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GILIANELLES: LATE CRETACEOUS MICROPROBLEMATICA FROM EUROPE AND CENTRAL AMERICA

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Abstract: During the last two decades, a range of microfossils have been collected from strata of Late Cretaceous (Coniacian–Maastrichtian) age. The name gilianelles has been coined to accommodate these microproblematica. On the basis of many thousands of specimens, typical features of this group have now been assessed. Distinctive traits are calcareous unilocular, basically axially symmetrical test, in the size range 80–200 μm, with a single-layered wall of radially arranged crystals, 15 μm thick, the outer surface with a crochet-like nanostructure, a small-sized aperture (one tenth of test diameter), situated on the upper surface *in vivo*. Secondary criteria include modification of axial test symmetry into radial or bilateral symmetry, development of expansions, either spiny or laminar and presence of longitudinal and latitudinal ornament. To date, 60 taxa have been described from northern Spain to northern Germany and from Central America. Evolutionary patterns of gilianelles are diverse, with both short- and long-ranging forms, some of which comprise lineages that were affected by a marked crisis dated at about 73 Ma. This event is here illustrated by the tribe Coraliellini, of which a key taxon, *Coraliella cognatio*, is described as new. Previous interpretations of Gilianelles as dinoflagellate cysts are discussed and rejected.

Key words: Gilianelles, microproblematica, Upper Cretaceous, evolution, taxonomy, biological crisis.

Gilianelles were first recognized in the GSSP section of the Campanian/Maastrichtian boundary at Tercis les Bains (near Dax, south-west France), where the platform carbonate facies has proved rich in organic remains, with common macrofossils throughout and microfossils collected primarily from less indurated levels (Odin 2001). Additional sampling of indurated levels, using acetolysis, was carried out in an attempt to determine whether or not such levels contained microfossils. The resultant residues yielded previously unknown minute microfossils, for which Odin (2007) coined the term gilianelles (feminine in French). Subsequent analyses allowed the group to be defined in more detail to distinguish it from associated microproblematica. Several morphologies have been described since, confirming that gilianelles constitute an original, cohesive group. Similar microproblematica were illustrated twenty years ago by Willems (1990), but their significance as an original microfossil group has been realized only recently (Odin and Lethiers 2006; Odin 2008*a*). A summary of current knowledge of this group is presented here in English for the first time, with the hope of arousing the attention of the palaeontological community. General characteristics and patterns of evolution are illustrated using one of the five tribes recognized to date (Odin 2009*b*) as an example. Added is an overview of the geographical and stratigraphical distribution of gilianelles, a review of the palaeoenvironment inhabited by the entire group and a discussion of traits which differentiate these microproblematica from dinoflagellate cysts. In south-west France, continuous sedimentation and good preservation has been conducive to the recognition of more than 50 species of gilianelles and to the documentation of their evolution, anatomy and palaeoenvironment during the Campanian and Maastrichtian. Gilianelles may ultimately lead to improving stratigraphical correlation between the Tethyan and Boreal realms and between Europe and America.

MATERIAL

In sections in south-west France, the first microproblematica were collected in 2005, after which a systematic search and sampling campaign was initiated. Since then, the number of specimens collected has increased markedly. To date, residues obtained by acetolysis of 50–200 g of sediment from the Campanian/Maastrichtian series in three sections near Dax, documenting sixty levels (inclusive of the stratotype boundary sequence), have been studied. Similar microproblematica have also been

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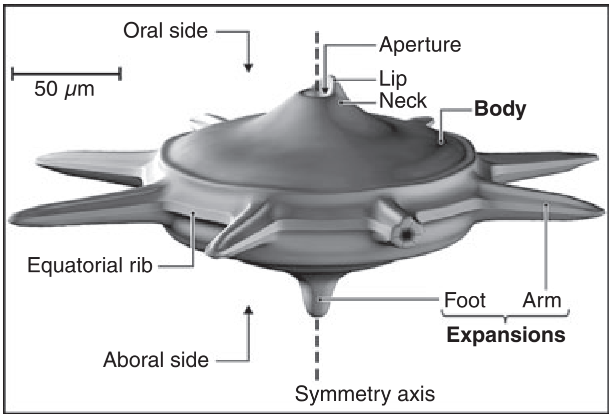
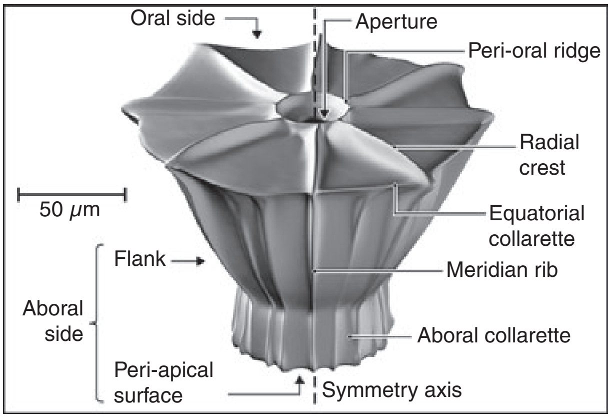


TEXT-FIG. 1. Terminology used in descriptions of gilianelles with discoidal body (genus *Gilianella*; modified from Odin 2007).

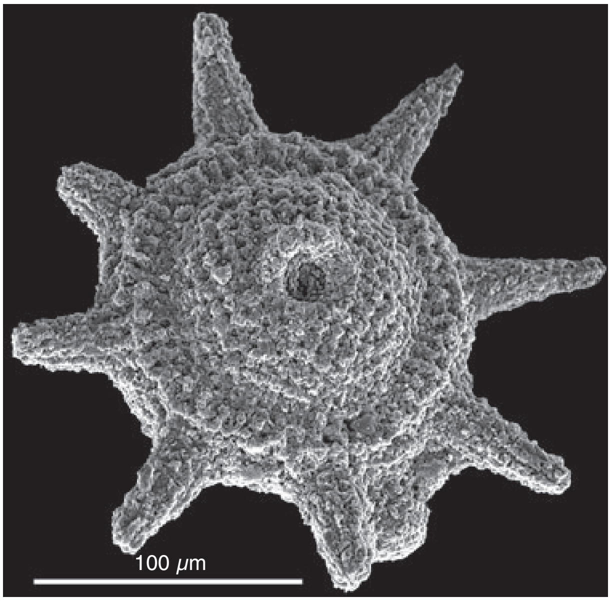


TEXT-FIG. 2. Terminology used in description of gilianelles with a cupula-like body (genus *Pocillella*).

collected from a section in Navarra, northern Spain (Odin 2008*b*). In south-west France, the number of microproblematica per residue sample commonly varies between 50 and 200 specimens/g (Odin 2009*a*). Each level may yield up to 20–30 distinct taxa, most of them representing gilianelles, but some other forms of microproblematica as well.

Selected individuals among thousands of specimens have been photographed and scanned by electron microscope to facilitate description. Odin (2007) introduced a terminology, first in French, to describe these microproblematica. This is here revised to include the diversity of morphologies shown by this group, as illustrated by two models. The first model is based on a test of the genus *Gilianella* Odin, 2007 (Text-fig. 1). The body of the test is discoidal with an axial symmetry. It has expansions (spiny processes) in an equatorial position, referred to as arms, and an additional, axial expansion, referred to as foot. At the other end of the test is an axial aperture which allows the term oral side (upper side) to be applied as distinct from the aboral (or lower) side. Gilianelles with a discoidal body commonly have an equatorial rib and, occasionally, circular, latitudinal ridges.

The second model (Text-fig. 2) is based on a test of the genus *Pocillella* Odin, 2008*a*. The aperture is situated on the upper surface, along the axis of symmetry. It is delimited by a narrow peri-oral surface which in turn is bounded by a peri-oral ridge from which prominent radial crests project. A more or less well-developed equatorial expansion, named a collarette, marks the outer limit of the upper surface. It is deflected outwards at the junction of crests and collarette, forming short arms. The aboral side is subdivided into a flank (a truncated cone) and a peri-apical surface perpendicular to the axis of symmetry. The flank often has meridian ribs and terminates downwards in an aboral collarette.



TEXT-FIG. 3. Oral view of a specimen of the genus *Gilianella* collected from level 79.8 (Grande Carrière at Tercis les Bains, south-west France) (SEM).

GENERAL CHARACTERISTICS AND DIVERSITY OF GILIANELLES

Text-figure 3 is an SEM image of the species on which the first model (Text-fig. 1) is based. The general traits of gilianelles not only characterize that group, but also distinguish it from other microfossil groups. These traits may be subdivided into seven primary (1–7) and three secondary (A–C) characteristics as follows:

1. Gilianelles represent the remains of living organisms, in the form of a calcareous unilocular envelope called a test.
2. A single aperture invariably is present, its diameter being about one-tenth of that of the test.

3. Exclusive of expansions, test size ranges between 80 and 200 μm.
4. Tests invariably display basic axial symmetry.
5. In life, the aperture was situated at the top (see video in Odin and Lethiers 2006).
6. Test wall thickness is fairly constant (15 μm); wall consists of a single layer of carbonate crystals, arranged roughly radially.
7. Test surface with a crochet-like nanostructure ('structure en napperon' in French), the 'stitches' being 5–10 μm wide and usually arranged radially and concentrically.

A. Some gilianelles have expansions which can be subdivided into four types: hollow spines (formed by elongate lamellae, resulting in a rosette-like aspect in section), filled spines (either cylindrical or flattened like helicopter blades), X-section spines ('en cornière' in French) and collarettes.

B. Axial symmetry is commonly altered in the direction of radial symmetry by the addition of radial ornament or expansions. Another alteration of axial symmetry is by elongations of the test in a direction perpendicular to the axis of symmetry, which together lead to differentiation into anterior and posterior portions as deduced from the hydrodynamical profile (Odin 2008*a*).

C. At times, the nanostructure develops stronger relief which produce elaborate ornament such as meridian ribs and latitudinal ridges.

Gilianelles display widely divergent morphologies which can be subdivided into five groups referred to as tribes (Odin 2009*b*). The tribe Tercensellini comprises spherical, axially symmetrical tests which lack expansions. The sole genus of this tribe, *Tercensella* Odin, 2008*a*, includes species that range in form from strictly spherical (Pl. 1, fig. 3) to barrel-like. The tribe Scutellellini consists of discoidal forms which may have been derived from spherical ancestors by compression along the axis. Among them, a few display a homogeneous, canvas-like nanostructure (Pl. 1, fig. 5); the single genus, *Azymella* Odin, 2008*a*, accommodating these may in fact constitute a different kind of microproblematicum. Most Scutellellini have a differentiated nanostructure on the oral and aboral sides; this tribe includes various genera some of which are characterized by the development of an equatorial collarette and an aboral, crown-like collarette. *Scutellella longivelifera* (Pl. 1, fig. 1) displays a wide equatorial collarette which prolongs and accentuates the oval form of the slightly elongated body (central portion of the specimen), thus increasing the secondary bilateral symmetry, a common feature in members of this tribe. The differentiation into an anterior side (to the right) and a posterior side (to the left) is more or less developed in the several species. Included in this tribe are tests with a flattened oral side and an aboral side which is elongated downwards to form a funnel-like body. The funnel shape is even more clearly defined by the development of an equatorial collarette towards the top. In *Corniculum clausum* Odin, 2008*a*, the narrowing of the aboral collarette leads to a spiny aboral foot (Pl. 1, fig. 8).

The third tribe, Gilianellini, comprises discoidal tests which have radially distributed equatorial expansions. Most have arms of hollow spines formed by elongated lamellae which cause a rosette-like section, as in the genus *Gilianella* (Text-fig. 3). A single genus, *Orculiella* Odin, 2008*a*, with equatorial expansions, has short flat arms and an extremely well-developed neck (Pl. 1, fig. 6). It might have been excluded from this tribe, because it is the only one displaying such a morphology. Note also the diverse nanostructures on different portions of its body. For all members of this tribe, it should be noted that the number of arms is not constant in any species.

The fourth tribe, Aquilegiellini, comprises those cupula-like tests which possess spine-like expansions at both terminations of their flank, thus leading to radial symmetry. These expansions can be flattened, as in the genus *Pennigerella* Odin, 2008*a* (Pl. 1, fig. 7, only equatorial expansions visible) or cylindrical as in the genus *Aquilegiella* Odin, 2008*a* (Pl. 1, fig. 2). Similar to the tribe Gilianellini, the number of expansions in any given species is not constant, either in equatorial or in aboral locations.

The last tribe, Coraliellini, accommodates those tests that are characterized by a cupula-like body with expansions in collarettes, 'en cornière' or both. Neither the Coraliellini nor the Aquilegiellini shows any tendency to bilateral symmetry. The oral side of tests of the Coraliellini presents a sun-like ornament, i.e. a peri-oral ridge from which high radial crests project as in the genus *Coraliella* (Pl. 1, fig. 4). The morphology of taxa contained in this tribe displays interesting evolutionary patterns, as illustrated in Text-figure 4.

Among microfossils that, on the basis of their general characteristics, are referable to gilianelles are two taxa from northern Germany [note that Versteegh *et al.* (2009) independently reached the same conclusion], initially assigned to a new genus, *Tetratropis* (four 'keels'), by Willems (1990), namely *Tetratropis corbula* and *T. patina*. A third, *Amphora coronata*, was erected subsequently (Willems 1994). This was later renamed to *Coronadinium coronata* (see Willems in Williams *et al.* 1998). A fourth taxon, *T. terrina*, was described by Bison *et al.* (2004), who also redefined the genus *Tetratropis*. However, the morphology of the last-named species differs from that of the original genus in displaying only two 'keels'. This trait made Odin (2009*b*) to decide to transfer that species to the genus *Scutellella* Odin, 2008*a*; that author also redescribed the genus

Tetratropis. The features of this species are identical to those of *Scutellella longivelifera* from Tercis les Bains, one of 44 taxa recorded subsequently from south-west France by Odin (2008*a*). Eleven additional ones have recently been published (Odin 2009*b*), and yet another one is defined here (see below). Together, these 60 gilianelles constitute a cohesive microfossil group, in spite of the fact that relationships with other organisms remain insufficiently known.

Repository. All illustrated specimens here are deposited at the Musee du Site Geologique de Tercies near the type section of the Campanian/Maastrichtian boundary.

SYSTEMATIC PALAEONTOLOGY

GILIANELLES Odin, 2007 (Microproblematica)
Tribe CORALIELLINI Odin, 2009*b*

Genus CORALIELLA Odin, 2008*a*

Type species. *Coraliella simplex* Odin, 2008*a*, by original designation.

Coraliella cognatio sp. nov.
Text-figure 5

Derivation of name. From Latin *cognatio* meaning link, connection.

Holotype. TCS.G104 (= Tercis, Gilianelle type number 104) (Text-fig. 5).

Diagnosis. *Coraliella* with a test similar to that of genus *Pocillella* in size (150 μm); outline conical typical of the genus *Coraliella*; equatorial collarette without indentation; aboral collarette short.

Description. Cupuloid test with a conical profile; height and equatorial diameter comparable (150 μm); oral side a low cone with an axial aperture, 15 μm in diameter, at the centre of a narrow peri-oral surface bounded by a circular peri-oral ridge from which 11 radial crests branch; crests interrupted at the inner side of the equatorial collarette that rises slightly above them; outline roughly conical with an angle of about 60 degrees prolonged by an aboral collarette < 50 μm in diameter; flank with about 40 meridian ribs in its widest portion; nanostructure partly obscured by the strong microstructure.

Material. A single test from level 50.0 at Tercis les Bains (Landes, south-west France).

Discussion. The microstructure is similar to that of other species of the tribe with the same 'sun-like' oral ornament. The genus *Coraliella* comprises species generally larger than 200 μm in diameter and height; the diameter of the equatorial end of the cone is more than twice that of the aboral end; it is known from between levels 47.2 and 260. In the same section, species of the related genus *Pocillella* are smaller, generally 100–150 μm in diameter and height, with the equatorial end of the cone less than twice the diameter of the aboral end; these occur between levels −5.0 and 25.0. The new species is important because it is intermediate between two genera: it is not large enough to be a 'regular' *Coraliella*, but already has a significantly conical flank. It is also intermediate between

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EXPLANATION OF PLATE 1

Fig. 1. *Scutellella longivelifera* Odin, 2008*a*, oral side showing aperture and thin, elongated equatorial collarette with the anterior part to the right, level +5.0 (SEM mount VIII, specimen no. 33).

Fig. 2. *Aquilegiella varia* Odin, 2008*a*, a specimen with nine arms and four feet, oral oblique view, level 57.9. Note the presence of aperture and peri-oral surface bounded by circular ridge (SEM mount XII, specimen no. 58).

Fig. 3. *Tercensella globosa* Odin, 2008*a*, oral oblique view, axial aperture obscured by sediment, level 62.5 (SEM mount X, specimen no. 22).

Fig. 4. *Coraliella brachialis* Odin, 2008*a*, oral oblique view, level 69.0. Note 'en cornière' structure of arms and their relationships with structures of oral and aboral sides (SEM mount XII, specimen no. 55).

Fig. 5. *Azymella cannabinata* Odin, 2008*a*, oral side with canvas-like nanostructure unique to this genus, level −5.0 (SEM mount VIII, specimen no. 21).

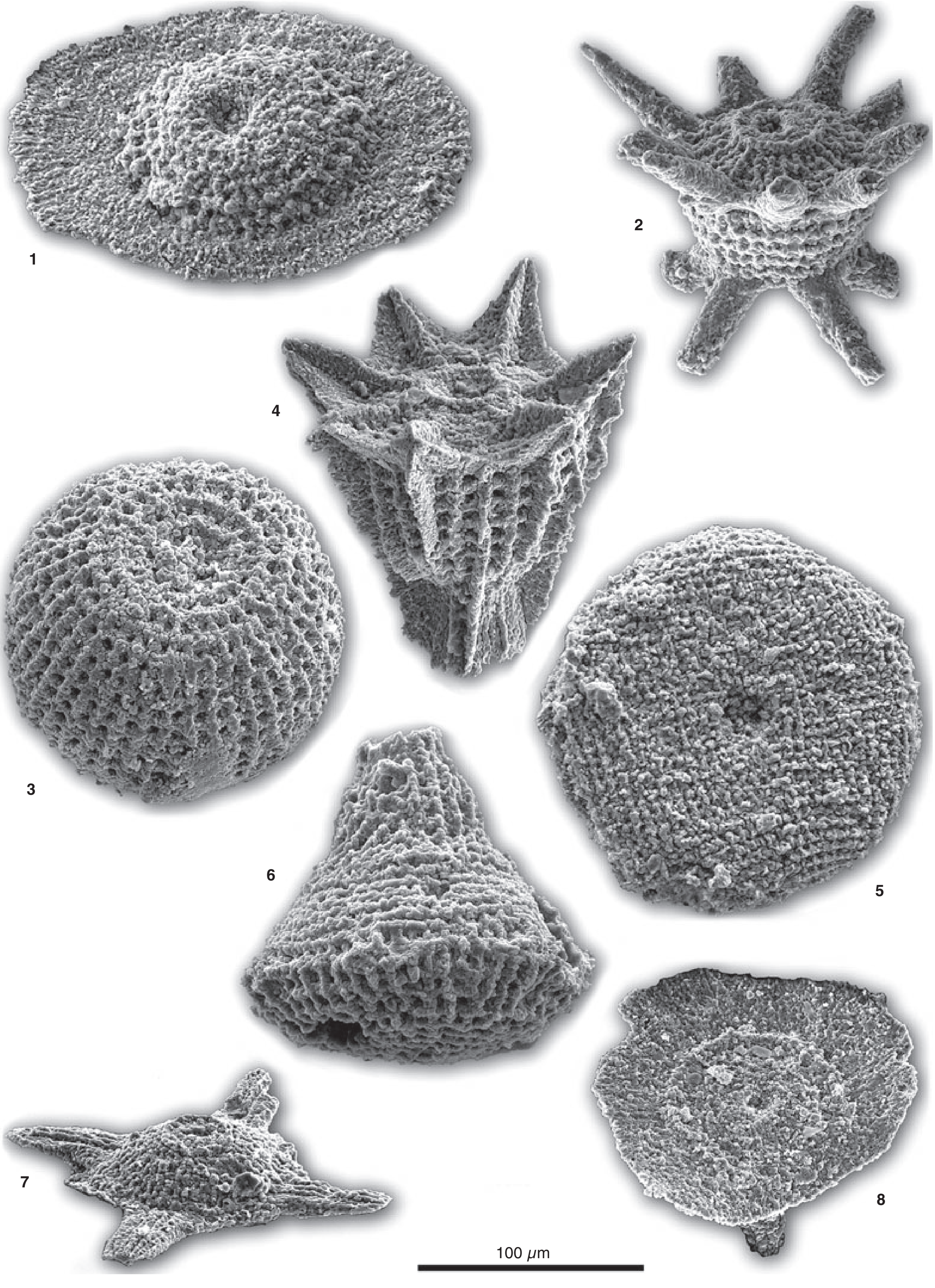
Fig. 6. *Orculiella niduseumenei* Odin, 2008*a*, profile showing different nanostructures on several test portions; six small, flat arms at test circumference eroded away, level 11.0 (SEM mount VI, specimen no. 51).

Fig. 7. *Pennigerella palmata* Odin, 2008*a*, only oral side visible, oblique view showing flat arms, level 11.0 (SEM mount XII, specimen no. 10).

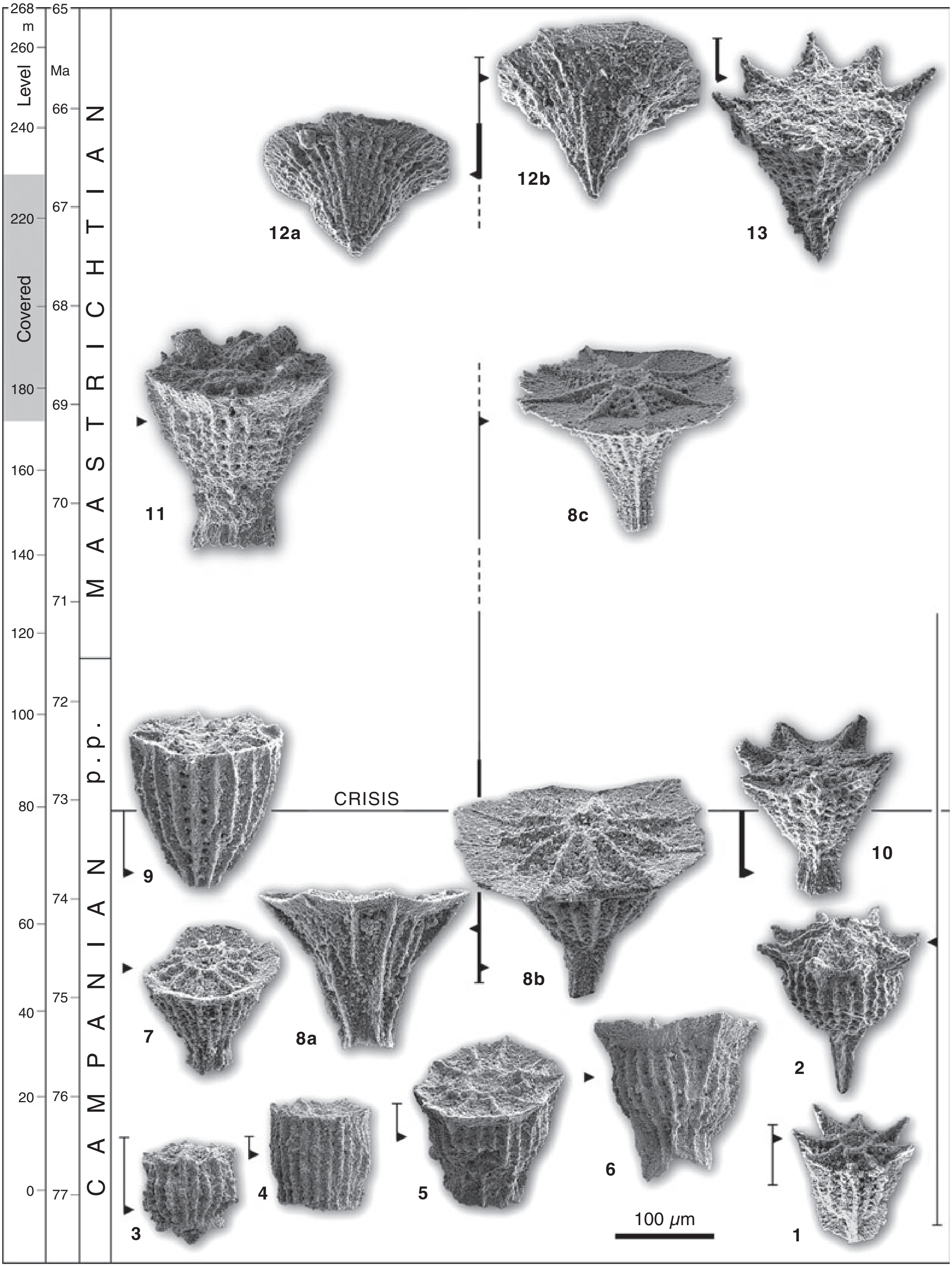
Fig. 8. *Corniculum clausum* Odin, 2008*a*, oral side; part of axial aboral foot visible below extended equatorial collarette; diagnostic crochet-like nanostructure obliterated (holotype), level 79.8 (SEM mount VII, specimen no. 21).

Scanning electron microscopy images of gilianelles, illustrating surface nanostructure of specimens collected below the biological crisis (upper Campanian, Tercis les Bains, south-west France).

PLATE 1



ODIN, surface nanostructure of gilianelles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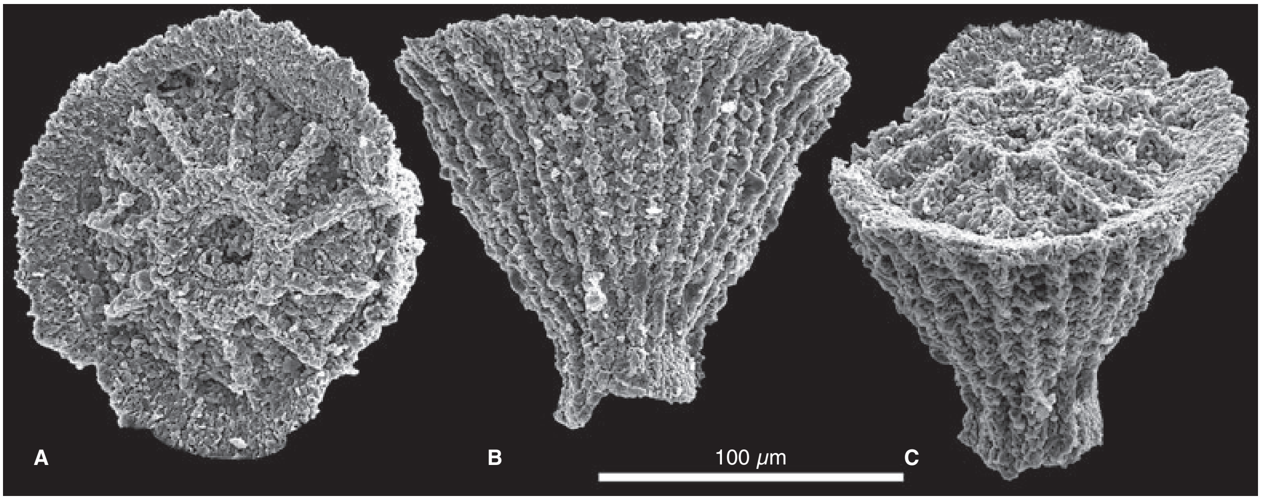

TEXT-FIG. 5. *Coraliella cognatio* sp. nov., level 50.0, upper Campanian, Tercis les Bains, south-west France. A, in oral veiw. B, in lateral (profile) veiw. C, oblique oral views.

older and younger taxa of the same tribe and is a key species in the documentation of the continuous evolution in the tribe (see Text-fig. 4).

Distribution. The type stems from level 50.0, at the very bottom of the range of the genus *Coraliella* (see Text-fig. 4, species 7); it co-occurs with the planktonic foraminifer *Radotruncana calcarata* and slightly younger than the heteromorph ammonite *Bostrychoceras polyplocum*.

EVOLUTIONARY PATTERNS

At Tercis les Bains, where the evolution of gilianelles is known in considerable detail, several types of evolutionary patterns have been recognized in strata of Campanian and Maastrichtian age. A few taxa are long ranging (3–4 Ma, or more), but exhibit no apparent morphological changes. A number of taxa have short ranges (< 1 Ma), including *Tetratropis terrina* Bison, Wendler, Versteegh and Willems, 2004, while others are confined to only a single level. However, there are taxa that seem to represent persistent lineages which existed for 10 Ma or more, and in which evolutionary trends can be traced. Finally, the entire group suffered from a marked biological crisis at the 79.8 level at Tercis les Bains, dated at *c.* 73 Ma (Odin 2009*a*). Thus, gilianelles have real potential for stratigraphical correlation.

In Text-figure 4, the tribe Coraliellini illustrates one of these patterns. Stocky forms are shown to the left and slender forms to the right. Previous age estimates by Odin (2001, p. 796) are revised on the basis of data presented by Odin and Walaszczyk (2003). The specimens are illustrated at their relative stratigraphical provenance (levels are given in approximate metres), and their ranges are indicated by the length of the associated vertical bars. No data are available for the section between levels 172 and 229, which represent an overgrown interval.

Species with an axial aboral foot ‘en cornière’ (four small wings, more or less at 90 degrees) have been placed in the genus *Obbella* Odin, 2008*a*. *Obbella alatopedata* Odin, 2008*a* is restricted to levels 1.1–14.8 (representing *c.* 0.5 Ma of deposition, see Text-fig. 4, species 1). In contrast, *Obbella caryophyllum* Odin, 2008*a* is known from between levels −5.0 and 125.5, representing 6 Ma of deposition (Text-fig. 4, species 4). In short, among two morphologically similar (and probably genetically related) forms present at the base of the section, one becomes extinct relatively soon while the other survives for a much longer period.

TEXT-FIG. 4. Evolutionary patterns in the tribe Coraliellini at Tercis les Bains, south-west France (1–6 and 8–10 species erected by Odin 2008*a;* 11–13 species erected by Odin 2009*b*). 1, *Obbella alatopedata*. 2, *Obbella caryophyllum*. 3, *Pocillella minuta*. 4, *Pocillella cylindrata*. 5, *Pocillella grandicula*. 6, *Pocillella cochleare*. 7, *Coraliella cognatio* sp. nov., holotype. 8a, *Coraliella cantharella* form A. 8b, *Coraliella cantharella* form B. 8c, *Coraliella cantharella* form C. 9, *Coraliella simplex*. 10, *Coraliella brachialis*. 11, *Coraliella mortarium*. 12a, *Coraliella apedata*. 12b, *Coraliella apedata* evolved form. 13, *Coraliella delicata*. The time scale is proportional to time, the metre scale is contracted where deposition was slow. The known range of a taxon is indicted by the length of the vertical bars; the carat indicates the level from which the specimen came. Dashed lines indicate assumed occurrences in the section. Thicker bars indicate greater abundance.

The other taxa in this tribe were assigned to *Pocillella* (small, with an equatorial diameter/aboral diameter ratio ≤ 2) or to *Coraliella* (larger forms with an equatorial diameter/aboral diameter ratio > 2; see Systematic Palaeontology). Four small species (Text-fig. 4, species 3–6) were short-lived and occurred at the base of the section. Above them an intermediate form (Text-fig. 4, species 7) is small but significantly conical in profile; this morphology is intermediate between that of *Pocillella* and *Coraliella* (this key taxon is *Coraliella cognatio* sp. nov. described above) The new form co-occurs with the very first representatives of larger sized *Coraliella* (Text-fig. 4, species 8a and b). Form A of this species, *C. cantharella*, is short with a broad, tube-like foot and 7–9 radial oral crests. Form B has a narrower and longer foot and 11–15 radial oral crests. In the central part of the range of *C. cantharella,* forms A and B (i.e. between levels 50 and 120), two other, quite discrete, species are known (Text-fig. 4, species 9–10). One is stocky and heavy, without expansions (*C. simplex*), while the other, *C. brachialis*, is a slender, delicate form with spindle-like expansions. In some variants, the body assumes a subspherical aspect quite at variance with the conical specimen illustrated, thus resembling the silhouette of *O. caryophyllum* Odin, 2008*a* and exhibiting a good example of convergent evolution. *Coraliella simplex* and *C. brachialis* may represent divergent tentative adaptations, both unsuccessful, because both disappear at level 79.8. This level is critical in the evolution of gilianelles, for it is there that they underwent a biological crisis (Odin 2009*a*). This crisis presumably evinces increased population densities of a commensal microfossil which adhered to their tests.

Higher up in the same section, *C. cantharella* is represented by a single morphology which, at level 172 and immediately below the covered section, acquired a more slender profile than lower in the section (Text-fig. 4, species 8c). This *C. cantharella* form C clearly is a descendant of form B. Another species that appears abruptly at level 172 is *C. mortarium* Odin, 2009*b* (Text-fig. 4, species 11). This seems to represent a new adaptation towards a more stocky, squatter profile. Above the covered portion of the outcrops, two discrete species occur. The first has an entire, uninterrupted collarette like *C. cantharella,* but the tubular aboral expansion is absent from between levels 230 and 240 (*C. apedata* Odin, 2009*b*; Text-fig. 4, species 12a). Very shortly thereafter, at level 252 and above, the same species regained a foot by elongation of the aboral portion on which small wings are present (Text-fig. 4, species 12b). The second species (Text-fig. 4, species 13) has a spiny aboral foot with meridian crests forming small wings and is also characterized by 'en cornière' arms formed by four small wings. In profile, it resembles the slender *O. caryophyllum*.

Gilianelles repeatedly evolved to make use of newly available food sources that in turn imply recently vacated environmental niches. The question which organisms they replaced or which niches became available cannot be answered yet. A final matter should be stressed: below the crisis level, members of the tribe illustrated here have up to five species occurring simultaneously; in contrast, above this level, only one or two remain. The same reduction in the number of species occurs in all tribes of gilianelles (Odin 2009*a*).

DISTRIBUTION

At Tercis les Bains, gilianelles range through a section of rocks which represents *c.* 12 Ma of time below the Cretaceous/Paleogene boundary. Material from northern Germany comprises older taxa dated as middle Coniacian (Willems 1990; Hildebrand-Habel and Willems 1997), which represents a downward range extension of about 10 Ma. In addition to Tercis les Bains, coeval deposits in northern Spain (Odin 2008*b*, *c*) and northern Germany (Willems 1990; Bison *et al.* 2004) document the currently known distribution of gilianelles. So far, there are no data from other areas, but according to J. A. Arz (pers. comm. 17 November 2008), gilianelles have also been recognized in Central America, in the Cretaceous/Paleogene clastic boundary unit in Cuba (Smit *et al.* 1996; Alegret *et al.* 2005). Pictures provided by J. A. Arz show that the morphology of the Cuban material is consistent with that of the late Maastrichtian *C. delicata* (Odin 2009*b*) at Tercis les Bains (Text-fig. 4, species 13).

The pattern that emerges from these outcrops suggests that the presence of gilianelles is linked to platform palaeoenvironments at depths in excess of 50 m and up to more than 150 m. Such depths have been postulated for the European Chalk in general and have also been deduced from a study of echinoids from Tercis les Bains (Odin 2001, p. 615). Observations in south-west France and northern Spain (Odin 2008*b*, *c*) suggest that gilianelles were restricted to clear seas without detrital input.

Tests of gilianelles show morphological adaptations which make it likely that they occupied various niches. Most are clearly consistent with a planktonic mode of life, but a few possibly were benthic (Odin and Lethiers 2006; Odin 2009*b*). An adaptation to a planktonic life style was assumed by Odin and Lethiers (2006) to be reflected in the development of projections (Pl. 1, species 2, 7), the orientation of the test along an axis of symmetry with an aboral prolongation acting as a ballast keel (see Pl. 1, fig. 4; Text-fig. 4, species 6c, 8, 11–12); this keel tends to maintain the aperture upwards. Perpendicular to the major axis of symmetry, there are common features indicating a preferred direction of movement relative to that of water (Pl. 1, fig. 1). Unkeeled tests without projections and in particular those with an oral surface more clearly developed than the aboral one (Pl. 1, fig. 6) are thought to have been better suited to a benthic mode of life. Other tests such as simple discs (Pl. 1, fig. 5) do not show obvious adaptations, and their range within the water column is uncertain.

DISCUSSION

That a new group of microfossils has only now been discovered may appear surprising after so many years of studies of organic remains in carbonate rocks by numerous experts. Gilianelles have previously been considered to represent microcrinoids, calcitized radiolarians, benthic foraminifera, calcareous algae or pseudarcellids (Odin 2007), but no convincing evidence has been put forward in favour of any of these groups. Here, the discussion essentially rejects their interpretation as dinoflagellate cysts, because such was the only interpretation offered in the literature for German taxa (Willems 1990, 1994; Bison *et al.* 2004). To date, 60 taxa have been described, making a well-founded interpretation feasible. The sum of the morphological features displayed by gilianelles in Campanian/Maastrichtian strata in south-west France does not support their affiliation to dinoflagellate cysts for the following reasons.

According to experts (see e.g. Keupp 1979), calcareous dinoflagellate cysts range between 30 and 100 μm in their major dimension. This is also the size range of organic-walled dinoflagellate cysts at Tercis les Bains (Odin 2001, chapters C2a–d). The body of some gilianelles is around 100 μm in diameter, but many of them are larger (up to 200 μm) than usual calcareous dinoflagellates, and their mean size generally exceeds that of co-occurring dinoflagellates.

Gilianelles do not show a tabulation of the cell wall which characterizes dinoflagellates. It is accepted that there are dinoflagellate cysts without paratabulation (an imprint of the tabulation of the motile forms); however, all dinoflagellate cysts must have at least one element of paratabulation, i.e. the archeopyle. This feature is addressed below.

Authors commonly referred to paratabulation and other dinoflagellate terms in the descriptions of the four taxa from Germany, erected prior to the discovery of 56 additional ones in France. However, it proved difficult to apply those terms in their description because the morphology of gilianelles differs in many details from that of dinoflagellates. For example, Willems (1994, p. 67) described the arms of his *Amphora coronata* (a true gilianelle) as, 'a ring of (…) six spines, but five, seven, and occasionally eight can be observed…The precingular paraplates 1″–7″ are represented by the number of seven spines'. His description indicated six to be the commonest number of spines and went on to state that, 'Some of them may however be considerably reduced in length, or they are even absent (…) an additional eight spine (…) may reflect the apical plate'. The same difficulty arose for the aboral expansions of *A. coronata* for which the same author noted, 'the antapical end of the test itself bears at least two more long spines (…) which certainly reflect the location of the two antapical plates (1⁗ + 2⁗). An occasional additional third spine can best be considered as a homologue to the postcingular plate 3‴'. The varying number of expansions that characterize gilianelles can hardly be described as a rigorously tabulated organization. As a result, an expansion may be taken to be in association with more than one paraplate, while the spines linked to similar paraplates may be either expressed or not. Finally, in gilianelles the spines are regularly spaced around the body and cannot have come from paraplates in different locations. Similar difficulties were encountered when authors tried to find traces of the sulcus of the flagellate motile system where the vertical flagellum is housed (Willems 1990, pl. 1, fig. 1b), and the horizontal cingulum, the furrow sheltering the horizontal flagellum, was taken to be the equatorial rib or collarette in my interpretation. This view is hardly consistent with the morphology of the equatorial collarette which has no furrow and is interrupted by arms in some genera, thus making it impossible for a flagellum to undulate if the tests involved represent free forms.

The central opening on the oral surface in gilianelles does not represent the absence of an apical operculum because it is invariably present, whereas the opening in a dinoflagellate cyst indicates only that plates sealing the cyst were removed when the occupant of the cell departed. The aperture of gilianelles is small (i.e. one-tenth of test diameter), whereas the site of an archeopyle commonly occupied a third of total cyst diameter (Keupp 1984, 1995). The dimensions and configurations of archeopyles were also discussed by Streng *et al.* (2004), who noted that archeopyles had different shapes and that the groups of plates removed when the cyst opened differed in location. Furthermore, an opening that represents only 12–18 per cent of the test is too small to have been the site of an archeopyle, because the dinoflagellate could not have emerged through such a small exit. The small size of the opening alone possibly does not reject the cyst nature of the remains because, 'We know some mineralized cysts of other microorganisms showing always similar small openings which are closed during the phase of encystment by an organic stopper, e.g. the archaeomonades' (HK pers. comm. 2009). Finally, in the three papers describing German material, different structures of gilianelles were interpreted as archeopyles. For example, Bison *et al.*

(2004) assumed the 'small central opening' in their *Tetratropis terrina* (= *Scutellella terrina*) to be the trace of an archeopyle; alternatively, the peri-apical surface bounded by a 'suture' was referred to as the archeopyle (compare Willems 1990, p. 247, 1994, p. 67). Note that in a number of gilianelles (e.g. Pl. 1, fig. 2) the peri-apical circular ridge, interpreted as the 'suture' which 'possibly mark the existence of… an archaeopyle' (Willems 1994, p. 67), occurs alongside the central opening called the archeopyle by Bison *et al.* (2004, p. 131). Therefore, two different morphological features are interpreted as the archeopyle by different authors; only one of them could be correct.

Most dinoflagellate experts (see Keupp 1979) agree that the presence of both open and closed forms of test is a requirement for their identification as a cyst. Among gilianelles, no closed forms are known, although it cannot be ruled out that an organic closure could occasionally have been present. That gilianelles probably do not represent cysts is supported by the fact that many show an adaptation to facilitate hydrodynamic movement. Such an adaptation may also occur in cysts, and the argumentation is not unequivocal *per se*. However, the adaptation is more sophisticated in gilianelles with a variety of adapted general forms of the test and of added specific structures (Odin 2009*b*). They were not simply passive cradles for dormant remains; for at least some of them were mobile, to a certain degree, probably as swimming plankton as suggested by the presence of adjustments in test form which indicate increased motility (see Pl. 1, fig. 7) and the occurrence of hydrodynamic equilibrium which kept the aperture up (Odin 2008*a*). There are no known 'features that show indications for the presence of flagella, cilia, muscles for active movement or oil vesicles for regulating density' (GV pers. comm. 2009), but at least some species did not simply float in the water column. Relative movement between sea water and the test can be seen in *Scutellella longivelifera* (see Odin 2008*a*, pl. 5, figs 71, 75) and in various species of the genera *Aturella* Odin, 2008*a* (see Odin 2008*a*, pls 2–3) and *Corniculum* Odin, 2008*a* (see Odin 2008*a*, pl. 6).

Gilianelles, in particular those that acquired a bilateral symmetry, must have moved differently from dinoflagellates. Gilianelles moved perpendicularly to their axis of symmetry, in the sense of the elongation of the tests, while dinoflagellates move along their apical–antapical axis using the vertical flagellum and turn around this axis using the equatorial flagellum. Note also that a vertical flagellum on a form like *Scutellella longivelifera* or the flat genus *Pennigerella* Odin, 2008*a* would have had to exert a huge amount of energy to move their tests vertically. In short, there is a fundamental difference between the modes of movement of these two groups. The fundamentally axial symmetry of gilianelles cannot be assimilated to the dorso-ventral organization of dinoflagellates and their cysts.

The terms gilianelloid or gilianellioid, as introduced by Versteegh *et al.* (2009) in favour of gilianelle(s), do not 'facilitate communication among micropalaeontologists and carbonate sedimentologists' (Versteegh *et al.* 2009) and should be avoided. Gilianelles have also been qualified as 'another enigmatic group of Mesozoic calcispheres' or 'Calcisphaeres' (see Versteegh *et al.* 2009, pp. 344–345). If a polyphyletic group of 'Calcitarcha' to include 'all calcareous microfossils with a central cavity for which the biological affinities remain unknown' and 'a variety of… both plants and animals' is accepted, then gilianelles would pertain to such a group. However, if this heterogeneous group of single-chambered, calcareous microfossils incertae sedis would be generally related to 'organisms of phytoplanktic nature' and described under 'botanical nomenclature', gilianelles are not 'Calcitarcha' (see Versteegh *et al.* 2009, p. 346).

In my opinion, gilianelles comprise micro-organisms with both planktonic and benthic habits. At Tercis les Bains, benthic life occurred at depths significantly > 50 m, which appears incompatible with an interpretation of gilianelles as algae dependent of photosynthesis. In contrast, my proposal (see Odin 2008*a*) is to consider them as protozoans and probably rhizopods, by comparison with foraminifera. The reasoning behind this is that they have an opening allowing prey to be ingested and they were relatively mobile permitting wider access to prey items. Although gilianelles are insufficiently known microproblematica, there is no need to replace the group's name by any other, less precise term.

CONCLUSIONS

Gilianelles are microfossils identified by a set of seven fundamental morphological features supplemented by three secondary traits. In spite of this narrow definition, they comprise a variety of tests which can be subdivided into five tribes with some 'strays' in the Scutellellini and Gilianellini. The 60 taxa known to date contribute to the diversity of Cretaceous biota, which require additional studies, as the discovery at Tercis les Bains of a dozen other microproblematica. These are not gilianelles, nor are they assignable to any other groups with which they have been compared so far. The known stratigraphical range of gilianelles comprises the final 20–25 Ma of the Late Cretaceous in the Tethyan and Boreal realms. This palaeogeographical distribution suggests that they might be a good tool for correlation, a potential that has already been demonstrated on either side of the Pyrenees.

Evolutionary patterns of gilianelles are diverse; the rapid evolution seen in some lineages provides clues to the mechanisms of adaptation. It appears that the niches occupied by some new forms are those left open by the disappearance of earlier taxa of the same group. This seems to have been the case particularly following the biological crisis at level 79.8, dated at *c.* 73 Ma.

Earlier interpretations of gilianelles as dinoflagellate cysts are discredited by the more detailed data available now. The main purpose of the present paper is the presentation of a new microfossil group which shows evolutionary trends of stratigraphical interest. Future studies of the Upper Cretaceous in areas between south-west France and northern Germany and other regions of the Boreal and Tethyan realms may be expected to yield a valuable supplement to current knowledge.

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