cainozoic nautiloids;
- the mineralized nacreous septal necks of the siphuncular tube in *Aturia* are much longer than in *Nautilus* and cross the whole of one chamber in front of the last formed septum.

The nacreous septum, therefore, is continuous into the siphuncular tube and extends across a whole chamber. Its continuation is an organic tube that also extends across a whole chamber. The segment of the siphuncular tube formed together with a new chamber, consists of a length amounting to a little more than two chambers. At the point where two successive siphuncular segments meet, a succession from the innermost layer of a spherulitic-prismatic, an inner prismatic, a nacreous, a spherulitic-prismatic, an inner prismatic, and again a nacreous layer is found. This is in fact the double tube already noted by Spath (1933). Thus, between nacreous outer tube wall and inner organic tube a porous space is held open by mineral pillars and porous mineral deposits of the same type as the chalky layer in *Nautilus*.

Miller (1947) and Sturani (1959) observed a lamellar or porcellaneous innermost layer in the shell and siphuncular tube. Since this layer is certainly present, the conclusion that this layer is continuous is not correct. The wall structure of the shell is similar to that of *Nautilus*, with a thin more prismatic layer below the periostracum and a thick nacre layer, which may be covered by a thin non-nacreous layer on the inner side. Thus, Spath (1933) noted the structure as being double layered, but did not understand the nature of the spiculous layer as homologous with the spherulitic prismatic layer in *Nautilus*.

The thick porcellaneous layer noted by Sturani (1959) probably represents a film of cement that was formed at early diagenesis and is also found on the shells we studied (Fig. 6(G)). However, it must be noted that Miller (1947) and Sturani (1959) studied the shell of *Aturia* before it had been recognized how the phragmocone of shell-bearing cephalopods functions as an apparatus of buoyancy. This began with the studies of Denton and Gilpin Brown (1966).

5.3. Palaeobiological interpretation

The double-walled siphuncular tube of *Aturia* as well as the attachment line of the septum to the inner shell wall distinguishes *Aturia* well from *Nautilus*. Shell construction is like that of *Nautilus* and the layers of the siphuncular tube are also seen in *Nautilus*, but in a different arrangement. The embryonic shell of *Aturia* is clearly smaller than that of *Nautilus* and it has been recognized early that hatching probably occurred with three chambers completed (Spath, 1933; Sturani, 1959). Embryonic development of *Nautilus* is extremely long while that of *Aturia* was shorter, but probably also took several months.

The double-walled tube of the siphuncle in many ways resembles that of Recent *Spirula* (Bandel and Boletzky, 1979; Mutvei, 1997), that of Ordovician endocerids (Mutvei, 1997), that of the belemnoid *Megateuthis* (Mutvei, 1971), and that of aulacocerid *Dictyoconites* (Bandel, 1985) (Fig. 8) which are all clearly not closely related to *Aturia*, with the last common ancestors of all these taxa having lived during the early Palaeozoic. Still, with respect to the construction, the siphuncular tube of *Spirula* has also the outer nacre tube crossing one chamber, the inner porous pillar supported zone separating the innermost organic layers. This inner layer is composed of the non-mineralized organic part of the nacre-bearing anterior part of the tube, so that each tube segment crosses two chambers. Access of liquid from the porous inner tube zone to the liquid of the chamber is along the inner side of the septum where it forms the septal neck. While the nacreous part of the tube continues into the organic portion of the tube, the pillar zone is found only in half the tube's length. *Spirula* differs by having another type of tube end in the first chamber as found in *Aturia* (Bandel and Boletzky, 1979). Also the type of nacre in the septa and nacreous tube section of *Spirula* is of the lamello-fibrillar nacre type while that of *Aturia* is of the normal stack of nacre plates type. Last but not least, the shells of *Spirula* and *Megateuthis* are held within the body of the animal, while that of *Aturia* was an external shell.
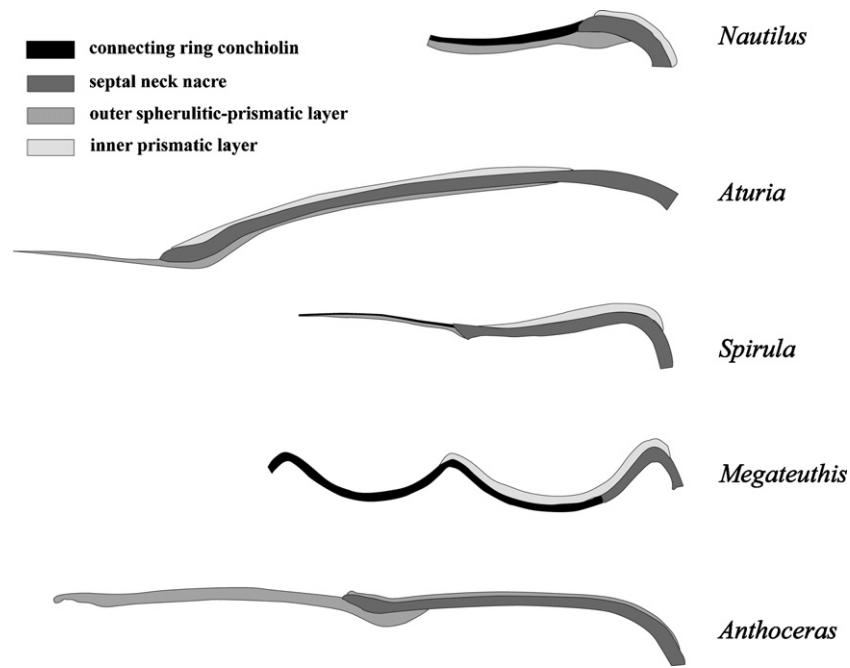
Fig. 8. Comparison of segments of the siphuncular tube of macrochoanitic cephalopods of different orders. In all cases, the inner prismatic layer (ipl) and the outer spherulitic layer (spl) are modified to provide a porous, liquid-permeable ring between the succeeding nested nacreous septal necks (n). Because all species illustrated here belong to different orders of different subclasses that have their last common ancestor in the Early Palaeozoic, we consider the characteristic siphuncle morphology as a homeomorphy in cephalopod evolution. Schemes of *Nautilus* and *Anthoceras* from Mutvei (1997), of *Megateuthis* from Mutvei (1971), and of *Spirula* from Mutvei and Donovan (2006). Not to scale.

Comparaison entre des segments du tube siphonculaire chez des céphalopodes macrochoanitiques appartenant à différents ordres. Dans tous les cas, la couche prismatique interne (ipl) et la couche sphérulitique externe (spl) sont modifiées pour offrir un anneau poreux, perméable au liquide, situé entre les trompes septales nacrées (n) successives qui s'emboîtent les unes dans les autres. Puisque toutes les espèces montrées ici appartiennent à des ordres différents représentant différentes sous-classes dérivées d'un ancêtre commun du Paléozoïque précoce, nous considérons cette morphologie siphonculaire typique comme une homéomorphie dans l'évolution des céphalopodes. Schéma de Nautilus *et* Anthoceras *d'après* Mutvei (1997), *de* Megateuthis *d'après* Mutvei (1971), *et de* Spirula *d'après* Mutvei et Donovan (2006). Échelle arbitraire.*

This brings us to another difference noted from *Nautilus*. *Aturia* has a more complex septum shape, somewhat resembling that found among some Palaeozoic ammonites. It is suggested that the double tube of *Aturia* had its function in providing a decoupling space similar to that known from *Sepia* (Denton and Gilpin Brown, 1966, p. 724) (Note: The decoupling space is not to be confused with Denton and Gilpin Brown's (1966) "hypothesis of decoupling", see discussion and review in Kröger, 2003, p. 48). An enhanced decoupling space at the siphuncle-chamber volume interface is interpreted as functional in the context of an active buoyancy regulation (Kröger, 2003). Thus, the telescoped elongated septal necks and the porous tube-like interspace in between two succeeding siphuncular segments possibly enhanced the ability of *Aturia* to pump small amounts of water out of the phragmocone and back into it more easily than is the case in *Nautilus*. In *Nautilus*, we know due to the studies carried out by Ward (1987, and references therein) that liquid pumping is a slow process, and the buoyancy apparatus of the phragmocone is not functional in the daily trips from 50 m depth to more than 250 m undertaken by these animals. It functions only as a general decrease of body weight in water to a few grams and all mobility is carried out by action of the funnel. In case of *Aturia*, this may quite well have been different. Assuming that, as in *Nautilus*, the tissue within the siphuncular tube was able to pump along all of its length, some liquid could be pumped from the porous layer and also, in contrast, allowed to flood back without pumping simply due to the pressure of the surrounding water, *Aturia* then had an aid in its daily migrations within the water column. In this way, it could more easily follow the daily migration of planktonic crustaceans from near water surface at night to more than 100 m depth during the day.

One of the puzzles is why *Aturia*, which was so well equipped for living in the oceans during Neogene times, much more, it appears, than *Nautilus*, became extinct when its seemingly primitive relative survived.

6. Conclusions

An autochthonous occurrence of *A. cubaensis* in the Eocene-Oligocene of Tierra del Fuego and in the Late Miocene of southern and central Chile is proposed. This interpretation opposes either the generally accepted interpretation that *Aturia* lived in subtropical to tropical environments or the supposed presence of a cool near-coast Humboldt Current at that time (Flower and Kennett, 1993). A relatively warm environment during the Miocene, however, is also indicated by several gastropod genera occurring together with *A. cubaensis*, such as *Nerita* (Nielsen et al., 2004), *Xenophora* (Nielsen and DeVries,

2002), *Strombus* (Nielsen, 2005), *Zonaria* (Groves and Nielsen, 2003), *Olivancillaria* (Nielsen, 2004), architectonicids (Nielsen and Frassinetti, 2007), *Sinum*, *Echinophoria*, *Distorsio*, *Ficus*, and *Terebra* (own data). It is possible that a cool ocean current flowed northwards relatively far off the Chilean coast and forced a warm southward counter-current, which enabled a warm water fauna to live along the coast of central and southern Chile during the Miocene. Contemporary faunas of Peru and northern Chile, however, contradict such a scenario and call for a different interpretation. This warm climate changed dramatically during the late Miocene and Pliocene and the molluscan fauna was replaced by a cool-water fauna resembling that of today in this region (Nielsen and Valdovinos, 2008).

The functional morphology of the siphuncular tube suggests that *Aturia* was much better adapted to an energy-efficient buoyancy regulation and therefore to vertical migration than *Nautilus*. However, it remains unclear if *Aturia* migrated in the open seas, or like *Nautilus* was a coast dweller.

Acknowledgements

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