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A REVISED CHITINOZOAN CLASSIFICATION

FLORENTIN PARIS, YNGVE GRAHN, VIIU NESTOR, AND ISKRA LAKOVA

Laboratoire de Paléontologie, UPR 4661 du CNRS, Université de Rennes I, 35042 Rennes-cedex, France <florentin.paris@univ-rennes1.fr>,
Universidade de Estado do Rio de Janeiro-UERJ, Faculdade de Geologia, 20559-900 Rio de Janeiro, Brazil <grahn@uerj.br>,
Tallinn Technical University, Institute of Geology, 7 Estonia Avenue, 10143 Tallinn, Estonia <vnestor@gi.ee>, and
Geological Institute, Bulgarian Academy of Sciences, 1113 Sofia, Bulgaria <lakova@geology.acad.bg>

ABSTRACT—The successful definition of chitinozoan genera depends primarily on the precision of the criteria used. A standardized morphological terminology based upon details from scanning electron microscope observations of the most representative taxa bearing these characters is therefore proposed. The 143 genera, or subgenera, described so far in the literature are reviewed in order to exclude invalid taxa and obvious junior synonyms. Particular attention is paid to preventing the overlap of generic definitions of the 56 genera ultimately retained. A brief account of the diagnostic features and stratigraphic range of selected genera is given, and basic information concerning the type material of these genera is listed. Finally, a suprageneric classification of the whole Chitinozoa group based on diagnostic features whose hierarchy is established on statistical and evolutionary grounds, is given. One new subfamily, Pogonochitininae, three new genera, *Baltochitina, Hyalochitina,* and *Saharochitina,* and a new species *Baltochitina nolvaki,* are defined. The subspecies *Fungochitina fungiformis spinifera* is elevated to a specific rank.

INTRODUCTION

CHITINOZOANS CONSTITUTE a group of organic-walled microfossils, well represented in Early Ordovician (late Tremadoc) to latest Devonian (latest Famennian) marine sediments from nearly all Paleozoic oceans. They are found isolated or in chainlike structures in most sedimentary or low grade metamorphic rocks, where their abundance usually ranges from a small number of specimens to several hundred (exceptionally up to several thousand) specimens per gram of rock. The length of a chitinozoan vesicle (basic isolated element) ranges from ca. 50 to 2,000 μm (with an average size of around 150–250 μm). They constitute an enigmatic group of fossils whose biologic affinities and significance are still interpreted in a variety of ways (see review in Miller, 1996), more than 60 years after their first description by Eisenack (1931). Personally, we favor the hypothesis of eggs of soft-bodied metazoans (Paris, 1981, p. 84; Paris and Nõlvak, in press) referred as chitinozoophorans by Grahn (1981). They have proven to be very efficient stratigraphic tools, and they are extremely useful for paleogeographic reconstructions. However, a unanimously accepted taxonomy is now strongly needed in order to make application of chitinozoan genera for paleogeographic and paleoenvironmental investigations more reliable.

There have been many attempts to classify chitinozoans. They were carried out through individual initiatives (Eisenack, 1931, 1968, 1972; Van Oyen and Calandra, 1963; Jansonius, 1964, 1967, 1970; Tappan, 1966; Taugourdeau, 1966, 1981; Paris, 1981; Achab et al., 1993) or under the authority of the chitinozoan Subcommission of the "Commission Internationale de Microflore du Paléozoïque" (CIMP) (Taugourdeau et al., 1967). In the last 25 years, major improvements in the knowledge of chitinozoan morphology have been achieved, primarily due to the routine use of the Scanning Electron Microscope (SEM). In addition, numerous new occurrences have greatly increased the chitinozoan record, so that it now includes more than 1,000 taxa described from almost all continents. We are convinced that sufficient data exist to propose a standard terminology and a general classification of chitinozoans that integrates the taxa described since the last extensive revision (Taugourdeau et al., 1967; Combaz et al., 1967). Our aim is to integrate all original morphologies recorded during the last 30 years into a general classification of the group. Particular attention is paid to the definition of the morphologic characters, and to the establishment of a hierarchy among these morphologic elements. A critical review is made of all 143 genera described and, after excluding those genera regarded as invalid by ICZN (third version), we propose a synonymy list based on the criteria we consider to be essential. Because many of the existing generic diagnoses are not sufficiently definite, we supplement the original definition of selected genera with their respective diagnostic features. By doing so, we hope to prevent overlapping of the generic definitions, which has proven to be one of the greatest and most constant problems in chitinozoan taxonomy.

CHITINOZOAN MORPHOLOGY

General terminology.—A chitinozoan individual may be defined as a small organic-walled vesicle with an opening. Well-preserved chitinozoans (i.e., in full relief and not eroded or distorted) share three major characteristics (Fig. 1): 1) they are made up of an organic membrane delimiting a cavity; 2) they have an aperture sealed with a plug; and 3) they normally display a radial symmetry. The actual chemical composition of the chitinozoan vesicle remains unknown. Therefore, this definition is so broad that various organisms, or part of organisms may be included. Size limits (<2,000 μm and >50 μm) or stratigraphic range restriction (exclusively of Paleozoic age, unless reworked) restrict this definition and allow various present day cysts, cocoons, or eggs of invertebrates (insects, annelids, molluscs, etc.) to be excluded from the chitinozoans. When present, the external ornamentation of a chitinozoan vesicle is fairly distinctive compared to the ornament of almost all other organic-walled microfossils of similar age (i.e., acritarchs, spores, and foraminiferal linings).

A detailed morphological terminology was first introduced by Combaz and Poumot (1962) and then subsequently completed by Combaz et al. (1967) under the direction of the Chitinozoa Subcommission of CIMP. Most recent papers dealing with chitinozoan systematics have used either the English adaptation proposed by Laufeld (1974) or the French terminology adopted by Paris (1981). These terminologies are still valid and well adapted for the description of the chitinozoans. Only a few modifications or additions are necessary in order to integrate the most recent morphological details revealed by SEM observations. One of our aims is to promote a standard morphological nomenclature that would be unanimously accepted and used.

The main parts of a chitinozoan vesicle are illustrated, showing the three principal morphological types of chitinozoans (Fig. 1). The basic element is the vesicle, with a bulging part called

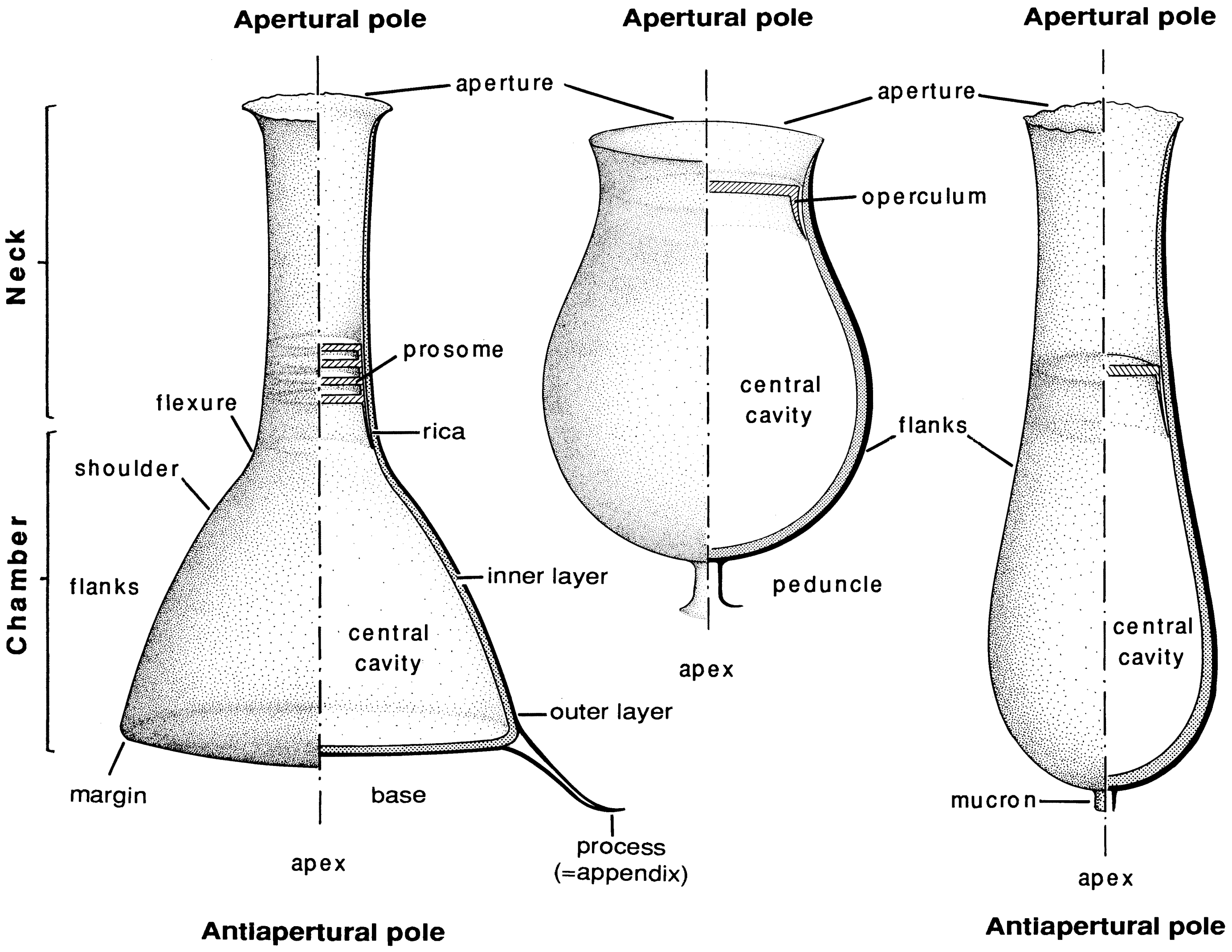

FIGURE 1—Main morphological features of the three principal types of chitinozoans (modified from Paris, 1981, fig. 56).

the chamber. The aperture is either situated directly on the chamber or at the distal end of a tubelike neck. In order to clarify discussion and descriptions, an arbitrary orientation of the vesicle has been adopted. The apertural pole is regarded as representing the top of the vesicle. This means that, in a chainlike structure, the upper (or last) vesicle has a free aperture. However, no biological nor physiological significance has to be given to this orientation, which is exclusively conventional. A collarette, frequently corresponding to a thinning of the wall, may be present around the aperture. The plug sealing this aperture is either called an operculum or a prosome depending on its internal or external position and on its role in inter-vesicle linking (see definitions below). The base, which corresponds to the antiapertural end of the vesicle, may display various linkage structures around the apex. This base is separated from the flanks by the margin. This zone proves to be of prime importance for chitinozoan taxonomy, as it frequently bears peculiar ornamentation (e.g., processes or carina). The flanks themselves may be separated from the neck by the flexure (e.g., vesicles with well-differentiated necks).

Lexicon of the morphologic features and structures.—This lexicon is given in order to restrict some previous definitions that were not accurate enough or were already used with a different meaning. It also introduces the morphologic terms we use for the discrimination of the chitinozoan genera we have selected. In addition, references are made to recently published SEM images which illustrate almost all of these terms.

1) antiapertural pole: lower part of the vesicle, opposite the aperture.

2) aperture: large opening at the top of the vesicle, delimited either by the lips of the neck or collarette, or if these two other elements are absent, by the border of the chamber (Fig. 1). This term is preferred instead of "mouth", which has physiological significance.

3) apertural plug: general term designating the simple or complex plug sealing the aperture, represented either by the operculum or by the prosome (see definitions below).

4) apertural pole: arbitrarily designated as the upper part of the vesicle.

5) apex: point of emergence of the axis of symmetry on the base of the chamber (Fig. 1).

6) apical pit: circular, depressed area surrounded by the rim of the mucron. [N.B. the apertural pit does not open in the vesicle in well-preserved specimens (see Miller, 1996, pl. 1, fig. 1; Verniers et al., 1995, fig. 6K)].

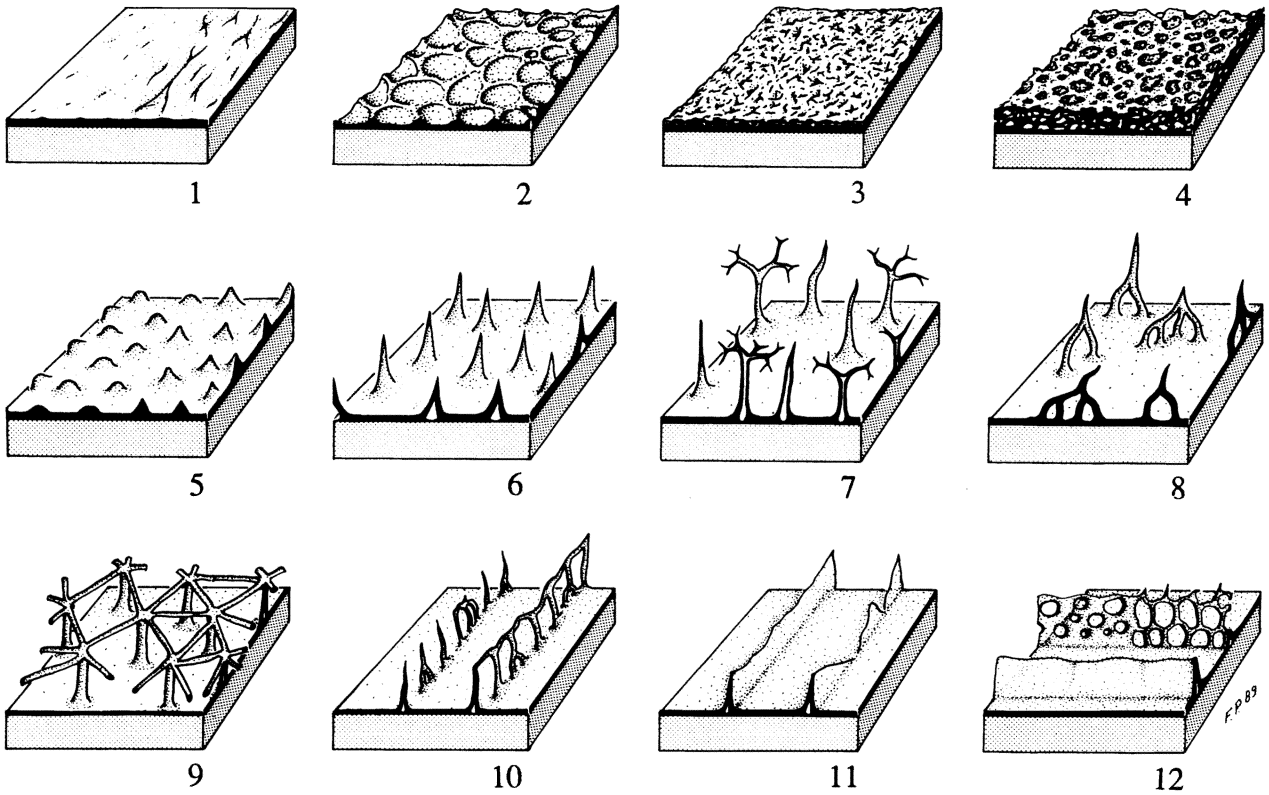

FIGURE 2—Different kinds of vesicle wall surfaces of chitinozoans. *1,* Smooth, scabrate, vermiculate; *2,* foveolate; *3,* feltlike; *4,* spongy; *5,* verrucate (granules, tubercules and/or cones less than 2 microns high); *6,* simple spines; *7,* simple and branched hairs or spines; *8,* bi and multirooted spines; *9,* meshlike structure; *10,* crests with vertical rows of free or connected spines; *11,* crests of weblike to discontinuous membranes; *12,* complete or perforated/reticulated carina. Stippled = inner layer; black = outer layer.

7) apical structure: includes the scar, callus, mucron, copula and peduncle; the bulb is also regarded as an apical structure.

8) axis: imaginary line joining the center of the aperture to the apex and representing the axis of symmetry of the vesicle.

9) base: part of the chamber opposite to the aperture (=antiapertural end or chamber bottom).

10) bulb (=siphon): membranous ampoule extending from the base of a vesicle (e.g., in *Siphonochitina formosa*) (see Jenkins, 1967, pl. 75, figs. 2–5).

11) callus: short stublike thickening on the apex (e.g., in *Desmochitina densa* illustrated by Laufeld, 1974, fig. 39D).

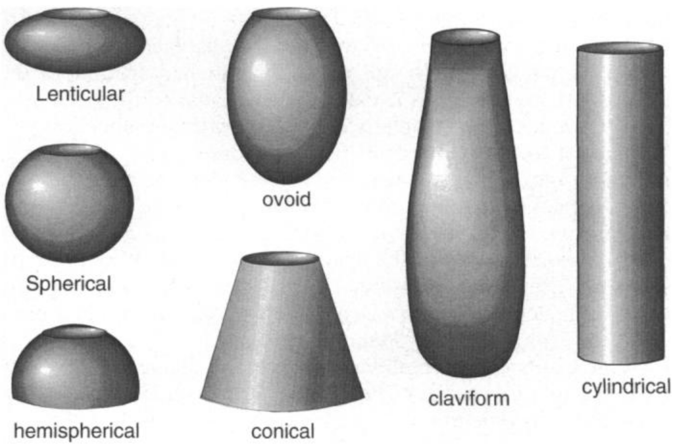

FIGURE 3—The basic chamber shape of the chitinozoans.

12) carina: circular expansion of the wall (outer layer) round the chamber; it may be located below, on, or above the margin (Fig. 2.12).

13) catenary structure (=chainlike structure): vesicles connected "aperture to base", along their axis (straight, curved or coiled chain) (see Jenkins, 1970b, pl. 6, figs. 4–6; Paris and Nõlvak, in press, pl.1, figs. 1, 3–4), or vesicles connected "neck to margin", with a coiled pattern (e.g., *Lagenochitina navicula* in Paris, 1981, pl. 31, figs.1–3).

14) central cavity: inner cavity corresponding to the chamber (Fig. 1) (contained the embryo if one adopts the egg hypothesis).

15) chamber: part of the vesicle (frequently bulging) situated below the neck or below the collarette when present (see Fig. 3 for the different chamber shapes).

16) cluster: group of vesicles belonging to the same species and connected by their flanks (aperture free); they are usually arranged in a coiled pattern (see Koslowski, 1963, fig. 3; Miller, 1996, pl. 5, figs. 1–2; Paris and Nõlvak, in press, pl. 1, figs. 5–8).

17) coiled chain (=helicoidal chain): vesicles connected "neck to margin" i.e., with a free aperture, or "aperture to base" i.e., aperture linked to the succeeding vesicle.

18) collarette (=collar): thinned cylindrical or flaring part of the neck, or of the vesicle wall when the neck is absent. The collarette surrounds the aperture.

19) copula: tubular, membranous expansion surrounding the apex (see Paris, 1981, pl. 1, figs. 7, 13).

20) crests: vertical rows of free or connected spiny ornamentation (Fig. 2.10), or of weblike to continuous membranes (Fig. 2.11) (see Achab et al., 1993, pl. 1, figs. 1–2; Miller, 1996, pl. 2, figs. 2–3).

21) diameter: refers to the maximum diameter of the chamber (D), neck (dn), or aperture (da); a coefficient of correction (e.g., 0.7 or 0.8, depending on the degree of flattening) (see Paris *in* Babin et al., 1979) must be used to restore the full-relief measurement where the vesicle is flattened or collapsed.

22) equatorial plane: corresponds to the maximum diameter of lenticular or spherical chambers.

23) external structures: include the carina and apical structures as well as the sleeve.

24) flanks: part of the chamber situated between the margin and the neck or collarette (Fig. 1).

25) flexure: concave zone separating the flank from the neck (Fig. 1).

26) glabrous: state of the vesicle surface when lacking spiny ornamentation (Fig. 2.1–5).

27) inner layer: internal membrane of the wall usually acting as a framework for the vesicle (Figs. 1, 2).

28) laciniated: deeply indented borders of a carina (e.g., *Pogonochitina spinifera* in Paris, 1996, pl. 1, fig. 9).

29) linear chain: straight, curved, or coiled catenary structure where the apertural pole of one vesicle is fixed to the base of the following one; the aperture is not free (see above).

30) linkage structures: elements intervening in the connection of two successive vesicles in a catenary structure (e.g., operculum, apical structures, lips, base).

31) lip: distal part of the collarette (or of the neck), surrounding the aperture.

32) margin (=basal edge sensu Laufeld, 1974): transition zone between the base and the flanks; may be inconspicuous, rounded, blunt or sharp. The margin bears the major morphologic elements (e.g., carina, processes).

33) mucron: thickened, raised rim surrounding the apical pit (e.g., see Laufeld, 1974, fig. 29D).

34) meshlike: spiny ornamentation making up a net-work or a trellis-work on the surface of the wall (Fig. 2.9) (e.g., *Acanthochitina barbata* in Nõlvak and Grahn, 1993, pl. 4, fig. A, or *Muscochitina muscosa* in Paris, 1981, pl. 30, figs.17–19).

35) neck (=apertural tube): tubular structure expanding aperturalward from the chamber; frequently terminated by a collarette.

36) operculum: disklike plug sealing the aperture of the vesicles lacking a neck (see Paris and Nõlvak, in press, pl. 1, fig. 2); a membranous expansion flaring antiaperturalward ("rica" sensu Bockelie, 1981) is common (e.g., see Paris, 1996, pl. 1, fig. 4).

37) ornamentation: includes all the spiny, hairlike or linear expansions (e.g., crests) of the outer layer (Fig. 2.6–11).

38) outer layer: external membrane forming the vesicle wall together with the inner layer; the vesicle ornaments (carina, processes, spiny ornamentation) arise from evaginations of this outer layer (Figs. 1, 2), which may also be glabrous (Fig. 2.1–5).

39) peduncle: solid short (e.g., *Margachitina catenaria* in Paris and Grahn, 1996, fig. 2) or elongated cylindrical structure extending from the apex (e.g., *Urochitina simplex* in Paris, 1996, pl. 3, fig. 12).

40) perforated: refers to closely distributed holes occurring on the carina (e.g., *Sagenachitina oblonga* in Paris, 1981, pl. 9, fig. 8) or on the collarette (e.g., *Fungochitina fenestrata* in Paris, 1996, pl. 1, fig. 1); the ultimate stage is the reticulate pattern when holes are only separated by threadlike remains (e.g., *Parisochitina perforata* in Paris, 1996, pl. 3, fig. 2).

41) processes (=appendices): simple or complex spines (e.g., *Ancyrochitina desmea* in Paris, 1996, pl. 2, fig. 6) arranged in a crown on the margin, or near the margin in the case of an ovoid to claviform chamber; the processes are usually hollow but may have a cell-like structure (e.g., *Plectochitina*); they may be short or very long (see Wood and Miller, 1991, pl. 1, figs. 1–5). (N.B. the processes never communicate with the interior of the chamber).

42) prosome: internal plug situated at the base of the neck; may be simple (disklike) or complex (tubular structure with several or numerous horizontal septa, i.e., "accordion pleated prosome" of previous authors; see Miller, 1996, pl. 4, fig. 8); it is not involved in vesicle linkage.

43) reticulum: reticulated outer layer strongly attached to the flanks; may extend beyond the base of the vesicle as a perforated carina (e.g., *Parisochitina perforata* in Paris, 1996, pl. 2, fig. 2); reticulum bearing vesicles are regarded as glabrous.

44) rib: annular (horizontal) thickening of the wall (e.g., *Margachitina catenaria* in Paris and Grahn, 1996, pl. 3, fig. 2).

45) rica: membranous, flanging part of the prosome or operculum, lining the upper part of the chamber (see Miller, 1996, pl. 2, fig. 4).

46) ridge: vertical linear thickening of the wall (e.g., *Laufeldochitina stentor* in Grahn et al., 1996, pl. 2, fig. 6).

47) scar: circular mark (depressed or slightly protruding) corresponding either to a thinning or to a thickening at the apex (see Grahn et al., 1996, pl. 1, figs.1, 10); may also exist on the center of the operculum (see Paris and Nõlvak, in press, pl. 1, fig. 2).

48) septa: horizontal membranous partition (from a few to more than 20) within a prosome (see Laufeld, 1974, fig. 72B; Miller, 1996, pl. 2, fig. 4 and pl. 4, fig. 8).

49) sheathing process: process whose proximal end extends horizontally from the margin (e.g., *Salopochitina monterrosae*; see Tekbali and Wood, 1991, pl. 19, figs. 4–5).

50) shoulder: convex area at the top of the flanks, just below the flexure; when both shoulder and flexure are present, the upper part of the chamber has a sigmoid profile (Fig.1).

51) sleeve: partially or totally attached membrane (usually the outer layer) covering the vesicle and extending beyond the base (see Achab et al., 1993, pl. 2, figs. 2–6).

52) spines: all kinds of simple to complex elongate expansions of the outer layer (see below); spine length must be at least twice their width and exceed two microns; most frequently hollow (Fig. 2.6–10). (N.B. the hollow spines never communicate with the interior of the vesicle).

53) spiny ornamentation: vesicle bearing spines, crests, and/or processes randomly distributed or arranged in rows or crowns (see below for additional information).

54) vesicle: basic chitinozoan individual, including the wall of the chamber and the neck (and collarette when present) as well as the apertural plug (Fig. 1).

55) wall (=test): organic envelope of a chitinozoan; includes both the outer and inner layer.

Shape of the chamber.—The following characteristics (Fig. 3) concern only vesicles in full relief. In flattened specimens the collapse of the vesicle is usually perpendicular to the equatorial plane for lenticular and spherical chamber without a neck. It will be parallel to the axis for all the other cases. The collarette is not taken into account when defining the shape of the chamber.

1) lenticular: width significantly larger than length ($D > L$); margin rounded; base convex (e.g., *Calpichitina, Fungochitina*).

2) spherical: width of the chamber equal or close to its length ($D = {\sim}L$); margin inconspicuous; base rounded (or exceptionally evaginated such as in *Margachitina elegans*); shoulder present (e.g., *Hoegisphaera, Sphaerochitina*).

3) hemispherical: length close to half the diameter ($L = D/2$); base flat; margin sharp or blunt; shoulder conspicuous (e.g., *Bulbochitina, Cyathochitina*).

4) ovoid: length of the chamber greater than its diameter but less than three times this diameter ($3D > L > D$); margin and

flexure inconspicuous; base convex to rounded (e.g., *Desmochitina, Angochitina*), more rarely truncated (e.g., *Lagenochitina dalbyensis*) or ogival (e.g., *Lagenochitina conifundus*).

5) claviform: the chamber length exceeds three times the maximum diameter (L > 3D), base rounded; margin inconspicuous; shoulder absent (e.g., *Clavachitina, Laufeldochitina*).

6) conical: straight, tapering flanks; base flat; margin sharp or blunt (e.g., *Bursachitina, Euconochitina, Cyathochitina*).

7) cylindrical: length usually several times the diameter; flanks straight and parallel; base flat; margin sharp or blunt (e.g., *Rhabdochitina*).

Vesicle characteristics.—The vesicle surface may be glabrous or spiny; it may also bear a carina or an apical structure. All combinations of these patterns may exist, with the exception of both glabrous and spiny surfaces together.

1) Surface pattern of the wall (Fig. 2; see also Grahn et al., 1996, pl. 1, figs. 1–11, and pl. 2, figs.1–3, 5–6, 9–10): this pattern includes both totally smooth surfaces (Fig. 2.1) as well as scabrate, vermiculate (Fig. 2.1), foveolate (Fig. 2.2), feltlike (Fig.2.3), spongy (Fig. 2.4), or microgranulous surfaces, including tubercles and cones (Fig. 2.5). When these granules are less than two microns high, the wall surface is regarded as glabrous. A glabrous surface may or may not be associated with a carina or with apical structures. Corrugations (e.g., *Armoricochitina reticulifera* in Nõlvak and Grahn, 1993, pl. 3, fig. c) as well as ridges (e.g., *Laufeldochitina stentor* in Nõlvak and Grahn, 1993, pl. 1, fig. G) or ribs (e.g., *Margachitina catenaria* in Paris et al., 1996, pl. 3, figs. 1–2) may occur on glabrous surfaces.

2) Spiny ornamentation (Fig. 2.6–11): this ornamentation includes all kinds of spiny extensions longer than two microns, occurring on the vesicle, i.e., simple (Fig. 2.6), bifurcated or branching spines (Fig. 2.7), bi- or multirooted spines (Fig.2.8), anastomosed spines (Fig. 2.10) or those connected by a meshlike structure (Fig. 2.9), spines in rows (Fig. 2.10), crowns or crests (Fig. 2.11), or randomly distributed on part or all of the vesicle. The spiny ornament, which is usually hollow, may coexist with any of the other elements (i.e., carina, apical structures) with the exception of a glabrous surface. It is of prime importance to distinguish eroded spines (rounded scars) from a truly glabrous surface.

When located on the margin, the spines arranged into a crown are called processes. They display the same range of complexity as the spines occurring on the flanks; in addition they may have a spongy or a cell-like texture (e.g., *Plectochitina*).

External structures.—These include the carina, the apical structures, and the sleeve.

1) Carina: this corresponds to an extension (annular evagination) of the outer layer, perpendicular or not to the axis of the vesicle; the carina may be located either below, on, or above the margin; it may be fairly thick (e.g., *Laufeldochitina*), membranous (e.g., *Cyathochitina kuckersiana, Pterochitina perivelata*), extending horizontally (e.g., *Cyathochitina vaurealensis*), or flaring antiaperturalward (e.g., *Laufeldochitina*). The carina may also be complete (Fig. 2.12) (e.g., *Cyathochitina*), perforated, reticulated (Fig. 2.12) (e.g., *Sagenachitina, Baltochitina*) or laciniated (e.g., *Pogonochitina spinifera* in Paris, 1996, pl. 1, fig. 9). The carina may be associated either with a glabrous or spiny wall and/or apical structures.

A carina does not coexist with processes (homologous elements); however, the threadlike expansions extending from insertion zones partially enveloping the margin of some taxa (e.g., "*Conochitina filifera*" in Tekbali and Wood, 1991, pl. 19, figs.1, 4–6) are regarded here as the ultimate case of processes (i.e., sheathing processes).

2) Apical structures: they include the scar, callus, mucron, copula and peduncle (see definitions above); they usually serve as a linkage medium with the operculum of the preceding vesicle. The bulb is also considered as an apical element, but it is not clearly involved in intervesicle linkage.

3) Sleeve: this corresponds to a partially or totally unstuck outer layer that may extend beyond the margin and even far beyond the base of the vesicle (e.g., *Pellichitina, Cutichitina, Velatachitina* in Achab et al., 1993, pl. 2, figs; 2, 4, 6). This term is not extended to various types of vertical folding (e.g., *Calpichitina velata* in Paris and Grahn, 1996, pl. 1, figs. 7, 9) or to irregular detachment of the outer layer (e.g., *Desmochitina juglandiformis* in Paris, 1981, pl. 17, figs. 16–17). Significant flattening of the vesicle may be responsible for a secondary detachment of this outer layer mirroring a sleeve (especially in the Desmochitinidae).

PRINCIPLE AND METHODOLOGY

Since the first description of chitinozoans by Eisenack (1931), two systems have prevailed in the classification of these organic microfossils. One involves the suprageneric subdivisions first introduced by Eisenack (1931) and subsequently improved by this author (1968, 1972). This classification was adopted, and in some cases further developed by other authors (Van Oyen and Calandra, 1963; Jansonius, 1964, 1967, 1970; Tappan, 1966; Taugourdeau, 1966, 1981; Paris, 1981; Schallreuter, 1981; Achab et al., 1993; Nestor, 1994; Paris and Grahn, 1996; Miller, 1996). The chitinozoan group was there by progressively subdivided into Orders, Families, and even into Subfamilies (see Paris, 1981; Achab et al., 1993; Miller, 1996).

The second system involves an alphabetical listing of genera. It was principally advocated by Laufeld (1967, 1974) and Jenkins (1970b). Many supporters of this simpler method argued that the affinities and the biologic significance of the chitinozoans were too poorly known to justify any classification. In reality, when grouping several species within a genus on morphological grounds, a paleontologist has already started to classify these taxa. Despite the fact that alphabetic sorting has been widely used by numerous authors, it proves to be of no help for taxonomic purposes. The only positive aspect of alphabetic classification is to facilitate a rapid search and location of genera within a long list of taxa.

Utility of a classification for chitinozoans.—Chitinozoan workers have unanimously adopted the Linnean binominal taxonomy, grouping species into genera, and therefore have already initiated a classification at a higher rank than the basic biological entity, i.e., the species. Consequently we see no serious reasons to dismiss a suprageneric classification of the chitinozoans. In addition, we believe that a formal classification, including suprageneric subdivisions, may enhance the knowledge and study of the chitinozoans for the following reasons:

1) It encourages chitinozoan workers to adopt a logical taxonomic approach, based on careful morphological analysis, rather than on a superficial survey of the general outline of the taxon.

2) It promotes a clearly defined hierarchy of morphological characters used in the chitinozoan identification, consequently preventing overlap of generic diagnoses.

3) It provides a level of identification compatible with the state of preservation of the material, while still remaining informative for broad stratigraphical purposes.

4) It gives a framework for cladistic analysis.

5) It gives a better ground for phylogenetic analysis, even if such approaches are still very tentative in an enigmatic group such as the Chitinozoa.

6) It prevents redundancy in generic diagnosis because it requires direct reference to family or subfamily characteristics.

7) A suprageneric classification also provides an excellent

framework for a computer-assisted system of identification, involving large and very informative chitinozoan databases which may include digitalized photos (Paris and Bernard, 1994).

The most common argument against suprageneric classification is the poor knowledge of the biological significance of the chitinozoans. We, however, are less pessimistic than the supporters of the alphabetic classification. Indeed, converging arguments have progressively emerged that convincingly support the hypothesis (first advocated by Koslowski, 1963) that chitinozoans represent eggs of soft-bodied marine metazoans (Paris, 1981; Paris and Nõlvak, in press), i.e., of the "chitinozoophorans" sensu Grahn (1981). This explanation, however, is not yet unanimously accepted, and other diverse hypotheses (see discussion in Miller, 1996) have been proposed, e.g., a possible relationship with cysts of tintinids (Reid and John, 1981), fungi theory (Locquin, 1976), or rhizopod affinities (e.g., Cashman, 1990). Because the two latter hypotheses are based either on unreliable arguments or on obvious misinterpretations of chitinozoan morphology, they are not considered here. Nevertheless, regardless of the affinities or the biological significance of chitinozoans, these microfossils are in any case related to fossil organisms. The morphology of the chitinozoans is certainly genetically controlled, as demonstrated by the occurrence of populations, that are statistically homogenous during time intervals ranging from several hundred thousand to a few million years. These populations display diagnostic morphologies, indicating that they belong to the same species. Because the time intervals involved exceed the usual duration of the life of any individual by numerous orders of magnitude, they clearly represent numerous successive generations of individuals. The stability of their morphology through time is controlled by genetic mixing (i.e., interfecundity of the organisms producing each "species" of chitinozoans) that was efficient enough to prevent speciation processes for periods of time corresponding to the total-range of the involved species. In addition, the existence of evolutionary processes is unquestionably demonstrated by the short range of many chitinozoans species, making the group an outstanding biostratigraphic tool. Therefore, we are convinced that the morphology of chitinozoans reflects evolutionary processes just as in any complete organism, even if the tempo might be slightly different. Consequently, the usual rules, especially those of classification used for "around" true organisms, should also be applied to the chitinozoans.

Sorting of the available morphologic characters.—In order to select the most suitable characters for generic and suprageneric classification of the chitinozoans, we list the criteria used by previous authors for the definition of the 143 previously published chitinozoan genera. We eliminated from this general survey the redundant characters, i.e., those which correspond with fragmentary or dissociated descriptors of a single morphologic feature (e.g., "rounded base," "rounded flanks," and "rounded margin" for a spherical chamber). We excluded dubious elements or features obviously related to misinterpretation or to artifacts of preservation (e.g., crystal casts, folding of the vesicle wall). After this preliminary sorting we ran a number of statistical analyses on the remaining data set in order to control the "weight" of each character and to identify the most definitive criteria. The ultimate aims were to detect morphological features that allow the separation of all genera by at least one character and can be used to cluster large groups of genera (e.g., subfamilies, families, and order).

We utilized different techniques and software for simple statistical analyses (histograms), multivariate analysis [e.g., Factorial Analysis of Correspondence (FAC), Ascendant Hierarchic Classification (AHC)], or cladistic approach. These sorting techniques were employed in order to identify both the morphologic characters shared by the greatest number of genera and those restricted to a single genus (Fig. 4). A general database was set up as a table of the morphologic characters regarded as the "variables" and reported in columns. In all calculations, genera were referred to as "individuals" and reported on rows.

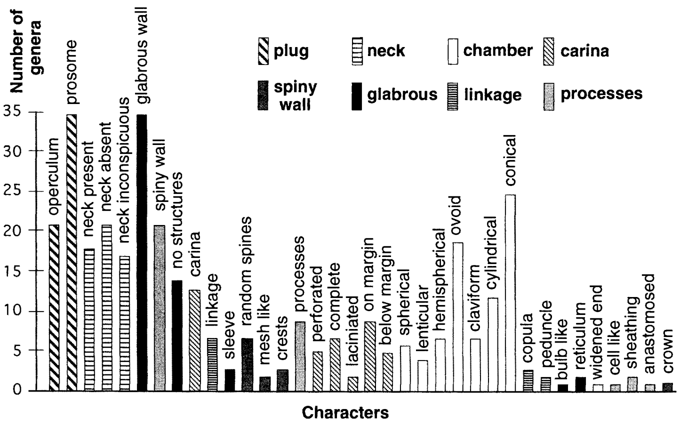

FIGURE *4*—Histogram of frequency of the characters recorded in the 56 selected chitinozoan genera.

A better approach would have been to apply these sorting procedures to all known chitinozoan species and subspecies; however this was not undertaken because too many species are poorly described.

Weight of the different morphologic characters.—The morphologic characters we selected were generally of the same "weight" for each calculation when they were taken separately; all were of Boolean type (i.e., on the general table they are quoted by "1" if present, and by "0" if absent). However, some criteria were directly subordinate to the presence of another, which was therefore considered to be of a higher magnitude, e.g., the characteristics "spines in rows" or "spine in crown" (second order characters) were subordinate to the existence of a "spiny wall" (first order character). Similarly, the criterion "anastomosed" (third order character) was subordinate to the existence of "processes", themselves depending on the existence of a "spiny wall". For taxa sharing this feature, the ornamentation of the surface of the vesicle had a "higher weight" (three levels of answers) than the character "glabrous" shared by other taxa (only one level of answer). Other characters were totally dependent on each other, e.g., "operculum" and "neck absent". Criteria related to the shape of the chamber, e.g., "cylindrical," "claviform", and to a lesser extent "conical", were closely tied (see Fig. 6) to the character "neck inconspicuous" because in this type of chamber, neither the flexure nor the shoulder were well distinct enough to indicate precisely the position of the boundary between the chamber and the neck.

Some discrepancies may have been introduced by a few features satisfying several states. This concerned exclusively the shape of the chamber and results both from some old definitions (not conforming with the sorting procedure adopted here) and from the existence of intrageneric, and even intraspecific variations of this parameter. Therefore, several genera may have included up to three states for the "shape of the chamber" (e.g., "lenticular," "conical," and "ovoid" for *Ancyrochitina*). These multiple answers influence the results of the multivariate analysis (Fig. 6).

Frequency histogram.—The histogram (Fig. 4) of all of the 36 characters finally selected reveals that only 5 variables are restricted to only one genus ("widened base" in *Pistillachitina*; "bulblike ampoule" in *Siphonochitina*; "cell-like processes" in

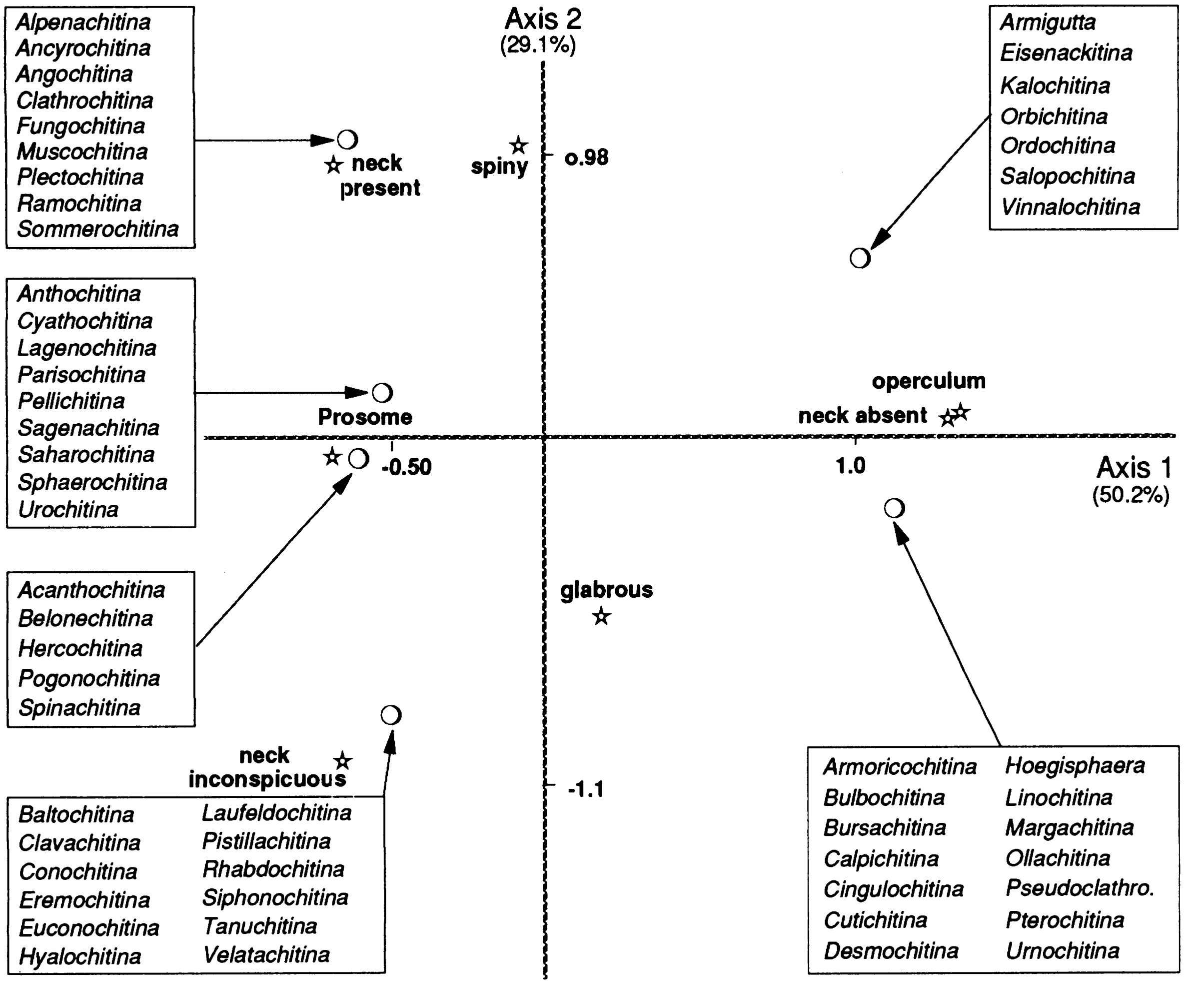

FIGURE 5—Factorial Analysis of Correspondence (FAC) of the chitinozoan genera (open circles) and of seven character states (open stars) of the apertural plug, neck, and wall surface.

Plectochitina; "anastomosed hollow processes" in *Clathrochitina*; and "crown of spines on the shoulder" in *Alpenachitina*). In contrast, 12 variables among the 36 selected are present in at least 10 genera, and two of them ("prosome" and "glabrous wall") are shared by 35 genera among the 56 accepted herein. In the construction of this diagram (Fig. 4) we dissociated some morphologic elements into their two mutually exclusive characteristics. The apertural plug was therefore divided into "operculum" and "prosome", while the wall surface was defined by its two exclusive states "glabrous" and "spiny wall". In both cases, the sum of the positive ("1") and negative ("0") answers is 56, i.e., the total number of accepted chitinozoan genera. In some other cases (e.g., the chamber shape) the sum of the dissociated answers (i.e., "spherical," "lenticular," "hemispherical," "ovoid," "claviform," "cylindrical," and "conical") is much greater than the total number of the selected genera, because some of them have several states (see above).

Multivariate analysis.—We used the multivariate analysis programs ANALMUL program for Factorial Analysis of Correspondence (FAC) on Macintosh (Febvay and Bonnot, 1991), and STAT ITCF program for the construction of Ascendant Hierarchic Classification (AHC using Euclidean distances). We ran these successively with different combinations involving some, or all, of the characters quoted in the 56 selected genera in order to distinguish the most diagnostic and discriminating characters. Our ultimate goal was to detect morphological features that would allow us to separate all of the selected genera by at least one character.

Based on the Factorial Analysis of Correspondence (FAC) diagrams, we tested different combinations of characters (Figs. 5–7). Some are totally independent from each other (e.g., neck differentiation/ornamentation, chamber shape/occurrence of a carina). On the other hand, the FAC diagram of the variables dealing with the apertural plug, the neck differentiation, and the shape of the chamber indicates clear relationships between these variables (Fig. 6).

The most discriminate combination involves only four characters, i.e., "operculum," "neck present," "neck inconspicuous," and "spiny wall". It yields a perfect clustering of the genera into six groups with 43.7 percent of the variance explained by the first axis and 40.9 percent by the second axis. It is worth noting that a similar clustering is obtained when using characters complementary to those chosen for this combination (the answer "operculum present" is identical to "prosome absent" and the lack of a "spiny wall" implicates a "glabrous wall"). Consequently, the introduction of all the variables describing the first order characters (apertural plug, characteristics of the neck, surface of the vesicle wall) does not improve the distinctiveness of the clusters. In the corresponding FAC, using seven variables, the main axis explains 50.2 percent of the variance whereas the second axis explains only 29.1 percent of this variance (Fig. 5).

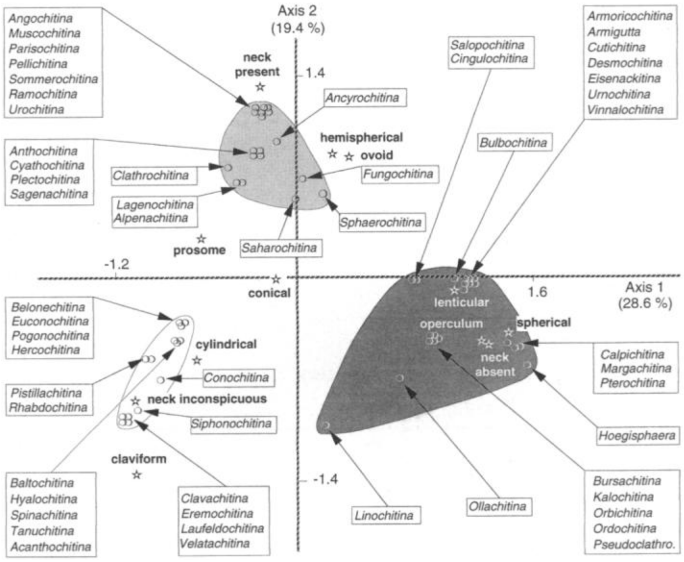

FIGURE 6—Factorial Analysis of Correspondence (FAC) of the chitinozoan genera (open circles) and of the characteristics of the apertural plug, neck, and chamber shape (12 variables) (open stars). Dark grey = Desmochitinidae; light grey = Lagenochitinidae; open = Conochitinidae.

When we replaced the characters describing the wall surface (i.e., "spiny wall" and "glabrous") with different chamber shapes, the clusters were poorly defined, but all genera may be referred to one of the three groups distinguished on the diagram (Fig. 6). The "lenticular" and the "spherical" chambers are closely tied with the characters "neck absent/operculum," while the "claviform" and "cylindrical" chamber shape (and to a lesser extent "conical") are well related to the characteristic "neck inconspicuous". In this FAC, the weight of each axis is fairly reduced (28.6 percent for axis 1, 19.4 percent for axis 2; the first seven axes explain 92.8 percent of the variance).

The FAC performed using all 36 variables (dissociated characters) and all 56 individuals (genera) does not show any well-defined clusters (Fig. 7). An important point is that all the genera are clearly separated from each other. This means that the morphologic criteria selected are distinctive enough to prevent the occurrence of synonyms (total overlapping). The clustering of the taxa from the same subfamily is not totally satisfactory, as a slight overlap occurs in some circumstances (Fig. 7). This is due mainly to the "dilution effect" introduced by the greater number of low rank criteria (second or third order characters) with respect to the first order ones. For that reason, we retained all complementary characters of the first order.

The Hierarchic Ascendant Classification (HAC), using Euclidean distances does not itself provide totally distinct clusters at the suprageneric level. A partial mixing of the Lagenochitinidae and the Conochitinidae was observed in different tests, and as in the FAC, can be explained by the excessive "weight" of the second and third order characters with regard to the first order ones. A more satisfactory HAC is obtained at a suprageneric level when using only first and second order criteria (Fig. 8), even if the Conochitinidae and the Lagenochitinidae are not completely separated because of the higher "weight" of the ornamentation ("spiny wall" and "processes") with regard to the differentiation of the neck. The subfamilies, however, are perfectly clustered, with the exception of *Cingulochitina* (this genus shares both Pterochitininae and Margachitininae characteristics).

Innovations through time.—In order to evaluate the tempo of the morphological changes of the chitinozoan vesicle through time, we plotted the first occurrence of successive major innovations recorded from the appearance of the group in the Tremadoc to its extinction in the topmost Famennian (Fig. 9.1–2). These innovations should provide the best support for establishing tentative phylogenetic trees. However, we have noted that the appearance of some peculiar characteristics may occur at different times in different families, e.g., the carina is present as early as middle Arenig in the Conochitinidae (e.g., *Tanuchitina*) and the Lagenochitinidae (e.g., *Cyathochitina*), whereas it is reported for the first time in the late Abereiddian in the Desmochitininae (e.g., *Pterochitina retracta*). Similar observations have also been made of the first occurrence of processes (of whatever type), which appeared during the Caradoc in the Conochitinidae (e.g., *Spinachitina*) and the Lagenochitinidae (e.g., *Ancyrochitina*) but not before the late Llandovery for the Desmochitinidae (e.g., *Salopochitina*), if we exclude the single individual representing *Armigutta* in the Middle Ordovician of Sweden (see Schallreuter, 1981). Depending on the families, second order features such as crests or meshlike ornaments also display a clear diachronism in their first appearance. It must be stressed that the order of appearance of innovations during the Ordovician (earlier in the Lagenochitinidae and in the Conochitinidae than in the Desmochitinidae) was inverted after the global crisis that affected the chitinozoan group (see Grahn, 1988; Paris, 1989) at the Ordovician–Silurian boundary.

Another important observation is the diachronism between the first occurrence of some innovations through space, i.e., in well-separated tectonic plates (for the timing of the same innovations in northern Gondwana and in Baltica (Fig. 9.1–2). This diachronism suggests an allopatric pattern of speciation for some chitinozoan taxa.

One of the most fruitful approaches for separating a general character from a minor one involves tracing the evolution of each of the characters through time. When a morphologic feature displays no obvious changes from the appearance of the group until its extinction, it indicates that the character was not affected by evolutionary processes. Such a character is likely to be plesiomorphic. However, when a character facilitates a recognizable differentiation (demonstrates a marked sorting with only a few subdivisions) among the accepted genera, it may be regarded as a high rank criterion (e.g., Family or Subfamily level). In chitinozoans, the three categories of neck, or the differentiation of the apertural plug either as a prosome or as an operculum, may play such a role, because no other innovations within these characters have been recorded from their first occurrence in the Early Ordovician until the extinction of the group in the latest Devonian (Fig. 9). In addition, the surface of the vesicle wall, i.e., either a glabrous or a spiny wall, should be discriminating characters in suprageneric subdivisions. The "glabrous" wall is present in the first chitinozoans, and the character state "spiny" is first reported in chitinozoan taxa not older than the middle Arenig in Gondwana and Baltica regions (Fig. 9.1–2). Since these character states were still present until the latest Famennian when the group disappeared, they may be considered plesiomorphic features.

Cladistic approach.—The application of a cladistic approach to test the relationship between the different chitinozoan genera is justified by the assumption that changes in chitinozoan morphology reflect genetic changes in the genetic patrimony of the "chitinozoophorans" (i.e., the organisms producing the chitinozoan vesicles). The hypothesis we have adopted—chitinozoans are reproductive stages (eggs) of an extinct marine metazoan group(s)—is not in conflict with this statement. Indeed, extant birds or insects clearly demonstrate a correspondence between morphology and genetics because they can be readily

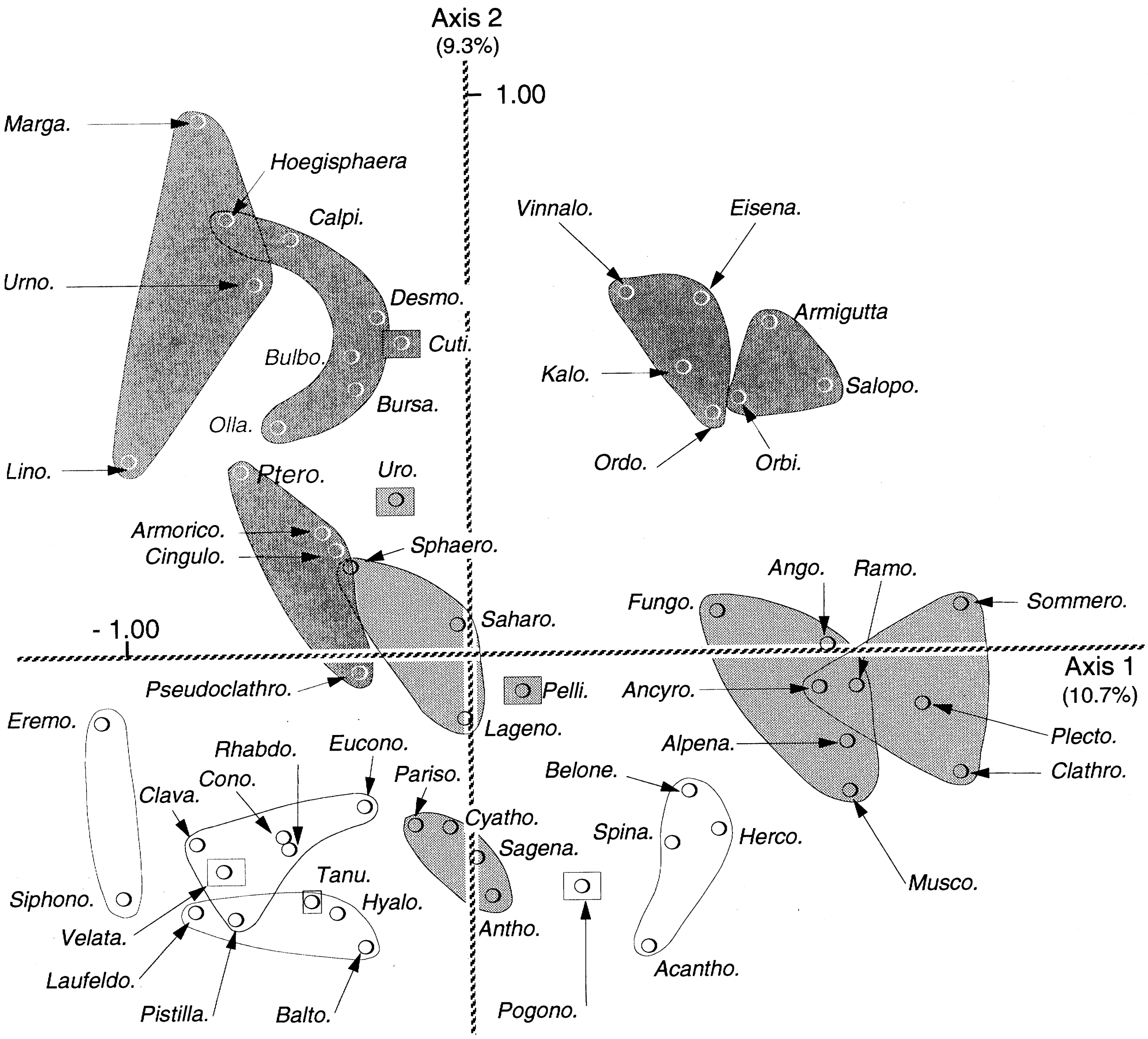

FIGURE 7—Factorial Analysis of Correspondence (FAC) of the chitinozoan genera (open circles) and of the 36 morphological variables of the vesicle. The subfamilies are surrounded. Dark grey = Desmochitinidae; light grey = Lagenochitinidae; open = Conochitinidae. Rectangles indicate monogeneric subfamilies.

identified to genus and sometimes even to species level, based exclusively on the external aspect of their eggs exclusively. Since the characteristics of the eggs of living metazoans can be used in generic identification, the morphology of the egg may be fairly strictly tied to the processes of speciation. Hence, the relationships existing between different metazoan genera should also be reflected by their eggs. Based on this argument, we have tried through a cladistic approach to depict the relationships between chitinozoan genera (Fig. 10). The application of the cladistic principle to the chitinozoans is relatively straightforward as long as the procedure is applied to taxa within the same family. However, difficulties arise when we attempt to include all the chitinozoan genera in a single cladogram. This is due to a diachronism of the appearance of apomorphic characters in several chitinozoan families.

Some apomorphic characters occur earlier in the Conochitinidae and the Lagenochitinidae than in the Desmochitinidae, at least up to the global faunal crisis at the Ordovician–Silurian boundary (see above). This is illustrated in northern Gondwana (Fig. 9.1) by the apomorphic character "carina below margin," which is already present in the middle Arenig in the Conochitinidae (e.g., *Tanuchitina*), whereas it appears for the first time in the late Abereiddian in the Desmochitinidae (e.g., *Armoricochitina*). Conversely, after the topmost Ordovician faunal event, the Desmochitinidae show the best potential of innovation, e.g., the apomorphic character "reticulum with perforated

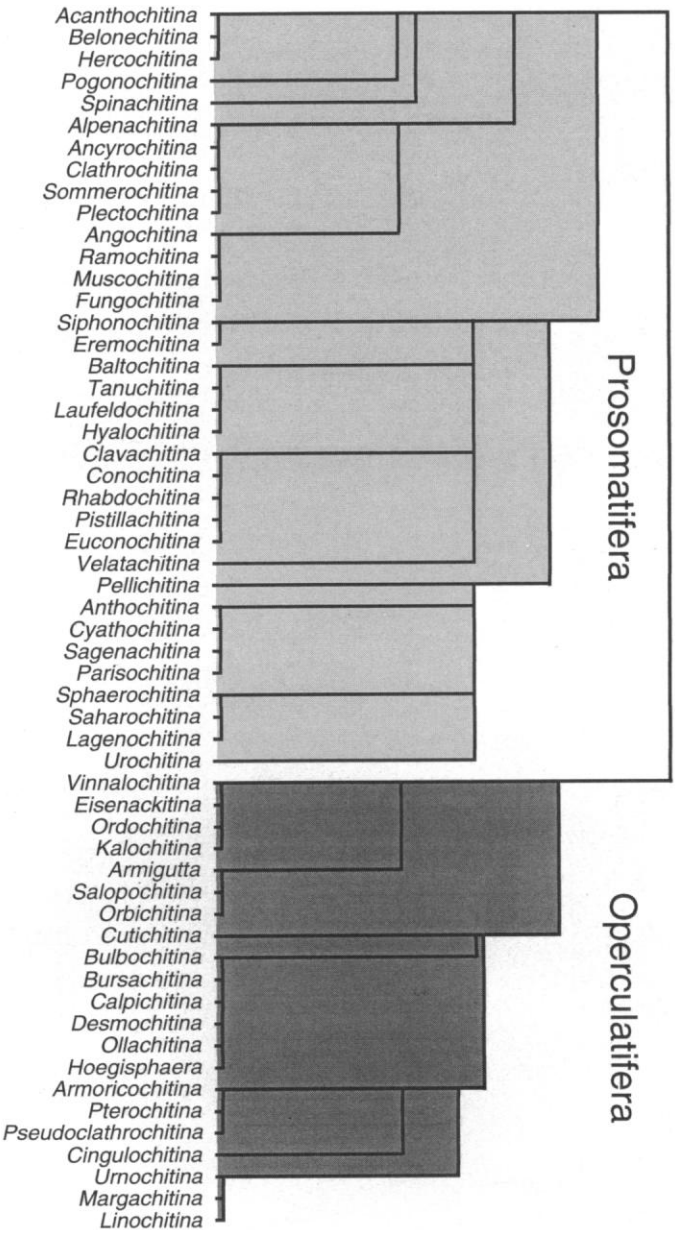

FIGURE 8—Hierarchic Ascendant Classification (HAC) using Euclidean distances for the 56 selected genera and the characteristics of the apertural plug, neck, surface pattern, and vesicle structures (12 states). Dark grey = Operculatifera; light grey = Prosomatifera.

expansion" occurs as early as the Wenlock (Al-Hajri and Paris, 1998) in the Desmochitinidae (e.g., *Pseudoclathrochitina*) but is not reported in the Lagenochitinidae before the late Givetian (e.g., *Parisochitina*). Similar observations are made for the apomorphic character "sheathing processes" which occur for the first time in *Salopochitina,* a Late Llandovery–Early Wenlock Desmochitinidae, but only in the late Frasnian–early Famennian for *Sommerochitina,* a genus belonging to the Lagenochitinidae.

This diachronism of some apomorphic characters leads to poorly resolved cladograms when all chitinozoan genera are analyzed together. This may be related to a possible polyphyletism of the Chitinozoa.

Hierarchy of the used criteria.—Mathematical treatments of all the morphological data, using either a simple histogram (Fig. 4) or more sophisticated multivariate analysis (Figs. 5–8), revealed which characters are shared by the greatest number of taxa. The highest subdivision is provided by the apertural plug, i.e., either a prosome or an operculum. Together with the chamber, aperture, neck and glabrous wall, the prosome was one of the very basic characteristics of a chitinozoan vesicle when the group appeared during the Tremadoc. The neck and the surface of the walls themselves showed modifications as early as those of the apertural plug (Fig. 8). However, for the stability of the nomenclature, as recommended by the International Code of Zoological Nomenclature, we prefer the preservation of the plesiomorphic characters "prosome" and "operculum" for the highest suprageneric subdivision of the group of the chitinozoans. The basic reason for this is because Eisenack (1972) had already used them, as the diagnostic elements of his widely accepted Prosomatifera and Operculatifera orders respectively. This scheme has been used for more than 20 years by almost all the chitinozoan workers who have accepted and used a suprageneric classification (see discussion in Paris, 1981; Achab et al., 1993), and there are no serious reasons to change it.

Other highly diagnostic features shared by several genera (see Figs. 5–6) are the various character states applied to the differentiation of the neck (i.e., "neck present," "neck absent," "neck inconspicuous"), the surface of the vesicle wall (i.e., "glabrous" and "spiny wall") and the shape of the chamber (i.e., "lenticular," "hemispherical," "spherical," "ovoid," "claviform," "conical," "cylindrical"). The most distinctive combinations of characters are those that relate neck differentiation to apertural plug. These combinations allow the division of the Chitinozoa into three main categories regarded here as families, i.e., the Conochitinidae, the Lagenochitinidae, and the Desmochitinidae (Fig. 11).

CLASSIFICATION OF THE ACCEPTED GENERA

Discussion.—In numerous publications, original generic diagnoses are too vague or introduce inconstancies in application of terminology. Consequently, under the heading "diagnosis", and in order to promote a more standardized terminology, we have indicated the discriminate character(s) (=diagnostic features) for each genus we accept.

The emended diagnoses proposed by Paris (1981, p. 110) respectively for the Desmochitinidae, the Conochitinidae and the Lagenochitinidae are strictly adopted here.

Age assignment of Ordovician taxa is given by reference to the recently modified British chronostratigraphy (Fortey et al., 1995).

SYSTEMATIC PALEONTOLOGY

Order PROSOMATIFERA Eisenack, 1972
Family CONOCHITINIDAE Eisenack, 1931 emend. Paris, 1981
Subfamily CONOCHITININAE Paris, 1981
Genus CLAVACHITINA Taugourdeau, 1966

Type species.—Rhabdochitina claviformis Taugourdeau, 1961. Holotype in Taugourdeau, 1961, p. 150, pl. 4, fig. 69, Avensac 101 borehole, 2051 m, Avensac Formation, Llandeilian, south-western France, collections of the Museum National d'Histoire Naturelle de Paris, France.

Diagnosis.—Conochitinidae with a glabrous claviform chamber and without mucron.

Occurrence.—Ordovician.

Genus CONOCHITINA Eisenack, 1931
emend. Paris, Grahn, Nestor, and Lakova

Type species.—Conochitina claviformis Eisenack, 1931. Lost holotype in Eisenack, 1931, p. 84, pl. 1, fig. 17, from erratic graptolitic rocks ("Graptolithengestein"); neotype: in Eisenack,

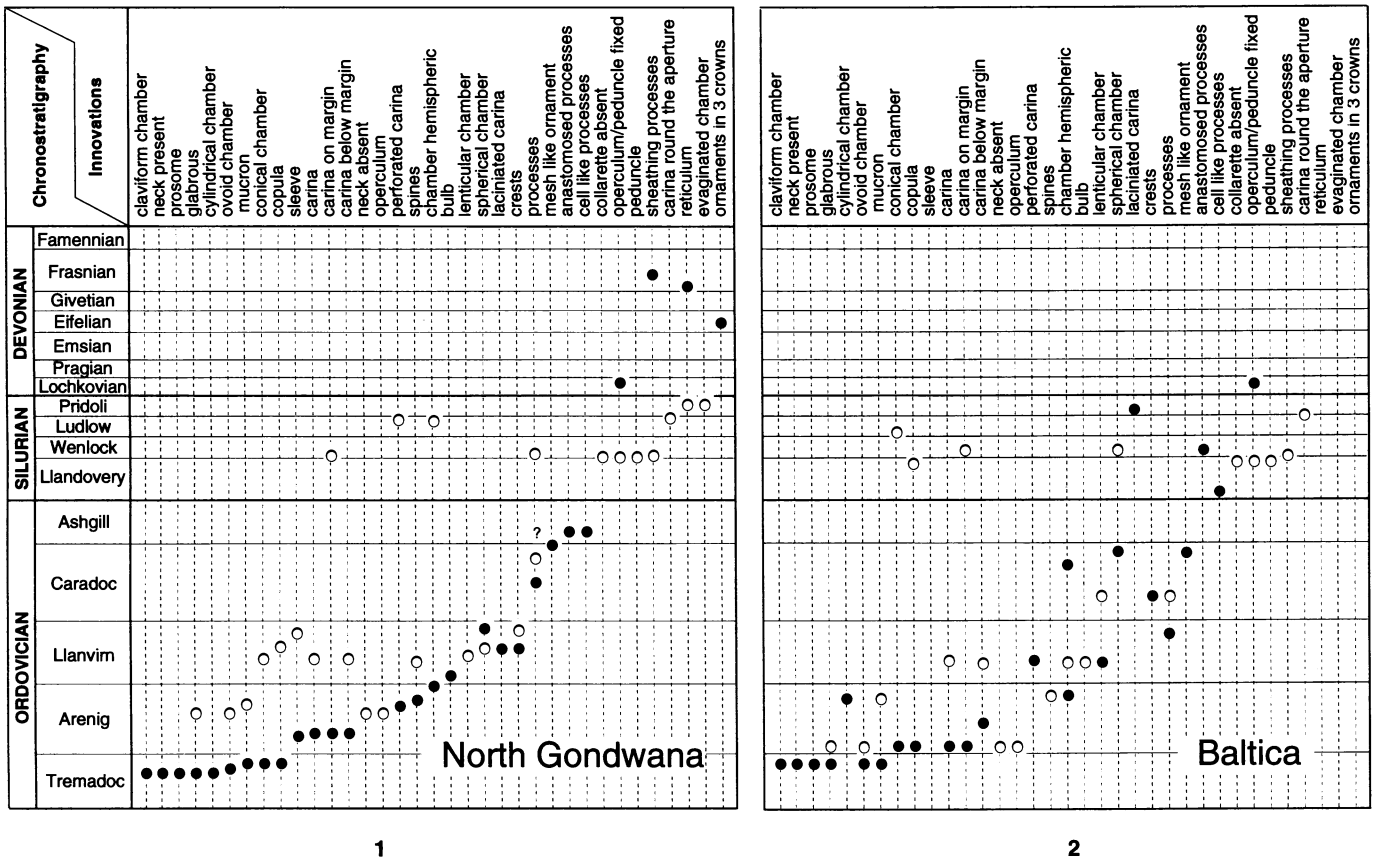

FIGURE 9—Innovations through time in the chitinozoans. Black circles = Prosomatifera; open circles = Operculatifera; *1,* northern Gondwana chitinozoans; *2,* chitinozoans from Baltica Plate.

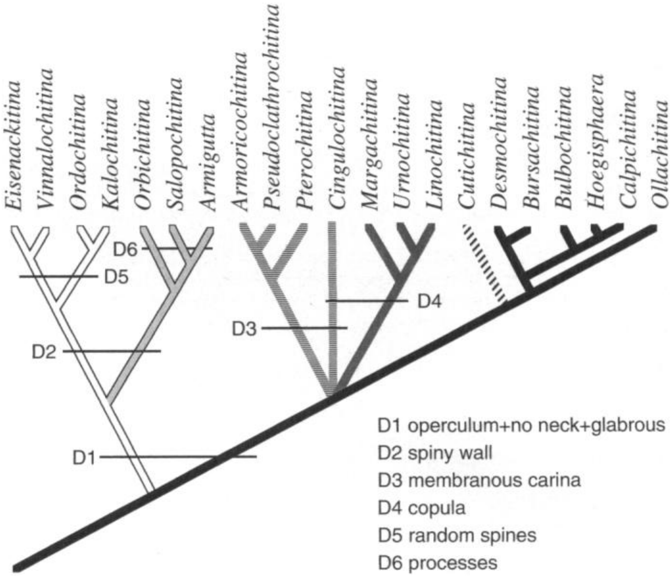

FIGURE *10*—Cladogram of the Desmochitinidae with the main synapomorphies. Black = Desmochitininae; oblique hatching = Cutichitininae; dark grey = Margachitininae; horizontal hatching = Pterochitininae; light grey = Orbichitininae; white =Eisenackitininae.

1968, p. 159, pl. 25, fig. 5, erratic graptolitic rocks, early Ludlow, collections of the Geologisch-Paläontologischen Institute der Universität, Tübingen, Germany.

Diagnosis.—Conochitinidae with a conical to claviform glabrous chamber provided with a mucron.

Occurrence.—Ordovician–Silurian.

Discussion.—Several authors (Eisenack, 1955b, p. 311; Taugourdeau, 1966, p. 35; Eisenack, 1968, p.158; Paris, 1981, p. 178) successively emended or restricted the definition of this genus. The present diagnosis is very close to the definition given by Paris, 1981.

Genus EUCONOCHITINA Taugourdeau, 1966
emend. Paris, Grahn, Nestor, and Lakova

Type species.—*Conochitina conulus* Eisenack, 1955b. Holotype in Eisenack, 1955b, p. 212, pl. 1, fig. 1, erratic, likely boundary beds between Lasnamägi and Uhaku stages (=middle part of the Llanvirn), Tallinn, Estonia, collections of the Senckenberg Museum, Frankfurt am Main, Germany.

Diagnosis.—Conochitinidae with a conical glabrous chamber and without mucron.

Occurrence.—Ordovician–Silurian.

Discussion.—The present diagnosis excludes the specimens with an ornamented vesicle.

Genus PISTILLACHITINA Taugourdeau, 1966

Type species.—*Rhabdochitina pistillifrons* Eisenack, 1939. Holotype in Eisenack, 1939, p. 145, pl. B, fig. 12, unknown

Order Plug	**Family** Neck differentiation	**Sub-family** Chamber surface	**Genera** Chamber shape and arrangement of ornamentation	
OPERCULATIFERA (operculum)	**DESMOCHITINIDAE** (no neck)	Desmochitininae (glabrous)	lenticular	*Calpichitina*
			spherical	*Hoegisphaera*
			hemispherical	*Bulbochitina*
			conical	*Bursachitina*
			ovoid	*Desmochitina*
			cylindrical	*Ollachitina*
		Cutichitininae (sleeve)	ovoid	*Cutichitina*
		Pterochitininae (carina)	lenticular to spherical	*Pterochitina*
			ovoid (below margin)	*Armoricochitina*
			conical (reticulum, perforated)	*Pseudoclathrochitina*
			conical to ovoid (on margin)	*Cingulochitina*
		Margachitininae (copula)	lenticular to spherical (peduncle)	*Margachitina*
			ovoid	*Urnochitina*
			claviform to cylindrical	*Linochitina*
		Eisenackitininae (spiny)	hemispherical	*Vinnalochitina*
			conical	*Kalochitina*
			conical (with crests)	*Ordochitina*
			ovoid	*Eisenackitina*
		Orbichitininae (processes)	conical	*Orbichitina*
			ovoid	*Armigutta*
			conical to ovoid (sheathing)	*Salopochitina*
PROSOMATIFERA (prosome)	**CONOCHITINIDAE** (flexure unconspicuous)	Conochitininae (glabrous)	conical	*Euconochitina*
			conical to claviform (with mucron)	*Conochitina*
			claviform	*Clavachitina*
			cylindrical (with widened base)	*Pistillachitina*
			cylindrical	*Rhabdochitina*
		Velatachitininae (sleeve)	claviform	*Velatachitina*
		Eremochitininae (copula)	claviform	*Eremochitina*
			claviform to cylindrical (bulb)	*Siphonochitina*
		Tanuchitininae (carina)	conical to cylindrical (on margin)	*Hyalochitina*
			claviform (below margin)	*Laufeldochitina*
			conical to cylindrical (perforated)	*Baltochitina*
			cylindrical (below margin)	*Tanuchitina*
		Pogonochitininae (carina/spiny)	conical (laciniated, on margin)	*Pogonochitina*
		Belonechitininae (spiny)	conical	*Belonechitina*
			conical to cylindrical (mesh-like)	*Acanthochitina*
			conical (with crests)	*Hercochitina*
		Spinachitininae (processes)	conical to cylindrical	*Spinachitina*
	LAGENOCHITINIDAE (flexure conspicuous)	Lagenochitininae (glabrous)	lenticular to conical	*Saharochitina*
			spherical	*Sphaerochitina*
			ovoid to cylindrical	*Lagenochitina*
		Cyathochitininae (carina)	conical to hemispherical (laciniated)	*Anthochitina*
			conical to hemispherical (perforated)	*Sagenachitina*
			conical to hemispherical (complete)	*Cyathochitina*
			ovoid (reticulum, perforated)	*Parisochitina*
		Pellichitininae (sleeve)	ovoid	*Pellichitina*
		Urochitininae (copula)	ovoid (peduncle)	*Urochitina*
		Angochitininae (spiny)	lenticular to conical	*Fungochitina*
			ovoid	*Angochitina*
			ovoid (mesh-like)	*Muscochitina*
			ovoid (with crests)	*Ramochitina*
		Ancyrochitininae (processes)	lenticular to conical	*Ancyrochitina*
			conical (anastomosed)	*Clathrochitina*
			conical to ovoid (cell-like)	*Plectochitina*
			ovoid to cylindrical (3 crowns)	*Alpenachitina*
			claviform (sheathing)	*Sommerochitina*

FIGURE *11*—Suprageneric and generic classification of the chitinozoans.

formation from the Rheinischen Schiefergebirges, Llanvirn–early Caradoc, Germany, collections of the Senckenberg Museum, Frankfurt am Main, Germany.

Diagnosis.—Conochitinidae with a glabrous cylindrical chamber ended by a lenticular to hemispherical widening.

Occurrence.—Middle-Upper Ordovician.

Discussion.—It must be stressed the transition between chamber and neck (position of the prosome) is within the tubular part of the vesicle.

Genus RHABDOCHITINA Eisenack, 1931

Type species.—Rhabdochitina magna Eisenack, 1931. Lost holotype in Eisenack, 1931, p. 90–91, pl. 3, fig. 18, erratic Baltic limestones ("Ostseekalk"); neotype in Eisenack, 1962, p. 292–293, pl. 14, fig. 1, erratic Baltic limestones, Ordovician, collections of the Geologisch-Paläontologischen Institute der Universität, Tübingen, Germany.

Diagnosis.—Conochitinidae with a glabrous elongated cylindrical vesicle.

Occurrence.—Ordovician.

Discussion.—Mucron may occur.

Subfamily EREMOCHITININAE Paris, 1981

Genus EREMOCHITINA Taugourdeau and de Jekhowsky, 1960

Type species.—Eremochitina baculata Taugourdeau and de Jekhowsky, 1960. Lost holotype in Taugourdeau and de Jekhowsky, 1960, p. 1228, pl. 8, fig. 107, Or-1 borehole, core sample from 2930 m, Arenig, Sahara, Algeria; neotype: in Taugourdeau, 1967, pl. 1, fig. 19, (DD. 52), same references as for the holotype, collections of the Museum National d'Histoire Naturelle de Paris, France.

Diagnosis.—Conochitinidae with claviform glabrous chamber with a tubular copula.

Occurrence.—Lower Ordovician.

Genus SIPHONOCHITINA Jenkins, 1967

Type species.—Siphonochitina formosa Jenkins, 1967. Holotype in Jenkins, 1967, p. 469–471, pl. 75, fig. 2, Shelve area, upper Hope Shale, early Abereiddian, Shropshire, England, S 17593, collections of the Centre for Palynological Studies, University of Sheffield, England.

Diagnosis.—Conochitinidae with a claviform to cylindrical chamber with a membranous bulb.

Occurrence.—Lower-Middle Ordovician.

Subfamily TANUCHITININAE Paris, 1981

Genus BALTOCHITINA Paris and Grahn new genus

Type species.—By original designation: *Baltochitina nolvaki* Paris and Grahn new species. Holotype: *Sagenachitina* sp. in Nõlvak and Grahn, 1993, pl. 5, figs. A and B, Rapla borehole, Vöo Formation, Lasnamägi Stage, late Abereiddian, south of Tallinn, Estonia; collections of the Institute of Geology, Estonian Academy of Sciences, Tallinn, Estonia.

Diagnosis.—Conochitinidae with a conical to cylindrical chamber with a perforated carina on the margin.

Etymology.—from Baltic, its type area.

Occurrence.—Middle Ordovician.

Discussion.—This genus differs from *Sagenachitina* Jenkins, 1970a and from *Parisochitina* Boumendjel, 1985, which have a well-defined neck.

BALTOCHITINA NOLVAKI Paris and Grahn new species

Sagenachitina sp. NÕLVAK AND GRAHN, 1993, pl. 5, figs. A and B

Diagnosis.—Conochitinidae with an elongate subcylindrical vesicle (ratio of vesicle length to chamber diameter >five), a smooth wall surface, straight lip, sharp margin bearing a carina turning reticulated distally and extending more or less perpendicular to the axis.

Description.—Long and slender chitinozoan (length of the holotype: 440 microns, chamber diameter: 60 microns) with a subcylindrical to slightly conical chamber; cylindrical neck ended with straight lips; chamber bottom flat; wall surface entirely smooth; perforated to reticulated carina erected on the margin; this fairly short membranous carina extends more or less perpendicularly to the flanks.

Etymology.—Dedicated to our colleague Jaak Nõlvak (Estonian Academy of Sciences, Tallinn, Estonia) for his outstanding investigations on Ordovician chitinozoans from the Baltic area.

Holotype.—fig. A, pl. 5 in Nõlvak and Grahn (1993), Ch. 1416/7631, collections of the Institute of Geology, Estonian Academy of Sciences, Tallinn, Estonia; late Abereiddian, Lasnamägi Stage, Vöo Formation, Rapla borehole (depth 179.2 m), south of Tallinn, Estonia.

Occurrence.—Late Abereiddian.

Discussion.—No other chitinozoan species has a subcylindrical vesicle and a reticulated carina.

Genus HYALOCHITINA Paris and Grahn new genus

Type species.—By original designation: *Cyathochitina hyalophrys* Eisenack, 1959. Holotype in Eisenack, 1959, p. 11–12, pl. 2, fig. 6, Cincinnati Group, Cincinnati, Ohio, late Maysvillian–early Richmondian (early Ashgill), collections of the Geologisch-Paläontologischen Institute der Universität, Tübingen, Germany.

Diagnosis.—Conochitinidae with a conical to cylindrical chamber provided with a complete membranous carina on the margin.

Occurrence.—Upper Ordovician.

Discussion.—This new genus is separated from *Tanuchitina* Jansonius, 1964, which has a carina below the margin, and from *Cyathochitina* Eisenack, 1955b emend. Paris, Grahn, Nestor, and Lakova herein, which has a conspicuous flexure.

Genus LAUFELDOCHITINA Paris, 1981

Type species.—Cyathochitina stentor Eisenack, 1937 (lost holotype in Eisenack, 1937, p. 221–222, pl. 15, fig. 2, grayish Ordovician limestones; neotype in Eisenack, 1962, p. 300, pl. 14, fig. 10, allochthonous Kukruse equivalents, Halde bei Metzingen, Würtemberg, Germany, collections of the Geologisch-Paläontologischen Institute der Universität, Tübingen, Germany).

Diagnosis.—Conochitinidae with a claviform, glabrous chamber and a complete, flaring membranous carina, below the margin.

Occurrence.—Ordovician.

Genus TANUCHITINA Jansonius, 1964
emend. Paris, Grahn, Nestor, and Lakova

Type species.—Tanuchitina ontariensis Jansonius, 1964. Holotype in Jansonius, 1964, p. 910–911, pl. 1, fig. 6, cuttings from Imperial-Calvan Anderson no. 9-6 borehole, depth 738 m (2,420 ft), Anderson Township, Essex County, Ontario, Canada, collections of Imperial Oil Limited, Calgary, Alberta, Canada.

Diagnosis.—Conochitinidae with a cylindrical chamber and a complete membranous carina below the margin.

Occurrence.—Ordovician–Silurian.

Discussion.—The conical forms with a carina on the margin are transferred into *Hyalochitina* Paris and Grahn, n. gen.

Subfamily VELATACHITININAE Achab, Asselin and Soufiane, 1993
Genus VELATACHITINA Poumot, 1968

Type species.—*Velatachitina nebulosa* Poumot, 1968. Holotype in Poumot, 1968, p. 50–51, pl. 1, fig. 9, borehole SN-1, core sample from 3,082–3,083 m (referred to "Llandeilo" by the author, but likely Abereiddian), Tunisia, CZ 244, collections of the Service Palynoplanctologique de la SNPA-Elf, France.

Diagnosis.—Conochitinidae with a claviform chamber enveloped within a membranous sleeve.

Occurrence.—Lower-Middle Ordovician.

Discussion.—The membranous sleeve may extend beyond the margin.

Subfamily BELONECHITININAE Paris, 1981
Genus ACANTHOCHITINA Eisenack, 1931

Type species.—*Acanthochitina barbata* Eisenack, 1931 (Lost holotype in Eisenack, 1931, p. 82–83, pl. 1, fig. 10, erratic limestone from the Baltic ["Ostseekalk"]; proposed neotype: in Nõlvak, 1980, pl. 29, fig. 1, Hullo borehole, 21.0 m, late Vormsi Stage (early Ashgill), Estonia, Ch. 701/5670, collections of the Institute of Geology of the Estonian Academy of Science, Tallinn, Estonia.

Diagnosis.—Conochitinidae with a conical to cylindrical chamber and raised meshlike ornamentation; may be surrounded with a membranous sleeve.

Occurrence.—Middle Ordovician (?)–Upper Ordovician.

Genus BELONECHITINA Jansonius, 1964

Type species.—*Conochitina micracantha* subsp. *robusta* Eisenack, 1959. Holotype in Eisenack 1959, p. 9–10, pl. 3, fig. 4, Koppelmann, Saku Member of the Wasalemma Formation, Oandu Stage, D3 (late Caradoc), Estonia, collections of the Senckenberg Museum, Frankfurt am Main, Germany.

Diagnosis.—Conochitinidae with a conical chamber and randomly distributed spines.

Occurrence.—Lower Ordovician–Silurian.

Genus HERCOCHITINA Jansonius, 1964

Type species.—*Hercochitina crickmayi* Jansonius, 1964. Holotype in Jansonius, 1964, p. 908–909, pl. 1, fig. 9, Gamache Princeton Lake 1 borehole, core sample from 210 m (690 ft.), Vauréal Formation, Ashgill, Anticosti Island, Canada; collections of Imperial Oil Limited, Calgary, Alberta, Canada.

Diagnosis.—Conochitinidae with a conical chamber and distinct crests (vertical rows of spiny or membranous ornamentation).

Occurrence.—Middle Ordovician–Upper Ordovician.

Subfamily POGONOCHITININAE new subfamily

Diagnosis.—Conochitinidae with a spiny ornamentation and a carina.

Genus POGONOCHITINA Taugourdeau, 1961

Type species.—*Pogonochitina simplex* Taugourdeau, 1961. Holotype in Taugourdeau, 1961, p. 148, pl. 4, fig. 59, Avensac 101 borehole, 1,902 m, Avensac Formation, Llandeilian, southwestern France, collections of the Museum National d'Histoire Naturelle de Paris, France. Representative specimen in Paris, 1996, pl. 1, fig. 9.

Diagnosis.—Conochitinidae with a spiny conical chamber and with a laciniated carina on the margin.

Occurrence.—Middle Ordovician–Silurian.

Subfamily SPINACHITININAE Paris, 1981
Genus SPINACHITINA Schallreuter, 1963
emend. Paris, Grahn, Nestor, and Lakova

Type species.—*Conochitina cervicornis* Eisenack, 1931. Lost holotype in Eisenack, 1931, p. 89, pl. 2, fig. 12, erratic calcareous sandy siltstones; proposed neotype: *Spinachitina cervicornis* in Nõlvak and Grahn, 1993, pl. 3, fig. A, Rapla borehole, core sample from 142.70 m, Kahula Formation, Keila Stage (early Caradoc), south of Tallinn, Estonia, collections of the Institute of Geology, Estonian Academy of Sciences, Tallinn, Estonia.

Diagnosis.—Conochitinidae with a conical to cylindrical chamber bearing a crown of processes.

Occurrence.—Upper Ordovician–Lower Silurian.

Discussion.—In addition to the emendation of Laufeld (1967), the genus is here restricted to forms without conspicuous flexure. *Coronochitina* Eisenack, 1965 is here regarded as a junior synonym of *Spinachitina*.

Family LAGENOCHITINIDAE Eisenack, 1931
emend. Paris, 1981
Subfamily LAGENOCHITININAE Paris, 1981
Genus LAGENOCHITINA Eisenack, 1931
emend. Paris, Grahn, Nestor, and Lakova

Type species.—*Lagenochitina baltica* Eisenack, 1931. Lost holotype in Eisenack, 1931, p. 80–81, pl. 1, fig. 1, erratic Ordovician Baltic limestones ("Ostseekalk"); neotype in Eisenack, 1959, p. 2, pl. 3, fig. 6, from Ordovician erratic limestones of the Baltic shore ("Ostseekalk"), collections of the Geologisch-Paläontologischen Institute der Universität, Tübingen, Germany.

Diagnosis.—Lagenochitinidae with an ovoid to cylindrical glabrous chamber.

Occurrence.—Lower Ordovician–Upper Devonian.

Discussion.—Forms with glabrous spherical chambers are transferred into *Sphaerochitina* Eisenack, 1955a, emend. Paris, Grahn, Nestor, and Lakova, herein.

Genus SAHAROCHITINA Paris and Grahn new genus

Type species.—By original designation: *Fungochitina*? *jaglini* Oulebsir and Paris, 1993. Holotype in Oulebsir and Paris, 1993, p. 274–279, pl. 4, fig. 1, Gd-1 bis borehole, north of Hassi Messaoud, north-eastern Sahara, Hassi Touareg Formation, Azzel Member, core sample at 4,033.50 m, late Abereiddian, IGR 60509 (R 41), collections of the Institut de Géologie de l'Université de Rennes, France.

Diagnosis.—Lagenochitinidae with a glabrous conical to lenticular chamber.

Occurrence.—Middle Ordovician–Silurian.

Discussion.—This genus differs from *Fungochitina* Taugourdeau, 1966 in being smooth and from *Pistillachitina* Taugourdeau, 1966, which displays a tubular chamber with an antiapertural widening.

Genus SPHAEROCHITINA Eisenack, 1955a
emend. Paris, Grahn, Nestor, and Lakova

Type species.—*Lagenochitina sphaerocephala* Eisenack, 1932. Lost holotype in Eisenack, 1932, p. 271, pl. 12, fig. 14, erratic *Beyrichia* Limestone ("Beyrichia-kalk"); neotype in Eisenack, 1955a, p. 162, pl. 1, fig. 6, erratic *Beyrichia* Limestone from the Baltic sea floor?, Pridoli, collections of the Senckenberg Museum, Frankfurt am Main, Germany.

Diagnosis.—Lagenochitinidae with a glabrous spherical chamber.

Occurrence.—Upper Ordovician–Devonian.

Discussion.—The spiny forms (spines exceeding two microns) as well as those with a conical or a lenticular chamber are here excluded from the genus.

Subfamily CYATHOCHITININAE Paris, 1981
Genus ANTHOCHITINA Eisenack, 1971

Type species.—*Anthochitina superba* Eisenack, 1971. Holotype in Eisenack, 1971, p. 452–454, fig. 1–1, erratic *Beyrichia* limestones from the Baltic bottom?, Pridoli(?), collections of the Geologisch-Paläontologischen Institute der Universität, Tübingen, Germany. Representative specimens in Wrona, 1980, pl. 26, figs. 1–9.

Diagnosis.—Lagenochitinidae with a conical to hemispherical chamber with a laciniated, spongy to cell-like carina.

Occurrence.—Upper Silurian–Lower Devonian.

Discussion.—Occasionally proximal perforations may exist.

Genus CYATHOCHITINA Eisenack, 1955b
emend. Paris, Grahn, Nestor, and Lakova

Type species.—*Conochitina campanulaeformis* Eisenack, 1931. Lost holotype in Eisenack, 1931, p. 86–87, pl. 2, fig. 2, erratic calcareous to sandy siltstone of Ordovician age; neotype: *Cyathochitina campanulaeformis* in Eisenack, 1962, p. 297–298, pl. 14, fig. 5, from Harku near Tallinn, likely lower Uhaku Stage (Llandeilian), Estonia, collections of the Senckenberg Museum, Frankfurt am Main, Germany.

Diagnosis.—Lagenochitinidae with a conical to hemispherical glabrous chamber and with a complete membranous carina on a sharp margin.

Discussion.—Conical species without a conspicuous flexure are transferred into *Hyalochitina* Paris and Grahn n. gen.

Occurrence.—Ordovician–lower Silurian (Llandovery).

Genus PARISOCHITINA Boumendjel, 1985

Type species.—*Parisochitina perforata* Boumendjel, 1985. Holotype in Boumendjel, 1985, p. 164–166, pl. 2, fig. 5, borehole Taouratine-3, 1,352 m, Gazelle Formation, late Devonian, Illizi Basin, south-eastern Sahara, Algeria, IGR 60319 (M 39), collections of the Institut de Géologie de l'Université de Rennes, France.

Diagnosis.—Lagenochitinidae with an ovoid chamber and with a reticulum extending beyond the base as a perforated carina.

Occurrence.—Upper Devonian.

Genus SAGENACHITINA Jenkins, 1970a

Type species.—*Clathrochitina oblonga* Benoît and Taugourdeau, 1961. Holotype in Benoît and Taugourdeau, 1961, p. 1406, pl. 1, fig. 1, Amg-1 borehole, 1,482 m, "Complexe argilo-gréseux supérieur" Formation, late Arenig, Sahara, Algeria, collections of the Museum National d'Histoire Naturelle de Paris, France.

Diagnosis.—Lagenochitinidae with a glabrous conical to hemispherical chamber and with a perforated or reticulated carina extending from the margin.

Occurrence.—Lower-Middle Ordovician.

Subfamily PELLICHITININAE Achab, Asselin and Soufiane, 1993
Genus PELLICHITINA Achab, Asselin and Soufiane, 1993

Type species.—*Desmochitina pellucida* Benoît and Taugourdeau, 1961. Holotype in Benoît and Taugourdeau, 1961, p. 1408–1409, pl. 4, fig. 37, Amg-1 borehole, core sample from 1,577 m, lower part of the Hamra Quartzite Formation, middle Arenig, Central Sahara, Algeria, collections of the Museum National d'Histoire Naturelle de Paris, France.

Diagnosis.—Lagenochitinidae with an ovoid chamber enveloped by a membranous sleeve.

Occurrence.—Lower-Middle Ordovician.

Subfamily UROCHITININAE Paris, 1981
Genus UROCHITINA Taugourdeau and de Jekhowsky, 1960

Type species.—*Urochitina simplex* Taugourdeau and de Jekhowsky, 1960. Holotype in Taugourdeau and de Jekhowsky, 1960, p. 1233, pl. 11, fig. 160, borehole Ge-1, core sample from 1,586 m, Oued Saret Formation, latest Lochkovian, Sahara, Algeria, collections of the Museum National d'Histoire Naturelle de Paris, France.

Diagnosis.—Lagenochitinidae with an ovoid chamber bearing a long solid peduncle.

Occurrence.—Lower-Middle Devonian.

Subfamily ANCYROCHITININAE Paris, 1981
Genus ALPENACHITINA Dunn and Miller, 1964

Type species.—*Alpenachitina eisenacki* Dunn and Miller, 1964. Holotype in Dunn and Miller, 1964, p. 725, pl. 119, fig. 1, Dock Street Clay Member, Alpena Limestone, Alpena, Michigan, USA, Middle Devonian, USNM collections 144880.

Diagnosis.—Lagenochitinidae with ovoid to cylindrical chamber and three distinct horizontal crowns of spiny ornamentation.

Occurrence.—Middle Devonian.

Genus ANCYROCHITINA Eisenack, 1955a

Type species.—*Conochitina ancyrea* Eisenack, 1931. Lost holotype in Eisenack, 1931, p. 88–89, pl. 4, fig. 4, erratic limestones of the Baltic ("Ostseekalk"); neotype: *Ancyrochitina ancyrea* in Eisenack, 1955a, p. 163–164, pl. 2, fig. 7, erratic *Beyrichia* limestones from the Baltic bottom?, Pridoli; collections of the Senckenberg Museum, Frankfurt am Main, Germany.

Diagnosis.—Lagenochitinidae with a lenticular to conical chamber bearing a crown of nonanastomosed hollow processes on the margin.

Occurrence.—Upper Ordovician–Upper Devonian.

Genus CLATHROCHITINA Eisenack, 1959

Type species.—*Clathrochitina clathrata* Eisenack, 1959. Holotype in Eisenack, 1959, p. 15 pl. 1, fig. 3, Dalhem canal, *Pentamerus gotlandicus* beds from south east Slite Marls, late Sheinwoodian, Wenlock, Gotland, Sweden, collections of the Geologisch-Paläontologischen Institute der Universität, Tübingen, Germany.

Diagnosis.—Lagenochitinidae with a conical chamber and a crown of anastomosed processes on the margin.

Occurrence.—Silurian.

Discussion.—In order to separate *Clathrochitina* from *Anthochitina,* the emendation proposed by Laufeld (1974) focusing on a membranous carina (cingulum) is not followed.

Genus PLECTOCHITINA Cramer, 1964

Type species.—*Plectochitina carminae* Cramer, 1964. Lost holotype in Cramer, 1964, p. 346–347, pl. 20, fig. 21, La Vid de Gordõn section, upper San Pedro Formation, Pridoli, northwestern Spain; neotype: *Plectochitina carminae* in Priewalder, 1997, p. 77, pl. 2, fig. 1, pl. 4, figs. 1, 7–8, slide 1997/1/1 (M. 35.3); collections of the Geological Survey of Austria, Vienna.

Diagnosis.—Lagenochitinidae with a conical to ovoid chamber provided with a crown of cell-like processes.

Occurrence.—Upper Ordovician–Silurian.

Discussion.—The processes may be anastomosed.

Genus SOMMEROCHITINA Costa Cruz and Quadros, 1985

Type species.—*Sommerochitina langei* Costa Cruz and Quadros, 1985. Holotype in Costa Cruz and Quadros, 1985, p. 289–293, pl. 1, fig. 1–2, 2-PM-1-MA borehole, core sample from 1,258–1,262 m, Cabeñas Formation (in Longa Formation according Grahn, 1992), early Famennian, Parnaíba Basin, Brazil, collections of departamento de Geologia e Paleontologia, Museu Nacional, Rio de Janeiro, Brazil.

Diagnosis.—Lagenochitinidae with a claviform chamber with sheathing processes.

Occurrence.—Upper Devonian.

Discussion.—When partly broken, threadlike expansions simulate a deeply laciniated carina located below the margin.

Subfamily ANGOCHITININAE Paris, 1981
Genus ANGOCHITINA Eisenack, 1931

Type species.—*Angochitina echinata* Eisenack, 1931. Lost holotype in Eisenack, 1931, p. 82, pl. 1, fig. 7, erratic *Beyrichia* limestones ("Beyrichia-kalk") from the Baltic bottom?; neotype: *Angochitina echinata* in Eisenack, 1964, p. 139, pl. 29, fig. 10, from the topmost part of the Hemse beds, Ludlow, early Ludfordian, Gotland, Sweden, collections of the Geologisch-Paläontologischen Institute der Universität, Tübingen, Germany.

Occurrence.—Upper Ordovician–Devonian.

Diagnosis.—Lagenochitinidae with ovoid chamber and randomly distributed simple or complex spines.

Genus FUNGOCHITINA Taugourdeau, 1966

Type species.—*Conochitina fungiformis* Eisenack, 1931. Lost holotype in Eisenack, 1931, p. 89, pl. 2, fig. 17, erratic grayish limestones ("grauer Kalk") referred to the lower Silurian but likely from the Rakvere Stage (late Caradoc); proposed neotype: *Conochitina fungiformis* subsp. *spinifera.* Eisenack, 1962, p. 310, pl. 14, fig. 15, Rakvere Stage (late Caradoc), Wesenberg, Estonia, collections of the Geologisch-Paläontologischen Institute der Universität, Tübingen, Germany.

Diagnosis.—Lagenochitinidae with conical to lenticular chamber and randomly distributed spines.

Occurrence.—Upper Ordovician–Upper Devonian.

Discussion.—Eisenack's original holotype for the species *fungiformis* was spiny. The subspecies *spinifera* is therefore chosen as the neotype for the genus and elevated to a specific rank.

Genus MUSCOCHITINA Paris, 1981

Type species.—*Muscochitina muscosa* Paris, 1981. Holotype in Paris, 1981, p. 269–270, pl. 30, fig. 17, Saint-Germain-sur-Ay section, upper part of LaHaye-du-Puits Formation, early Lochkovian, western France, IGR 51761 (M40/1), collections of the Institut de Géologie de l'Université de Rennes, France.

Diagnosis.—Lagenochitinidae with an ovoid chamber and a meshlike ornamentation.

Occurrence.—Lower Devonian.

Genus RAMOCHITINA Sommer and van Boekel, 1964
emend. Paris, Grahn, Nestor, and Lakova herein

Type species.—*Ramochitina ramosi* Sommer and van Boekel, 1964. Holotype in Sommer and van Boekel, 1964, p. 426, pl. 1, fig. 3, Tocantiná, middle Devonian, Paraná Basin, Goías, Brazil. Representative species of the genus in Laufeld, 1974, figs. 49–50.

Diagnosis.—Lagenochitinidae with an ovoid chamber and distinct crests (vertical rows of spines or membranes).

Occurrence.—Silurian–Devonian.

Discussion.—The vertical rows of spines (crests) occurring on the holotype and confirmed by SEM observation on material from the type locality (Grahn, unpublished), necessitate the emendation of this genus. *Gotlandochitina* Laufeld, 1974 which has the same characters is therefore a junior synonym.

Order OPERCULATIFERA Eisenack, 1931
Family DESMOCHITINIDAE Eisenack, 1931, emend. Paris, 1981
Subfamily DESMOCHITININAE Paris, 1981
Genus BULBOCHITINA Paris, 1981

Type species.—*Bulbochitina bulbosa* Paris, 1981. Holotype in Paris, 1981, p. 134–135, pl. 35, fig. 10, la Lézais section, Bois-Roux Formation, Aubriais Member, late Pragian, western France, IGR 51138 (P 36/3), collections of the Institut de Géologie de l'Université de Rennes, France.

Diagnosis.—Desmochitinidae with a hemispherical glabrous chamber.

Occurrence.—Upper Silurian–Lower Devonian.

Genus BURSACHITINA Taugourdeau, 1966
restrict. Paris, 1981

Type species.—*Desmochitina bursa* Taugourdeau and de Jekhowsky, 1960. Lost holotype, in Taugourdeau and de Jekhowsky, 1960, p. 1225, pl. 7, fig. 89, Tb-1 borehole, core sample from 1,268 m, Early Devonian, Sahara, Algeria; neotype: in Taugourdeau, 1967, p. 256, pl. 1, fig. 3, Nm-1, core sample from 1,200 m, Early Devonian (likely lower Emsian), Sahara, Algeria, collections of the Museum National d'Histoire Naturelle de Paris, France).

Diagnosis.—Glabrous Desmochitinidae with a conical chamber.

Occurrence.—Ordovician (?)–Middle Devonian.

Discussion.—We have adopted the position of Paris (1981, p. 137) who restricted the genus to glabrous species.

Genus CALPICHITINA Wilson and Hedlund, 1964

Type species.—*Calpichitina scabiosa* Wilson and Hedlund, 1964. Holotype in Wilson and Hedlund, 1964, p. 164, pl. 1, fig. 1, lower Sylvan Shale, south of Davis, Murray County, Oklahoma, early Ashgill, OPC 235-113-1, collections of the University of Oklahoma, Norman.

Diagnosis.—Desmochitinidae with a glabrous lenticular chamber.

Occurrence.—Ordovician–Lower Devonian.

Discussion.—*Calpichitina* has been selected despite the fact that Wilson and Dolly (1964) considered it as a junior synonym of *Hoegisphaera.* The latter, however, is here restricted to species with a subspherical chamber (see discussion below). The present definition includes the two subgenera *Calpichitina* (*Calpichitina*) and *Calpichitina* (*Densichitina*), erected by Paris (1981, p.127 and 131), but no longer maintained.

Genus DESMOCHITINA Eisenack, 1931

Type species.—*Desmochitina nodosa* Eisenack, 1931. Lost holotype in Eisenack, 1931, p. 92, pl. 3, fig. 1, erratic Ordovician calcareous sandy siltstone; proposed neotype: *Desmochitina nodosa* in Laufeld, 1967, p. 330–332, fig. 26 from the Keila Stage (Caradoc), Fjäka section, Dalarna, Sweden, collections of the Institute of Palaeontology of the University of Lund, Sweden.

Diagnosis.—Desmochitinidae with an ovoid, glabrous chamber.

Occurrence.—Lower Ordovician–Lower Devonian.

Discussion.—The present definition includes the two subgenera *Desmochitina* (*Desmochitina*) and *Desmochitina* (*Pseudodesmochitina*), erected by Paris (1981, p. 116–117), but no longer maintained as the presence of a mucron in the Desmochitinidae is not regarded here as a generic character.

Genus HOEGISPHAERA Staplin, 1961
emend. Paris, Grahn, Nestor, and Lakova herein.

Type species.—*Hoegisphaera glabra* Staplin, 1961. Holotype in Staplin, 1961, p. 419–420, pl. 50, fig. 5, Socony Vegreville no. 1, Duvernay Member, Woodbend Formation, cuttings from 1,067–1,097 m (3,500–3,600 ft), Late Devonian (Frasnian), Alberta, Canada; collections of Imperial Oil Limited, Calgary, Alberta, Canada.

Diagnosis.—Desmochitinidae with a spherical, glabrous chamber.

Occurrence.—Upper Devonian.

Discussion.—The genus is restricted here to forms with a subspherical chamber. Species with a lenticular chamber are transferred into *Calpichitina.* The emendations proposed by Urban (1972) and by Legault (1973b), based on the occurrence of a membranous matlike structure, are not adopted as the primary or secondary origin of such a structure is not yet demonstrated.

Genus OLLACHITINA Poumot, 1968

Type species.—*Ollachitina ingens* Poumot, 1968. Holotype in Poumot, 1968, p. 47–48, pl. 1, fig. 1, Gs-2 borehole, core sample from 3,451.50 m, El Gassi, northern Sahara, Algeria, unknown formation, Tremadoc, collections of the Service Palynoplanctologique de la SNPA-Elf, France.

Diagnosis.—Desmochitinidae with a glabrous, cylindrical chamber.

Occurrence.—Lower Ordovician.

Subfamily MARGACHITININAE Paris, 1981
Genus LINOCHITINA Eisenack, 1968
restrict. Paris, 1981

Type species.—*Desmochitina erratica* Eisenack, 1931. Lost holotype in Eisenack, 1931, p. 92, pl. 3, fig. 6, erratic graptolitic rock of early Ludlow age ("Graptolithengestein"); neotype in Eisenack, 1962, p. 307, pl. 17, fig. 11, erratic graptolitic rock, Wenlock to early Ludlow, collections of the Geologisch-Paläontologischen Institute der Universität, Tübingen, Germany.

Diagnosis.—Desmochitinidae with a claviform to cylindrical chamber and a hollow tubular copula.

Occurrence.—Middle Ordovician–Middle Devonian.

Discussion.—As expressed by Paris (1981, p. 148), forms bearing a carina are excluded from this genus.

Genus MARGACHITINA Eisenack, 1968

Type species.—*Desmochitina margaritana* Eisenack, 1937. Lost holotype in Eisenack, 1937, p. 221, pl. 15, fig. 9, erratic bluish-gray marly limestones of early Silurian age; neotype in Eisenack, 1962, p. 306, pl. 17, fig. 13, erratic Silurian graptolitic rocks, collections of the Geologisch-Paläontologischen Institute der Universität, Tübingen, Germany. Representative specimens in Laufeld, 1974, fig. 62.

Diagnosis.—Desmochitinidae with a lenticular to spherical, glabrous chamber and a solid peduncle linking the apex to the operculum of the preceding vesicle.

Occurrence.—Silurian–Lower Devonian.

Discussion.—Collarette is absent.

Genus URNOCHITINA Paris, 1981

Type species.—*Desmochitina urna* Eisenack, 1934. Lost holotype, in Eisenack, 1934, p. 69–70, pl. 5, fig. 7, late Silurian (Pridoli) limestones from Karlstejn, Bohemia, Czech Republic; proposed neotype: *Desmochitina urna* in Paris, Laufeld and Chlupac, 1981, p. 15–16, pl. 1, fig. 1, bed 29, late Pridoli limestones from Karlstejn, Bohemia, Czech Republic, IGR 51365(O 35), collections of the Institut de Géologie de l'Université de Rennes, France.

Diagnosis.—Desmochitinidae with an ovoid, glabrous chamber, and short tubular copula.

Occurrence.—Silurian–Lower Devonian.

Discussion.—Granules may be present on the wall.

Subfamily PTEROCHITININAE Paris, 1981
Genus ARMORICOCHITINA Paris, 1981

Type species.—*Linochitina*? *ceneratiensis* Paris, 1976. Holotype in Paris, 1976, p. 107, pl. 23, fig. 1, Saint-Céneré section, upper part of the Saint-Céneré Formation, Pragian, Western France, IGR 50160 (N 48/4), collections of the Institut de Géologie de l'Université de Rennes, France.

Diagnosis.—Desmochitinidae with an ovoid chamber and a membranous carina extending below the margin.

Occurrence.—Middle Ordovician–Lower Devonian.

Discussion.—Granules may be present on the wall.

Genus CINGULOCHITINA Paris, 1981

Type species.—*Desmochitina cingulata* Eisenack, 1937. Lost holotype in Eisenack, 1937, p. 220, pl. 15, fig. 6 from erratic graptolitic shale ("Graptolithengestein"); neotype: *Linochitina cingulata,* in Eisenack, 1968, p. 170–171, pl. 29, fig. 29, from erratic graptolitic shale, Ludlow; collections of the Geologisch-Paläontologischen Institute der Universität, Tübingen, Germany. Representative specimens from outcrops in Laufeld, 1974, fig. 37 B and D, Valbyte 1, Slite Marls, Sheinwoodian, Wenlock, Gotland, Sweden.

Diagnosis.—Desmochitinidae with a thin-walled, conical to ovoid glabrous chamber bearing a complete membranous carina on the margin; a short tubular copula is present.

Occurrence.—Silurian–Lower Devonian.

Genus PSEUDOCLATHROCHITINA Cramer, 1966
emend. Priewalder, 1997

Type species.—*Clathrochitina carmenchui* Cramer, 1964. Holotype in Cramer, 1964, p. 346, pl. 24, fig. 18, La Vid de Gordõn section, upper San Pedro Formation, Pridoli, north-western Spain; neotype: *Pseudoclathrochitina carmenchui* in Priewalder, 1997, p. 78–81, pl. 1, figs. 2, 6, pl. 5, fig. 8, slide 1997/1/2 (L. 39.3); collections of the Geological Survey of Austria, Vienna.

Diagnosis.—Conical Desmochitinidae with a reticulum extending in a perforated carina.

Occurrence.—Silurian.

Discussion.—The emendation proposed by Priewalder (1997, p. 78) is accepted. However, we consider the folding of the meshwork around the margin as a structure equivalent to a carina.

Genus PTEROCHITINA Eisenack, 1955a

Type species.—*Bion perivelatum* Eisenack, 1937. Lost holotype in Eisenack, 1937, p. 229–230, pl. 16, fig. 4, erratic *Beyrichia* limestones ("Beyrichia-kalk"); neotype in Eisenack, 1955a, p. 177, pl. 3, fig. 10, erratic *Beyrichia* limestones from the Baltic bottom?, Pridoli; collections of the Senckenberg Museum, Frankfurt am Main, Germany.

Diagnosis.—Desmochitinidae with a lenticular to spherical, glabrous chamber with a membranous carina.

Occurrence.—Middle Ordovician–Lower Devonian.

Subfamily CUTICHITININAE Achab, Asselin and Soufiane, 1993
Genus CUTICHITINA Achab, Asselin and Soufiane, 1993

Type species.—*Cutichitina legrandi* Achab, Asselin and Soufiane, 1993. Holotype in Achab et al., 1993, p. 7, pl. 1, fig. 9, QD-1 borehole, core sample from 3,361 m, upper part of the Ouargla Sandstone Formation, Arenig, Central Sahara, Algeria, GSC 103 969 (J.55.3), collections of the Geological Survey of Canada, Ottawa, Ontario, Canada.

Diagnosis.—Desmochitinidae with an ovoid chamber enveloped by a membranous sleeve.

Occurrence.—Ordovician.

Subfamily Eisenackitininae Paris, 1981

Genus Eisenackitina Jansonius, 1964
restrict. Paris, 1981

Type species.—*Eisenackitina castor* Jansonius, 1964. Holotype in Jansonius, 1964, p. 912–913, pl. 2, fig. 16, Imperial Cartridge borehole, core sample from 253 m (758 ft.), Hume Formation, early Givetian, northern Canada, collections of Imperial Oil Limited, Calgary, Alberta, Canada.

Emended diagnosis.—Desmochitinidae with an ovoid chamber and a randomly distributed, spiny ornamentation.

Occurrence.—Middle Ordovician–Middle Devonian.

Discussion.—In agreement with Paris (1981, p. 155), smooth, ovoid forms are transferred into *Desmochitina* and smooth, conical ones into *Bursachitina.*

Genus Kalochitina Jansonius, 1964

Type species.—*Kalochitina multispinata* Jansonius, 1964. Holotype in Jansonius, 1964, p. 909–910, pl. 2, fig. 21, Imperial-Calvan Anderson 9-6 borehole, cuttings from 736–737 m (2,420–2,425 ft), Anderson Township, Essex County, Ontario, Canada Maeford-Dundas Formation, Cincinnatian (late Caradoc-Ashgill), collections of Imperial Oil Limited, Calgary, Alberta, Canada.

Diagnosis.—Desmochitinidae with a conical chamber and random spines.

Occurrence.—Upper Ordovician.

Genus Ordochitina Achab, Asselin and Soufiane, 1993

Type species.—*Ordochitina tadlaiensis* Achab, Asselin and Soufiane, 1993. Holotype in Achab et al., 1993, p. 6, pl. 1, fig. 1, Bj-103 borehole, cuttings sample from 849 m, unnamed formation, early Caradoc, Tadla Basin, Morocco, GSC 103 965 (P 27.2), collections of the Geological Survey of Canada, Ottawa, Ontario, Canada.

Diagnosis.—Desmochitinidae with a conical chamber covered by crests (vertical rows of spiny or membranous ornamentation).

Occurrence.—Middle Ordovician–Upper Ordovician.

Genus Vinnalochitina Sutherland, 1994

Type species.—*Vinnalochitina granosa* Sutherland, 1994. Holotype in Sutherland, 1994, p. 36–37, pl. 1, fig. 7, Ludlow area, Lower Leintwardine Formation, Ludfordian, Shropshire, England, MPK 9847, collections of British Geological Survey, Keyworth, England.

Diagnosis.—Desmochitinidae with a hemispherical chamber and randomly distributed spines.

Occurrence.—Silurian.

Subfamily Orbichitininae Achab, Asselin and Soufiane, 1993

Genus Armigutta Schallreuter, 1981

Type species.—*Armigutta hillmeri* Schallreuter, 1981. Holotype in Schallreuter, 1981, p. 109, pl. 7, fig. 1, erratic Sularp shale, Keila Stage (Caradoc), Sweden, collections of Geologisch-Paläontologisches Institute der Universität Hamburg, Germany.

Diagnosis.—Desmochitinidae with an ovoid chamber and a crown of processes on the margin.

Occurrence.—Upper Ordovician.

Discussion.—This genus is based on a single specimen, which may be a teratologic specimen, from anerratic rock sample.

Genus Orbichitina Achab, Asselin and Soufiane, 1993

Type species.—*Orbichitina vulpina* Achab, Asselin and Soufiane, 1993. Holotype in Achab et al., 1993, p. 7, pl. 1, fig. 5, Riviére-au-Renard, Gaspé Peninsula, Québec, Canada, lower part of the Rosebush Cove Member of the Indian Point Formation, Pridoli, GSC 103967 (E 44.3), collections of the Geological Survey of Canada, Ottawa, Ontario, Canada.

Diagnosis.—Desmochitinidae with a conical chamber and a crown of processes.

Occurrence.—Silurian (Pridoli).

Genus Salopochitina Swire, 1990
emend Paris, Grahn, Nestor, and Lakova

Type species.—*Conochitina*? *monterrosae* Cramer, 1969. Holotype: *Salopochitina bella* Swire, 1990 (=*S. monterrosae*), p. 109–110, pl. 2, fig.3, Lover Hill Farm borehole, Buildwas Formation, Sheinwoodian, Shropshire, England, MPK 5913, collections of the British Geological Survey, Keyworth, England.

Diagnosis.—Desmochitinidae with a conical to ovoid chamber, and sheathing processes.

Occurrence.—Silurian (Wenlock-Ludlow).

Discussion.—The chamber surface may be granulous and, when damaged, the remaining processes may simulate a laciniated carina. The original diagnosis of the genus includes misinterpretations (e.g., central process); in addition we consider *S. bella* Swire, 1990 to be a junior synonym of *S. monterrosae* (Cramer, 1969).

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APPENDIX: LIST OF THE REJECTED GENERA

Acmochitina Tsegelnyuk, 1982. Type species: *Acmochitina corollata* Tsegelnyuk, 1982. Junior synonym of *Ancyrochitina* Eisenack, 1955a.

Agathochitina Tsegelnyuk, 1982. Type species: *Ancyrochitina primitiva* Eisenack, 1955a. Junior synonym of *Ancyrochitina* Eisenack, 1955a.

Aleurochitina Locquin, 1976. Type-species: *Desmochitina erinacea* Eisenack, 1931. Nomen nudum.

Amphorachitina Poumot, 1968. Type species: *Amphorachitina conifundus* Poumot, 1968. Junior synonym of *Lagenochitina* Eisenack, 1931.

Aqualichitina Locquin, 1976. Type species: *Lagenochitina ovoidea* Taugourdeau and de Jekhowsky, 1960. Nomen nudum.

Ampullachitina Collinson and Schwalb, 1955. Type species: *Ampullachitina laguncula* Collinson and Schwalb, 1955. Remarks: *Ampullachitina laguncula* Collinson and Schwalb was published on 16 May 1955. It is therefore a senior synonym of *Ancyrochitina* Eisenack, 1955a published on 5 June 1955. However, despite the fact that it is not a nomen oblitum, *Ampulachitina* has not been used since 1955, thus for stability of nomenclature, it is suggested to maintain *Ancyrochitina* because Collinson himself adopted this genus (see Collinson and Scott, 1958).

Ascochitina Tsegelnyuk, 1982. Type species: *Ascochitina seccata* Tsegelnyuk, 1982. Junior synonym of *Angochitina* Eisenack, 1931, emend. Eisenack, 1968.

Baculochitina Locquin, 1976. Type species: *Cyathochitina cylindrica* Taugourdeau and de Jekhowsky, 1960. Nomen nudum.

Biconigutta Schallreuter, 1981. Type species: *Biconigutta catinus* Schallreuter, 1981. Considered here as a junior synonym of *Armigutta* Schallreuter, 1981. Remarks: this genus is based on a single specimen from an erratic rock sample.

Calpichitina (*Densichitina*) Paris, 1981. Type species: *Desmochitina densa* Eisenack, 1962. This subgenus, sometimes used at a generic rank (e.g., Grahn and Paris, 1992), is here included within *Calpichitina* emend. Paris 1981.

Calychitina Tsegelnyuk, 1982. Type species: *Desmochitina*? *urna* Eisenack, 1934. Junior synonym of *Urnochitina* Paris, 1981.

Catenachitina Jansonius, 1967. Type species: *Desmochitina erratica* Eisenack, 1931. Nomen nudum, see Jansonius, 1967, p. 351.

Catenochitina Locquin, 1976. Type species: *Desmochitina elegans* Taugourdeau and de Jekhowsky, 1960. Nomen nudum.

Ceratochitina Tsegelnyuk, 1982. Type species: *Ceratochitina cornuta* Tsegelnyuk, 1982. Junior synonym of *Ancyrochitina* Eisenack, 1955a

Cingulochitina Locquin, 1976. Type species: *Cyathochitina dispar* Taugourdeau and de Jekhowsky, 1960. Nomen nudum.

Cladochitina Lange, 1967. Type species: *Conochitina biconstricta* Lange, 1949. Junior synonym of *Spinachitina* Schallreuter, 1963.

Clathrochitinella Cramer, 1967. Type species: *Clathrochitina oblonga* Benoît and Taugourdeau, 1961. Invalid taxon according to the code of Zoological Nomenclature (no definition given).

Combachitina Locquin, 1976. Type species: *Lagenochitina dubia* Taugourdeau and de Jekhowsky, 1960. Nomen nudum.

Coronochitina Eisenack, 1965. Type species: *Coronochitina coronata* Eisenack, 1965. Junior synonym of *Spinachitina* Schallreuter, 1963.

Cramerochitina Locquin, 1976. Type species: *Halochitina retracta* Eisenack, 1968. Nomen nudum.

Cupulachitina Jansonius, 1967. Type species: *Desmochitina elegans* Taugourdeau and de Jekhowsky, 1960. Nomen nudum.

Cylindrochitina Schallreuter, 1963. Type species: *Cylindrochitina granata* Schallreuter, 1963. Junior synonym of *Angochitina* Eisenack, 1931, restrict., 1968.

Dasychitina Tsegelnyuk, 1982. Type species: *Dasychitina implexa* Tsegelnyuk, 1982. Junior synonym of *Ancyrochitina* Eisenack, 1955a.

Deflandrochitina Locquin, 1976. Type species: *Angochitina milanensis* Collinson and Scott, 1958. Nomen nudum.

Desmochitina (*Pseudodesmochitina*) Paris, 1981. Type species: *Desmochitina*? *cocca* Eisenack, 1931. This subgenus, sometimes used at generic rank (e.g., Schallreuter, 1983), is here included within *Desmochitina* Eisenack, 1931, emend. Paris, 1981.

Diabolochitina Locquin, 1976. Type species: *Conochitina symmetrica* Taugourdeau and de Jekhowsky, 1960. Nomen nudum.

Discochitina Tsegelnyuk, 1982. Type species: *Discochitina discoides* Tsegelnyuk, 1982. Junior synonym of *Ancyrochitina* Eisenack, 1955a.

Earlachitina Collinson and Scott, 1958. Type species: *Earlachitina latipes* Collinson and Scott, 1958. Junior synonym of *Ancyrochitina* Eisenack, 1955a.

Edouardochitina Locquin, 1976. Type species: *Angochitina communis* Jenkins, 1967. Nomen nudum.

Erinaceochitina Locquin, 1976. Type species: *Sphaerochitina collinsoni* Dunn, 1959. Nomen nudum.

Eurychitina Tsegelnyuk, 1982. Type species: *Bursachitina oviformis* Eisenack, I972. Junior synonym of *Bursachitina* Taugourdeau, 1966.

Flascachitina Jansonius, 1967. Type species: *Angochitina flasca* Collinson and Schwalb, 1955. Nomen nudum (see Jansonius, 1967, p. 351).

Fustichitina Achab, 1980. Type species: *Fustichitina ventriosa* Achab, 1980. Junior synonym of *Conochitina* Eisenack, 1931, restrict. Eisenack, 1955b, 1965 and restrict. Paris, 1981.

Giraffachitina Locquin, 1985. Type species: *Giraffachitina poignantii* Locquin, 1985. We exclude this taxon from the chitinozoans.

Gotlandochitina Laufeld, 1974. Type species: *Gotlandochitina martinssoni* Laufeld, 1974. Junior synonym of *Ramochitina* Sommer and van Boekel, 1964 emend.

Guizhouchitina Lai, 1982. Type species: *Guizhouchitina lagena* Lai, 1982. Junior synonym of *Lagenochitina* Eisenack, 1931 if the vesicle is glabrous. Remarks: the "reticulate" pattern of the holotype is an artifact related to pyrite crystal casts.

Halochitina Eisenack, 1968. Type species: *Pterochitina retracta* Eisenack, 1955b. Junior synonym of *Pterochitina* Eisenack,1955a.

Haplochitina Grignani and Mantovani, 1964. Type species: *Haplochitina omdoulensis* Grignani and Mantovani, 1964. Junior synonym of *Sphaerochitina* Eisenack, 1955a.

Helicochitina Locquin, 1976. Type species: *Helicochitina viticula* Locquin, 1976. Nomen nudum.

Iberichitina Jansonius, 1967. Type species: *Clathrochitina carmenchui* Cramer, 1964. Nomen nudum.

Idiochitina Tsegelnyuk, 1982. Type species: *Idiochitina platycera* Tsegelnyuk, 1982. Junior synonym of *Ancyrochitina* Eisenack, 1955a.

Illichitina Collinson and Schwalb, 1955. Type species: *Illichitina crotalum* Collinson and Schwalb, 1955. Remarks: the authors of this genus later considered it to be a synonym of *Cyathochitina* Eisenack, 1955b (see Taugourdeau et al., 1967, p. 62). Normally *Illichitina* has the anteriority (16 May 1955, instead of 12 December 1955 for *Cyathochitina*) but for stability of the taxonomy and because the definition was too broad, we follow the decision of CIMP (see Taugourdeau et al., 1967, p. 62) and do not retain *Illichitina*.

Jansoniuchitina Locquin, 1976. Type species: *Kalochitina* cf. *inflata* (Taugourdeau, 1961) in Jansonius, 1964, pl. 2, fig. 23. Nomen nudum.

Jenkinochitina Paris, 1981. Type species: *Conochitina oelandica* Eisenack, 1955b. Junior synonym of *Euconochitina* Taugourdeau, 1966.

Labrochitina Locquin, 1976. Type species: *Conochitina elegans* Eisenack, 1931. Nomen nudum.

Lachkarichitina Locquin, 1976. Type species: *Cyathochitina elongata* Bouché, 1965. Nomen nudum.

Lambdachitina Lakova, 1986. Type species: *Lambdachitina coronata* Lakova, 1986. Junior synonym of *Angochitina* Eisenack, 1931 restrict. Eisenack, 1968.

Leiochitina Locquin, 1976. Type species: *Cyathochitina elenitae* Cramer, 1964. Nomen nudum.

Leiochitina Tsegelnyuk, 1982. Type species: *Lagenochitina elegans* Beju and Danet, 1962. Junior synonym of *Lagenochitina* Eisenack, 1931.

Ligulachitina Locquin, 1976. Type species: *Rhabdochitina virgata* Taugourdeau, 1961. Nomen nudum.

Lissochitina Tsegelnyuk, 1982. Type species: *Sphaerochitina resupina* (Dicevichius, 1971). Junior synonym of *Sphaerochitina* Eisenack, 1955a

Macrostomachitina Taugourdeau, 1965. Type species: *Lagenochitina macrostoma* Taugourdeau and de Jekhowsky, 1960. Nomen nudum; see Jansonius (1967, p. 352).

Mirachitina Eisenack, 1931. Type species: *Mirachitina quadrupedis* Eisenack, 1931. No longer included in the chitinozoans.

Monicachitina Locquin, 1976. Type species: *Cyathochitina striata* Eisenack, 1937. Nomen nudum.

Monilichitina Locquin, 1976. Type species: *Desmochitina sommeri* Lange, 1952. Nomen nudum.

Mucrochitina Locquin, 1976. Type species: *Lagenochitina esthonica* Eisenack, 1955b. Nomen nudum.

Mycetochitina Locquin, 1976. Type species: *Mycetochitina hypha* Locquin, 1976. Nomen nudum.

Nanochitina Nestor, 1994. Type species *Nanochitina nana* Nestor, 1994. Regarded as a junior synonym of *Bursachitina* Taugourdeau, 1966.

Nematochitina Locquin, 1976. Type species: *Ancyrochitina longicornis* Taugourdeau and Jekhowsky, 1960. Nomen nudum.

Oochitina Tsegelnyuk, 1982. Type species: *Oochitina fugax* Tsegelnyuk, 1982. Junior synonym of *Ancyrochitina* Eisenack, 1955a.

Orochitina Tsegelnyuk, 1982. Type species: *Orochitina inflata* Tsegelnyuk, 1982. Junior synonym of *Angochitina* Eisenack, 1931 restrict 1968.

Pallachitina Costa, 1970. Type species: *Pallachitina wilhelmi* Costa, 1970. Junior synonym of *Bursachitina* Taugourdeau, 1966.

Palenchitina Schweineberg, 1987. Type species: *Palenchitina pisuergensis* Schweineberg, 1987. Junior synonym of *Ancyrochitina* Eisenack, 1955a.

Parachitina Eisenack, 1937. Type species: *Parachitina curvata* Eisenack, 1937. Incertae sedis (see Jansonius, 1967, 1970). No longer included in the chitinozoans.

Parvichitina Locquin, 1976. Type species: *Conochitina vasculiformis* Bouché, 1965. Nomen nudum.

Phiolachitina Montenari and Maass, 1996. Type species: *Phiolachitina silvanegratica* Montenari and Maass, 1996. Not included in the chitinozoans.

Poteriochitina Legault, 1973a. Type species: *Poteriochitina briarca* Legault, 1973a. Junior synonym of *Eisenackitina* Jansonius, 1964.

Poumochitina Locquin, 1976. Type species: *Ancyrochitina multiradiata* Eisenack, 1959. Nomen nudum.

Retrochitina Locquin, 1976. Type species: *Halochitina retracta* Eisenack, 1955b. Nomen nudum.

Rhizochitina Tsegelnyuk, 1982. Type species: *Rhizochitina laufeldi* Tsegelnyuk, 1982. Junior synonym of *Ancyrochitina* Eisenack, 1955a.

Sclerochitina Tsegelnyuk, 1982. Type species: *Conochitina intermedia* Eisenack, 1955a. Junior synonym of *Belonechitina* Jansonius, 1964.

Solenochitina Tsegelnyuk, 1982. Type species: *Solenochitina fistulata* Tsegelnyuk, 1982. Junior synonym of *Conochitina* Eisenack, 1931, emend. Paris, 1981.

Spathachitina Costa, 1970. Type species: *Spathachitina cruzi* Costa, 1970. Junior synonym of *Conochitina* Eisenack, 1931, emend. Paris, 1981

Steneyochitina Zaslavskaya, 1980. Type species: *Steneyochitina ovatoelongata* Zaslavkaya, 1980. Junior synonym of *Spinachitina* Schallreuter, 1963.

Stephanochitina Grignani and Mantovani, 1964. Type species: *Stephanochitina africana* Grignani and Mantovani, 1964. Probably a junior synonym of *Angochitina* Eisenack, 1931, but the diagnoses and illustration of the type material do not allow a definite statement.

Striatolagenochitina Schallreuter, 1981. Type species: *Striatolagenochitina clava* Schallreuter, 1981. Junior synonym of *Lagenochitina* Eisenack, 1931.

Subulochitina Locquin, 1976. Type species: *Acanthochitina secunda* Schallreuter, 1963. Nomen nudum.

Taugourdochitina Locquin, 1976. Type species: *Conochitina micracantha* Eisenack, 1931. Nomen nudum.

Togachitina Wood, 1994. Type species: *Togachitina eamesi* Wood, 1994. Junior synonym of *Pellichitina* Achab, Asselin, and Soufiane, 1993

Trochochitina Miller, 1976. Type species *Trochochitina radiata* Miller 1976. Nomen nudum.

Urnichitina Locquin, 1976. Type species: *Desmochitina rhenana* Eisenack, 1939. Nomen nudum.

Virgilochitina Tasch and Hutter, 1978. Type species: *Virgilochitina kansasensis* Tasch and Hutter, 1978. Junior synonym of *Lagenochitina* Eisenack, 1931.

Vitreachitina Nestor, 1994. Type species: *Sphaerochitina vitrea* Taugourdeau, 1962. Regarded as a junior synonym of *Euconochitina* Taugourdeau, 1966 because the wall thickness is not used as a discriminate character in the present classification.

Discussion.—Locquin's document (1976), including new chitinozoan genera and distributed to some chitinozoan workers by this author, is not registered in the official record for French publications in the Bibliothèque Nationale de France. Concerning valid publications, the International Code of Zoological Nomenclature (third edition, 1985) stipulates: Article 8a(i) "it must be issued for the purpose of providing a permanent scientific record." We consider that this requirement and point (i) of Article 13a of the code are not fulfilled in Locquin's document (1976). Therefore, we consider the taxa described in this document as nomina nuda, like the taxa described in unpublished theses.

Four new genera, *Grahnichitina, Nanochitina, Retiachitina,* and *Sericochitina,* have been erected recently by Geng et al. (1997). Because they were published after the submission of our manuscript, it was not possible to include them in our multivariate analysis and therefore, they are not discussed herein. It should be noted that *Nanochitina* Geng et al., 1997 is an homonym of *Nanochitina* Nestor, 1994. However, if the synonymy of *Nanochitina* Nestor, 1994 with *Bursachitina* Taugourdeau, 1966 is accepted, then the name *Nanochitina* can be used again as a generic name.