Definition and composition of the class Spirillinata (Foraminifera)

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A new diagnosis and revised composition of the class Spirillinata Maslakova, 1990 are given. The subclass Ammodiscana includes the orders Ammodiscida, Ammovertellida, Tournayellida, Palaeospiroplectamminida, Koskinobigenerinida, Biseriamminida, Tetrataxida, Endothyrida, Fusulinida, and Ozawainellida. The subclass Spirillinana includes the orders Archaediscida, Lasiodiscida, Involutinida, Hottingerellida, Spirillinida, and Patellinida.

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The subclass Spirillinata was separated as a group of high taxonomic rank equal to that of Miliolata and Rotaliata by Maslakova (1990). It included the order Spirillinida (Triassic – Holocene) which representatives have a pseudotwochambered shell throughout or only initially, and a calcareous shell wall. This order was described by Hohenegger & Piller (1975). Later the rank of the group was elevated to class and its composition widened (Mikhalevich, 1992, 1993, 1997a, 1997b, 1998). All representatives of Spirillinata are pseudotwochambered or derived from that arrangement. Those having microgranular or agglutinated shell wall were separated in the subclass Ammodiscana (Cambrian – Holocene); they were previously placed in the suborder Textulariina sensu Loeblich & Tappan (1988). Those having lime secreted walls were placed in the subclass Spirillinana in which were included not only the former Spirillinida and the Patellinida which were later separated from them, but also more ancient forms (orders Archaediscida, Involutinida, and orders having canal systems: Lasiodiscida and Hottingerellida).

I regard the subclass Ammodiscana as a more primitive step in the evolution of this class than the subclass Spirillinana which appeared in the Carboniferous and developed not only a more progressive shell wall, but also the canal system – a unique system of the organism level met only in Foraminifera. Previously the similarity of the foraminiferans of the two subclasses was regarded as a convergent one. The evolution of the shell wall from agglutinated in Ammodiscana to fully calcareous in Spirillinana is similar to transformations in some other foraminiferal classes (in Miliolata, from Sclumbergerinana to Miliolana; in Nodosariata, from Hormosinana to Nodosariana; in Rotaliata, from Textulariana to Rotaliana) (Mikhalevich, 1992, 1997a, 1997b, 1998).

Spirillinata is one of the most ancient foraminiferal classes combining in its morphology some plesiomorphic features (presence of pseudotwochambered or pseudomultichambered shells with primitive septation, abundance of irregular glomerate types of coiling, terminal aperture lacking any internal structures) with apomorphic ones (multichambered and even supermultichambered shells arising in the later stages of evolution; trochospiral types of coiling; additional apertures; canal systems).

Class **SPIRILLINATA** Maslakova, 1990, emend.

Diagnosis. Shells pseudotwochambered (with long tubular second chamber around proloculus) or derived from them (pseudomultichambered, multichambered in advanced representatives, but often with initial tubular part preserved during 1-2 volutions), with different coiling types: glomerate (very frequent, especially in the initial part), planospiral (more frequent in the adult stage, being initially streptospiral), some-

times biserial in the last part or trochospiral; in advanced supermultichambered forms, the shell may become spherical or fusiform; pseudochambers formed by constrictions of the outer shell wall, endoskeletal thickenings or short septula; chambers in multichambered forms usually bearing primitive features showing their origin from the tubular ones (being somewhat irregular, with short, straight or only slightly curved septa); fluted septa are met only in this group; chambers in advanced groups becoming more regular. Integrative systems: tunnels in advanced supermultichambered forms, primitive canal systems in some advanced tubular forms. Wall (still not sufficiently studied) monofontinal, agglutinated (often with ferrugineous cement) or microgranular in primitive forms (Ammodiscana) and in their multichambered representatives sometimes very thick, with different layers, not principally differing from those of the thick-walled Textulariana, but with special additional inner shell depositions (nodes, nodosites, hooks, chomata) on the chamber floor not met in other groups. Wall in the advanced subclass (Spirillinana) fully secreted, radial, may be pitted by regular pseudopores (according to published data); layers of growth are not formed; in ancient forms, often two layers are marked (microgranular and radial), in Involutinida usually radial; in recent Spirillinida, radial crystal units act optically as a single crystal, outer sculpture and inner pillars well developed. Growth of the tubular part uninterrupted, occurs by lateral accretion along the edge of the chamber, in multichambered forms not clarified. Aperture terminal or derived from terminal (in trochoid forms, tending to displace on the umbilical side), always simple, never forming inner apertural structures, single or (rarely) multiple (in advanced multichambered forms); in multichambered trochoid forms, outer apertural stuctures sometimes present (valvular flap, T-shaped or S-shaped plate); additional apertures often met. Agamonts of recent Spirillinata homokariotic (their proloculus larger than that of the gamonts); gametes (if known) amoeboid. Bottom-dwelling, mostly free-living forms. Cambrian – Holocene.

Remarks. This is one of the most ancient and not adequately studied foraminiferal groups having some convergent resemblance to Miliolata (descending from tubular forms, preserving initial tubular part in many multichambered forms, having terminal aperture, forming fusulinoid tests, having tunnels) and to Rotaliata (in multichambered plano- or trochospiral forms). It differs from Miliolata not only in the absence of inner apertural structures (their characteristic teeth), chamber form (non-tubular) in most of the multichambered forms and ultrastucture of calcareous wall in the advanced subclasses of both classes, but also in the tendencies of their development, i. e. formation in multichambered representatives of mostly non-tubular chambers resembling those of Rotaliata and mostly planospiral and often trochospiral (practically not represented in Miliolata) shells, and in presence of additional apertures and canal systems. It differs from Rotaliata in the tubular pseudotwochambered and pseudochambered shells, terminal position of the aperture without inner apertural structures as opposed to basal aperture of Rotaliata with its complex inner structures (Mikhalevich & Debenay, 1998), character of their chambers, septa and chamber conjunctions (as well as in the monofontinal wall in the advanced subclass). The terminal position of the aperture in Spirillinata is clearly seen not only in the pseudotwochambered tubular forms, but also in the pseudomultichambered and multichambered ones, especially in *Tournayella* and *Endothyranella* with their circular aperture resembling the end of the tubular chamber or in *Endothyranopsis*, *Endothyra* and *Globoendothyra* with their semicircular aperture, also resembling the end of a tube (see Loeblich & Tappan, 1988, pl. 232 (figs 6-14), 248 (figs 7-11), 244 (figs 1-6), and 245 (fig. 5)). The similarity with the tubular *Fischerina* and *Fischerinella* (Miliolata) is stricking. This terminal (not basal, in spite of their original diagnoses) position of their large aperture is reflected in its form and the structure of their inner short septa dividing chambers. The true basal aperture of Rotaliata leads to another form of septa. The chambers of Rotaliata represent the result of additional polymerization while those of Spirillanata mostly the result of fissation (Mikhalevich, 1981, 1997a, 1997b).

Some genera previously placed in Textulariina also have an initially terminal circular or semicircular aperture and some features of chamber arrangement showing their origin rather from the tubular ancestors and should be moved to Spirillinata: *Lituotuba* and the whole family Lituotubidae, some Charentiinae (*Melathrokerion*, *Karaisella*, may be some other genera), Hottingeritidae,

Buccicrenatinae, *Kutsevella* of Ammomarginulininae, may be also some species included previously in the genus *Evolutinella* (*E. darwini* (Dain), *E. schleiferi* (Sharovskaja) (Loeblich & Tappan, 1988, pl. 48, figs 16-21), the genus *Budashevella* and some others. Many planospirally coiled lituolid forms need to be revised as the apertural stucture of their initial stage is unknown.

As was shown earlier (Mikhalevich, 1992, 1997b), the wall of the palaeozoic forms (former Fusulinacea) does not differ principally from the agglutinated and microgranular wall of Textulariana, but Fusulinacea is a heterogeneous group and needs a profound revision. Based on the principle of the shell structure priority, I moved some taxa of Fusulinacea to other groups according to the plan of their organization (for instance, Parathuramminida and Paratikhinellidae to Astrorhizata; Collaniellida, Pseudopalmulinidae and some of Paleotextulariidae to Nodosariata; Biplanatidae and Nezzazatidae to Textulariana). This revision cannot be considered as finished.

In the subclass Ammodiscana, only pseudotwochambered tubular forms or the forms whose origin from the first ones seems to be undoubtful are left. The palaeozoic forms are regarded here less detailly than the recent ones.

In the text below, authors and dates are given only for families described after 1988, and diagnoses and included genera only for those described in 1999.

Subclass AMMODISCANA Mikhalevich, 1980

Diagnosis. Shells with agglutinated or microgranular shell wall. Cambrian – Holocene.

Included orders. Ammodiscida Mikhalevich, 1980 (Ammodiscidae, Pseudoammodiscidae, Pseudolituotubidae, Tolypamminidae), Ammovertellida Mikhalevich, 1999 (Ammovertellidae, Usbekistaniidae), Tournayellida Hohenegger & Piller, 1973 (Lituotubidae, Moravamminidae, Tournayellidae, and Plagioraphidae Mikhalevich, 1999 (shell high conical or cylindrical; each of the tubular chambers following proloculus forms one volution or a little more than one; *Plagioraphe* Kristan-Tollmann, 1973)), Palaeospiroplectamminida Mikhalevich, 1999 (Palaeospiroplectamminidae), Koskinobigenerinida Mikhalevich, 1999 (Koskinobigenerinidae, ? Semitextulariidae), Biseriamminida Mikhalevich, 1981, Tetrataxida Mikhalevich, 1981, Endothyrida Fursenko, 1958 (to which I add here the genera *Melathrokerion* and *Karaisella* from Charentiinae (Textulariana)), Fusulinida Fursenko, 1959, and Ozawainellida Solovieva, 1980.

Subclass SPIRILLINANA Maslakova, 1990, emend.

Diagnosis. Shells with calcareous wall, of radial ultrastructure throughout or only in the outer layer, with rich additional skeletal structures on the outer surface and/or in the umbilical area, often with inner pillars; a primitive canal system may be present. Carboniferous – Holocene.

Remarks. Glomerate tubular forms with a radial wall are a blind alley; trochospiral forms developed a primitive canal system. There is a succession in the development of forms with a radial wall: Archaediscida (Carboniferous) – Lasiodiscida (Carboniferous – Permian) – Involutinida (Permina – Cretaceous) – Spirillinida (Triassic – Holocene). I regard them as different steps in the evolution of one phyletic branch. Shell wall ultrastructure is not adequately studied in the representatives of the families Chilostomellidae and Seabrookinidae, but the terminal position of their aperture allows me to move them from Rotaliata to Spirillinata.

Included taxa. Superorder **Archaediscoida** Pojarkov, 1980: orders Archaediscida Pojarkov, 1980 (Archaediscidae, Planoarchaediscidae Gubenko, 1989, Glomodiscidae Mikhalevich, 1999 (shell pseudotwochambered with the last part of the inner lumen of the second tubular chamber subdivided by inner lateral skeletal thickenings; genera *Glomodiscus* Malakhova, 1973, *Uralodiscus* Malakhova, 1973, *Tournarchaediscus* Conil & Pirlet, 1974, *Permodiscus* Dutkevich, 1948)), Lasiodiscida Mikhalevich, 1993 (Lasiodiscidae, Monotaxinoididae Mikhalevich, 1999 (weakly trochoid shell without additional apertures and lateral bridges; *Monotaxinoides* Brazhnikova & Yartzeva, 1956)). Superorder **Involutinoida** Hohenegger & Piller, 1977: orders Involutinida Hohenegger & Piller, 1977 (superfam. Involutinoidea: Involutinidae, Triadodiscidae, Aulotortidae, Hirsutospirillinidae, Planispirillinidae; superfam. Triasinoidea: Triasinidae), Hottingerellida Mikhalevich, 1993 (Hottingerellidae Mikhalevich, 1993). Superorder **Spirillinoida** Hohenegger & Piller, 1975: orders Spirillinida

Hohenegger & Piller, 1975 (suborder Spirillinina Hohenegger & Piller, 1975: Spirillinidae, Conicospirillinidae Mikhalevich, 1999 (test trochospiral; umbilical area filled with secondary shell matter; *Conicospirillina* Cushman, 1927); suborder Spirotrocholinina Mikhalevich, 1993: Spirotrocholinidae Mikhalevich, 1993), Patellinida Mikhalevich, 1992 (superfam. Hergottelloidea: Hergottellidae, Placentulinidae (without Ashbrookininae, but with the genus *Metapatellina* transferred here from Ungulatellidae), Ungulatellidae (without *Metapatellina*), Panellainidae; superfam. Patellinoidea: Patellinidae, Paleopatellinidae Mikhalevich, 1999 (test like in Patellinidae, but without initial coil of the tubular chamber; *Paleopatellina* Kasimova et al., 1973, *Pseudopatellinella* Takayanagi, 1960, *Patelinella* Cushman, 1928, *Subpatelinella* McCulloch, 1977, possibly also *Paalzowella* Cushman, 1933, all from Ashbrookinidae), Annuloplatellinidae) and possibly Seabrokinida Mikhalevich, 1980 (Seabrokinidae).

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