



Very Small Ammonites (Micromorphs) from Lower Oxfordian Marls (Mariae Zone)

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8 Text-Figures and 1 Plate

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Sehr kleine Ammoniten (Micromorphe) aus Mergeln des Unteren Oxfordiums (Mariae-Zone)

Zusammenfassung

Die Untersuchung von Ammonitenpopulationen aus den *Creniceras renggeri*-Mergeln (Unteres Oxfordium) ergab, dass viele Arten bei sehr kleinen Durchmessern (<30 mm) geschlechtsreif wurden (Lobendrängung, entrollter Umbilikalgrat, modifiziertes Ornament auf der Wohnkammer, geschlechtsreife Mündung). Diese Ammoniten werden als Mikromorphe bezeichnet. Sie werden drei Unterfamilien zugeordnet:

- 1) Taramelliceratinae. Die häufigste Art ist *Scaphitodites scaphitoides* (COQUAND), deren Adultstadium 7–5 mm erreicht. Die nächsthäufigste Spezies ist *Taramelliceras heimi* DE LORIOI. Wir nehmen hier Sexualdimorphismus an mit *T. heimi* DE LORIOI als Makrokonch (20–30 mm) und *T. langi* DE LORIOI als Mikrokonch (11–16 mm). *Sphaerodomites* cf. *globosus* (DE LORIOI) in HAAS ist selten; *Sphaerodomites calcaratus* (COQUAND) und *Sphaerodomites ? puellaris* sind äußerst selten. Sexualdimorphismus bei den drei letztgenannten ist unbekannt.
- 2) Pachyceratinae. Die einzig auftretende Art ist selten: *Tornquistes chapuisi* (DE LORIOI) non OPPEL. Sie ist dimorph mit "*Macrocephalites*" *greppini* DE LORIOI als Makrokonch und *Sphaeroceras chapuisi* (OPPEL) in DE LORIOI als Mikrokonch.
- 3) Hecticoceratinae. Beide Arten sind sehr selten: "*Hecticoceras*" *kobyi* DE LORIOI und "*Hecticoceras*" *baylei* (COQUAND).

Die übrigen kleinen Adultformen sind Mikrokonche zugehörig zu Makrokonchen jenseits dieser Größenklasse. *Hecticoceras matheyi* DE LORIOI ist selten. Es kann einen Adultdurchmesser von 12 mm erreichen. Geschlechtsreife Makrokonche wurden nicht gefunden. *Creniceras renggeri* (OPPEL) ist der häufigste Kleinammonit. Er wurde oft als der zugehörige Mikrokonch von *Taramelliceras richei* DE LORIOI betrachtet. Im Gegensatz zu *Taramelliceras* tritt *Creniceras renggeri* nicht in den "Terres Noires" des südostfranzösischen Beckens auf. Dies lässt Zweifel aufkommen, ob diese Paarung richtig ist. *Mirosphinctes*, der dimorphe Partner von *Euaspidoceras* wird im Allgemeinen als geschlechtsreifer Phragmokon von weniger als 30 mm Durchmesser gefunden.

Keine der anderen Gattungen mit adulten Mikrokonchen größer als 30 mm (*Cardioceras*, *Peltoceratoides*, *Properisphinctes*, *Prososphinctes*, *Taramelliceras*) zeigt Anzeichen von Maturität. Diese stellen keine Zwergformen dar, wie manche Beobachter annehmen.

Zwei Gattungen treten in dieser Fazies massenhaft auf: *Scaphitodites*, der auf Mergel mit pyritiserten Fossilien beschränkt ist und *Creniceras*, der auch in eher proximaler Fazies vorkommt. Beide Arten sind häufig, wenn *Sowerbyceras* selten ist, und sind selten, wenn *Sowerbyceras* häufig ist.

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Abstract

Examination of Lower Oxfordian ammonite populations from "Creniceras renggeri marls" reveals that many species reach maturity (closely spaced suture lines, uncoiled umbilical ridge, modified body chamber ornament, mature aperture) at very small sizes (diameter less than 30 mm). Such ammonites are termed micromorphs. They are classified into three subfamilies:

- 1) Taramelliceratinae. The commonest species is *Scaphitodites scaphitoides* (COQUAND) whose mature size range is from 7 mm to 15 mm. The next commonest is *Taramelliceras heimi* DE LORIOI. We suggest here that it is sexually dimorphic, with *T. heimi* DE LORIOI as macroconch (20–30 mm) and *T. langi* DE LORIOI as microconch (11–16 mm). *Sphaerodomites* cf. *globosus* (DE LORIOI) in HAAS is rare; *Sphaerodomites calcaratus* (COQUAND) and *Sphaerodomites ? puellaris* are extremely rare and dimorphism is unknown in these last three species.
- 2) Pachyceratinae. The only species is rare: *Tornquistes chapuisi* (DE LORIOI) non OPPEL. It is dimorphic with "Macrocephalites" *greppini* DE LORIOI as macroconch and *Sphaeroceras chapuisi* (OPPEL) in DE LORIOI as microconch.
- 3) Hecticoceratinae. The two species are very rare: "Hecticoceras" *kobyi* DE LORIOI and "Hecticoceras" *baylei* (COQUAND).

The other small adult species found are microconchs of macroconchs outside the size range. *Hecticoceras matheyi* DE LORIOI is rare. It attains a mature size of 12 mm. Mature macroconchs are not found. *Creniceras renggeri* (OPPEL) is the most abundant small ammonite. It is often considered to be the microconch of *Taramelliceras richei* DE LORIOI. However, unlike *Taramelliceras*, *C. renggeri* is not found in the "Terres Noires" of the SE France Basin, this casts doubt on the pairing. *Mirosphinctes*, the sexual dimorph of *Euaspidoceras*, is commonly found as a mature phragmocone of less than 30 mm.

None of the other genera with adult microconchs greater than 30 mm (*Cardioceras*, *Peltoceratoides*, *Properisphinctes*, *Prososphinctes*, *Taramelliceras*) display mature characters. They do not represent dwarves in pyritic marls as some observers suggest.

Two species are commonplace in this facies: *Scaphitodites*, which is largely confined to marls with pyritic fossils and *Creniceras*, which occurs also in more proximal facies. Both of these species are common when *Sowerbyceras* (Phylloceratina) is rare and are absent when *Sowerbyceras* is common.

1. Introduction

Lower Oxfordian marl deposits in many parts of Europe contain pyritised ammonite fossils that are often small (less than 25 mm in diameter in 90 % of cases). Of these ammonites, some are mature adults less than 30 mm in diameter and most belong better to what are known as micromorph species.

In this paper we draw up an inventory of Lower Oxfordian (Mariae zone) micromorphs, describe them and attempt to identify dimorphic couples. We also attempt to identify morphological criteria for distinguishing between the inner whorls of species of larger adult diameter (termed macromorphs here) and microconchs (sometimes mature at less than 30 mm diameter).

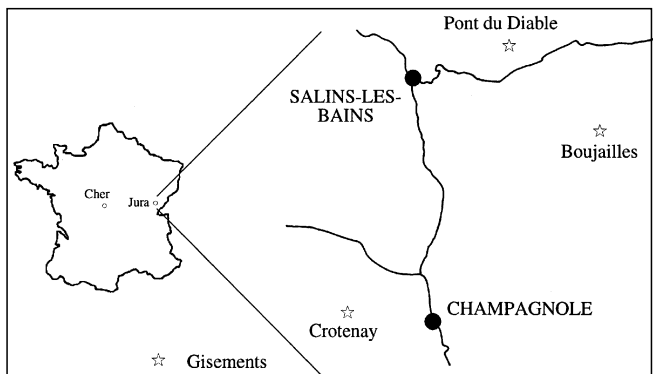
Three major facies types are found in the Lower Oxfordian:

- 1) Invariably thin carbonate sediments often containing ferruginous ooliths (proximal platform; upper shoreface to top of the lower offshore; COURVILLE & COLLIN, 1997; COLLIN et al., 1999).
- 2) Often thick marls with pyritised fossils (more distal platform; lower offshore).
- 3) Invariably thick, black marls with unpyritised fossils (Terres Noires) ("basin"; more distal lower offshore).

We shall attempt to pin down the geographical distribution of the different species, particularly the micromorph species, by comparative synecological analysis. This should improve our understanding of the environmental constraints and ecological requirements.

2. Methods

This study is based essentially on three large fossil sites in the Jura (France) (Text-Fig. 1). The first faunal collection comes from the *Creniceras renggeri* Marls (Pont du Diable, Doubs); it consists of ammonites from the Mariae zone (Woodhamense, Praemartini and Alphacordatum horizons, i.e. the equivalent of a subzone). The second is from marls containing ferruginous fossils (Boujailles, Jura) which yield fauna from the summit of the Praecordatum subzone. The third is a section (Crotenay, Doubs) surveyed bed by bed (by P.C.) and covering the entire Lower and Middle Oxfordian. The zonation used here was published by FORTWENGLER & MARCHAND (1994) and FORTWENGLER et al. (1997) (Text-Fig. 2).



Text-Fig. 1.
Map of outcrops studied.

Text-Fig. 2.
Biozonation of the Lower Oxfordian (FORTWENGLER et al., 1997).

		Zone	Ss-Zone	Horizon
OXFORDIEN INFERIEUR	CORDATUM		CORDAT.	
			COSTIC.	
			BUKOW.	
	MARIAE		PRAECORDATUM	Praecordatum
				Alphacordatum
				Praemartini
	SCARBURGENSE			Woodhamense
				Scarburgense
				Thuouxensis

Each ammonite from each site was observed with a magnifying glass for characters marking the mature stage, namely:

- 1) closely spaced suture lines,
- 2) open umbilicus,
- 3) changes in whorl section and in ornament that commonly occur at the end of the body chamber and, of course,
- 4) adult aperture shape.

This procedure yielded the following general observations:

- Where mature macroconchs are invariably large (greater than 7–8 cm) in other facies, as with the genera *Cardioceras*, *Hecticoceras* s.l., *Properisphinctes*, *Prososphinctes*, *Peltocheratoides*, *Euaspidoceras* and most *Taramelliceras*, no individuals are found with any of these four adult characters.
- When microconchs are small, as with *Creniceras* (considered by PALFRAMAN [1966] as the microconch of *Taramelliceras*), *Hecticoceras* s.l., and *Mirosphinctes* (microconch of *Euaspidoceras*), mature characters are consistently (*Creniceras*) or sometimes (*Hecticoceras* s.l. and *Mirosphinctes*) found for diameters of less than 30 mm.
- "Micromorph" species (adult diameter less than 30 mm) are often complete in the pyritised fossil marls and in the ferruginous oolitic limestones

3. Micromorph Ammonites from the Pyritised Fossil Marls

In this section we describe all the species with adult diameters of less than 30 mm. After reviewing the main morphological characteristics used by observers – especially DE LORIO – to create these species, we refine the descriptions, discuss the possibility of microconch/macroconch dimorphism and propose new generic attributions when necessary.

3.1. Taramelliceratinae

Taramelliceras heimi (DE LORIO)

(Pl. 1, Figs. 1–3; Text-Fig. 3)

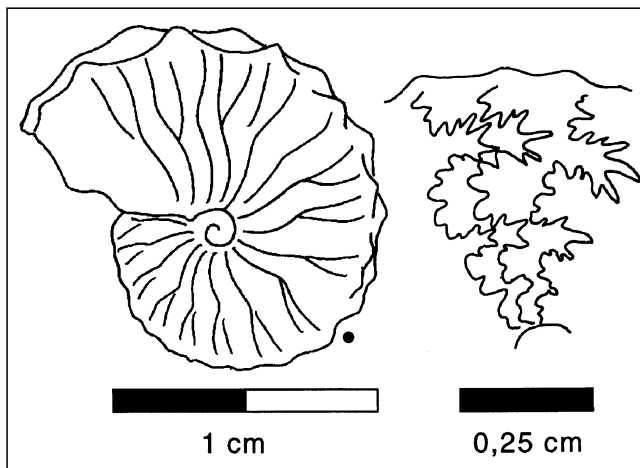
This species as understood here includes two species created by DE LORIO:

- *Taramelliceras langi* (DE LORIO)
= *Oppelia langi* DE LORIO 1898

DE LORIO (1898, p. 56–58, Pl. IV, Figs. 18–20) created the species *langi* for five specimens of which, as he himself said, "the characters are generally very constant". DE LORIO considered them "very nearly complete" and reported a maximum diameter ranging from 16 to 20 mm. The apertures were missing. The general ornamentation is that of *Taramelliceras*. However, the species is original in that, a series of four or five tubercles "arise along the outer circumference" of the body chamber that are "widely spaced, protuberant, pointed or sharp and markedly more developed than those of the median series". He also reported that the suture line was "not very deeply indented".

In 1900 DE LORIO reported (p. 47–48, Pl. IV, Figs. 2–7) that the 23 specimens of his collection all had partial or complete body chambers. He also reported that the largest specimen (D = 17 mm) had a sulcus "immediately preceding (...) the aperture proper". He counted as many as seven ventrolateral tubercles on one body chamber. He also emphasised

- 1) the attenuation of the median tubercles on the body chamber, which could even give "a divided keel";



Text-Fig. 3.

Taramelliceras heimi (DE LORIO) [m] = *T. langi* (DE LORIO).

- 2) the reduction of the ventrolateral tubercles, and
- 3) the progressive erasure of ornamentation from the flanks at the end of growth.

Examination of our material (15 samples ranging from 11 to 15.5 mm) confirms all of DE LORIO's data. However, we can add that:

- the final two septa are systematically closely spaced and slightly simplified, while the antepenultimate is seldom more closely spaced;
- the sulcus preceding the aperture proper is neither straight nor unbroken;
- the aperture margin is complex: the bottom third is radial and lined by a sulcus of variable depth; thereafter, it is sigmoidal and lined by an indistinct sulcus;
- the umbilical margin is consistently if only slightly unfolded in the final quarter whorl;
- the many small axial tubercles on the phragmocone become larger and therefore more widely spaced on the body chamber, where they are sometimes partly or entirely connected by a thin, sharp, low keel;
- the ventrolateral tubercles never appear on the phragmocone, seldom on the phragmocone/body chamber boundary and almost always around the end of the first third of the body chamber.

It can be noticed that *Oppelia langi* DE LORIO was included by SCHAIRER (1984) in his new genus *Flexispinites*. For SCHWEIGERT (oral communication), that species is considered as a minute macroconch rather than a microconch, as in this paper.

- *Taramelliceras heimi* (DE LORIO)
= *Oppelia heimi* DE LORIO 1898

In 1898 DE LORIO (p. 48–50, Pl. IV, Figs. 8 & 10) created this species for some 15 individuals, four of which possessed mature body chambers, ranging in diameter from 20 to about 30 mm. He reported that "approaching the final chamber the siphuncular tubercles develop, becoming very protuberant on the final chamber". He added "at the same time (...) others appear on either side of the outer circumference becoming on the final chamber (...) very tall and very elongate". When they appear, the venter tends to narrow and flatten. The suture line is very indented of course. In 1900 (p. 44–45) DE LORIO did not give further details although he reported possessing some forty more specimens from the Ledonian Jura.

We examined 37 mature specimens ranging in size from 17.8 to 28.2 mm. They have all or part of their body

chamber intact. All display umbilical uncoiling and many have two or three closely spaced septa. Thirty-three specimens have ventrolateral tubercles. These appear suddenly in the first third of the body chamber. In the other four specimens the tubercles appear at the end of the phragmocone. It seems that five other specimens (15.2–21.5 mm) can be ascribed to this species because, although they are preserved only as phragmocone, they bear already prominent ventrolateral tubercles. The axial tubercles, which are never very distinct on the phragmocone, suddenly become stouter when the ventrolateral tubercles appear. For this reason the specimen figured by DE LORIO (1900, Pl. III, Fig. 25) cannot belong to this species and should be classified with the *Taramelliceras minax* (see BUKOWSKI, 1887).

DE LORIO's two species *Taramelliceras langi* and *T. heimi* are always found together. As they display very similar ontogenetic patterns (unknown in other species of the genus *Taramelliceras*) and despite the fact that the *heimi* forms are more compressed than the *langi* forms at the same diameter, we consider them to be the microconchs and macroconchs of one and the same species. This dimorphic species should be called *Taramelliceras heimi* (DE LORIO).

This species is rare in the pyritised fossil marls of the Jura (less than 1 %). It is found somewhat more commonly in the ferruginous oolite facies and sporadically in the Terres Noires.

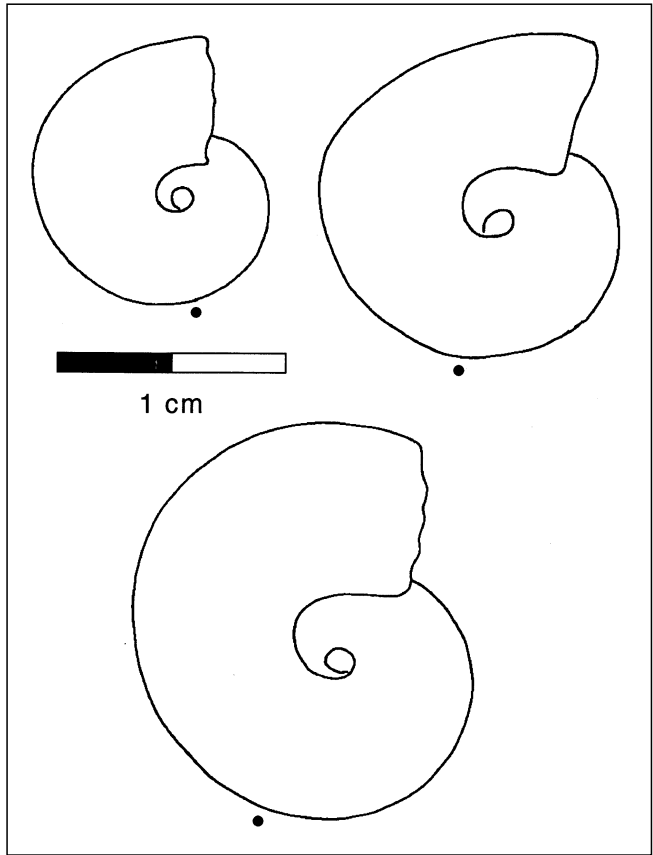
***Scaphitodites scaphitoides* (COQUAND)
= *Ammonites scaphitoides* COQUAND 1853**
(Pl. 1, Figs. 4–5 and Text-Fig. 4)

This is the most abundant micromorph species in the pyritised fossil marls, representing up to 3 % of the fauna as at Boujailles (collected by Q.S.). DE LORIO (1900, p. 55) observed more than 500 specimens from a site at La Billed (Jura). When creating the species, COQUAND (1853) emphasised its scaphitoid shell morphology and its very small size. This species has been described again recently (NEIGE et al., 1997) from a sample of 150 individuals. Of that sample, 105 mature specimens have closely spaced final two septa and most have a body chamber formed by a shaft and hook giving the species a characteristic scaphitoid appearance. It should be noticed, though, that the whorls remain in contact despite the clearly uncoiled umbilicus.

Measurements of this sample (and confirmed by measurements of 165 new specimens) show that the mature phragmocone ranges from 4.5 mm to 11.6 mm, a ratio of 1 : 2.6, with a mean value of 9.4 mm (NEIGE et al., 1997). The histogram for this character is somewhat positively skewed but is not bimodal: no size-related dimorphism can be detected. The largest mature shell diameter measured is less than 16 mm.

By contrast, a plot of thickness versus diameter reveals a bimodal distribution. However, as there is no bimodal distribution for mature phragmocone diameter and as umbilical uncoiling displays a whole array of intermediate morphologies between regular uncoiling and shaft-hook type uncoiling, the hypothesis of intraspecific polymorphism has been preferred to that of sexual dimorphism. For SCHWEIGERT (oral communication), *Scaphitodites* is a microconch genus and his macroconch partner has to be searched in another genus: *Proscaphites*.

In this species – save exceptions – a ventral sulcus appears, beginning on average some five septa ahead of the mature body chamber. As the siphuncle is invariably lo-



Text-Fig. 4.
Scaphitodites scaphitoides (COQUAND).

cated under the sulcus it is possible to think that the slight shift of the siphuncle towards the dorsal margin induces the formation of the ventral sulcus, all the more so as the sulcus terminates at the beginning of the body chamber. While this interpretation is logical enough, it does not account for the rare specimens (4 reported) where the ventral sulcus extends just beyond the beginning of the body chamber. Three explanations are possible:

- 1) The shell follows a similar growth pattern without being induced by the siphuncle.
- 2) the organic siphuncle extends very slightly beyond the phragmocone.
- 3) The final septum is too thin to be visible on the internal mould.

Interestingly, there is also one specimen (GAUDRY's collection) where the sulcus extends over the first half of the body chamber. This sulcus might also be a muscle insertion site.

This species is also found in the ferruginous oolite limestones but much more sporadically than in the pyritised fossil marls. It is very scarce in the Terres Noires (FORTWENGLER & MARCHAND, 1994). *Scaphitodites scaphitoides* (COQUAND) apparently preferred open but shallow environments as the *C. renggeri* Marls contain few phylloceratids and in particular few specimens of the genus *Sowerbyceras*.

***Sphaerodomites calcaratus* (COQUAND)
= *Oppelia calcarata* COQUAND 1853**
(Pl. 1, Fig. 6)

In 1898, DE LORIO (p. 61–62, Pl. V, Fig. 2) used the name created by COQUAND for a small, moderately inflated specimen with a very small umbilicus, comparatively thick

and not very flexuous ribs, characterised on the venter by a median keel "accompanied, on either side, by a broad, deep sulcus". DE LORIOLE also reported that the (final?) body chamber occupied at least a half whorl. But contrary to COQUAND'S sample, DE LORIOLE'S did not have a ventral swelling or "spur" as COQUAND called it.

In 1900, DE LORIOLE when observing the holotype, reported that:

- 1) the keel and one of the two sulci cross over the spur (p. 52), which is contradicted by Fig. 9b (Pl. IV);
- 2) the suture line is not very indented, and
- 3) the final septum is partly preserved. In 1928, MAIRE (Pl. 3, Fig. 18–19) depicted two individuals (D = 14 and 17 mm) from the Praecordatum zone exhibiting all the characteristics of the specimen of DE LORIOLE (1898) as re-figured in 1983 by OLORIZ & SCHAIRER.

We know only one specimen of this extremely rare species (Pont du Diable; coll. P.C.). Its final two suture lines are closely set (but not concertinaed) and its umbilicus opens to give a short shaft, indicating it is a mature form. The aperture is partly preserved. The lower third is radial, edged by a rather indistinct sulcus while the umbilical end folds back toward the shell centre prefiguring an "aborted" hook. It is 24 mm in diameter. The body chamber extends for scarcely half a whorl.

The phragmocone venter bears slight axial tubercles which give way to a smooth, unbroken keel over the final two or three chambers. The keel is edged by two sulci which form at the same time as the keel and then become clearly deeper. The keel never stands above the sulci edges. To adopt the definition of ROLLIER (1909), who created the genus, we have a tricarinate and bisulcate tabular venter. Furthermore, half way along the body chamber, the collateral sulci become shallower and the keel becomes less prominent and broadens out. This phenomenon intensifies as far as the aperture.

Ornamentation consists of low, radial primary ribs that bifurcate at the middle of the flanks. Alternate ribs are rare. The secondary ribs become slightly stouter on the ventrolateral shoulder and cross the venter at two points:

- 1) on the unkeeled part of the phragmocone, and
- 2) at the end of the body chamber when the keel and sulci become less prominent; the ribs then form an indistinct proverse chevron over the keel.

This species is reported in the ferruginous oolith marls. However, it is apparently absent from the Terres Noires.

***Sphaerodomites cf. globosus* (DE LORIOLE 1898)**

in HAAS 1955

= *Oppelia episcopalis* DE LORIOLE 1898

(Pl. 1, Figs. 8–9)

One of the authors (P.C.) found four specimens at the Crotenay site (two in the Woodhamense horizon and two in the Alphacordatum horizon) having points in common with a number of specimens described as *Oppelia episcopalis* by DE LORIOLE, *Oppelia (Phlycticeras) reynelensis* by MAIRE and *Taramelliceras (Proscaphites) globosum* by HAAS.

The resemblances with MAIRE'S species are:

- spiral striae on one of the two specimens from the Alphacordatum horizon similar to those found in *Phlycticeras* in the Callovian. These four striae are located near the ventral margin rather than the middle of the flanks;
- very small umbilicus;

- median tubercles on the phragmocone, although they are "barely detectable" in MAIRE'S species;
- ventral keel on the body chamber although that described by MAIRE is low and lined by two narrow sulci;
- constriction behind the aperture margin.

Before comparing our specimens with those of *T. episcopalis*, it should be recalled that in his original description, DE LORIOLE (1898, p. 45–48) reported the ventrolateral tubercles appear at the end of the phragmocone and the suture lines are highly indented. But he fails to mention any individuals of the species with ventral keel and sulci, or alterations in ornamentation on the rare body chambers that are preserved. However, in 1900 (Pl. III, Figs. 21–24) he depicts four phragmocones displaying original characters under the name *Oppelia episcopalis*. Figs. 21 and 22 show individuals with rounded venters displaying a series of tubercles on the median axis which progressively change into a tuberculate keel standing proud of the lateral flats. On the specimen in Fig. 23, the tuberculate keel becomes smooth and is lined by two deepening sulci. The small form in Fig. 24 is interesting as DE LORIOLE shows very fine spiral striae in high position which he terms "epidermal granulous lines"; but the specimen does not (yet?) display any incipient keel or sulci. DE LORIOLE (1900, p. 42) considers that these "singularly monstrous" individuals should be classified in the species *O. episcopalis* on the basis of their other morphological characters, including the suture line.

Resemblances between our four specimens and those few forms described by DE LORIOLE are as follows:

- small ("*Taramelliceras*" type) tubercles on the ventral axis which vanish before the beginning of the body chamber;
- the keel appears suddenly at the beginning of the body chamber; in the two individuals from the Alphacordatum horizon, the keel is smooth but may display faint crenulations towards the end of growth;
- the two ventral flats appear shortly after the keel, towards the end of the body chamber. They do not change into sulci and the cross-section remains clearly ogival;
- "*Taramelliceras*" type ornamentation on the phragmocone. However, on the body chamber, the primary ribs may become slightly retroverse and the forked secondary ribs may become stouter at their ends (individuals from the Alphacordatum horizon).

Insofar as DE LORIOLE'S original description of *Oppelia episcopalis* does not mention specimens with keel and sulci, we cannot ascribe our individuals to this species. However, since these forms are very similar to *Taramelliceras (Proscaphites) globosum* DE LORIOLE in HAAS (*globosa* being for DE LORIOLE the variety of *Oppelia episcopalis* with the most inflated individuals) it seems reasonable to use the name given by HAAS for our four specimens.

SCHWEIGERT et al. (1999) depict under the name of *Oxydiscites pidanceti* (COQUAND, 1853) a topotype and two small individuals, one from the "Marnes de Villers" (Normandy) (Fig. 6; Houlgate, coll. Ilg), the other from the *C. renggeri* marls of Champagnole (Jura) (Fig. 7). As the specimen from Normandy "shows a weak but remarkable spiral striation", SCHWEIGERT et al. (1999) consider it to be an inner whorl of *Oxydiscites*, a genus (DACQUÉ, 1934) with a spiral striation, and classify DE LORIOLE'S *episcopalis* species (but only *globosus* variety) as synonymous with *pidanceti* (COQUAND). However, COQUAND'S holotype, which must have been greater than 40 mm in diameter, is relatively com-

pressed and differs from all the specimens described by a very marked "prominent keel", sulci which are merely flat and the absence of axial tubercles on the phragmocone. Moreover, COQUAND does not report any spiral striation. Given the current state of knowledge, it seems wiser not to consider the species of DE LORIOL in HAAS as synonymous with *pidanceti* (COQUAND).

Sphaerodomites cf. *globosus* as described here seems to be rare. But as the nuclei are very difficult to identify it may be more common than is thought. It is found both in the ferruginous oolite facies and in the Terres Noires but mature forms are rare.

***Sphaerodomites ? puellaris* (DE LORIOL)
= *Oppelia puellaris* DE LORIOL 1898**

(Pl. 1, Fig. 7 and Text-Fig. 5)

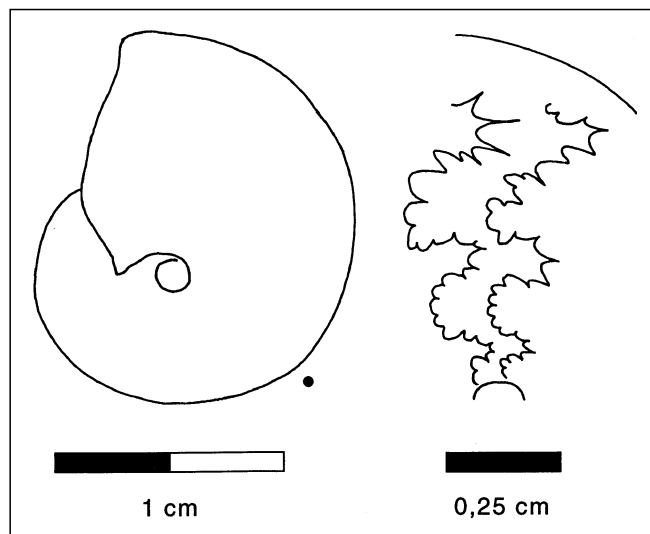
This species was created by DE LORIOL in 1898 from a single 15 mm specimen with part of its body chamber preserved. It is an inflated form, with a very small umbilicus and no marked ornamentation. The suture line is fairly simple. A second specimen, also 15 mm in diameter, was described but not figured in the Ledonian Jura (DE LORIOL, 1900, p. 53).

In our collections a single specimen from Crotenay (bed 65, Praemartini horizon; COURVILLE et al., 2000) is a representative of this species. It is a complete specimen with the final two septa telescoped, an uncoiled umbilicus and part of the mature aperture. It must have been about 17 mm in diameter.

The very faint ornamentation consists of radial primary ribs and often forked secondary ribs that do not cross the venter. At the end of the phragmocone a faint narrow, uncrenulated keel appears along the centre line of the venter. On the body chamber the keel is lined by two very slender shoulders. About half way along the body chamber, which covers half a whorl, there is a break in coiling which tends to become scaphitoid. The umbilical part of the aperture, the only part intact, shows there was a sulcus ahead of the aperture margin.

The specimen becomes more compressed at the phragmocone/body chamber boundary. A few spiral striae can be seen near the ventral edge when illuminated at a low angle.

This specimen therefore displays characters reported in *S.* cf. *globosus* DE LORIOL in HAAS, although much at-



Text-Fig. 5.
Sphaerodomites ? puellaris (DE LORIOL).

tenuated. Accordingly, we ascribe it tentatively to the genus *Sphaerodomites*.

This form is not found in the Terres Noires but is purportedly found in the ferruginous oolite limestones.

3.2. Pachyceratinae

***Tornquistes chapuisi* (DE LORIOL) non OPPEL**

(Pl. 1, Figs. 11–12 and Text-Fig. 6–7)

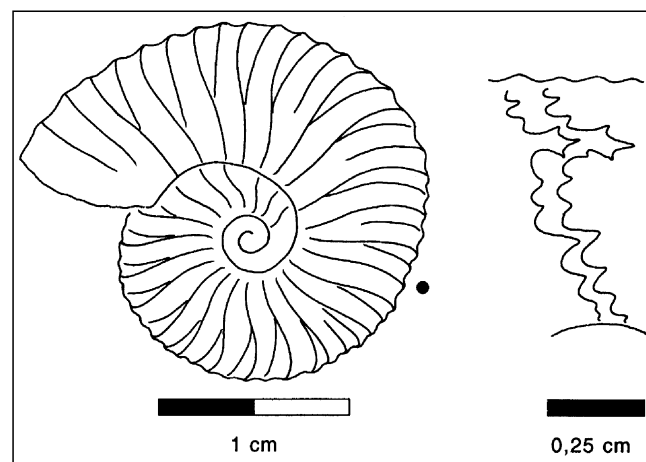
This species, as understood here, encompasses two species created by DE LORIOL.

● ***Tornquistes chapuisi* (DE LORIOL) non OPPEL
= *Sphaeroceras chapuisi* OPPEL in DE LORIOL**

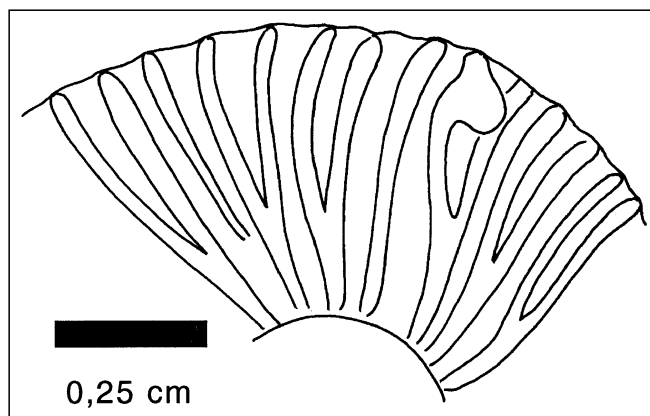
DE LORIOL (1900, p. 59–61) reported 12 specimens of *S. chapuisi* several of which had part of the body chamber intact. Mature size ranges from 17 to 20 mm. In his description, he emphasised the whorls tube as high as they are wide, the venter rounded, and the ribs bifurcating midway along the flank. He also reported that a slight ventral sulcus may occur on the phragmocone and, above, all parabolic nodes on the venter, including on the body chamber, "analogous to those of certain *Perisphinctes*". Additionally, he mentioned too that the terminal part of the body chamber seems to contract. Finally he showed (Fig. 10, p. 60) that the suture line is not very indented and has very broad saddles.

This species is invariably very rare in the pyritised fossil marls (approximately 0.5 % of the population). Our collections (seven adults ranging from 16 to 18.5 mm and three phragmocones) allow the following clarifications:

- closer sutural spacing may start three septa before the final septum which is consistently concertinaed with the penultimate septum;
- the body chamber does not apparently exceed half a whorl;
- the body chamber becomes characteristically narrower towards the aperture; this progressive contraction is common in many sphaerocone species;
- there may be a slight break where the ribs cross the venter; this is actually a slight flattening or even a sulcus which may give rise to two faint rows of very small tubercles; this feature is absent or less pronounced on the body chamber;
- the parabolic nodes seem to be more common on the phragmocone than on the body chamber. DE LORIOL (1900, p. 61) reports a geniculate individual. Our observations suggest the geniculation is related to a more



Text-Fig. 6.
Tornquistes chapuisi DE LORIOL non OPPEL [m].



Text-Fig. 7.

Tornquistes chapuisi DE LORIO non OPPEL [M].

prominent parabolic node, since the whorl is consistently modified to a greater or lesser degree at each node;

- depressed, narrow radial zones occur on the phragmocone suggesting constrictions;
- the umbilical margin uncoils clearly but evenly; only one individual displays shaft and hook type uncoiling. Uncoiling generally begins at the end of the phragmocone except in one specimen where the phragmocone is sca-phitomorphic;
- the primary ribs are radial in the first half of the flanks and then retroverse after the bifurcation point;
- the secondary ribs are consistently less prominent than the primaries, above all on the inner whorls;
- the suture line is simple.

● ***Tornquistes chapuisi* (OPPEL) in DE LORIO**
= ***Macrocephalites greppini* DE LORIO 1898**

In 1898 DE LORIO described (Pl. V, Figs. 15, 15a) a single specimen of a large ammonite (phragmocone up to 60 mm) under the obviously incorrect generic name *Macrocephalites*. The specimen is very inflated and shows an open but deep umbilicus, rounded venter, straight and stout primary ribs on the lower part of the flanks, two or three times as many secondary ribs crossing the ventral margin without interruption. The suture line has lobes and saddles which "are not very deeply incised".

In 1900 DE LORIO classified 16 specimens in this new species. All of them were phragmocones ranging from 10 to 22 mm. For DE LORIO these specimens were "indisputably juvenile *Macr. Greppini*".

Oddly though, DE LORIO did not report the often faint parabolic nodes on either side of the siphuncular axis although such nodes cause the ribs on the median part of the venter to be slightly raised. Similarly he did not report that the suture line at these diameters already has a lobe in the upper part of the umbilical margin.

The two individuals depicted by DE LORIO in 1900 (Pl. IV, Figs. 17 & 18) as *M. greppini* are in fact very different from each another. We made the same observation in our material which contains two groups of forms distinguished by a similar set of characters. The first group exhibits:

- a rounded umbilical margin;
- radial ornamentation;
- a fairly uneven whorl;
- well developed parabolic nodes;
- an axial flat on the venter;
- close-set suture lines from 15 mm diameter.

This first group, matching Fig. 17 in DE LORIO (1900), shares many points in common with the species "*chapuisi*"

as described by DE LORIO and also above in this paper. Insofar, as this first group is larger in size, it is legitimate to think it contains macroconchs while the *chapuisi* group contains microconchs.

The only genus known to display this type of morphology in the Lower Oxfordian is *Tornquistes*. Accordingly we propose to use this genus to replace the genera *Sphaeroceras* and *Macrocephalites*. The species name should rightly be *chapuisi* DE LORIO because the name *greppini* cannot be used since the holotype (DE LORIO, 1898, Pl. V, Fig. 15) is a large (60 mm) phragmocone that clearly belongs to the genus *Cardioceras*.

One ammonite described by BUKOWSKI (1887) as *Sphaeroceras insociale* is close to *T. chapuisi* but suture and parabolic nodes are, in our opinion, different.

Last remark: as suggested by SCHWEIGERT (oral communication), that species may be a primitive form of *Protophites*.

Tornquistes chapuisi (OPPEL) is found in the ferruginous oolite limestones but is rare. It does not seem to occur in the Terres Noires.

***Tornquistes* sp.**

(Pl. 1, Fig. 10)

The second group matching Fig. 18 of DE LORIO (1900) is distinctive from the inner whorls in having a slightly more open umbilicus, a more prominent umbilical margin with a vertical – or even overhanging – umbilical wall, more even coiling, and more numerous and fainter parabolic nodes. The secondary ribs are more proverse on the upper half of the flanks. The venter has no flat on the axial part and may be slightly ogival. Moreover, at the same diameter the suture line is more complicated. Finally the three individuals in our collection are all phragmocones whose final suture lines are not close-set.

These specimens are clearly not micromorphs; therefore, they are the inner whorls of a large growing genus. The only possible genus in the Lower Oxfordian is *Tornquistes*. However, as there are no published reports of *Tornquistes* species in the Mariae zone, we shall keep the nomenclature of this form open.

A few *Tornquistes* belonging to a large species have been reported in the ferruginous oolite limestones and in the Terres Noires, but these specimens have not yet been described in detail.

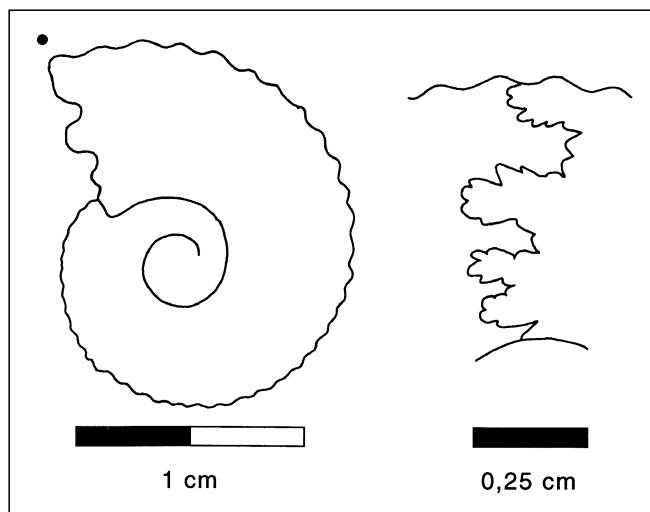
3.3. Hecticoceratinae

"*Hecticoceras*" *kobyi* (DE LORIO)
= ***Oekotraustes kobyi* DE LORIO 1898**

(Pl. 1, Figs. 13–14)

DE LORIO (1898, p. 70–71) considered his new species to be common. It is characterised generally by a final body chamber (more than half a whorl) with "somewhat irregular" coiling marked by "a slight elbow". For DE LORIO the venter is either rounded or somewhat angular and slightly keeled. He reported that ornamentation is often absent except on the "final septum" where the "ribs are arched forwards and stouter towards the external margin ... and soon weakening" before they disappear. He reported the suture lines are not very indented. The individual shown in Pl. V, Fig. 11 is probably an *Eocheloceras*.

In 1900 (p. 56) he confirmed the species was commonplace. He also indicated that while the species is often smooth, ornamented specimens do occur. Most of DE LORIO'S specimens have their body chambers partly or entirely preserved, implying a small species. An individual



Text-Fig. 8.
"Hecticoceras" baylei (COQUAND).

measuring 13.7 mm is even depicted (Pl. IV, Fig. 22) with its aperture "a siphuncular rostrum and very short lappets in the middle of each flank". He confirmed that a geniculation is observed in some specimens. He did not consider this to be a fundamental character.

Four geniculate specimens were collected from the Scarburgense sub-zone, Praemartini horizon and the base of the Alphacordatum horizon in the Crotenay section. They are all mature individuals whose final two septa are concertinaed.

The specimen from the Scarburgense horizon has its body chamber and the internal part of its phragmocone intact. The latter is smooth, whereas the body chamber has distinct secondary ribs. These are broad but not sharp and become proverse as they thin out beyond the ventrolateral margin. These ribs are more distinctive ahead of the geniculation which occurs towards the end of the first third of the body chamber. Beyond that point, they become fainter and disappear. Primary ribs are absent throughout.

The other three specimens too display the characteristic geniculation, i.e. a sudden increase in height while the umbilical diameter remains constant. At the end of growth, a second smaller geniculation occurs in three specimens. In one of them, the geniculation is at the phragmocone/body chamber boundary. In the other two, it appears at the end of the first third of the body chamber. Just one specimen displays prominent secondary ribs ahead of the geniculation but these disappear quickly beyond it.

In the current state of knowledge we cannot tell whether this morphology is characteristic of a species or whether, as DE LORIOI seemed to think, these are "abnormal" specimens within a population with classical planispiral coiling.

This species is rare in the ferruginous oolite limestones and in the Terres Noires (FORTWENGLER & MARCHAND, 1994).

***"Hecticoceras" baylei* (COQUAND)
 = *Oppelia baylei* COQUAND 1853
 (Pl. 1, Fig. 15; Text-Fig. 8)**

In 1900 DE LORIOI classified 15 small specimens (12–21 mm) of which one only had an intact body chamber, with COQUAND's species. He described them as compressed forms, with a rather narrow umbilicus and round-

ed venter. On the median line is "an even series or tubercles ... not very prominent, closely-spaced"; on each side of the line is a very fine keel that is invariably difficult to observe. The flanks are smooth and the suture line not very indented.

We have only one individual of this species; it was collected from ferruginous fossil marls in the Boujailles area (Jura, coll. Q.S.) and dated to the top of the Praecordatum subzone. It is a 16 mm phragmocone with evenly spaced and increasingly large axial tubercles from 7–8 mm in diameter onwards. There are no primary ribs. The secondary ribs are small and proverse. They can be seen only on the ogival venter. They end in a small tubercle. The suture lines are not very indented; they are unusual in that in the first two thirds of the phragmocone they close up two-by-two at three points but are not concertinaed.

The same beds have yielded two individuals of 10–11 mm with parts of their body chambers intact. They are apparently mature specimens although the final two septa are not close-set. The overall shape and the presence of very small tubercles (associated with the secondary ribs) mean that these forms are likely microconchs. However, the more indented suture lines in comparison with the specimen described above argue against this hypothesis.

This species is apparently absent from the Terres Noires and the ferruginous oolite limestones.

***"Hecticoceras" mayeri* DE LORIOI 1898
 = *"Oppelia" mayeri* DE LORIOI 1898
 (Pl. 1, Figs. 16–17)**

In 1898 DE LORIOI created this species from eight specimens whose body chamber was not preserved (15–29 mm). He listed the following main characteristics:

- narrow umbilicus;
- thick, widely spaced, radial primary ribs, terminating without a tubercle ahead of the radial sulcus midway up the flank;
- arched secondary ribs ending with a prominent rounded tubercle;
- slight keel without tubercles;
- suture lines with deeply indented lobes and saddles.

In 1900 he described four small (less than 20 mm) septate specimens. He added that the keel is "to a greater or lesser extent divided into fragments or thin elongate tubercles", and that the suture line is less deeply indented as the individuals are small.

Six specimens come either from ferruginous fossil marls, dated to the bottom of the Lower Oxfordian (Mariae zone, Scarburgense subzone, Scarburgense horizon) of the Cher (coll. M. DUBUGET), and *C. renggeri* marls. They are all phragmocones, the largest of which reaches 25 mm. They display all the main characteristics listed by DE LORIOI. The following clarifications can be added:

- towards the radial sulcus the primary ribs may become stouter and form a blunt tubercle;
- towards the ventrolateral margin, the secondary ribs fill out and may become raised to give true tubercles;
- the secondary ribs may cross the axial part of the venter forming a slightly proverse and raised chevron;
- the great development of lobes induces a decrease in the number of septa. Spacing between septa increases during ontogeny.

Four specimens (two from the Cher and two from Crotenay) are from the Woodhamense horizon (Scarburgense subzone). They have more morphological af-

finities with the form from the Ledonian Jura (DE LORIO, 1900, Pl. IV, Fig. 8) than with those from the Bernois Jura (DE LORIO, 1898, Pl. IV, Figs. 21–23). It is observed that:

- the suture line has shorter lobes;
- the ornamentation is less marked and the lateral sulcus fainter;
- the venter is narrow with first a fine, uncrenulated keel that progressively becomes a keel with secondary rib chevrons forming small rises before becoming properly individualised tubercles. These tubercles are sometimes associated with a small tertiary rib;
- the ventrolateral tubercles appear very early in ontogeny, becoming progressively stouter. They are better individualised than on the Scarburgense sub-zone specimen.

A single specimen found at Pont du Diable comes from the top of the Praecordatum subzone. It is a 14.5 mm phragmocone characterised by:

- a not very indented suture line;
- no primary ribs but short secondary ribs, pairs of which end with a very marked tubercle from less than 10 mm in diameter;
- a very indistinct lateral sulcus at this diameter;
- a narrow venter with a low, uncrenulated keel along the midline.

As no specimens of this species have yet been found with their intact body chamber, we are unable to say whether or not it is a micromorph species. However, we can report that this morphology is unknown in the beds of the Lower Oxfordian riches in carbonates where larger ammonites are preserved. It is very rare in the Terres Noires.

4. Small Adult Ammonites (Microconchs) from the Pyritised Fossil Marls

4.1. Hecticoceratinae

Hecticoceras matheyi DE LORIO 1898

(Pl. 1, Figs. 18–20)

In 1898 (p. 43–44) DE LORIO created this species for three specimens with intact body chambers ranging from 18 to 20 mm. He reported the venter is rounded with no keel, the ornamentation on the body chamber “bears a few very slight sinuous ribs ... somewhat more prominent in the umbilical area ... weakened on the ventral margin”. The phragmocone furrow is smooth. The umbilicus is largely open and the suture line not very indented. In 1900 (p. 35–36) he classified 43 specimens with this species, often with complete or part of the body chamber. He specified little other than that on the umbilical circumference “often appeared a few very short ribs” and that there may be a slight fold on the ventral margin.

Most specimens in our material matching DE LORIO’s description have a body chamber that extends for half a whorl; moreover the final suture lines either close up or the last two suture lines are concertinaed. If we use only complete adulte specimens (37 individuals from Pont du Diable), the mature phragmocone can be seen to range from 6 to 19 mm. The same values are found for the 28 specimens from Boujailles.

In the smaller specimens, the umbilicus is very open and ornamentation indistinct. The body chamber above all displays a very proverse swelling, which is sometimes distinct, the centre line of which extends from the “inner lateral lobe” to use DE LORIO’s terminology. In larger individuals, this swelling can be seen to be part of a sickle-

shaped rib, the umbilical part of which is more prominent than the ventrolateral part. This rib morphology foreshadows a lappet.

We consider these small adult forms to be microconchs of macroconch forms *H. bonarelli* DE LORIO for the most faintly ribbed, *H. chatillonense* DE LORIO for forms with more distinct ribs and even *H. punctatum* STAHL (in DE LORIO) for the rare individuals with coarse ribs.

This microconch is found in all the environments considered here.

4.2. Taramelliceratinae

Creniceras renggeri (OPPEL) 1862

This species is always very abundant in the pyritised fossil marls and remarkably easy to recognise. In most cases the body chamber is preserved (rarely with the lappets), the last two suture lines are closely spaced and the umbilical margin is largely uncoiled. A recent study (NEIGE, 1997) reports that *Creniceras renggeri* includes individuals exhibiting all the intermediate morphologies from large forms (mature size more than 20 mm) with many prominent ventral crenulations to much smaller forms (mature diameter less than 10 mm) with few, indistinct ventral crenulations if any.

In 1963 PALFRAMAN proposed considering this species as the microconch of the macroconch *Taramelliceras richei* (DE LORIO). This is plausible for the following reasons:

- the inner whorls of the two groups are very similar, even if *C. renggeri* consistently has simpler suture lines than contemporaneous *Taramelliceras*;
- the genus *Taramelliceras* first appears at the base of the Upper Callovian as does the genus *Creniceras*.

However, two observations apparently contradict PALFRAMAN’s hypothesis:

- *Creniceras* is completely unknown in the South-East France Basin while *Taramelliceras* is not rare;
- *Creniceras* can disappear from the fossil record, reappearing later, as shown by ZIEGLER (1974).

As yet we do not know for certain whether *Creniceras* includes only microconchs or whether it is a micromorph genus with indistinct sexual dimorphs. In the latter case, the slightly crenulated small forms would be the microconchs and the larger more crenulated forms the macroconchs.

This species is very common in the *C. renggeri* marls (sometimes more than 10 %) and is found in ferruginous oolitic limestones, but it is less common. However, although found in Ardèche, the species is completely absent from the Terres Noires. It seems then that it preferred shallow, open water environments like *S. scaphitoides*.

4.3. Euaspidoceratinae

In this subfamily the specimens interpreted as macroconchs (subgenus *Euaspidoceras*) are invariably associated with specimens interpreted as microconchs (subgenus *Mirosphinctes*) (BONNOT, 1995; BONNOT et al., 1994; BONNOT & GYGI, 1998).

In the pyritised fossil marls, *Mirosphinctes* are rarely preserved with their intact body chamber. Generally, they are phragmocones only. However, in many specimens the final septa are closely spaced and are therefore probably mature. These phragmocones range in diameter from 19 mm to 30 mm, values similar to those of complete specimens, sometimes with lappets, collected from carbonate facies. As the body chamber usually occupies half a whorl, mature size is between 30 and 45 mm. Phragmocone ornamentation comprises:

- 1) a smooth section;
- 2) a stage with parabolic ribs and no parabolic intermediate ribs, and
- 3) a stage with more or less prominent parabolic nodes.

In the Lower Oxfordian, the adult body chamber with divided ribs never displays parabolic formations (specimens with body chambers showing parabolic nodes never have closely spaced final septa and are therefore juveniles).

Ornamentation of the macroconchs associated with *Mirosphinctes* includes a stage with parabolic formations followed by a bituberculate stage. They can be easily distinguished from the microconchs as the parabolic formation stage is always brief and the bituberculate stage often appears before they reach diameters of 20 mm.

The *Mirosphinctes* microconchs are relatively abundant in the carbonate facies and pyritised fossil marls. However, they are very rare indeed in the black marls with no pyritised fossils (Terres Noires) and nearly as rare as the macroconchs.

5. Conclusion

Pyritised fossil marls contain diverse ammonite fauna and their abundance means that even some extremely

rare forms can be collected. These forms are small (termed micromorphs) and cannot readily be ascribed to any known genus as their ornamentations are indistinct and their suture lines not very significant. The question is whether these specimens are representatives of a true palaeospecies or whether they are teratological specimens characterised by their unusual ontogeny and doomed in evolutionary terms.

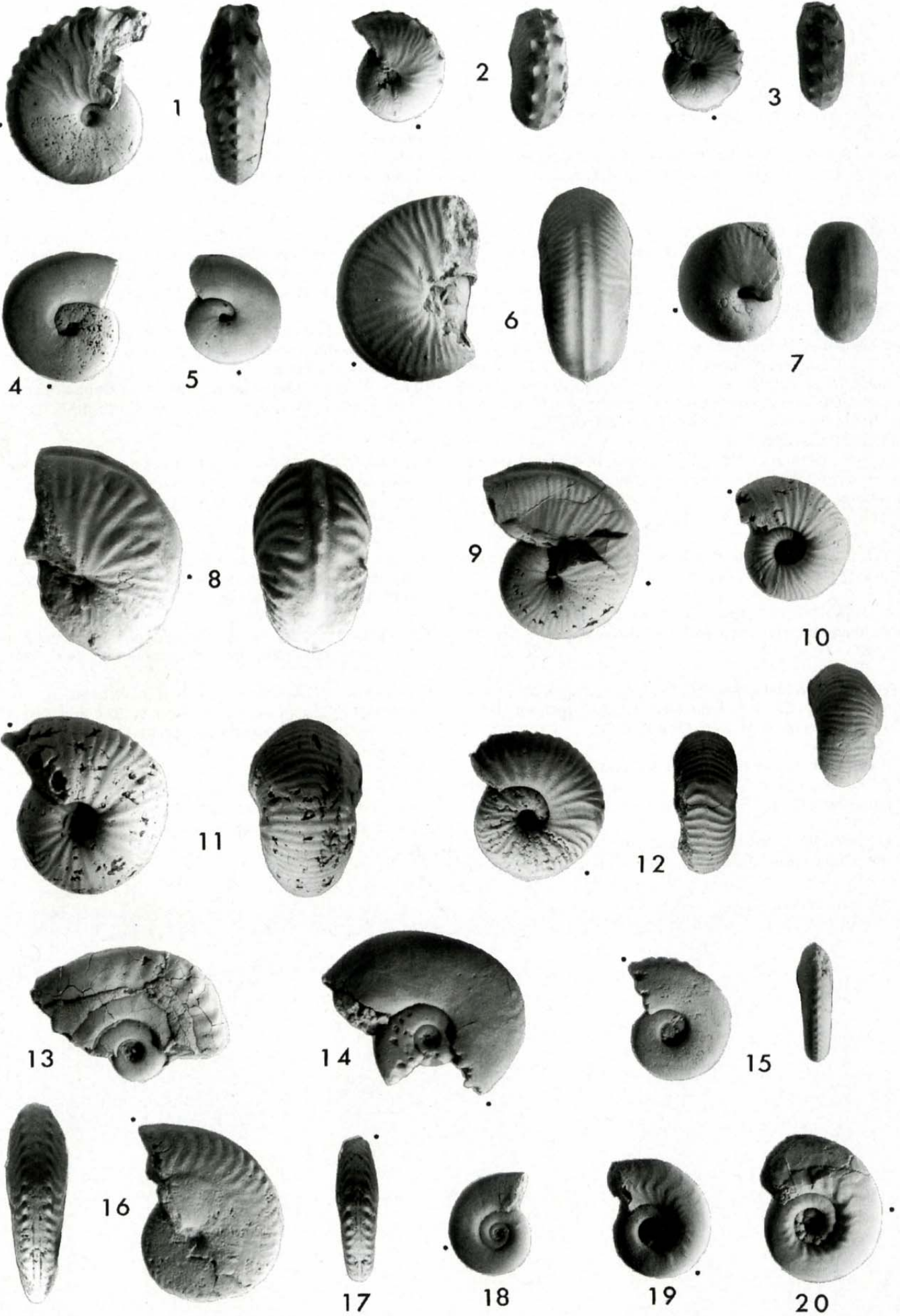
The relative abundance of some micromorph ammonites (*Scaphitodites scaphitoides*) or microconch/macroconch pairings (*Creniceras renggeri*) shows that the clear reduction in size could be tolerated in open environments rich in organic material which could therefore form an original biotope for these species.

Those specimens of known large species found in pyritised fossil marls and measuring less than 30 mm in diameter are invariably immature. This proves that the ammonite fauna was not a dwarf fauna even if very small species are reminiscent of dwarf (or progenetic) species.

It is important that further data should be collected on "micromorph" species so that comparisons and correlations can be made between populations, speciations and environments.

Plate 1

- Fig. 1: *Taramelliceras heimeii* (DE LORIO) [M].
Pont du Diable (Doubs).
Praecordatum sz. (JR).
- Figs. 2–3: *Taramelliceras heimeii* (DE LORIO) [m]
= *T. langi* (DE LORIO).
Pont du Diable (Doubs).
Praecordatum sz. (JR).
- Figs. 4–5: *Scaphitodites scaphitoides* (COQUAND).
Crottenay (Doubs).
Praecordatum sz. (PC).
- Fig. 6: *Sphaerodomites calcaratus* (COQUAND).
Pont du Diable (Doubs).
Praecordatum sz. (PC).
- Fig. 7: *Sphaerodomites? puellaris* (DE LORIO).
Crottenay (Doubs).
Praecordatum sz., Praemartini horizon (PC).
- Fig. 8: *Sphaerodomites* cf. *globulus* (DE LORIO) in HAAS.
Crottenay (Doubs).
Scarburgense sz., Woodhamense horizon (PC).
- Fig. 9: *Sphaerodomites* cf. *globulus* (DE LORIO) in HAAS.
Crottenay (Doubs).
Praecordatum sz., Alphacordatum horizon (PC).
- Fig. 10: *Tornquistes* sp.
Pont du Diable (Doubs).
Praecordatum sz. (PC).
- Fig. 11: *Tornquistes chapuisi* DE LORIO non OPPEL [M]
= *T. greppini pars* (DE LORIO).
Pnt du Diable (doubs).
Praecordatum sz. (JR).
- Fig. 12: *Tornquistes chapuisi* DE LORIO non OPPEL [m].
Pont du Diable (Doubs).
Praecordatum sz. (JR).
- Figs. 13–14: *Hecticoceras kobyi* (DE LORIO).
Crottenay (Doubs).
Praecordatum sz. (PC).
- Fig. 15: *Hecticoceras baylei* (COQUAND).
Boujailles (Jura).
Praecordatum sz. (QS).
- Fig. 16: *Hecticoceras mayeri* (DE LORIO).
Montlouis (Cher).
Scarburgense sz., Woodhamense horizon (MD).
- Fig. 17: *Hecticoceras mayeri* (DE LORIO).
Scay (Cher).
Scarburgense sz., Scarburgense horizon (MD).
- Figs. 18–20: *Hecticoceras matheyi* DE LORIO [m].
Pont du Diable (Doubs).
Praecordatum sz. (JR).
- = Last sutures.
All the ammonites are × 1.5.
They are preserved in the typothèque of the "Centre des Sciences de la Terre" of the Burgundy University.
Photos A. BONNOT.
- Figs. 1, 2, 3, 11, 12, 18, 19, 20: Jacques ROSSI' s collection.
Figs. 4, 5, 6, 7, 8, 9, 10, 13, 14: Philippe COURVILLE' s collection.
Figs. 15: Quentin SCOUFFLAIRE' s collection.
Figs. 16, 17: Michel DUBUGET' s collection.



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