

Morphology of Cephalic Structures in Late Cretaceous Radiolarians of the Order Nassellaria

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Abstract—Eight morphological types of the initial chamber (cephalis) of Late Cretaceous radiolarians of the order Nassellaria are described; seven of them, i.e., *Perseus*, *Napora*, *Arcanicsapsa*, *Cornutella*, *Theocoronium*, *Sciadiocapsa*, and *Squinabollum*, are established for the first time. These types are distinguished by the structure of the cephalic spicule (presence or absence of various spines, incorporation of elements into the cephalic wall, etc.) and the subdivision of the cephalis into upper and lower parts. These data allow one to introduce clarity into the taxonomic position of species of the Late Cretaceous Nassellaria.

Key words: Radiolaria, Upper Cretaceous, cephalis, cephalic spicule, cephalic types.

INTRODUCTION

Radiolarians from the Late Cretaceous display a high morphological and taxonomic diversity. However, the currently accepted taxonomy is based on an artificial system, and precise criteria for the higher taxa have not been developed.

The nassellarian system based on the morphology of the cephalis and its spicule was proposed by Petrushevskaya (1981) in her famous fundamental work *Radiolyarii otryada Nassellaria Mirovogo okeana* (Radiolarians of the Order Nassellaria of the World Ocean). The main criterion for the higher taxa is similarity in the features manifested at the early developmental stage. Such features of the Nassellaria are the cephalic structure and the morphology of the cephalic spicule. Petrushevskaya (1981) established 11 structural types of the cephalis of the Meso-Cenozoic Nassellaria, three of which (at most) occur in the Mesozoic: (III) artostrobiid (similar to the *Sciadiocapsa* type), (VIII) acropyramidal of the second type (similar to the *Perseus* type), and (X) theoperidial (similar to the *Arcanicsapsa* type). The study of the cephalic structure performed by the author of this paper for Late Cretaceous radiolarians from the Russian Plate (Bragina, 1994; Bragina *et al.*, 1999), Crimea (Bragina, 1999), Mediterranean (Bragin and Bragina, 1991; Khokhlova *et al.*, 1994; Bragina and Bragin, 1995, 1996), and the Far East (Bragina, 1991a, 1991b; Bragina and Vitukhin, 1997), and analysis of published data, including the classical papers by Pessagno (1969, 1970), Dumitrica (1970), and Takemura (1986), allow for the establishment of eight structural types of cephalis in Late Cretaceous radiolarians.

Nassellarian shells usually consist of the cephalis (first chamber) enclosing the cephalic spicule; the tho-

rax (second chamber); the abdomen (third chamber); and postabdominal chambers, which widely vary in number. When describing the cephalic elements, the generally accepted terminology and designations are used (Petrushevskaya, 1981; Takemura, 1986). Figure 1 shows the structure of the cephalic spicule. It consists of the median bar MB and the following spines: (A) apical, (V) vertical; (Lr) and (Ll) two main lateral; (D) dorsal; (lr) and (ll) right and left supplementary lateral, and (Ax) axobate. In addition, I introduced the designation for a new spine named (Lm) *lateral middle*; this spine gently slopes downwards and is positioned in almost the same plane as the median bar and the two lateral spines or slightly above the lateral spines (under the vertical spine) (Fig. 2, 4b). In contrast to the axobate (Foreman 1968; Petrushevskaya, 1981), one end of the new spine is always incorporated in the lower part of the cephalic wall (Pl. 3, fig. 6) or the upper part of the thorax (Bragina and Bragin, 1996, pl. III, figs. 2–4). This spine was registered in nassellarians displaying the *Theocoronium* type of the cephalic chamber. The plane containing the median bar and positioned perpendicular to the main shell axis is named the *basal plane*, the thickening on the internal wall of the cephalis in the plane of the median bar MB and the main lateral spines Lr and Ll is the *cervical ring* (Takemura, 1986).

RESULTS AND DISCUSSION

Figure 2 demonstrates the results of detailed analysis of types of the cephalic structure, each cephalic type is shown in various planes.

(1) *Perseus* type (Figs. 2, 1a–1c) (Pl. 3, figs. 3, 4; Pl. 4, figs. 4, 10, 11). This type was first discovered by Takemura (1986) in the Middle Jurassic Nassellaria. It

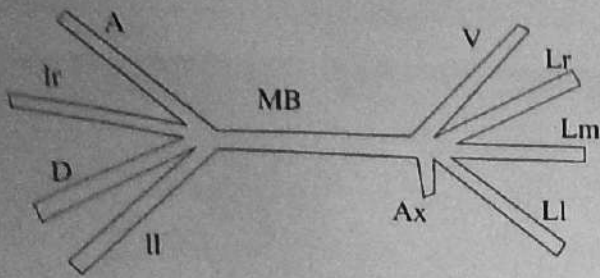


Fig. 1. The main morphological elements of the nassellarian spicule: (MB) median bar; (A) apical, (V) vertical, (D) dorsal, (Lr) and (Ll) main lateral, (Lm) lateral middle, (lr) and (ll) right and left supplementary, and (Ax) axobate spines.

main shell axis (Fig. 2, 1a), the Lr, Ll, lr, and ll are positioned almost perpendicular to apical spine A. The basal plane (Figs. 2, 1c) displays five pores; three are relatively larger and formed by Lr and lr, lr and ll, and ll and Ll; the other two pores are smaller and located between Lr and V, V and Ll.

occurs in such Cretaceous taxa as *Xitus asymbatos* (Foreman) and *Stichomitra warzigita* Empson-Morin (Pl. 3, fig. 4; Pl. 4, fig. 11). The median bar of the cephalic spicule is located in the central part of the cephalic chamber (Fig. 2, 1b). Spine A is connected to the end of the MB at an almost right angle; external to the cephalis, it becomes a stout apical horn. Spine V is more inclined with reference to the median bar than the apical spine and positioned at an acute angle to the median bar (Fig. 2, 1b); external to the cephalic wall, it is occasionally shaped into a small horn. In the plane of the

(2) *Napora* type (Figs. 2, 2a-2c). The taxa assigned to this type of the cephalic structure first emerged approximately in the Middle Jurassic, where they were first discovered by Takemura (1986), and persisted to the Late Cretaceous (O'Dogherty, 1994, pl. XLI, figs. 15-17). In this type, the apical spine is often almost completely incorporated in the cephalic wall; occasionally, this is accompanied by a thickening of the wall at the point of incorporation. In this case, the supplementary spines lr and ll connected to this part of the cephalic spicule are reduced (Figs. 2, 2b). The spine D is perfectly developed, pierces the shell wall, and extends far beyond its outline. The median bar MB is displaced from the central position, its end that is continued by spine D closely approaches the internal surface of the cephalis; the base of spine D is located inside the wall of the lower part of the cephalic chamber. As a result, the base of the cephalis contains six pores; four are approximately equal in size and formed

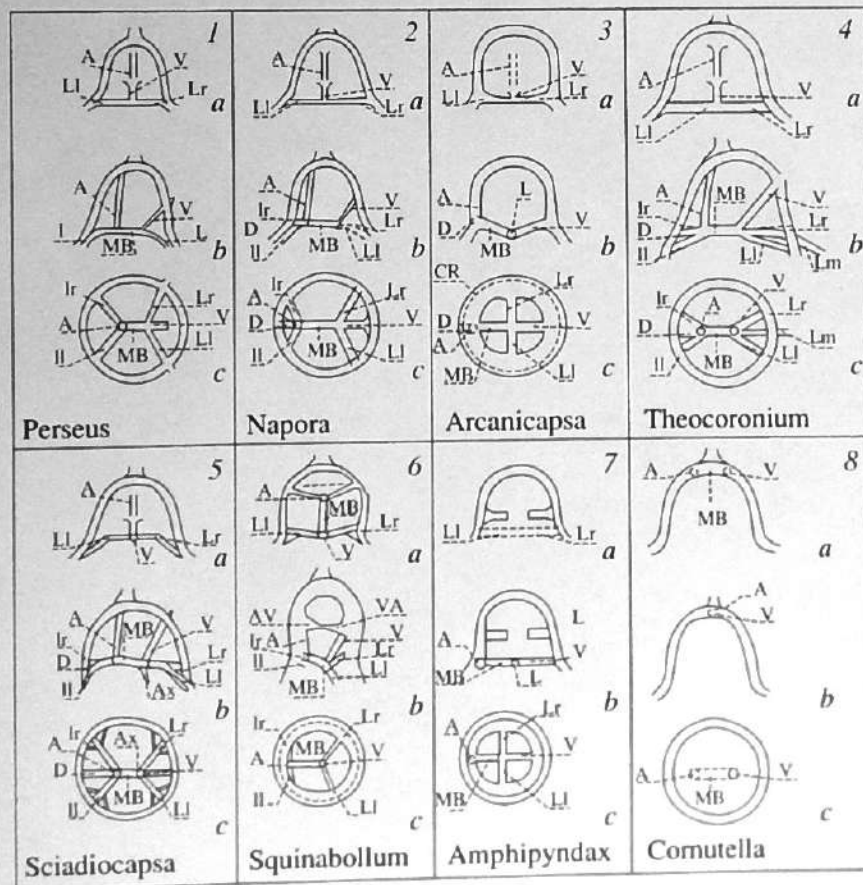
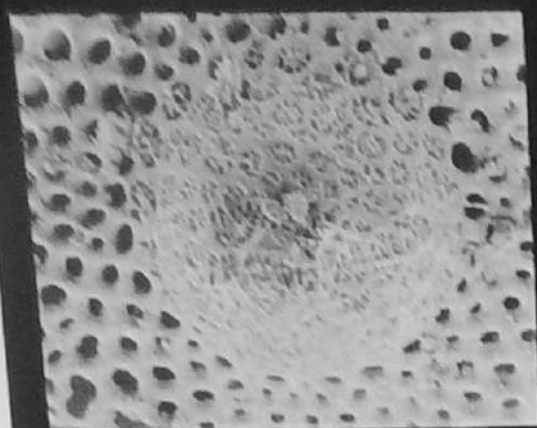
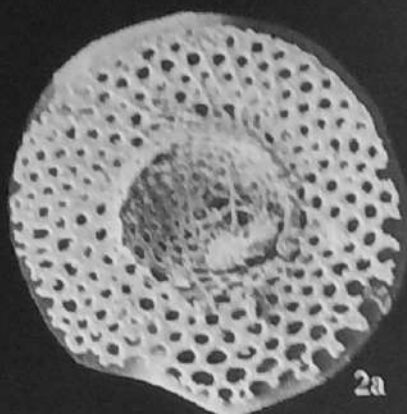


Fig. 2. The cephalic types of Late Cretaceous radiolarians. Designations: structure of the cephalic chamber: (1a, 2a, 3a, 4a, 5a, 6a, 7a, 8a) lateral view, section along the main shell axis in the plane perpendicular to the median bar MB and containing the Lr and Ll spines; (1b, 2b, 3b, 4b, 5b, 6b, 7b, 8b) lateral view in the plane of the median bar MB; and (1c, 2c, 3c, 4c, 5c, 6c, 7c, 8c) structure of the cephalic spicule through the apex of the cephalis in the basal plane.



1



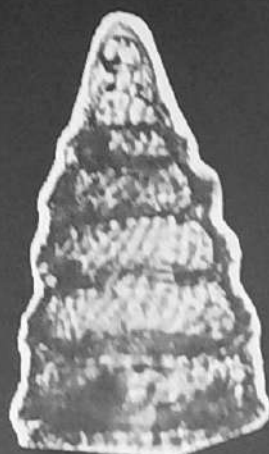
2a



2b



3



4a



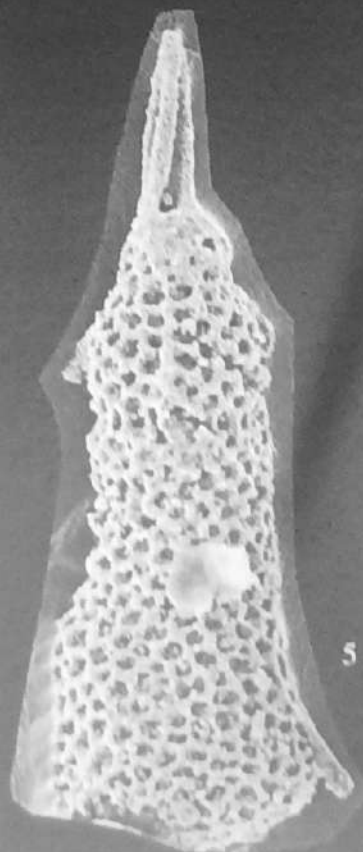
6a



6b



4b



5

Explanation of Plate 3

Structural types of the cephalis in Late Cretaceous radiolarians: (Figs. 1, 2) *Sciadiocapsa* type, (Figs. 3, 4) *Perseus* type, (Fig. 5) *Napora* type, and (Fig. 6) *Theocoronium* type.

Figs. 1 and 2. *Neosciadiocapsa jenkinsi* Pessagno: (1) specimen GIN, no. 4849/1, Santonian–Campanian of the Russian Plate (Khot'kovo Group), $\times 500$; (2) specimen GIN, no. 4850/1, Upper Cenomanian of southern Sakhalin: (2a) $\times 500$ and (2b) $\times 250$.

Fig. 3. *Dietyomitra* sp. ex gr. *D. densicostata* Pessagno, specimen GIN, no. 4849/2, Santonian–Campanian of the Russian Plate (Khot'kovo Group), $\times 500$.

Fig. 4. *Stichomitra* sp. ex gr. *S. communis* Squinabol, specimen GIN, no. 4848/1, Santonian–Campanian of the northwestern Kamchatka (Penzhina): (4a) $\times 175$ and (4b) $\times 250$.

Fig. 5. *Rhopalosyringium euganeum* (Squinabol), specimen GIN, no. 4870/1, Lower Turonian of the Mountainous Crimea, $\times 350$.

Fig. 6. *Theocoronium ornatum* Bragina, specimen GIN, no. 4848/2, Santonian–Campanian of the northwestern Kamchatka (Penzhina), $\times 250$.

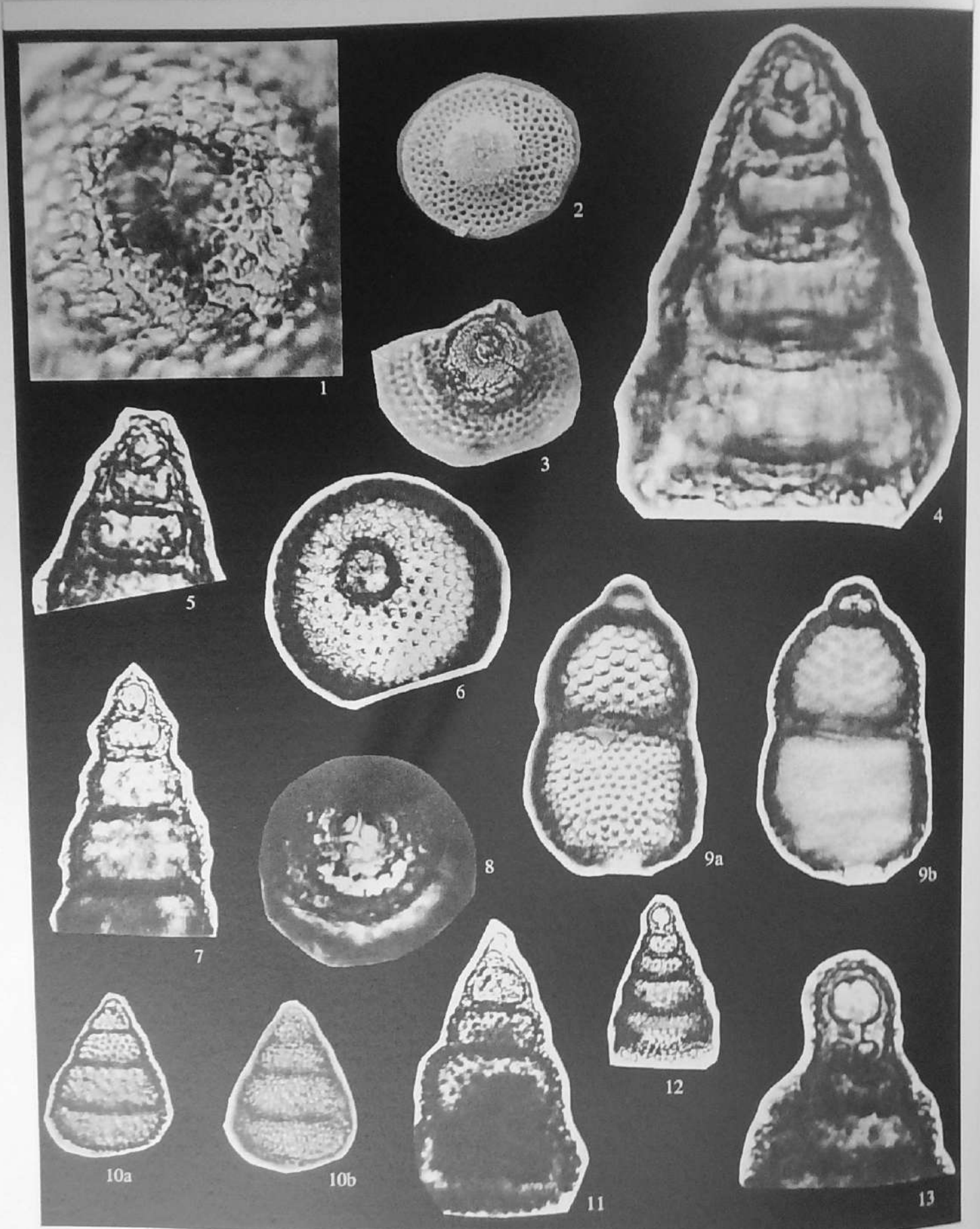
by the median bar MB, the gently sloping spine V, and the main lateral spines Lr and Ll (Fig. 2, 2c) extending far beyond the shell, as does spine D; two other pores formed by the spines ll and D, D and lr are very small and scarcely visible in the basal plane. In the basal plane, the spines D, Lr, and Ll are directed to the apices of an isosceles triangle (Fig. 2, 2c; Pl. 3, fig. 5). The nassellarian shells showing this cephalic type, for example, Late Cretaceous representatives of the genera *Rhopalosyringium* and *Ultranapora*, usually have a well-developed apical horn, which is complicated by a small thorn at the base, on the surface of the cephalic chamber. In earlier members of the family Ultranaporidae assigned to the genus *Napora*, the apical horn is in the central position and passes through the uppermost point of the cephalis (Takemura, 1986, pl. III, figs. 9, 10). It was shown that radiolarians assigned to this type were widespread in the Jurassic and Early Cretaceous (Baumgartner *et al.*, 1995), became relatively scarce in the Late Cretaceous (Thurrow, 1988; Erbacher, 1994; O'Dogherty, 1994; Salvini and Marcucci Passerini, 1998), and almost entirely disappeared in the Santonian.

(3) *Arcanica* type (Figs. 2, 3a–3c; 3a–3h) (Pl. 4, figs. 6, 9). This type was first established by Takemura (1986) for Middle Jurassic nassellarians. It persisted unchanged from the Middle Jurassic to the Late Maastrichtian. In the taxa assigned to this type, for example, representatives of the genus *Holocryptocanium*, spine A is completely incorporated in the cephalic wall; spine V is so low that, tending to the horizontal (Pl. 4, fig. 6), it looks like a continuation of the median bar MB (Figs. 2, 3b). Four pores formed by the MB and spines V, Lr, and Ll are distinctly visible in the basal plane (Figs. 2, 3c; Pl. 4, fig. 6). This type is characterized by the development of the cervical ring in the basal plane; the cephalis appears as if isolated by the ridge from the second chamber, the thorax. The cervical ring is formed by the arches incorporated in the internal wall of the cephalis and connecting in pairs the MB and Lr, Lr and V, V and Ll, and Ll and MB. In the Late Cretaceous, a similar cephalic structure is characteristic of the abundant cryptocephalic taxa of the family Williriedellidae. A continuous series of genera displaying a similar structure is observed from the Middle Jurassic to the terminal Late Cretaceous: *Arcanica* (Takemura,

1986, pl. VII, figs. 1–3), *Zhamoidellum* (Calloviaan–Oxfordian) (Dumitrica, 1970, pl. X, fig. 63), *Holocryptocanium* (Baumgartner *et al.*, 1995) emerging in the Early Cretaceous, and many genera described by Dumitrica (1970) from the Late Cretaceous of Romania: *Holocryptocapsa* (Dumitrica, 1970, pl. XV, figs. 99c, 100d), *Excentropyllomma*, *Hemicryptocapsa* (pl. XIII, figs. 79b, 83a), *Heliocryptocapsa* (pl. IV, fig. 21b), and *Holocryptocanium*. Each genus has a cervical ring. It should be noted that the genus *Williriedellum* occupies an intermediate position; in this case, the presence of the cervical ring and four pores at the base of the cephalis is combined with an incomplete incorporation of the A, ll, and lr spines in the cephalic wall. The structure of the cephalic spicule in the genus *Diacanthocapsa* (Dumitrica, 1970, pl. VII, fig. 36) is distinguished from that of the *Arcanica* type by the development of the axobate (Dumitrica, 1970, pl. VII, fig. 43).

(4) *Theocoronium* type (Figs. 2, 4a–4c). This type was discovered during the morphological study of Santonian–Campanian associations from the Penzhinskaya Guba (northwestern Kamchatka) (Bragina, 1991b, pl. 1, fig. 3; text-fig. 1a) (Pl. 3, fig. 6). It is characterized by the development of all spines, except for the axobate. A characteristic feature of this type is the presence of the Lm spine in the middle position between the Lr and Ll spines and in the same plane as these spines. In contrast to the *Napora* type, the supplementary spines lr, ll, and Lm extend beyond the shell and are directed to the apices of an isosceles triangle in cross section (Fig. 2, 4c). One species of this genus, *Theocoronium subtriquetrus* Bragina, displaying a similar cephalic structure is known from an Early Campanian tropical association discovered in the Perapedhi Formation of Cyprus (Bragina and Bragin, 1996, pl. III, figs. 2–4).

(5) *Sciadiocapsa* type (Figs. 2, 5a–5c) (Pl. 3, fig. 2). This type is widespread in Late Cretaceous radiolarians. It is especially well-pronounced in the genera *Neosciadiocapsa* (Pessagno, 1969, pl. XXXVI, figs. 1, 2), *Microsciadiocapsa* (Pessagno, 1969, pl. XXX, figs. 1, 2; pl. XXXIV, figs. 1, 2), and *Sciadiocapsa* (Pessagno, 1969, pl. XXXVII, fig. 5). This type is characterized by perfectly developed spines A and V. In this case, the cephalic apex is usually crowned by the apical horn, and the vertical spine external to the cephalic wall is



Explanation of Plate 4

Structural types of the cephalis in Late Cretaceous radiolarians: (Figs. 1–3) *Sciadiocapsa* type, (Figs. 4, 7, 10, 11) *Perseus* type, (Figs. 5, 8) *Squinabollum* type, (Figs. 6, 9) *Arcanica* type, and (Figs. 12, 13) *Amphipyndax* type.

Figs. 1–3. *Neosciadiocapsa jenkinsi* Pessagno: (1) specimen GIN, no. 4848/3, Santonian–Campanian of the northwestern Kamchatka (Penzhina), $\times 500$; (2) specimen GIN, no. 4850/2, Upper Cenomanian of southern Sakhalin, $\times 200$; and (3) specimen GIN, no. 4848/4, Santonian–Campanian of the northwestern Kamchatka (Penzhina), $\times 200$.

Fig. 4. *Dictyomitra formosa* Foreman, specimen GIN, no. 4849/3, Santonian–Campanian, Khot'kovo Group of the Russian Plate, $\times 500$.

Figs. 5 and 8. *Nassellaria* gen. et sp. indet.: (5) specimen GIN, no. 4849/5, $\times 350$; (8) specimen GIN, no. 4849/4, $\times 500$; Santonian–Campanian, Khot'kovo Group of the Russian Plate.

Fig. 6. *Cryptamphorella conara* (Foreman), specimen GIN, no. 4849/6, Santonian–Campanian, Khot'kovo Group of the Russian Plate, $\times 250$.

Fig. 7. *Xitus asymbatos* (Foreman), specimen GIN, no. 4849/7, Santonian–Campanian, Khot'kovo Group of the Russian Plate, $\times 250$.

Fig. 9. *Tricolocapsa granti* Campbell et Clark, specimen GIN, no. 4849/8, Santonian–Campanian, Khot'kovo Group of the Russian Plate, $\times 350$.

Fig. 10. *Stichocapsa* (?) sp., specimen GIN, no. 4848/5, Santonian–Campanian of the northwestern Kamchatka (Penzhina), $\times 250$.

Fig. 11. *Stichomitra warzigita* Empson-Morin, specimen GIN, no. 4849/9, Santonian–Campanian, Khot'kovo Group of the Russian Plate, $\times 300$.

Figs. 12 and 13. *Amphipyndax stocki* (Campbell et Clark): (12) specimen GIN, no. 4849/10, $\times 150$; (13) specimen GIN, no. 4849/11, $\times 500$; Santonian–Campanian, Khot'kovo Group of the Russian Plate.

often visible through a relatively large pore, which extends the shell wall to form a small and short tube, as is observed in the species *Neosciadiocapsa diabloensis* Pessagno (Pessagno, 1969, pl. XXXV, figs. 7–9) and *Ewingella jonesi* Pessagno (Pessagno, 1969, pl. XXVII, fig. 2; pl. XXVIII, figs. 2–4) (Figs. 2, 5b). The spines A, V, D, lr, ll, Lr, and Ll are well developed. A distinctive feature of the *Sciadiocapsa* type is the development of paired secondary spinules at the ends of the spines listed above (Fig. 2, 5c; Pl. 3, fig. 2; Pl. 4, fig. 1), which are oriented in opposite directions with reference to the ends of these spines. The neighboring spines are connected in pairs by arches (Pessagno, 1969, pl. XXX, figs. 1, 2.). The spine Ax (axobate) is directed perpendicularly downwards to the distal part of the shell. The basal plane contains six pores positioned symmetrical to each other with reference to the median bar MB (Fig. 2, 5c).

(6) *Squinabollum* type (Figs. 2, 6a–6c; 3i–3m). In each type considered above, the median bar MB is in an almost horizontal position, as is evident from Figs. 2, 1b, 4b, and 5b. Let us consider the changes in the cephalis where the spine A is almost completely incorporated in the cephalic wall and the median bar is strongly inclined (its end is shaped into the apical spine A and positioned closer to the apex of the cephalis) (Figs. 2, 6a, 6b) (Dumitrica, 1970, pl. XIX). In this case, the vertical spine V is positioned at an angle of a little less than 90° to the median bar MB and almost immediately incorporates in the cephalic wall; the supplementary spines (lr, ll) and the spine D are reduced; and the median bar MB and the main lateral spines Lr and Ll form three large pores distinctly seen through the thorax (Dumitrica, 1970, pl. XIX, fig. 121b) and through the apex of the cephalis (Fig. 2, 6c); the upper part of the cephalic chamber is obliquely constricted by arches (Fig. 2, 6b), which extend from the upper part of the

spine A incorporated in the wall of the cephalic chamber to the vertical spine V and form a ridgy ring on the internal wall of the cephalis (Dumitrica, 1970, pl. XIX, fig. 121c). The edge of the ridge that adjoins spine V is somewhat lower than the edge adjoining spine A. Such a cephalic structure has been registered with certainty only in *Squinabollum fossilis* (Dumitrica, 1970; Petrushevskaya, 1981) and in individual taxa from the associations of the Santonian and Campanian of the Moscow Region (Pl. 2, figs. 5, 8).

In a paper devoted to the cephalic structure of the genus *Amphipyndax*, Foreman (1966, text-figs. 4–6) gave a reconstruction of the cephalis closely resembling that of *Squinabollum*. Nevertheless, this reconstruction displays a number of distinctions, i.e., the cephalis is divided into three parts instead of two, and the spines Lr and Ll are in somewhat different positions.

(7) *Amphipyndax* type (Figs. 2, 7a–7c). This type was first established by Foreman (1966, text-figs. 7–9). It is characterized by the complete incorporation of apical spine A in the cephalic wall (Figs. 2, 7b, 7c) and a special position of spine V, which, in the genus *Amphipyndax*, is positioned so close to the horizontal that it looks like a continuation of the straight line of the median bar MB without an inflection at their joint (Fig. 2, 7b). The spines Lr and Ll are in the same plane as the median bar MB and the spine V (Figs. 2, 7b, 7c). The upper part of the cephalis is detached by arches forming a ridge on its internal surface and located at a right angle to the main shell axis (Fig. 2, 7a).

Riedel (1967) combined the taxa having a detached upper part of the cephalis in the family Amphipyndacidae. In the Middle Jurassic, such forms were characterized by the cephalic spicule of the *Yamatoum* type (Takemura, 1986), while in the Cretaceous, they have the spicule of the *Amphipyndax* and *Squinabollum*

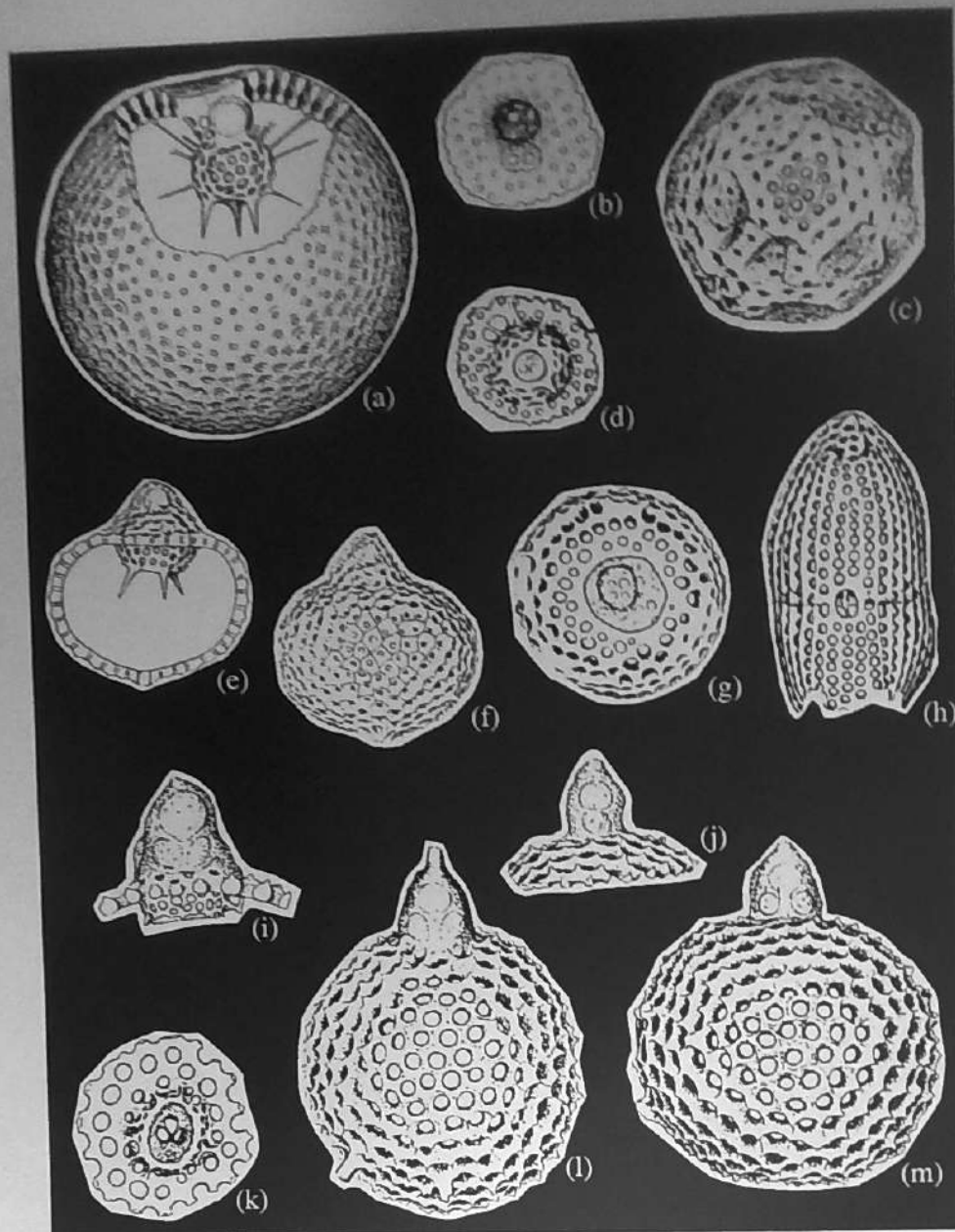


Fig. 3. *Arcanica* and *Squinabollum* cephalic types compiled on the basis of figures produced by Dumitrica (1970): (a, b) *Holocryptocanium barbui* Dumitrica, (b) cephalic structure; (c, d) *Hemicryptocapsa polyhedra*, (d) cephalic structure; (e, f) *Hemicryptocanium simplex*, (e) inner shell structure; (g) *Diacanthocapsa umbilicata*, cephalic structure; (h) *Diacanthocapsa* sp.; (i–m) *Squinabollum fossilis*, cephalic structure: (i, l) plane of the main shell axis and spines Lr and Ll, (j) plane of the main shell axis and spines A and I, arches formed by spines Lr, Ll, and V are seen, and (k) transverse plane at the thorax base.

types. However, some researchers (Empson-Morin, 1982; O'Dogherty, 1994) disagree with the presence of the cephalis divided into parts in representatives of the genus *Amphipyndax*. I agree with the point of view proposed by Takemura (1986) that Empson-Morin (1982) mistakenly considered the lower part of the divided cephalis to be the thorax. In actual fact, the cephalic structure of *Amphipyndax* is clearly seen under a light microscope in all members of this genus at the base of the lower part of the cephalis rather than in the lower part of the thorax (Foreman, 1978, pl. IV, figs. 1–5) (Pl. 4, figs. 12, 13). The division of the cephalis in the genus *Amphipyndax* is even more clear in photos produced with the aid of a scanning electron microscope

given by Empson-Morin (1982, text-figs. 1A, 1C, 1H, 2G, 2H, 2I).

(8) *Cornutella* type (Figs. 2, 8a–8c). This type was first discovered by Takemura (1986) in problematic Middle Jurassic nassellarians. It is characterized by an almost entirely reduced cephalic spicule. A perfectly developed apical horn is clearly seen external to the shell (Fig. 2, 8a); however, internally, the cephalic chamber is hollow and smooth (Figs. 2, 8a–8c). This is most likely accounted for by a complete incorporation of the median bar and all other elements in the cephalic wall.

Thus, the present study has shown that Late Cretaceous nassellarians have eight types of cephalic structure; in two of them, *Squinabollum* and *Amphipyndax*, the upper part of the cephalis is detached. It is shown

that the subfamilies Neosciadiocapsinae and Rotaforminae of the family Neosciadiocapsidae are similar in cephalic structure. This conclusion agrees with the assumption of Pessagno (1970) that these subfamilies (ranked by Pessagno as families) belong to the same phylogenetic lineage. The study of the cephalic structure in the family Williriedellidae allows one to revise its composition and exclude the genus *Williriedellum*, since its cephalic structure is atypical of this family. The *Theocoronium*, *Sciadiocapsa*, and *Squinabollum* types of the cephalic spicule are established for the first time. The presence of the *Perseus*, *Cornutella*, *Napora*, and *Arcanicapsa* types in the Late Cretaceous is noted for the first time. This study shows that the description of new taxa should be provided with an examination of the cephalic structure.

The material examined in the present study is stored at the Geological Institute of the Russian Academy of Sciences, collection nos. 4848, 4849, 4850, and 4870.

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