JOURNAL OF PALEONTOLOGY, VOL. 22, NO. 2, PP. 233–263, PLS. 33–35, 14 TEXT FIGS., MARCH 1948

FOSSIL TINTINNIDS: LORICATED INFUSORIA FO THE ORDER OF THE OLIGOTRICHA

G. COLOM
Lucas Mallada Institute for Geological Research, Madrid

ABSTRACT—The Upper Jurassic (Tithonian) and Neocomian beds of the Balearic Islands include sediments of very fine structure on a basis of calcite in very small grains, *Nannoconus colomi* (a microorganism *incertae sedis*), Radiolaria, and an enormous quantity of coccolith discs. These sediments are pelagic, with no terrigenous influences. They contain great numbers of loricas of tintinnids (loricated, oligotric infusoria) preserved as calcium carbonate. A few species of fossil tintinnids were already known from other Mediterranean regions under the name of *Calpionella*. The true nature of the Calpionellae was unknown and they were assigned to the Foraminifera by some and to the Radiolaria by others until the author demonstrated that they were tintinnids, and his conclusions were confirmed by Professor Deflandre in 1936. In the present work new forms belonging to different genera and very similar to living forms, are described.

INTRODUCTION

THE STUDY of the Calpionellae, or fossil tintinnids, from the Tithonian and Lower Cretaceous formations of Spain, is one to which I have devoted several earlier papers. In returning to this subject after an interval of some years I am presenting a résumé of our present knowledge concerning this peculiar and interesting group of planktonic infusoria. This is a subject that the geologist working in the Balearic Islands, and especially in Majorca, will find difficult or impossible to slight, for the fine textured sublithographic limestones of these ages are brought forcibly to his attention both by reason of their wide extent and the importance of the geological facies they represent. The greater part of them is replete with the remains of these organisms and they offer a vast field of study not only to the paleontologist who cultivates this specialty but to the geologist as well, because the data they furnish are important for a detailed understanding of the sediments left by Mesozoic seas in Spain.

In the Tithonian and Lower Cretaceous beds of the Balearics, as well as in strata of the same ages in the eastern part of the Iberian peninsula, myriads of representatives of a plankton characterized chiefly by Radiolaria and tintinnids are preserved. The latter fossils possess the delicate structures of living marine tintinnids and it is remarkable that the extremely fragile and delicate tests or loricas of these Mesozoic species could be so perfectly fossilized.

Since the appearance of my first notes on the Calpionellae in 1934 and 1939, I have continued this study. The following pages present descriptions of new species, both Tithonian and Cretaceous, as well as previously known forms and remarks on the composition and extent of the facies which they characterize. I have also compiled and reviewed all existing data on the Calpionellae, in order to give the most exact idea possible of our present knowledge of them. I have been able to examine in detail various Majorcan deposits containing a very complete pelagic record ranging from the upper Lias to the Aptian-Albian and to follow the tintinnids step by step from their first appearance in the basal beds of the Tithonian to their disappearance in the Barremian.

That the Calpionellae are true fossil tintinnids is no longer doubted by most paleontologists and they are now recognized as such in various authoritative works (Lombard 1945, Murgeanu 1938). This determination is similar in a way to that made in recent years with respect to the Peridiniidae, hystricosferids, etc., which have been found in chert. Such discoveries confirm the words of the famous paleontologist Gaudry who stated, in his work "Fossiles Secondaires" (Vol. II, p. 37, 1890), "Little by little we shall discover in the earth's strata

the ancestors of all the creatures that surround us, however frail they be."

I wish to thank my good friend Dr. Massuti, Director of the Oceanographical Laboratory of Palma (Majorca) and author of numerous works on the western Mediterranean plankton, for constant help in the interpretation of fossil loricas as well as for access to his bibliography on living tintinnids. With his help I have been able to obtain the remains of fossil plankton from the Balearic rocks that were previously unknown. I am also indebted to Professors J. Cadisch and G. Deflandre, of the Universities of Bâle and Paris respectively, both authors of interesting works on the Calpionellae, for information and suggestions and I wish to express my thanks for their assistance.

SUMMARY OF MORPHOLOGY AND BIOLOGY OF THE LIVING ANIMAL

The tintinnids are oligotric infusoria, generally marine, pelagic and free-swimming, whose protoplasmic mass is lodged in and protected by an organic test or lorica. Some groups live in the ocean (holoplankton) and others inhabit neritic waters (mesoplankton) as, for example, most species of the genus *Tintinnopsis*. Still others exist in fresh water, but at present this is a small group of species. Fossil representatives have been found in Quaternary peat-bogs (Lagerheim 1901).

Plankton samples usually include tintinnid loricas in great numbers, but the body of the animal is nearly always missing. Therefore it is only by laborious investigation on the part of zoologists that an exact knowledge of the complete structure of these infusoria has been obtained.

The first investigator to publish an extensive monograph on this group was Daday (1887), who described the shape of the living animal, the manner in which it is attached to the lorica, the structure of the membranelles, which he considered to be of generic significance, and the number of nuclei in a varied group of species. He also described many new genera and species. Similar investigations were carried on in later years by Laackman (1906) who also studied the nuclear changes which occur during reproduction. Entz, Jr. (1909) published an important work on lorica sections and their histological staining. It was not until Fauré-Fremiet (1924), however, that a detailed work on the vital organization of this group appeared by the French zoologist Fauré-Fremiet who reported new and interesting facts concerning their organization.

The living cell of tintinnids has a bell-shaped or conic form adapted to the size and structure of the lorica. Its lower portion is generally pointed and attached by a narrow, more or less contractile, protoplasmic prolongation, to the bottom or to the side of the lorica. At the opposite end, the thick cylindrical protoplasmic mass is abruptly truncated, forming a disc or peristome varying in width in different species, which is surrounded by a collar bearing on its upper side a wreath of long and narrow ciliary plates, termed *membranelles*. The peristomial disc carries the mouth in a more or less deep pre-oral cavity, into which some of the ciliary plates descend. The latter are delicate and thin, turned outwards and bordered by strong rims. Inwardly, they form a fringe of more or less long ciliated bristles. The peristome is commonly bordered by rounded lobes. In some species there exist at the base of the *membranelles*, on the inner side of the peristomes, peculiar, fine, tentacle-shaped organs—the *tentaculoids*—which seem to be quite variable in length and shape and probably are highly contractile in the living animal. In many species the body bears external fields of cilia, which have been described in detail by Fauré Fremiet. Most marine tintinnids have two large ovoid or rounded macronuclei, each accompanied by a diminutive micronucleus. According to Entz, Jr. the number of nuclei is much greater in certain genera, but this abundance may be related to sporulation which occurs during the reproductive cycle.

The bristles and cilia enable the tintinnids to swim rapidly. Their bodies can extend far out from the lorica and in this position movement is free and easy.

The shapes of tintinnid loricas are very diverse and it is on them alone that the systemmatic arrangement of the group is founded. Little is known about their chemical composition and many investigators of the living plankton have described them as

gelatinous or pseudo-chitinous. The most important morphological features for the determination of living genera and species are characters of the lorica as seen in thin section. Some have prismatic or alveolar structure or a tendency to accumulate various kinds of mineral or organic particles on their surfaces (Fig. 1).

The simplest lorica wall consists of a delicate membrane, apparently structureless, as in *Tintinnus lusus-undae*. A more advanced and complex type is finely reticulated, termed by Brandt "*primary structure.*" In a way this wall is "double" with a single layer of "prismatic elements" between outer and inner laminae. Still more complex loricas possess several layers of "prismatic elements" between the outer laminae.

The loricas of certain genera also show a marked tendency to include or become incrusted with numerous foreign particles, which gives them a more or less agglutinated appearance. These particles are varied and may consist of extremely fine mineral grains or coccoliths produced by microscopic planktonic algae.

The relative proportions of the loricas, the form (dentate or smooth) or the oral collars, the shape and size of the oral openings, the presence of rings or rims around the tests, and the direction and anastomosis of longitudinal striae are other characters on which the present systematic arrangement of this group is based. According to Kofoid and Campbell, size is rarely distinctive as it is generally correlated with temperature and varies considerably within the geographic area of each species.

Only rarely can the standards and methods of planktologists working with living material be applied to fossil species, especially to those, like the Calpionellae, preserved by calcite in sedimentary rocks, although they can be used for Tintinnids preserved in chert. In thin sections of rock, however, nothing can be seen but the simple, more or less well preserved, outlines of the loricas, most of which retain nothing of their characteristic detailed structure. These silhouettes appear white in contrast to the gray color of the enclosing rock. It is not possible to govern the orientation of the sections, because the of minute size of these organisms, and few sections are obtained following the longitudinal axis of the lorica, although this orientation is the most desirable and the only one that gives an unmistakable representation. For this reason I believe that one must be very prudent in distinguishing fossil species within this group, for it is easy to go astray in trying

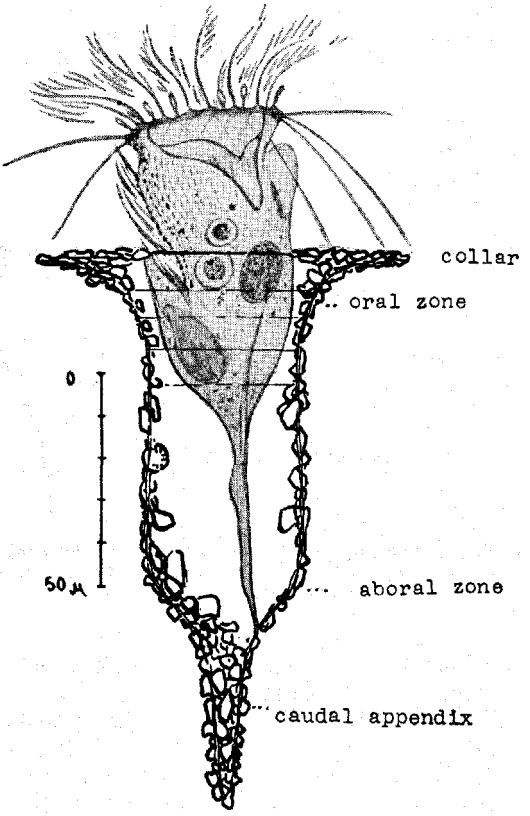

FIG. 1—*Tintinnopsis campanula* (Ehrenb.) after Fauré Fremiet, 1924. A living species, greatly enlarged, indicating terminology of the lorica.

to interpret the numerous random sections that are obtained. For example: sections of *Tintinnopsella carpathica* (Murgeanu and Filipescu) seem to show a considerable variety of loricas (fig. 2, a–c). Some are bell-shaped, with a wide oral opening; some are long and narrow and some have a globular apical region and a small oral opening. None reveals the existence of a caudal prolongation at the apical end. All, however, are the

same species but they are differently oriented.

An even more striking example occurs in a slide from the Tithonian of Cape Pinar, Alcudia (Majorca) which shows a lorica similar in shape to *Calpionella elliptica* Cadisch but differing from all other sections of this species in having a long caudal appendage, greater in length than the lorica itself (Fig. 11—*64*). Does this represent a species similar to *C. elliptica* but distinct because of its long caudal appendage? Or is such an appendage characteristic of *C. elliptica*, many of whose sections (Fig. 11—*65*, *67*, *68*, *73–75*) show a pointed and abruptly truncated extremity? It would be easy to accept the latter view, as the perfection of a section depends upon its orientation. The answer to this question, however, is even more involved. Professor Deflandre (1936) observed and figured a specimen of *C. elliptica* suggesting the existence of a cylindrical prolongation, or long neck, surmounting its oral opening (fig. 3, no. 27; text). Similar and even more perfect examples occur among my own slides and a particularly notable lorica appears in a section obtained from the Tithonian limestones of Cala Blanca, Andraitx (Majorca). This specimen is typically preserved and through the calcite granules can be seen, slightly blurred but unmistakable, a long cylindrical neck with a wide outward-turned lip at its outer and extending beyond the oral portion of a test of *C. elliptica* (Fig. 11—*72*). Professor Deflandre compared such specimens, with good reason, to living tintinnids of the genus *Codonellopsis* and especially to *Codonellopsis lusitanica* Jörg (Fig. 3, no. 28). If we compare the two sections just mentioned, the first with its long caudal appendage (Fig. 11—*64*) and the second with its long cylindrical neck (Fig. 11—*72*), with sections of *Calpionella elliptica* Cadisch showing the existence of a caudal appendage

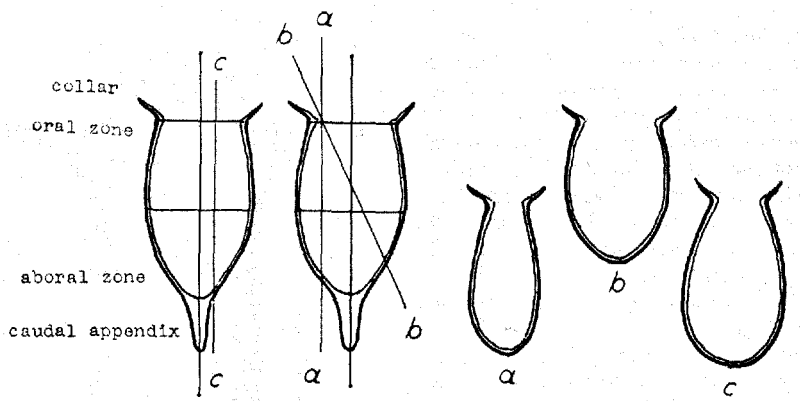

FIG. 2.—Drawings of *Tintinnopsella carpathica* (Murgeanu and Filipescu) showing how three different sections (*a*, *b*, *c* at right) might be obtained from a single form (*a*—*a*, *b*—*b*, and *c*—*c* on the two figures at left.) Greatly enlarged.

(Fig. 11, *65*, *67*, *68*, *73–75*), could they not all be assigned to a single species of the genus *Codonellopsis*? Quite possibly. However, if anyone should affirm that these different sections represent three distinct species, it would be difficult to oppose him with definite arguments, because differences of this kind are found among living forms and commonly they are described as different species. Consequently the "species" among fossil tintinnids may be understood quite differently according to the views of those who study them, a situation general to all ages and to very different groups of organisms, and I believe that the question of speciation among extinct tintinnids will always be a debatable one. This problem is nonetheless interesting, since these very facts are evidence that confirm the presence of true tintinnids in the beds of the Tithonian and Lower Cretaceous.

EARLY STUDIES OF FOSSIL TINTINNIDS

The Jurassic or Cretaceous cherts in which many admirably preserved microorganisms have been found (Dinoflagellata, Peridiniidae, etc.) have not yet furnished

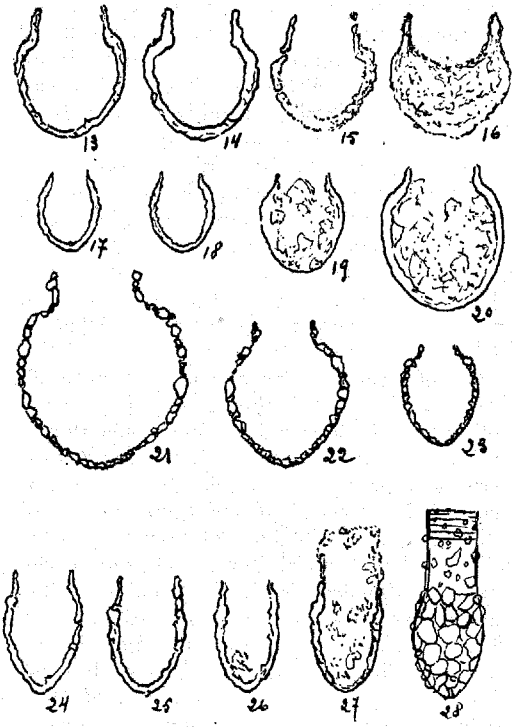

FIG. 3—Copies of figures *13* to *28* from Deflandre (Bull. Soc. Française de Micr., vol. 5, 1936). *13, 14, Calpionella alpina* Lorenz (Mesozoic, Alpine Tithonian Brunig); *15, 16* two tangential sections of *C. alpina* from the Alpine Tithonian, one (*15*) very oblique and showing an apparent lengthening of the oral collar, the other (*16*) very superficial and almost transverse to the upper level of an oblique lorica; *17–19*, small form of *C. alpina* from the Majorcan Hauterivian; *20*, *C. alpina* from the smal slide; *21, 22*, two extreme forms of the living *Stenosemella ventricosa*, longitudinal section; *23*, *S. nucula*, living species, longitudinal section. All figures ×250.

any examples of tintinnids. According to Deflandre (1936), however, the German paleontologist Rüst discovered tintinnid loricas in Jurassic rocks associated with Radiolaria. Such findings should be confirmed by new investigations.

Lorenz (1901) noted in the calcareous cement of the Falknis breach, pertaining to the uppermost levels of the Malm, numerous extremely small microorganisms of very simple structure. He compared them with similar fossils discovered by Steinmann in 1890 in the Jurassic limestones of the torrent of Morgorabbia in the southern part of the Alps and named them *Calpionella alpina*. Lorenz emphasized the stratigraphic importance of these microscopic forms as characteristic of the Vindelician facies of the Tithonian, belonging to the region of the "klippes" of Switzerland. In the following year, Kilian (1902) recorded the presence of *C. alpina* in the Swiss autochthonic series of the environs of Grenoble and wrote, "Le même auteur (Lorenz) a décrit sous le nom de *C. alpina* Lor., un petit foraminifère uniloculaire que se retrouve en quantité dans les calcaires a facies vaseux du tithonique Delphine-Provençal (Bastille, près Grenoble, Col de Cabre). Ces deux organismes peuvent être cités parmis les plus caracteristiques, le premier . . . le second (*C. alpina*) des calcaires tithoniques de la région subalpine." Steinmann (1913) cited these microorganisms in rocks both from the Carpathians and from Spain, localized likewise in Upper Jurassic and Lower Cretaceous strata.

Leon Moret (1925) noted the presence of *Calpionella* and numerous Radiolaria in a series of marly Tithonian limestones in the Isère Valley, near Grenoble. He did not indicate nor distinguish the species observed in his slides, but stated that the presence of tintinnid plankton seemed closely related to the purity of the marly sediment, which is strongly calcareous where they predominate.

In 1927 Andrussoff and Koutek devoted an extensive work to sediments with *C. alpina* Lorenz in the western Carpathians, thus verifying their wide dispersion throughout this zone. They mentioned only the one species, but stated that Radiolaria and *Calpionella* do not occur everywhere with equal frequency in the same strata. This observation is likewise true for their occurrence in strata of the same age in Majorca. The French geologist M. Solignac (1929) in a stratigraphic report recorded *Calpionella* in the Upper Jurassic of Tunis. At about the same time Professor E. Kraus (1929)

again called attention to the stratigraphic value of *C. alpina* and its significance as a type fossil of the Upper Jurassic. Professor J. Cadisch (1932) published an important work on *Calpionella* which includes a detailed study of *C. alpina* and descriptions of two new species, *C. elliptica* and *C. oblonga*. One chapter is devoted to a consideration of their stratigraphic and geographic distribution. This first comprehensive work on *Calpionella* is of great paleontological value. It called attention to these diminutive organisms and no doubt encouraged their investigation by others. The Roumanian geologists Murgeanu and Filipescu (1933) recorded a new species which is common in the Tithonian of the Carpathians of their country, *C. carpathica*. At about the same time another Roumanian, Dr. O. Protescu (1933) mentioned a new species which, so far as I am aware, has never been described and its name, therefore, is a *nomen nudum*.

LATER STUDIES OF FOSSIL TINTINNIDS

In writing on the Lower Cretaceous sediments of the Balearic Islands in 1930 and 1932 I noted the occurrence of *Calpionella* and reported on its vertical distribution in the stratigraphic series. In 1934, in a paleontological paper devoted to these microorganisms from the Balearics, I described a new species, *C. darderi*, summarized what was then known about the Calpionellae in general, and identified them with the loricated, planktonic infusorians of the family Tintinnidae of Claparède and Lachmann. Coinciding with the appearance of this study, an identical reference of *Calpionella* to the Tintinnidae was published in a bibliographical review in the "Palaeontologisches Zentralblatt" (Vol. 5, 1934–35) by Dr. Thalmann. Later, in his review of foraminiferal species published during the year 1933, Thalmann again drew attention to *Calpionella* as well as to another microorganism which is considered at the end of this paper. In this work Thalmann (1935) stated:

> The writer has suggested (he refers to the Palaeont. Zentr.) that the genus *Calpionella* should be removed from the Foraminifera and be classed within the family of the Tintinnidae (Ciliata). Colom, independently, arrived at the same conclusion (Soc. Esp. H. N. 1934).

The genus *Nannoconus* Kamptner, 1939, listed below, in the writer's opinion most probably represents what has been called by de Lapparent (1925) "embryons de Lagena." Thus *Nannoconus steinmanni* Kamptner becomes a synonym of *Lagena colomi* de Lapp, 1931.

Subsequently, study of the Calpionellae has attracted numerous investigators and increased interest in them has paralleled the modern intensification of interest in all kinds of fossil Protozoa. The widespread occurrence of fossil tintinnids in the pelagic faunas of the Tithonian and Neocomian throughout the Mediterranean Tethys has been revealed by the work of numerous geologists and they are now known to extend from the mountains of the Caucasus and Crimea, as reported by Vassoevitch in 1936, to the region of the Spanish Riff, where they were noted by Blumenthal in 1937.

Before the appearance of my note on *Calpionella* in 1934, the taxonomic position of these microoorganisms had been uncertain. They were assigned to the Foraminifera by some, to the Radiolaria by others, or considered to be an indefinite group of "incertae sedis." Dr. Galloway in his "Manual of Foraminifera," referred to the genus *Calpionella* with the remark, "This genus may be a calcareous alga." Dr. Cushman made no mention of them in the various editions of his well-known "Foraminifera." Dr. Kraus, in his study of 1929 previously referred to, denied the validity of the genus *Calpionella* and maintained that forms referred to it belong to the genus *Orbulina*, Foraminifera of the family Globigerinidae, which at the end of their development enclose all their early chambers of globigerinoid growth within a large, spherical, terminal chamber. He supposed that when the tests sank to the sea floor after death, gases formed by decomposition of organic matter within them broke through violently and formed the opening that is the oral aperture of the loricas. This supposition is of course, now untenable.

Professor A. Lombard of Switzerland devoted several papers (1937, 1945) to the study of a diminutive chlorophyllaceous alga belonging to the lowest and simplest groups, *Proto-* and *Pleurococaceas*, to which he gave the name of *Globochaeta alpina*. Its remains abound, according to this author

in certain pelagic Tithonian facies of the Alps. I have found these diminutive algae of Lombard's to be numerous in lower Tithonian strata of Majorca and probably at certain times they constituted an important part of the plankton of that epoch. Lombard believes that the numerous tintinnid loricas which are locally associated with *Globochaeta* represent a phase in the reproductive cycle of the latter (empty zygotes abandoned after sporulation).

I think this is not a reasonable conclusion. The loricas of the very different tintinnid species described and figured in the present work show such diversity of structure that it does not seem possible to interpret them all as simple zygotes, spores etc. of *Globochaeta alpina*. Moreover, the morphological similarities of fossil and living tintinnid loricas seem to me so close and definite that I am content to leave judgment in this matter to the reader.

THE WORK OF PROFESSOR DEFLANDRE

In the "Bulletin de la Société Microscopique de France," Professor Deflandre (1936), well-known author of numerous works on living and fossil Protozoa, agreed with my opinion that the Calpionellae belong to the group of pelagic infusoria of the family Tintinnidae which is well represented in existing seas. In this work, revisional and critical rather than a contribution of new data, he stated that the tintinnids most likely to be fossilized are those having richly agglutinated loricas, and explained the possible process of their fossilization.

One of the most disputed and difficult points in admitting the existence of fossil tintinnids in Mesozoic sediments concerns the explanation as to how it has been possible for the delicate organic loricas of these planktonic infusoria to persist embedded in fine mud until they were replaced by calcite. As I have already stated, much has been published on the morphology of the loricas of living species but it is remarkable how little is known about their actual chemical composition.

Professor Deflandre believes that only loricas containing agglutinated particles could become fossilized in beds of highly calcareous ooze and that completely organic loricas can have left no trace in such strata. He compares species like *Calpionella alpina* Lombard and *C. elliptica* Cadisch with existing forms of the genera *Codonella*, *Codonellopsis* and *Stenosemella*, many of whose species have tests laden with agglutinated particles, and his drawings of thin sections suggest that such a conclusion is substantiated by observed structures. He also compares forms similar to *Calpionella carpathica* Murgeanu and Filipescu with various existing species of the genus *Tintinnopsis*, whose loricas are covered with minute grains of sand, etc. Such loricas, deposited with enormous numbers of the diminutive discs of *Coccolithoforidae* in the extremely fine Tithonian-Neocomian oozes would be rapidly buried and soon fossilized by the action of abundant calcium carbonate.

I have noticed some *Calpionella* loricas, which I included in 1939 in the genus *Favelloides*, that show extremely delicate structure when highly magnified. Within the thin mass of calcite of uniform optical orientation which reveals no grains, it is possible to distinguish a series of very fine, compressed partitions, transverse to the axis of the test, apparently similar to structures described by different investigators for certain living species. These are not uniformly orientated calcite crystals formed on the lorica walls such as occur on many specimens but rather an arrangement within the calcite which certainly reveals the primitive structure of the lorica. These observations, I believe, indicate the possibility that rapid replacement of the delicate primary structure of loricas lacking agglutinated material may have occurred, although I must admit that such preservation is not abundant among the innumerable sections of fossil tintinnids that appear in my slides. Although agglutinated tests are more likely to have been fossilized in Mesozoic strata, I am convinced that under certain conditions completely organic loricas have been replaced by calcite. This is not the only example that paleontology offers of delicate soft parts being replaced in such a manner.

Deflandre compares *Calpionella alpina* Lorenz with the existing species *Stenosemella ventricosa* (Claparède and Lachmann), common in the Mediterranean plankton, whose loricas are abundantly covered with

grains of quartz or calcite. He also found in the Tithonian limestones of Majorca a form of *C. alpina* characterized by its small size and comparable for that reason to another existing species of the same genus, *S. nucula*, with which it coincides in shape and dimensions. These comparisons are very convincing and for that reason I reproduce his drawings (fig. 3). Also, according to the same author, *Calpionella elliptica* Cadisch presents, as I have pointed out above, a strange analogy to *Codonellopsis lusitanica* Jörgensen of the existing plankton. This modern genus, and especially this species of Jörgensen, has a strongly arenaceous lorica continued by a long hialine neck which also may be covered with sand granules. Except for this neck *Codonellopsis lusitanica* bears an extraordinary resemblance to the fossil loricas of *Calpionella elliptica*, as is clearly shown by Deflandre's figures reproduced here (fig. 3). The resemblance between these two species is even more striking if one takes into consideration the existence of specimens of *C. elliptica* possessing a hialine neck (more or less blurred but unmistakable) such as Deflandre has figured and I have described above and illustrated by fig. 11—*72*.

Calpionella carpathica Murg.-Filip. is compared by Deflandre with different species of the genus *Tintinnopsis*, especially with *T. schotti*, *T. orientalis* (Fig. 10—*11*) and *T. loricata* (Fig. 10—*4*). All these living species have agglutinated loricas which could be fossilized in calcareous sediments. Also they all have oral openings similar to that of *C. carpathica*.

Professor Deflandre points out that he does not make these comparisons to suggest the identification of fossil forms with living ones, but only to emphasize the identity of structures in fossil Mesozoic Calpionellae and living tintinnids. He states: "Les calcaires a Calpionelles sont donc des calcaires a Tintinnoidiens." And in concluding his paper he remarks: "Est-il désirable d'appliquer dès maintenant aux Tintinnoidiens fossiles les noms des genres actuels? Je ne le pense pas, car les biologistes eux-mêmes ne sont pas encore entièrement d'accord sur l'acceptation de ces derniers. Disons seulement que les genres actuels *Tintinnopsis*, *Codonellopsis* et *Stenosemella* florissaient déjà vers la fin de l'époque jurassique et reservons encore quelque temps aux espèces fossiles le nom de Calpionella, en évitant bien entendu de créer abusivement des genres nouveaux pour les Tintinnoidiens fossiles. Il reste, c'est bien certain, d'autres espèces de Calpionelles a découvrir."

I have no desire to complicate the systematic arrangement of fossil tintinnids (in this I agree with Professor Deflandre) but it has been necessary to create new genera. Upon the discovery in 1939 of fossil loricas whose characters coincide perfectly with those of the living genera *Favella* and *Rhabdonella*, I decided to propose two new fossil genera, *Favelloides* and *Rhabdonelloides*, because it did not seem prudent to include them in Lorenz' primitive genus *Calpionella*, which they do not resemble. In continuing this study, it has not seemed advisable to include in *Calpionella* a series of newly discovered loricas whose structural features differ greatly from those characteristic of that genus. Accordingly, I have been obliged (Deflandre anticipated this would be necessary) to alter the whole systematic arrangement of this group, adapting it to the newly discovered fossils and also to our present knowledge of all the species described. For that reason I have distinguished a few new genera and have distributed the species in different groups according to their more notable affinities but I have retained in Lorenz' genus, *Calpionella*, the forms most intimately related to *C. alpina*, the type of this genus. I have been careful not to distinguish numerous species because of the uncertainties previously discussed.

Before describing new genera and species I have studied, whenever possible, numerous well-oriented sections in order to minimize the possibility of basing determinations on differently oriented sections or deformed specimens. With few exceptions, new species are abundant at certain particular Balearic localities.

The data presented by Deflandre and my own investigations have profoundly modified concepts regarding the morphology of the loricas of these fossils and their systematic arrangement. With the new information presented here, the simplicity of the earlier classification of the Calpionellae,

when only five species—*C. alpina*, *C. elliptica*, *C. oblonga*, *C. carpathica*, *C. darderi*—were known, disappears and a group of well defined but quite variable organisms becomes apparent that is similar to a living group now inhabiting marine waters in great abundance.

The systematic strictness of definition and description used by investigators of the living animals cannot be applied to fossil material preserved as calcite replacements in limestone. The Tithonian or Neocomian fossils of Majorca do not provide the micropaleontologist with as exact and conclusive data as might be desired and ample margin for varied interpretations of certain features will always remain. A study of all the species described in the following pages reveals the existence of a large group of organisms exhibiting great specific and generic diversity of structures which would be classified by planktologists in many different groups. A similar classification of fossil specimens, however, is not possible because the fine structural details of the Tithonian or Neocomian loricas have mostly been destroyed and the simple outlines that remain are not easy to interpret.

DESCRIPTION OF GENERA AND SPECIES

Genus CALPIONELLA Lorenz, 1901

Genotype, *Calpionella alpina* Lorenz

This genus includes those species whose loricas are morphologically similar to Lorenz' type species, *C. alpina*.

Lorica globular, oval or cylindrical, usually rounded at the aboral end but in some specimens pointed. Certain species have an oral collar extending straight forward from the lorica and a thickening of the test near its point of insertion, but in others the collar is wanting.

CALPIONELLA ALPINA Lorenz, 1901

Figure 11—*1, 22–33, 35–43*

C. alpina LORENZ, 1901, Geolog. Stud. Grenzg. Zwischen Helv. Ostalp. Faz., Naturf., Ges., Freiburg.—CADISCH, 1932, Geolog. Rundschau vol. 23, p. 248, figs. 1–2 (text) and fig. 3 (text), no. 1–9.—COLOM, 1934, Bol. R. Soc., Española Hist. Nat., vol. 34, p. 380, pl. 30, figs. 1–3.—DEFLANDRE, 1936, Bull. Soc. Française Microscop., vol. 5, p. 116, figs. 13–23.—COLOM, 1939, "Las Ciencias" Año 4, no. 4, p. 8.

The more typical specimens of *C. alpina* have spheroidal loricas with rather prominent, forward projecting collars. The walls are thin, somewhat sinuous and tend to narrow slightly at the lowered end of the lorica (Fig. 11—*22–26, 31–33, 35, 36*) other specimens are more oval in section or even almost elliptical (Fig. 11—*28, 40–42*. In both groups loricas with more or less pointed aboral portions have been observed but I have found none with any clearly visible caudal prolongation, such as occurs in other species.

The largest loricas measure 110μ in length by about 80μ in width but are rather exceptional. A common average is 80μ in length by 60μ in width but forms 70 by 55μ are nearly as abundant. Measurements of 31 typical specimens may be grouped as follows:

Length of the lorica	50–60–70–80–90–100–110 microns.
Number of specimens	1 6 3 12 6 0 2

Two modes are apparent, one at about 60μ and another, more prominent, between 80 and 90μ. Width measurements show corresponding modes at 40 and 60μ, of which the former is more prominent. These data might reasonably justify the distinction of two races in *C. alpina*, as Deflandre has suggested but to determine adequately variations within this species a much larger number of individual measurements are required.

The study of large populations of *C. alpina* seems to confirm the existence of a diminutive race of this species. Deflandre compared it to the living species *Stenosemella nucula* (Fol.), which is always found associated with *S. ventricosa* (Clap.-Lach.), of larger size. Figs. 11—*22, 23, 28, 38, 39* illustrate various specimens of this small form. The smallest loricas are 43μ long by 38μ wide. These measurements differ somewhat from those given by Deflandre which vary from 35 to 47μ in length. Most of his specimens measure about 50 by 40μ (fig. 3, text).

In considering the possible existence of a small race, it must not be forgotten, however, that many small lorica sections may correspond to somewhat tangential cuttings of loricas of normal dimensions.

Calpionella alpina is common in tintinnid-

bearing facies. Its tiny, horse shoe-shaped sections appear white against the greenish-gray matrix of the sediment. This species seems to be very widely distributed in the Tithonian of the Mediterranean region.

CALPIONELLA ELLIPTICA Cadisch, 1932
Figure 11—*2, 51–81*

C. elliptica CADISCH, 1932, Geol. Rundschau. vol. 23, p. 241, fig. 3 (text), n. 10–11, 17, 25–26. —COLOM, 1934, Bol. R. Soc. Española Hist, Nat., vol. 34, p. 380, pl. 30, figs. 4–6.—COLOM, 1939, "Las Ciencias," Año 4, no. 4, p. 8.—DEFLANDRE, 1936, Bull. Soc. Française Microscop., vol. 5, no. 3, p. 118, figs. 24–26 (text).

In general characters this species is closely related to the last. It has the same oral zone and collar. It differs from *C. alpina*, however, in having a longer lorica, with parallel sides, which gives the whole test an elliptical form in section. In many specimens the aboral zone is pointed and seems to reveal the existence of a caudal extension (Fig. 11—*65–68, 73, 75–77*). This supposition seems well founded if one takes into account the specimen with characters typical of *C. elliptica* figured in Figure 11—*64*, and provided with a long caudal appendage.

The largest specimens of *C. elliptica* measure 110μ in length by 56μ in width but they are not common. Those that appear in greatest abundance reach a length of about 85μ, and a width of 50μ. The smallest are about 60 by 38μ respectively.

This species almost always is associated with the last but I agree with Dr. Cadisch that there are no intermediate forms. The size distribution indicates that *C. elliptica* is a very homogenous group with only a single mode.

The measurements of 31 specimens are grouped as follows:

Length of the lorica	50–60–70–80–90–100 microns.
Number of specimens	2– 4– 4–13– 6– 2
Width of the lorica	30–40–50–60 microns.
Number of specimens	10–11– 8– 3

The figures of the two species, *C. alpina* and *C. elliptica*, (Fig. 11) show this constancy clearly. Although certain sections may not appear so distinctive, it must be remembered that if they are not cut parallel to the longitudinal axis of the lorica slight discrepancies will result.

As previously mentioned, some specimens of *C. elliptica* show traces of a long, more or less altered, cylindrical neck, set upon the oral collar. Deflandre in his paper of 1936 figured a specimen of this kind (fig. 3, no. 27; text) from the Alpine Tithonian and my slides from Majorca also show sections with similar structures. In one of my sections the neck is very complete (Fig. 11—*72*) and flaring at its free end. It is shown by a series of fine calcite granules, faintly marking its outline and is not as clear as the rest of the lorica but there can be no doubt as to its existence or interpretation (fig. 3, no. 27).

It might be possible to completely reconstruct this species on the basis of the three different but related kinds of loricas (with or without a caudal prolongation, or with a long cylindrical neck) and classify it as a species of the existing genus *Codonellopsis* very close to the living species *C. lusitanica* Jörgenson, as Deflandre has done. If so it would be the first exact reconstruction of a fossil tintinnid but certain doubts would necessarily remain. Therefore I consider it inadvisable to separate this species from its original genus by transfering it to *Codonellopsis*, and I only wish to point out how reasonable Professor Deflandre's comparisons seem to be, in view of the new information furnished by my Balearic material.

C. elliptica is commonly present in the upper strata of the Tithonian and in the Berrasian of Majorca.

CALPIONELLA UNDELLOIDES Colom, 1939
Figures 11—*3, 34, 47, 49, 55*

C. undelloides COLOM, 1939, "Las Ciencias" Año 4, no. 4, p. 6, pl. 2, fig. 12.

This is a small species with an oval lorica

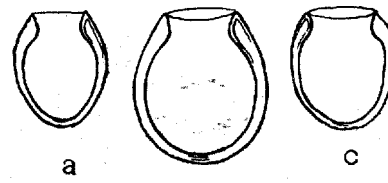

FIG. 4—*Undella claparedei. a, U. claparedei* form *angustior* Jörgensen; *b, U. claparedei* (Entz) Daday, after Jörgensen; *c, U. claparedei* form *fastigata* Jörgensen. Median longitudinal sections.