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Morphostructure and paleobiology of Mesogean orthophragminids (Discocyclininidae and Orbitoclypeidae, Foraminifera)

CARLES FERRÀNDEZ-CAÑADELL

Departament d'Estratigrafia i Paleontologia, Facultat de Geologia, Universitat de Barcelona, Martí Franqués s/n, 08071-Barcelona (Spain). cferran@natura.geo.ub.es

Orthophragminids are Paleocene-Eocene bilamellar-perforate larger foraminifers characterized by a lenticular test with an equatorial layer of rectangular chamberlets arranged in concentric rings and lateral chamberlets on either side. Usually called "discocyclinids", orthophragminids include genera from two families: Discocyclinidae and Orbitoclypeidae.

This paper presents a detailed study of the morphostructure of the four Mesogean orthophragminid genera: the Discocyclinidae *Discocyclina* and *Nemkovella,* and the Orbitoclypeidae *Orbitoclypeus* and *Asterocyclina* using exceptionally well-preserved specimens from the early Cuisian sites of Gan and Bosdarros (southern France). Following the morphostructural study, a revision of the systematics and a study of the ontogeny, the functional morphology, the morphogenesis and biocalcification of the test, and the phylogeny and evolution of the group are undertaken.

Morphostructure

Three-dimensional models reflecting the lamellar construction, the arrangement of chambers and chamberlets, and the structural elements (pores, stolons, apertures, "pillars", etc) were built for each genus (Fig. 1).

Lamellar construction: One of the main results of the morphostructural study was the identification of the tridimensional lamellar construction of the test in all four genera studied. The model obtained differs from those described in other foraminiferal groups. The test is built from additive chambers. Each chamber is delimited by an outer lamella, which forms a new annulus and which completely covers the previous test. The annuli are subdivided by box-like independent inner lamellae, one for each equatorial rectangular chamberlet. On the lateral surfaces, the involute outer lamellae form lateral chamberlets, which are internally covered by inner lamella.

Chamber and chamberlet: Given these characteristics of the lamellar construction, and taking the definition of chamber as all the structures formed in one growth step (Hottinger, 1978), in orthophragminids a chamber is delimited by an outer lamella and comprises several geometrically separated elements: an *annulus* of rectangular *equatorial chamberlets* plus a number of *lateral chamberlets*, scattered on the lateral surfaces. The term "chamber" must, thus, be used only for megalospheric embryonic chambers and microspheric proloculus and initial spiral chambers.

Stolons and apertures: The chambers and chamberlets are connected by cylindrical passages called stolons. Four types of stolon were differentiated: *radial*

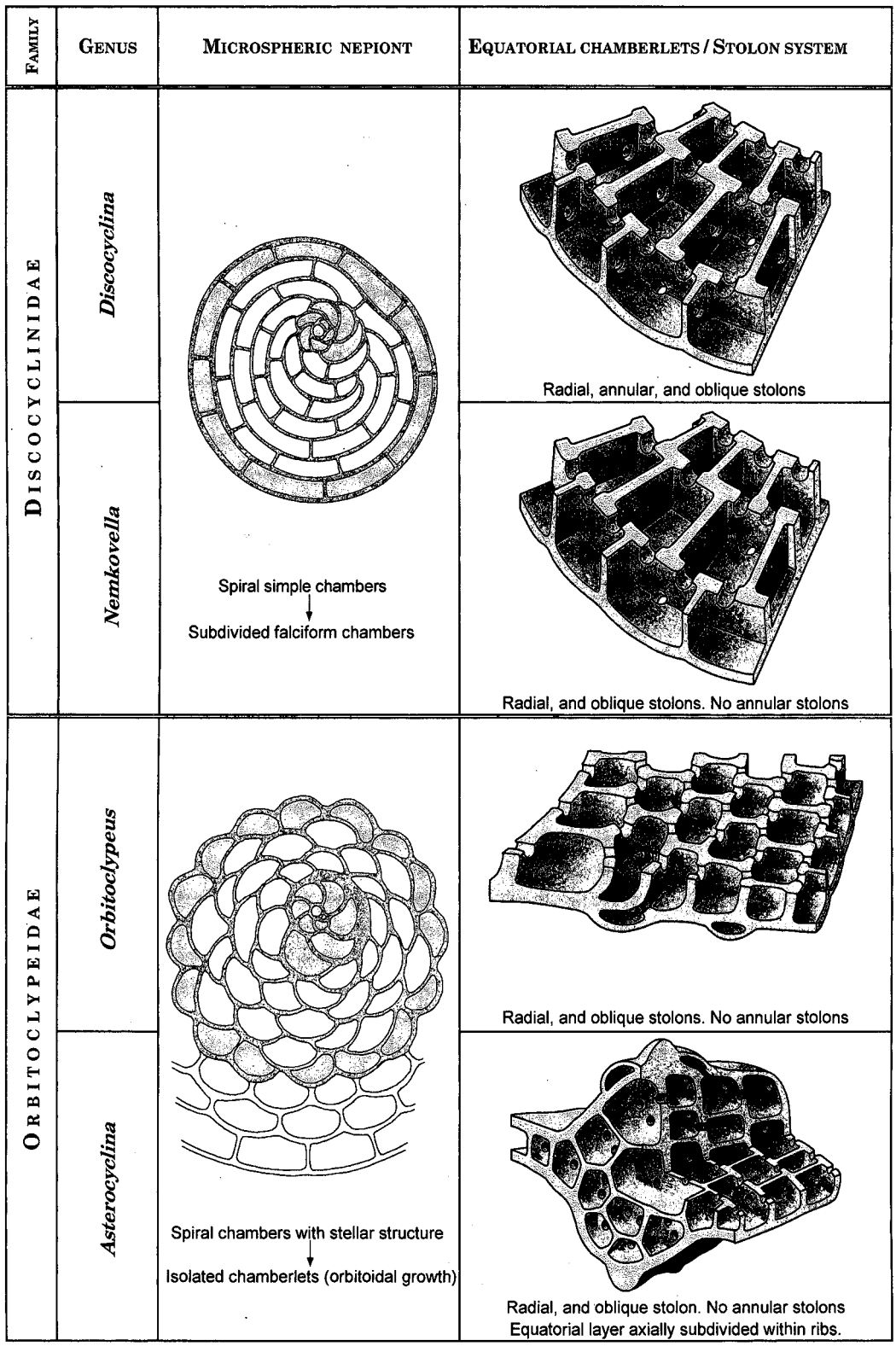

Figure 1.- Summary of the main morphostructural characters in Mesogean orthophragminids Orthophragminids comprise two families, Discocyclinidae and Asterocyclinidae, that are differentiated according to their microspheric nepiont. Within the Discocyclinidae, Discocyclina is differentiated from Nemkovella by the presence of annular stolons in the former. The Orbitoclypeidae also lack annular stolons; only in Asterocyclina the annuli are locally enlarged and subdivided into equatorial chamberlets axially superposed.

stolons (those connecting equatorial chamberlets of adjacent annuli), *annular stolons* (those connecting equatorial chamberlets of the same annulus), *oblique stolons* (those connecting equatorial and lateral chamberlets) and *interlateral stolons* (those interconnecting lateral chamberlets). The stolons are arranged in stolon systems. The radial stolon system runs radially from the centre of the test towards the periphery within the equatorial plane, and ends in the *equatorial apertures* in the periphery of the test. The annular stolons form annular circuits within each annulus crossing the septula. The interlateral stolon system forms a three-dimensional network in the lateral layers, connected to the annuli by the oblique stolons, and opening to the exterior by the *lateral apertures* in the lateral surfaces of the test. The equatorial, oblique and lateral apertures become stolons when a new chamber is formed, thus extending the stolon systems.

Crystalline cones: A new term, crystalline cone is proposed, instead of "pillar" (which is also used in agglutinated and porcellaneous foraminifers), for the imperforate conical structures formed by the superposition of thickened imperforate sectors of the involute outer lamellae. The crystalline cones originate as hemispherical granules on the lateral walls of embryonic chambers and equatorial and lateral chamberlets. The preferential formation on the equatorial chamberlets produces the concentric arrangement of granules on the lateral surfaces found in several orthophragminid species.

Embryonic chambers: In all four genera the embryo is bilocular, with a subspherical protoconch and a kidney-shaped deuteroconch, of a size and shape characteristic for each species. The two embryonic chambers are connected by the *protoconchal stolon*. The deuteroconch is connected to each equatorial chamberlet of the first annulus by a *deuteroconchal equatorial stolon*, and to the first lateral chamberlets by the *deuteroconchal lateral stolons*.

Microspheric forms: Two models of ontogeny were characterized (Fig. 1), differentiated into three stages: spiral, transitional, and neanic. In Discocyclinidae, the chambers of the spiral stage are simple and do not form a thickened wall, while those of the transitional stage are falciform and subdivided into chamberlets by septula of inner lamella, becoming progressively larger until they form a complete annulus. In the Orbitoclypeidae, the spiral chambers form a thickened spiral wall and have stellar structure, with the ventral side subdivided into a main chamberlet and a stellar chamberlet (Fig. 2), whereas the transitional stage follows the orbitoidal growth model.

Morphogenesis and biocalcification

A model for the morphogenesis of the test is proposed. Each new chamber is formed from previous apertures. Consequently, the shape of each new chamber and the number of chamberlets within it are determined by the number and arrangement of apertures in the previous test. In megalospheric forms, the first annulus after the embryo is formed from the deuteroconchal equatorial apertures, and the subsequent new annuli from the equatorial apertures in the previous one. The lateral chamberlets are formed either from the deuteroconchal lateral apertures in the embryo, from the oblique

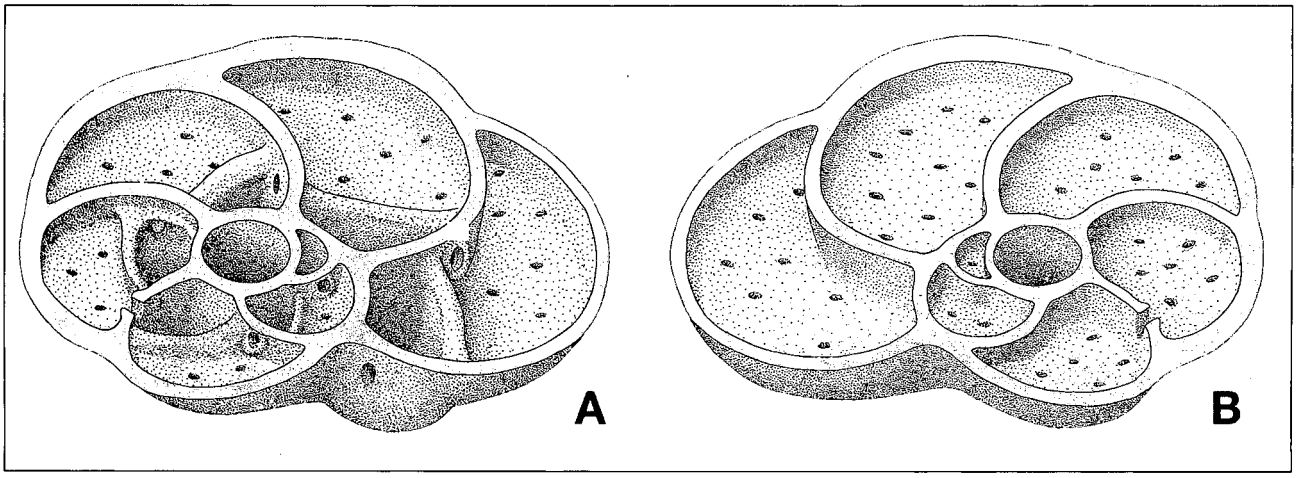

Figure 2.- Equatorial section of the microspheric nepiont of Asterocyclina and Orbitoclypeus showing the ventral (A) and dorsal (B) halves. Each chamber is subdivided in its ventral half into a main chamberlet and a stellar chamberlet. This stellar structure indicates a relationship with the Asterigerinacea.

apertures in the equatorial chamberlets, or from the lateral apertures in previous lateral chamberlets.

A biocalcification model is proposed for the formation of the lamellae in each chamber from organic matrices made up of different materials. Two types of organic matrices are differentiated: In the first case, the organic matrix is constituted by a central polysaccharide layer, acting as a mould for the new chamber, covered at both sides by a proteinic epitaxial layer from which the calcitic inner and outer lamellae are formed. This first type of organic sheath corresponds to the *median layer* of the primary bilamellar wall and produces the septa, the lateral walls, and the radial septula of the annuli, and the walls of lateral chamberlets. The second type of organic matrix consists only of a proteinic layer that covers a previous wall, and produces the septal flap (inner lamella on previous outer lamella) and the involute part of the outer lamella.

Functional morphology

The functionality of each morphostructural element, their arrangement and the general features of the test were analyzed. The results point to a general adaptation of the foraminifer to symbiosis with photosynthetic unicellular algae. The main features of such an adaptation would be the flat shape of the test to provide a large surface/volume ratio; the presence of lateral chamberlets, to harbour the symbionts, whereas the main cytoplasmatic fluxes take place in the equatorial plane; and the thin, trasparent walls, with the calcite crystallites oriented with the optical axes normal to the wall, to enhance light penetration. In this sense, the crystalline cones, located on the lateral walls of chamberlets, would act as lenses to concentrate light in the interior of the test for symbiont insolation. Extrusion of the protoplasm took place through the apertures, for feeding, excretion, movement and chamber formation, whereas the function of pores was restricted to gas exchange.

Systematics, phylogeny and evolution

The morphostructural study allowed taxonomic characters to be revised and revealed new features, such as the deuteroconchal lateral stolons, the equatorial ridge and the stellar structures in the microspheric initial chambers. The evaluation of the taxonomic criteria led to a revision of the systematics, with the following main results (Fig. 1): Mesogean orthophragminids comprise two families, Discocyclinidae and Orbitoclypeidae, differentiated by the microspheric nepiont. The Mesogean Discocyclinidae include only two genera, *Discocyclina* and *Nemkovella*, differentiated by the presence of annular stolons in the former and their absence in the latter. The Mesogean Orbitoclypeidae include two genera, *Orbitoclypeus* and *Asterocyclina*, both without annular stolons, differentiated by the axial subdivision of annuli, only present in *Asterocyclina*. The genus *Nemkovella*, proposed by Less (1987) is shown to be valid, it is better characterized, and a new species, *N. rota* is defined. The genus *Actinocyclina* must be abandoned, as it is defined from taxonomic features of specific value that are found in *Discocyclina*, *Nemkovella*, and *Orbitoclypeus* (Fig. 3). The presence of stellar structures in the microspheric nepion in *Asterocyclina* and *Orbitoclypeus* (Fig. 2) indicates a phylogenetic relationship of the Orbitoclypeidae with the asterigerinaceans.

The revision of the systematics is extended to non-Mesogean orthophagminids, their validity and synoniymies are discussed, and afterwards, a tentative phylogeny of the group is proposed: The Asterocyclinids originated in the Caribbean region in the Paleocene from an asterigerinacean ancestor from which *Hexagonocyclina* arosed, probably triggered by the acquisition of algal symbiosis. In the Lower Paleocene, *Hexagonocyclina* migrated to Europa, giving rise to *Orbitoclypeus* from which *Asterocyclina* split in the lowermost Eocene by the development of the stellate-ribbed pattern. In America a similar, parallel evolution occurred. The American orbitoclypeid *Neodiscocyclina* differs from the Tethyan *Orbitoclypeus* in possessing proximal annular stolons. There is no obvious ancestor for the Discocyclinidae. In the Mesogea, *Discocyclina* appeared in the upper Paleocene (*D. seunesi*), giving rise to *Nemkovella* in the lowermost Eocene. In America, Discocyclinidae are represented by the genera *Athecocyclina*, *Pseudophragmina* and *Proporocyclina*. The presence of true *Discocyclina* in America is questioned, as no clear microspheric forms were found in the literature. A further genus of Discocyclinidae, *Asterophramina* has been reported only in Israel, Burma and Pakistan.

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