Invertebrate Zoology, 2017, 14(1): 2–7

Conch ornamentation in nonammonoid cephalopods: form and function

I.S. Barskov

A.A. Borissiak Paleontological Institute Russian Academy of Sciences, Profsoiuznaya Str. 123, Moscow, 117321 Russia. E-mail: is_barskov@mail.ru

ABSTRACT. The initial appearance and the functional significance of external conch ornamentation in main orders nonammonoid cephalopods (Plectronocerida, Ellesmerocerida, Orthocerida, Pseudorthocerida, Actinocerida, Endocerida, Oncocerida, Discosorida, Tarphycerida, Barrandeocerida) is discussed. The origin and primary functions of conch ornamentation is considered. The first type of ornamentation to appear was the annulated shell of some Early Ordovician Plectronocerida and Ellesmerocerida, and its function was increase in buoyancy of the phragmocone. Annulated conchs only appeared from the Middle Ordovician in Orthocerida, Pseudorthocerida, Actinocerida, Endocerida. The functional significance of longitudinal ornamentation in cyrtoceraconic and orthoceraconic and spiral ornamentation in coiled conch not apparent. The lateral apertural flanges (lappets), present in some Devonian and late Paleozoic Nautilida probably served as directing planes/wings, which allowed the animal to maintain an oriented position while moving rapidly using its hyponome.
How to cite this article: Barskov I.S. 2017. Conch ornamentation in nonammonoid cephalopods: form and function // Invert. Zool. Vol.14. No.1. P.2–7. doi: 10.15298/invertzool.14.1.01

KEY WORDS. Nonammonoid cephalopods, conch ornamentation, comparative morphological analysis, Paleozoic.

Орнаментация раковины неаммоноидных цефалопод. Форма и функция

И.С. Барсков

Палеонтологический институт им.А.А. Борисяка РАН, Профсоюзная ул., 123, Москва, 117321 Россия. E-mail: is_barskov@mail.ru

РЕЗЮМЕ: Обсуждается появление и функциональное значение орнаментации раковины в основных отрядах неаммоноидных цефалопод (Plectronocerida, Ellesmerocerida, Orthocerida, Pseudorthocerida, Actinocerida, Endocerida, Oncocerida, Discosorida, Tarphycerida, Barrandeocerida). Появление кольчатой орнаментации раковин у раннеордовикских Plectronocerida и Ellesmerocerida было первым типом орнамента. Ее функциональное значение — повышение плавучести фрагмокона. Со среднего ордовика известны кольчатые раковины в отрядах Orthocerida, Pseudorthocerida, Actinocerida, Endocerida. Функциональное значение продольной орнаментации у циртоцераконовых и ортоцераконовых раковин и спирального орнамента у свернутых не ясно. Приустьевые выросты у некоторых девонских и позднепалеозойских Nautilida вероятно служили для поддержания ориентированного положения животного при быстром движении с помощью воронки.

Как цитировать эту статью: Barskov I.S. 2017. Conch ornamentation in nonammonoid cephalopods: form and function // Invert. Zool. Vol.14. No.1. P.2–7. doi: 10.15298/invertzool.14.1.01

КЛЮЧЕВЫЕ СЛОВА: неаммоноидные цефалоподы, орнаментация раковины, сравнительно-морфологический анализ, палеозой.

Introduction

Two major types of external conch ornamentation are recognized in cephalopods: growth lines and the stronger and more elaborate shell surface ornamentation. Growth lines are not considered further in this paper. The latter kind of ornamentation (considered here) includes (Shimansky, 1962; Teichert, 1964): lirae and ribs — spiral and/or transverse positive structures, which are not reflected on the inner side of the shell, or on the mold. Larger elements of external ornamentation (sculpture): annulations, costae or ridges, nodes, spines, and apertural flanges, may be reflected on the inner surface of the shell and on the mold. I will discuss these structures using examples from non-ammonoid cephalopods, in the context of the general question of the origin of cephalopod conch ornamentation (when, why and for what purpose this ornamentation appeared).

Material and methods

The materials for the discussion are descriptions and pictures in global cephalopod genera handbooks (Ruzhencev, 1962a,b; Moore, 1964) and my experience in studies of these matters.

Results and discussion

With regard to the functional significance of ornamentation in ammonoids, the simplest view is "that ornamentation is the most economical way to increase the strength of an otherwise thin and fragile conch, i.e., using the least material and adding the least weight" (Ruzhencev, 1962, p. 261). This was associated with minimizing the energy used on building the outer shell wall, allowing this energy to be used for other purposes, e.g., to secrete increasingly complex septa. This interpretation is further supported by comparison of shell wall thickness in smooth and ornamented conchs. However, this interpretation is insufficient to explain the initial appearance of ornamentation, or its diversity.

There are three issues to consider: (1) The conch of the earliest orthoceraconic and cyrtoceraconic cephalopods (Plectronocerida, Ellesmerocerida, Orthocerida, Pseudorthocerida, Actinocerida, Endocerida, Oncocerida, Discosorida, Bactritida) was originally smooth, while the ornamentation appeared later, independently in the above groups. (2) The adult shell in the modern *Nautilus* is smooth, while the embryonic shell, as in all fossil nautilids, has a reticulate ornamentation (Fig. 1A). Evidently, ancestors of this order had an ornamented shell. In the family Rutoceratidae, accepted as ancestral to nautilids, sculptured shells do indeed prevail. The dominance of smooth shells in the Nautilida is therefore secondary. (3) The earliest ammonoids (*Anetoceras*, *Erbenoceras*, *Mimosphinctes*) had a transversely ribbed conch (Fig. 1Q). Ammonoid conchs are usually ornamented, and an incredible diversity of ornamentation in ammonoids is well known, especially in Mesozoic groups, but is discussed more by artists than by scientists.

Thus, the origin and primary functions of conch ornamentation should be discussed using examples from the earliest ortho- and cyrtoceraconic taxa. The succession of appearance of different types of ornamentation in non-ammonoid cephalopods is interesting to follow. Cyrtoceraconic and orthoceraconic conchs of all late Cambrian (Furongian) cephalopods (two orders, 28 genera) lack ornamentation, except for growth lines. The first type of ornamentation to appear was the annulated shell of some Early Ordovician Plectronocerida and Ellesmerocer-

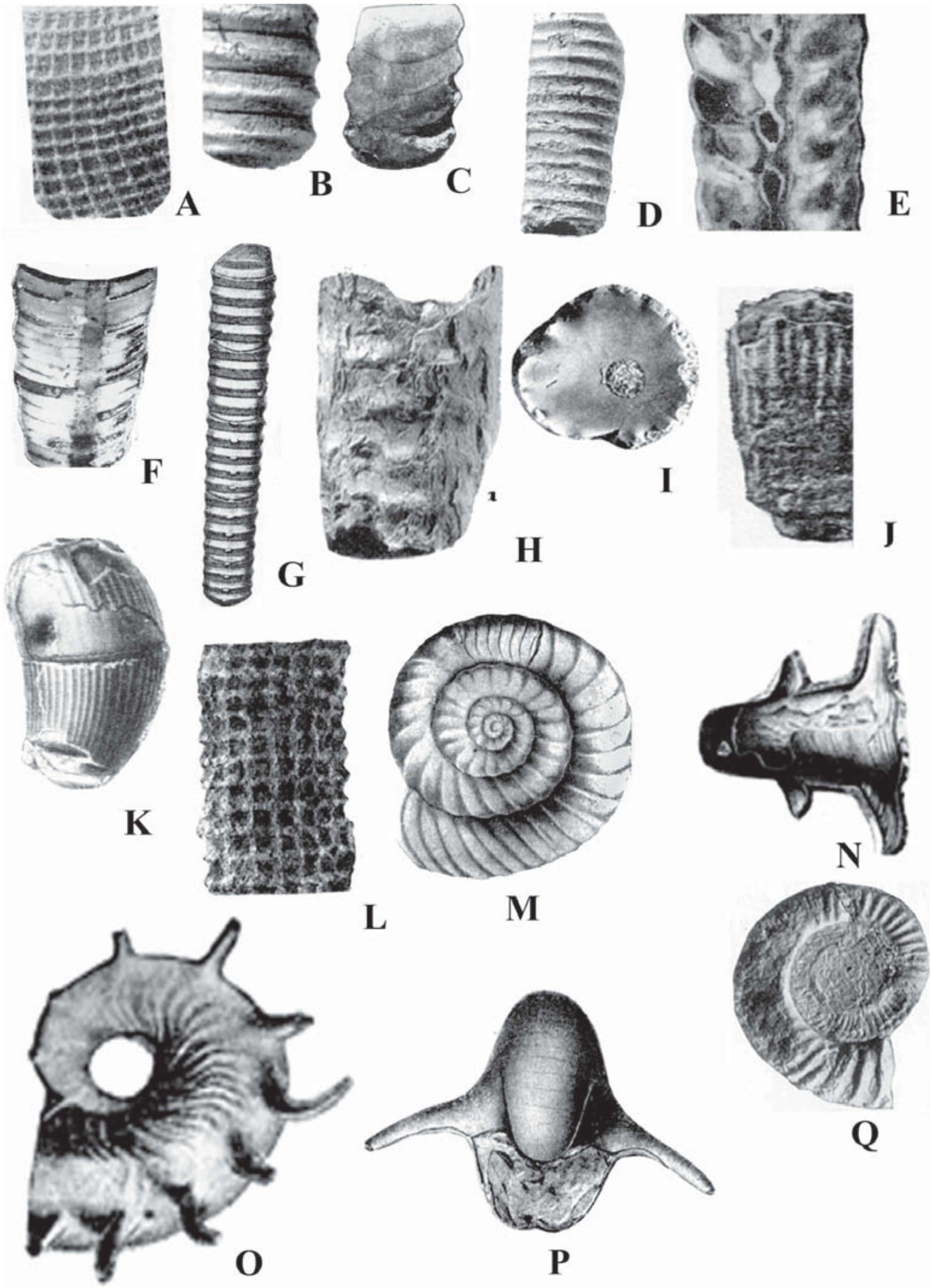

Fig. 1. Main types of conch ornamentation in nonammonoid cephalopods. A — *Nautilus stenomphalus* Sowerby, recent, embryonal conch ornamentation; B — *Lopingoceras lopingens* (Stoyanov), Orthocerida, Upper Permian, annulate conch, lateral view: C — the same species, longitudinal section; D — *Protocycloceras lamarcki* (Billings), Ellesmerocerida, L. Ordovician, annulate conch; E — *Spyroceras karpinskyi* Zhuravleva, Pseudorthocerida, Middle Devonian, annulate conch; F — *Pseudeskimoiceras* sp., Pseudortho-

ida (the family Protocycloceratidae and several genera in other families). This was the only type of conch ornamentation present in these orders. The orthoceraconic and cyrtoceraconic members of the Endoc?rida, the Actinocerida, and the Orthocerida, which appeared in the Early Ordovician, did not have conch sculpture. Annulated conchs only appeared from the Middle Ordovician (a few genera only: three in the Endocerida, two in the Actinocerida, and nine in the Orthocerida). The appearance of annulations has a rational functional explanation. Cephalopods that developed a hydrostatic mechanism that allowed them to be lifted above the seafloor and colonize a new adaptive zone (pelagial), where in the Cambrian-Ordovician they had no competitors, faced three main functional problems: (1) increase in buoyancy, (2) suitable orientation in the water column, (3) developing a new means of locomotion (Barskov et al., 2008). The last of these three problems was solved by transforming the foot of the originally crawling ancestors, probably monoplacophorans, into a jet device (funnel), whereas the second problem was approached in various ways in the major groups: development of intrasiphonal and cameral deposits and coiling in a laterally flattened spiral (Barskov et al., 2008). At the early evolutionary stages, the main problem was to increase buoyancy. This could be achieved by increasing the volume of the chambers by making them longer. This trend is distinctly recognized in the evolution of the earliest plectronocerids, ellesmerocerids, and other taxa. However, there is also another way of achieving this, i.e., a cylindrical shape (phragmocone chamber in smooth shells) has a smaller volume than a barrel shape of the same height. This was the original function of the annulation, i.e., the original functional significance of an annulated shell was to increase buoyancy. Over time, the primary hydrostatic function of the annulation was apparently lost, while the buoyancy was controlled by modifications of the shell hydrostatics. However, the ribbing of the shell surface remained. This hypothesis is apparently sup-

cerida, Middle Ordovician, annulate conch, three chambers per annulus; G — *Bohemites aculeatum* (Barrande), Upper Silurian, annulate conch, up to five chamber per annulus; H — *Ellinoceras septicurvatum* Balashov, Actinocerida, Middle Ordovician, annulate conch with strongly sinuous sutures, lateral view, I — longitudinal section; J — *Greenlandoceras lineatum* (Troedsson), Orthocerida, Upper Ordovician, longitudinal ornamentation; K — *Clathroceras sulcatum* (Barrande), Oncocerida, Silurian, longitudinal ornamentation; L — C*edarvilleoceras porkunense* Balashov, Orthocerida, Silurian, cancellate sculpture; M — *Discoceras antiquissimum* (Eichwald), Tarphicerida, Upper Ordovician, ribbed conch; N — *Ptenoceras alatum* (Barrande), Lower Devonian, apertural flanges; O — *Cooperoceras texanum* Miller, Nautilida, Lower Permian, conch with spines; P — *Permonautilus cornutus* (Golovkinsky), apertural flanges, Q — *Erbenoceras advolvens* (Erben), Agoniatitida, Lower Devonian, ribbed conch. The magnification in all picture is arbitrary.

Рис. 1. Основные типы орнамента раковины неаммоноидных цефалопод. A — *Nautilus stenomphalus* Sowerby, совр., орнамент эмбриональной раковины; B — *Lopingoceras lopingens* (Stoyanov), Orthocerida, верхняя пермь, кольчатая раковина, вид сбоку; C — тот же вид, продольный разрез раковины; D — *Protocycloceras lamarcki* (Billings), Ellesmerocerida, нижний ордовик, кольчатая раковина; E — *Spyroceras karpinskyi* Zhuravleva, Pseudorthocerida, средний девон, кольчатая раковина; F — *Pseudeskimoiceras* sp., Pseudorthocerida, средний ордовик, три камеры на кольцо; G — *Bohemites aculeatum* (Barrande), верхний силур, до пяти камер на кольцо; H — *Ellinoceras septicurvatum* Balashov, Actinocerida, средний ордовик, кольчатая раковина с синусоидной перегородчатой линией; вид сбоку; I — тот же вид, продольное сечение; J —*Greenlandoceras lineatum* (Troedsson), Orthocerida, верхний ордовик, продольный орнамент; K — *Clathroceras sulcatum* (Barrande), Oncocerida, силур, продольный орнамент; L — *Cedarvilleoceras porkunense* Balashov, Orthocerida, силур, ретикулятный орнамент; M — *Discoceras antiquissimum* (Eichwald), Tarphycerida, верхний ордовик, ребристая раковина; N — *Ptenoceras alatum* (Barrande), нижний девон, выросты устья; O — *Cooperoceras texanum* Miller, Nautilida, нижняя пермь, раковина с шипами; P — *Permonautilus cornutus* (Golovkinsky), apertural flanges; Q — *Erbenoceras advolvens* (Erben), Agoniatitida, нижний девон, ребристая раковина. Для всех рисунков увеличение произвольное.

Table 1. Shares of genera with an ornamented conch in the main orders of nonammonoid cephalopods.
Таблица 1. Пропорция родов с орнаментированной раковиной в основных отрядах неаммоноидных цефалопод.

Ornamentation/ Orders	Transverse ribs, ridges	Longitudinal lirae, ribs, ridges	Reticulate ribs, ridges	Nodes	Longitudinal furrows or projections	Total
Plectronocerida	–	–	–	–	–	–
Ellesmerocerida	15%	–	–	–	–	15%
Endocerida	5%	–	–	–	–	5%
Actinocerida	0.5%	0.5%	0.5%	–	–	1.5%
Discosorida	4%	4%	–	–	–	8%
Oncocerida	8%	2%	6%	–	–	16%
Orthocerida + Pseudorthocerida	28%	8%	1%	–	–	37%
Ascocerida	38%	–	–	–	–	38%
Tarphycerida	50%	–	–	–	–	50%
Barrandeocerida	52%	2,5%	2,5%	2%	–	59%
Nautilida	17%	8%	3%	8%	3%	39%
Total						24.4%

ported by the fact that one annulation originally corresponded to exactly one phragmocone chamber (Fig. 1B–E), whereas in later genera shells had three or even five annulations per chamber (Fig. 1F–G). The annulation of the conchs was associated with increased complexity of the suture in orthoceraconic actinocerids, i.e., the Late Ordovician genus *Ellinoceras* Balashov (Fig. 1H–I). The annulation, possibly, served to increase buoyancy, whereas an increased sutural complexity suggests a change in the hydrostatic control. This phenomenon is not observed in Paleozoic non-ammonoid cephalopods (only in some Mesozoic nautilids, the septum became more complicated: Triassic *Yakutionautilus* Barskov et Archipov, Cretaceous *Hercoglossa* Conrad, Paleogene *Aturia* Bronn), but was the main trend in the evolution of ammonoids.

Very diverse ribbing of the conch of coiled cephalopods was unlikely to have been associated with buoyancy. Whereas it is possible to suggest for the coarsely ribbed taxa that their widely spaced and raised ribs could improve stability during fast locomotion (Reyment, 1973), for taxa with a finely ribbed conch such a hypothesis cannot be supported.

The longitudinal conch ornamentation (ribs) (Fig. 1J–K) and reticulate one (Fig. 1L) are far less common in orthoceraconic and cyrtoceraconic shells, and only appeared at the end of the Ordovician. The early coiled members of the orders Tarphycerida (Fig. 1M) and Lituitida have only transverse ribbing but have no longitudinal ornamentation. Longitudinal ornamentation is more diverse in the late Paleozoic Nautilida: lirae, transverse ridges and spiral ribs, rows of nodes, ventral and lateral keels and furrows. The functional significance of this ornamentation is not apparent. The most prominent longitudinal sculpture elements, which essentially changed the shape of the shell, could be used to support the orientation of the animal in the water (idle and in motion). The functional significance of the lateral apertural flanges (lappets), present in some Devonian and late Paleozoic Nautilida, is more apparent. They probably served as directing planes/wings, which allowed the animal to maintain an oriented position while moving rapidly using its hyponome. Noteworthy, that the formation of these directing elements occurred at different stages of ontogeny (Fig. 1N–P).

Table 1 shows that more advanced, younger groups had more diverse ornamentation. All taxa of the order rank were dominated by transverse ornamentation being expressed by trans-

Table 2. Change in shares of genera with an ornamented conch in nonammonoid cephalopods over time.
Таблица 2. Изменение пропорций родов неаммоноидных цефалопод с орнаментированной раковиной во времени.

Cm	O1	O2+3	S	D	C	P	T	Total
0	13%	14%	19%	35%	49%	34%	7%	24.4%

verse annulations, ribs, or costa. Some groups only have this ornamentation (Ellesmerocerida, Endocerida, Tarphycerida, Ascocerida).The longitudinal ornamentation appeared later. Exotic types of ornamentation, represented by nodes, spines, or apertural flanges are known only in the coiled Barrandeocerida and Nautilida. The share of genera with ornamented shells increased until the Carboniferous, and slightly decreased in the Permian (Table 2). After the mass extinction at the end of the Permian, the share of ornamented conchs among newly appearing nautilids was very low. Later, in the Jurassic, Cretaceous, and Cenozoic, only taxa with smooth conchs existed, apart from two Cretaceous genera, the external surface of which had thin transverse ribs which were not reflected on the internal mold.

Acknowledgements

The author is deeply grateful to professor T.B. Leonova for stimulating of my cephalopod studies and Dr. S.V. Nikolaeva for help in English translation this paper. The study was supported by the Program No 28 of the Presidium of the Russian Academy of Sciences "Evolution of the Organic World and Planetary Processes" (subprogram 2).

References

Barskov I.S., Leonova T.B., Boiko M.S., Konovalova V.A., Nikolaeva S.V. 2008. Cephalopods in marine ecosystems of the Paleozoic // Paleontol. J. Vol.41. 118 p.

Moore R.C. (ed.). 1964. Treatise on Invertebrate Paleontology. Part K. Mollusca 3. Univ. Kansas Press. 519 p.

Reyment R.A. 1973. Factors in distribution of fossil cephalopods // Bull. Geol. Inst. Univ. Uppsala. New ser. Vol.4. Pt.3. P.7–41.

Ruzhencev V.E. (ed.). 1962. Osnovy Paleontologii. Molluski – Golovonogie 1. Moscow: AN SSSR Publ. 438 pp. [in Russian].

Ruzhencev V.E. 1962a. [Superorder Ammonoidea. General Part] // Ruzhencev V.E. (ed.). Osnovy Paleontologii. Molluski – Golovonogie 1. Moscow: AN SSSR Publ. P.243–33.[in Russian].

Shimansky V.N. 1962. [Superorder Nautiloidea. General Part] // Ruzhencev V.E. (ed.). Osnovy Paleontologii. Molluski – Golovonogie 1. Moscow: AN SSSR Publ. P.33–71.[in Russian].

Teichert C. 1964. Morphology of Hard Part // Moore R.C. (ed.). Treatise on Invertebrate Paleontology. Part K. Mollusca 3. Univ. Kansas Press. P.K13–K54.

Responsible editors
E.N. Temereva, K.G. Mikhailov