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SYSTEMATICS OF THE ALVEOLINIDS OF THE TREMP BASIN, SOUTH-CENTRAL PYRENEES, SPAIN

BY

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ABSTRACT

The Alveolinidae of the Ager Formation (Upper Paleocene–Lower Eocene) in the Tremp Basin have been studied systematically. The commonly used genus name *Alveolina* has been replaced by *Fasciolites* because the former is a junior synonym of the latter. One new subgenus, *Microfasciolites*, and one new species, *Fasciolites (Microfasciolites) agerensis*, have been established. The new species is the intermediate form between *F.* (*M.*) *subtilis* and *F.* (*M.*) *boscii*. Many species described by Hottinger (1962) and Drobne (1977) appear to be identical with other species, so that the picture of the evolution of the family becomes simpler and more easily surveyed.

INTRODUCTION

The primary aim of this study of the alveolinids of the Tremp Basin is to acquire a tool for the correlation of the measured sections in that area. A complete revision of the systematics of the alveolinids is not the intention; for this purpose this investigation of the alveolinids is not extensive enough, since it covers only part of one basin during a relatively short interval of time. Nevertheless it is necessary to treat some parts of the alveolinid systematics in some detail, especially when the concepts involved differ from those presented in the literature. Since Hottinger's work is the most recent important publication in this field, most references concern this work. For the identification of the alveolinid species Hottinger's publications of 1960 and 1962 were very helpful; the latter is usually incorrectly assumed to have been written in 1960 too because that is the year which has been printed on the cover. In addition the works of Reichel (1936, 1937), Checchia-Rispoli (1905, 1909), Schwager (1883) and Leymerie (1846) were also used for identification purposes.

The geographical position of the sections mentioned in this publication can be found in my PhD thesis (Gaemers, 1978) in which the palaeoecology and evolution of the alveolinids and biozonation based on these foraminifera are also discussed. The type material of the new species *F.* (*M.*) *agerensis* has been deposited in the Rijksmuseum van Geologie en Mineralogie (RGM), Hooglandse Kerkgracht 17, Leiden.

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METHODS

In the first instance the alveolinids were examined directly in thin sections under the microscope. The results were described in a previous paper (Gaemers, 1971). In this unpublished report an attempt was made to follow Hottinger's concepts (1960, 1962) entirely, assuming that all species which he described were separate species.

The disadvantage of the approach followed at that time was that the specimens could only be studied successively. This implies that every characteristic of each previously studied specimen had to be remembered. Thus comparison of the specimens was hampered and a total survey was not obtained. When not only the proportions and shapes but also the absolute sizes are important for identification of a group of fossils, memory cannot be relied upon. It then becomes rather easy for subjective ideas to interfere with the identifications.

Therefore the following method based on suggestions by Hottinger (1962, 1963) was now used. All perfect and nearly perfect axial sections present in the sections were photographed and printed at a twenty-fold magnification, so that they could be compared immediately with most of Hottinger's pictures (1962). Thus many hundreds of photographs were acquired. The alveolinids of each stratigraphic section were placed in vertical rows with the oldest known specimens at the bottom and the youngest at the top. By means of the identification of the species horizontal rows could be formed, which resulted in the biostratigraphical correlations.

In this manner a total survey was obtained and the similarities and differences between the alveolinid faunas of successive stratigraphical units could be studied more conveniently. It can easily be ascertained which intervals of

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which sections have not yet furnished enough well-oriented alveolinid sections for accurate correlation.

There can be two reasons for the shortage or deficiency of alveolinids. Firstly, more thin sections of the important alveolinids of a specific species may be necessary before the exact place within the lineage can be determined; secondly, it may be necessary to look for other as yet unknown alveolinid species because the available species do not yield an age determination of sufficient precision.

PROBLEMS OF IDENTIFICATION

With this method it soon became clear that many of the photographed specimens were transitional forms between two known species. Two possibilities exist: the transitional forms are either intermediate between two species of different stratigraphical horizons or are intermediate between two more or less extreme forms of the same geological age which apparently belong to one species of marked variability.

The only way of tackling this problem is to begin by studying the range of variation of the species in question. Here a difficulty arises. How do we know for sure that the specimens present in a certain stratigraphical horizon belong to one population? A thanatocoenosis may have been built up of elements that come from different places and ages. If the differences in space and time are insignificant or absent, we may assume that the differences between the specimens represent the true variability of that species. The state of preservation of the fossils, the sort of sediment in which they are found and the sedimentary structures can help us determine the environmental conditions which existed at the time of deposition. Then a reasonable estimation of the possible differences in space and time can be made. For most of the sediments within the Tremp Basin it is justifiable to presume that little mixing occurred (see also Gaemers, 1978, Chapter IV).

Another problem is that it is usually difficult to obtain numerous axial sections of the specimens of one species in one rock sample. Therefore the study of the variation depends on only a few axial sections from one sample; however we can make use of the study of specimens from horizons in the same section which are slightly higher or lower, at least when it is known that only slight differences in stratigraphic level exist. In this manner we begin to acquire some idea of the variability within a species. Then we look for specimens in other stratigraphical sections which fall within the known range of variation. If we find such material together with still other variants which can be assigned to the same species, our insight into the range of variation increases and true variability will be closely approximated.

In the next stage the transitional forms which exist as a result of differences in geological age must be distinguished from those which exist thanks to intraspecies variation. Hereby it has to be remembered that within an evolutionary lineage some specimens of a population of a given species can resemble the majority of the specimens of its forerunner species or its descendant species. Therefore it is always best to study as many specimens of a species from one sample as possible in order to have some degree of certainty regarding the kind of transition, the identification of the species and consequently the geological age.

Variability is usually pronounced in alveolinid species. Reichel (1936, 1937, p. 18) writes that the degree of elongation of the skeleton is the main variable characteristic of the alveolinids. This is confirmed by the present study. Since the elongation is also one of the most important characteristics used to distinguish the species within an evolutionary lineage, identification can be exceedingly difficult. This fact, together with the pronounced symmetry of these foraminifera (the coiling axis can be considered the axis of radial symmetry; the equatorial plane is a clear plane of symmetry) whereby the number of specific characteristics is considerably limited, makes it very difficult to distinguish many alveolinid species. Some investigators of alveolinids have therefore tried to keep the number of species as small as possible, for instance Osimo (1909). Unfortunately she lumped many different forms within one species, so that her system becomes illogical and intractable. On the other hand Hottinger (1960, 1962), who studied the alveolinids in much more detail and much more carefully, introduced a large number of new species. His ideas approximate the real relationships much better than those of investigators like Osimo, although he distinguished too many species. Unfortunately this has led to the disastrous tendency to split the alveolinids into still more species, as Drobne has done (1975, 1977).

Some remarks have to be made about Hottinger's concept of a species. Hottinger (1962, p. 10, 11) bases his concept of a species mainly on de la Harpe (1883) and Boussac (1911). De la Harpe's basic assumption was that an analogous form which is not precisely identical to a previously known species, and was found in a clearly different stratigraphic horizon, may definitely be considered as a different species, whereas the species concept should be interpreted as broadly as possible within a stratigraphic horizon – thus including as many variations as possible. This definition is dependent on two ideas which cannot be substantiated. The main difficulty is that such an analogous form usually falls within the range of variation of a known species. Certainly a new alveolinid species remains doubtful as long as we only have one or a small number of specimens. Moreover the problem is that we want to determine with the help of the alveolinids the age of the rock in which the fossils have been found. There is no other way to know whether, when we compare two rock samples from different places, the stratigraphic horizon is the same or not. In such a case it is unacceptable to start with the idea that the geological ages of the two samples are exactly the same or obviously different. We have to prove the stratigraphic relationship by means of the guide fossils.

Sometimes Hottinger (1960, 1962) seems to start with a fixed stratigraphic framework which the alveolinid species must follow, instead of using the reverse method of identifying the alveolinids first and then deriving the biostratigraphic zonation. Such mistakes are made easily if the species concept of de la Harpe is followed rigorously.

Stratigraphers have to look for fossils which answer the description of Boussac (1911): "En un mot, nos espèces seront étendues au sens très large dans la direction horizontale et au sens étroit du mot dans la direction verticale, de façon à leur donner le maximum de rendement au point de vue stratigraphique, l'utilisation géologique des fossiles restant toujours notre préoccupation dominante". In practice however no species can satisfy these requirements completely, because the time range of the best of fossils is still large compared to the subdivision we wish to make in stratigraphy. Many groups of fossils are even so restricted geographically or evolve so slowly that they are useless for accurate time identifications. It has to be remembered that each species, also a useful one, has its own limitations due to ecological, geographic and evolutionary factors. All of these factors have to be studied for each important species in order to obtain a general picture of the fossils that agrees as much as possible with reality. With this knowledge reliable biostratigraphic correlations can be made.

The problem of flosculinization (this phenomenon was named after the former subgenus *Flosculina* Stache in Schwager, 1883) is also important for the delimitation of alveolinid species. Hottinger (1962, p. 9) tried to resolve this problem statistically, but he did not succeed. It is hard to believe that flosculinization has no taxonomic value at all, for many flosculinized forms certainly do not have narrowly coiled counterparts which are geologically synchronous. Therefore Bakx's statement (1932) that flosculinization cannot be used for species identification is not correct. Hottinger (1962) on the other hand has exaggerated the value of this characteristic so much that he considers subtle differences in flosculinization to be sufficient for the differentiation of a large number of species. Variation in flosculinization within a species however is usually so marked that it is not justifiable to attach so much value to this characteristic. Many species defined by Hottinger indeed also show considerable variability in this respect.

Moreover the number of narrowly coiled first coils before the occurrence of flosculinization is more variable than Hottinger suggests. The same applied to the presence or absence of such coils. Unfortunately he has based many of his identifications on this characteristic; he has even introduced new groups of alveolinids on this basis.

Some of the results of the present investigation may be important as far as the problem of flosculinization is concerned. In the first place the Late Paleocene flosculinized alveolinids are highly variable with respect to flosculinization. These species are *Fasciolites avellanus, F. globulus* and *F. globosus*; they are common in the area studied and have been identified with certainty. Hottinger (1962, pl. 3, 4) also noted the marked variability of this characteristic in these species. It is very interesting to see that the shape and the size of the chamberlets change considerably with the degree of flosculinization. The chamberlets are small and low (flattened) if there is distinct flosculinization. If flosculinization is insignificant the chamberlets are relatively large and more rounded. With intermediate flosculinization the chamberlets are transitional in shape and size. We have to be careful when using these characteristics for identifications because they apparently are closely related. In species like *F. pasticillatus* which show a sudden change from the stage of accelerated growth with flosculinization to the senile stage without flosculinization, we observe a simultaneous rapid change in the shape and the size of the chamberlets. In the stage of accelerated growth they are small and flattened; in the senile stage they are much larger and moreover distinctly higher than long. The rapid increase in the size of the chamberlets during the transitional stage between these two forms of *F. pasticillatus* can easily be distinguished from the normal increase in the size of the chamberlets in the outer coils. The latter increase is present in all alveolinids and is characterized by gradual changes in shape and size. A good example of these gradual changes is *F. varians* (Hottinger, 1962, figs. 12 and 65).

Therefore if we want to use the shape and the size of the chamberlets as a means of identification, it will be necessary to study first the properties of the chamberlets in all growth stages.

SYSTEMATIC DESCRIPTIONS

Phylum PROTOZOA
Superclassis RHIZOPODA Siebold, 1845
(= SARCODINA Hertwig & Lesser, 1874)
Ordo FORAMINIFERA d'Orbigny, 1826
Familia ALVEOLINIDAE Ehrenberg, 1839

There is considerable confusion in the literature concerning the nomenclature of the Palaeogene alveolinids. Most investigators have used the genus name *Alveolina* d'Orbigny, 1826, but this is not in accordance with the rules of the International Code of Zoological Nomenclature (ICZN).

"The nominal genus *Alveolina* d'Orbigny, 1826, from which the family containing *Borelis* has been named and become widely known, is unquestionably a junior objective synonym, since *Nautilus melo* Fichtel & Moll, 1798, according to provisions of the international Rules of Nomenclature, is the type-species of both. For *Borelis* this is fixed by original designation. D'Orbigny did not designate any of the 7 species assigned by him to *Alveolina* as type-species and therefore the first author who selected one of these eligible species to be the type established it unalterably. Such first valid designation was made by Parker & Jones, 1860, when they choose *Nautilus melo,* one of the original 7 species named by d'Orbigny, as type-species of *Alveolina*" (Moore in Reichel, 1964, p. C506). "No named species originally were included in *Fasciolites*. *Alveolina oblonga* d'Orbigny was based on specimens collected by him from the Eocene (Cuisian) of France, and *Fasciolites* Parkinson was mentioned by d'Orbigny as a synonym of *Alveolina*" (Moore in Reichel, 1964, p. C508). *Alveolina oblonga* must be regarded as the type species of *Fasciolites* because the specimen shown by Parkinson (1811, pl. 10, figs. 28–31) belongs to this species. The designation of *Alveolina boscii* as the type species of the genus *Alveolina* by H. Douvillé (1906), as mentioned by Hottinger (1962), has no taxonomic value since this designation was established much later than that of Parker & Jones (1860).

The nominal subgenus *Glomalveolina* was introduced by Reichel (1936), but it has the status of a nomen nudum because Reichel did not designate a valid type species, viz.

Alveolina ovulum, as required by the ICZN for publications after 1930 (1961, Art. 13b). Moreover Reichel hid this subgenus quite well: he mentions *Glomalveolina* only once on p. 80 and in the caption of pl. 11. In the other plates and remaining text the name *Glomalveolina* never occurs.

Hottinger (1962) validated *Glomalveolina* with the designation of *Alveolina dachelensis* Schwager as its type species. "The provisional use of *A. dachelensis* by Schwager and attribution of *Glomalveolina* to Reichel by Hottinger have no effect on the validity of *A. dachelensis* and recognition of Hottinger as author of *Glomalveolina*. Also the date of this nominal subgenus must be given as 1962 – not 1936" (Moore in Reichel, 1964, p. C510).

Glomalveolina should indeed be regarded as a junior synonym of *Fasciolites* because the irregular nepionic coiling of the first spirals (Fr. pélotonnement) in the megalospheric forms is not a permanent characteristic during the evolution of the alveolinids. There are two clear-cut examples to prove this. The small species '*Alveolina* (*Glomalveolina*)' *dachelensis* with irregular nepionic coiling in microspheric and megalospheric forms is an ancestor of *Fasciolites ellipsoidalis* and probably also of other species such as *F. dolioliformis*, *F. globulus* and *F. avellanus*. All of these species only show irregular nepionic coiling in the microspheric forms. *Alveolina boscii* with practically no irregular nepionic coiling in the megalospheric forms is a descendant of *Fasciolites* (*Microfasciolites*) *subtilis* which is characterized by irregular nepionic coiling in both forms.

Genus FASCIOLITES Parkinson, 1811

Alveolina auctt. (partim) non d'Orbigny, 1826.
Flosculina Stache in Schwager, 1883, p. 102.
Eoalveolinella Silvestri, 1928, p. 35.

Subgenus MICROFASCIOLITES n. subg.

Diagnosis. – Small alveolinids; megalospheric specimens always possess a small proloculus. Spirals are tightly coiled. Basal layer is thin, chamberlets are small, septula are slender. In thin sections the appearance as a whole is therefore always very fragile and delicate. Flosculinization does not occur in the known species assigned to this subgenus. Dimorphism is rare, even in highly evolved species.

Species typicus. – *Alveolina boscii* (Defrance in Bronn, 1825).

Derivatio nominis. – Mikros (Gr.) = small. Named for the small size and the delicate internal structure.

Distribution. – Thanetian–Lutetian.

Remarks. – This subgenus includes *Fasciolites* (*Microfasciolites*) *levis*, *F.* (*M.*) *pilulus*, *F.* (*M.*) *lepidulus*, *F.* (*M.*) *telemetensis*, *F.* (*M.*) *subtilis*, *F.* (*M.*) *agerensis*, *F.* (*M.*) *boscii*, *F.* (*M.*) *minutulus* and unidentified forms from the Lutetian found by Hottinger (1962).

How the subgenera *Fasciolites* and *Microfasciolites* are related to one another is not yet clear. Hottinger (1962) suggested that *Fasciolites primaevus* might be the ancestral form for all Palaeogene alveolinids. Distinct transitional forms between the two subgenera have not however been found as yet in sufficient numbers.

In the area studied the following species were identified with certainty in the thin sections: *F.* (*M.*) *lepidulus*, *F.* (*M.*) *pilulus*, *F.* (*M.*) *minutulus*, *F.* (*M.*) *boscii*, and the new species *F.* (*M.*) *agerensis*.

F. (*M.*) *lepidulus* is by far the most common species of this group and is most numerous in the *F. cucumiformis* and *F. ellipsoidalis* Zones, but has been found up to and including the *F. trempinus* Zone; this confirms Hottinger's findings (1962). *F.* (*M.*) *pilulus* is much less abundant; moreover its stratigraphic range is much shorter. *F.* (*M.*) *boscii* has been assigned definitely to this group, because an intermediate form between this species and *F.* (*M.*) *subtilis* has been discovered which is also intermediate stratigraphically. Hottinger (1962, p. 150; 1963, p. 301) had already observed that *F.* (*M.*) *boscii* has many characteristics in common with the other small alveolinids. Its delicate and fragile structure, its small size compared with contemporary species, and its slight dimorphism had already indicated that *F. boscii* together with most small alveolinids might be placed in a distinct group, that is in a subgenus of *Fasciolites*.

Fasciolites (*Microfasciolites*) *boscii* lineage

Fasciolites (*Microfasciolites*) *agerensis* n. sp.
(Pl. 1, Figs. 1–18; Pl. 2, Fig. 8)

Type. – Holotype: megalospheric form; Pl. 1, Fig. 2; Pl. 2, Fig. 8, Coll. RGM 248 615. Paratypes: Pl. 1, Figs. 1, 3–18.

Locus typicus. – Section F, 1 km SE of Sant Cerni, province of Lérida, Spain.

Stratum typicum. – Base of *F. corbaricus* Zone (sample F-45), Ager Formation, Early Eocene.

Derivatio nominis. – Named for the Ager Formation in which the species was found.

Diagnosis. – A distinctly elongated *Microfasciolites* species which normally has clearly pointed poles. Usually the elongation index varies between 2.5 and 2.8 in full-grown specimens.

Description. – External characteristics: small alveolinids which generally have clearly pointed poles. Sometimes the poles are slightly rounded. Elongation index using the outermost preserved spiral of the holotype (11th spiral) is 2.55. For the most slender megalospheric specimen a value of 2.83 was obtained using the tenth regular spiral. Microspheric forms seem to be more variable in this respect; the most extreme values measured for the eleventh regular spiral are 2.35 and 3.29. The largest equatorial diameter, 1.41 mm, was found for the shortest microspheric specimen. The greatest axial length is 3.6 mm (microspheric form). As a rule the axial length does not exceed 2.9 mm.

Internal characteristics: no distinct differences were found between megalospheric and microspheric specimens, only the number of irregular nepionic coils generally differed. Microspheric forms have two or three coils which are irregularly wound like a clew as in the Miliolidae. Megalospheric forms generally have no or only one irregular nepionic coil; however in one example, which also has the smallest proloculus, two such coils occur. The spherical or slightly oval proloculus of megalospheric forms varies from 70 to 120 μm (8 measurements). In an equatorial section of a microspheric form (sample F-42) with three irregular nepionic coils, 6 chambers were counted in the fifth regular spiral, 7 in the sixth spiral, 8 in the seventh spiral, 10 in the eighth spiral and 11 in the ninth spiral. The chamberlets are predominantly circular in shape. In the internal spirals they can be slightly flattened and in the external spirals they are often slightly oval, being somewhat higher than they are long. The size of the chamberlets does not increase very much towards the senile spirals. The basal layer and the roof of the chambers are equally thick near the equatorial section. The basal layer is only thickened at the poles; this is clearly visible. The septula are fragile as a result of their thin mid-sections.

Material. – 9 well-oriented thin sections of microspheric forms and 5 good sections of megalospheric forms. 9 thin sections parallel to the axial section close to the proloculus. 4 oblique sections of megalospheric forms through the proloculus. A large number of poorly oriented sections. Nearly all of these specimens are from section F (1 km SE of Sant Cerni); a few specimens are from section J (near Guardia de Tremp). The species also occurs in sections A, B, C, E, I, K, L, M, N, O, W and X'.
F. ellipsoidalis Zone: sample F-24, 1 thin section, Coll. RGM 248 607.
F. moussoulensis Zone: sample F-33, 3 thin sections, Coll. RGM 248 608, 248 609, 248 610; sample F-42, 2 thin sections, Coll. RGM 248 611, 248 612.
F. corbaricus Zone: sample F-44, 2 thin sections, Coll. RGM 248 613, 248 614; sample F-45, 6 thin sections, Coll. RGM 248 615 (holotype), 248 616–248 620; sample F-45t, 1 thin section, Coll. RGM 248 621; sample J-29, 1 thin section, Coll. RGM 248 622.

Stratigraphic distribution. – Upper part of the *F. ellipsoidalis* Zone – lowermost part of *F. corbaricus* Zone (Upper Paleocene–lowest Lower Eocene).

In the area studied *F. (M.) agerensis* occurs in sediments which belong to the upper part of the *F. ellipsoidalis* Zone up to and including the base of the *F. corbaricus* Zone. Romani (1974) found specimens which can be assigned to this new species together with *F. oblongus* and *F. (F.) ruetimeyeri*, which also proves that *F. (M.) agerensis* occurs in the lowermost part of the *F. corbaricus* Zone.

Ecology. – The most characteristic occurrence of *F. (M.) agerensis* is in a foraminifera association with perforate elements (mainly nummulites) as well as imperforate species (other alveolinids, miliolids and sometimes *Orbitolites*). In some cases it is the only alveolinid species occurring together with nummulites. The alveolinids usually found together with *F. (M.) agerensis* in the Tremp Basin are *F. (F.) subpyrenaicus* (35×), *F. (F.) pasticillatus* (24×) and *F. (F.) leupoldi* (20×). Furthermore the new species often occurs with *F. (M.) lepidulus* (18×), *F. (F.) moussoulensis* (15×) and *F. (F.) corbaricus* (10×). Occasionally the species is found together with *F. (F.) dolioliformis, F. (F.) globosus, F. (F.) ellipsoidalis, F. (F.) decipiens* (5–7×). Only once or twice was the species accompanied by *F. (F.) fornasinii, F. (F.) parvus* or *F. (F.) oblongus*. The number of times *F. (M.) agerensis* was found together with the other species is given in parentheses. From these data we may conclude that *F. (M.) agerensis* certainly lived in biocoenoses with all of the species of the first group.

Within the stratigraphic sequence F-22 to F-45t, *F. (M.) agerensis* is almost continuously present. It is only missing in the few cases when *F. moussoulensis* is common to very common or when the sediment was not appropriate. *F. (M.) agerensis* flourished on pure or fairly pure lime mud bottoms, since it has been found almost exclusively in such sediments. It tolerated only a small amount of clay, silt or sand.

It is striking that large quantities of fossil fragments nearly always accompany this species. The fragments are generally parts of various foraminifera but also include skeletons of larger animals such as solitary corals and pelecypods; the presence of these fragments proves that current velocities were considerable at these locations.

Its presence in a mixed perforate-imperforate foraminifera association (facies XI and XII; see Gaemers, 1978) means that *F. (M.) agerensis* lived at depths of at least 20–30 metres. It evidently could not live in very shallow waters, because many sections containing only imperforate associations in the stratigraphic range of *F. (M.) agerensis* do not include this species. The maximum depth of occurrence can be placed at about 50 metres. Conditions were not suitable for *F. (M.) agerensis* in numerous sections along the axis of the basin. In many places the rate of sedimentation was rather high, as was the rate of subsidence; mainly clay was deposited in such an area. Large quantities of clay could not be endured by alveolinids.

Discussions. – In all respects *F. (M.) agerensis* is the intermediate form between *F. (M.) subtilis* and *F. (M.) boscii*. The size of the proloculus, the number of chambers in the spirals, the elongation index, and the thickening of the basal layer at the poles are always intermediate between those of the two previously known species. Stratigraphically and ecologically the new species is also intermediate.

Fasciolites (Microfasciolites) boscii (Defrance in Bronn, 1825)
(Pl. 1, Figs. 19–24)

Discussion. – As can be seen from the photographs the variability within this species is high. The variation in elongation is the most conspicuous, although compact forms like that seen in Pl. 1, Fig. 21 are rare. The size of the proloculus of megalospheric forms also varies markedly.

The architecture of the skeleton is generally quite regular. Pl. 1, Fig. 22 shows the most aberrant specimen in this respect; here the elongation increases suddenly after the first seven spirals. Microspheric forms tend to be somewhat more elongated than megalospheric ones.

Subgenus FASCIOLITES Parkinson, 1811

Species typicus. – *Alveolina oblonga* d'Orbigny, 1826.

Type of Alveolina oblonga. – Lectotype: text-fig. 75 in Hottinger, 1962, p. 142; Coll. d'Orbigny, Muséum National d'Histoire Naturelle, Paris; vicinity of Soissons, Paris Basin, France, Cuisian, Lower Eocene.

Diagnosis. – Generally large alveolinids; megalospheric specimens possess a distinct proloculus. Spirals are loosely coiled. Basal layer always well-developed. Chamberlets are usually large. Septula are strong. In thin sections the appearance as a whole therefore is always solid. Flosculinization can be present. Dimorphism is slight in primitive species and is very obvious in the more highly developed species.

Remarks. – The subgenus *Fasciolites* includes all species which Hottinger (1962) assigned to the subgenus *Alveolina* s.s. Moreover *Alveolina* (*Glomalveolina*) *primaeva*, *A*. (*G*.) *primaeva ludwigi* and *A*. (*G*.) *dachelensis* also belong to this subgenus.

Fasciolites (*Fasciolites*) *oblongus* lineage

All members of this group formed by Hottinger were found again in the Tremp Basin. They are easily distinguished from one another and also from all other groups of alveolinids. The only species which is seldom found is *F*. (*F*.) *trempinus*, the others are frequent and sometimes even abundant.

In contrast to Hottinger (1960, 1962), who prudently assigned *F*. (*F*.) *oblongus* to a group of its own, it seems to me that this species fits within the ellipsoidalis group. Because of the importance of this species for the correlations within the Tremp Basin *F*. (*F*.) *oblongus* is treated here in somewhat more detail.

Fasciolites (*Fasciolites*) *oblongus* d'Orbigny, 1826
(Pl. 1, Fig. 25; Pl. 2, Figs. 1–5; Pl. 3, Figs. 1–6; Pl. 7, Fig. 3)

Alveolina oblonga d'Orbigny, 1826, p. 306.
Alveolina oblonga d'Orbigny; Hottinger, 1962, p. 141, pl. 9, figs. 4–16; text-figs. 5 (no. 10–12), 16, 17, 22k, 75, 76.
Alveolina cf. *oblonga* d'Orbigny; Hottinger, 1962, p. 144, text-fig. 77b.
Alveolina cylindrata Hottinger, 1962, p. 140, pl. 9, figs. 1–3; text-figs. 20f, 21i, 74.
Alveolina (*Alveolina*) *oblonga* d'Orbigny, 1826; Drobne, 1977, p 41, text-fig. 42b.
non *Alveolina* (*Alveolina*) *oblonga* d'Orbigny; Drobne, 1977, pl. 7, figs. 8, 9.
Alveolina (*Alveolina*) *cylindrata* Hottinger; Drobne, 1977, p. 41, pl. 7, fig. 7; text-fig. 42a.

Discussion. – Hottinger (1962) describes *A. cylindrata* as a new species which he found in only one section near Mur. He did not find typical forms of *F*. (*F*.) *oblongus* in the Tremp Basin. Forms, especially megalospheric ones, which are entirely comparable with the pictures of this species (Hottinger, 1962) are however very common in rock samples from many sections in the Tremp area. Sometimes they are accompanied by forms which cannot be distinguished from *A. cylindrata*. According to Hottinger it is difficult to differentiate between megalospheric forms of *A. oblonga* and *A. cylindrata*. For instance the diameter of the megalospheric proloculus of *A. cylindrata* (210–255 μm) falls entirely within the somewhat greater variability of that of *A. oblonga* (175–275 μm). Although *A. cylindrata* should have a less elongated skeleton than *A. oblonga*, the range of variation for the specimens of *A. oblonga* shown by Hottinger (1962) is already so large that some specimens are as short as *A. cylindrata* (see text-fig. 76e and pl. 9, figs. 5, 10, Hottinger, 1962).

Within the Tremp Basin and even within one rock sample it is not difficult to observe a large variation in the elongation of specimens of *F*. (*F*.) *oblongus*. Romani (1974), who has studied some alveolinids in the Ara-Cinca area (southern Pyrenees, province of Huesca, Spain), also found the same marked variability for this species. With multivariate statistical techniques he ascertained that all of his specimens of *F*. (*F*.) *oblongus* fall within a distinct cluster which is clearly separated from the clusters of several other alveolinid species. Moreover a principal coordinate analysis carried out by Romani shows that the specimens of *F. oblongus* described by Hottinger (1962) belong to the same cluster as the specimens collected by Romani himself.

Whereas megalospheric forms of *F. oblongus* are very common in the Tremp Basin, microspheric forms occur only occasionally. An example of a microspheric form is shown in Pl. 3, Fig. 1. Although the section is slightly oblique and does not intersect the proloculus, it is clear that this specimen is highly elongated in comparison with the microspheric forms of Hottinger's *A. cylindrata*.

In the same stratigraphical section (section O) as the highly elongated microspheric *F. oblongus* but much higher in the sequence are relatively short megalospheric specimens of the same species (Pl. 2, Fig. 4; Pl. 3, Fig. 3; Pl. 7, Fig. 3). As the evolution of alveolinids always tends towards more elongated forms, the above-mentioned data again suggest a large variation in the elongation of *F. oblongus*, which also includes *A. cylindrata*. Therefore the somewhat deformed specimen of *A*. cf. *oblonga*? from the Niveau de Coudures (Hottinger, 1962, text-fig. 77b) also easily falls within the range of variation of *F. oblongus*.

Drobne (1977) shows two alveolinids (pl. 7, figs. 8, 9) which she has assigned to *A*. (*A*.) *oblonga*. The shape of the spirals near the poles of both specimens however does not look like that of this species, but instead closely resembles that of *F*. (*F*.) *corbarica*. Therefore both specimens should be included in this latter species.

Fasciolites (*Fasciolites*) *corbaricus* (Hottinger, 1962)

Alveolina corbarica Hottinger, 1962, p. 68, pl. 2, figs. 20–24; text-figs. 6a, 35c–g.

Alveolina (Alveolina) oblonga d'Orbigny; Drobne, 1977, pl. 7, figs. 8, 9; non text-fig. 42b.
Alveolina (Alveolina) guidonis Drobne, 1977, p. 60, pl. 15, figs. 6–12.

Discussion. – There do not appear to be any differences between the specimens identified as *A.* (*A.*) *guidonis* by Drobne and *F.* (*F.*) *corbaricus*. The same applies for several specimens identified as *A.* (*A.*) *oblonga* by the same author (see discussion of *F.* (*F.*) *oblongus*). Strangely enough she does not discuss *F.* (*F.*) *corbaricus* at all.

Fasciolites (Fasciolites) cucumiformis lineage

This group includes not only *F.* (*F.*) *cucumiformis* and *F.* (*F.*) *tumidus* but also *F.* (*F.*) *ruetimeyeri*, which was placed in a group of its own by Hottinger (1960, 1962).

F. (*F.*) *cucumiformis* is frequent in the lower part of the marine Palaeogene beds of the Tremp Basin. *F.* (*F.*) *tumidus* is very scarce; Hottinger (1960, 1962) considers this form to be a subspecies of *F.* (*F.*) *cucumiformis* but because of its intermediate position, both morphologically and stratigraphically, between *F.* (*F.*) *cucumiformis* and *F.* (*F.*) *ruetimeyeri*, it is probably better to give this form the status of a species.

F. (*F.*) *ruetimeyeri* is abundant in certain beds, but generally this species is rare in the Tremp Basin. Therefore it is not strange that, like *F.* (*F.*) *tumidus*, it has not been found in this area before.

Fasciolites (Fasciolites) tumidus (Hottinger, 1962)
(Pl. 2, Fig. 7)

Alveolina cucumiformis tumida Hottinger, 1962, p. 139, text-fig. 71b.
Alveolina (Alveolina) cucumiformis tumida Hottinger; Drobne, 1977, p. 40, pl. 7, figs. 4–6.

Discussion. – A nearly perfectly oriented section was found in a thin section of a sample from the top of the *F. moussoulensis* Zone of section X[1] (La Fuente del Oro). Most characteristics of this specimen agree very well with Hottinger's description of *A. cucumiformis tumida*: the number of elongated coils is the same as that given by Hottinger (1962) as are the size, shape and arrangement of the chamberlets. Only the proloculus is relatively small: 125 μm versus 175–215 μm according to Hottinger. The range of variation in the size of the proloculus is most probably much greater than Hottinger mentions, because only megalospheric specimens were at his disposal. The species is evidently also rare in other areas investigated.

Fasciolites (Fasciolites) ruetimeyeri (Hottinger, 1962)
(Pl. 4, Figs. 1, 2; Pl. 5, Figs. 1, 2)

Alveolina ruetimeyeri Hottinger, 1962, p. 159, pl. 9, figs. 17, 18; pl. 11, figs. 13–15; pl. 14, figs. 20–22; pl. 15, figs. 5, 6; text-figs. 84, 85.
Alveolina cf. *ruetimeyeri* Hottinger, 1962, p. 160, text-fig. 77c.
Alveolina (Alveolina) ruetimeyeri Hottinger; Drobne, 1977, p. 64, pl. 17, figs. 2–5.

Discussion. – This species coils in the same manner as *F.* (*F.*) *cucumiformis* and *F.* (*F.*) *tumidus*. The size, the shape and the arrangement of the chamberlets and the thickness of the basal layer are also very similar for all three species, which for these reasons are placed in one group. The diameter of the proloculus of megalospheric forms varies from 200 to 475 μm according to Hottinger (1962). However he did not find any specimens representing the intermediate values between 250 and 350 μm, and the small sizes (200–250 μm) are only known to occur in one locality.

One sample (O-94) that is very rich in megalospheric forms of *F.* (*F.*) *ruetimeyeri* yielded three well-oriented sections and two slightly oblique ones. These specimens which may be considered as belonging to one and the same population show a remarkable variation in the size of the proloculi, ranging from 275 to 610 μm. Most proloculi are oval in shape; the respective largest and smallest diameters of the five specimens are: 610 and 505 μm, 430 and 305 μm, 370 and 305 μm, 305 and 275 μm, 275 and 275 μm. The smallest proloculus of *F.* (*F.*) *ruetimeyeri* which this author has found belongs to a specimen from sample K-53; the diameters are 300 and 225 μm, respectively (Pl. 5, Fig. 2).

The number of elongated coils in megalospheric forms ranges from 5 to 8 in sample O-94. Variation in this respect is thus somewhat greater than Hottinger found.

The specimen from the 'Niveau de Coudures' shown by Hottinger (1962, text-fig. 77c), who identified it cautiously as *A.* cf. *ruetimeyeri*, certainly belongs to the species. There is very close agreement for all properties. Unfortunately *F.* (*F.*) *ruetimeyeri* is a rare species in most deposits in the Tremp Basin, but the specimens found undoubtedly belong to this species.

Fasciolites (Fasciolites) subpyrenaicus lineage

Fasciolites (Fasciolites) dolioliformis (Schwager, 1883)

Alveolina regularis Hottinger, 1962, p. 116, pl. 7, fig. 7; text-fig 61f.
Alveolina piper Hottinger, 1962, p. 106, pl. 6, figs. 11–13; text-fig 58a–c.
Alveolina (Alveolina) regularis Hottinger; Drobne, 1977, p. 34, pl. 5, fig. 16; non text-fig. 15d.

Discussion. – The variability of this very common species is considerable. In *F.* (*F.*) *dolioliformis* flosculinization is never very pronounced, but nevertheless many variations occur. Sometimes it is even absent. If present the flosculinized spirals usually change gradually into normal spirals, but sometimes the transition is quite sudden. In that case only a few flosculinized spirals are present. Flosculinization starts usually after the third but sometimes also after the second or fourth juvenile spiral, the latter being tightly coiled.

As with most alveolinid species megalospheric forms are by far the most frequent. Their proloculi vary considerably more in size than Hottinger records. Specimens with the size of that of *A. piper* (70–100 μm) have been found fairly often, whereas the manner of coiling of these shells is usually typical of *F.* (*F.*) *dolioliformis*. There is a gradual transition from the juvenile stage to the older spirals in these specimens and thus no clear separation from the flosculinized part of the skeleton, as is the case in *A. piper*. Because of the existence of such transitional forms *A. piper* has to be considered a synonym of *F.* (*F.*) *dolioliformis*.

Although the chamberlets of *F* (*F.*) *dolioliformis* usually increase rapidly in size, reaching respectable dimensions in the senile stage, the enlargement can also take place much more slowly. Then forms which resemble *A. regularis* quite closely occur next to the normal forms of *F.* (*F.*) *dolioliformis*. Since in addition Hottinger (1962) based his new species *A. regularis* upon only a few specimens, it is better to regard this species as a synonym of *F.* (*F.*) *dolioliformis*. As a result most specimens of *A.* (*A.*) *regularis* mentioned by Drobne (1977) must also be assigned to *F.* (*F.*) *dolioliformis*.

Fasciolites (*Fasciolites*) *subpyrenaicus* (Leymerie, 1846)

Alveolina (*Alveolina*) *regularis* Hottinger; Drobne, 1977, p. 34, text-fig. 15d; non pl. 5, fig. 16.
Alveolina (*Alveolina*) *dedolia* Drobne, 1977, p. 32, pl. 5, figs. 9–11; text-fig. 15a.
Alveolina (*Alveolina*) aff. *dedolia* Drobne, 1977, p. 33, pl. 5, fig. 12; text-fig. 15b.

Discussion. – This species, which normally becomes larger than *F.* (*F.*) *dolioliformis*, is also very common in the area studied. The size of the proloculus in megalospheric forms as given by Hottinger (1962) is again in fact more highly variable. The diameter of the proloculus is often small; values of 150 µm are not exceptional, sometimes even smaller values (up to 100 µm) were measured. Proloculi larger than those found by Hottinger also occur.

F. (*F.*) *subpyrenaicus* in most cases can be distinguished from *F.* (*F.*) *dolioliformis* by its more regular spirals, which start with fewer or no tightly coiled juvenile spirals.

In no respect do the alveolinids described by Drobne as *A.* (*A.*) *dedolia* and *A.* (*A.*) aff. *dedolia* differ from *F.* (*F.*) *subpyrenaicus*. They fall within the range of variation of the latter species. At least one specimen which Drobne has identified as *A.* (*A.*) *regularis* and which comes from the *F.* (*F.*) *moussoulensis* Zone belongs to *F.* (*F.*) *subpyrenaicus*. Probably the specimens not shown which were found in the same biozone also belong to this species.

Fasciolites (*Fasciolites*) *fornasinii* (Checchia-Rispoli, 1909)
(Pl. 4, Figs. 3–6)

Alveolina fornasinii Checchia-Rispoli, 1909, p. 62, pl. III (I), fig. 3; text-fig. 2.
Alveolina fornasinii Checchia-Rispoli; Hottinger, 1962, p. 112, pl. 6, figs. 1–4; text-fig. 60a.
Alveolina aragonensis Hottinger, 1962, p. 109, pl. 6, figs. 5–10; text-figs. 20e, 22h, 60b–f.
Alveolina (*Alveolina*) *fornasinii* Checchia-Rispoli; Drobne, 1977, pl. 5, figs. 7, 8; text-fig. 14d.
Alveolina (*Alveolina*) *aragonensis* Hottinger; Drobne, 1977, pl. 5, figs. 1–6; text-figs. 14a–c.
Alveolina (*Alveolina*) *pisella* Drobne, 1977, p. 34, pl. 5, fig. 19.
Alveolina (*Alveolina*) *citrea* Drobne, 1977, p. 36, pl. 6, figs. 5–9; text-figs. 19a–c.

Discussion. – It is truly remarkable that Hottinger (1962) has given the new species name *A. aragonensis* to these globular to oval forms, which cannot be distinguished from the holotype of *A. fornasinii* Checchia-Rispoli (1909, pl. III(I), fig. 3). The spherical shape of both species is identical. The shape, size and arrangement of the chamberlets and the manner of coiling are so similar that no distinction can be made. The ontogenetic stages of the holotype of *A. fornasinii* are even typical of many of the specimens which Hottinger assigns to *A. aragonensis*: the juvenile spirals are small and close together; the following 2–4 spirals are more or less flosculinized and the adult and senile spirals are again closer together. Consequently we have to consider *A. aragonensis* as a synonym of *F.* (*F.*) *fornasinii*.

A big problem is the extreme variability of this species. Not only does the degree of flosculinization range from zero to very pronounced but also the elongation index varies enormously. In addition to exactly spherical shapes there are also specimens with an axial diameter twice as long as the equatorial diameter. In the course of time nevertheless some changes are visible in these alveolinids. The oldest known specimens in the Tremp Basin are always spherical to slightly oval; no elongated specimens existed at that time. Among the youngest known specimens from the Tremp Basin however nearly spherical shapes are found next to highly elongated ones. In different stratigraphic sections it is frequently observed that rather elongated specimens are followed by nearly spherical ones in younger beds. Although one would gladly distinguish two different species (a spherical and an elongated one), it does not seem to be justifiable.

Without a doubt the holotype of *A.* (*A.*) *pisella* is a microspheric form of *F.* (*F.*) *fornasinii*. The large chamberlets of the adult spirals make another identification impossible. Curiously the other specimens which are included in this species by Drobne have much smaller chamberlets. The taxonomic position of these specimens remains uncertain for the present.

Forms resembling those placed by Drobne in the new species *A.* (*A.*) *citrea* are common in the uppermost part of the *F.* (*F.*) *corbaricus* Zone and in the *F.* (*F.*) *trempinus* Zone of the Tremp Basin. Since all intermediate forms were found together with the typical specimens of *F.* (*F.*) *fornasinii* (which are not as highly flosculinized) in the same stratigraphic horizons, there is no reason to split this group into two species. Nevertheless the more highly flosculinized forms described as *A.* (*A.*) *citrea* have a certain stratigraphic value, because their range is more limited than that of the typical forms of *F.* (*F.*) *fornasinii*.

Fasciolites (*Fasciolites*) *decipiens* lineage

F. (*F.*) *varians* (Hottinger, 1962) as well as *F.* (*F.*) *decipiens* (Schwager, 1883) regularly occurs in the Tremp Basin. Transitional forms between *F.* (*F.*) *varians* and *F.* (*F.*) *dolioliformis* seem to exist.

Fasciolites (*Fasciolites*) *decipiens* (Schwager, 1883)

Alveolina (*Flosculina*) *decipiens* Schwager, 1883, p. 103, pl. 26, fig. 1.

Alveolina decipiens Schwager; Hottinger, 1962, p. 123–126, pl. 8, figs. 1–3; text-figs. 66a, e, 70g.
Alveolina (Alveolina) decipiens Schwager; Drobne, 1977, p. 35, pl. 5, figs. 20, 21; text-fig. 17.
Alveolina (Alveolina) subpyrenaica Leymerie; Drobne, 1977, pl. 5, figs. 13–15; text-fig. 15c.

Discussion. – The alveolinids described by Drobne as *A. (A.) subpyrenaica* are too elongated for this species. Their shape as a whole agrees well with that of *F. (F.) decipiens.*

Fasciolites (Fasciolites) schwageri (Checchia-Rispoli, 1905)
(Pl 2, Fig. 9; Pl. 5, Figs. 3–5; Pl. 6, Figs. 1–6; Pl. 7, Figs. 1, 4)

Alveolina schwageri Checchia-Rispoli, 1905, p. 162, pl. XII(I), figs. 11–14.
Alveolina schwageri Checchia-Rispoli; Checchia-Rispoli, 1909, p. 64, pl. III(I), fig. 6.
Alveolina oblonga d'Orbigny; Checchia-Rispoli, 1909, p. 62, pl. III(I), fig. 4.
Alveolina ilerdensis Hottinger, 1962, p. 119, pl. 7, figs. 14–20; text-fig. 64.
Alveolina schwageri Checchia-Rispoli; Hottinger, 1962, p. 155, pl. 10, figs. 5–7; pl. 11, fig. 3; text-figs. 20g, 21h.
Alveolina (Alveolina) schwageri Checchia-Rispoli; Drobne, 1977, pl. 15, figs. 13–16; text-fig. 34a.
Alveolina (Alveolina) distefanoi Checchia-Rispoli; Drobne, 1977, pl. 16, fig. 1; non pl. 16, figs. 2–4; text-fig. 34b.

Discussion. – Because this species is very common in the Tremp Basin, many well-oriented thin sections could be studied. It soon became clear that the range of variation is pronounced in many respects. In addition to the forms with rounded or truncated poles which match the specimens of *A. ilerdensis* shown by Hottinger, the best, many specimens with more or less pointed poles and a fusiform outline occur in the same samples from the Tremp Basin; the latter resemble *F. (F.) schwageri* very closely. Many transitional forms exist between these two extremes.

In all forms specimens with a small proloculus in the megalospheric stage are known, in contrast to Hottinger's findings. Thus the variation in the size of the proloculus seems to be considerable, which is compatible with the conspicuous variability noted for the other species of this group.

The pointedness of the poles of specimens of *F. (F.) schwageri* can decrease as these foraminifera grow older. This had already been described by Hottinger (1962) and is confirmed by the present study. One microspheric form illustrates this property very well (Pl. 7, Fig. 1). Also the megalospheric form shown by Checchia-Rispoli (1909, pl. III, fig. 4) and identified as *A. oblonga* clearly possesses this feature. Here the transition from the fusiform outline to the truncated shape takes place very rapidly within two spirals.

The specimens of *F. schwageri* shown by Hottinger (1962) and Drobne (1977) are not full-grown. The same applies for the type specimen of this species (Checchia-Rispoli, 1905). A more adult specimen of *F. (F.) schwageri* was not recognized by Drobne; she described it as *A. (A.) distefanoi.*

Fasciolites (Fasciolites) globosus lineage

Fasciolites (Fasciolites) globulus (Hottinger, 1962)

Alveolina aff. *globula* Hottinger, 1962, p. 80, pl. 3, figs. 12–14; text-figs. 38a, b.
Alveolina aramea Hottinger, 1962, p. 72, pl. 3, figs. 4–7; text-fig. 36.
Alveolina avellana aurignacensis Hottinger, 1962, p. 85, pl. 4, figs. 14, 15; text-figs. 41a–c.
Alveolina (Alveolina) aff. *globula* Hottinger; Drobne, 1977, p. 21, pl. 2, figs. 6–8; text-fig. 41a.
Alveolina (Alveolina) pasticillata Schwager; Drobne, 1977, text-fig. 11b; non pl. 4, figs. 1–7.
Alveolina (Alveolina) avellana aurignacensis Hottinger; Drobne, 1977, p. 24, pl. 3, figs. 9–11.
Alveolina (Alveolina) aramaea aramaea Hottinger; Drobne, 1977, p. 18, pl. 1, figs. 11–13; text-figs. 6a, 39a.
Alveolina (Alveolina) aramaea latior Drobne, 1977, p. 19, pl. 1, figs. 14, 15; text-figs. 6b, 7a–c, 39b; non pl. 1, fig. 16.
Alveolina (Alveolina) daniensis Drobne, 1977, p. 20, pl. 1, figs. 17–20; text-figs. 6c, 39c.

Discussion. – This frequently occurring species is highly variable, especially as far as the flosculinization of megalospheric forms is concerned. Some (megalospheric) specimens only possess very slightly thickened basal layers and resemble *F. (F.) dolioliformis* fairly closely. They can be differentiated by the much larger size of the proloculus of *F. (F.) globulus.* Usually two or three, sometimes four, spirals are flosculinized, while the thickness of the basal layer can differ greatly. Microspheric forms have three to five flosculinized spirals which are always clearly developed.

The megalospheric forms shown by Hottinger are often only slightly flosculinized; the megalospheric specimens of *A. aramaea* are more highly flosculinized, just like the majority of the specimens of *F. (F.) globulus* from the Tremp Basin. In contrast the microspheric forms of *F. (F.) globulus* have more flosculinized spirals than the microspheric forms of *A. aramaea* shown by Hottinger (1962). The variation found during this study in the flosculinization of microspheric forms of *F. (F.) globulus* equals exactly the variation of both of Hottinger's species together. Therefore there does not seem to be an obvious reason for designating *A. aramaea* as a separate species.

As the flosculinization of *F. (F.) globulus* is much more variable than indicated by Hottinger (1962), *A. avellana aurignacensis* also falls within the range of variation of *F. (F.) globulus.* The same applies for the alveolinids described by Drobne as *A. (A.) daniensis, A. (A.) aramaea aramaea* and some of the specimens of *A. (A.) aramaea latior.*

Fasciolites (Fasciolites) globosus (Leymerie, 1846)

Alveolina globosa (Leymerie, 1846); Hottinger, 1962, p. 80, pl. 3, figs. 15–20; text-figs. 10, 22i, 40.
Alveolina pisiformis Hottinger, 1962, p. 85, pl. 4, figs. 1–6; text-figs. 43a–e.
Alveolina (Alveolina) globosa (Leymerie); Drobne, 1977, p. 22, pl. 2, figs. 9–11; text-figs. 9, 41b.
Alveolina (Alveolina) pisiformis Hottinger; Drobne, 1977, p. 24, pl. 3, figs. 12–17; text-fig. 11a.

Discussion. – This species is as variable as the preceding species but attains a larger size than *F.* (*F.*) *globulus* and possesses more flosculinized spirals. The thickness of the basal layer can vary considerably, even within one specimen so that the pattern of coiling becomes highly irregular. Regular and generally very pronounced flosculinization is also common.

Most of the megalospheric forms of *A. pisiformis* shown by Hottinger (1962, pl. 4, figs. 4–6) agree in all respects with those of *F.* (*F.*) *globosus*. A juvenile stage with tightly coiled spirals is not apparent in these specimens. According to Hottinger the presence of these tightly coiled spirals is in fact the most important characteristic for the group of *A. avellana* and consequently for the species *A. pisiformis*. Moreover the microspheric forms of *A. globosa* and *A. pisiformis*, both having a juvenile stage with tightly coiled spirals, show no taxonomically valuable differences.

Because of the disappearance of *A. pisiformis* from the synonymy of *F.* (*F.*) *globosus*, and *A. avellana aurignacensis* from the synonymy of *F.* (*F.*) *globulus*, only *F.* (*F.*) *avellanus* is left in Hottinger's group of *A. avellana*. In my opinion *F.* (*F.*) *avellanus* shows a close relationship with the alveolinids of the group *F.* (*F.*) *pasticillatus* and therefore I have incorporated this species in this latter group.

Fasciolites (*Fasciolites*) *triestinus* (Hottinger, 1962)

Alveolina triestina Hottinger, 1962, p. 75, pl. 3, figs. 1–3; text-figs. 21d, 22d, 37a–c.
Alveolina (*Alveolina*) *triestina* Hottinger; Drobne, 1977, p. 21, pl 2, figs. 4, 5; text-figs. 8, 40b.
Alveolina (*Alveolina*) *brassica* Drobne, 1977, p. 22, pl. 2, figs 12–14; pl. 3, figs. 1–3; text-figs. 10, 41c.
Alveolina (*Alveolina*) aff. *brassica* Drobne, 1977, p. 23, pl. 3, fig. 4; text-fig. 41d.

Discussion. – In no respect do the alveolinids described by Drobne as *A.* (*A.*) *brassica* and *A.* (*A.*) aff. *brassica* differ essentially from the typical specimens of *F.* (*F.*) *triestinus*. Therefore there is no reason to maintain this species as a separate taxon.

Group of *Fasciolites* (*Fasciolites*) *pasticillatus*

Fasciolites (*Fasciolites*) *avellanus* (Hottinger, 1962)

Alveolina avellana Hottinger, 1962, p. 82, pl. 4, figs. 7–13; text-figs. 7e, 21b, c, 41d–i, 42, 58d.
non *Alveolina* (*Alveolina*) *avellana* Hottinger; Drobne, 1977, p. 24, pl. 3, figs. 5, 6.
Alveolina (*Alveolina*) cf. *avellana* Hottinger; Drobne, 1977, p. 24, pl. 3, figs. 7, 8.
Alveolina (*Alveolina*) *aramaea latior* Drobne, 1977, p. 19, pl. 1, fig. 16; non pl. 1, figs. 14, 15; text-figs. 6b, 7a–c, 39b.

Discussion. – This moderately flosculinized species is always small. Because of its frequent occurrence a good insight into the variability of this species was obtained. The range of variation is not great and is mainly restricted to the flosculinization and the elongation. After two-four narrowly wound juvenile spirals flosculinization usually starts immediately and normally comprises the subsequent three or four, sometimes five or six, spirals. Only occasionally is flosculinization pronounced; the basal layer is almost always moderately thickened. The senile spirals are again tightly coiled and the transition from the earlier spirals can be gradual or abrupt.

Some specimens with a more highly developed flosculinization resemble *F.* (*F.*) *pasticillatus* rather closely (Hottinger, 1962, p. 83, text-figs. 41e, f). This suggests a close relationship between both species.

The holotype of *A.* (*A.*) *aramaea latior*, a subspecies which has been established by Drobne, does not differ essentially from typical specimens of *F.* (*F.*) *avellanus*.

Fasciolites (*Fasciolites*) *pasticillatus* (Schwager, 1883)

Discussion. – This common species as a rule cannot be confused with other species. Generally three or four highly flosculinized spirals are present. The transitions from the juvenile to senile spirals are always abrupt. Sometimes only two flosculinized spirals occur. In that case the resemblance to *A. minervensis* Hottinger, 1962, is striking. Most probably *A. minervensis* is a synonym of *F.* (*F.*) *pasticillatus*.

Fasciolites (*Fasciolites*) *leupoldi* (Hottinger, 1962)

Alveolina leupoldi Hottinger, 1962, p. 92–94, pl. 4, figs. 20-23; text-figs. 6b, 47.
Alveolina (*Alveolina*) *leupoldi* Hottinger; Drobne, 1977, p. 26, pl. 4, fig. 10.
Alveolina (*Alveolina*) aff. *leupoldi* Hottinger; Drobne, 1977, p. 27, pl. 4, figs. 11–12.

Discussion. – It is not always easy to distinguish this species from *F.* (*F.*) *pasticillatus*. In its most characteristic form only two flosculinized spirals are present, while the elongation index is greater than that of *F.* (*F.*) *pasticillatus* which has a spherical or even a nautiloid shape. Unfortunately less typical specimens with three flosculinized spirals also occur which sometimes do not even possess a clear elongation along the coiling axis. In such cases the distinction between *F.* (*F.*) *leupoldi* and *F.* (*F.*) *pasticillatus* becomes rather arbitrary. The species is not rare.

Fasciolites (*Fasciolites*) *parvus* (Hottinger, 1962)

Discussion. – The variability of this species which occurs rather frequently in the Tremp Basin is considerable. The number of flosculinized spirals varies from two to four. The thickness of the basal layer is in many cases moderate, but very pronounced flosculinization can also occur resulting in a remarkable resemblance to *F.* (*F.*) *pasticillatus*. It is therefore not inconceivable that *F.* (*F.*) *parvus* belongs to the group *F.* (*F.*) *pasticillatus*. The two species can always be distinghuished by means of the number of tightly coiled juvenile spirals. *F.* (*F.*) *pasticillatus* has less than four of these spirals, *F.* (*F.*) *parvus* four or more.

It is the question whether *A. recondita* Hottinger, 1962, can be considered as a separate species. Probably the range of variation of *F.* (*F.*) *parvus* is so great that it is a synonym of this latter species.

Fasciolites (Fasciolites) canavarii lineage

Fasciolites (Fasciolites) laxus (Hottinger, 1962)
(Pl. 7, Fig. 2; Pl. 8, Fig. 4)

Discussion. – Flosculinization of this species varies enormously. In the first place the degree of flosculinization is highly variable. Moreover not only do specimens exist which consist of regular spirals with always the same degree of flosculinization as shown by Hottinger (1962), but there are also specimens in which only the first two or three spirals are flosculinized while the more adult spirals are tightly coiled. This species is rare in the Tremp Basin.

Fasciolites (Fasciolites) canavarii (Hottinger, 1962)
(Pl. 8, Figs. 1–3, 6, 7)

Alveolina coudurensis Hottinger, 1962, pl. 9, figs. 19, 20; non text-fig. 77a.
Alveolina rotundata Hottinger, 1962, pl. 6, figs. 18–21; text-figs. 20i, 22a, 70a–f.
Alveolina (Alveolina) canavarii Checchia-Rispoli; Drobne, 1977, p. 39, pl. 6, figs. 12–14.
Alveolina (Alveolina) aff. *canavarii* Checchia-Rispoli; Drobne, 1977, p. 39, pl. 6, fig. 15; text-fig. 20.
Alveolina (Alveolina) aff. *coudurensis* Hottinger; Drobne, 1977, p. 43, pl. 7, figs. 14, 15.

Discussion. – Specimens of this species occur rather regularly in the Tremp Basin. Sample O-94 which yielded beautiful specimens of *F. (F.) ruetimeyeri,* also provided three thin sections that allowed recognition of *F. (F.) canavarii.* They fall within the range of variation of the species, as far as their size, shape and internal structure are concerned. In no respect can *A. coudurensis* (Hottinger, 1962, pl. 9, fig. 20) be distinguished from *F. (F.) canavarii.* This specimen obviously falls within the range of variation of this latter species.

The holotype of *A. coudurensis* is an aberrant form of this species with more highly flosculinized coils and therefore at the same time smaller chamberlets.

Fasciolites (Fasciolites) aff. *canavarii* (Hottinger, 1962)
(Pl. 8, Fig. 5)

Alveolina aff. *rotundata* Hottinger, 1962, pl. 134, pl. 6, fig. 21; text-fig. 70c.
Alveolina (Alveolina) aff. *rotundata* Hottinger; Drobne, 1977, p 40, pl. 7, figs. 1–3.

Discussion. – Elongated forms which resemble *F. (F.) canavarii* rather closely (Pl. 8, Fig. 1) occasionally occur in the top of the marine Palaeogene sequence in the Tremp Basin, together with the more compact specimens. Often the typical specimens of the very compact and small forms described by Hottinger (1962) as '*A.* aff. *rotundata,* forme trapue' were also found. In samples J-81, L-92 and M-77 good examples of these forms occur.

Group of *Fasciolites (Fasciolites) levantinus*

Only one specimen of this group was found in the area studied and it cannot be determined more specifically (Pl. 1, Fig. 26).

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PLATE 1

Figs. 1, 13. *Fasciolites* (*Microfasciolites*) *agerensis* n. sp. Paratypes, microspheric forms, axial sections. Sample J-29, section J, west of Guardia de Tremp, basal bed of the *F. corbaricus* Zone, Coll. RGM 248 622.

Figs. 2, 3, 4, 7, 10, 14, 18. *Fasciolites* (*Microfasciolites*) *agerensis* n. sp. Sample F-45, section F, 1 km southeast of Sant Cerni, basal part of *F. corbaricus* Zone.
Fig. 2. Holotype, megalospheric form, axial section, Coll. RGM 248 615.
Fig. 3. Paratype, megalospheric form, axial section, Coll. RGM 248 615.
Figs. 4, 7. Paratypes, microspheric forms, axial sections, Coll. RGM 248 616, 248 617.
Figs. 10, 14. Paratypes, nearly axial sections, Coll. RGM 248 618, 248 619.
Fig. 18. Paratype, axial section, pyrite crystals in proloculus, Coll. RGM 248 620.

Figs. 5, 9, 11, 17. *Fasciolites* (*Microfasciolites*) *agerensis* n. sp. Sample F-42, section F, 1 km southeast of Sant Cerni, uppermost bed of *F. moussoulensis* Zone.
Fig. 5. Paratype, megalospheric form, axial section, Coll. RGM 248 611.
Fig. 9. Paratype, nearly axial section, Coll. RGM 248 612.
Fig. 11. Paratype, microspheric form, equatorial section, Coll. RGM 248 612.
Fig. 17. Paratype, nearly axial section, regenerated specimen, Coll. RGM 248 611.

Fig. 6. *Fasciolites* (*Microfasciolites*) *agerensis* n. sp. Paratype, megalospheric form. axial section. Sample F-45t, section F, 1 km southeast of Sant Cerni, basal part of *F. corbaricus* Zone, Coll. RGM 248 621.

Figs. 8, 12. *Fasciolites* (*Microfasciolites*) *agerensis* n. sp. Sample F-33, section F, 1 km southeast of Sant Cerni, middle part of *F. moussoulensis* Zone.
Fig. 8. Paratype, microspheric form, axial section, Coll. RGM 248 608.
Fig. 12. Paratype, megalospheric form, axial section, Coll. RGM 248 609.

Fig. 15. *Fasciolites* (*Microfasciolites*) *agerensis* n. sp. Paratype, nearly equatorial section. Sample F-44, section F, 1 km southeast of Sant Cerni, basal part of *F. corbaricus* Zone, Coll. RGM 248 613.

Fig. 16. *Fasciolites* (*Microfasciolites*) *agerensis* n. sp. Paratype, megalospheric form, axial section. Sample F-24, section F, 1 km southeast of Sant Cerni, upper part of *F. ellipsoidalis* Zone, coll. RGM 248 607.

Figs. 19, 22, 23. *Fasciolites* (*Microfasciolites*) *boscii* (Defrance, 1825). Megalospheric forms, axial sections, sample A. van Vliet, Tremp section, 10–15 m above horizons with *Turritella figolina* and *Patallophyllia*, lower part of *F. corbaricus* Zone, Coll. RGM 248 623, 248 624, 248 625.

Fig. 20. *Fasciolites* (*Microfasciolites*) *boscii* (Defrance, 1825). Megalospheric form, axial section. Sample O-67, section O, 5.5 km south of Puente de Montañana, middle part of *F. corbaricus* Zone, Coll. RGM 248 626.

Fig. 21. *Fasciolites* (*Microfasciolites*) *boscii* (Defrance, 1825). Megalospheric form, axial section. Sample M-68, section M, 0.3 km northeast of Beniure, upper part of *F. corbaricus* Zone, Coll. RGM 248 627.

Fig. 24. *Fasciolites* (*Microfasciolites*) *boscii* (Defrance, 1825). Microspheric form, axial section. Sample A. van Vliet, Tremp section, 10–15 m above horizons with *Turritella figolina* and *Patallophyllia*, lower part of *F. corbaricus* Zone, Coll. RGM 248 628.

Fig. 25. *Fasciolites* (*Fasciolites*) *oblongus* (d'Orbigny, 1826). Megalospheric form, juvenile specimen, axial section. Sample M-48, section M, 0.3 km northeast of Beniure, middle part of *F. corbaricus* Zone, Coll. RGM 248 629.

Fig. 26. *Fasciolites* (*Fasciolites*) *levantinus* group. Megalospheric form, axial section. Sample F-44, section F, 1 km southeast of Sant Cerni, lower part of *F. corbaricus* Zone, Coll. RGM 248 611.

All specimens reproduced at a magnification of 20×.


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PLATE 2

Fig. 1. *Fasciolites (Fasciolites) oblongus* (d'Orbigny, 1826). Megalospheric form, axial section. Sample A-76, section A, 2 km east of Llimiana, lower part of *F. trempinus* Zone, Coll. RGM 248 630.

Figs. 2, 3. *Fasciolites (Fasciolites) oblongus* (d'Orbigny, 1826). Megalospheric forms, juvenile specimens, axial sections. Sample M-50, section M, 0.3 km northeast of Beniure, middle part of *F. corbaricus* Zone.

Fig. 4. *Fasciolites (Fasciolites) oblongus* (d'Orbigny, 1826). Megalospheric form, axial section. Sample O-95t, section O, 5.5 km south of Puente de Montañana, lower part of *F. trempinus* Zone.

Fig. 5. *Fasciolites (Fasciolites) oblongus* (d'Orbigny, 1826), resembling *F. (F.) moussoulensis* (Hottinger, 1962). Megalospheric form, axial section. Sample K-53, section K, 2 km west of Guardia de Tremp, basal bed of *F. trempinus* Zone, Coll. RGM 248 631.

Fig. 6. Transitional form between *F. (F.) moussoulensis* and *F. (F.) oblongus*. Megalospheric form, axial section. Sample C-21, section C, 3 km east of Sant Miguel de la Vall, basal bed of *F. corbaricus* Zone.

Fig. 7. *Fasciolites (Fasciolites) tumidus* (Hottinger, 1962). Megalospheric form, axial section. Sample 300b, section X', La Fuente del Oro (north of La Puebla de Roda), upper part of *F. moussoulensis* Zone.

Fig. 8. *Fasciolites (Microfasciolites) agerensis* n. sp. Holotype, megalospheric form, axial section. Sample F-45, section F, 1 km southeast of Sant Cerni, basal part of *F. corbaricus* Zone, Coll. RGM 248 615.

Fig. 9. *Fasciolites (Fasciolites) schwageri* (Checchia-Rispoli, 1905). Megalospheric form with more than one proloculus, axial section. Sample M-86, section M, northeast of Beniure, lower part of *F. trempinus* Zone.

Fig. 8. Reproduced at a magnification of 40×, all other specimens at a magnification of 20×.

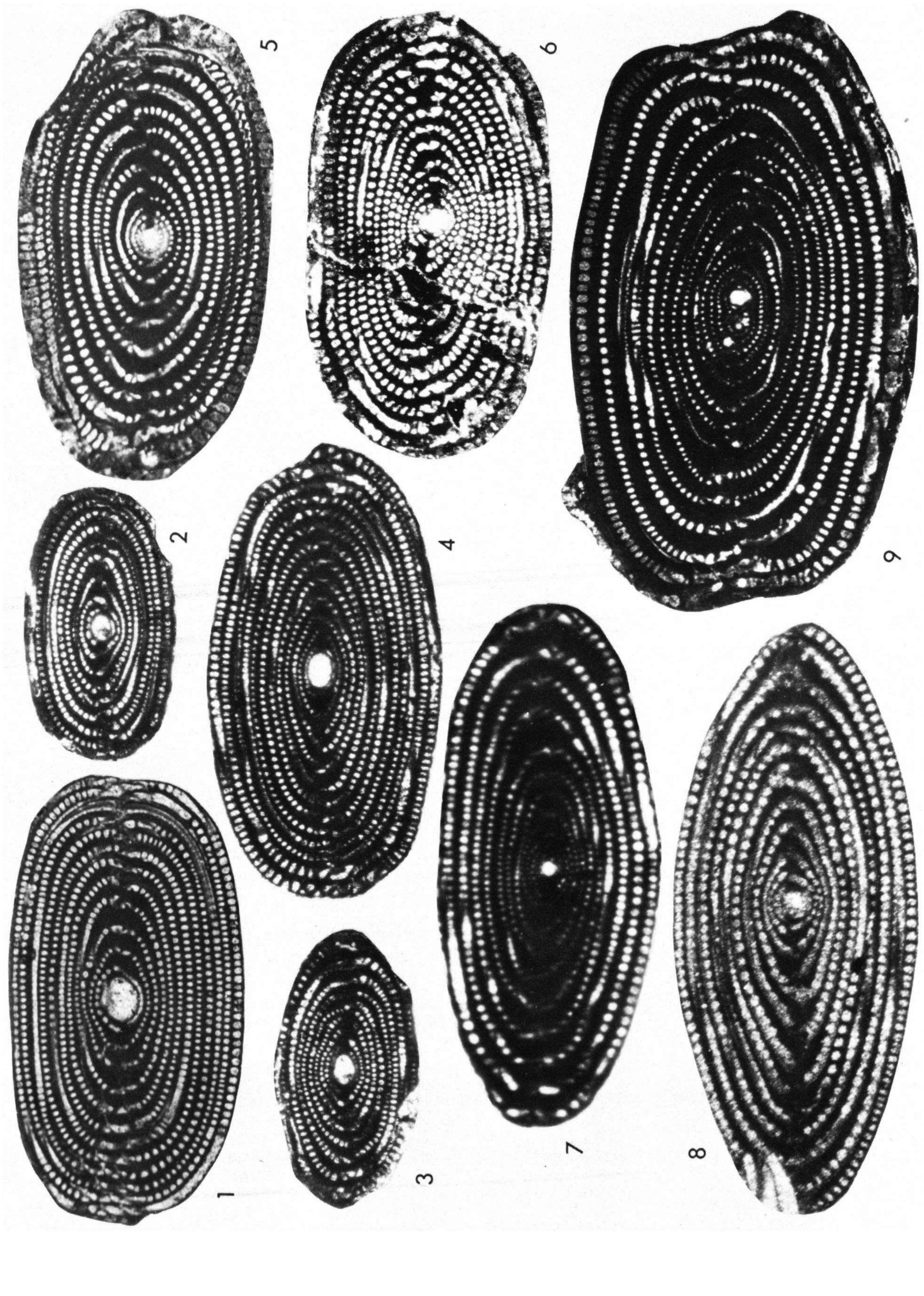
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PLATE 3

Fig. 1. *Fasciolites (Fasciolites) oblongus* (d'Orbigny, 1826). Microspheric form, nearly axial section. Sample O-67, section O, 5.5 km south of Puente de Montañana, middle part of *F. corbaricus* Zone.

Fig. 2. *Fasciolites (Fasciolites) oblongus* (d'Orbigny, 1826). Megalospheric form, juvenile specimen, axial section. Sample 433a, section X, La Puebla de Roda, lower part of *F. trempinus* Zone.

Fig. 3. *Fasciolites (Fasciolites) oblongus* (d'Orbigny, 1826). Megalospheric form, axial section. Sample O-95t, section O, 5.5 km south of Puente de Montañana, lower part of *F. trempinus* Zone, Coll. RGM 248 632.

Fig. 4. *Fasciolites (Fasciolites) oblongus* (d'Orbigny, 1826). Microspheric form, axial section. Sample J-51, section J, west of Guardia de Tremp, lower part of *F. corbaricus* Zone, Coll. RGM 248 633.

Figs. 5, 6. *Fasciolites (Fasciolites) oblongus* (d'Orbigny, 1826). Megalospheric forms, axial sections. Sample A. van Vliet, Tremp section, 10–15 m above horizons with *Turritella figolina* and *Patallophyllia*, lower part of *F. corbaricus* Zone, Coll. RGM 248 634, 248 635.

All specimens reproduced at a magnification of 20×.


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PLATE 4

Figs. 1, 2. *Fasciolites (Fasciolites) ruetimeyeri* (Hottinger, 1962). Megalospheric forms, axial sections. Sample O-94, section O, 5.5 km south of Puente de Montañana, lower part of *F. trempinus* Zone, Coll. RGM 248 637, 248 638.

Fig. 3. *Fasciolites (Fasciolites) fornasinii* (Checchia-Rispoli, 1909). Microspheric form, axial section. Sample J-54, section J, west of Guardia de Tremp, lower part of *F. corbaricus* Zone.

Fig. 4. *Fasciolites (Fasciolites) fornasinii* (Checchia-Rispoli, 1909). Megalospheric form, axial section. Sample M-77, section M, 0.3 km northeast of Beniure, top of *F. corbaricus* Zone.

Fig. 5. *Fasciolites (Fasciolites) fornasinii* (Checchia-Rispoli, 1909). Megalospheric form, axial section. Sample D-16t, section D, 2 km south of Sant Salvador de Tolo, middle part of *F. corbaricus* Zone.

Fig. 6. *Fasciolites (Fasciolites) fornasinii* (Checchia-Rispoli, 1909). Megalospheric form, axial section. Sample C-38, section C, 3 km east of Sant Miguel de la Vall, upper part of *F. corbaricus* Zone.

All specimens reproduced at a magnification of 20×

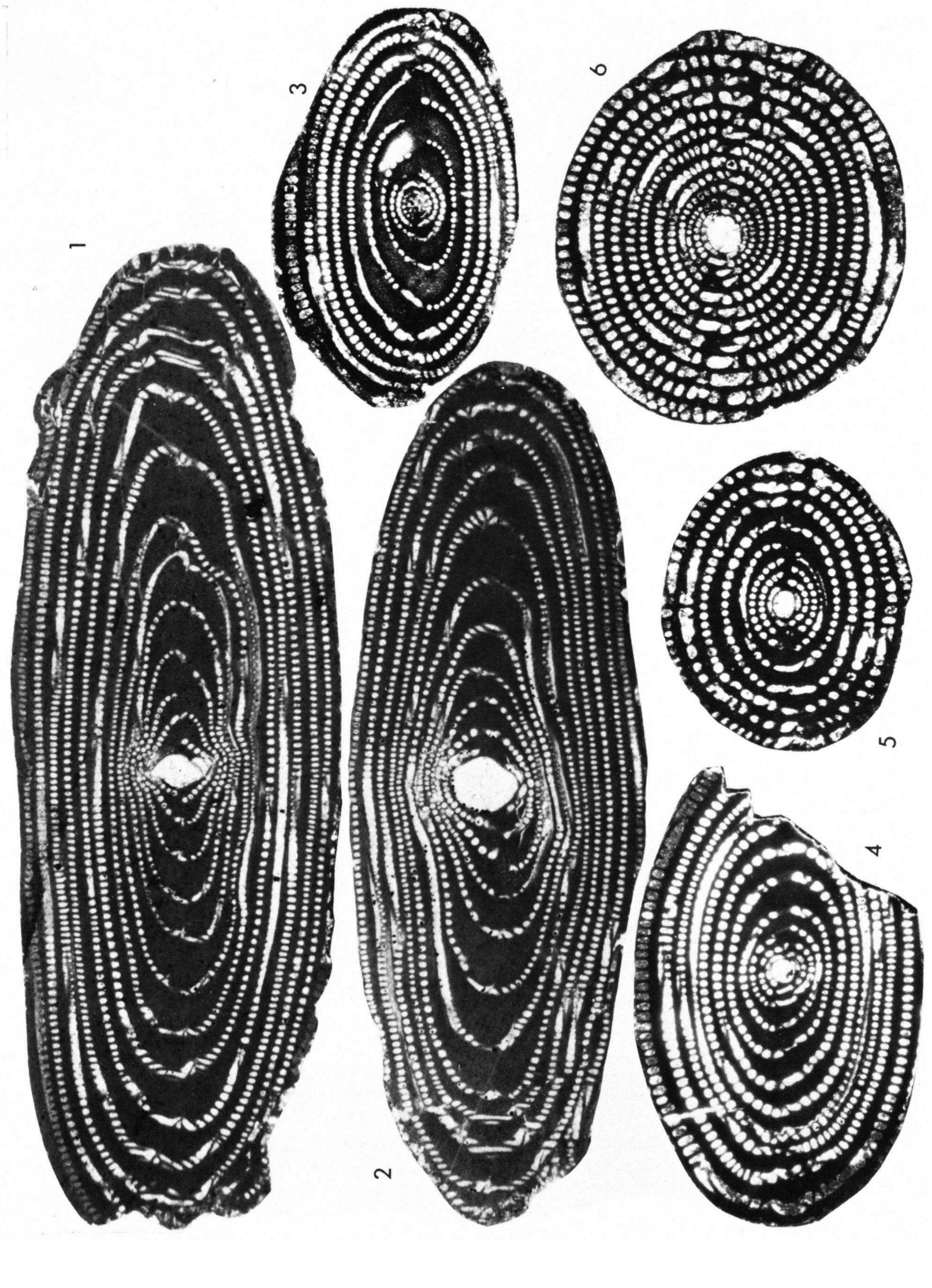
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PLATE 5

Figs. 1, 2. *Fasciolites (Fasciolites) ruetimeyeri* (Hottinger, 1962). Megalospheric forms, axial sections. Sample K-53, section K, 2 km west of Guardia de Tremp, basal bed of *F. trempinus* Zone, Coll. RGM 248 639 (Fig. 1).

Fig. 3. *Fasciolites (Fasciolites) schwageri* (Checchia-Rispoli, 1905). Microspheric form, nearly axial section. Sample A-76, section A, 2 km east of Llimiana, lower part of *F. trempinus* Zone, Coll. RGM 248 640.

Fig. 4. *Fasciolites (Fasciolites) schwageri* (Checchia-Rispoli, 1905). Megalospheric form, axial section. Sample C-50, section C, 3 km east of Sant Miguel de la Vall, lower part of *F. trempinus* Zone.

Fig. 5. *Fasciolites (Fasciolites) schwageri* (Checchia-Rispoli, 1905). Megalospheric form, axial section. Sample O-109, section O, 5.5 km south of Puente de Montañana, middle part of *F. trempinus* Zone, Coll. RGM 248 641.

All specimens reproduced at a magnification of 20×.


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PLATE 6

Figs. 1–6. *Fasciolites (Fasciolites) schwageri* (Checchia-Rispoli, 1905). Megalospheric forms, axial sections. Sample C-48, section C, 3 km east of Sant Miguel de la Vall, basal bed of *F. trempinus* Zone.
Fig. 1. Coll. RGM 248 642.
Figs. 2, 4. Coll. RGM 248 643.
Fig. 3. Coll. RGM 248 644.
Fig. 5. Coll. RGM 248 645.

All specimens reproduced at a magnification of 20×.

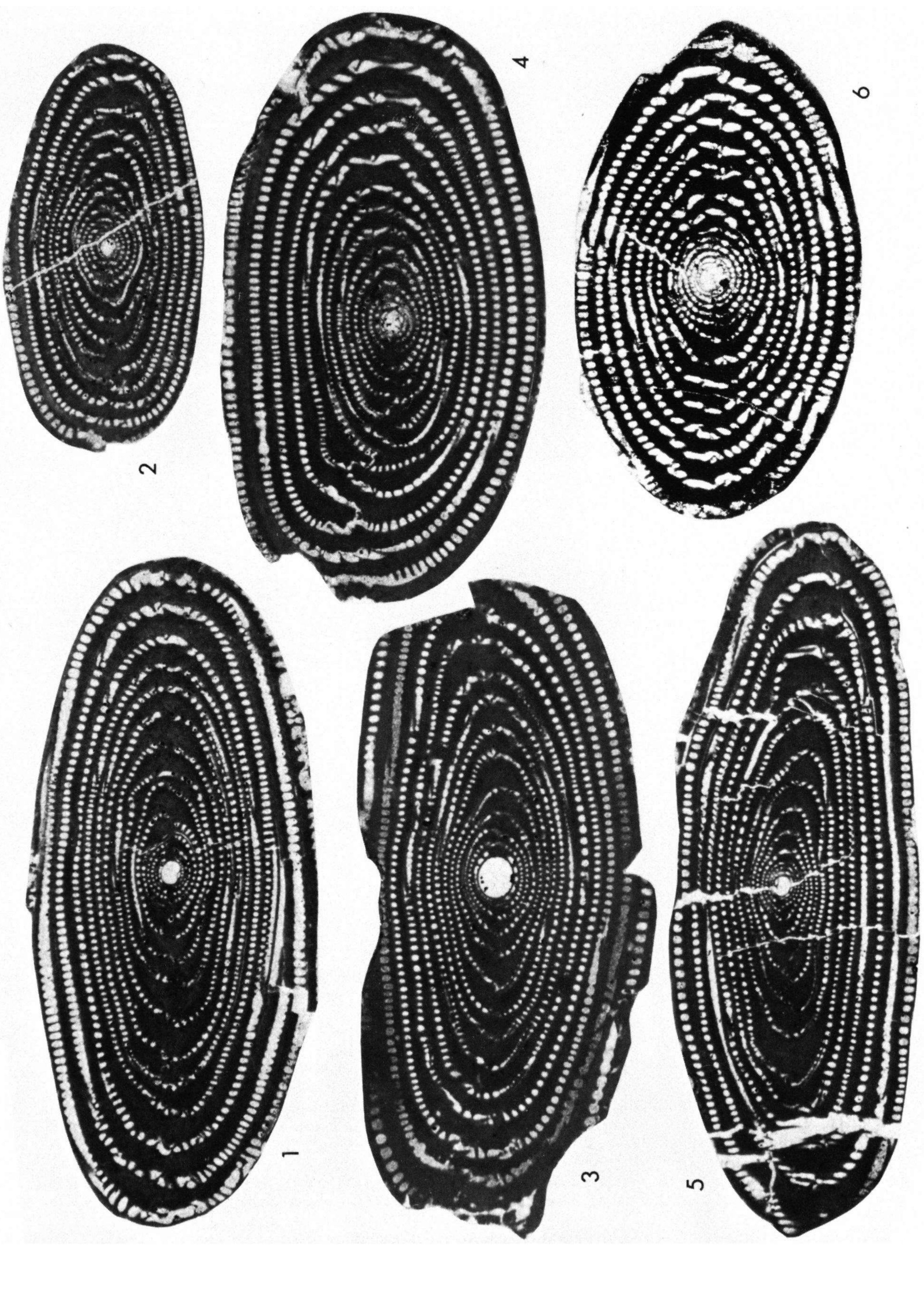
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PLATE 7

Fig. 1. *Fasciolites (Fasciolites) schwageri* (Checchia-Rispoli, 1905). Microspheric form, nearly axial section. Sample K-37, section K, 2 km west of Guardia de Tremp, middle part of *F. corbaricus* Zone.

Fig. 2. *Fasciolites (Fasciolites) laxus* (Hottinger, 1962). Microspheric form, nearly axial section. Sample G-25, section G, 3.5 km south of Sant Salvador de Tolo, basal bed of *F. corbaricus* Zone.

Fig. 3. *Fasciolites (Fasciolites) oblongus* (d'Orbigny, 1826). Megalospheric form, axial section. Sample O-95t, section O, 5.5 km south of Puente de Montañana, lower part of *F. trempinus* Zone, Coll. RGM 248 636.

Fig. 4. *Fasciolites (Fasciolites) schwageri* (Checchia-Rispoli, 1905). Megalospheric form, axial section. Sample J-96, section J, west of Guardia de Tremp, lower part of *F. trempinus* Zone.

All specimens reproduced at a magnification of 20×.

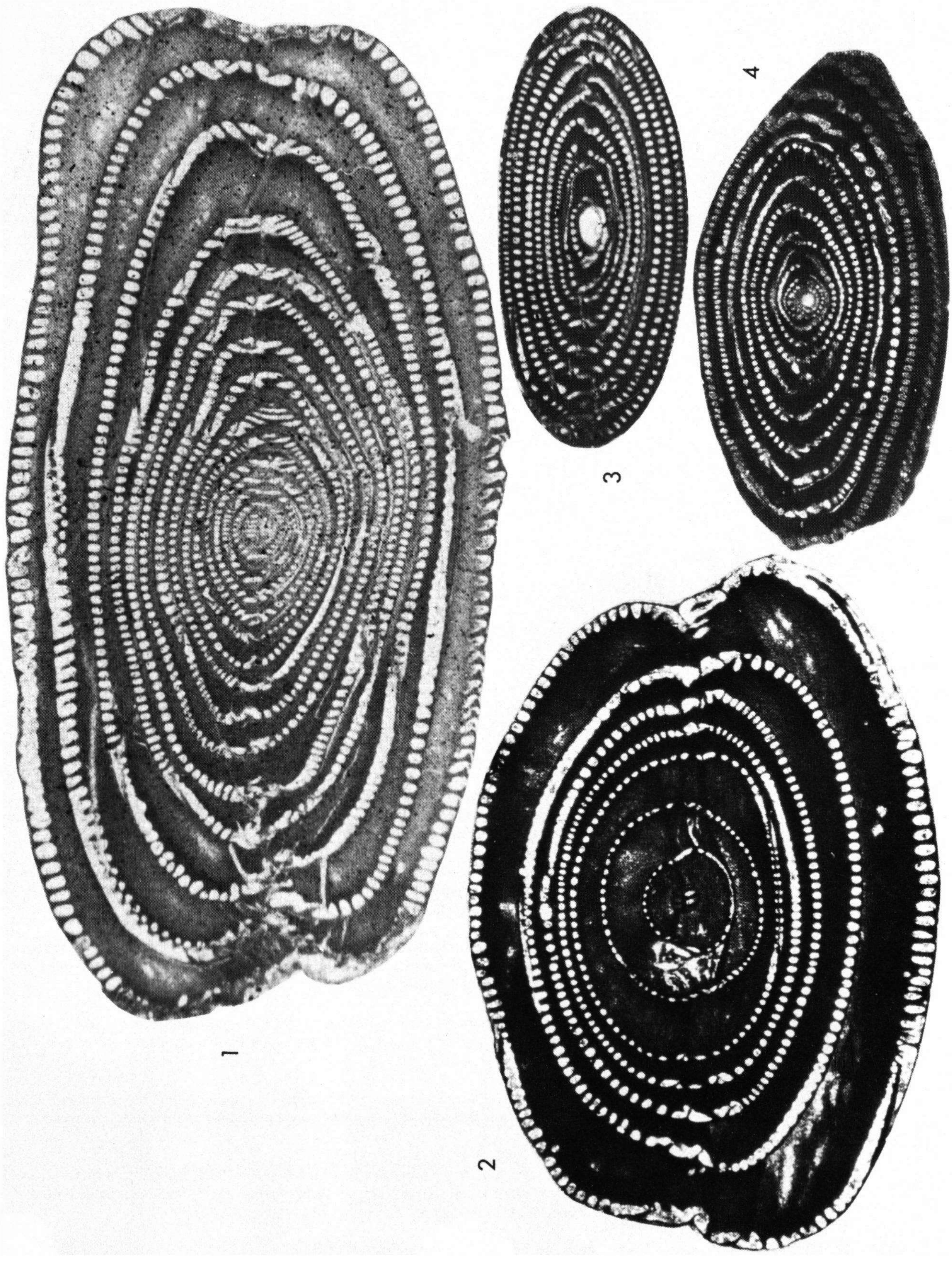
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PLATE 8

Fig. 1. *Fasciolites (Fasciolites) canavarii* (Checchia-Rispoli, 1905), transitional form to *F. (F.) vicentinus* (Hottinger, 1962). Megalospheric form, axial section. Sample O-95t, section O, 5.5 km south of Puente de Montañana, lower part of *F. trempinus* Zone, Coll. RGM 248 646.

Fig. 2. *Fasciolites (Fasciolites) canavarii* (Checchia-Rispoli, 1905). Microspheric form, juvenile specimen, axial section. Sample K-53, section K, 2 km west of Guardia de Tremp, basal bed of *F. trempinus* Zone, Coll. RGM 248 647.

Figs. 3, 7. *Fasciolites (Fasciolites) canavarii* (Checchia-Rispoli, 1905). Megalospheric forms, axial sections, Sample O-94, section O, 5.5 km south of Puente de Montañana, lower part of *F. trempinus* Zone, Coll. RGM 248 648, 248 649.

Fig. 4. *Fasciolites (Fasciolites) laxus* (Hottinger, 1962). Megalospheric form, axial section. Sample 291c, section X′, La Fuente del Oro (north of La Puebla de Roda), lower part of *F. ellipsoidalis* Zone.

Fig. 5. *Fasciolites (Fasciolites)* aff. *canavarii* (Checchia-Rispoli, 1905). Megalospheric form, dwarf form, axial section. Sample J-81, section J, west of Guardia de Tremp, upper part of *F. corbaricus* Zone.

Fig. 6. *Fasciolites (Fasciolites) canavarii* (Checchia-Rispoli, 1905). Megalospheric form, axial section. Sample O-95t, section O, 5.5 km south of Puente de Montañana, lower part of *F. trempinus* Zone, Coll. RGM 248 650.

All specimens reproduced at a magnification of 20×.