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INSOLENTITHECA EMEND., *PROTOINSOLENTITHECA* N. GEN., AND CALIGELLIDAE EMEND., PERMANENT CYSTS OF PALAEOZOIC FORAMINIFERA?

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Abstract. Insolentitheca was interpreted as a microproblematicum, a foraminiferal test, or a syzygial cyst. Arguments are listed versus syzygial cysts or ordinary foraminiferal agglutinates, and for permanent cysts with probable infaunal life. *Protoinsolentitheca fundamenta* n. gen. n. sp. is described, which links *Insolentitheca* and the Caligellidae. Some elements of nomenclature are introduced to describe the particular tests of the Caligellidae. These taxa could be basically represented by an infaunal naked or chitinaceous foraminifer, which secretes during its lifetime a calcified perimeter denominated the chimney, only present in the Caligellidae. To this initial secretion are added two types of «agglutinated» and bioeroded tests: the fundamental in *Protoinsolentitheca* and *Insolentitheca*, and the bricks, in *Insolentitheca* only.

Riassunto. Insolentitheca è stato interpretato come un microproblematico, un guscio di foraminifero oppure una cisti sigiziale. In questo articolo sono elencati gli argomenti contro l'interpretazione di cisti sigiziale o di un normale foraminifero agglutinante, e sono esposti quelli a favore di una cisti permanente con probabile vita infaunale. Viene descritta *Protoinsolentitheca fundamenta* n. gen. n. sp., ritenuta collegare *Insolentitheca* alle Caligellidae. Sono introdotti alcuni elementi di nomenclatura per descrivere il guscio particolare delle Caligellidae. Questi taxa possono essere sostanzialmente rappresentati da un foraminifero infaunale nudo o chitinoso, che secerne durante la sua vita un perimetro calcificato denominato camino, presente solo nelle Caligellidae. A questa secrezione iniziale si aggiungono due tipi di guscio "agglutinato" e bioeroso: le fondamenta *Protoinsolentitheca* e *Insolentitheca*, e i mattoni nella sola *Insolentitheca*.

Introduction

Vachard (1994) assigned the controversial genus *Insolentitheca* Vachard in Bensaid et al., 1979 to the Caligellidae (Foraminifera, Fusulinida), because of the lack of proloculus and aperture, and the resemblance with the general morphology of this group, especially *Baituganella*. The discovery of the genus *Protoinsolentitheca* n. gen., confirms this interpretation. Our analysis of *Insolentitheca* and *Protoinsolentitheca* contributes new insight into the Caligellidae, and their interpretation as a special group of foraminifera. Basically *Insolentitheca* is similar to *Caligella* or *Baituganella*, with an irregular «test», without proloculus, repetitive septation and terminal aperture, but in contrast *Insolentitheca* is able to collect, cement and bioerode some foraminiferal tests previously located at the water/sediment interface or within the sediment.

Groves (1987, 1988) interpreted *Insolentitheca* as a syzygial cyst of foraminifera. However, many taphonomical and palaeontological arguments are inconsistent with this hypothesis. Our position in this paper is: (1) *Insolentitheca* and Caligellidae are foraminifera of the order Fusulinida because they secrete a microgranular skeleton; (2) *Insolentitheca* is not a syzygial cyst; (3) *Insolentitheca* is not a typical agglutinated test; (4) no proloculus occurs; (5) no wide aperture occurs, but some small communications are observed; (6) morphological similarities exist with cysts of some foraminifera; (7) the growth of *Insolentitheca* and Caligellidae is not representative of the building of a true test, and does not correspond to exact outlines of the protoplasm; (8) complete *Insolentitheca* show internal bioerosion affecting systematically the incorporated material; (9) the irregularity and asymmetry of *Insolentitheca* are totally unknown among typical foraminiferal tests; (10) despite the relatively large, wide and thin-walled (interpreted to be not resistant to degrading hydraulic processes produced over the water/sediment

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interface), it never occurs to be externally abraded, mechanically broken or encrusted. Hence *Insolentitheca* is probably an infaunal taxon, as those foraminifera which are living in the upper few centimeters of bottom sediment (e.g. Jones & Charnock 1985; Murray 1991; Debenay et al. 1996).

Consequently, *Insolentitheca* is considered as a permanent cyst (a notion introduced by Le Calvez 1938, for the Recent genus *Iridia*) of an infaunal chitinaceous naked foraminifer. This permanent cyst needs for its description a new nomenclature (Fig. 1). It is not directly adhesive to the cytoplasm (Fig. 2.1). This cyst, replacing the test, is developed in all the Caligellidae (Fig. 2. 2-15), but particularly advanced in *Insolentitheca*.

The aim of this work is: (a) to discuss the previous interpretations of *Insolentitheca*; (b) to propose a new nomenclature of *Insolentitheca*; (c) to apply a part of this nomenclature to the Caligellidae emend. (Fig. 2); (d) to highlight new interpretations of some genera of the family Caligellidae; (e) to describe a new genus, *Protoinsolentitheca* n. gen.; (f) to summarize the geographic and stratigraphic distribution of *Insolentitheca*.

Previous work on *Insolentitheca*

The foraminiferal test

The first described species of *Insolentitheca* have been interpreted as test of foraminifera, and assigned to the questionable *Ammobaculites* or to a new subgenus *Haplophragmina* (*Haplophragmoides*) (Brazhnikova et al. 1967; Aizenverg et al. 1983; Perret 1993). Adachi (1980) described similar specimens as three new foraminiferal genera of a unknown family: *Fukujia, Ichinotania, Parahaplophragmella*. Most authors synonymize these three genera with *Insolentitheca* (Loeblich & Tappan 1986, 1988; Pinard & Mamet 1998). Loeblich & Tappan (1986) erected the subfamily Insolentithecinae, which was successively considered as related to the family Archaesphaeridae (Loeblich & Tappan 1986, 1988, 1992), Chernyshinellidae (Lipina 1989), Caligellidae (Vachard & Beckary 1991; Vachard 1994), and Parathuramminacea (Perret 1993). More recently, the name *Insolentitheca* has newly been regarded as valid but not necessarily belonging to the foraminifera (Mamet et al. 1993; Vachard 1994; Mamet 1996; Rauzer-Chernousova et al. 1996, Mamet & Isaacson 1997; Pinard & Mamet 1998; Vdovenko 2000; Sebbar 2000).

Groves (1987) has yet summarized the arguments against the truly agglutinated foraminifera, which are recognized by the parallel orientation of the agglutinated particles, the thick calcareous layer of cement including completely the particle, the small number of agglutinated tests, and the weak selectivity. Moreover, no calcisphaerid *Pachysphaerina* has been observed in *Insolentitheca*. Although *Haplophragmina* and *Insolentitheca* can be morphologically similar [compare: pl. 44 and 45 of Brazhnikova et al. (1967); pl. 3, figs. 1-10 and pl. 3, fig. 11 of Aizenverg et al. (1983); pl. FV, fig. 12-16 and pl. FV, figs. 17-20 of Perret (1993); pl. 43, figs. 6-8 and pl. 43, figs. 9-12 of Pinard & Mamet (1998)], *Haplohragmina* differs by its spherical proloculus and a planispiral juvenarium, well developed septa, and rather regular chambers and apertures.

The initial proposed attribution of *Insolentitheca* to *Ammobaculites* (?) can also correspond to a morphological similarity due to the infaunal life of *Ammobaculites* (e.g. Jones & Charnock 1985; Murray 1991). According to Bignot (1999), the fragile tests of *Ammobaculites* are broken by post-mortem transports, but they can easily fossilized in situ, in the sediment where they lived. The fossilization of *Insolentitheca* is probably identical.

The problematicum

Insolentitheca was created as a problematicum and a probable result of activity of a protista (Bensaid et al. 1979), for instance an encystment or moulting stage. According to Delvolvé & Perret (1987), *Insolentitheca* is a «pseudoforaminifer». Pinard & Mamet (1998) provide a good recent summary of the history of *Insolentitheca*, considered also as incertae sedis within the protozoans.

The syzygial cyst

After the interpretation as a syzygial cyst by Groves (1987), Groves (1988) and Tappan & Loeblich (1988) regarded Insolentithecinae and *Insolentitheca* as inappropriate names, for which the rules of the Code of International Zoological Nomenclature cannot be used. Consequently for ten years, «syzygial cysts» replaced *Insolentitheca* in the literature (Tappan & Loeblich 1988; Villa & Sánchez de Posada 1991; Ueno et al. 1994; Altiner & Savini 1995; Einor et al. 1996; Rauzer-Chernousova et al. 1996). The arguments for the syzygial cysts were: (a) the lack of characteristic foraminiferal features, including the proloculus, the apertures and the septation; (b) the supposed monospecificity of the linked tests; (c) the great number of tests participating to such cysts, up to 14 in *Patellina corrugata* Williamson (see Lee et al., 1991); (d) a supposed alternation of small and large tests, representing sexual dimorphism; (e) the internal dissolution of the agglutinated tests.

Arguments against a syzygial cyst

1. The components of *Insolentitheca* exist stratigraphically largely before, and remain after *Insolentitheca* itself. For instance, the distribution of *Tetrataxis* included in «*Fukujia*» (= *Insolentitheca*) *typica* subsp. B Adachi, 1985 is late Tournaisian to Late Permian, and the genus *Endothyranella* that makes up the «test» of «*Fukujia*» *typica* subsp. A Adachi, 1980 ranges only from late Bashkirian to late Early Permian, whereas *Insolentitheca* is late Viséan to latest Carboniferous (earliest Permian?).

2. An evolution of *Insolentitheca* exists. It is very rare and incompletely developed during the late Viséan (with *Protoinsolentitheca* and true *Insolentitheca*), typical and relatively abundant during the Middle Carboniferous (Bashkirian-Moscovian), rare again in the Late Carboniferous-Early Permian? interval. However, during the Middle Carboniferous, *Insolentitheca* includes some short-ranged taxa, e. g. *Semistaffella, Profusulinella, Aljutovella.*

3. A new genus, *Protoinsolentitheca*, is interpreted here as the ancestor of *Insolentitheca* because morphological similarities exist, and because the «tests» are usually generated from one kind of included test, in some cases two.

4. In modern equivalents, a syzygial cyst includes one, or rarely two species of the same genus (Le Calvez 1950). In *Insolentitheca* two or three genera (or families) are commonly present in the same specimen (Adachi 1980, fig. 3. 7; pl. 29, fig. 4; Aizenverg et al. 1983, pl. 4, fig. 2; Mamet et al. 1993, pl. 16, fig. 16; Vachard 1994, pl. 7, fig. 6) and sometimes their sizes are very different (Vachard 1994, pl. 7, fig. 6). Small foraminiferal tests are dominant in *Insolentitheca*, but a bimodality is frequent (Maslov 1929, fig. 10; Brazhnikova et al. 1967, pl. 45, fig. 1; Aizenverg et al. 1983, pl. 4, fig. 2; Perret 1993, pl. F5, fig. 18; Vachard 1994, pl. 7, fig. 6). However, *Insolentitheca* usually shows different sizes of foraminiferal tests. In contrast to the Groves' (1987) opinion as dimorphism, significant differences in the size has been only observed in the syzygial cysts composed of two specimens, and not in multi-specimen cysts. In a few exceptions, all the agglutinated tests are large (Adachi 1980, pl. 29, figs. 13-14; Loeblich & Tappan 1988, pl. 208, figs. 1-3; Villa & Sánchez de Posada 1991, pl. 1, fig. 3; Vachard & Beckary 1991, pl. 3, fig. 2). In fact, all the intermediate sizes exist (Adachi 1980 figs. 3. 1-11, 4. 1-6; pl. 30, figs. 1-20).

5. In modern equivalents, the cyst is composed of a thin wall, which is destroyed before the expulsion of the gamonts, so its preservation in the geological record should be extremely rare, while *Insolentitheca* can be relatively common and widespread, in the Middle Carboniferous.

6. No fossil examples of syzygial cysts occur in younger periods, especially those of maximal diversity of the foraminifera, i. e. Jurassic, Cretaceous or Paleocene.

7. Most syzygial cysts comprise trochoidal genera (e. g. *Discorbis*, *Glabratella*, *Rubratella*, *Patellina*), linked by the ventral area. In *Insolentitheca*, most of the foraminiferal morphologies and types of coiling are present (e.g. endothyroid, lenticular, biserial-coiled, fusiform, though rarely trochospiral because this type of coiling is rare in the Carboniferous-Permian) and the tests are not linked by the ventral areas, but randomly or with the long axes radiating out.

8. In syzygy, the dissolution of the tests is restricted to the ventral areas in contact. This dissolution affects randomly the tests constituting *Insolentitheca*. It is probably a bioerosion, which is accomplished, before the incorporation of the foreign tests, by the pseudopodia through chemical dissolution, as speculated for the Recent *Cymbaloporella* (Smyth 1988). Pseudopodia may penetrate individually and in several directions. This bioerosion by individualized pseudopodia might explain the misshapen morphology of *Insolentitheca.*

9. The syzygy can explain the internal dissolution, but cannot explain the secretion of a microgranular cement (modern examples of syzygial cysts among hyaline foraminifera are only linked by an organic cement).

10. *Insolentitheca* occurs at the same time and in different geological basins with constituents of many families (e. g. Endothyridae, Tetrataxidae, Biseriamminidae, Ozawainellidae, Schubertellidae, Profusulinellidae, Fusulinidae). It could be an unique case of «trans-family» evolution, without any ancient or modern equivalents in foraminiferal evolution.

11. The selectivity of *Insolentitheca* is high but not exclusive (see above, arguments 4 and 10). In fact, the selectivity is still poorly explained among the modern foraminifera (Debenay et al. 1996, p. 20).

New nomenclature for *Insolentitheca, Protoinsolentitheca* and Caligellidae

As exemplified by the well oriented, and apparently most complete specimens, found in Spain (Villa & Sánchez de Posada 1991, pl. 2, figs. 1, 4; Vachard 1994,

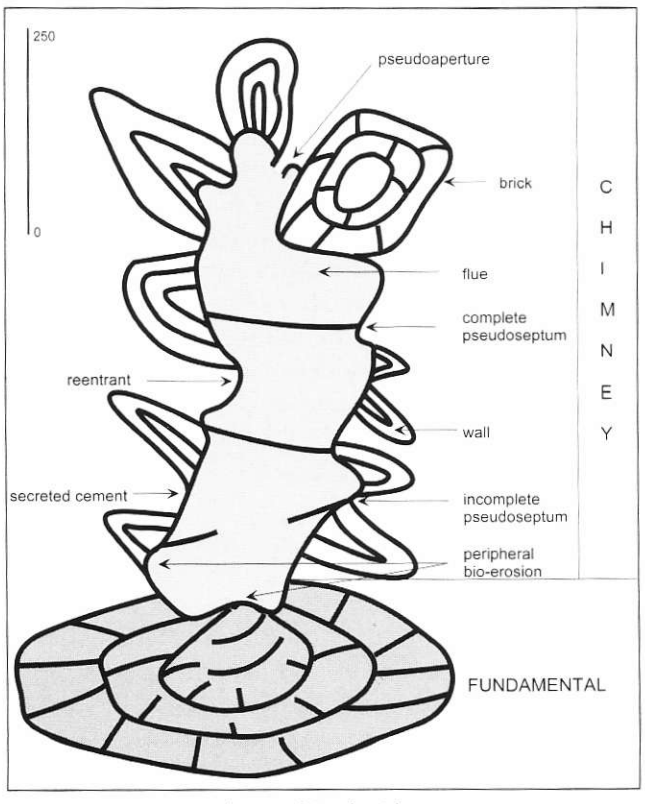


Fig. 1 - New nomenclature of *Insolentitheca.*

pl. 7, fig. 6), the initial part of the permanent cyst of *Insolentitheca* appears composed of a relatively large test: the «fundamental» (Fig. 1). A part of the endostructure of this fundamental is strongly eroded. The absence of the fundamental may be caused by oblique sections, but is probably characteristic of some morphotypes (see the material of Adachi 1980, for instance fig. 4. 3, pl. 30, figs. 12, 16, 19). Several cases of «isolated fundamentals» have been illustrated in the literature (see hereafter the synonymy list of *Protoinsolentitheca fundamenta* n. gen. n. sp.).

From the fundamental, extends a large, more or less tubular, closed part named herein «chimney» (Fig. 1). The chimney is hollow, and its cavity is the «flue». The flue is more or less interrupted by incomplete, or rarely complete pseudosepta, and generally does not show a wide aperture but presents sometimes «pseudoapertures», i. e. some interruptions or small channels of the wall and septa (Groves 1987 fig. 1. I, 1988, fig. 1. 4; Perret 1993, pl. F V, figs. 17, 20; Pinard & Mamet 1998, p. 132). The inner surface of the flue in *Insolentitheca* appears relatively regular and secondary bioeroded (Fig. 1). Either the flue is completely bioeroded, and no septum appears, or the bioerosion is incomplete, and pseudosepta are present.

The chimney is constituted of «bricks», that are «agglutinated» tests of foraminifera. The number of bricks varies from 1 up to more than 50. Some bricks have almost the same size as the fundamental, but they are generally smaller. The largest brick is generally adjacent to the fundamental (Adachi 1980, fig. 3. 1-4, 6, 10-11), but diametrically opposed locations of the fundamental and the biggest brick exist also (Villa & Sánchez de Posada 1991, pl. 2, fig. 1). The bricks are internally bioeroded and dissolved but externally well preserved, and linked by an undulating film of microgranular cement. The resorption of the bioeroded calcite of the bricks can contribute to produce periodically this cement, which shows several irregularities, sinuosities and «re-entrants» (Fig. 1).

This cement is similar to the microgranular walls of the Fusulinida tests incorporated into the wall. Bricks are absent in the cysts of Caligellidae, and rarely observed in *Protoinsolentitheca*. The hypothesis is slightly simpler in this case, because after trapping and bioeroding the fundamental, the foraminifer was able to secrete the rest of the chimney, and rarely, it needed other tests to generate the chimney.

Systematics

Class **Foraminifera** d'Orbigny, 1826 nomen translat. Lee, 1990

Order **Fusulinida** von Moeller, 1878 nomen translat. Fursenko, 1958

Superfamily ?Earlandioidea Cummings, 1955 nomen translat. Loeblich & Tappan, 1982

Family Caligellidae Reitlinger in Rauzer-Chernousova & Fursenko, 1959 emend. herein

Composition. 2 subfamilies: Caligellinae (only with cement) and Insolentithecinae (cement, fundamental and bricks). Caligellinae are composed of (Fig. 2. 2-13): *Caligella*; *Ademassa*; *Baituganella*; *Eocaligella*; *Eotikhinella*; *Glubokoevella*; *Paracaligella*; *Paracaligelloides*; *Petchorina*; *?Yukonella*; *? Halenopora*; *?Eoammosphaeroides*; *? Vulgarella* (references in Loeblich & Tappan 1988 and Vachard 1994). Insolentithecinae are represented by *Insolentitheca* and *Protoinsolentitheca* n. gen. (Fig. 2. 14-15).

The Caligellidae may belong to the superfamily Earlandioidea with an infaunal adaptation (Fig. 3), or to a particular group related with the Irregularinidae (*Eoammosphaeroides* seems to be a morphological intermediary), in this case Caligellidae and Irregularinidae can constitute together a superfamily, particularly diversified during the Devonian.

Emended diagnosis. Permanent cysts of elongate chitinaceous naked foraminifera secreting a microgranular chimney. The shape is more or less cylindrical (e. g. *Caligella*, *Paracaligella*, *Glubokoevella*, *Eotikhinella*, *Eocaligella*, *Insolentitheca*), polygonal (*Ademassa*) or irregular (*Baituganella*). No proloculus but occasionally a fundamental, i.e. a firstly trapped, bioeroded and dissolved foraminifer test, followed by a secreted microgranular to granular (Caligellinae), sometimes «agglutinated» (Insolentithecinae) chimney. The growth is partly or completely infaunal, probably vertical as in *Ammobaculites*. Rare pseudoapertures are visible in the wall. Some septa, perforated or not, occur within the flue. The pseudoapertures are numerous in *Yukonella*, and the septa are very regular in *Halenopora*. Wall microgranular (*Caligella*, *Paracaligella*, *Glubokoevella*), sometimes granular (*Paracaligelloides*, *Baituganella*), bilayered with a pseudofibrous layer (*Ademassa*), or calcareous «agglutinated» (*Insolentitheca*).

Discussion. Despite their uncommon aspects, the Caligellidae are almost unanimously accepted as a family of Fusulinida foraminifera (Rauzer-Chernousova & Fursenko 1959; Loeblich & Tappan 1988, 1992; Vdovenko et al. 1993; Vachard 1994), because of (a) the microgranular wall; (b) morphological similarities with oblique sections of more advanced foraminifera (e. g. Tournayelloidea, see Lipina 1989). Some breakages of the caligellids might be interpreted as apertures, but true foraminiferal apertures are apparently lacking.

An infaunal life cycle of the Caligellidae was suggested by Vachard (1994). The principal arguments are: (a) the rather good preservation of these fragile microfossils; (b) the absence of abrasion, i. e. transport by bottom or turbulent currents; (c) the absence of encrusting biofilms of cyanobacteries or other calcimicrobes.

The growth of all the other caligellids is probably similar to that of *Insolentitheca*. As indicated by Bensaid et al. (1979), some specimens of *Insolentitheca* are similar to *Baituganella* (for instance the different *Ichitonania* of Adachi 1980, pl 30, figs. 15-18). Other figured specimens

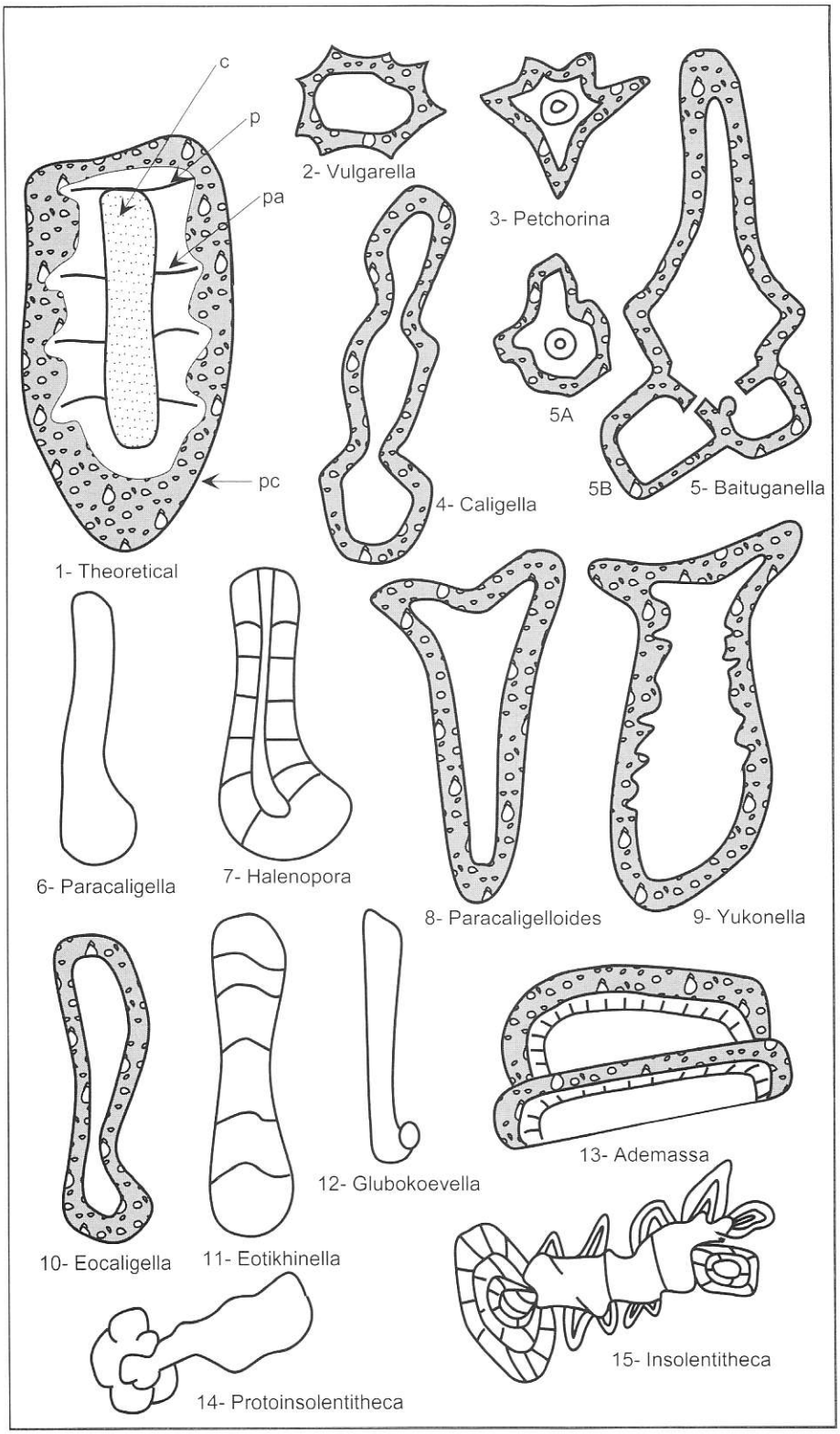


Fig. 2 - An interpretation of the tests of Caligellidae as permanent cysts. Abbreviations: c = cytoplasm; p = pseudopode, pa = pseudoaperture, pc= permanent cyst.

look like *Caligella* (see Adachi 1980, pl. 30, fig. 19). The morphology of *Caligella, Eotikhinella* and *Baituganella* can be easily explained by a succession of permanent cysts (Fig. 2. 2, 5 A-B, 11). *Eocaligella, Glubokoevella, Paracaligella* and *Paracaligelloides* consist in a single permanent cyst (Fig. 2. 6, 8, 10, 12). *Yukonella* is interpreted as an advanced form of *Paracaligelloides* with numerous perforations caused by bioerosion (Fig. 2. 9); the explanation of *Yukonella* as a dasyclad alga is inconsistent with the types of wall and perforations. *Halenopora* is interpreted here as an advanced form of *Paracaligella* with possible calcification of the cytoplasm and the pseudopodia (compare Figs. 2. 1 and 2.7). The previous interpretation as codiacean alga is inconsistent with the size, the microgranular calcitic wall, and the general organization.

A first growth stage, analogous to the fundamental and composed of a spherical monolocular foraminifer (such as *Cribrosphaeroides*) may exist (Fig. 2. 12) in some primitive caligellids (e. g. *Caligella, Paracaligella, Glubokoevella*), this spherical fundamental has been sometimes confused with a true proloculus (see Vachard 1994).

The pre-Silurian ancestors of the Caligellidae could be (1) an *Earlandia* secondarily adapted to an infaunal life (Fig. 3), with the lineage *Earlandia-Eocaligella-Caligella*, (2) an irregularinid form similar to *Cribrospheroides, Parphia, Bisphaera* or *Irregularina*, but these genera appear in the Devonian; (3) some enigmatic forms, as such as *Sorosphaera* (?) sp., allied the oldest foraminifera from the Early Cambrian (Culver 1991, 1994); (4) a pre-Silurian unknown naked foraminifer beginning to secrete in the Ludlovian the type of chimney of the caligellids.

The descendents of the Caligellidae are unknown. The Triassic representatives are very questionable, and correspond more probably to *Ammobaculites* (see Salaj et al. 1983, pl. 32, fig. 1; Trifonova 1992, p. 40-41, pl. 5, figs. 14-15).

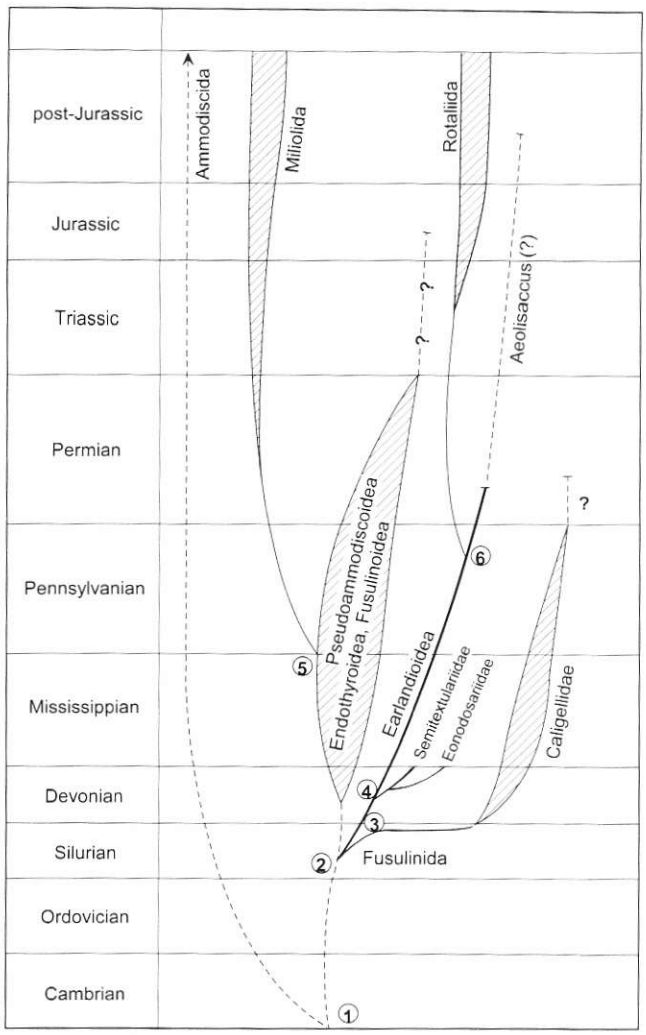


Fig. 3 - Phylogenetic hypothesis of the Caligellidae compared to other Fusulinida and to the other orders of foraminifera, and their importance in the foraminiferal phylogenies during the Paleozoic (according to Vachard, 1994). (1) = appearance of the Ammodiscida (agglutinated tests); (2) appearance of the secreted foraminifera with the Fusulinida (microgranular); (3) bifurcation of Earlandioidea and Caligellidae (tests passing to permanent cysts); (4) first diversification of the foraminifera (Givetian-Frasnian); (5) appearance of the Miliolida (secreted, porcelaneous); (6) appearance of the Rotaliida (secreted, hyaline).

Range. Cosmopolitan in the late Silurian (Ludlovian) to the latest Carboniferous (Orenburgian), and perhaps earliest Permian (Fig. 3). The primitive forms during the Silurian-Devonian are *Caligella*, *Eocaligella*, *Eotikhinella*, *Glubokoevella*, *Petchorina*, and *Eoammosphaeroides*. The Strunian (latest Devonian) is biostratigraphically characterized by *Paracaligelloides*, very abundant in the Etroeungt stratotype (Vachard & Mistiaen, work in progress). In the Tournaisian-Viséan the main genera are *Paracaligella*, *Halenopora*, *Baituganella*, *Ademassa* and *Yukonella*. The Caligellinae are rare in the Serpukhovian: Ukraine (Aizenverg et al. 1983), southern Spain (Cózar & Rodríguez 2000) and Qinghai, China (Vachard & Laveine, work in progress). The youngest forms are figured in the earliest Bashkirian of southern Urals [as *Haplophragmina* (?) sp. sensu Sinitsyna & Sinitsyn 1987, pl. 1, figs. 1-2]. The more advanced representatives of the Caligellidae survive, with *Insolentitheca* alone, from the late Serpukhovian to the Orenburgian (latest Carboniferous) and may be earliest Permian.

PLATE 1

Protoinsolentitheca n. gen. and contemporaneous Caligellidae (collections of the thin-sections are PC = P. Cózar, DV = D. Vachard, except in those case in which the author collection is specified).

Figs. 1-7 - *Protoinsolentitheca fundamenta* n. gen. n. sp. Fig. 1 - Holotype. The fundamental is a *Palaeotextularia*. Thin-section PC1198. Specimen 2175/4. Late Asbian, Ballyadams Formation, Ballyadams Quarry (Ireland). x 30. Fig. 2 - A fundamental, as a result of the bioerosion of *Koskinotextularia* (compare with Vachard and Tahiri, 1991, pl. 12, fig. 19). Thin-section 288 (section A). Late Viséan. Oulmes area, central Morocco. x 70. Fig. 3 - Bioerosion of a *Eostaffella mosquensis acuta* Rauzer-Chernousova (compare with Vachard, 1977, pl. 5, fig. 22). Brigantian, Montagne Noire (southern France). Thin-section DV 246G-18. x 85. Fig. 4 - Bioeroded *Endothyra* as fundamental. Thin-section PC1135. Specimen 2175/18. Late Asbian, Ballyadams Formation, Ballyadams Quarry (Ireland). x 140. Fig. 5 - A complete paratype with *Plectogyranopsis* as fundamental. Thin-section PC1137. Specimen 2175/15. Late Asbian, Ballyadams Formation, Ballyadams Quarry (Ireland). x 50. Fig. 6 - Bioeroded palaeotextulariid as fundamental. Thin-section PC1143. Specimen 2175/14. Late Asbian, Ballyadams Formation, Ballyadams Quarry (Ireland). x 16. Fig. 7 - Slightly modified palaeotextulariid. Thin-section PC1198. Specimen 2175/3. Late Asbian, Ballyadams Formation, Ballyadams Quarry (Ireland). x 75.

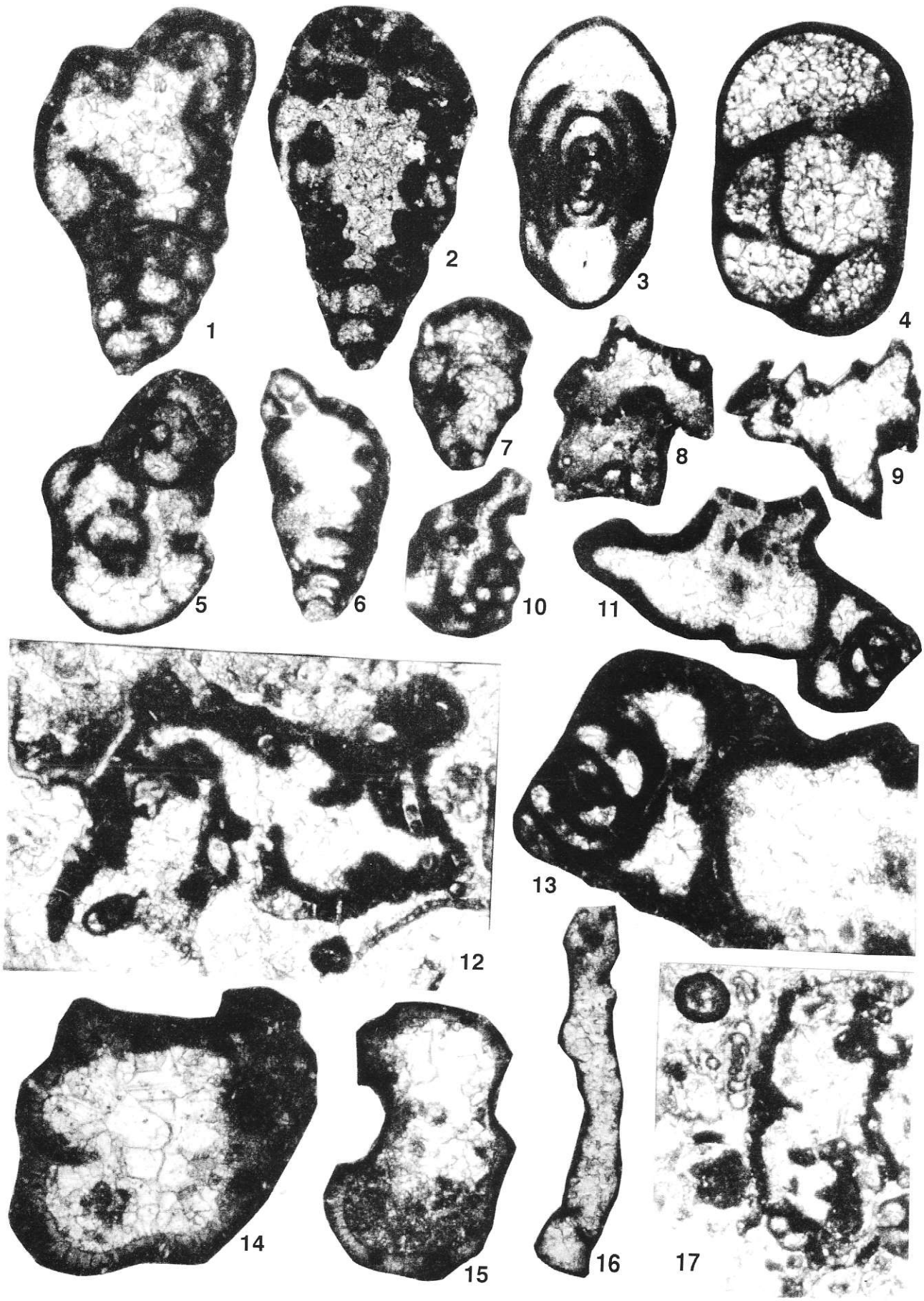
Fig. 8 - *Baituganella* (?) sp. Transverse section. Angular periphery, with granular wall and some spherical bricks. Thin-section PC1150. Specimen 2175/12. Late Asbian, Ballyadams Formation, Ballyadams Quarry (Ireland). x 75.

Fig. 9 - *Baituganella chernyshinensis* Lipina. Longitudinal section. Thin-section PC1117. Specimen 2175/24. Late Asbian, Ballyadams Formation, Ballyadams Quarry (Ireland). x 75.

Figs. 10-13, 17 - *Protoinsolentitheca serpuchoviensis* (Brazhnikova in Aizenverg et al., 1983). Late Asbian, Ballyadams Formation, Ballyadams Quarry (Ireland). Fig. 10 - Narrow flue. Thin-section PC1615. Specimen 2175/27. x 50. Fig. 11 - The fundamental is an *Endothyra* (right). Thin-section PC1151. Specimen 2175/10. x 75. Fig. 12 - Longitudinal section with a *Kamaenella* (left in the wall) and a large and roomy chimney and flue, similar to *Baituganella*. Thin-section 27/8/5. Specimen 2175/26. x 30. Fig. 13 - Detail of Fig. 10 showing the fundamental (left) and the base of the chimney. x 150. Fig. 17 - Longitudinal section. Thin-section PC1117. Specimen 2175/23. x 50.

Fig. 14- 15 - *Ademassa inuncta* Vachard. Late Asbian, Ballyadams Formation, Ballyadams Quarry (Ireland). Fig. 14 - Oblique section. Thin-section PC1118. Specimen 2175/21. x 50. Fig. 15 - Thin-section PC1151. Specimen 2175/8. x 50.

Fig. 16 - *Baituganella* cf. *serpiensis* Chuvashov. Longitudinal oblique section looking like *Paracaligella* or *Eocaligella*. Thin-section PC1200. Specimen 2175/2. Late Asbian, Ballyadams Formation, Ballyadams Quarry (Ireland). x 50.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Subfamily Insolentithecinae Loeblich & Tappan, 1986

Genus *Protoinsolentitheca* n. gen.

Type species. *Protoinsolentitheca fundamenta* n. sp., designated herein.

Diagnosis. Caligellidae with a bioeroded fundamental, followed by a mostly secreted wall, rarely with agglutinated bricks into the chimney. The flue is only composed by an enlargment of the chambers of the fundamental, or caligellid-shaped. Large aperture absent, but small pseudoapertures are observed. Pseudosepta usually present, but always as remains of the previous fundamental septa. Secreted wall microgranular.

Composition. *Protoinsolentitheca fundamenta* n. gen. n. sp., *Paracaligelloides* (?) *serpuchoviensis* Brazhnikova in Aizenverg et al. 1983 (due to the presence of a fundamental and a brick in the type-material of Aizenverg et al. 1983, pl. 1, fig. 8).

Comparisons. *Protoinsolentitheca* differs from the Caligellinae by the presence of a fundamental. In contrast with *Insolentitheca*, bricks are nearly absent and most of the wall was directly secreted.

Significant differences (morphotypes)exist between the specimens of *Protoinsolenthica*, as in *Insolentitheca* (see hereafter) but they depend on the size and type of wall of the fundamental, and of the level of bioerosion of the fundamental.

Protoinsolentitheca differs from some probable reproductive chambers of the tetrataxids, e. g. the «genus» *Globotetrataxis* and some uncommon *Tetrataxis* (*T. mirus*, *T. fortis*, *T. exornatus* partim) (e.g. Aizenverg et al. 1983; Conil & Lys 1964; Bogush & Juferev 1976; Adachi 1985), because of the lack of internal bioerosion of the tetrataxids.

Stratigraphic range and palaeobiogeography. Late Viséan from Ireland, Southern France, Morocco, and Alaska (see the synonymy list of *P. fundamenta* n. sp.). Serpukhovian from Donbass (Ukraine).

Protoinsolentitheca fundamenta n. gen., n. sp.

Pl. 1, figs 1-7

v. 1977 *Eostaffella mosquensis acuta* Rauzer-Chernousova - Vachard, pl. 5, fig. 22.

p. 1983 various deformed or apparently archaic sections - Aizenverg et al., pl. 2, fig. 23 (only).

1983 - *Mediocris ovalis* forma globosa - Aizenverg et al., pl. 12, figs. 5, 11.

1983 - *Mediocris evolutis grandiosa* forma recta - Aizenverg et al., pl. 12, figs. 6-7.

1983 - *Mediocris* ex gr. *breviscula* forma recta - Aizenverg et al., pl. 12, fig. 6a.

1983 - *Mediocris crassitheca* forma recta - Aizenverg et al., pl. 12, fig. 11.

v. p. 1991 - *Koskinotextularia bradyi* (von Moeller) - Vachard & Tahiri, pl. 12, fig. 19 (non pl. 4, fig. 11, nec pl. 5, fig. 18 = true *Koskinotextularia*).

1993 - *Pseudoendothyra densa* Rozovskaya - Mamet et al., pl. 11, fig. 16.

Derivatio nominis. Latin fundamenta, because it is situated at the foundations of the *Insolentitheca* lineage, and because it exhibits the first fundamentals.

Locus typicus. Ballyadams Quarry, about 7 km southwest of Athy, Ireland (McConnell & Philcox 1994).

Stratum typicum. Late Asbian, 20.60 m below of the top of the quarry, close to the base of the upper working bench (this quarry is active, so the base is periodically deepened).

Holotype. Pl. 1, fig. 1 (thin-section PC 1198).

Paratypes. The material is distributed throughout the late Asbian in the Ballyadams Quarry (Ballyadams Fm.), more than one hundred sections, and tens of specimens in the Brigantian in the Clogrenan, Aghmaddock and Dunamase quarries (Clogrenan Fm.), Ireland (Pl. 1, figs. 4-7).

Repository of the types. Department of Paleontology, Facultad de Ciencias Geológicas, Universidad Complutense Madrid (Spain).

Diagnosis. Insolentithecinae composed of a fundamental. Bricks are very scarce or absent. Chimney and flue are well-developed in complete specimens. Wall microgranular, thin.

Description. The fundamentals are composed of small (e.g. *Endothyra*, *Omphalotis*, *Plectogyranopsis*, *Eostaffella*, *Pseudoendothyra*, *Consobrinella*, *Koskinotex-*

PLATE 2

Several morphotypes of *Insolentitheca horrida*

Figs. 1, 3, 7 - Morphotype *endothyroidea* (Adachi). Fig. 1 - Numerous bricks of *Endothyra*. Bashkhirian. Valdeteja (northern Spain). Thin-section PC34. x100. Fig. 3 - Serpukhovian. Donbass basin (Ukraine). Collection M.F. Perret (sampling E. Groessens). Thin-section Up E1. x 50. Fig. 7 - Numerous bricks of *Mediocris breviscula* (Ganelina) and pseudosepta. Early Bashkirian. Truebano (northern Spain, located in Vachard & Beckary 1991). x 50.

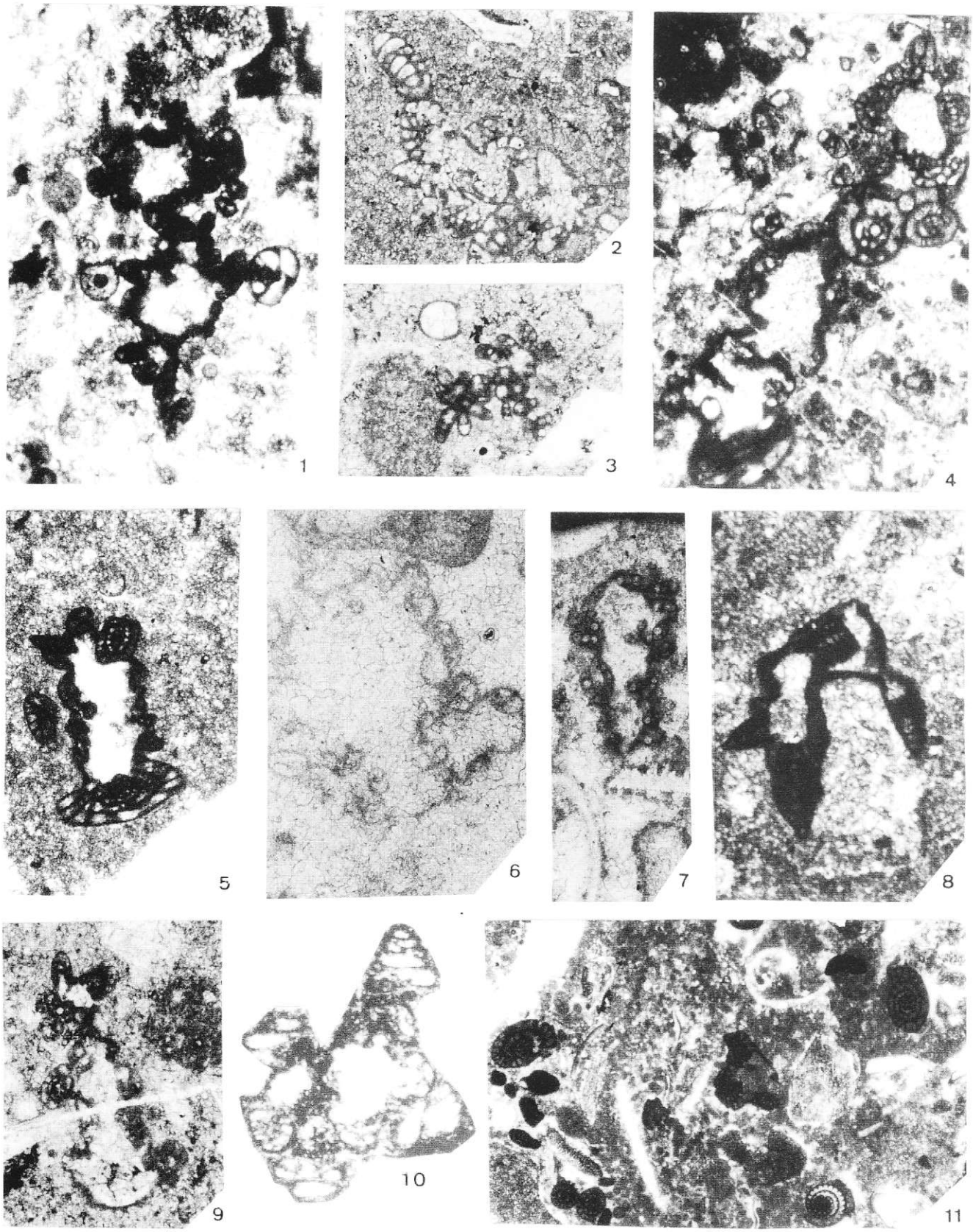
Figs. 2, 4-5, 9 - Morphotype *horrida* (Brazhnikova). Fig. 2 - Bricks of *Plectomillerella*. Serpukhovian. Donetz basin (Ukraine). Thin-section 2/7. Collection M.F. Perret (sampling E. Groessens). x 50. Fig. 4 - Plurigeneric composition of the bricks: *Endothyra*, *Eostaffella*, *Semistaffella* and *Eoschubertella*. Moscovian. Villanueva de la Tercia (northern Spain). Thin-section PC20. Specimen 34. x 75. Fig. 5 - Fundamental of *Fusiella*, bricks of *Fusiella*, *Endothyra* and *Pseudostaffella*. Late Moscovian (Podolskian). Xinjiang (northern China). Thin-section Sjg.An.1.2. Collection J.P. Laveine. x 45. Fig. 9 - Bricks of eostaffellids. Serpukhovian. Donetz basin (Ukraine). Thin-section Up E1. Collection M.F. Perret (sampling E. Groessens). x 50.

Fig. 6 - Morphotype *variabilis* (Brazhnikova). Bricks are composed of globivalvulinids. Moscovian. Thailand. Thin-section DV 8950 (=T2723) (sampling H. Fontaine). x 50.

Fig. 8 - Morphotype *ozawainelloidea* (Adachi). Bricks are composed of ozawainellids. Podolskian. Xinjiang (northern China). Thin-section Sjg.Buya.a. Collection J.P. Laveine. x 45.

Fig. 10 - Morphotype 6 (=*Fukujia typica* subsp. B = pl. 22, fig. 27 of Adachi 1985). Bashkirian. Japan. x 40.

Fig. 11 - Morphotype *gigantea* (Adachi), (centre) accompanied by *Aljutovella* sp. Early Moscovian. Tin Hieddan (Illizi basin, Algeria) (located in Massa & Vachard 1979). Thin-section OC 827. Collection Total. x 17.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tularia) and medium-sized material (Palaeotextulariinae such as *Palaeotextularia, Cribrostomum*). Bricks are usually absent, or rarely small *Endothyra* are observed. «Pseudosepta» are frequent, but clearly correspond to previous parts of the wall of the fundamental. The phenomenon of bioerosion is observed in *Protoinsolentitheca*, although it is less significant than in *Insolentitheca*, because it only bioeroded 1 or 2 agglutinates. No possible misinterpretation exists with taphonomical dissolution, because in the case of *Protoinsolentitheca* it is also followed by precipitation and generation of new parts of the test. *Protoinsolentitheca,* in those specimens in which their fundamental was originally a Palaeotextulariinae. In these exceptional cases, *Protoinsolentitheca* dissolved both layers of the foraminifer, but the new precipitated cement is exclusively microgranular. Parts with fibrous layer are original, not bioeroded, test remains.

The size of the specimens varies in function to the size of the fundamental and the development of the chimney. Pseudoapertures are distinctively present in many specimens.

Comparison. Differs from *P. serpuchoviensis* by a thinner wall, a small chimney and a larger fundamental.

Range. Type material from the late Viséan: Asbian-Brigantian of Ireland. Late Viséan-late Serpukhovian from Southern France, Morocco, Ukraine, Alaska (see the synonymy list).

Genus *Insolentitheca* Vachard in Bensaid et al., 1979 emend. herein

Type species. *Ammobaculites* (?) *horridus* forma typica Brazhnikova in Brazhnikova et al., 1967; by original designation.

Emended diagnosis. Permanent cyst of Caligellidae, with a relatively large fundamental, (i. e. a first trapped foraminifer, bioeroded and dissolved), followed by a secreted and agglutinated chimney constructed with bricks, i.e. rare to numerous, monospecific or not, tests of foraminifera, internally bioeroded and truncated. Small pseudoapertures exist, and some residual pseudosepta can be present in the flue, i. e. central cavity. Bricks are linked by a microgranular cement.

Composition. *Insolentitheca horrida* (Brazhnikova, 1967) seems the unique species (Pinard & Mamet 1998). Among the very numerous «species» of Adachi (1980), some morphotypes are relatively particular and can correspond to selectivity stages due to the biostratigraphical evolution of the incorporated material, for instance the supplementary morphotypes: «*variabilis*» (Brazhnikova in Aizenverg et al. 1983), «*endothyroidea*» (Adachi, 1980), «*ozawainelloidea*» (Adachi, 1980), «*gigantea*» (Adachi, 1980) and «morphotype 6» (Pl. 2, figs. 1-11). These subdisions differ by the following characters: (a) nature and presence of fundamentals, (b) size and bimodality of bricks, (c) nature of the flue, (d) importance of pseudosepta, (e) shape of the chimney.

Stratigraphic range. *Insolentitheca* is very rare in the late Viséan (Mamet 1970, pl. 11, fig. 3, left bottom. re-interpreted; Ivanova 1973 a-b; Conil 1980; Aizenverg et al. 1983, p. 48; Laloux 1988; Vdovenko 2000); rare in the early Serpukhovian (Morocco; Chalot-Prat & Vachard 1989); common and cosmopolitan from the late Serpukhovian to the late Moscovian; limit Moscovian/Kasimovian from Kazakhstan (collection Lys, sample ML IV-2, unpublished). Apparently absent in the late Carboniferous, the genus reappears in the Orenburgian of the Carnic Alps (Auernig Formation) (Vachard & Krainer 2001). *Insolentitheca* is also present in the early Wolfcampian (= early Bursumian = Orenburgian of northern Mexico) (collection F. Rangin, unpublished). The specimen of Mamet (1996, pl. 1, fig. 47) from Bolivia is «Asselian or Sakmarian», consequently can correspond to this part of the Wolfcampian now put into latest Pennsylvanian, as well as the «Sakmarian» specimen of Pinard & Mamet (1998, pl. 43, fig. 12). Therefore, the presence of *Insolentitheca* in the early Permian is not definitively confirmed. The last occurrence of *Insolentitheca* might be more probably Orenburgian in age.

Concerning the first occurrence in the stratotypical Viséan of Belgium, the early Viséan Cf 4α dating (Conil 1980, pl. 1, fig. 4) is probably misinterpreted (due to a confusion between two numbers of thin-sections?), and the first specimen seems to appear in the late Viséan Cf 6γ2 («V 3 bγ» séquence 2) (Laloux 1988, pl. 1, fig. 13). In the latest Viséan Cf6δ, Caligellinae and *Protoinsolentitheca* n. gen. coexist with the first true *Insolentitheca.*

Palaeobiogeography. Late Viséan-early Serpukhovian specimens are quoted or simply figured in Belgium, Poland, Donbass, southern Urals, western Canada and eastern Morocco. The genus is cosmopolitan in the late Serpukhovian-Bashkirian, from Pyrenees to Algeria (Bechar, Reggan) and Central Morocco, from Turkey to Afghanistan, from Thailand to China (Xinjiang and Qinghai, Vachard & Laveine, work in progress) and Japan, and from Spitsbergen to USA (including Alaska)/Mexico/Bolivia/Brazil. The post-Bashkirian distribution is sporadic but also cosmopolitan.

Conclusions

1. The existence of Palaeozoic syzygial cysts of foraminifera are not confirmed.

2. The new genus *Protoinsolentitheca* is a taxon more evolved than some Caligellidae, such as *Baituganella*, *Paracaligelloides*, and less evolved than *Insolentitheca*. It links the Caligellinae and Insolentithecinae. Despite their advanced life stage, *Insolentitheca* and *Protoinsolentitheca* belong to the primitive family Caligellidae. All the

genera secreted permanent cysts but no tests. As the cement of these cysts is microgranular, they belong to the foraminifera Fusulinida.

3. The permanent cyst of *Insolentitheca* is interpreted as composed of an initial part: the fundamental, and a second part, the chimney, agglutinating some bricks, which belong to a small number of foraminifer families. The fundamental can be absent and the chimney only present. The cavity or flue of the chimney shows some incomplete figures of bioerosion/dissolution: the pseudosepta. The wall is composed of bricks of Fusulinida and thin secreted microgranular cement, similar to the secretions of the true Fusulinida.

4. The morphological similarities with *Ammobaculites* are probably due to the infaunal growth.

5. All the caligellids are similarly infaunal and more or less constructed as *Insolentitheca* and *Protoinsolentitheca*.

6. The generic range of *Insolentitheca* is late Viséan to late Carboniferous (Orenburgian), and may be earliest Permian. *Protoinsolentitheca* is late Viséan to late Serpukhovian in age. The caligellids exist from the late Silurian to the latest Carboniferous/earliest Permian? They form a particular group of the microgranular foraminifera Fusulinida.

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