

Origin of the Kimmeridgian-Tithonian Boreal perisphinctid faunas: migration and descendants of the Tethyan genera *Crussoliceras* and *Garnierisphinctes*

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Abstract

Kimmeridgian perisphinctid faunas from England and eastern France have been studied in order to try to clarify the relationships between the Late Kimmeridgian perisphinctids of the Boreal Faunal Realm, whose forerunners are unknown in the Subboreal Province, and their possible ancestors in the Submediterranean Province of the Tethyan Faunal Realm. From Late Oxfordian times onward eastern France was occupied by the Western Europe Swell, a shallower water area that acted as a transitional faunal region between the Subboreal and Submediterranean Provinces. Different biozones have been developed within the provinces, and these are still imperfectly correlated. They are discussed in the present account. Here, we describe the stratigraphical and geographical distributions of the perisphinctid genera that form the basis for the study. They include the Submediterranean forms *Crussoliceras* and *Garnierisphinctes*, the Subboreal *Subdichotomoceras* and *Pectinatites*, and *Tolvericeras* and *Pseudogravesia* of the Western European Swell. Many of the English specimens studied are preserved as crushed impressions, but their positions are accurately located within a well-defined chronostratigraphical succession. In contrast, the stratigraphical relationships of much of the material from France, mostly museum specimens in solid preservation in old collections, are uncertain or have yet to be clarified. The palaeontological descriptions include 18 species or subspecies of which 8 species (*Crussoliceras dubisense*, *lamberti*, *lotharingicum*, *petitclerci*, ? *Subdichotomoceras praecursor*, *Tolvericeras anglicum*, *popeyense*, *robertianum*) and 1 subspecies (*Subdichotomoceras lamplughii dorsetense*) are new. The last part of the paper discusses the origin of the Subboreal perisphinctids, including the possibility that *Subdichotomoceras* evolved from *Crussoliceras* and that *Pectinatites* may have evolved from *Subdichotomoceras*. However, with the possible exception of ? *S. praecursor* n. sp. from the Western Europe Shelf of eastern France, there is no published description of a transitional form between *Crussoliceras* and *Subdichotomoceras*. An evolution quantum jump is needed to explain the sudden morphological differentiation of *Subdichotomoceras*. This probably occurred via peripatric speciation.

Keywords

Perisphinctid ammonites, Subboreal and Submediterranean faunas, Kimmeridgian, England, France, Western Europe Swell.

Résumé

Origine des faunes de périsphinctidés boréales du Kimméridgien-Tithonien : migrations et descendance des genres téthysiens *Crussoliceras* et *Garnierisphinctes*. - L'étude a pour objet les faunes de Périsphinctidés du sud de l'Angleterre et de l'est de la France. Le but est d'essayer de comprendre les relations probables entre les Périsphinctidés boréaux du Kimméridgien supérieur, dont on ne connaît aucun précurseur dans les régions subboréales, et leurs probables ancêtres subméditerranéens. Le matériel du sud de l'Angleterre est souvent écrasé et conservé à l'état de compression, mais il est bien situé stratigraphiquement dans un cadre lithostratigraphique et biostratigraphique précis. Au contraire du matériel de l'est de la France, issu principalement de collections anciennes, dont la localisation stratigraphique est incertaine ou doit être interprétée. En outre, à partir de l'Oxfordien, l'est de la France faisait partie du Haut-Fond d'Europe occidentale, un domaine intermédiaire et de faible profondeur entre les domaines subboréal et subméditerranéen. Les différents schémas zonaux utilisés pour chacun de ces territoires sont encore imparfaitement corrélés et sont discutés. Dans la partie paléontologique sont décrits et discutés les genres de Périsphinctidés les plus significatifs de l'étude : *Crussoliceras* et *Garnierisphinctes* (Subméditerranéen), *Subdichotomoceras* et *Propectinatites* (Subboréal), *Tolvericeras* et *Pseudogravesia* (Haut-Fond d'Europe occidentale). Les descriptions paléontologiques comptent 18 espèces ou sous-espèces, dont 8 espèces (*Crussoliceras dubisense*, *lamberti*, *lotharingicum*, *petitclerci*, *Subdichotomoceras praecursor*, *Tolvericeras anglicum*, *popeyense*, *robertianum*) et une sous-espèce (*Subdichotomoceras lamplughii dorsetense*) sont nouvelles. La dernière partie du travail traite de l'origine des Périsphinctidés subboréaux, en particulier la possibilité que *Subdichotomoceras* ait évolué à partir de *Crussoliceras* et que *Pectinatites* puisse être dérivé de *Subdichotomoceras*. Cependant, à l'exception de ? *S. praecursor* du Haut-Fond d'Europe occidentale de l'est de la France, aucune forme de transition entre ces genres n'a été identifiée ; d'où la nécessité d'admettre un saut morphologique et

un processus d'évolution quantique pour expliquer la différenciation de *Subdichotomoceras*, probablement réalisée dans le cadre du modèle de spéciation péripatrique.

Mots-clés

Ammonites périsphinctidés, faunes subboréale et subméditerranéenne, Kimméridgien, Angleterre, France, Haut-Fond d'Europe occidentale.

1. INTRODUCTION

The present study of museum and new material from the Kimmeridgian of England and parts of France (Paris Basin, Jura and SE France) was undertaken to clarify the relationships between the Late Jurassic Subboreal and Submediterranean perisphinctid faunas which are as yet poorly understood. During the Late Jurassic, differentiation of the faunas in the Boreal and Tethyan Faunal Realms increased from Late Oxfordian times

onward. In Late Kimmeridgian times the boundary between the Subboreal and Submediterranean faunal provinces ran through the Paris Basin and the northern part of the Jura (Fig. 1). As a result, the ammonite faunas of Normandy and the Boulonnais are closely related to those of England and the Boreal Realm, and those of the northern Aquitaine Basin and the Paris Basin from Poitou-Charentes as far south as Lorraine display clear-cut relationships with the Tethyan Realm. The latter area is the western part of the Middle European Shelf

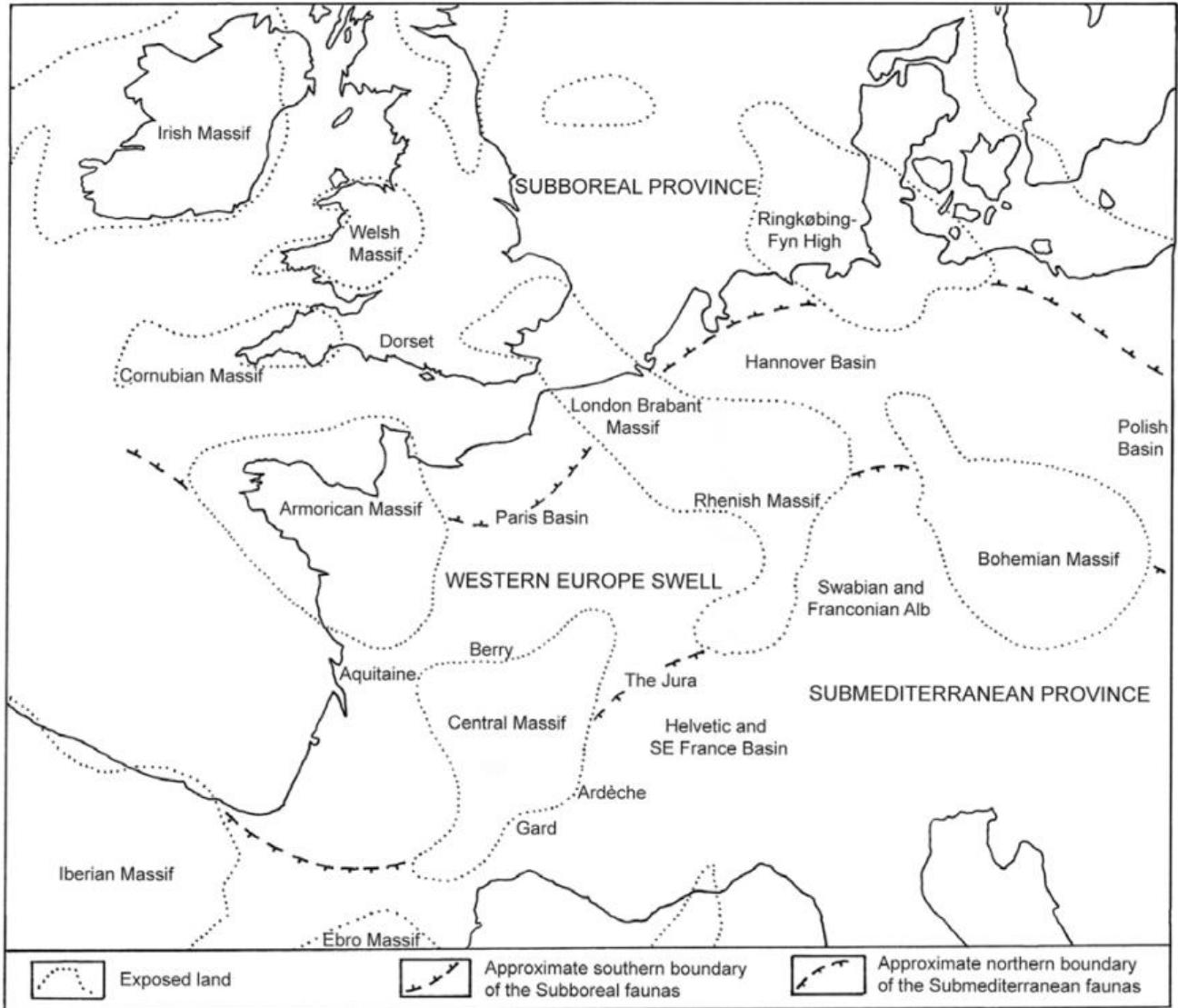


Fig. 1: Palaeogeographical reconstruction for Western Europe during Kimmeridgian times showing the principal outcrop areas referred to in the text.

of Énay (1980) which extended from western France to Eastern Poland (Fig. 1). It was subsequently named the French-German Biome and the Western Europe Swell by Hantzpergue (1987, 1989) when referring to its ecological significance. Only the last of these names is used in this account.

The present study is the culmination of an interest in the relationships of the contemporaneous Subboreal and Submediterranean perisphinctid ammonites which began in the 1980s with the identification by one of us (RE) of ammonites collected by Roberts (1892) from Cambridgeshire, England as the Submediterranean *Crussoliceras sevogodense* (Contini & Hantzpergue, 1975). It was thought at that time that *Crussoliceras* might be related to *Subdichotomoceras* Spath, but the latter was considered to be a Subboreal genus. The phyletic relationship between *Crussoliceras* and *Subdichotomoceras* was suggested by one of us (Énay,

1985); Van der Vyver (1986) came to a similar conclusion based on study of their stratigraphical distribution in England.

From the Late Oxfordian onward, the Subboreal Province was populated by the Aulacostephanidae (Pictoniinae and Aulacostephaninae) which did not include a possible ancestral form of *Subdichotomoceras*. Bed-by-bed collecting of the ammonites and photography of crushed *in situ* specimens exposed in the type Kimmeridgian sections at Kimmeridge, Dorset has enabled one of us (R.E.) to re-examine the relationships of the Subboreal perisphinctids that gave rise to the radiation of the dorsoplanitids and the Submediterranean forms that are likely to have been ancestral to them. In addition, specimens in museum collections in Oxford, Cambridge, Geneva and Lyon from throughout the Kimmeridgian part of the Kimmeridge Clay outcrop (Fig. 2) have been examined, and the recorded occurrences of

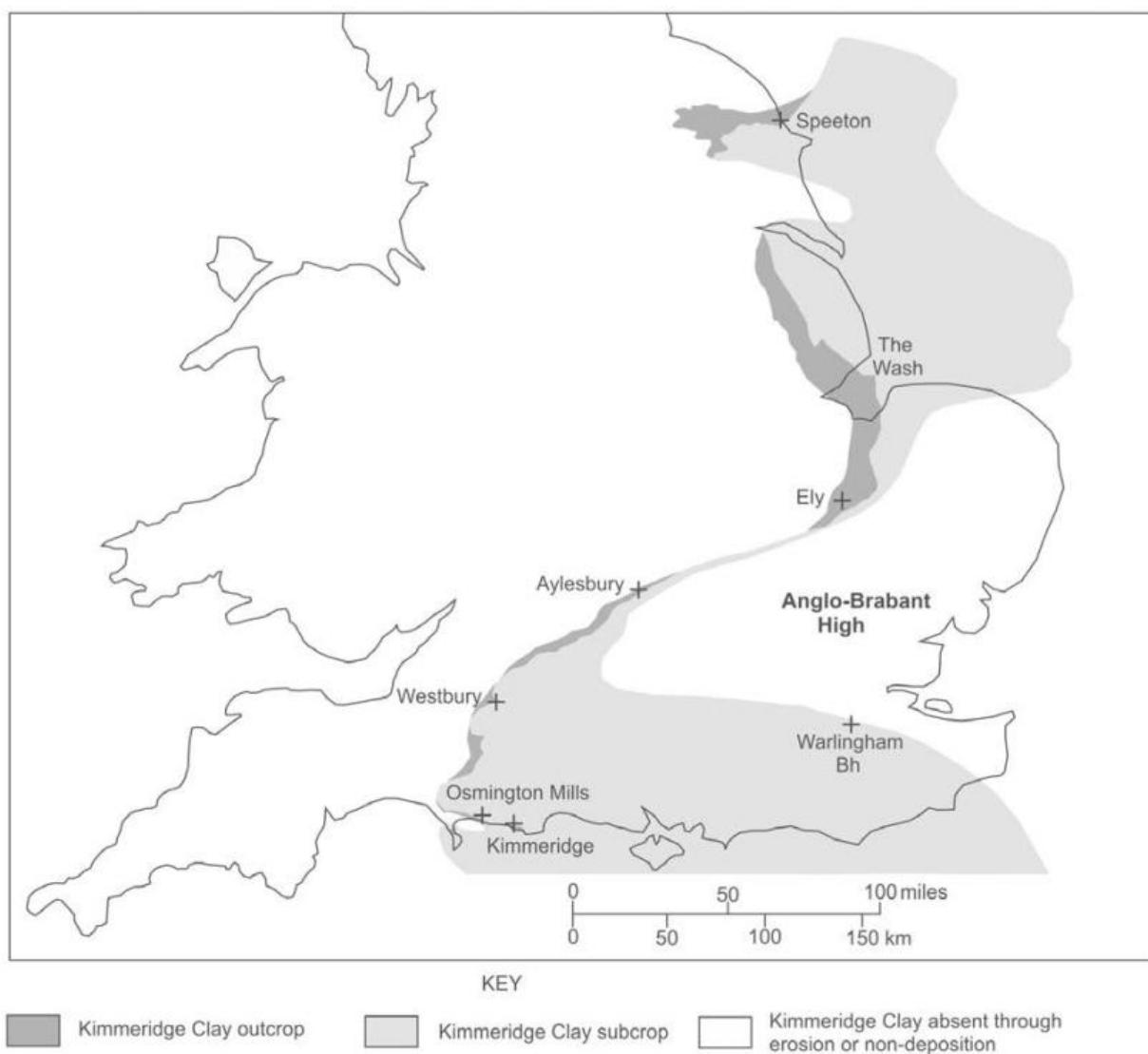
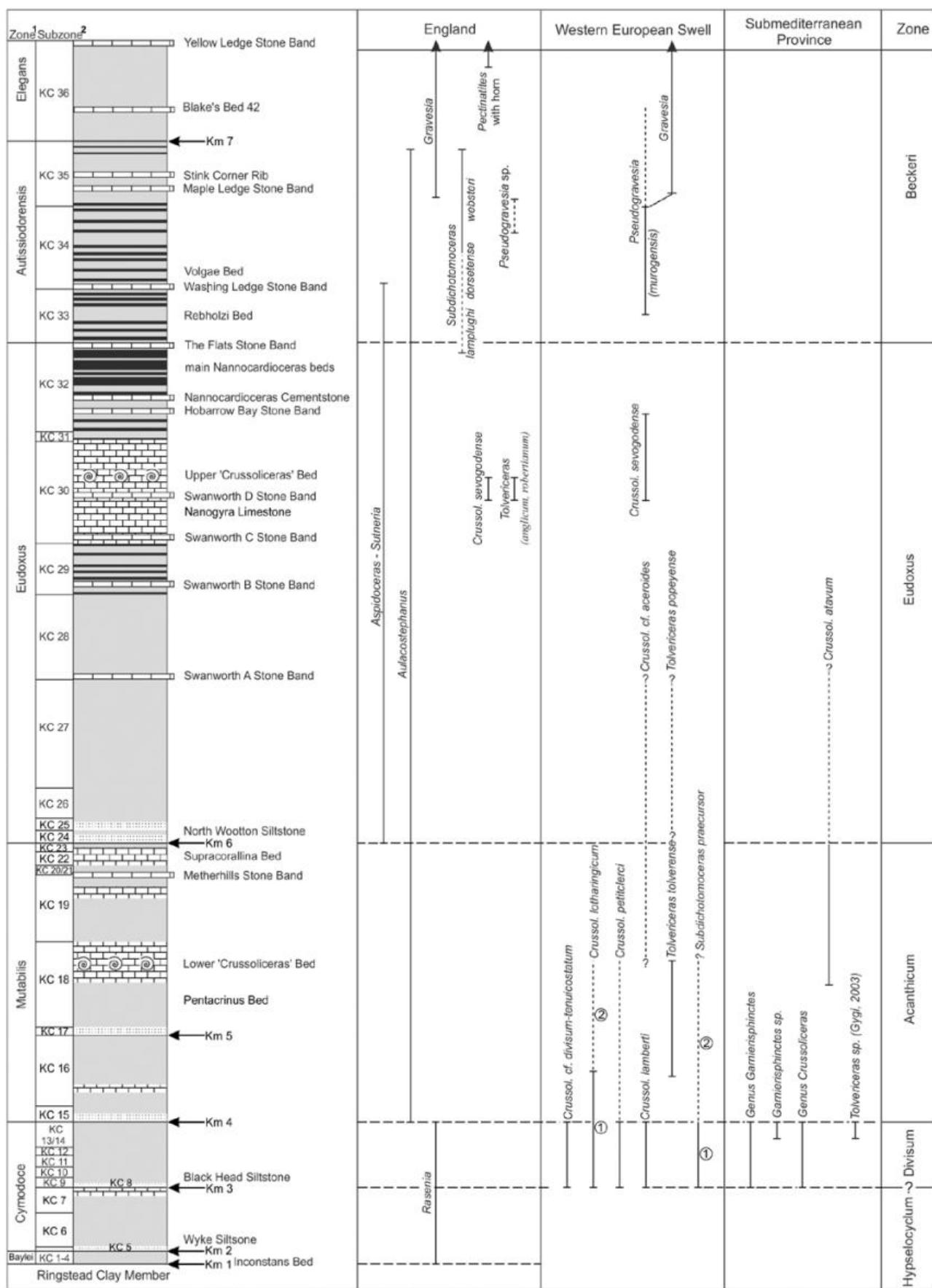


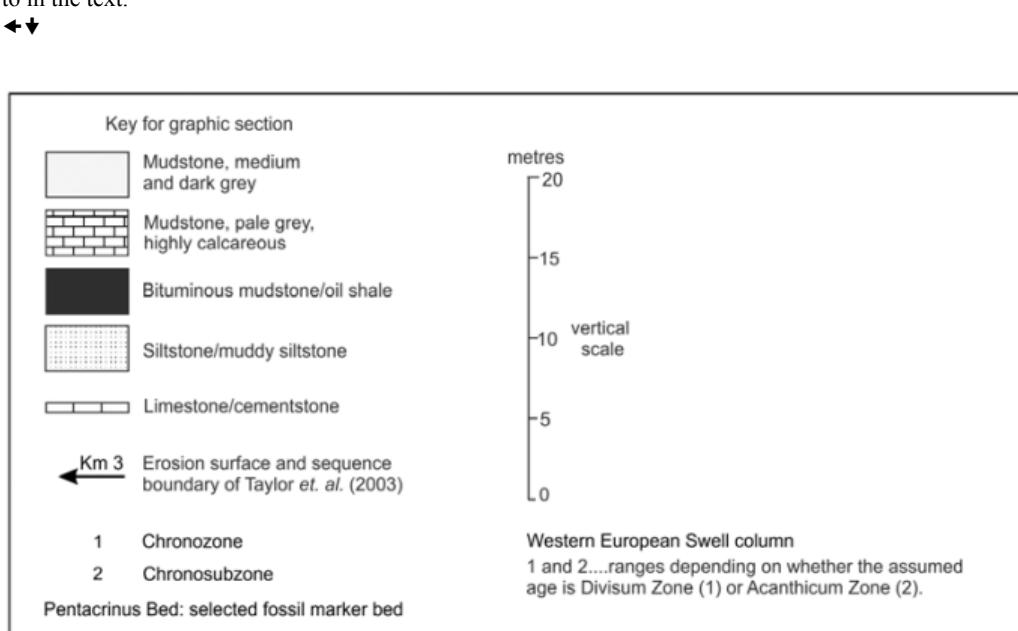
Fig. 2: Geological sketch map of the English outcrop and subcrop of the Kimmeridge Clay showing the positions of localities referred to in the text (after Gallois, 1979).



Kimmeridgian perisphinctids in boreholes and former exposures has been reviewed. All the relevant, readily accessible specimens from the Kimmeridgian rocks of eastern and south eastern France were also examined. Several genera are common to the Subboreal and Submediterranean provinces in the Late Kimmeridgian. These confirm that following a period of geographical faunal differentiation in the Late Oxfordian-Early Kimmeridgian (Énay, 1980, 1985; Hantzpergue, 1987, 1989) marine pathways were present from time to time during the Kimmeridgian that allowed ammonites to migrate between the two provinces. These are represented in the Kimmeridge Clay by species of *Aspidoceras*, *Aulacostephanus*, *Crussoliceras*, *Gravesia* and *Sutneria* (Callomon & Cope, 1971; Gallois & Cox, 1976). They enable correlations to be made at some stratigraphical levels between the different zonal schemes in the Subboreal and Submediterranean Provinces. For example, the Eudoxus Zone and several of the included faunal marker beds are common to both provinces. However, the situation is complicated by the presence of faunas with parallel but independent evolutionary paths, homoeomorphic features that are difficult to interpret in the absence of reliable biochronological data, and migratory pulses that introduced new faunas and taxa. These problems are particularly applicable to the perisphinctids, a group that was well represented in Tethyan faunas but which, with the exception of the *Pictoniinae*-*Aulacostephaninae* branch, disappeared from NW Europe at the end of the Oxfordian. Their evolution provides the basis for the standard zonal

scheme in the Subboreal Province based on species of *Pictonia*, *Rasenia* and *Aulacostephanus*, forms derived directly from Oxfordian ancestors (Wright, 2010). Other perisphinctids are present at several restricted horizons in the Subboreal Kimmeridgian whose ancestry cannot be traced back to the Oxfordian in that province. Ammonites collected by Roberts (1892) from limestone nodules in exposures in the Kimmeridge Clay in the Ely, Cambridgeshire area include specimens that were identified by one of us (Énay, 1976 and 1978 MS) as macroconchs of the Tethyan genera *Crussoliceras* (Sedgwick Museum, Cambridge University J 69855 and J 69856) and *Garnierisphinctes* (J 61311). The *Crussoliceras* are close to *Tolvericeras sevogodense* (Contini & Hantzpergue, 1975). They occur in association with *Aulacostephanus* spp., *Aspidoceras* and *Sutneria* indicative of the Eudoxus Zone. All three specimens probably came from an ammonite-rich marker bed which had until that time been called the *Propectinatites*? Band (Gallois & Cox, 1976). This bed was thereafter referred to as the *Crussoliceras* Band (Fig. 3). *Propectinatites* Cope was subsequently shown by Birkelund *et al.* (1983, p. 302) to be a junior synonym of *Subdichotomoceras* Spath. Pavlow & Lamplugh (1891a, b) and Sheppard (1907) figured specimens of two distinctively different perisphinctids from the Kimmeridge Clay of Speeton, Yorkshire which they identified as *Perisphinctes lacertosus* Fontannes, a species of the *Crussoliceras crusoliense* (Font.) group (= *Crussoliceras* Énay, 1959). Spath (1924) described these as two species of a new genus *Subdichotomoceras*. For many years the genus

Fig. 3: Generalised vertical section of the Kimmeridgian succession in the Dorset type area (after Gallois, 2000) showing the recorded range in England, the Western European Swell and the Submediterranean Province of the ammonite genera and species referred to in the text.



was rarely identified in England, but was used profusely for homoeomorphic specimens in the Indo-Malagasy Province and, more scarcely, for Submediterranean specimens of the *C. crusoliensis* group. Other records of *Crussoliceras?* in the Kimmeridge Clay include a marker bed in the Mutabilis Zone with abundant “indeterminate perisphinctids” (Gallois & Cox, 1976). Van der Vyver (1986) identified *Crussoliceras* in this bed in Dorset, and it is probably the same bed in which Kitchin & Pringle (1926, MS, in Gallois, 1988, p. 38–39) recorded ‘*Subdichotomoceras*’ in Cambridgeshire.

In continental Europe, the *Crussoliceras* group was identified as a characteristic component of the Kimmeridgian faunas of the Marnes à *Crussoliceras* (= *Crusoliensis* Mergel) in Swabia, Franconia, the Jura, south-eastern France, northern Italy and Spain where it is used to define the Divisum Zone (Table 1). Rarer examples of the same group have been recorded or figured in the eastern Paris Basin and adjacent areas by Petitclerc (1917), Durand (1933) and Contini & Hantzpergue (1973, 1975). In the Submediterranean Province the oldest *Crussoliceras* has been recorded from the highest part of the Hypselocyclus Zone. It reaches its acme in the Divisum Zone, and continues into the Acanthicum and Eudoxus Zones as *C. atavum* Schneid., 1914 and *C. sevogodense* (Contini & Hantzpergue, 1975) (Fig. 3). The former has unusual features that suggest that it is an end species.

In the French Southern Jura, on the northwestern margin of the South-East-France Basin, a change from open-ocean environments in the southeast to platform environments in the northwest is accompanied by lateral variations in the ammonite assemblages. When traced north westwards, the oppeliids and ataxioceratids rapidly become scarce or absent, but the perisphinctids, particularly the *C. crusoliense* group commonly accompanied by *Aspidoceras*, remain. When traced westwards, a calcareous mudstone/muddy limestone facies with common *Crussoliceras* and *Garnierisphinctes* has the greatest geographical extent. This association is in accord with the suggestions of Ziegler (1963b, c, 1967), Cecca (1992) and Westermann (1990, 1996) that the perisphinctids were more able to survive and/or adapt to shallower-water platform environments than other groups, and that this enabled them to colonise territories in the Subboreal Province.

2. REGIONAL VARIATIONS IN THE AMMONITE ZONAL SCHEMES

Some of the material discussed in this account came from the Western Europe Swell, the intermediate area between the Subboreal and Submediterranean Provinces and for which different zonal schemes are in use that have yet to be correlated in detail. Those used in this account are summarised in Table 1. Many of the correlations

suggested to date between the provinces are based on faunal marker beds and/or faunal ranges that have been variously described as episodes, horizons, biohorizons and flood occurrences.

In the U.K. part of the Subboreal Province 5 chrono-zones and 35 chronosub-zones have been based on a combination of lithological, palaeontological and sedimentary features (Fig. 3). These were initially identified in borehole cores in the Kimmeridge Clay in Norfolk (Gallois & Cox, 1976), and subsequently in boreholes throughout the Kimmeridge Clay outcrop and subcrop in England (Gallois, 1979a), and in the cliff sections in the Dorset type Kimmeridgian area (Cox & Gallois, 1981). Prior to this, five ammonite bio-zones had been recognised in the Subboreal Province in the U.K. and northern France based on the Aulacostephanidae. The bio-zones, in ascending order, are named after *Pictonia baylei*, *Rasenia cymodoce*, *Aulacostephanus mutabilis*, *Aul. eudoxus* and *Aul. autissiodorensis*. For continuity, the ammonite names have been retained for the five chrono-zones even though the zonal boundaries are no longer based solely on ammonite ranges. To avoid possible confusion with bio-zones, the chronosub-zones (KC 1 to KC 35) have not been named after fossils.

Not all the biozone boundaries are defined in precisely the same way in the Subboreal and Submediterranean Provinces (see below). Birkelund *et al.* (1983) suggested dividing the Mutabilis Zone into three Biosub-zones (*Rasenia askepta*, *Aul. mutabilis* and *Orthaspidocepheras orthocera*), but these were not formalised. Elsewhere, Matyja & Wierzbowski (2000) have used the *askepta* and *mutabilis* Biosub-zones in a proposed correlation between the bio-zonal schemes of the two provinces (Table 1).

Correlations have been suggested between some of the ammonite assemblages in the Subboreal Province with some of the *faunal horizons* recognised by Hantzpergue (1987, 1989) in the Western European Swell, notably by Birkelund *et al.* (1983) and Van der Vyver (1986) in southern England and by Samson *et al.* (1996) in Normandy. These horizons were given formal status and referred to as subdivisions of Sub-zones and named Horizons (Table 1). They correspond with the horizons of Gabilly (1964, 1974) and Callomon (1964, *non* 1984) that are currently in use in France (Cariou & Hantzpergue, 1997). Really they are junior equivalents of the zonules of Hedberg (1976) as Phelp (1985) well noticed. They are more similar to the *fossiliferous episodes* of Mattéi (1974) which are considered to be sedimentary events, and also close to the *faunal horizons* of Callomon (1984; Callomon & Chandler, 1990) or *biohorizons* (Page, 1992, 1995) which are considered to be biological events of short duration.

The ammonite assemblages and index species of the Hantzpergue’s (1987) faunal horizons fall into three taxonomic units: the Perisphinctidae (*Subdiscosphinctes*, *Ardesia*, *Lithacosphinctes* and *Gravesia*), Aulacostephanidae (*Pictonia*, *Rasenia*, *Eurasenia* and *Rasenioi-*

Correlation of the Submediterranean Kimmeridgian zonal scheme of Geyer (1961) and Atrops (1982) and the Western Europe Swell of Hantzpergue (1987, 1989) according to Matyja & Wierzbowski proposal (2000) concerning the Hypselocyclus (*pars*), Divisum and Acanthicum (*pars*) Zones, and Atrops (1982), Zeiss (2003) and Hantzpergue *et al.* (1997) concerning the Platynota (and Galar) Zones.

des) and the Aspidoceratidae (*Paraspidooceras*, *Physodooceras*, *Orthaspidooceras* and *Aspidoceras*). The sequence of these horizons was strongly influenced by the evolution of the ammonite assemblages, the palaeogeography and sea-level changes that opened or closed migratory pathways, and local changes in the environmental conditions on the Western Europe Swell (Hantzpergue, 1991, 1993, 1995). As a result, successive faunas show alternating Submediterranean and Subboreal influences that gave rise to the taxonomic heterogeneity of the index-species. The episodic arrival of taxa from an adjacent province influenced the assemblages in such a way as to give rise to local zones (topozones) and teilzones of the type graphically illustrated by Arkell (1933, fig. 1).

2.1. The Mutabilis Zone in the Subboreal Province and the Western European Swell

The base of the Mutabilis Zone was originally defined as an upward change from species of *Rasenia* to species of *Aulacostephanus*. In practice this involves the recognition of a change from finely ribbed *Rasenia* of the subgenera

Rasenioides and *Semirrasenia* to *Aulacostephanus* of the subgenera *Aulacostephanooides* and *Aulacostephanites*. Many authors (e.g. Ziegler, 1962, 1964; Cox & Gallois, 1981; Birkelund *et al.*, 1983) noted that the dividing line between the genera is arbitrary, and not all authors have used the same definition of *Aulacostephanus*. Geyer (1961) and Ziegler (1963a) interpreted *Aulacostephanus* as a genus in which the majority of all individuals in every population show interruption of the external ribs throughout life, but Arkell & Callomon (1963) identified those that have a smooth ventral band only on the later whorls as *Aulacostephanus*. Birkelund *et al.* (1978) used the former definition and included their *Rasenioides askepta* Biosubzone in the Cymodoce Zone, but Birkelund *et al.* (1983) used the latter definition and placed the *Askepta* Biosubzone in the Mutabilis Biozone. In the Submediterranean Province, the base of the Mutabilis Biozone was taken by Geyer (1961) and Ziegler (1962) at the level at which *Aulacostephanus* with a smooth ventral band “throughout life” first appears: the same definition was used by Hantzpergue (1979, 1989). In Britain, the base of the Mutabilis Zone is marked by a widespread erosion surface, Sequence Boundary Km 4

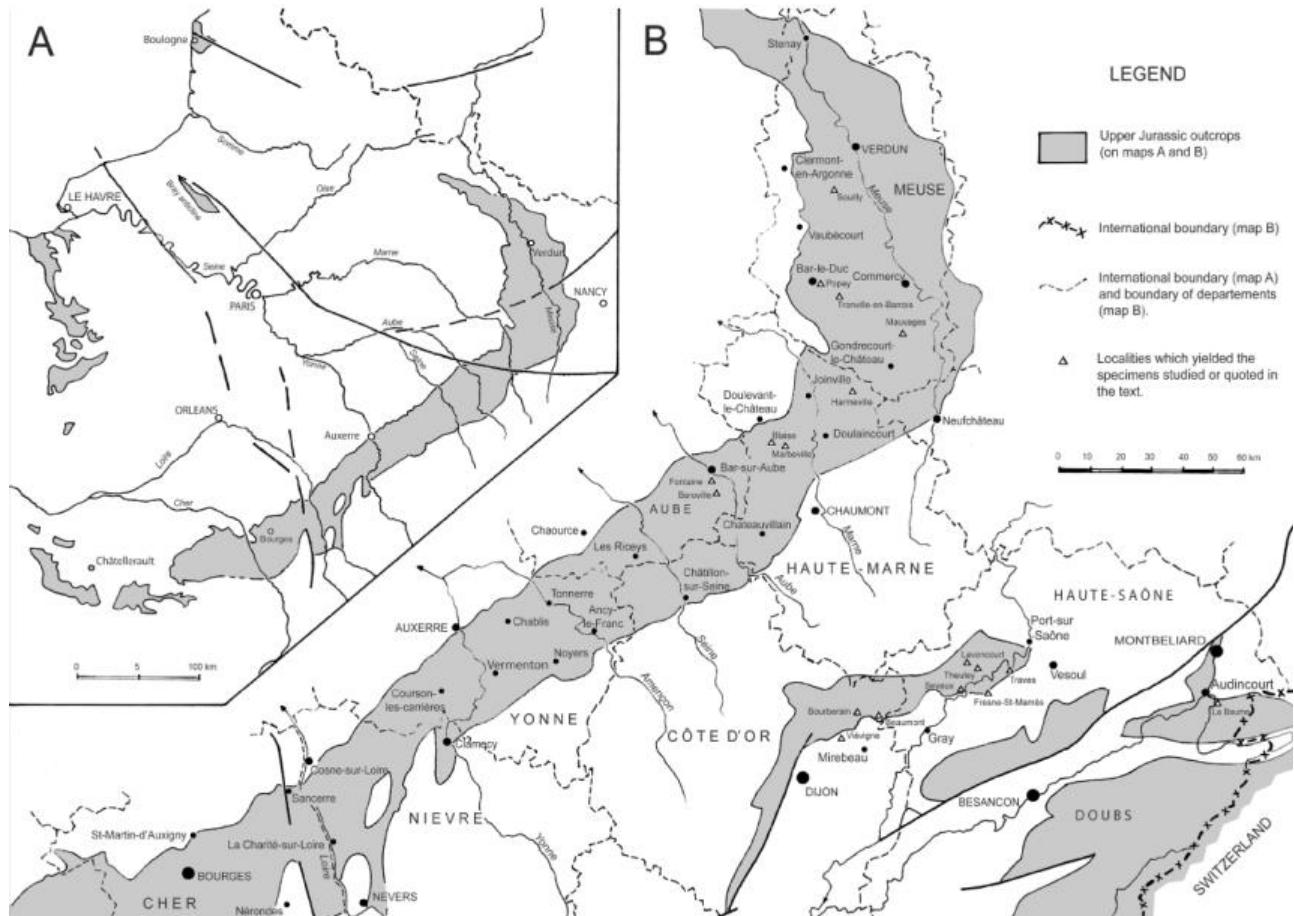


Fig. 4: Map showing the Upper Jurassic outcrops and the positions of the localities quoted in the text, corresponding to the 1/50000 scale geological maps (black circles) and those which yielded the studied specimens (open set triangles).

of Taylor *et al.* (2001), which marks a sudden upward change from raseniids to aulacostephanids. A similar, but more pronounced erosion surface is present at the base of the Argiles de Croquet on the Normandy coast (Gallois, 2005) and may be the correlative of Disconformity 7 in Northern Aquitaine (Hantzpergue, 1987, 1989).

2.2. The Eudoxus Zone in the Subboreal Province and the Western European Swell

In the Kimmeridge Clay the base of the Eudoxus Zone is everywhere taken at an erosion surface and Sequence Boundary Km 6 (Taylor *et al.*, 2001) which marks an upward change from predominantly finely ribbed *Aulacostephanus* of the subgenera *Aulacostephanoides* and *Aulacostephanites* to coarsely ribbed *Aulacostephanus* and *Aulacostephanoceras* (following Ziegler, 1962), and above which *Aspidoceras* and *Sutneria* suddenly appear. On the Normandy coast, the base of the Eudoxus Zone is also marked by an erosion surface at the base of the Argiles d'Ecqueville médian that is the correlative of Sequence Boundary Km 6 (Gallois, 2005). Samson *et al.* (1996) recorded *A. eudoxus* and *Orthaspidoceras orthocera* in the lowest part of the Argiles d'Ecqueville médian which they correlated with the *Orthocera* Horizon of Charentes. A similar succession is present at Westbury, Wiltshire and at Osmington Mills, Dorset where *Orthaspidoceras* occurs in association with *Aul. eudoxus* in a thin (1 m thick) succession between two erosion surfaces, those at the bases of Chronosubzones KC 24 and KC 25 (Gallois, 1979b; Birkelund *et al.*, 1983).

In the Western European Swell the base of the Eudoxus Biozone was initially defined by the single known occurrence of *Aulacostephanus eudoxus* together with *Aspidoceras* in the Caletanum Horizon (Hantzpergue, 1979). It is currently taken at the base of the Orthocera Horizon following Hantzpergue (1984, 1989). *A. eudoxus* occurred later in northern Aquitaine as assumed by Hantzpergue (1989) and Geyssant (1994). The reason for the change in the zonal boundary is that in Southern Germany *Orthaspidoceras* of the *schilleri-orthocera* group occur together with *A. eudoxus*, *pseudomutabilis* and *S. cyclodorsata* (Aldinger, 1945; Schmidt-Kaler, 1962; Bantz, 1970).

2.3. Correlation with the Submediterranean Province

Correlation of the Submediterranean zonal scheme with that of the Subboreal Province remains uncertain even though the faunas of the Western European Shelf are in an intermediate geographical position between the two. The definition of the base of the Kimmeridgian Stage and its GSSP remains undecided at the time of writing (e.g. Wierzbowski *et al.*, 2006; Wierzbowski, 2010). In Table 1, the correlation of the Divisum Zone (*sensu*

Atrops, 1982 *non* Geyer, 1961 and Énay *et al.*, 1971) with the upper part of the Chatelaillonense Subzone is taken from Matyja & Wierzbowski (2000). The suggestion by Zeiss (2003), that the Divisum Zone is the correlative of the whole of Chatelaillonensis Subzone is inconsistent with the occurrence of *Ataxioceras lothari* (Hantzpergue, 1989, p. 45) in the lowermost Aulnisa Horizon. The acme of the species is in the Semistriatum Horizon (Atrops, 1982), the correlative of the Manicata and Aulnisa Horizons (Tab. 1).

The correlation between the Eudoxus/Autissiodorensis zonal boundary and the Eudoxus/Beckeri zonal boundary remains unclear. Schweigert (1993, 1996, 1999) and Baier & Schweigert (2001) correlated the Contejeani Subzone of the Western Europe Swell with the Subeumela Subzone of the Submediterranean Province (Schweigert, 1999), but also (Schweigert, 1993b) with the Pedinopleura and Subeumela Subzones, Beckeri Zone.

3. SOURCES OF SPECIMENS EXAMINED IN THE PRESENT STUDY

The specimens used in the present study came from the English Kimmeridge Clay and the Kimmeridgian rocks of eastern France including the Paris Basin, Côte d'Or and the French Jura (Fig. 1). The French material is mostly well preserved, uncrushed museum specimens that are suitable for taxonomic study, but many are stratigraphically poorly documented. In contrast, museum specimens from English localities such as those in the Sedgwick Museum, Cambridge are tied in to well defined localities and measured sections. Similarly, new material from outcrops in the Dorset type area is located within a detailed stratigraphical succession. However, these specimens are almost all crushed and difficult to compare with specimens in solid preservation. National Grid References (e.g. ST 882 528 for Westbury, Cement Works, Wiltshire) are given for localities in England; those in France refer to the Institut Géographique National (IGN) grid (e.g. x: 758, 150, y: 294,600 Malet Quarry, Mount Crussol, Ardèche).

3.1. Kimmeridgian of England

Speeton, Yorkshire : nodules found loose, probably from the Autissiodorensis Zone, include the holotype (Pictet Collection, Geneva) of *Subdichotomoceras lamplughii* Spath, type-species of the genus *Subdichotomoceras* Spath, 1924, and a specimen (Sedgwick Museum J 35941), complete with the peristome, recorded as *Subdichotomoceras crassum* (Neaverson, 1925), which is here considered as the macroconch dimorph of *S. lamplughii*.

Ely, Cambridgeshire: two incomplete *Cru ssoliceras* collected *in situ* by Roberts (1892) (Sedgwick Museum

J. 59855 and 59856) attributed to *Per. biplex* Sow. One specimen (Sedgwick Museum, J. 61311), originally ascribed to *Garnierisphinctes* sp., probably a new species of *Tolvericeras*.

Kimmeridge, Dorset: crushed microconch and macroconch dimorphs of *Subdichotomoceras* photographed *in situ* in the highest part of the Eudoxus Zone and throughout the Autissiodorensis Zone for the present study. Crushed and solid preservation specimens of the same genus in the Etches, Énay, National Museum of Wales and Oxford University collections from the Autissiodorensis and Elegans Zones.

Osmington Mills, Dorset: loose material containing *Subdichotomoceras*. A large specimen in solid preservation, loose, probably from the Eudoxus or Autissiodorensis Zone. *In situ*, but fragmentary, poorly preserved *Crussoliceras* from the Mutabilis Zone.

Westbury, Wiltshire: an adult specimen in solid preservation from the Eudoxus Zone; probably a new species of *Tolvericeras*.

3.2. Kimmeridgian of the eastern and southern border of the Paris Basin (Meuse, Haute-Marne, Aube and Cher Departments) (Fig. 4)

The geology of the Upper Jurassic was reviewed in Mégnien & Mégnien (ed.), 1980. The stratigraphy of the area is summarized in Figures 5 and 6 in which the biochronological ages assumed in the *Geological Synthesis of the Paris Basin* (Debrand-Passard *et al.*, 1980) are partly revised in the light of data from the Berry area (Hantzpergue & Debrand-Passard 1980; Debrand-Passard, 1982) and from the northern Aquitaine Upper Jurassic (Hantzpergue, 1979, 1987, 1989). More precise data on the stratigraphy and ammonite occurrences in the various formations are given by Maubeuge (1953, 1955, 1965) and in the descriptions of the Bureau de Recherches Géologiques et Minières (BRGM) 1:50,000 scale geological maps.

Aulacostephanid specimens in the P. and M. Curie-Paris 6 University Collection support the ages assumed in

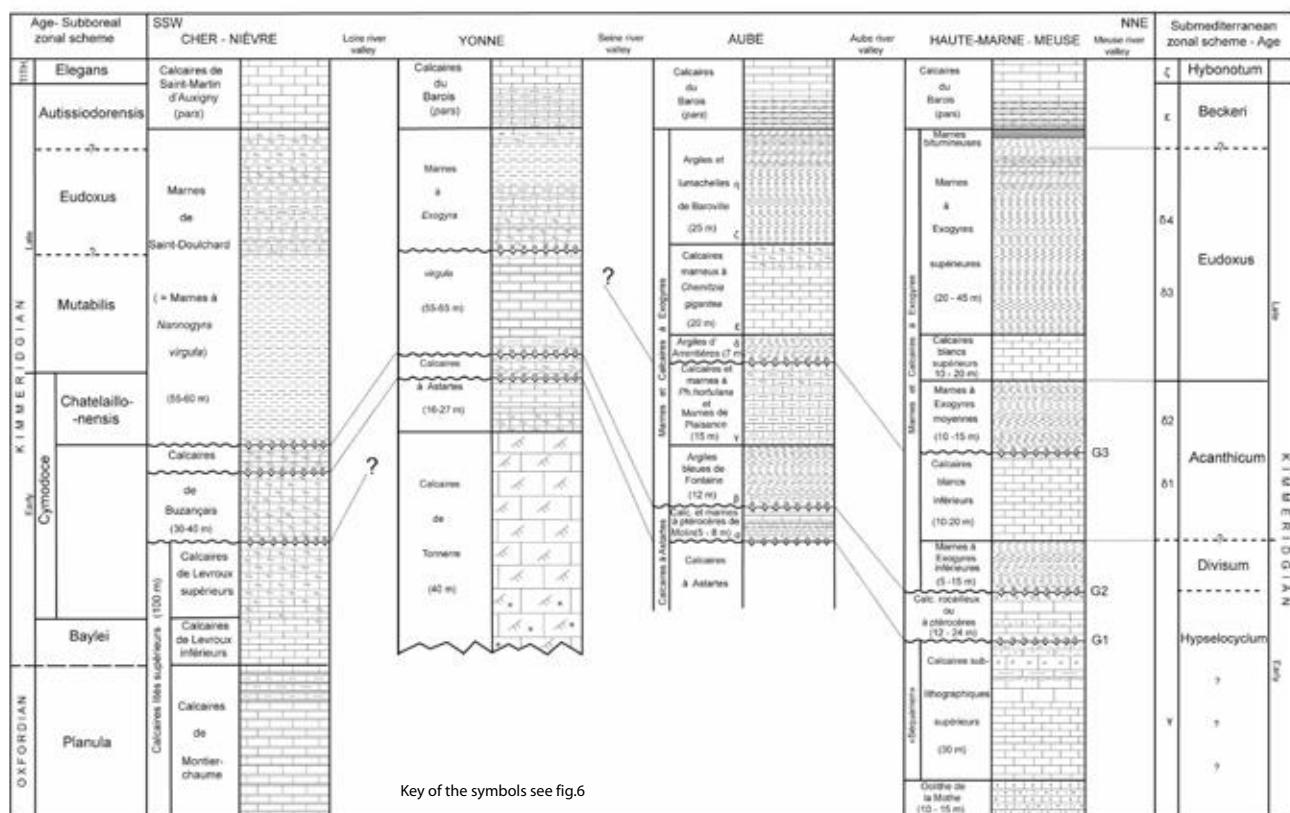


Fig. 5: Simplified vertical sections for the Kimmeridgian succession of the Eastern and Southern borders of the Paris Basin. Meuse and Haute-Marne area from Le Roux (1969) and Maubeuge (1965, 1970, 1976); Aube area from De Lorol & Lambert (1893) and Lemoine & Rouyer (1902, 1904); Yonne area from Mégnien & Turland (1972) and Debrand-Passard & Lefavrais (1990); Nièvre and Cher area from Debrand-Passard (1982) and Hantzpergue & Debrand-Passard (1980). * Lemoine & Rouyer (1902, 1904) nomenclature α to ε is often used as Kimmeridgian A to E.

Fig. 6: Simplified vertical sections for Kimmeridgian rocks succession, biostratigraphy and ages of Côte d'Or and Haute-Saône Plateau and Northern French Jura. Côte d'Or from Pascal (1973), Haute-Saône from Contini (1972) and Contini & Hantzpergue (1973, 1975), Montbéliard area from Contini & Hantzpergue (1973). ➔

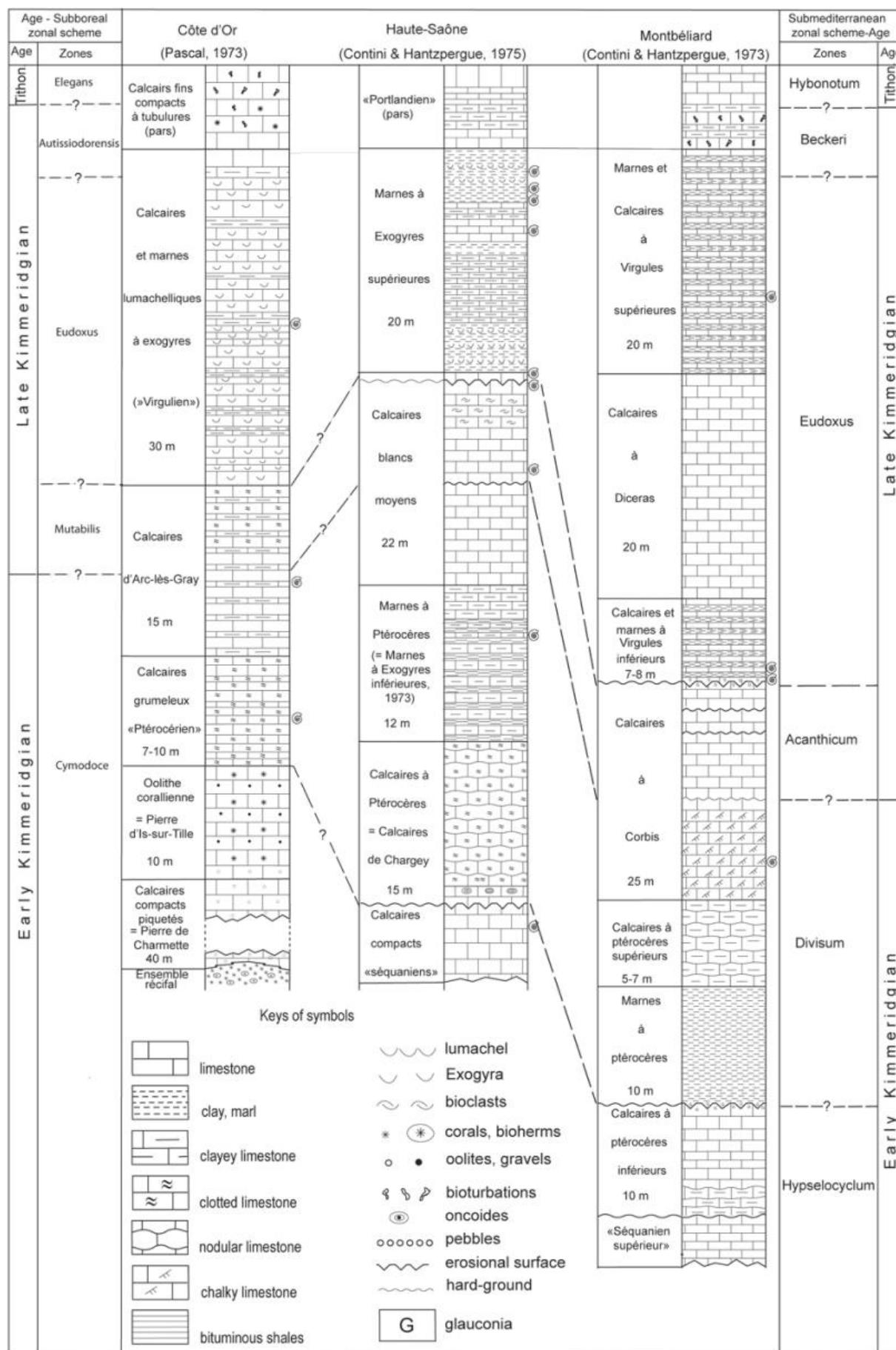


Figure 5. These include *A. gr. mutabilis* (without precise stratigraphical assignment) from Baroville, Aube; *A. cf. quenstedti* from the Calcaires inférieurs (Acanthicum/Mutabilis Zone); *A. cf. eudoxus* from the Calcaires supérieurs of Fontaine, Aube (Eudoxus Zone); *A. phorcus* from Kimmerigien D (Acanthicum/Mutabilis Zone) and *A. quenstedti* from Kimmeridgien E (Eudoxus Zone).

The studied specimens are housed in the collections of the P. and M. Curie-Paris 6 University and the National High School of Geology in Nancy (ENSG). Most of them are newly figured here and, with the exception of a specimen from Aube quoted by Loriol & Lambert (1893) and Lemoine & Rouyer (1902), have not previously been referred to in publications.

Souilly, Meuse: a complete adult specimen of *Crussoliceras* (ENSG Nancy Collection) from the Hypselocyclus-Divisum Zones or possibly from the Mutabilis Zone.

Popey, Meuse: an adult macroconch specimen of *Tolvericeras* from the Marnes à Exogyres Formation, Eudoxus Zone.

Mauvages, Meuse: *Perisphinctes* sp. ind. (Durand, 1933, p. 306, 324; pl. 21, fig. 4), not found in the Buvignier Collection but a plaster cast is preserved in Lyon (FSL 175 911). Probably from the Eudoxus Zone.

Tronville, Meuse: an early complete specimen (Durand Collection, ENSG Nancy) an inner cast of grey limestone with adherent *Exogyra* which agrees with the label "Upper Kimmeridgian", Eudoxus Zone.

Bar-le-Duc, Meuse: Two fragmentary body chambers from the same locality quoted by Durand (1933, p. 306) as *Perisphinctes acerrimus* Siemiradzki, 1898 (N° 17) and *Perisphinctes garnieri* Fontannes, 1876 (N° 19), Acanthicum/Mutabilis or Eudoxus Zone.

Harméville, Haute-Marne: a single specimen (coll. UPMC 153) identified as "*Ammonites eupalus* d'Orbigny, and labelled "Middle Kimmeridgian, Pterocerian".

Fontaine, Aube: a specimen in the Lambert Collection (UPMC 151) ascribed to *Ammonites eupalus* d'Orb., quoted by Loriol & Lambert (1893, p. 209) and by Lemoine & Rouyer (1902, p. 105), Divisum Zone.

Baroville, Aube: the last whorl preserved and less than a half-whorl of a microconchiate *Crussoliceras* labelled as Kimmeridgian B (Divisum Zone) (MNHN Paris R 2921).

Saint-Martin-d'Auxigny, Cher: the type specimens (m and M) of *Tolvericeras (T.) murogense* Hantzpergue (1989), Autissiodorensis Zone, Dépont Collection, Natural History Museum, Bourges.

3.3. Kimmeridgian of the Plateaus of Haute-Saône and Côte d'Or Departments, and the Montbéliard area (Fig. 4)

The more useful data on the biostratigraphy and palaeontology of the ammonites are those published by

Contini (1972) and Contini & Hantzpergue (1973, 1975) for the Haute-Saône and Montbéliard areas, and Pascal (1973) and Rat *et al.* (1978) concerning the Côte d'Or. **Fresne-Saint-Mamès**, Haute-Saône: *Perisphinctes crusoliensis* Font. in Petitclerc (1917) (UPMC 152) possibly from the Acanthicum Zone or from the uppermost Divisum Zone.

Traves, Haute-Saône: *C. aceroides* Geyer in Contini & Hantzpergue (1975, p. 13; pl. 2, fig. a; pl. 5, fig. 1) from the Divisum or Acanthicum/Mutabilis Zone.

Savoyeux, Haute-Saône: a plaster-cast (FSL 175912) of the holotype of "*Katroliceras*" *sevogodense* Contini & Hantzpergue (1975, p. 12; pl. 4, fig. 4a, b) based on a well documented specimen from the upper Eudoxus Zone.

Theuley-lès-Lavoncourt and **Lavoncourt**, Haute-Saône: two specimens from the Divisum or Acanthicum/Mutabilis Zone (FSL 175917 and 175918), the only *Subdichotomoceras* recorded from the Western Europe Swell.

Audincourt, Doubs: a nearly complete adult specimen of a large species of a *Crussoliceras* species of which a plaster cast is housed in the Lyon Collection (FSL 175 915), from La Baume Quarry, Divisum Zone.

Beaumont-sur-Vingeanne, Côte d'Or: "*Perisphinctes lacertosus*" Font. (Authorship P. de Loriol), in the Martin Collection, Geneva (MHNG 92-37724), assigned to the Calcaires à Astartes, from the Divisum or Acanthicum/Mutabilis Zones.

Viéville, Côte d'Or: a poorly preserved specimen (Earth Sciences Institute of Dijon Collection) showing some inner whorls preserved and half a whorl of the body chamber, assigned to *Katroliceras* (*Crussoliceras*) sp. by Tintant and to the Orthocera Subzone.

For a better understanding of the Submediterranean genera *Crussoliceras* and *Garnierisphinctes*, specimens from the Southeastern France Basin and the adjacent areas were also studied.

3.4. South-eastern France Basin (Ardèche, Gard, Hautes-Alpes Departments) (Fig. 4)

Mount Crussol, Ardèche: Holotype and two topotypes of the type species of *Crussoliceras crusoliense* from the Crusoliensis Marls, Divisum Zone; two topotypes, one well preserved complete full-grown adult and another less well preserved in the Boselli Collection. *Crussoliceras divisum* (Qu.) from the Crusoliensis Marls, Divisum Zone, Boselli Collection.

Conqueyrac, Gard: two specimens of *Crussoliceras divisum* (Qu.) in the Atrops Collection (FSL 185005, 185014);

Châteauneuf-d'Oze, Hautes-Alpes: a specimen in the Atrops Collection (FSL 188841) from the topmost bed of the Divisum Zone (Atrops, 1982, p. 302, tab. 51), initially labelled "*Progeronia*" before being referred to *Garnierisphinctes* sp.

3.5. Helvetic-Southeastern France Basin margins (Ain, Savoie and Isère Departments and Switzerland)

Saint-Jean-de-Gonville, Ain: a nearly complete adult specimen (Énay Collection, FSL 101153) of *C. crussoliense* from the Divisum Zone.

Saint-André-Val-de-Fier, Savoie: a complete adult specimen (Hirtz Collection, FSL 101124) of *Crussoliceras sayni* from the Divisum Zone.

Creys-Pusignieu, Isère: two incomplete specimens (Énay Collection, FSL 175 913 and 175 914) of *Crussoliceras atavum*, the smaller restricted to the inner whorls, the larger corresponding to the living chamber of an adult individual without the aperture, Acanthicum Zone (Énay, 1958).

Mellikon, Aargau, Switzerland: part of the body chamber of *C. tenuicostatum* group with eight ribs preserved, Divisum Zone.

Additional specimens that were examined are referred to in the descriptions.

4. PALAEONTOLOGICAL DESCRIPTIONS

The present account describes those species of the genera *Crussoliceras*, *Subdichotomoceras*, *Tolvericeras* that are considered to have a bearing on the relationships between the Kimmeridgian Subboreal and Submediterranean perisphinctids, and undetermined species of *Pseudogravesia* (formerly described as *Gravesia*, Gallois & Etches, 2010). Their relationship to *Garnierisphinctes* is also discussed, although none of the specimens studied in the present work are attributable to that genus.

4.1. Measurements and other descriptive data

They follow the traditional scheme: maximum or final diameter (Dm); actual or measured diameter (D); end of phragmocone diameter (ph); where the specimen is wholly septate (nucleus = n); (?) indicates where the end of the septate whorls is unknown; whorl height and ratio to corresponding diameter (Wh; Wh/D); the whorl thickness or breadth (Wb, Wb/D), umbilicus width (Ud, Ud/D), the ratio Wb/Wh and the number of primary ribs (N1) per half-whorl; ratio of whorl heights on opposite sides at same diameter (Wh/Wh'). Values in brackets indicate estimates; the dash means that there is no corresponding value.

The following abbreviations are used in the synonymies and descriptions: (V) the corresponding synonymous specimen has been seen; (Vm) plaster cast; (*pars*) partial synonymy; (?) doubtful synonymy; (*non*) synonymy not accepted; (m) and (M) microconchiate and macroconchiate forms. The rib-curves (N1 vs Dm or D) have been plotted for all the specimens that are sufficiently well preserved. They illustrate the changes in

rib density during growth and show common trends, but not all of these trends are significant at the species level.

4.2. Studied material

Several institutions and individuals have assisted in the loan of specimens from their collections and from private collections, including the following:

Muséum National d'Histoire naturelle de Paris (MNHN); Université Pierre et Marie Curie, Paris 6 (UPMC); École Nationale Supérieure de Géologie de Nancy (ENSG); Musée Aquarium of Nancy (MAN); Université de Nancy (UN); Université Claude Bernard-Lyon 1, Département des Sciences de la Terre, R. Énay, F. Huguenin and J. Martin Collections (FSL); Musée d'Histoire naturelle de Bourges, Cher, Depont Collection (MHB); P. Boselli private collection, Bourg-de-Péage, Drôme, Musée d'Histoire Naturelle de Genève (MHNG); Oxford University Museum, Oxford, UK (OUM); Sedgwick Museum, Cambridge University, UK (SM); National Museum of Wales (NMW); S. M. Etches Collection, Kimmeridge Fossil Museum, UK (KFM); Museum für Naturkunde, Stuttgart, Germany (MNS).

Superfamily Perisphinctoidea Steinmann, 1890

Family Perisphinctidae Steinmann, 1890

The following genera and their accepted synonyms (in brackets), including selected species, are described in the present account: *Crussoliceras* (*Badenia*), *Garnierisphinctes*, *Subdichotomoceras* (*Propectinatites*), *Tolvericeras* and possible *Pseudogravesia*. Atrops (1982) considered the origin of *Crussoliceras* to be within *Lithacosphinctes*, a genus which Atrops (1982) presumed to be the root-stock of the Ataxioceratids (subfamily Ataxioceratinae). *Garnierisphinctes* and *Progeronia* also appear to have also been derived from *Lithacosphinctes*. Hantzpergue (1989) also considered that *Crussoliceras* was derived from *Lithacosphinctes* and described the routes by which this had occurred.

Genus *Crussoliceras* Énay, 1959

Type-species: *Ammonites (Perisphinctes) crusoliensis* Fontannes, 1876, in Dumortier & Fontannes, 1876, p. 97, pl. 14, fig. 3. Pl. II, fig. 1 in the present account.

Synonym: *Badenia* Énay, 1959. Type-species: *Badenia wegelei* nom. mut. (= *Perisphinctes acerrimus* Wegele, 1929 [*non* Siemiradzki, 1891], Wegele, 1929, p. 62, pl. 5, fig. 4), Énay, 1959, p. 229: Pl. I, fig. 1 in the present account.

Homonym: The name *Badenia* was preoccupied by *Badenia* Finlay, 1930 (= nom. nov. for *Powellia* Finlay, 1926), a recent gastropod genus.

Remarks: *Badenia* was not accepted by Geyer (1961, p. 37) and later by Oloriz (1978), Pavia *et al.* (1987) and Gygi (2003) who regarded *Badenia* and *Crussoliceras* as synonyms, with *Crussoliceras* having the priority. The assumed synonymy of the type-species of *Badenia* with *C. tenuicostatum* n. sp. by Geyer (1961, p. 44) is now irrelevant by reason of the homonymy with *Badenia* Finlay.

Énay's (1959) original description of *Crussoliceras* referred to "Perisphinctes" sp. ind. Durand (1933, pl. 21, fig. 4). This was later ascribed to *Katroliceras sevogodense* by Contini & Hantzpergue (1975) and subsequently to *Crussoliceras* (Énay, 1976 MS; Birkelund *et al.*, 1983) and *Tolericeras* (Hantzpergue, 1987, 1989). The type-species of *Badenia* Énay was assumed to be a variant of *C. crusoliense* from which it was distinguished by its smaller size and different ribbing pattern. The original description of *Crussoliceras* referred only to the macroconchs with *Badenia* proposed for small microconchs, including the type species and the lectotype of *C. divisum* (Qu.) and a specimen of *C. sayni* (Pl. III, fig. 2) with the lappets preserved.

Undescribed specimens from the Crusoliensis Marls at Mount Crussol collected by Martin (FSL 35110 and 35114) and originally attributed to *C. wegelei* (Énay) are now thought to be microconchiate forms closely related to *C. crusoliense* (Pl. I, fig. 2-4). The holotype of the type species of the genus, *C. crusoliense* (Font.), is an incomplete specimen showing a wholly septate nucleus and a quarter whorl of the body chamber. The latter bears four swollen ribs divided high on the side, with a rapid change in ribbing style following a constriction that occurs before the end of the phragmocone at c. 70 mm diameter. It was incorrectly presumed from the presence of an early variocostate stage to be a macroconch. The true macroconch dimorph of *C. crusoliensis* is a nearly complete specimen from the Divisum Beds of the French southern Jura (Énay Collection, FSL 101 153, Pl. III, fig. 1). It is also represented in the *Crussoliceras* Marls (Bed 171) at Mount Crussol by a large, almost complete specimen (Boselli Collection, Pl. IV, fig. 2). Strengthening of the ribbing occurs more slowly than in the microconchs in both specimens.

The macroconch forms are large (300 to 400 mm in diameter), evolute and with slow coiling. The whorl section is circular to rounded quadratic, more compressed and oval shaped on the end of the body chamber. The ornamentation can be divided into three stages:

Initial stage: The Early whorls bear rectiradiate relatively close ribs that are regularly divided and they bifurcate high on the side. The secondary ribs cross the venter without change.

Middle stage: More or less early depending on the species, the ornamentation becomes stronger with

intercalatory simple ribs that can result in a polygyrate structure (false virgatotome in Énay, 1959). This stage occurs early and abruptly in *C. lamberti* n. sp., but more progressively in *C. crusoliense*, *C. aceroides* Geyer and *C. peticlerci* n. sp.

Terminal stage: This stage commonly starts at a constriction at the beginning of the body chamber or a little before. Strong simple ribs, swelling or varix-shaped, are developed sometimes with traces of weakened secondaries on the venter. This variocostate stage is well developed in *C. atavum* (Schneid, 1914), one of the end forms of the genus, from the Acanthicum and ?Eudoxus Zones in southern Germany. These mimic the Oxfordian *Perisphinctes* st. s. (see reference in Schneid, 1914 to the "gr. of Per. bplex-martelli").

The microconchs display two morphologies which are more obviously distinguishable than those of the macroconchs. In the first type the two first stages are more strongly developed and, in some cases, are the only stages that are developed with stronger and stronger biplicate ribs continuing to the lappeted aperture [e.g. *C. lotharingicum* n. sp. (m), Pl. VII, fig. 2]. The second type are characterised by the microconchs for which the genus *Badenia* was proposed (Énay, 1959). A survey of the specimens illustrated by Quenstedt (1887), Wegele (1929), Geyer (1961), Ziegler (1977, 1987) and Gygi (2003), and those examined in the present study show a wide variability in the microconchiate adults of *Crussoliceras*. Some of these specimens (e.g. the type-specimen of *C. divisum* (Qu.)) show a biplicate ribbing stage with intercalatories lasting until the aperture. Others [e.g. *C. tenuicostatum* Geyer] are distinguished by swollen simple ribs, sometimes with branching obvious on the ventral area (e. g. *C. crusoliense/wegelei*), but commonly absent and similar to the last stage of the macroconchs. Geyer (1961, p. 45) recognised two varieties within *C. divisum* that corresponded to these co-existing morphologies.

A complete survey of the genus *Crussoliceras* would not be complete without a discussion of *C. divisum* (Qu.) of the *C. divisum* group and *C. sayni* Camus & Thieuloy which resemble *Subdichotomoceras*. In addition, *C. divisum* has features that might be a special form of dimorphism (Tab. 2). Two specimens (Atrops Collection, FSL 185005, 185014) from Le Bois Noir (Le Vigan, x: 725,625, y: 186,675), Conqueyrac, Gard are identified as *C. divisum*. The better preserved specimen (FSL 185014) is figured (Pl. IV, fig. 3). The second specimen (FSL 185005), less well preserved but more complete, shows the same constriction at the same diameter (d=118 mm), this being followed by three prominent swollen ribs. Another specimen in the Boselli Collection from Bed 171 of the Crusoliensis Marls is identified as *C. divisum* (Pl. IV, fig. 2). Apart from the differences in the adult sizes (180 mm vs 120 mm in diameter), it is clearly closely related to the specimen attributed to *K. (C.) divisum* by Ziegler (1977, pl. 4, fig. 2 and 1987, pl. 2, fig. 3). The

Table 2: Measurements of *Crussoliceras divisum* (Quenstedt) (m + M)

Name/n°	Dm/D	Ph	Wh	Wh/D	Wb	Wb/D	Ud	Ud/D	Wb/Wh	N1/1/2 whorl			
Holotype (m)	143									141	14	70	16
Cast Lyon FSL 14079	140		37.7	0.26	28	0.20	73.7	0.52	0.740	130	14	60	16
	105		27.9	0.26	26	0.24	54.8	0.52	0.930	120	15	50	16
										90	15	40	16
										80	15	30	15
<i>Per. acerrimus</i> Siem. de Loriol, 1877, pl. 5, fig. 7	140	?	30	0.27	29	0.26	60	0.54	0.960	111	c 13	30	17
	111		22.4	0.26	26.5	0.31	45	0.52	1.180	85	18		
	85		—	—	—		27.5	0.5	—	50	18		
Conqueyrac (Gard) (m) FSL 185005	135	? 120	33.5	0.27	—	—	60	0.5	—	135	11		
	120									120	12		
Conqueyrac (Gard) (m) FSL 185014	122	70											
	120		32	0.26	27	0.22	61	0.5	0.843	120	11	30	18
	103		29.6	0.28	23	0.22	53.5	0.51	0.777	100	14	20	17
	90		25	0.27	23	0.25	45	0.5	0.920	80	16		
	70		21	0.3	21	0.3	34	0.48	1.000	50	22		
Crussol (Ardèche) (m) P. Boselli Collection	134	?								134	12	60	22
	127		33.9	0.26	—	—	65.5	0.51	—	120	13	40	20
	98		26.6	0.27	—	—	50.3	0.51	—	100	16	30	17
										80	18		
in Ziegler, 1977, 1987	180	115								180	12	90	24
Mus. Stuttgart 22916 (?M)	175		50	0.28	31.6	0.18	91	0.52	0.63	150	13	70	25
Cast Lyon FSL 175919	140		37.5	0.26	26.3	0.18	71.7	0.51	0.7	130	17	50	c 23
	105		27.7	0.26	—	—	53.5	0.5	—	110	22	30	20

morphologies are similar, but the rib-curves (Fig. 7) show clear differences in the number of ribs per half whorl and their change during growth. The question therefore arises as to whether these individuals belong to the same species with a wide range of sizes, two distinct species with different sizes, or are dimorphs of the same species. The last is assumed here with the lectotype and the Gard and Mount Crussol specimens as microconchs and the Ziegler specimen as the corresponding macroconch. However, the incomplete preservation of the aperture of the Ziegler specimen means that this cannot be confirmed. *Crussoliceras sayni* Camus & Thieuloy (1963, p. 277, fig. 4, 5) is another interesting species of *Crussoliceras* (a

microconch). Although it was not figured, the description of the paratype agrees well with the specimen from the Couches à Céphalopodes of Saint-André-Val-de-Fier (Seysse, x: 876,000, y: 109,840), Savoie figured here as Pl. III, fig. 2 (Hirtz Collection FSL 101124). The inner whorl is preserved as a compression, and the body chamber, a whole whorl long and complete with aperture, is in a solid but crushed preservation. The aperture, a simple rounded sinuous margin with a short reduced lappet, is similar to that of *Subdichotomoceras lamplughii* Spath. However, this is only one of several features in *Crussoliceras* microconchs that are reminiscent of *Subdichotomoceras*. They include the inner whorls before

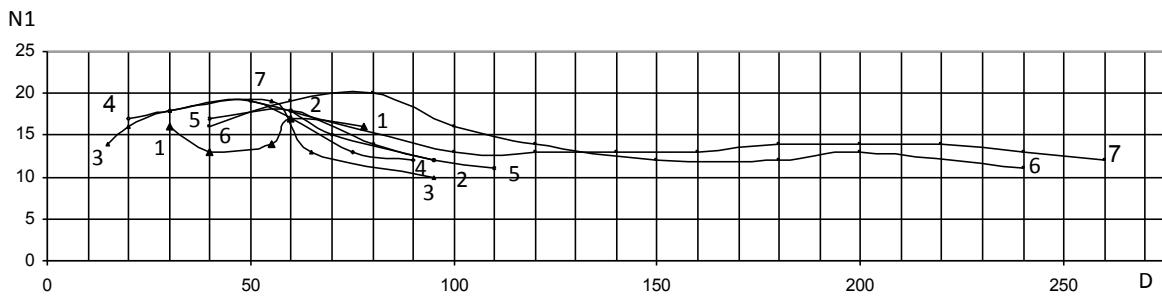


Fig. 7: Rib curves of *Crussoliceras divisum* (Qu.). 1, Lectotype (Quenstedt, 1888, pl. 106, fig. 1); 2, Geyer (1961, pl. 5, fig. 1); 3, Atrops Collection, FSL 185005; 4, Atrops Collection, FSL 185014; 5, Boselli collection; 6, Énay collection; 7, Ziegler (1977, pl. 4, fig. 2; 1987, pl. 2, fig. 3).

they develop their adult morphology, the thick whorl section which is even thicker than high and depressed, and strong, distant ribs that are regularly biplicate with strong oblique constrictions and few intercalatory ribs.

Crussoliceras crusoliense (Fontannes, 1876) (m + M)

Pl. I, figs 1-4; Pl. II, figs 1-3; Pl. III, fig. 1;
Text-figs 7, 9; Tab. 3.

- V 1876. *Perisphinctes crusoliensis* Fontannes, in Dumortier & Fontannes, 1876, p. 279, pl. 14, fig. 3.
- non 1877. *Ammonites (Perisphinctes) crusoliensis* Fontannes, de Loriot, p. 53, pl. 5, fig. 6-8 (= *Perisphinctes acerrimus* Siemiradzki, 1891, p. 65).
- 1879. *Perisphinctes crusoliensis* Fontannes, p. 60.
- 1898. *Perisphinctes crusoliensis* Fontannes.—Siemiradzki, p. 286.
- non 1925. *Ammonites (Perisphinctes) crusoliensis* Fontannes.—Beurlen, p. 21.
- non 1929. *Ammonites (Perisphinctes) crusoliensis* Fontannes.—Wegele, p. 61, pl. 6, fig. 1-2.
- 1929. *Ammonites (Perisphinctes) acerrimus* Siemiradzki.—Wegele, p. 62, pl. 5, fig. 4.
- ? 1943. *Katroliceras crusoliensis* Fontannes.—Butticaz, p. 25.
- 1959. *Badenia wegelei* Énay, p. 230 [= *Perisphinctes acerrimus* Wegele, 1929 (non Siemiradzki, 1891).—Wegele, 1929, p. 62, pl. 5, fig. 4].
- 1959a. *Crussoliceras crusoliense* Fontannes.—Énay, p. 230.
- 1959b. *Crussoliceras crusoliense* Fontannes.—Énay, p. 126.
- 1961. *Katroliceras (Crussoliceras) crusoliense* Fontannes.—Geyer, p. 43, pl. 3, fig. 6 and pl. 4, fig. 4 (= new figure of Fontannes holotype).
- 1968. *Katroliceras (Crussoliceras) crusoliense* Fontannes.—Martin, p. 69.
- V 1975. *Crussoliceras (Crussoliceras) crusoliense* Fontannes.—Hantzpergue, p. 215, pl. 26, fig. b, c; pl. 45, fig. a.

Material: *Microconch*: holotype (FSL 12631) from Mount Crussol; Malet Quarry (Valence, x: 758, 150, y: 294,600); two topotypes from Mount Crussol, Malet Quarry, Bed 171, Boselli Collection; two additional

topotypes (FSL 35110 and 35114) from Mount Crussol, Martin (1968) Quarry A (Valence, x: 798,080, y: 294,400) and eastern cliffs (Valence, x: 798,500, y: 295,460), Bed 22 of Martin (1968, = Beds 168-169 of Atrops, 1982); plaster cast of the holotype of *B. wegelei* (FSL 14078).

Macroconch: two topotypes from Malet Quarry, Bed 171,

a well preserved complete full-grown adult and one not so well preserved, Boselli Collection; a nearly complete adult with the body chamber in solid preservation and the inner whorls crushed or partly missing, Couches à Céphalopodes, Arête de la Roche (Saint-Julien-en-Genevois, x: 875,750, y: 143,075), Saint-Jean-de-Gonville, Ain (Énay Collection, FSL 101153).

Description: *C. crusoliense* (Font.) is confirmed as a dimorphic species.

Microconch: The difficulties inherent in interpreting the type-species were resolved by comparing specimens collected by Martin from the Crusoliensis Marls of Crussol. These are incomplete but complement each other at about the same growth stage ($d = 95$ mm). The Boselli Collection includes one well preserved incomplete specimen and a second that looks close to the holotype. The holotype is incomplete and includes the wholly septate nucleus ($D = 78$ mm) and a quarter whorl of the body chamber with an estimate diameter of about 125 mm. Four strong ribs branch high on the whorl-side, with a rapid change in ribbing style following a constriction that occurs before the end of the phragmocone at $D = 70$ mm. This is followed by stronger and more distant ribs. The rib count is unusual with a maximum of 18-19 ribs at $D = 30$ mm and $D = 70$ mm and a minimum of 15 ribs between $D = 40$ and $D = 50$ mm, decreasing again on the end of the septate whorls. However, a single specimen is insufficient to determine whether or not this ribbing style is characteristic of the species.

At the same growth stage ($d = 95$ mm), Martin's specimens from Bed 22 show some differences. They preserve half a whorl of the body chamber covered with strong and distant primary ribs, bi- or trifurcate, the secondary ribs forming together a bulge but still obvious on the ventral area. The whorl-section is initially depressed to strongly depressed, and more compressed on the body chamber

Table 3: Measurements of *Crussoliceras crusoliense* (Fontannes) (m+ M)

Name/n°	Dm/D	Ph	Wh	Wh/D	Wb	Wb/D	Ud	Ud/D	Wb/Wh	N1/1/2 whorl			
Holotype (m), Crussol Lyon FSL 12631	125	?								78	16	30	16
	78		18.5	0.23	—	—	41.5	0.53	—	60	17		
	60		15	0.25	—	—	32.5	0.54	—	55	14		
Topotype (m) DES Martin	50	?	12.8	0.25	—	—	23.5	0.47	—	40	13		
Crussol, bed 22	95		25	0.26	26.9	0.28	47	0.5	1.076	95	12		
Lyon FSL 35110	70		18.8	0.26	21	0.3	33	0.47	1.117	70	15		60
Topotype (m) DES Martin Crussol, bed 22 Lyon FSL 35114	c 95	?	25	0.26	27	0.28	—	—	—	95	10	30	18
	60		17	0.28	25	0.41	30	0.5	1.47	65	13	20	16
										55	19	15	14
Topotype (m), Crussol, bed 171	90	?								90	13	30	18
Boselli Collection	83		20	0.24	—	—	43	0.51	—	75	13	20	17
	75		19	0.25	24	0.32	38.7	0.51	1.26	50	19		
	58		15.8	0.27	—	—	28.5	0.48	—				
Topotype, Crussol bed 171	110	75	18	0.16	—	—	59.5	0.54	—	110	11	60	18
Boselli Collection (m)	80		20	0.25	23.5	0.29	44	0.55	1.175	95	12	40	17
	65		15	0.24	22	0.33	36	0.55	1.466	80	14		
“Badenia” wegelei Enay (= <i>P. acerrimus</i> Siem.) (m) Lyon FSL 14078 (cast)	c 105	?	27	0.27	27	0.27	—	—	1.00	105	11		
Sain-Jean-de-Gonville (M)	260		65	0.25	46	0.17	141	0.54	0.7	260	12	160	13
Enay coll., Lyon	220		59	0.26	43	0.19	93	0.42	0.72	240	13	140	13
FSL 101153	190	c 44	55	0.28	43	0.22	? 80	0.42	0.78	220	14	120	13
	150			0.29	—	—	? 75	0.5	—	200	14	100	13
										180	14	50	23
Topotype, Crussol, bed 171	240	?								240	11	100	16
Boselli Collection (M)	230		56	0.24	—	—	117	0.5	—	200	13	80	20
	190		54	0.24	—	—	95.7	0.51	—	180	12	60	19
	140		37.8	0.27	—	—	72	0.51	—	150	12	40	16
										120	14		

($Wb/Wh = 1,436$ at $d = 60$ vs $1,018$ at $d = 95$ mm in FSL 35114). Strong, distant ribs occur early on the inner whorls. They are more pronounced at a smaller diameter (45/50 mm) on specimen FSL 35114 than on the type-specimen. In contrast, the body-chamber of FSL 35110 is closer to the type-specimen with high branching on the whorl-side. As an example of intraspecific variability, FSL 35114 has bundles of well defined secondary ribs on the ventral mid-part of the flank. The rib-curves (Fig. 8) show a steady increase in rib count to a maximum of 18–20 ribs per half a whorl between 30 and 55 mm diameter, followed by a sharp decline at about 60 mm until 10–12 ribs at 95 mm diameter. This is closely similar to the estimated number (11 ribs at $D = 111$ mm) for the type specimen of *C. wegelei*.

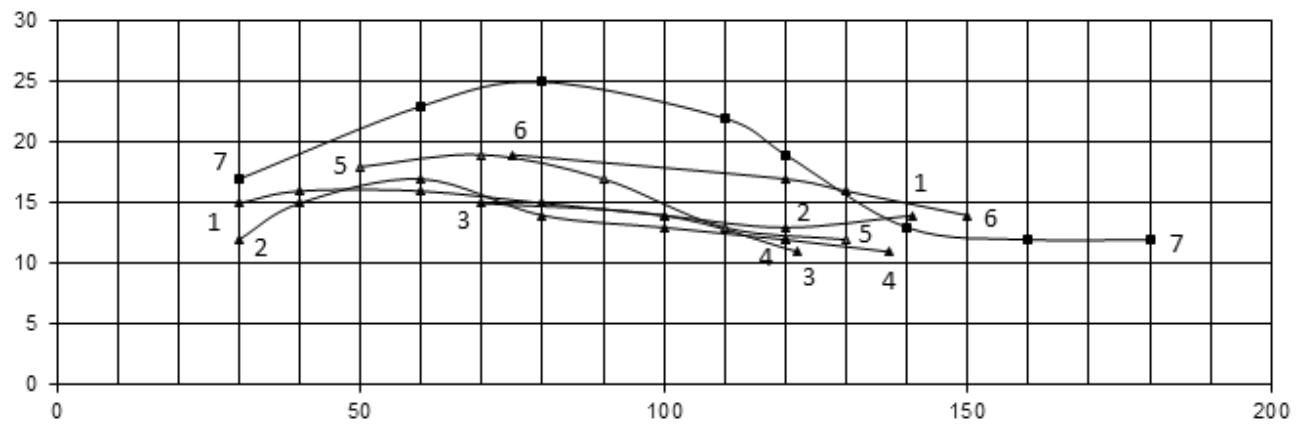
The more complete specimen ($d = 110$ mm) in the Boselli Collection from Crussol Bed 171 (Atrops, 1982), hence a little younger, is considered to be a small-size variant of the holotype (estimated maximum diameter 130–140 mm). The rib-curve shows the same trend as the Martin specimens. The second specimen is incomplete with the adult stage missing, but the middle whorls are complete and similar to the holotype. The rib-curve is the same as the Martin specimens but differs from that of the holotype. This confirms that the ribbing on the type specimen is unusual.

Macroconch: An example from the French Jura (Hantzpergue, 1975) is nearly complete at 260 mm diameter with the body chamber preserved more than a whorl long, but without the aperture. Coiling is evolute, except for the last whorl which shows slight uncoiling. At the end of the septate whorls and the beginning of the body chamber, the whorl section is thick and almost circular, more compressed and oval-shaped on the last whorl. This change might be due to slight crushing.

The few ribs that are visible at the small diameters are delicate and rectiradiate, becoming stronger and more distant at about 80 mm diameter. The branchings points are high on the whorl side and never apparent in the umbilicus. On the last whorl, the branchings are faintly outlined or absent and the ribs appear large, swollen and sharply prominent on the ventral area. Coarsening of the last three ribs suggest the vicinity of the aperture, but this is not preserved. The topotype in the Boselli Collection (Pl. IV, fig. 2) is slightly smaller ($d = 240$ mm), but better preserved, especially the inner whorls. The ribbing, with a constriction at about 80 mm diameter, is well displayed. The ribs are strong and regularly spaced with several deep constrictions with associated single ribs. Another, less well preserved specimen in the Boselli Collection, reaches the same size as the Jura specimen.

Discussion: The absence of the suture on the outer whorl of the microconch holotype led to doubt about its growth stage. This latter combined with the early appearance of variocostate ribbing contributed to its initial interpretation as a macroconch. The present study has confirmed that it is a microconch. The two specimens unpublished since Martin (1968), as well as the more complete specimen in Boselli Collection, first ascribed to *C. wegelei*, show the same evolute coiling, the same thick and depressed whorl section of the young whorls, the same ribbing with strengthening of the ribs until the large swollen ribs of the last whorl. Hence, *C. wegelei* was accepted as a species close to *C. crusoliense*, from which it was distinguished by its smaller adult size and the rib-curve. It is more likely and assumed herein, that *C. wegelei* falls within the species *C. crusoliense* as a small-sized variant and that the type-species exhibits an anomalous rib number. The better knowledge of the microconchiate dimorph has led to the assumption that that in *Crussoliceras*, variocostate ribbing characterizes the microconch dimorph.

N1



D

Fig. 8: Rib curves of *Crussoliceras crusoliense* (Font.). Microconch dimorphs: 1, Holotype; 2-3, Crussol, Martin collection, FSL 35110 and 35114; 4-5, Crussol, Boselli collection. Macroconch dimorphs: 6, Crussol, Boselli collection; 7, Saint-Jean-de-Gonville, Ain, Énay collection, FSL 101153.

Ribbing changes are more uniform in the macroconchiate dimorph, but differences in the rib-curves for diameters of 50 to 100 mm are the result of data missing from the French southern Jura specimen. Ribbing strengthening at about 80 mm in the Boselli Collection adult specimen is gentle, and that occurring in the French southern Jura specimen at about 150 mm in diameter results from different crushing at about the end of the septate whorls. *C. lamberti* n. sp. (described below) shows very Early strong prominent ribs, but the ribbing change is gradual. **Distribution:** *C. crusoliense* (Fontannes) is a characteristic species of the Divisum Zone. *Microconchs*: Mount Crussol, Ardèche: Holotype, Huguenin Collection, FSL 12631; Martin Collection, FSL 35110, 35113, Bed 22 (= Beds 168-169 in Atrops, 1982); Boselli Collection (2 specimens), Bed 171. *Macroconchs*: Mount Crussol, Ardèche, Boselli Collection (2 specimens), Bed 171; Arête de la Roche, Saint-Jean-de-Gonville, Ain, Énay Collection, FSL 101153.

Crussoliceras lamberti n. sp. (M)

Pl. V, fig. 1; Text-fig. 9; Tab. 4.

V 1893. *Ammonites eupalus* d'Orbigny.—Lambert in de Loriol & Lambert, p. 209.

V 1902. *Ammonites eupalus* d'Orbigny.—Lemoine & Rouyer, p. 105.

V 1904. *Ammonites eupalus* d'Orbigny.—Lemoine & Rouyer, p. 18.

Holotype: The complete specimen figured Pl. VI, fig. 1.

Locus typicus : Fontaine, Aube.

Stratum typicum: Argiles bleues de Fontaine (= unit β in Lemoine & Rouyer, 1902), Divisum Zone.

Derivatio nominis: From the name of the collector.

Material: The holotype is a complete macroconch adult that was referred to as *Am. eupalus* d'Orbigny in de Loriol & Lambert (1893) and Lemoine & Rouyer (1902, 1904); Lambert Collection (UPMC 151). The dorsal part of the aperture and a half-whorl-long body chamber are preserved: the end of the phragmocone is missing. The coiling is relatively evolute, the whorl height grows slowly and the whorls have a small overlap. The whorl section is depressed becoming slowly more compressed on the last whorl. The sides and the ventral area are rounded with a high umbilical wall and a rounded umbilical margin. The poorly preserved ribs on the umbilicus indicate that the early ribbing is strong and prominent. The number of ribs shows little change, from 12 per half whorl at D = c. 100 mm to 11 on the last whorl with a minimum of 10 ribs (Fig. 9). In that part of the shell in which they are well preserved, from c. d = 150 mm onwards, the primary ribs are prominent swellings arising on the umbilical

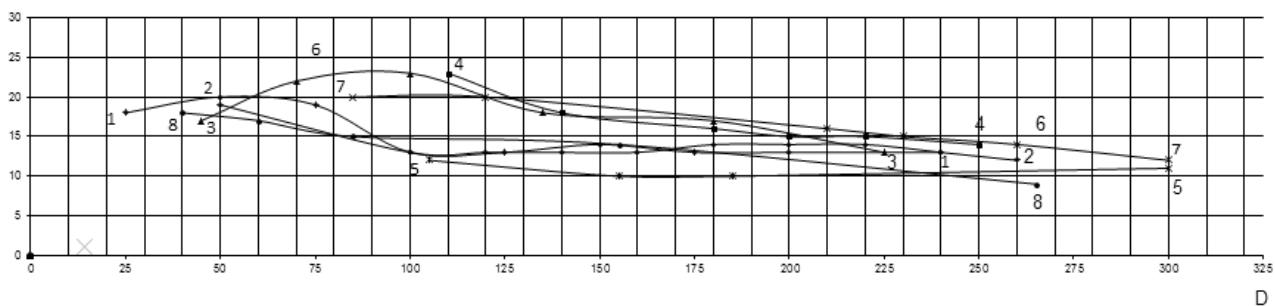


Fig. 9: Rib curves of some macroconch dimorph of *Crussoliceras* species. 1, *C. crusoliense* (Font.), topotype, Boselli collection; 2, *C. crusoliense* (Font.), Saint-Jean-de-Gonville, Ain, Énay collection, FSL 101153 ; 3, *C. petitclerci* n. sp. Fresnes-Saint-Mamès, Petclerc collection, UPMC 152; 4, *C. aceroides* Geyer, Durand collection, ENSG Nancy; 5, *C. lamberti* n. sp., Lambert collection, UPMC 151; 6, *C. dubisense* n. sp., plaster cast, FSL 175915; 7, *C. atavum* (Schneid), Énay collection, FSL 175913 and 175914 ; 8, *C. sevogodense* Contini & Hantzpergue, specimen figured in Durand (1933, pl. 21, fig. 4), Buvignier collection, ENSG Nancy, plaster cast FSL 175911.

Table 4: Measurements of *Crussoliceras lamberti* n. sp. (= *Amm. eupalus* Lambert) (M).

Name/n°	Dm/D	Ph	Wh	Wh/D	Wb	Wb/D	Ud	Ud/D	Wb/Wh	N1/1/2 whorl
= <i>Am. eupalus</i> Lambert	295	?	82	0.27	—	—	153	0.51	—	295 11
Univ. Paris 6, UPMC 151	240		61	0.25	59	0.24	124	0.51	0.96	185 10
Fontaine (Aube)	185		c 51	0.27	54	0.29	97	0.52	1.05	155 10
	125		38	0.3	41	0.32	67	0.53	1.07	105 12

margin. They bifurcate about at mid-height on the whorl side. The secondaries are weaker and symmetrically spaced, with branching barely visible on the umbilicus except where they are adjacent to the single constriction. The only clear ribs on the body chamber are primary ribs, mostly simple but some with unclear branching, the last ribs being stronger on the ventral area. The last two ribs adjacent to the peristome are less sharp on the whorl side. Constrictions are doubtless present, but only one can be clearly seen, on the last but one whorl where it is fringed by two simple ribs. At the diameters where they can be counted, the number of ribs is the lowest of the *Crussoliceras* species studied. The peristome shows a simple apertural margin. Only the dorsal part is well preserved with evidence on the ventral part favouring a flexuous margin with a dorsal sinus and a forward inflexion in the median part.

Discussion: This is one of the more complete *Crussoliceras* macroconchs. The early occurrence of strong ribbing is a significant feature which distinguishes *C. lamberti* from other species of *Crussoliceras*. It is larger than *C. crusolicense*, more involute, has a greater overlap of the whorls, and the whorl section more depressed. These differences are sufficient for it to be proposed as a new species. The specimen in the Royer Collection figured by Loriol *et al.* (1872) as *Ammonites eupalus* from the Orthocera Zone is unrelated to the new species described here.

Distribution: Only one specimen is known, that from Fontaine, Aube. A microconchiate *Crussoliceras* (MNHN Paris R 2921) of the *C. divisum-tenuicostatum* group from the same formation and locality dates the formation as Divisum Zone.

Crussoliceras cf. aceroides (Geyer, 1961) (M)

Pl. V, figs 2-3; Text-fig. 9; Tab. 5

- V 1933. *Perisphinctes acer* Neumayr.— Durand, p. 306.
 V 1933. *Perisphinctes garnieri* Fontannes.— Durand, p. 306.

- Vm cf. 1961. *Katroliceras (Katroliceras) aceroides* Geyer, p. 41-42; pl. 3, fig. 3; pl. 5, fig. 5-7.
 ? 1975. *Crussoliceras (Badenia) aceroides* (Geyer).— Contini ? Hantzpergue, p. 13; pl. 2, fig. a; pl. 5, fig. 1 [= ? *C. atavum* (Schneid.)].
 ? 1992. *Crussoliceras cf. aceroides* (Geyer).— Finkel, p. 245, fig. 52.

Material: The Durand Collection (ENSG, no collection number) contains two specimens, a large, reasonably well preserved adult specimen from Tronville, Meuse that was listed by Durand (1933, p. 306) as *Per. acer*, and a whorl fragment from Bar-le-Duc with part of the living chamber and the very last sutures preserved which is listed as *Perisphinctes garnieri*. The large specimen is labelled Kimmeridgian, probably from the Marnes à Exogyres moyennes of Acanthicum/Mutabilis Zone age. The incomplete specimen is labelled “Pterocerian”, possibly from the Marnes à Exogyres inférieures according to Durand (1933, fig. 10) which would make it a little older.

Description: The large specimen preserves the adult living chamber, the middle part weathered, but without the aperture. The coiling is evolute, the growth of the whorl height is slow, and the umbilicus is wide and relatively shallow. The whorl section is quadratic rounded to subcircular, the umbilical margin rounded, and the umbilical wall high and vertical. The incomplete body chamber is more than three quarter of the last whorl. Ribs are not well preserved on the inner whorls, but locally seem strong enough, rectiradiate, the branching points not visible in the umbilicus. The first obvious branchings are mostly bifurcate, with some intercalatories that are not well connected to the normal branchings and falsely polygyrate. The ribbing strengthens progressively on the body chamber with the branching point's secondary ribs still visible in spite of being weathered.

Discussion: None of the specimens attributed to *C. aceroides* by Geyer are complete and so the adult stage is not known. At the same growth stage, the Tronville specimen shows differences from the type material

Table. 5: Measurements of *Crussoliceras cf. aceroides* Geyer (M). (* Inferred from the H/D and E/D ratio given by Geyer).

Name/n°	Dm/D	Ph	Wh	Wh/D	Wb	Wb/D	Ud	Ud/D	Wb/Wh	N1/1/2 whorl		
Durand, 1933, (M)	250	170								250	14	110 23
Durand Coll.	220		55	0.25	—	—	126	0.57	—	220	15	
ENSG Nancy	200		53	0.26	—	—	105	0.52	—	200	15	
	180		49	0.26	48	0.26	91	0.50	0.97	180	16	
	160		45	0.28	—	—	82	0.51	—	140	18	
<i>C. aceroides</i> Geyer, 1961												
Holotype, (M)	140		41*	0.29	—	—	70*	0.50	—	140	23	100 30
										120	26	80 37

which explains the uncertain naming. The coiling is more evolute and the growth of the whorl height is slower at all diameters, and the ribs are less prominent and more numerous with 5-6 ribs per half whorl. The type material looks more homogeneous, and the features restricted to the specimens studied here are undoubtedly more related to age differences than to geographical variations.

The weathering of the ornamentation on the last whorl does not preclude the possibility of placing the Tronville specimen near to *C. aceroides* Geyer. However, it has numerous features in common with *C. sevogodense* (Contini & Hantzpergue) from the Eudoxus Zone. The precise stratigraphical level from which the specimen was obtained is not known. The label says "Upper Kimm." which, in Durand's terminology, begins with the Orthocera Beds. This would make it younger than *C. aceroides* and a possible forerunner of *C. sevogodense*. The assignment of the specimen figured by Contini & Hantzpergue (1975, p. 13, pl. 5, fig. 1) to *C. aceroides* is presumably based largely on its derivation from the Calcaires Blancs Moyens. These range in age from the Divisum Zone to the Acanthicum Zone. The preservation is not good enough to allow *C. aceroides* to be differentiated from *C. atavum*.

Distribution: All the specimens Geyer described came from the Divisum Zone, from the Upper White Jura (Malm γ) in southern Germany or from the Baden Beds in northern Switzerland. Kimmeridgian, Acanthicum/Mutabilis Zone, Tronville, Meuse, Durand Collection, ENSG Nancy (no collection number). "Pterocerian", Bar-le-Duc, Meuse, Durand Collection n° 19, ENSG Nancy (no collection number),? Divisum Zone.

? *Crussoliceras dubisense* n. sp. (M)

Pl. VI, fig. 1; Text-fig. 9; Tab. 6

Holotype: Complete specimen figured Pl. VIII, fig. 1.

Locus typicus: La Baume Quarry (Delle, x: 941,250, y: 285,000), Audincourt, Doubs.

Stratum typicum: Calcaires à Corbis (lower part), Divisum Zone.

Derivatio nominis: From the Latin name (*Dubis*) of the river Doubs (and the Doubs Département).

Material: The holotype, a large, well preserved,

nearly complete macroconch in which the last ribs are approximated and without the aperture, is housed in the Town Museum, Besançon, Doubs. There is a plaster cast in Lyon University (FSL 175915).

Description: The holotype is nearly complete at 280 mm diameter, the body chamber preserved over a little more than half a whorl. The section is compressed, the greatest thickness on the dorsal part, the umbilical wall high, the umbilical margin rounded, the whorl sides converging toward the rounded ventral area. Slightly prorsiradiate, primary ribs rise from the upper part of the umbilical wall, at first narrow and sharp and then progressively more distant and strongly prominent at the umbilical margin. Branching is not visible in the umbilicus, but it is likely that the initial stages of the inner whorls have regularly bifurcate primary ribs. The earliest visible bifurcations, at the beginning of the last whorl, are associated with intercalatory ribs that are joined to the bifurcation to form pseudoschizotomous bundles of polygyrate or fasciopartite ribs in the middle stage. These are replaced on the body chamber by dorsally prominent ribs in which the distal part is widened and slightly cuneiform in shape. The secondary ribs are irregularly indicated by furrows on the swellings crossing the venter with a forward sinus fading on the medio-ventral line.

Discussion: The specimen is assigned to a new species on the grounds that it is more densely ribbed than *C. cf. aceroides* and *C. petitclerci* n. sp. (Fig. 9). Except for the ribbing, the holotype is similar to the macroconch topotype in the Boselli Collection (Pl. II, fig. 3). The tendency to the distal enlargement of the ribs on the body chamber is known in other species of *Crussoliceras*, for example, *C. atavum* (Schneid) and *C. petitclerci* n. sp.

Distribution: Calcaires à Corbis, (Beds Ba 01 to Ba 15 in Contini & Hantzpergue, 1973, p. 144), Divisum Zone, La Baume Quarry, Audincourt, Doubs.

Crussoliceras petitclerci n. sp. (M)

Pl. VII, fig. 1; Text-figs 9, 11, Tab. 7

1916. *Perisphinctes* aff. *crusoliensis* Fontannes.— Petitclerc,

1917, p. 48, pl. 7, fig. 1 (non pl. 6, fig. 16, 17).

? 1975. *Crussoliceras (Badenia)* n. sp. B, Hantzpergue, p. 220, pl. 27, fig. c; pl. 46, fig. a, b.

Table 6: Measurements of *Crussoliceras dubisense* n. sp. (M)

Name/n°	Dm/D	Ph	Wh	Wh/D	Wb	Wb/D	Ud	Ud/D	Wb/Wh	N1/1/2 whorl			
Holotype (M), Audincourt, Doubs, Univ. Besançon Cast Lyon FSL 175915	280 180	190	75 62	0.26 0.34	59 42.5	0.21 0.23	140 82	0.5 0.45	0.78 0.68	267 250 230 200 175	14 15 16 17 20	150 120 100 80 75	22 27 26 25 22

Table 7: Measurements of *Crussoliceras petitclerci* n. sp. (M)

Name/n°	Dm/D	Ph	Wh	Wh/D	Wb	Wb/D	Ud	Ud/D	Wb/Wh	N1/1/2 whorl		
Holotype (M)	225	155/160	63	0.28	64	0.28	113	0.50	1.01	225	13	70 22
Fresne-Saint-Mamès, Hte Saône, Petitclerc Coll., Paris 6 ,UPMC 152	170		48	0.28	58	0.34	83	0.48	1.20	180	17	45 17
										135	18	
										100	23	

Holotype: The complete specimen figured in Pl. VII, fig. 1. Petitclerc Collection (UPMC 152).

Locus typicus: Railway station (Port-sur-Saône, x: 864,700, y: 289,950), Fresne-Saint-Mamès, Haute-Saône.

Stratum typicum: Petitclerc (1917) referred the specimen to the Séquanien, part of the succession in which there are few ammonites. Following Contini (pers. comm.), it is more likely that the specimen came for the Calcaires Blancs Moyens, most of which is Divisum Zone to Acanthicum Zone in age.

Derivatio nominis: From the name of the collector.

Material: The holotype (Petitclerc Collection, UPMC 152) is a well preserved almost complete adult from Fresne-Saint-Mamès Railway Station, Haute-Saône.

Description: The holotype is almost complete, probably an adult with the aperture missing, but with the body chamber preserved on nearly two thirds a whorl. The preservation is good except for the beginning of the last whorl, a little before the end of the septate whorls. Coiling is regular, rather quick with a slight uncoiling of the end of the last whorl, and the umbilicus is wide and moderately deep. The whorl section is nearly quadratic, the height and thickness about the same, and the umbilical margin rounded. It seems to be more circular on the inner whorls. The ribbing is well defined at all diameters with strong, prominent, and subradiate to slightly prorsiradiate primary ribs that are already well defined on the umbilical wall. They are regularly bifurcated high on the whorl side with the branching points not visible in the umbilicus except on the external last quarter whorl in connection with its uncoiling. The secondary ribs cross the ventral area without change, the anterior secondary being slightly proverse. At the beginning of the last half a whorl, normal branchings are added with scarce (2) intercalatories. The ribs on the last quarter whorl are in places unbranched and look like swellings. The rib count increases regularly until a maximum at $d = c. 100$ mm and then soon decreases. Oblique, deep constrictions with a simple rib in front occur on the youngest whorl and on the latest whorl a little more than half a whorl before the end of the specimen.

Discussion: Although only known from a single specimen *C. petitclerci* displays enough distinctive features to justify its proposal as a new species. The

adult body chamber with its strong ‘swollen’ ribs looks similar to *C. atavum* (see Pl. VI, figs. 2, 3) from the Acanthicum to Eudoxus Zones (Schneid, 1914; Ziegler, 1958). *C. petitclerci* has even more features in common with *C. lotharingicum* n. sp. (see below). The rib-curves (Figs. 9, 11) are closely similar at the same diameters and there are numerous common features. The principal difference is the size, which might mean that they belong to a single species. The uncertainty relating to the ages of the type material suggests that they are best regarded as two species until such time that more specimens become available.

Distribution: The age of the holotype is uncertain. The acme of *Crussoliceras* falls in the Divisum Zone. Some of the features that distinguish *C. petitclerci* from the *Crussoliceras* of the Divisum Zone suggest that a later age (Acanthicum Zone?) cannot be excluded. Fresne-Saint-Mamès, Haute-Saône, Petitclerc Collection, UPMC 152.

Crussoliceras atavum (Schneid, 1914) (M)

Pl. VI, figs 2, 3; Text-fig. 9, Tab. 8

- 1888. *Ammonites divisus coronatus* Quenstedt, p. 961, pl. 106, fig. 6-8.
- 1914. *Perisphinctes atavus* Schneid, p. 94, pl. 2, fig. 2; pl. 9, fig. 1.
- 1958. *Katroliceras (?) atavum* Schneid.– Ziegler, p. 183.
- ? 1959. *Perisphinctes atavus* Schneid.– Seeger, p. 56
- non 1961. *Katroliceras (Katroliceras) atavum* Schneid.– Geyer, p. 42, pl. 4, fig. 1; pl. 4, fig. 6.
- non 1962. *Katroliceras (Katroliceras) atavum* Schneid.– Geyer, p. 342.
- ? 1975. *Crussoliceras (Badenia) aceroides* (Geyer).– Contini & Hantzpergue, p. 13, pl. 2, fig. a; pl. 5, fig. 1.
- ? 1983. *Crussoliceras cf. atavum* (Schneid).– Birkelund et al., p. 294.
- non 1993. *Tolvericeras atavum* (Schneid).– Schweigert, p. 144, Abb. 5 (renamed *T. hantzperguei* Zeiss, 1994, p. 514, pl. 2, fig. 1).

Material: Two incomplete specimens (Énay Collection, FSL 175913 and 175914) from the Calcaires à Aspidoceras, Acanthicum Zone, La Gorge (Belley, x: 843,500, y: 85,200), Creys-Pusignieu, Isère (Énay, 1958) in the Isle Crémieu. The smaller specimen, 155 mm

Table 8: Measurements of *Crussoliceras atavum* (Schneid) (M)

Name/n°	Dm/D	Ph	Wh	Wh/D	Wb	Wb/D	Ud	Ud/D	Wb/Wh	N1/1/2 whorl			
Creys-Pusigneau, Isère. Enay Coll.Lyon FSL 175914	c. 155 c. 85	?	45 —	0.29 —	— —	— —	76 43	0.49 0.5	— —	155 85 60	14 15 17	40	18
Creys-Pusigneau, Isère. Enay Coll.Lyon FSL 175913	265	c. 200	60	0.22	—	—	145	0.54	—	265	9		

diameter, comprises the inner whorls. The larger specimen is the body chamber of an adult, but without the aperture. The two specimens complement one another and give a good idea of the complete ammonite, a species which has been the subject of various interpretations.

Description: The smaller specimen (FSL 175914) has only one side preserved. The opposite side is irregularly corroded and has a green (glauconite?) coating. The coiling is relatively evolute, the umbilicus wide and deep because of the whorl thickness, the whorl section at least as broad as high, and the whorl side and the ventral area rounded. The primary ribs are visible as early as 35/40 mm diameter, rectiradiate and thick, becoming progressively thicker and sharper. The branching points are not visible in the umbilicus except for one which bifurcates. On the last quarter whorl preserved, the secondary ribs combine with bifurcate ribs and intercalatories, the latter often connected to the former in a polygyrate style. The larger specimen (FSL 175913) is half a whorl of an adult specimen with the end part of the phragmocone and the beginning of the body chamber preserved on about one third of a whorl. A small part of the preceding whorl preserves 6-7 ribs and a constriction. At the adult stage the whorl section is wider than high and depressed, and the venter flat and smooth. The ornamentation is restricted to strong and swelling-shaped ribs, the distal part twisted forward, with a cuneiform style recalling the Oxfordian perisphinctids of the *Perisphinctes martelli* group as noted by Schneid (1914).

Discussion: In spite of their poor preservation, the Creys-Pusigneau specimens include all the most characteristic features of *C. atavum* and the assignment to Schneid's species is not in doubt. We accept Schweigert (1993) rejection of the two specimens illustrated by Geyer (1961) with a doubt about the specimen figured in pl. 4 fig. 6 which has much in common with the inner whorls of the holotype of *C. atavum*. However, Geyer assumed that it had come from the White Jura upper γ (Divisum Zone) and was therefore older. Similarly, the specimen pictured in Contini & Hantzpergue (1975) as *Crussoliceras (Badenia) aceroides* (Geyer) is assumed to have come from the Divisum Zone, even though the Calcaires Blancs Moyens Formation which yielded the

specimen ranges up into the Acanthicum Zone and the precise locality is uncertain.

The form identified as *C. atavum* Schneid in Schweigert (1993) was given the new name *Tolvericeras hantzperguei* by Zeiss (1994). This specimen is discussed below.

Distribution: Schneid attributed *C. atavum* to the Pseudomutabilis Zone (*recte* Eudoxus Zone) and Ziegler (1962) referred the species to the Acanthicum Zone. The two specimens from Creys-Pusigneau figured here (Énay Collection, FSL 175913 and 175914) are from the later zone.

Crussoliceras sevogodense

(Contini & Hantzpergue, 1975) (M)

Pl. VIII, figs 1, 2; Pl. IX, figs 1, 2; Text-figs 9, 10; Tab. 9

- V 1892. *Ammonites biplex* Sowerby.—Roberts, p. 50, 67.
 Vm 1933. *Perisphinctes* sp. ind., Durand, p. 324, pl. 21, fig. 4 a, b.
 Vm 1972. *Aulacostephanus* cf. *crassicosta* (Durand).—Contini, p. 77.
 Vm 1975. *Katroliceras (Katroliceras) sevogodense* nov. sp. Contini & Hantzpergue, p. 12, pl. 1, fig. a, b, c; pl. 4, fig. 4 a, b.
 1983. *Katroliceras (Katroliceras?)* cf. *Sevogodense* Contini & Hantzpergue.—Hantzpergue & Lafaurie, p. 605.
 V 1983. *Crussoliceras* cf. *sevogodense* (Contini & Hantzpergue).—Birkelund et al., p. 294, 302 (= Roberts' specimens).
 1985. *Crussoliceras sevogodense* (Contini & Hantzpergue).—Énay, p. 207
 Vm 1987. *Tolvericeras sevogodense* (Contini & Hantzpergue).—Hantzpergue, p. 178, pl. 11, fig. 6.
 V 1988. *Crussoliceras*, Gallois, p. 42 (= Roberts' specimens).
 Vm 1989. *Tolvericeras sevogodense* (Contini & Hantzpergue).—Hantzpergue, p. 156, fig. 128/9; pl. 11, fig. a.
 ? 1993a. *Tolvericeras (Tolvericeras) sevogodense* (Contini & Hantzpergue).—Schweigert, p. 173.
 ? 1993b. *Tolvericeras (Tolvericeras) sevogodense* (Contini & Hantzpergue).—Schweigert, p. 144, fig. 6.

Material: The holotype from Seveux (Champlitte, x: 855,000, y: 288,800), Haute-Saône, preserved in the

Table 9: Measurements of *Crussoliceras sevogodense* Contini & Hantzpergue (M)

*Measurements according to Hantzpergue, 1989. ** Measurements and number of ribs following Schweigert's figure, 1993a.

Name/n°	Dm/D	Ph	Wh	Wh/D	Wb	Wb/D	Ud	Ud/D	Wb/Wh	N1/1/2 whorl		
Holotype* (M)	265	180	65	0.24	50	0.189	137	0.52	0.77	265	17	140 27
Seveux, Hte Saône										180	25	130 25
Univ. Besançon,										170	26	80 22
Cast FSL 175912										160	26	70 20
										150	26	65 20
<i>Per.</i> sp. in Durand, 1933	300	?195	75	0.25	66	0.22	170	0.56	0.88	300	12	120 21
Bar-le-Duc, Meuse										260	14	85 20
Cast FSL 175911										230	15	
										210	16	
Chettisham, Ely (M)	212	173	—	—	—	—	—	—	—	210	17	120 23
Roberts Collection	200		48	0.24	—	—	114	0.57	—	180	18	100 23
Sedg.Mus J.59855	170		44	0.258	—	—	86	0.5	—	160	23	80 22
										140	24	
Chettisham, Ely (M)	220	175	54	0.245	—	—	123	0.559	—	220	19	100 24
Roberts Collection	180		52	0.288	—	—	102	0.566	—	200	21	80 24
Sedg.Mus J.59856	160		42	0.262	—	—	80	0.50	—	180	21	60 21
										160	22	40 19
										140	26	30 16
										120	25	
Beaumont, Côte d'Or	110	77	27	0.24	30	0.27	56	0.50	1.111	110	18	70 19
J.B. Martin Coll. Geneva,	85		29	0.34	30	0.35	50	0.58	1.034	80	19	50 17
MHNG 92-37724												
“ <i>Katroliceras</i> ” <i>mosense</i>	220	145	56	0.25	63	0.31	127	0.63	1.125	220	15	175 17
Maubeuge, 1996.	200		49	0.24	60.5	0.30	116.5	0.58	1.234	200	16	145 18
MNHN Paris A 25411	175		41.6	0.23	54.4	0.31	104	0.59	1.307			
	145		38	0.26	49	0.33	83	0.57	1.289			
“ <i>Katroliceras</i> ” <i>nasiunmense</i>	165	120	38.4	0.23	45.4	0.27	92.8	0.56	1.182	165	13	95 18
Maubeuge, 1996	135		37.6	0.27	39	0.28	75	0.55	1.037	135	14	70 18
MNHN Paris A2 5412	115		29	0.25	32	0.27	65.2	0.56	1.103	115	16	
Gerhausen, Souabe **	342	?		0.26	—	—	178	0.52	—	342	13	180 18
SMNS Inv.-Nr 62467	275			0.26	—	—	140	0.50	—	300	14	150 20
in Schweigert, 1993a	215			0.27	—	—	104	0.48	—	270	17	120 21
										240	17	90 24
										210	17	

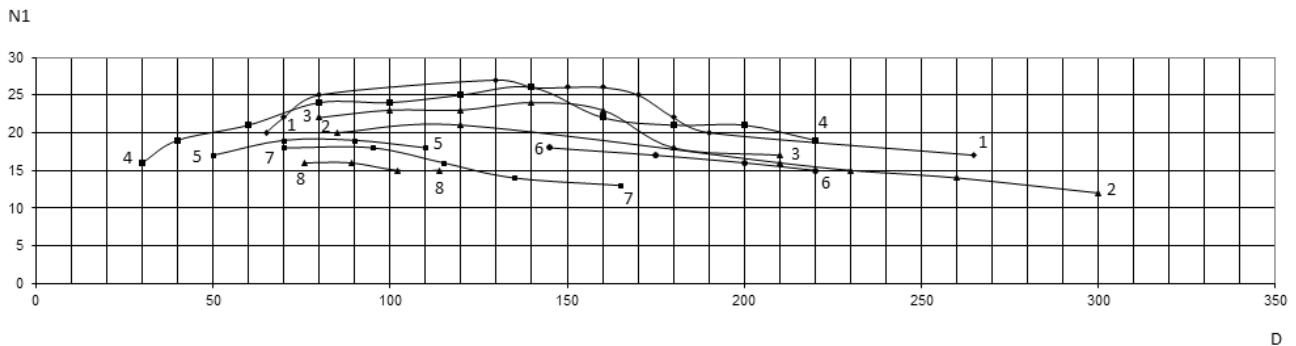


Fig. 10: Rib curves of *Crussoliceras sevogodense* (Contini & Hantzpergue) and some related forms. 1, Holotype, Univ. of Besançon, plaster cast, FSL 175912; 2, specimen figured in Durand (1933, pl. 21, fig. 4), Buvignier collection, ENSG Nancy, plaster cast FSL 175911; 3-4, specimens quoted in Roberts (1892), Roberts collection, Sedgwick Museum, Cambridge, J 59855 (3) and 59856 (4); 5, Martin collection, MHN Geneva 92-37724; 6, "Katroliceras" mosense Maubeuge, Holotype, MNHN A25411; 7, "K." nasumiense Maubeuge, Holotype, MNHN A25412; 8, *Pseudogravescia gravisiformis* Hantzpergue, Holotype.

University of Poitiers (Hantzpergue Collection, UP. SX.10A), and a plaster cast (FSL 175912) at Lyon University) are of Contejeani Subzone age; a specimen from Mauvages, Meuse figured in Durand (1933, pl. 21, fig. 4), in the Buvignier Collection at Nancy is presumed lost, but there is a plaster cast (FSL 175911) at Lyon University; two specimens (SM J 59855 and 59856) collected by Roberts (1892) from the Kimmeridge Clay Formation at Chettisham [TL 547 838], Cambridgeshire, Eudoxus Zone (Chronosubzone KC 30); a small specimen (MHNG 92-37724) from the Calcaires à Astartes at Beaumont-sur-Vingeanne, Côte d'Or; a badly preserved specimen in the Earth Sciences Institute of Dijon; the specimen with the inner whorls preserved in calcite and half a whorl of the body chamber preserved is probably that identified by Tintant as *Katroliceras* (*Crussoliceras*) sp. and dated as Orthocera Subzone). The same specimen was quoted as *Katroliceras divisum* (Quenstedt) from the Calcaires de Bourberain Formation of Orthocera Subzone age by Rat *et al.* (1978) which Pascal (1973) correlated with the Calcaires Blancs Moyens Formation of Haute-Saône.

Description: The description of the holotype by Contini & Hantzpergue (1975) was revised by Hantzpergue (1987, 1989). The final stage is poorly preserved in the holotype and is better displayed in the more complete specimen of *Perisphinctes* sp. ind. figured in Durand (1933). Despite a strengthening of the ribs on the body chamber the secondary ribs are clear especially on the ventral area where they do not coalesce to produce swellings. The two Chettisham specimens, each with about half a whorl of the body chamber, were identified by one of the authors as *Crussoliceras* (Énay MS, 1976). The diameters, 215 and 220 mm, and other measurements (Fig. 22) are similar with ends of the phragmocones at 173 and 175 mm in diameter. The ornamentation on the one side of each specimen that is preserved is identical. The coiling is slow and regular, the umbilicus wide and not very deep, the umbilical margin rounded and well

defined and the umbilical wall high. The whorl section is nearly quadratic rounded, but the complete shape is not known. Ribbing is regular, probably bifurcate on the inner whorls (initial stage), but the branching points are not visible in the umbilicus, unlike of the following intermediary stage. At c. D = 120-130 mm, secondary ribs occur in the umbilicus forming pseudoschizotomous trifurcate bundles of the polygyrate style. These continue until the end of the specimen in parallel with a progressive strengthening of the primary ribs and secondary rib bundles, but do not reach the terminal stage which is not preserved. The ribs-curves are similar to those of the holotype, the number of ribs per half whorl being higher or lower depending on the specimen.

The assignment of the Beaumont-sur-Vingeanne specimen to *C. sevogodense* is less obvious. The maximum diameter is 100 mm with the body chamber starting at c. D = 77 mm and is about three quarters whorl long. It could be a juvenile *C. sevogodense* or a microconch dimorph. However, at the small diameters the rib count is lower than that of the macroconchs. The similarity of the rib count to *K. nasumiense* is referred to in the discussion.

Discussion: *C. sevogodense* was included by Hantzpergue (1987, 1989) in his newly described genus *Tolvericeras* (see later discussion of phylogeny). When compared with the species of *Crussoliceras* described above, *C. sevogodense* is closest to those with slow coiling and uniformly developed strong ribs in the final stage, for example *C. crusoliense* and *C. aceroides*. In addition to the specimens studied here, Schweigert (1993a, b) ascribed a large (D = 342 mm) well preserved specimen from the Beckeri Zone (Subeumela Subzone) of Swabia to *T. sevogodense*. The successive ornamental stages, ribbing density and rib-curves (Fig. 10) fall within the range of the species of *Crussoliceras* described in this account. However, the Swabian specimen differs in having quicker coiling and height growth, and hence a less wide umbilicus.

The holotype (MNHN A 25411) of *Katroliceras mosense* Maubeuge (1996, p. 106, pl. 4 and pl. 6, fig. 1) from Demanges-aux-Eaux, Meuse, which has a complete body chamber, and the incomplete holotype (MNHN A 25412) of *K. nasumense* Maubeuge (1996, p. 108, pl. 5, fig. 2 and pl. 6n fig. 1) from Naix-aux-Forges, Meuse, were also examined. Although they were found loose in ploughed fields and presumed to be derived from the Couches à *Gravesia*, they are almost certainly of Autissiodorensis Zone age. *T. mosense* and *T. nasumense* resemble *C. sevogodense* in part, but have markedly lower rib counts (maximum 15 to 20 vs 20 to 27 in *C. sevogodense*). The holotype of *T. nasumense* is an almost complete specimen with the body chamber three quarters of a whorl long, and hence is probably a microconch. The holotype of *T. mosense* is a large ($D = 220$ mm), complete adult specimen with almost a whorl of body chamber and the peristome preserved. The limited development of the ribbing on the terminal stage to 3-4 simple ribs before the aperture probably means that the specimen is not fully mature. Until additional material is available these forms are best considered as species related to *T. murogense*.

Distribution: The holotype of *Crussoliceras sevogodense* is of Eudoxus Zone, Contejeani Subzone age (Hantzpergue, 1989). The Mauvages specimen is described as from the Kimmeridgian (Durand, 1933) and supposedly of the same age. The Chettisham specimens are from the Eudoxus Zone (Chronosubzone KC 30) (Gallois, 1988). The Beaumont-sur-Vingeanne specimen is from either the Divisum Zone or the Acanthicum/Mutabilis Zone, depending on its level within the Calcaires de Bourberain Formation.

Crussoliceras lotharingicum n. sp. (m)

Pl. VII, fig. 2; Text-fig. 11; Tab. 10

V ? 1975. *Crussoliceras (Badenia)* n. sp. B, Hantzpergue, p. 220, pl. 27, fig. c; pl. 46, fig. a, b.

Holotype: The complete specimen on Pl. VII, fig. 2. (ENSG, no collection number)

N1

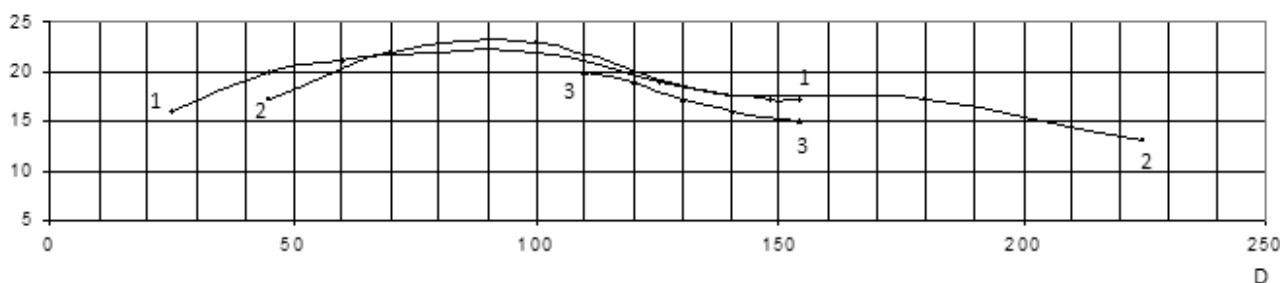


Fig. 11: Rib curves of *Crussoliceras petitclerci* n. sp. (M) and *C. lotharingicum* n. sp. (m). 1, *C. petitclerci* n. sp. Holotype, Petitclerc collection, UPMC 152; 2, *C. lotharingicum* n. sp., Holotype, Petitclerc collection, ENSG Nancy ; 3, *C. cf. lotharingicum*, Énay collection, FSL 101 114.

Locus typicus: Souilly, Meuse.

Stratum typicum: The holotype is labelled as from the Calcaires à Astartes although J. Le Roux (pers. comm.) concluded that it might have come from the Calcaires rocailleux. The matrix is a whitish chalky limestone similar to the local Calcaires Blancs Inférieurs which may mean that the specimen came from an unknown place in strata ranging from Divisum to Acanthicum Zone in age.

Derivatio nominis: The name refers to the source area in the former Lotharingia.

Material: The holotype is well preserved with the aperture complete. Another specimen, complete with aperture, (Énay Collection, FSL 101 114) from the Couches à Céphalopodes at Villes (Nantua, x: 863,050, y: 126,000), Ain was figured in Hantzpergue (1975, p. 220, pl. 46, fig. a, b).

Description: The holotype is a well preserved complete adult with the body chamber and aperture preserved. The coiling is slow and regular, the whorl height increases regularly, and the umbilicus is wide and deep. The whorl section is initially depressed, the whorl sides rounded, and then progressively more compressed and quadratic in shape. The whorl sides are flat and parallel when they reach the body chamber. The ribs are strong and prominent as soon as the early whorls, already obvious on the umbilical wall, and strengthen progressively until the end. A few are prorsiradiate on the whorl side, regularly bifurcate high on the whorl side with the branching points covered by the succeeding whorl and not visible in the umbilicus. The secondary ribs are hardly less strong than the primaries and pass over the venter without changing direction or weakening. The anterior branch curves slightly forward. The rib count increases regularly until the maximum is reached between $c. d = 80$ and 100 mm diameter, then decreases regularly. Constrictions are obvious in the umbilicus, fringed in front by a simple oblique rib connected to the preceding rib, with two on the last whorl followed by a simple rib. A third, bordered by two simple ribs, is present just before the aperture and there is a short lateral lappet high on the side. The Jura specimen is not as well preserved as the holotype, but

Table 10: Measurements of *Crussoliceras lotharingicum* n. sp. (m)

Name/n°	Dm/D	Ph	Wh	Wh/D	Wb	Wb/D	Ud	Ud/D	Wb/Wh	N1/1/2 whorl		
Holotype (m)	151	102								148	17	60 21
Souilly, Meuse.	150		39	0.26	37	0.24	77	0.52	0.94	125	19	45 20
Coll. ENSG Nancy	100		26	0.26	29	0.29	50	0.50	1.11	100	22	25 16
										80	22	
<i>C. (Badenia) n. sp. B</i> in Hantzpergue, 1975, Pra-Devant, Villes, Ain Coll. Enay, FSL 101 114	154	?	44	0.28	46	0.30	77	0.50	1.04	154	13	110 20
	125		36	0.28	34.6	0.27	62	0.49	0.96	140	16	
										130	16	
										120	19	

looks very similar in spite of a faster whorl height growth and more involute coiling. The end of the body chamber shows a thicker, slightly depressed whorl section, and the last ribs are more distant and prominent, especially on the ventral area. It is probably a variant of the species.

Discussion: The ribbing pattern is relatively similar to that of *C. lacertosum* (Fontannes) from which it is clearly distinguished by more evolute coiling, higher rib counts at early diameters, and with the maximum rib count occurring at a later stage. Within the genus *Crussoliceras*, *C. lotharingicum* illustrates a microconch dimorph that is less common than the one more commonly described and figured for the type-species of the genus and for the *Crussoliceras divisum* (Quenstedt)-*tenuicostatum* Geyer group. It looks closer to the morphologies more frequently displayed by the macroconch dimorphs. Although they are derived from geographically widely spaced localities and the precise ages are uncertain, it can be assumed with confidence that the new species *C. lotharingicum* is the microconchs dimorph of *C. petitclerci* described above.

Distribution: The age of the holotype is uncertain, probably Divisum to Acanthicum Zone age. Souilly, Meuse, ENSG Nancy (no collection number); Divisum Zone, Villes, Ain, Énay Collection (FSL 101 114).

Crussoliceras cf. divisum (Quenstedt, 1888)-*tenuicostatum* Geyer, 1961 (m)

Pl. IV, fig 1.

- cf. 1863. *Ammonites bplex* Schafhärtl, p. 416, pl. 86, fig. 1.
- cf. 1888. *Ammonites divisus* Quenstedt, p. 959, pl. 106, fig. 1, 2 et 4 (non fig. 10).
- cf. 1888. *Ammonites cf. divisus* Quenstedt, p. 961, pl. 106, fig. 5.
- cf. 1929. *Perisphinctes crusoliensis* Fontannes.—Wegele, p. 61, pl. 6, fig. 1 (non 2).
- 1933. *Perisphinctes acerrimus* Siemradzki.—Durand, p. 306.
- cf. 1961. *Katroliceras (Crussoliceras) tenuicostatum* Geyer, p. 44, pl. 4, fig. 3 et 5; pl. 5, fig. 3.

- cf. 1961. *Katroliceras (Crussoliceras) divisum* (Quenstedt).—Geyer, p. 44, pl. 3, fig. 5; pl. 5, fig. 1.
- cf. 1977. *Katroliceras (Crussoliceras) divisum* (Quenstedt).—Ziegler, pl. 4, fig. 2. ? (M)
- cf. 1987. *Katroliceras (Crussoliceras) divisum* (Quenstedt).—Ziegler, pl. 2, fig. 3. ? (M)
- non 1987. *Crussoliceras aff. divisum* (Quenstedt).—Pavia, Benetti & Minetti, p. 84, pl. 5, fig. 1.

Material: Part of the body chamber with four ribs labelled as *P. acerrimus* Siemradzki (Durand Collection, N° 17, ENSG, no collection number) from Bar-le-Duc, Meuse. Labelled Kimmeridgian, probably from either the Marnes à Exogyres Inférieures or the underlying beds, Hypselocyclum to Divisum Zone age.

Description: The whorl section and the strong, regularly bifurcating ribs agree with the illustrations of these two closely related species, the variability of which was underlined by Geyer (1961). The Bar-le-Duc specimen is distinguished by the zig-zag arrangement of the secondaries on the ventral area, a feature never reported or pictured previously. This pattern is present in the Gard specimens (FSL 185 005, 185 14) discussed and figured (Pl. IV, fig. 3) above as *C. divisum*, but is missing in the Crussol specimen of the same species (Boselli Collection, Pl. IV, fig. 2), all of which are closely similar to the large specimen pictured as “*Katroliceras*” (*Crussoliceras*) *divisum* (Quenstedt) in Ziegler (1977, 1987) except for the size. The possibility that they might be a dimorphic pair was discussed earlier (see above).

Discussion: One of the few microconch *Crussoliceras* known from the Kimmeridgian in the studied area. Contini (1972) and Contini & Hantzpergue (1975) recorded *C. tenuicostatum* from the Marnes à Ptérocerès at Arc-lès-Gray, Haute-Saône. Microconchs are much more common in the French southern Jura, especially in the Cluse du Fier section (Énay, 1959; Hantzpergue, 1975), and also in the Badener-Schichten of the Aargauer Jura (Gygi, 2003).

The peculiar feature of the ventral area increases the

variability shown by the figured specimens, which throws doubt on the value of the two species. Geyer distinguished two varieties within the species *C. divisum*, and Ziegler (1977, 1987) ascribed a specimen with all the characteristics of *C. tenuicostatum* except for the adult size to the same species (see p. 312). Following Geyer (1961), *C. tenuicostatum* is distinguished from *C. divisum* by its closer ribbing on the inner whorls to which should be added the faster whorl-height growth of the successive whorls. *C. wegelei* (the type-species of *Badenia* Énay), which Geyer tentatively identified as *C. tenuicostatum* Geyer (1961), is considered here to be a variant of *C. crusoliense*.

Distribution: *Crussoliceras* of the *divisum-tenuicostatum* group characterize the Divisum Zone. Bar-le-Duc, Meuse, Durand Collection N° 17, ENSG Nancy (no collection number), probably of the same age.

Crussoliceras sp. (m)

Pl. XIII, fig. 1; Tab. 11

Material: A specimen (MNHN R 2921) with a little less than half a whorl of the body chamber ($d = 105$ mm), the inner whorl very damaged, labelled as “*Ammonites* nov. sp. (syn. *A. eupalus* de Loriol, non *A. eupalus* d’Orbigny)” from Baroville, Aube. It is assumed to be from Kimmeridgian B, the same assignment as on the label of a large *Crussoliceras* from the Argiles de Fontaine in the Lambert Collection (here described as *C. lamberti* n. sp.), Divisum Zone. A closely related form (Énay Collection FSL 175921) was collected from the Badener Schichten, Divisum Zone, of Mellikon Quarry, Argovie, Switzerland.

Description: The partially preserved body chamber shows a depressed whorl section, maximum width near the umbilical margin, convex whorl sides, and a wide, rounded ventral area [$D = 100$ mm: $Wh = 27$; $Wh/D = (0,27)$; $Wb = 30$; $Wb/D = (0, 30)$; $Ud -$; $Ud/D = (-)$; $Wh/Wb = 1,110$; $N1 = 12$]. The 12 primary ribs are distant, strong and prominent, and regularly bifurcate at two thirds of the whorl height. The secondary ribs pass over the venter with little change, the posterior branch without a change in direction and, the anterior branch projected slightly forward.

Discussion: The Baroville specimen is a microconch *Crussoliceras* of the *C. divisum-tenuicostatum* group, but cannot be ascribed to a known species. The bifurcate

ribbing and the depressed whorl section are reminiscent of *Subdichotomoceras*. The similarity is more marked in the Argovie specimen which also has a partially preserved body chamber. This shows eight ribs and is clearly related to the Baroville specimen, but has a more depressed whorl section ($E/H = 1, 220$ vs $1,110$).

Distribution: Baroville, Aube, Divisum Zone (MNHN R 2921); Mellikon Quarry, Argovie, Switzerland, Divisum Zone (Énay Collection FSL 175921).

Genus *Garnierisphinctes* Énay, 1959

Type species: *Ammonites garnieri* Fontannes, 1876, in Dumortier & Fontannes, 1876, p. 263-265, pl. 10, fig. 2, 3. Énay, 1959, p. 229.

Remarks: Some of the features of *Garnierisphinctes*, in particular the ribbing style, are sufficiently similar to those of *Crussoliceras*, *Subdichotomoceras* and *Tolvericeras* to be relevant to the principal aim of the present study to clarify the relationships between these last three genera.

The holotype of the type species *G. garnieri*, from the Divisum Zone at Mount Crussol, is a complete adult microconch with the aperture preserved. It formed part of the Garnier Collection housed at Grenoble University, but is presumed to have been lost. There is a plaster cast at Lyon University (FSL 63797). The genus is known from several species that give a good picture of the microconch forms [*G. plebejus* (Neumayr), *G. semigarnieri* Geyer, *G. densicostatus* Camus & Thieuloy]. The type-species differs from other species of the genus by being more evolute, the whorl height grows less quickly, and the final ornamental stage is less well characterized. A second specimen (FSL 35127) from Mount Crussol is even more evolute (at $D = 130$ mm, $H/D = 0,50$ vs $0,46$). The genus is dimorphic with similar differences present in the coiling in the macroconch forms.

The microconch forms: These are discoidal in shape with the whorl height growing faster and the coiling more involute than in *Crussoliceras*. The whorl section is compressed, higher than thick, the umbilical wall and margin well defined, the sides flat, and the ventral area barely rounded. There are narrow, shallow constrictions at all growth stages. Where preserved, the aperture bears a simple rib and lappet. There are three stages of ribbing development: these are less strong than those in *Crussoliceras*.

Table 11: Measurements of *Crussoliceras* sp. ind. (m)

Name/n°	Dm/D	Ph	Wh	Wh/D	Wb	Wb/D	Ud	Ud/D	Wb/Wh	N1/1/2 whorl	
Baroville, Aube	c 105	?	—	—	—	—	—	—	—	—	—
MNHN Paris R 2921	100		27	0.27	30	0.30	—	—	1.11	—	—

The first stage of the inner whorls displays dense, prorsiradiate, sharp, regularly biplicate ribs that branch low on the upper part of the side. The secondary ribs cross the venter without change.

The middle stage begins with the appearance of intercalatory ribs that give rise to pseudoschizotomous triplicate branches similar to polygyrate ribbing (falsely virgatotome of Énay, 1959). The secondaries have a well-defined forward undulation where they cross the ventral area. This stage commences at different times and is more or less defined depending on the species. For example in the Geyer (1961) species *G. virgatocostatum* and *G. semigrarnieri*, which may be variants of the same species.

The final stage commonly follows a constriction which is the principal characteristic of the genus. This feature is not well developed in the type species, but the holotype may not be fully mature even though the aperture and lappet are present. A more complete specimen from a marly layer with *Crussoliceras* at Sermétrieu, Isère in which the peristome is not preserved, is interpreted as an adult. In this specimen, the last quarter to half-whorl before the peristome bears stronger, more distant ribs with schizotomous polyfurcate branchings of polygyrate type. Some are thickened as swellings, but the branchings and secondaries are still visible.

The rib-curves of the principal described species are similar in shape to one another with a depressed arch and a maximum at $d = 70$ to 90 mm. Other criteria are needed to differentiate the species. These include the size of the adult, small (*G. weilhemensis* Sapunov = *Perisphinctes crusoliensis* in Wegele non Fontannes; Geyer, 1961, pl. 10, fig. 1) or large (*G. championneti*); coiling (*G. garnieri*); position of maximum of rib count early (*G. championneti*, *G. weilhemensis*) or late (*G. plebejus*, *G. romanoi*); and the adult ribbing (*G. semigarnieri* and *G. virgatocostatum*).

The macroconch forms: These are poorly known and may include unpublished, badly preserved forms from the southern French Jura (Énay Collection, FSL 101115, 101118, 101161, 101163; Hantzpergue, 1975)

comprising numerous specimens, some of which are complete with a final diameter of 230 and 280 mm. Gygi (2003, p. 118, fig. 136, 137) attributed a similar specimen ($D = 220$ mm) to *Garnierisphinctes* sp. The coiling is evolute, the whorl section initially nearly trapezoidal and slightly depressed and then more compressed, the sides flat or barely rounded and convergent toward the ventral area.

The first stage shows numerous rectiradiate ribs that bifurcate at about three quarters of the whorl height.

The middle stage begins towards the end of the septate whorls or the beginning of the body chamber where the ribbing changes to a false polygyrate type in which ventral simple ribs are unconnected or poorly connected to the biplicate branchings.

The final stage occupies the body chamber where the primary ribs are represented by more or less prominently swollen ribs which are enlarged on the venter ("low tubercle" of Gygi, 2003). The aperture is unknown, but is probably simple.

The rib-curves of these macroconch forms are similar (Fig. 12), the range of rib counts per half-whorl being within 5 ribs with a maximum of 7 in a single specimen (FSL 101161). This homogeneity contrasts with the great variability of the microconch rib-curves. For this reason, the rib-curve of *G. championneti* (Fontannes, 1876) suggests that it is a macroconch. Fontannes noted that the body chamber was a little more than a whorl long which suggests that the type-specimen is not a mature adult. The species is distinguished by a relatively sudden change in the ribbing just after a constriction. This is less prominent in most other macroconch specimens of *Garnierisphinctes*, but it is present in the two described below.

Garnierisphinctes or *Tolvericeras*?

Three specimens with similar rib-curves (Fig. 12), but of different ages are discussed in order to clarify the relationship of *Garnierisphinctes* to *Tolvericeras*. Gygi (2003, p. 144, fig. 165, 166) described a large specimen of

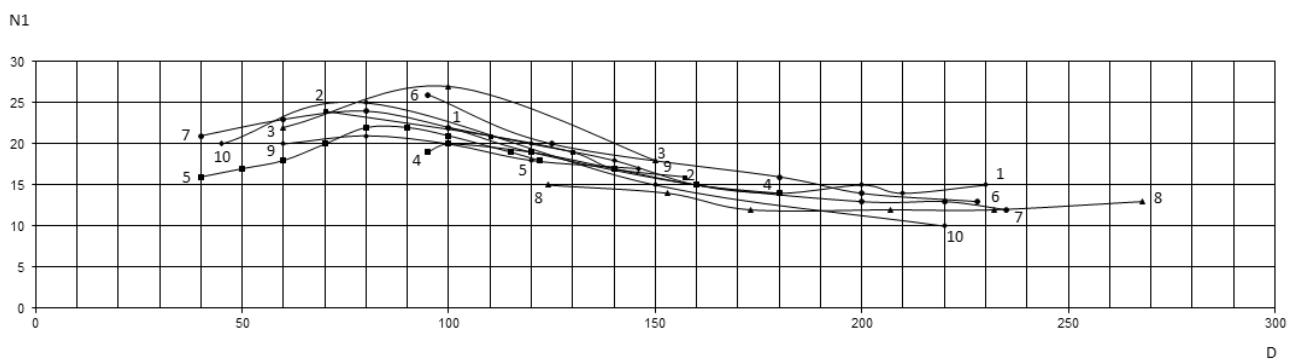


Fig. 12: Rib curves of the species of some macroconchs *Garnierisphinctes* and *Tolvericeras*. 1-4, *G. n. sp. A*, FSL 101115, 101118, 101161, 101163; 5, *G. championneti* (Font.); 6, *G. sp.* FSL 188847; 7, *G. n. sp.* Gygi (2003); 8, *T. tolverense* Hantzpergue, holotype; 9, *T. n. sp.* Gygi (2003, fig. 165); 10, *T. popeyense* n. sp.

Divisum Zone, Uhlandi Subzone age from the Wettinger Member of the Reuchenette Formation from Mellikon, Aargau, Switzerland as *Tolvericeras* (*Tolvericeras*) n. sp. The ribbing on the living chamber is similar to that of the type specimen of the type species of *Tolvericeras* (Hantzpergue, 1989, pl. 10, fig. b) which led Gygi (2003) to prefer his identification to that of *Progeronia* which would have been more consistent with the age. However, the final whorl on the Gygi specimen is incomplete and it might not be a mature adult. The adult morphology is probably the same as that of a specimen of Divisum Zone age figured by Quenstedt as *Ammonites divisus* Quenstedt (1887, pl. 10, fig. 1) and by Wegele as *Per. Crusoliensis* Fontannes (1929, pl. 6, fig. 2) and attributed by Geyer (1961, p. 46) to the microconchiate species *Garnierisphinctes semigarnieri* Geyer.

The same ornamentation style occurs in a specimen in the Atrops Collection (FSL 188841) from the topmost bed of the Divisum Zone at Châteauneuf-d'Oze (Gap, x: 881,700, y: 253,000 and x: 881,420, y: 253,570), Haute-Alpes (Atrops, 1982, p. 302, tab. 51). This was initially labelled “*Progeronia*” before being referred to *Garnierisphinctes* sp. (Pl. XIV, fig. 1; Fig. 12). This is larger than the specimen illustrated by Gygi and has a body chamber that occupies almost a whorl. It is distinguishable from the Gygi specimen by having more evolute coiling and with polygyrate style ribbing with three or four secondary ribs. Overall, it looks similar to the type species of *Tolvericeras*. The macroconchiate forms of *Garnierisphinctes* and *Tolvericeras* are distinguished from one another by a faster coiling and growth in whorl height in *Garnierisphinctes*. The Gygi (2003) specimen is significantly older than the oldest *Tolvericeras* described by Hantzpergue (1989) from the Mutabilis Zone. Half of a large specimen (ENSG no collection number) from the Eudoxus Zone of Popey, near Bar-le-Duc, Meuse is described below as *Tolvericeras popeyense* sp. nov.

Genus *Subdichotomoceras* Spath, 1925

Type species: *Subdichotomoceras lamplughii* Spath, 1925, p. 119 (= *nomen novum* for *Perisphinctes lacertosus* Pavlow, non Fontannes 1876, *in* Pavlow & Lamplugh, 1891a, p. 468-470, text-figure¹, 1891b, p. 515 table; 1892, p. 110-111. Spath, 1925, p. 119-120, MHNG 16252.

Synonym: *Propectinatites* Cope, 1968. Callomon (in Birkelund *et al.*, 1983, p. 302) concluded that *Subdichotomoceras* was the senior synonym of *Propectinatites* and Van der Vyver (1986) came to the same conclusion based on a study of the type material;

Oates (1991) also interpreted the type species of *Propectinatites* as *Subdichotomoceras*.

Material: The type specimen (Pictet Collection, MHNG 16252) of the species and genus of *Subdichotomoceras* is preserved in a calcareous nodule derived from the Kimmeridge Clay found loose on the beach at Speeton [TA 146 761], Yorkshire. Other specimens in museum collections, also found in loose nodules on the beach at Speeton, include examples of *S. lamplughii* and other species of *Subdichotomoceras*. The Kimmeridge Clay at Speeton is almost always covered by beach sand. When exposed, the outcrop can be seen to be disturbed by tectonic and glaciectonic faulting and folding. The most complete published section of the beach outcrop is that of Leckenby (1859) who recorded over 20 m of succession with nodule beds at several levels. However, some of the beds may have been repeated by faulting or folding. Callomon (in Callomon & Cope, 1971, p. 162) recorded *S. lamplughii* in the beach outcrops in association with *Aulacostephanus* spp. of the Autissiodorensis Zone. In the coastal outcrops in Dorset ? *Subdichotomoceras* spp. occur *in situ* in the highest part of the Eudoxus Zone (Chronosubzone KC 32) and in the Autissiodorensis Zone (Chronosubzones KC 33 to KC 35). The stratigraphical position of the type specimen cannot therefore be determined with certainty.

Spath (1925) accepted Tethyan species closely related to *Crussoliceras* (e.g. “*Katroliceras*” *crusoliense* (Fontannes) and “*K.*” *divisum* (Quenstedt)) into his new genus, and suggested that it was transitional between the Oxfordian genera *Perisphinctes* s. s. and/or *Dichotomoceras* and the Tithonian genus *Pallasiceras* (= *Pavlovia*). Arkell (in Arkell *et al.*, 1957) interpreted the genus in much the same way and accepted wide geographical and stratigraphical ranges for it. In contrast, other authors (e.g. Callomon in Callomon & Cope, 1971) regarded *Subdichotomoceras* as a Boreal genus, and Énay (1959) considered that it should not be used for the Tethyan genera *Crussoliceras* or *Katroliceras* and closely related genera.

The type species of *Subdichotomoceras* is a microconchiate form as Callomon (in Birkelund *et al.*, 1983) assumed. Arkell (in Arkell *et al.*, 1957) described the aperture as “simple or trumpet shaped, without lappets”, but this may refer to another Spath (1925) species, *S. speetonense*, which is probably a macroconch. In the holotype of the type species the sinuous apertural margin can be interpreted either as the beginning of lappet, a reduced lappet or as a residual lappet. Either the apertural margin is incompletely preserved in the type specimen or the sinuous apertural margin is the result of an evolutionary decrease of the lappet, a process well known in some ammonite groups. In some examples of *Subdichotomoceras* recorded *in situ* at Kimmeridge Bay, Dorset the lappets are short but well defined.

A macroconch *Subdichotomoceras* is the large (D = 180 mm) specimen (SM J 35 941) labelled

¹ The reference to the year 1892 and pages 110-111 given by Spath corresponds to a 1891 paper republished with continuous pagination in the issues 2, 3 and 4 of the *Bulletin de la Société Impériale de Russie*.

Subdichotomoceras crassum (the type species of the genus *Sphinctoceras* Neaverson, 1924). The specimen is well preserved with remnants of the test and the peristome, the beginning of the body chamber at D = 140 mm. Arkell (in Arkell et al., 1957) regarded *Subdichotomoceras* and *Sphinctoceras* as possible synonyms. The age difference (*Subdichotomoceras* Autissiodorensis Zone, *Sphinctoceras* Tithonian Wheatleyensis Zone) makes this unlikely. The *Subdichotomoceras* macroconchs include specimens recorded as *Propectinatites* by Cope (1968), as *Sphinctoceras* by Callomon & Cope (1971), and *Subdichotomoceras* by Spath (1925), Birkelund et al. (1983), Van der Vyver (1986) and Oates (1991). Specimens from the Eudoxus Zone referred to *Propectinatites?* by Gallois & Cox, (1976) were identified as *Crussoliceras* by Énay (1974, MS).

The rib-curves (Figs. 13-17) of the specimens examined in the present study [*S. speetonense* Spath, 1925; *P. websteri* Cope, 1968; *S. websteri* (Cope) sensu Oates, 1991; Sedgwick Museum specimen SM J 35 941 labelled “*Sphinctoceras crassum*” Neaverson; and two specimens from Brandy Bay, Callomon Collection OUMNH J. 70538 and Énay Collection, FSL 175920] form two homogeneous groups. The first is made up of two species with dense ribbing [*S. speetonense* and *S. websteri* (Cope) sensu Oates] and includes the holotype of the Spath species *S. speetonense* with a simple, splayed, trumpet-shaped aperture preserved. The specimens in the second group, which includes the holotype of *Propectinatites websteri* Cope and the specimen labelled *S. crassum*, are less densely ribbed. The latter is probably a complete adult with a simple aperture.

Subdichotomoceras and Tolvericeras

It is surprising that the relationship of *Subdichotomoceras* to *Tolvericeras* has not previously been discussed in view of the similarity of the microconch of *Tolvericeras*

murogense murogense Hantzpergue (1989, p. 182, pl. 12, fig. c, d) to *Subdichotomoceras* (see Pl. XIII, fig. 3-4 and Fig. 14). It is not known if the specimen of Hantzpergue (1989, pl. 12, fig. c) is an adult, but apart from the diameter, the general coiling, whorl section and ribbing are the same as those of some species of *Subdichotomoceras*. The specimens, in the Depont Collection in the Town Museum of Bourges have been examined for the present study. Except for the final stage, the rib-curves at a smaller diameter are close to that of English *Subdichotomoceras*, in particular one of the *S. lamplughi lamplughi* specimens (Fig. 13). Cariou (1984) and Hantzpergue (1987, p. 77, but not in the CNRS volume of 1989) considered that microconchs were more significant and had prior right when defining genera. An example of this was given by Sykes & Callomon (1979, p. 893) who showed that the microconchs of *Ringsteadia* displayed different morphologies, *Ringsteadia* or *Microbiplices*, depending on the species. Similarly, Bonnot (in Bonnot et al., 1995; Bonnot & Gygi, 1998) showed that for *Euaspidoceras* and its possible microconch *Mirospinctes*, it was necessary to know the stratigraphical positions of the specimens in order to be able to identify the macroconch and microconch partners.

In the case of *Subdichotomoceras*, the macroconchs display a different ribbing from *Tolvericeras* at the adult stage. They preserve bifurcate primaries to the final stage and the rib-curves are quite different at the adult stage (Fig. 14). They do not develop the strong swollen ribs that are characteristic of the final stage of *T. murogense*. Hence the *Subdichotomoceras*-like morphology of the microconch dimorph of *T. murogense* may not be relevant to its generic position, but even when limited to the microconch of a single species it must have a phylogenetic significance. It probably relates to a genetic patrimony inherited from a *Crussoliceras-Garnierisphinctes* group ancestor. This raises the question of where the *Tolvericeras* lineage fits in the ancestry.

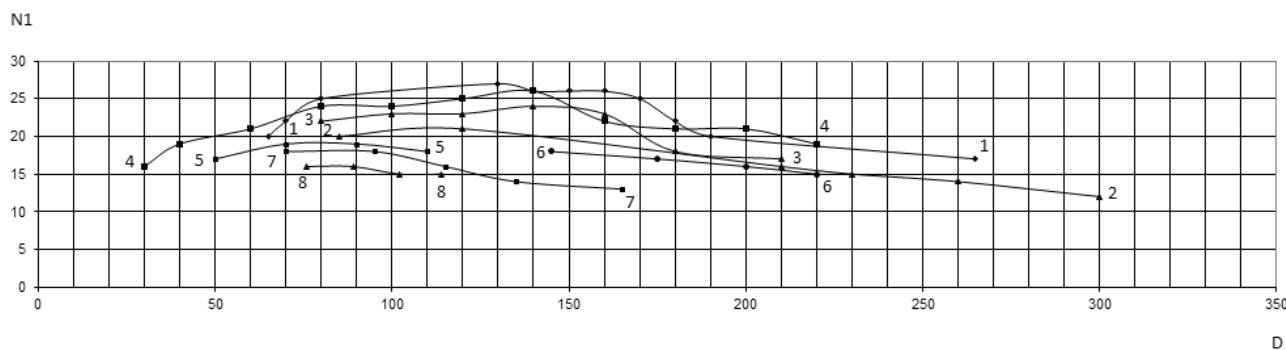


Fig. 13: Rib curves of some microconchs of *Subdichotomoceras* and *Subdichotomoceras*-like microconchs of “*Tolvericeras*” *murogense* Hantzpergue. 1, *S. lamplughi lamplughi* Spath, Holotype, Pictet collection, Geneva, MHNG 16252; 2, *S. lamplughi dorsetense* n. subsp., Holotype, Etches Collection K1715; 3, *S. websteri* (Cope) Paratype; 4, *S. websteri* (Cope), Etches collection K 1711; 5, *S. websteri* (Cope), photo *in situ* Sub 06; 6-8, “*T.*” *murogense* Hantzpergue (1989); 6, “*T.*” *murogense* Hantzpergue (1989, pl. 12, fig. c); 8, “*T.*” *murogense* Hantzpergue (1989, pl. 12, fig. d); 8, *T. murogense* Hantzpergue (1989, p. 59, not figured), ENSG Nancy collection (MAN).

***Subdichotomoceras lamplughii lamplughii* Spath, 1925**

(m + M)

Pl. X, figs 1, 2; Text-figs 13-15, 17-18; Tab. 12

- V 1891a. *Perisphinctes lacertosus* Dumortier & Fontannes.— Pavlow in Pavlow & Lamplugh, text-fig., p. 468.
- V 1892. *Perisphinctes lacertosus* Dumortier & Fontannes.— Pavlow in Pavlow & Lamplugh, text-fig., p. 111.
1925. *Subdichotomoceras lamplughii* Spath, p. 119 (= *Perisphinctes lacertosus* Palow).
1957. *Subdichotomoceras lamplughii* Spath.— Arkell in Arkell *et al.*, p. L.328, fig. 422.
1971. *Subdichotomoceras lamplughii* Spath.— Callomon & Cope, p. 62.
1971. *Sphinctoceras* sp. Callomon & Cope, p. 162

Holotype: The complete specimen of Pl. X, fig. 1, from Speeton, Yorkshire.

Locus typicus: Speeton, Yorkshire, England.

Stratum typicum: Kimmeridge Clay, Autissiodorensis Zone (*fide* Callomon & Cope, 1971, p. 162).

Material: *Microconchs*: The holotype (Pictet Collection MHNG 16252; plaster cast Lyon FSL 14 075) and a repaired broken specimen (SM J 48158) from Speeton. *Macroconch*: A complete specimen (SM J 35941) in a loose nodule from Speeton with the aperture preserved: labelled *Sphinctoceras crassum* Neaverson.

Description: The type specimen of the type species, a microconch in solid preservation, has never been fully described.

The microconch: Coiling is slow with few overlap of the preceding whorl, the whorl section clearly thicker than high and depressed ($Wb/Wh = 1, 29$ at $D = 80$ mm), the umbilical wall high and vertical, the umbilical margin rounded, the whorl sides convex, and the ventral area broadly rounded. The primary ribs are strong and prominent in the earliest visible whorls, rectiradiate and

uniformly bifurcate with symmetrical branching. The secondary ribs cross the ventral area without any smooth bands or furrows. The ribs are regularly disturbed by constrictions that are preceded by a rib joined to the preceding ribs and followed by a simple rib. At least three such structures are present on the well preserved three-quarter of the last whorl and others are visible on the inner whorls. The aperture, which is only partly preserved, shows a simple swelling-shaped rib just before the final flare with a sinuous margin. This is possibly the beginning of a lappet that was not preserved or a residual lappet. A second specimen (SM J 48158), too badly preserved to be figured, is a large ($D = 130$ mm), probable complete adult with the body chamber a whorl long. The coiling is evolute, the whorl height increases slowly with a broad umbilicus, the whorl section quadratic and thicker than the height and depressed, the ventral area is rounded, the umbilical margin is rounded, and the umbilical wall is vertical. The ribbing is made up of strong, regularly spaced bifurcate primary ribs.

The macroconch: This was not originally identified as a macroconch other than implicitly when Arkell (in Arkell *et al.*, 1957, p. L 328) suggested a link between *Sphinctoceras* and *Subdichotomoceras*. Specimen SM J 35941, identified here as *Subdichotomoceras* but erroneously ascribed to *S. crassum* Neaverson, is a very well preserved, large specimen ($D = 180$ mm) with part of the test preserved, complete with the aperture and half a whorl of body chamber. The coiling is fairly evolute, the umbilicus wide and deep, the whorl section thick and depressed, and the umbilical margin well defined. The ribbing comprises strong, slightly prorsiradiate ribs that bifurcate uniformly at about two thirds of the whorl height. The branching points are visible on the umbilicus and do not change until the latest ribs just before the aperture where they are closer and more projected

Table 12: Measurements of *Subdichotomoceras lamplughii lamplughii* Spath (m + M)

Name/n°	Dm/D	Ph	Wh	Wh/D	Wb	Wb/D	Ud	Ud/D	Wb/Wh	N1/1/2 whorl		
Holotype (m)	115	80	31.5	0.27	32.4	0.28	61	0.53	1.028	112	18	75 c 15
Speeton, Yorkshire	80		19	0.23	25	0.31	51.8	0.52	1.315	100	17	40 c 13
Genève, MHNG 16252										85	17	20 11
Speeton, Yorkshire (m)	130	c 85								100	18	
Sedgwick Museum J. 48158	100		25	0.25	30/32	0,30/32	50	0.5	—			
“S. crassum” (M)	180	140								175	25	100 19
Speeton, Yorkshire	175		42	0.24	50	0.28	101	0.57	1.19	160	25	80 17
Sedgwick Mus. J 35941	150		36	0.24	49	0.32	82	0.54	1.361	140	22	60 16
	120		31	0.25	42	0.35	62	0.51	1.354	120	20	45 14

N1

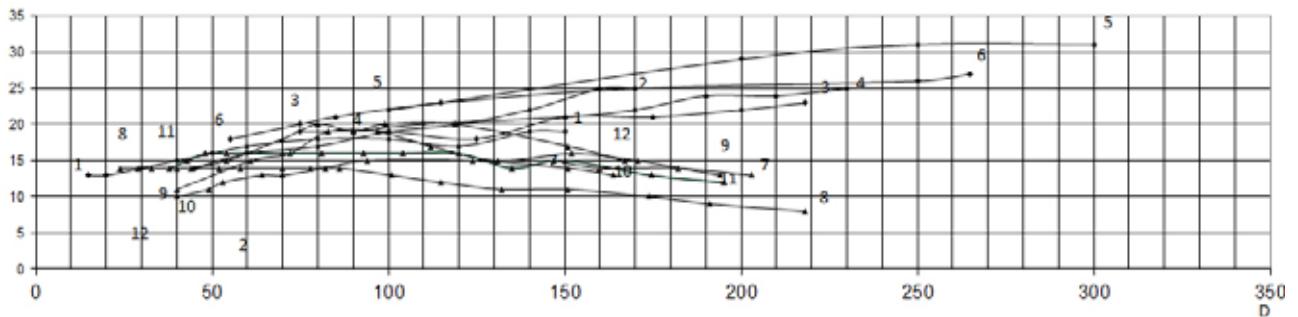


Fig. 14: Rib curves of the macroconchs of *Subdichotomoceras* and “*Tolvericeras*”. 1, *S. websteri* (Cope), Holotype; 2, *S. lamplughii lamplughii* Spath, Sedgwick Museum J 48158; 3, *S. lamplughii dorsetense* n. subsp., Callomon collection, OUMNH J.70538, 4, *S. lamplughii dorsetense* n. subsp. Énay collection, FSL 175920; 5, *S. speetonense* Spath, Holotype, in Sheppard (1907); 6, *S. speetonense* Spath, [= *S. websteri* (Cope), Oates (1991)]; 7-12, “*T.*” *murogenense* Hantzpergue, 1989, pl. 12 and p. 159; 7, Holotype, MNHN Paris; 8, specimen A, pl. 12, fig. a; 9, specimen B, pl. 12, fig. b; 10, specimen C, p. 159; 11, specimen D, p. 159; 12, p. 159, ENSG Nancy collection (MAN).

N1

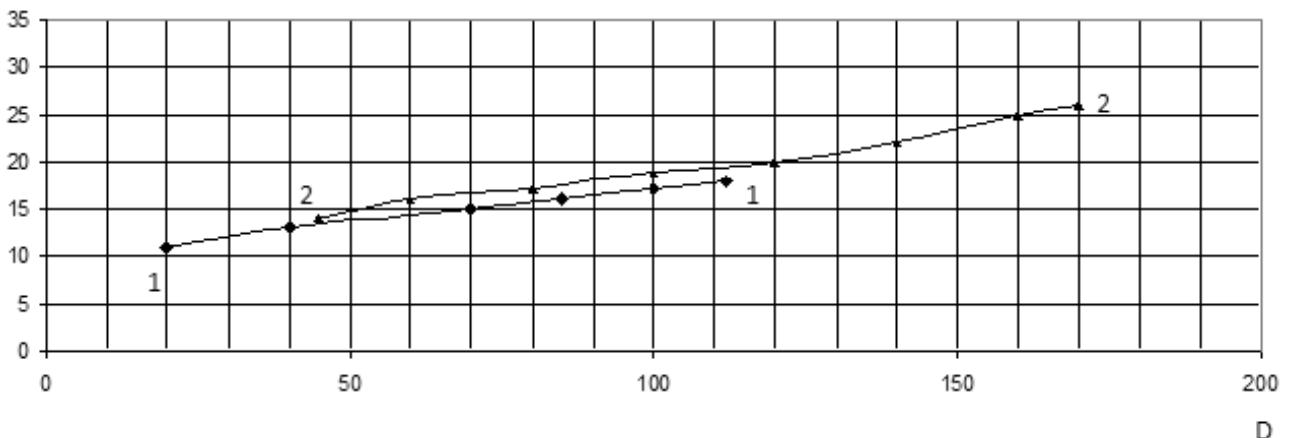


Fig. 15: Rib curves of *Subdichotomoceras lamplughii lamplughii* Spath. 1, Holotype, microconch dimorph, Pictet collection, Geneva, MHNG 16252; 2, macroconch, Sedgwick Museum J 48158.

forward. Constrictions are prominent, each fringed on the posterior side by a simple rib, the penultimate a scarcely modified rib on the last quarter a whorl. The shell ends with a sinuous margin and a lip-like extension of the ventral area. A large *Subdichotomoceras* ($D = c. 300$ mm) from Aylesbury, Bucks was figured by Oates (1991).

Discussion: The recognition of the specimen SM J 35941 as the macroconch of the holotype of the species is supported by the rib-curves (Fig. 15). These are almost identical at the same diameters (until $D = 115$ mm) and a similar upward trend in the rib count continues to the end of the macroconch. Distinguishing a nominal subspecies of *S. lamplughii* is the result of the establishment of the

new subspecies *S. lamplughii dorsetense*. This is justified by features that enable the microconchs and macroconchs of the Speeton and Dorset specimens to be distinguished from one another. Although not well preserved, an evolute specimen (Photo KFMP 24) from Brandy Bay ($D = 92$ mm, possibly a nucleus) with coarse strong ribbing has some features in common with *S. lamplughii lamplughii*.

Distribution: Kimmeridge Clay, Autissiodorensis Zone, Speeton, Yorkshire; Kimmeridge Clay, Autissiodorensis Zones, Chronosubzone KC 34, Kimmeridge Bay and Brandy Bay, Dorset.

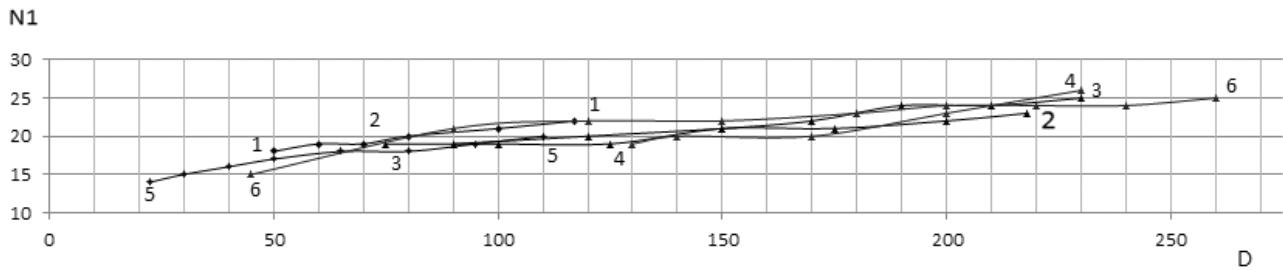


Fig. 16: Rib curves of *Subdichotomoceras lamplughii dorsetense* n. subsp. 1, Holotype (m), Etches collection, K 1715; 2, Paratype (M), Callomon collection, OUMNH J.70538, 3, Paratype (M), Énay collection FSL 175920; 4, Etches collection, K 1778 (m); 5, Paratype (M), Osmington, Etches Collection; 6, Van der Vyver Collection, NMW 82.26.44 (M).

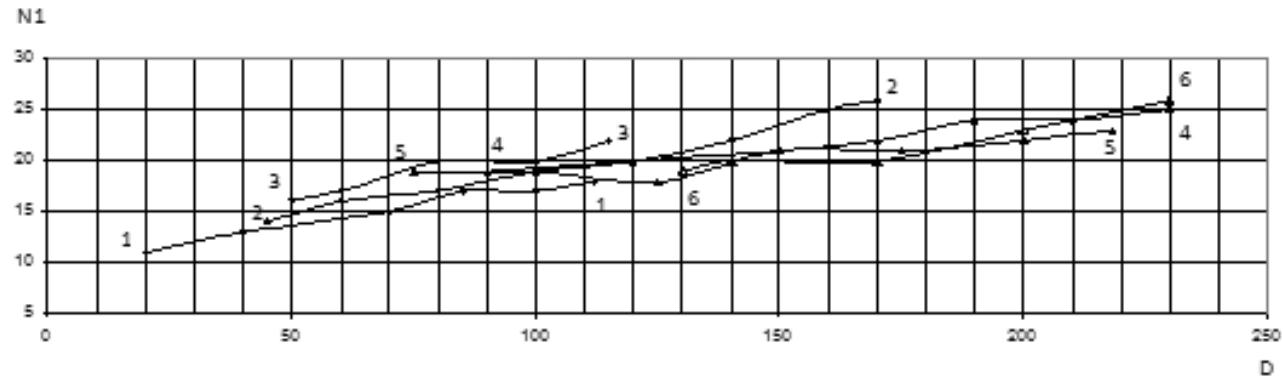


Fig. 17: Rib curves of *Subdichotomoceras lamplughii* Spath (m and M). 1-2: Subspecies *lamplughii*, 1, Holotype, microconch dimorph, Pictet collection, Geneva, MHNG 16252; 2, macroconch, Sedgwick Museum J 48158. 3-5, Subspecies *dorsetense*, 3, Holotype (m), Etches collection, K 1711; 4, Paratype (M), Callomon collection, OUMNH J.70538, 5, Paratype (M), Énay collection FSL 175920; 6, Paratype (M), Osmington, Etches collection.

Subdichotomoceras lamplughii dorsetense subsp. nov. (m + M)

Pl. XI, figs 1, 2; Pl. XIV fig. 2; Text-figs 14, 16-19;
Tab. 13

Holotype: Specimen figured Pl. XI, fig. 1, Etches Collection K1715 (m).

Locus typicus: Brandy Bay, Kimmeridge, Dorset.

Stratum typicum: Kimmeridge Clay, Autissiodorensis Zone, Chronosubzone KC 34.

Paratypes: The macroconch specimens from Brandy Bay, Callomon Collection OUMNH J.70538 (here Pl. XI, fig. 2) and Énay Collection FSL 175920; from Black Head Osmington Mills, Etches Collection.

Derivatio nominis: From the name of the type area Dorset.

Material: *Microconchs*: Loose calcareous nodules from Brandy Bay [SY 893 792] containing two specimens in solid preservation (Etches Collection K 1715 and K 1778), the former well preserved with the nacreous inner layer preserved and the latter a little crushed.

Macroconch: Two crushed *in situ* specimens (Callomon Collection, OUMNH J.70538 and Énay Collection, FSL 175 920), one specimen in Van der Vyver Collection (NMW 82.2G.44) from Brandy Bay; one specimen in solid preservation found loose at Black Head [SY 727 819], Osmington Mills, Dorset.

Description: *The microconch*: Specimen K 1715 is a little smaller than the type species, without the aperture, the whorl section thick and depressed, the ribbing bifurcate throughout with few simple ribs until a constriction at about half last whorl. The rib density is slightly greater than 3-4 ribs per half whorl. The subspecies differs from the nominal subspecies by having a slower growth rate in the height of the whorl and more evolute coiling. The secondary ribs cross the venter without change or weakening. Photographs of *in situ* specimens buried obliquely to the bedding show the ventral area to be identical to the holotype. Notwithstanding the incomplete preservation, Photo KMFP 24 with evolute coiling strong and distant ribs is determined as *S. lamplughii dorsetense* rather than the nominal subspecies. Crushing is probably

Table 13: Measurements of *Subdichotomoceras lamplughii dorsetense* n. subsp. (m + M)

	Dm/D	Ph	Wh	Wh/D	Wb	Wb/D	Ud	Ud/D	Wb/Wh	N1/1/2 whorl			
Holotype (m)	117.8	?	30	0.25	39.1	0.33	58.2	0.49	1.303	117	22	70	19
Kimmeridge, Dorset	100		22	0.22	-	-	56	0.56	-	100	21	60	19
Etches Coll. K 1715	75		19	0.25	-	-	37	0.49	-	80	20	50	18
Kimmeridge, Dorset (m)	115	?	32	0.27	-	-	55	0.47	-	115	20	70	18
Etches Coll. K 1778			26	0.28	-	-	44	0.48	-	100	19	60	17
			19	0.29	-	-	32	0.49	-	85	19	50	17
Paratype (M)	230	?	72	0.31	-	-	95	0.41	-	230	26	140	20
Osmington, Dorset										200	23	130	c 19
Etches Coll.										1270	20		
Paratype (M)	238	?	70	0.29	-	-	115	0.48	-	230	c 25	150	21
Kimmeridge, Dorset	190		50	0.26	-	-	100	0.52	-	210	24	120	20
Enay Coll., FSL 175920	180		50	0.27	-	-	90	0.50	-	190	24	90	19
	160		42	0.26	-	-	75	0.46	-	170	22		
Paratype (M)	218	?	57	0.26	-	-	120	0.55	-	218	23	125	18
Kimmeridge, Dorset	170		42	0.24	-	-	92	0.54	-	200	22	100	19
Callomon Coll.,										175	21	75	19
OUM J.70538													
KFMP 45 (M)	260	?	65	0.25	-	-	143	0.55	-	260	23	180	23
Van der Vyver coll.	220		53	0.24	-	-	115	0.52	-	240	24	150	22
NMW 82.2G.41	180		50	0.27	-	-	90	0.5	-	220	24	120	22
										200	24	90	21

responsible for the place of the branching points very low on the whorl side.

The macroconch: Despite their large size, the Callomon Collection ($D = 218\text{mm}$) and Énay Collection ($D = 230\text{ mm}$) crushed specimens from Brandy Bay are incomplete. The former preserves marks of nearly three quarters of a whorl which indicates a complete diameter of $c. 290\text{-}300\text{ mm}$. It was probably the size of the large specimen in Van der Vyver collection, the badly preserved outer quarter whorl being not considered (Fig. 19). When allowance is made for the distortion due to crushing, the morphology is in good agreement with that of the microconch. In particular, the coiling is fairly evolute and the ribbing regularly bifurcate until the end. The Black Head specimen, although found loose is identified here as *S. lamplughii dorsetense* on the basis of

the similarity of the coiling and the ribbing style to the specimens described above. The specimen is incomplete with the body chamber probably partly preserved, but the end of the septate whorls is not obvious. It provides a good illustration of the subspecies before crushing. When allowance is made for this it explains why the branching points (Fig. 18) on OUMNH J.70538 and FSL 175 920 are lower on the whorl than those on the Black Head specimen.

Discussion: The subspecies *S. lamplughii dorsetense* n. subsp. is distinguished from the nominal subspecies mainly by more evolute coiling connected to a very slow height growth on the succeeding whorls. Hence the ratio between the paired heights at the same diameters are $\text{Wh}/\text{Wh}' = 1, 1$ for the *S. lamplughii dorsetense* n. subsp. and $\text{Wh}/\text{Wh}' = 1, 5$ for *S. lamplughii lamplughii*. The small

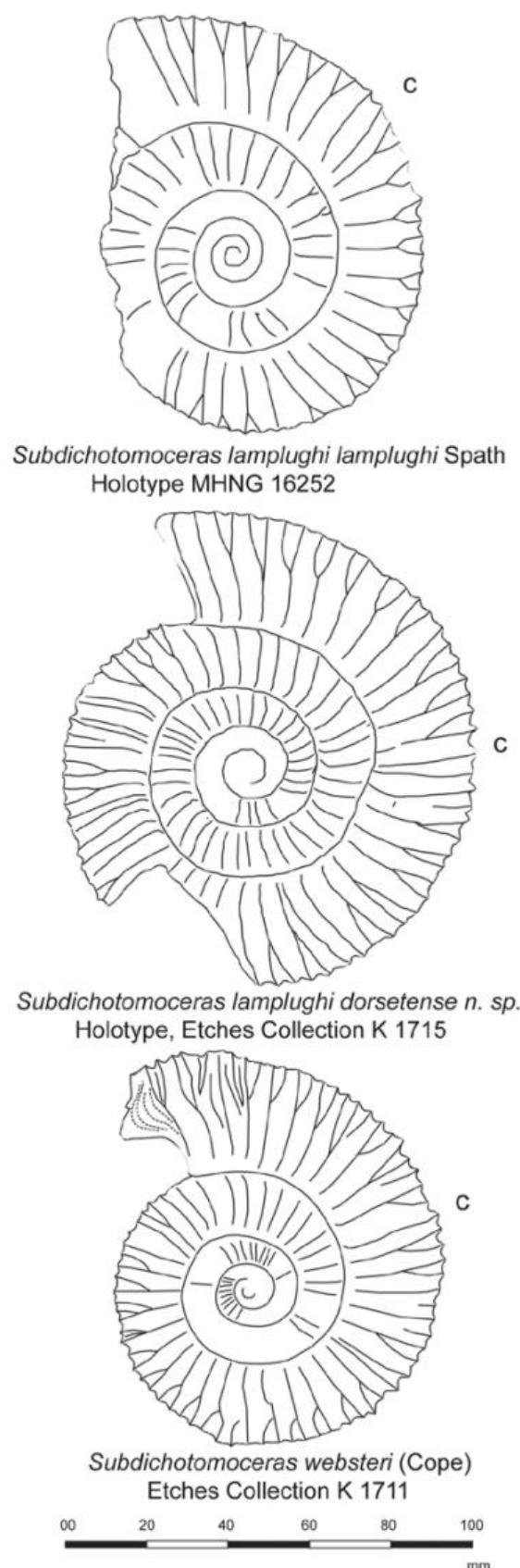


Fig. 18: Diagram illustrating differences in the coiling and ribbing of the species/subspecies of *Subdichotomoceras*. All specimens in solid preservation; c: constriction.

number of specimens available for study at the present time suggest that the two subspecies may be regional variants with *S. lamplughii lamplughii* in the north (e.g. Yorkshire) and *S. lamplughii dorsetense* n. subsp. in the south (e.g. Dorset). Some features in a single specimen from Dorset (e.g. Photo KFMP 24) that resemble those of *S. lamplughii lamplughii* may have resulted from crushing. **Distribution:** Kimmeridge Clay, Autissiodorensis Zone (Chronosubzone KC 34). *Microconchs:* loose calcareous nodules, Brandy Bay, Dorset; photographs of *in situ* specimens from the same beds and locality. *Macroconchs:* crushed specimens on mudstone layer (OUMNH J.70538, FSL 175 920 and NMW 82.2G.41), crushed *in situ* specimens from the same beds in Brandy Bay, and a loose specimen in solid preservation from Black Head, Osmington Mills.

Subdichotomoceras websteri (Cope, 1968) (m + M)

Pl. XII, fig. 2; Text-fig. 14, 18, 20; Tab. 14

- 1962. *Perisphinctes* "Subplanites" *ruepeleanus* (Quenstedt).—Ziegler, 1962, p. 13.
- 1968. *Propectinatites* *websteri* Cope, p. 17, pl. 1 fig. 1-2.
- non 1991. *Subdichotomoceras websteri* Cope.—Oates, p. 194, fig. 6b (p. 196).
- ? 1993b. *Propectinatites websteri* Cope.—Schweigert, p. 146, fig. 4.

Material: The holotype (M) and paratype (m) of the type species of the genus *Propectinatites* (BM C.73731 and 73732) from the Autissiodorensis Zone (Chronosubzone KC 34), Brandy Bay, Kimmeridge, Dorset. *Microconch:* A specimen (Etches Collection K 1711) in solid preservation found loose in a nodule adjacent to an *in situ* nodule bed in Chronosubzone KC 34 in Brandy Bay. Photographs of crushed *in situ* specimens from the same bed as the type specimen. (KFMP 06, 24). *Macroconch:* Photographs of *in situ* crushed specimens from Chronosubzones KC 34 and KC 35 in Brandy Bay and Kimmeridge Bay [KFMP 05, 11/22/35 = same specimen], 18];

Description: *The microconch:* The paratype is a relatively small specimen ($D_m = 92$ mm) and may be not an adult even though the aperture is complete with a lappet. Specimen K 1711, in solid preservation with the nacreous inner layer of the shell preserved, is slightly larger ($D_m = 105$ mm). Although slightly distorted, this specimen shows the shape of the whorl section to be thicker than high and depressed. The peristome is well preserved and bears a short well defined lappet, a little above mid-height, similar to that of the paratype. In addition to its larger size, K 1711 shows some differences from the type specimen including coiling and the whorl height growth, occurrence of intercalatory ribs more or less jointed to the bifurcate secondaries as false polygyrate branching. Four such branchings are present on the final quarter of the last whorl following a constriction. Cope (1968) noted the presence of polygyrate ribs in his description of *Propectinatites*.



Fig. 19: *Subdichotomoceras lamplughii dorsetense* n. subsp. The largest known specimen (actual diameter 260 mm, not considered the badly preserved outer half a whorl), Brandy Bay, Autissiodorensis Zone (Chronosubzone KC 34), Van der Vyver Collection, NWM 82.2G.41.

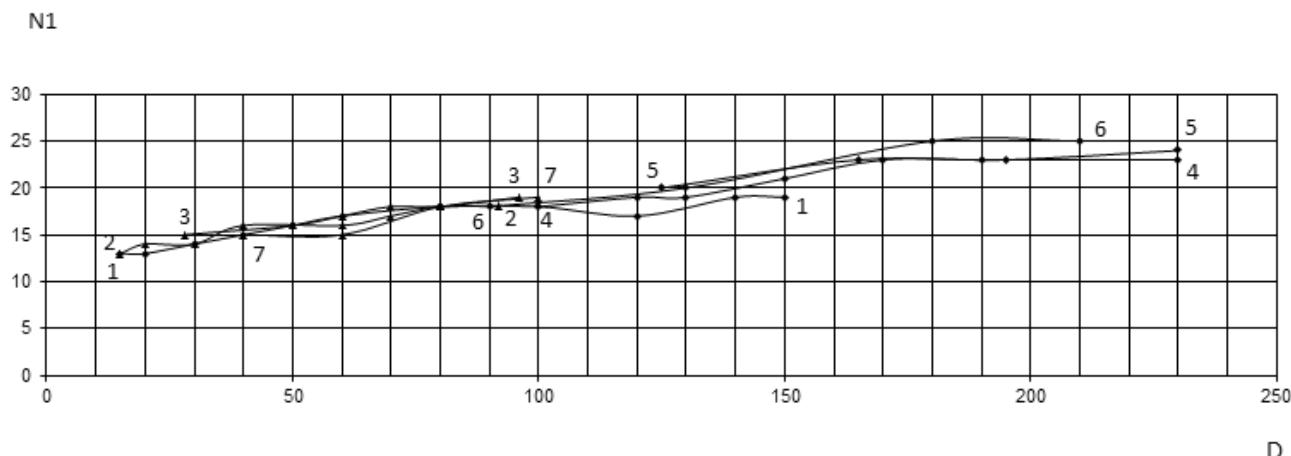


Fig. 20: Rib curves of *Subdichotomoceras websteri* (Cope). 1, Holotype (M), Cope collection, BM C.73731, 2, Paratype (m), Cope collection, BM C.73732; 3, Etches collection K 1711 (m); 4-7, specimens *in situ*: 4-6, KFMP 05, 11/22/35 (same specimen) and 18 (M); 7, KFMP 06 (m).

Specimen K 1711 differs from the paratype by branching higher on the whorl side. The low position on the paratype is the result of crushing and cannot be used as a feature to distinguish *Propectinatites* from *Subdichotomoceras*. *The macroconch:* Photographs of several *in situ* crushed specimens from Brandy Bay and Kimmeridge Bay include a probably complete specimen with slightly oblique crushing distortion in which the aperture is poorly preserved at *c.* D = 220-230 mm. The coiling and the ribbing and rib density are closely similar to those of the holotype. It differs from macroconch forms identified as *S. lamplughi dorsetense* by having more involute coiling and with a higher whorl height. Another crushed *in situ* specimen (11 = 22 and 35) from the same beds is smaller (D = 220 mm) and compressed, but not obliquely distorted; the specimen KFMP 18 (D = 245 mm) in the same state of preservation from the highest part of the Autissiodorensis Zone (Chronosubzone KC 35) is the youngest recorded to date.

When allowance is made for distortion caused by crushing, the diameter of the adults seems to be a useful feature for distinguishing between the macroconchs of *S. lamplughi* and *S. websteri*. The macroconch holotype of *P. websteri* (Cope, 1968) (BM C. 73731) is an incomplete, poorly preserved, crushed specimen *c.* 160 mm in diameter. Complete or nearly complete specimens from the same bed and adjacent beds have adult sizes of *c.* D = 220-230 mm in Chronosubzone KC 34, and up to 245 mm in Chronosubzone KC 35, a small increase during the biochron of the species. The specimens identified here as *S. lamplughi dorsetense* macroconchs have diameters of up 300 mm. In addition, *S. websteri* (Cope) can be distinguished from *S. lamplughi dorsetense* subsp. nov. by being more involute, having a greater whorl height and a narrower umbilicus diameter.

Discussion: All the specimens described here as

species or subspecies of *Subdichotomoceras* except *S. speetonense* Spath (see below) have similar rib-curves (Figs. 14, 20). The differences in the rib counts at the same diameters differ by only ± 5 in both the macroconchs and the microconchs. Among the solid-preservation microconchs, the holotype of *S. lamplughi lamplughi* (MHNG 16252) is less densely ribbed at any diameter than the holotype of *S. lamplughi dorsetense* subsp. nov. (K 1715) and *S. websteri* (K 1711). The rib-curves on the last two are almost identical. Among the macroconchs the only solid specimen (SM J 35941) is identified here as *S. lamplughi lamplughi*. It is initially less densely ribbed until *c.* D = 100 mm after which the ribbing is more dense than on any other specimen studied.

Distribution: Kimmeridge Clay, Autissiodorensis Zone (Chronosubzone KC 34 and KC 35), Brandy Bay and Kimmeridge Bay, Kimmeridge, Dorset. *Microconch:* BM 73732; Etches Collection (K 1711), photographs of *in situ* KFMP 06, 19. *Macroconch:* BM C.73731, photographs of *in situ* KFMP 05, 11/22/35 (same specimen), 18.

Subdichotomoceras cf. speetonense Spath, 1925 (M)

Pl. XII, fig. 3; Text-fig. 14, 21; Tab. 15

1907. *Perisphinctes lacertosus* Fontannes, Sheppard, p. 277.

1925. *Subdichotomoceras speetonense* Spath, p. 220.

1991. *Subdichotomoceras websteri* (Cope).— Oates, p. 194, 196, fig. 6b.

Material: Nucleus in solid preservation with the nacreous inner layer of the shell preserved (Etches Collection K 1365), loose calcareous nodule, Brandy Bay, Kimmeridge, Dorset, Autissiodorensis Zone (Chronosubzone KC 34).

Description: Spath proposed the name *S. speetonense* for a Speeton specimen (= *Perisphinctes lacertosus*

Table 14: Measurements of *Subdichotomoceras websteri* (Cope) (m + M)

Name/n°	Dm/D	Ph	Wh	Wh/D	Wb	Wb/D	Ud	Ud/D	Wb/Wh	N1/1/2 whorl			
Holotype (M)	152	?	50	0.32	—	—	73	0.48	—	150	19	50	16
BM C73731	125		35	0.28	—	—	54	0.43	—	140	19	40	15
	100		36	0.36	—	—	38	0.38	—	120	17	30	14
										100	18	20	13
										80	18	15	13
										60	17		
Paratype (m)	92	?	29	0.31	—	—	42	0.45	—	92	18	40	16
BM C73732										80	18	30	14
										70	17	20	14
										60	16	15	13
Topotype (m)	96.2		29.9	0.31	33.6	0.35	44.2	0.45	1.123	96	19	60	17
Etches Coll., K1711	70		20	0.28	—	—	35	0.5	—	80	18	50	16
	50		16	0.32	—	—	25	0.5	—	70	18	28	15
Photo <i>in situ</i> KFMP 06 (m)	100	?	36	0.36	—	—	43	0.43	—	100	19	60	15
										80	18	40	15
Photo <i>in situ</i> KFMP 05 (M)	230		70	0.3	—	—	110	0.47	—	230	23	130	19
	170		55	0.32	—	—	82	0.48	—	190	23	120	c 19
	150		45	0.30	—	—	77	0.51		170	23	100	c 18
										150	21		
Photo <i>in situ</i> KFMP 11/22/35 (M)	230	?	70	0.3	—	—	112	0.48	—	230	24	125	19
	195		50	0.25	—	—	100	0.51	—	195	23		20
	160		46	0.28	—	—	82	0.51	—	165	23		
Photo <i>in situ</i> KFMP 18 (M)	245	?	72	0.29	—	—	110	0.44	—	245	30		
	210		60	0.28	—	—	93	0.42	—	200	25		
	175		51	0.29	—	—	80	0.45	—	150	21		
	145		47	0.32	—	—	63	0.43	—	100	18		

Fontannes, in Sheppard, 1907, p. 277; Spath, 1925, p. 120), which was housed in Hull Museum and “lost by bombing during the last war” (Birkelund *et al.*, 1983, p. 302). The holotype is a complete adult specimen 305 mm in diameter with a flared, trumpet-like aperture preserved. The rib count increases uniformly during growth until 30 ribs per half a whorl on the final part of the body chamber. Specimen K 1365 is placed near Spath species solely on the evidence of the number of ribs. The rib-curve between 60 and 125 mm in diameter is exactly

the same as that of the type species at the same diameters (Fig. 21). Comparison is not possible beyond this as the inner whorls are not preserved in the type specimen.

Discussion: On the evidence of the number of ribs alone, *S. websteri* Oates, *non* Cope (Oates, 1991) seems to be close to *Subdichotomoceras cf. speetonense*.

Distribution: Kimmeridge Clay, Autissiodorensis Zone, Speeton, Yorkshire and, Kimmeridge, Dorset, Etches Collection (K 1365).

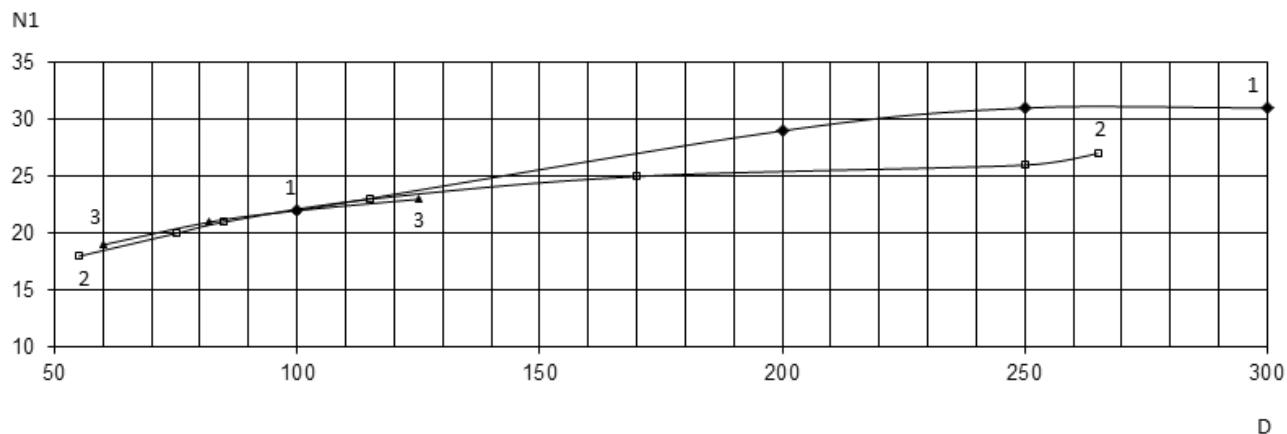


Fig. 21: Rib curves of *Subdichotomoceras speetonense* and cf. *speetonense* Spath. 1, Holotype, in Sheppard, 1907; 2, *S. "websteri"* (Cope), Oates, 1991; 3, Etches collection, K 1365.

Table 15: Measurements of *Subdichotomoceras speetonense* and cf. *speetonense* Spath (M). From Sheppard and Oates figures.

Name/n°	Dm/D	Ph	Wh	Wh/D	Wb	Wb/D	Ud	Ud/D	Wb/Wh	N1/1/2 whorl			
Coll. Etches, K 1365 (M)	125	?	33	0.26	—	—	65	0.52	—	125	23	60	19
Holotype (M) in Sheppard, 1907.	305	?	-	-	-	-	-	-	-	100	22	82	21
Hull Museum *										300	31	100	22
<i>S. "websteri"</i> Cope in Oates, 1991 *	288		80	0.27	—	—	160	0.55	—	265	27	85	21
										250	26	75	20
										170	25	55	18
										115	23		

Subdichotomoceras? praecursor sp. nov. (m)

Pl. XII, fig. 1; Pl. XIII, fig. 2; Text-fig. 22; Tab. 16

1917. *Perisphinctes* aff. *Crusoliensis* Fontannes.— Petitclerc, 1917, p. 48, pl. 6, figs. 16-17.

Holotype: The complete specimen figured in Pl. XIII, fig. 2. Caillet Collection, Lyon, FSL 175 917.

Locus typicus: Theuley-lès-Lavoncourt, Haute-Saône.

Stratum typicum: Labelled Séquanien; the matrix suggests that it is from the Calcaires Blançs Moyens Formation of Divisum-Mutabilis/Acanthicum Zone age.

Paratype: The specimen figured in Pl. XII, fig. 1, labelled Calcaires à Astartes, is probably from the Calcaires

Blancs Moyens Formation at Lavoncourt, Haute-Saône. Unknown collector, FSL 175 918.

Derivatio nominis: The name alludes to the possibility that the species is the earliest *Subdichotomoceras* and the only one described outside England.

Material: Two specimens (FSL 175917 and 175918) from geographically close localities at Theuley-lès-Lavoncourt and Lavoncourt, Haute-Saône. The more complete specimen (FSL 175917), in the Caillet Collection, is a plastic cast made from the external mould of a small, probably nearly complete individual. It matches the illustration by Petitclerc of the internal cast of an immature *Perisphinctes* aff. *crusoliensis* Fontannes (Petitclerc, 1917, p. 49-50, pl. 6, figs. 16-17) so closely

N1

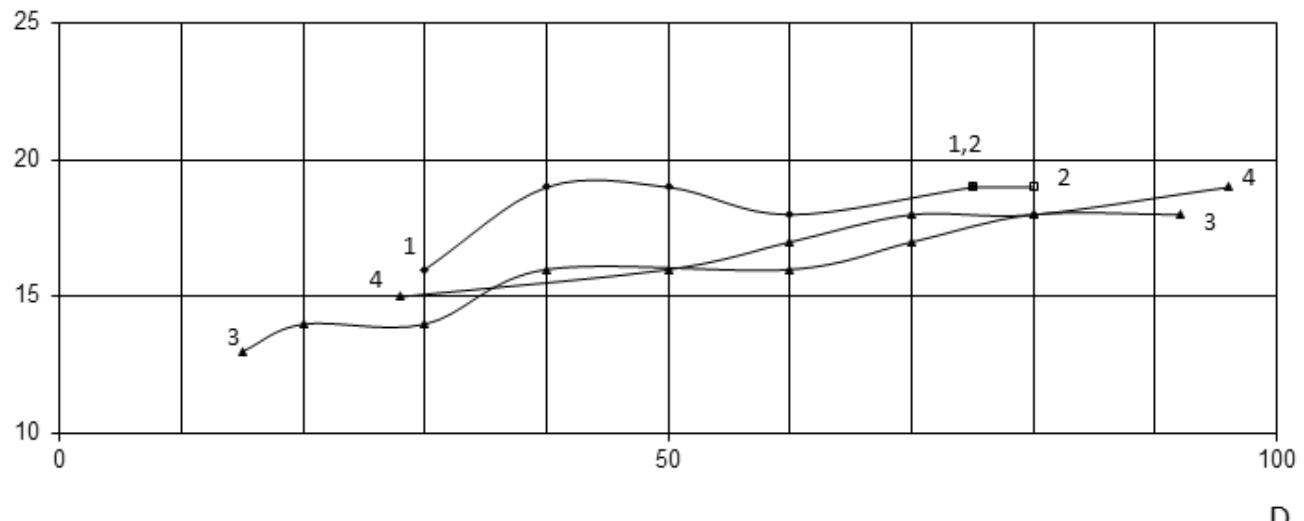


Fig. 22: Rib curves of *?Subdichotomoceras praecursor* n. sp. 1, Holotype, Caillet collection, FSL 175917; 2, Paratype, FSL 175918. *S. websteri* (Cope) for comparison, 3, Paratype, Cope collection, BM 73732; 4, Etches collection, K 1711.

Table 16: Measurements of *Subdichotomoceras praecursor* n. sp. (m).

* From the E/H value (0,29) given by Petitclerc (1916, p. 49, specimen 1)

Name/n°	Dm/D	Ph	Wh	Wh/D	Wb	Wb/D	Ud	Ud/D	Wb/Wh	N1/1/2 whorl	
Holotype (m), Theuley-lès-Lavoncourt, Haute-Saône Caillet Coll., FSL 175917	75 55	?	20 17	0.26 0.30	22* 0	0,29* 0	40 35	0.53 0.63	1,10* 0	75 60 50 40	19 18 19 19
Paratype (m) Lavoncourt, Haute-Saône ? Caillet Coll., FSL 175918	82 75	?	21 20.4	0.25 0.27	20 19	0.24 0.25	43 39.8	0.52 0.53	0.95 0.93	82 75	18 18

that there is no doubt that it is the same specimen. The label was recently discovered in the Paris 6 University collection, but not the specimen even though other specimens figured in Petitclerc, 1917 pl. 7, fig. 2, as *Perisphinctes* aff. *crusoliensis* Fontannes and pl. 8, fig. 1 as *Holcostephanus* (*Perisphinctes*) *trifurcatus* Rein. (= *Aulacostephanus quenstedti* Durand in Ziegler, 1962, p. 129, pl. 20, fig. 4) were found.

A second example (FSL 175 918) of the same species which reached about the same growth stage consists of a little more than half a whorl of a body chamber without any inner whorls.

Description: The holotype shows a fairly evolute coiling, very convex whorl sides, and a rounded umbilical margin

on the inner whorls which is better defined on the last quarter of a whorl. The ribs are close, prorsiradiate and prominent to sharp. They bifurcate uniformly with the branching points barely visible in the umbilicus except where they are related to what appears to be a constriction. Two constrictions are clearly visible on the last quarter whorl of the holotype and the paratype where they are followed by a simple rib and accompanied forward by either a simple rib or a related bifurcate rib. Scarce intercalatory ribs give rise to pseudoschizotomous trifurcations that appear as false polygyrate branches. The secondary ribs cross the ventral area without changes in direction or smoothing.

The view of the venter illustrated by Petitclerc (1917,

pl. 6, fig. 17) agrees with his published Wh/D value (= 0, 29) from which are deduced the values of Wh = 21, 75 mm and Wb/Wh = 1,08. The cross section is slightly depressed, at least on the last quarter of the whorl. It is almost circular and compressed, slightly higher than thick in the paratype, but a weak oblique distortion of the internal mould means it was partially crushed. The shape of the whorl section cannot be determined from the Caillet external cast.

Discussion: Many of the features of the two specimens, including the adult whorl shape and the ribbing style are so similar to those of *Subdichotomoceras* that Petitclerc (1917) identification of the holotype as an immature *Crussoliceras* is not adopted here. The rib-curves (Fig. 22) are in close agreement with those of *S. websteri* (e.g. the solid preservation K 1711) and the crushed BM C. 73732 (Fig. 21).

Distribution: At the present time *S.? praecursor* is only known from two specimens from the Haute-Saône region whose age is not well constrained. Both were probably from the Calcaires Blancs Moyens which ranges from Divisum Zone to Acanthicum/Mutabilis Zone in age. Theuley-lès-Lavoncourt, Haute-Saône, Caillet Collection (Lyon FSL 175917). Lavoncourt, Haute-Saône (FSL 175918).

Genus *Tolvericeras* Hantzpergue, 1989

Type-species: *Tolvericeras tolverense* Hantzpergue, 1989, p. 148-156, fig. 33, 34; tab. 2; pl. 10, fig. a-e; pl. 11, fig. a.

Hantzpergue (1989) recognised five species and one subspecies divided into two subgenera, *Tolvericeras* and *Pseudogravesia*. The species of *Tolvericeras* s. s. occur in chronological order from the Mutabilis Zone to the Autissiodorensis Zone and those of *Pseudogravesia* in the earliest Tithonian (Gigas Zone). *Tolvericeras* was largely confined to the Western European Swell where the environmental conditions were markedly different from those of the open-sea environments in Kimmeridgian times. The geographical extent of the individual species is patchy, which may in part be due to the occurrence of local species and in part to a lateral impersistence of some horizons. Hantzpergue noted (1989, p. 353-354) that the relationships and biochrons of the five species were at that time unknown and that the proposed evolutionary interpretation was provisional. Hence, the genus *Tolvericeras* can be understood in two different ways.

First, the genus can be based on the type species *T. (T.) tolverense*, which is represented by 41 specimens [19(M) and 22(m)] from a single bed (the Desmonotus Horizon) at one locality in the Mutabilis Zone (Mutabilis Subzone). This assemblage was initially identified as *Katroliceras* (*Crussoliceras*) *atavum* (Schneid), *K. (C.) gr. atavum* (Schneid), *K. (C.) acer* (Neumayr) and *Garnierisphinctes*

sp. (Hantzpergue, 1979). The same specimens were subsequently (Hantzpergue, 1987, 1989) interpreted as the population of a single species with a wide variability, not all of which has been illustrated. The similarity of *Tolvericeras* to the *Crussoliceras-Garnierisphinctes* group was interpreted by Hantzpergue (1987, 1989, p. 148) as an example of homeomorphism. The principal difference between these genera being that the bifurcation points in the *Crussoliceras-Garnierisphinctes* group occur on the upper third of the whorl side whereas those in *Tolvericeras* are less well defined and occur at mid-whorl height.

Except one all specimens of *T. (T.) tolverense* are too crushed for the thickness and E/D ratios to be determined. The whorl section, based on a single specimen, is initially subquadrate but soon becomes oval and compressed with a narrow, rounded ventral area (Hantzpergue, 1989, p. 153). None of the figured specimens of the type species, including the holotype and paratypes, clearly show the final stage described by Hantzpergue (1989, p. 154) as "being made of massive and cuneiform primary ribs" and "occurring often on a whole whorl long" (ibid., p. 157). The species ascribed to *Tolvericeras* were interpreted (Hantzpergue, 1987, 1989) as forming a '*Tolvericeras* lineage' from the oldest, *T. tolverense* to the youngest *T. murogense*. However, the thick, depressed whorl section of *T. murogense* distinguishes it from the type-species of *Tolvericeras* and links it to the later species of the subgenus *Pseudogravesia*. There is, therefore, a morphological break between *T. tolverense* and "*T.* *murogense*" (now shown as *P. murogensis* in Fig. 3). This break is emphasized by the *Subdichotomoceras*-like morphology of the microconch of *T. murogense*, which is markedly different from that of the microconch of *T. tolverense* Hantzpergue [pl. 10, fig. e only, not the "microconch of small size" (pl. 10, fig. d) which is probably a juvenile macroconch].

T. murogense occupies a position within the *Tolvericeras-Gravesia* lineage just before the earliest *T. (Pseudogravesia)* and its *Gravesia* off-shoot. Hantzpergue (1989, fig. 127) filled the morphological break and the biochron gap between *T. tolverense* and *T. murogense* with '*T.* *sevogodense*', even though the differences with *T. tolverense* are well defined (Hantzpergue, 1989, p. 157). The species "*T.* *sevogodense*" is interpreted here, as it was by Énay (1959, 1985), as a *Crussoliceras* macroconch (see above where it is described under *Crussoliceras*). The specimen (ENSG, no collection number) in the Durand Collection referred to here as *C. cf. aceroides* Geyer has more evolved features than those of Geyer (1961) *C. aceroides* and could be transitional to *C. sevogodense*. This interpretation breaks the *Tolvericeras* lineage and limits the nominal genus to the type-species and new species described by Gygi (2003) and in this account (see below). '*T.* *murogense*' is included here in *Pseudogravesia* which becomes a full genus.

Two unusual specimens are relevant to the discussion

of *Garnierisphinctes*. One figured by Gygi (2003, figs. 165, 166) as *Tolvericeras* sp., having a compressed oval whorl section ($Wb/Wh = 0.87$ at $D = 132$ mm). The other one, from Châteuneuf-d'Oze, Hautes-Alpes in the Atrops Collection (FSL 188841; Pl. IV, fig. 1), was initially assigned to *Progeronia* and subsequently to *Garnierisphinctes*. Both specimens are of Divisum Zone age and older than the oldest *Tolvericeras* (*Mutabilis/Acanthicum* Zone) described by Hantzpergue (1987, 1989). Both are morphologically similar to the holotype of *T. toloverense*.

Within the studied material, some specimens from the Eudoxus Zone have morphologies that are more similar to that of *T. toloverense* than to the other members of the *Tolvericeras-Gravesia* lineage. The first (ENSG, Pl. XVI, fig. 2) is from the Marnes à Exogyres at Bar-le-Duc area, the second (Etches Collection, K 321, Pl. XVI, fig. 1) from the Kimmeridge Clay at Westbury, Wiltshire and the third (SM J 61311, Pl. XIV, fig. 1) is from the Kimmeridge Clay at Ely. This raises again the question of the origin of *Tolvericeras*.

It is assumed here that some of the new species of *Tolvericeras* described below could have been derived from *Garnierisphinctes* rather than from *Progeronia*, and others derived from *Crussoliceras*. The *Subdichotomoceras*-like morphology of the microconch of *T. murogense* suggests that some species of *Tolvericeras*, including *T. murogense* and those of the subgenus *Pseudogravesia*, were derived from *Crussoliceras*.

Forms with a compressed whorl-section, including *T. popeyense*, *T. anglicum* and *?T. robertianum*, form a homogeneous group that is in accord with the type species of *Tolvericeras* and *Tolvericeras* sp. Gygi (2003, figs. 165, 166). These are forms that could have originated from a *Garnierisphinctes* which is morphologically similar to the specimen figured in Pl. XIV, fig. 1. They could also be related to the Tithonian genus *Hegovisphinctes* (Zeiss *et al.*, 1996) except for its larger size ($D_m = 380$ mm) which may also be a descendant of *Tolvericeras*.

Tolvericeras robertianum sp. nov. (M)

Pl. XV; Text-fig. 23; Tab. 17

Holotype: Specimen SM J 61311 figured Pl. XV, fig. 1.

Locus typicus: Roslyn Hole [TF 555 808], Ely, Cambridgeshire.

Stratum typicum: Kimmeridge Clay, Bed 3 in Roberts (1892), Eudoxus Zone (Chronosubzone KC 30).

Derivatio nominis: The species is devoted to T. Roberts who published a survey of the Jurassic rocks of the Cambridge region and made a large collection of ammonites from the area.

Material: Specimen SM J 61311 labelled *Perisphinctes* sp.; one side visible, the other embedded in a grey mudstone.

Description: A large ($D = 255$ mm) probably an adult specimen with the end of the septate whorls at about $D = 170$ - 175 mm and about half a whorl of body chamber. The coiling and the whorl height growth are slow, and the umbilicus is wide and shallow. The whorl sides are flat or barely rounded, the umbilical margin is almost absent, and the whorl section higher than thick and is compressed. The ornamentation is developed in three stages. The initial stage displays relatively numerous rectiradiate primary ribs that probably bifurcate, but the branching points are not visible in the umbilicus. The intermediate stage occurs a little before the beginning of the last whorl where trifurcate branching points give rise to 'false polygyrate' ribbing. This initially alternates with bifurcate ribs, and then continues along with a progressive strengthening of the primary and secondary ribs. The final stage is not well exposed partly because of the poor preservation and probably also because the shell is incomplete.

Discussion: The new species is distinguished from the type species of *Tolvericeras* by the more evolute coiling, wider umbilicus, branching high on the whorl side, and a constant rib density of 15 and 20 ribs per half a whorl in which the initial and final stages are similar with a higher number of primary ribs on the middle whorls (Fig. 23). The morphology of *T. robertianum* n. sp. suggests that it is a possible transitional form between *Garnierisphinctes* and *Tolvericeras*.

Distribution: Kimmeridge Clay, Eudoxus Zone, Chronosubzone KC 30, Ely, Cambridgeshire. Roberts Collection (SM J 61311).

Tolvericeras popeyense sp. nov. (M)

Pl. XVI, fig. 2; Text-fig. 23; Tab. 18

Holotype: The single specimen figured Pl. XVI, fig. 2.

Locus typicus: Railway cutting near the farm of Popey (Bar-le-Duc, x: 809,350, y: 121,300), south-east of Bar-le-Duc, Meuse.

Stratum typicum: The provenance of the specimen (ENSG, no collection number) is from the Calcaires Supérieurs (Marnes à Exogyres Formation) at Popey (J. Le Roux, pers. comm.), Eudoxus Zone.

Derivatio nominis: Latinized name derived from Popey.

Material: Half an adult specimen in which the body chamber is preserved on a little less than half a whorl, without the aperture.

Description: The holotype is incomplete but well preserved with successive whorls available for study from about $D = 20$ mm up to the fifth whorl. From the innermost whorl onwards the whorl section is compressed, higher than thick, the umbilical margin rounded and the umbilical wall vertical, and the whorl side slightly rounded. The ribbing is initially rectiradiate to fairly prorsiradiate primary and is probably bifurcate in the initial stage. The branching points are not visible in the umbilicus or the first three half whorls. The fourth whorl bears stronger and more distant ribs with the branching

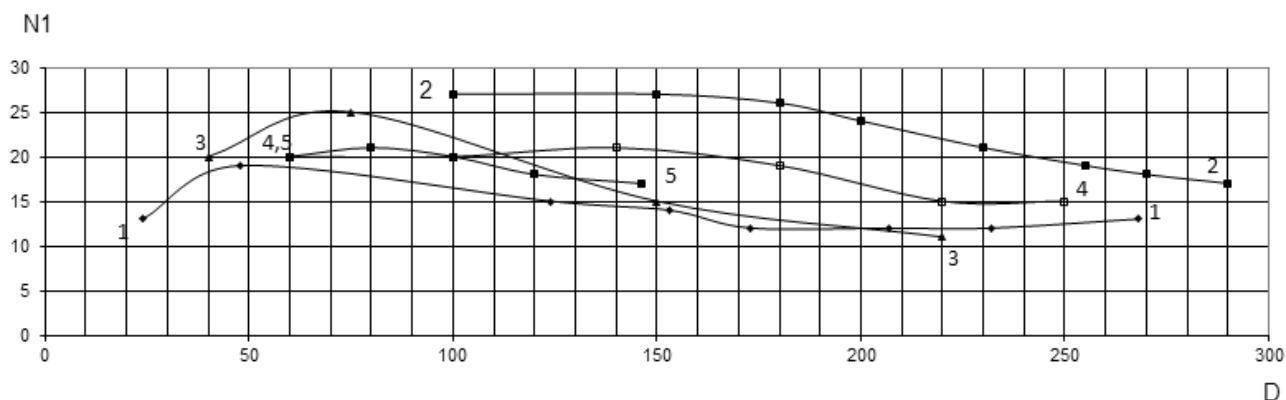


Fig. 23: Rib curves of some species of *Tolvericeras*. 1, *T. toloverense* Hantzpergue, Holotype (M), Hantzpergue collection, Poitiers, 40310; 2, *T. anglicum* n. sp., Holotype (M), Etches collection K 321; 3, *T. popeyense* n. sp., Holotype (M), ENSG Nancy; 4, *T. robertianum* n. sp., Holotype (M), Sedgwick Museum J. 61311; 5, *Tolvericeras* n. sp., Gygi, 2003, fig. 165.

Table 17: Measurements of *Tolvericeras robertianum* n. sp. (M)

Name/n°	Dm/D	Ph	Wh	Wh/D	Wb	Wb/D	Ud	Ud/D	Wb/Wh	N1/1/2 whorl		
Holotype (M), Roberts Coll.	255	170	75	0.29	—	—	135	0.52	—	250	15	140 21
Sedgwick Museum J 61311	200		53	0.26	—	—	104	0.52	—	220	15	100 20
	155		46	0.29	—	—	78	0.5	—	180	19	60 20

Table 18: Measurements of *Tolvericeras popeyense* n. sp. (M)

Name/n°	Dm/D	Ph	Wh	Wh/D	Wb	Wb/D	Ud	Ud/D	Wb/Wh	N1/1/2 whorl		
Holotype (M)	145	?	60		48				0.8	220	c 10	80 25
Popey, Bar-le-Duc, Meuse			46	0.31	39	0.26	65	0.44	0.84	150	15	45 20
ENSG Nancy (MAN)												

Table 19: Measurements of *Tolvericeras anglicum* n. sp. (M)

Name/n°	Dm/D	Ph	Wh	Wh/D	Wb	Wb/D	Ud	Ud/D	Wb/Wh	N1/1/2 whorl		
Holotype (M)	290	?								290	17	200 24
Kimmeridge, Dorset	287		81	0.27	—	—	152	0.53	—	270	18	180 26
Etches Coll. K321.										255	19	150 27
										230	21	100 27

points not visible until a constriction on the last quarter whorl. The middle stage is characterized by branching lower on the whorl side with the view of trifurcate bundles of polygyrate ribbing well displayed on the end of the penultimate whorl. The last half whorl corresponds to the final stage and bears strong rectiradiate ribs. The

first of these shows the same prominence throughout the whorl height. This is followed by two ribs that are flared at the distal end and cuneiform-shaped with no sign of secondary ribs. The apparent approximation of the last two prominent last ribs appears to be just before where the aperture would have been.

Discussion: The principal morphological characters of *T. popeyense* are closely similar to those of *Tolvericeras*, especially those of the type species with the exception that the terminal stage is more developed than in the holotype of the type species of *Tolvericeras*. At the diameter corresponding to that of the septate whorls of *T. popeyense*, the nearest similar form is a specimen described by Gygi (2003, p. 144, fig. 165) as *Tolvericeras* sp. The final stage of *T. popeyense* has strong swollen ribs that are absent in the Gygi (2003) specimen which preserves a whorl-long body chamber. In addition, the Gygi specimen came from the Badener Schichten Formation (Divisum Zone) of markedly different age from that of *T. popeyense*.

Distribution: The stratigraphical level of the single specimen *T. popeyense* from Popey, Meuse is poorly known. It is thought to have been collected from the Marnes à Exogyre Formation of Eudoxus Zone age.

***Tolvericeras?* *anglicum* sp. nov. (M)**

Pl. XVI, fig. 1; Text-fig. 23; Tab. 19

Holotype: The complete specimen figured in Pl. XVI, fig. 1.

Locus typicus: Westbury Cement Works [ST 882 528], Wiltshire.

Stratum typicum: Kimmeridge Clay, Eudoxus Zone, Chronosubzone KC 30 (*Propectinatites?* Bed, Cox & Gallois, 1981 = *Crussoliceras* Bed, Birkelund *et al.*, 1983), Etches Collection K 321.

Derivatio nominis: Latinized name derived from Anglia (England).

Material: A single specimen in solid preservation with the nacreous inner layer of the shell preserved; only one side visible, the opposite side embedded in a calcareous nodule.

Description: The holotype is a large ($D = 290$ mm), complete adult with the aperture and the body chamber preserved. The general shape is discoidal, the coiling fairly evolute, the whorl height increasing rapidly, and the umbilicus wide and relatively shallow. The whorls are high and thick, the whorl section quadratic and probably depressed, but width measurements are not possible because of the incomplete preservation. The umbilical margin is rounded and sloping and not prominent, and the ventral area fairly rounded. The ribbing comprises numerous and close primaries, bow-shaped and slightly proverse. The branching points are not visible on the initial stage where they are assumed to bifurcate. The branching points begin to be obvious on the penultimate whorl where bifurcations alternate with pseudoschizotomous trifurcate ribs on the middle stage. The rib strength and spacing increases progressively, the secondary ribs being irregularly visible except on the last quarter whorl which bears strong primary ribs and pseudoschizotomous bundles of secondary ribs. The rib-curve shows a high rib number at all diameters,

more than 25 ribs per half whorl until $d = 180$ mm, then decreasing regularly but never to less than 15b ribs per half whorl on the last whorl (Fig. 23). The aperture is simple, the margin bow-shaped as in the preceding ribs, and the peristome margin thickened.

Discussion: The general shape and coiling of *T. anglicus* sp. nov. are similar to that of the type species of *Tolvericeras*. It is distinguished from other species of the genus by its rib density and branching points high on the flank.

Distribution: Kimmeridge Clay, Eudoxus Zone (Chronosubzone KC 30), Westbury Cement Works, Wiltshire.

Genus *Pseudogravesia* Hantzpergue, 1987

Type species: *Tolvericeras (Pseudogravesia) hahni* Hantzpergue, 1987 (= *Gravesia polypleura* Hahn, 1963, pl. 2, fig. 2 and 3); Hantzpergue, 1987, p. 191, pl. 13, fig. a; Hantzpergue, 1989, p. 166, pl. 13, fig. a.

Described as a subgenus of *Tolvericeras* by Hantzpergue (1987), *Pseudogravesia* is here considered as a genus. The reasons of this change, which are elaborated in the discussion of *Tolvericeras*, are the *Subdichotomoceras*-like microconch *vs* the *Progeronia*-like microconch of *Tolvericeras* and the thick depressed whorl section *vs.* the compressed oval whorl section of *Tolvericeras*. As a genus, *Pseudogravesia* comprises a lineage of three successive species that evolved during the Late Kimmeridgian (*P. murogensis*) and the Early Tithonian (*P. hahni* and *P. gravesiformis*). The older, *P. murogensis*, is separated from the other two by an absence of specimens from the uppermost Kimmeridgian (upper part of the Irius Subzone). The geographical extent of the genus is mainly limited to the Western Europe Swell. The two specimens from southern England that are described below as undetermined species of *Pseudogravesia* are therefore of particular interest.

***Pseudogravesia* indet. nov. sp.? (m + M ?)**

Pl. XVII, figs. 1, 2a, b

- 2010. *Gravesia* sp., possible microconch, Gallois & Etches, p. 245, 247, fig. 7d.
- 2010. *Gravesia* sp., microconch, Gallois & Etches, p. 245, 247, fig. 7e.

Material: Two specimens in Etches Collection from Brandy Bay (K 1581) and Kimmeridge Bay (K 1757), Dorset, previously published as “Early undescribed form of *Gravesia*, possible microconch” or “Possible Early form of *Gravesia*, microconch” (Gallois & Etches, 2010, p. 245, 247, fig. 7d, e). They are crushed and more or less distorted, the former more than the latter. Specimen K 1757 is a complete adult microconch with the aperture preserved. The stage of growth reached by

specimen K 1581 is unknown, but it is suggested here that it is the inner whorls of a larger individual, possibly a macroconch. Autissiodorensis Zone, Chronosubzone KC 34.

Description: The two specimens are described separately with the common features highlighted in the discussion. Owing to the crushing, the descriptions deal only with the coiling and ribbing features.

The microconch K 1757 is complete and fully grown: the final part of the last whorl (and the living chamber) show strong single ribs. The coiling is fairly evolute, the whorl height increasing slowly. The ribbing comprises radiate coarse and strong primaries. These probably bifurcate on the inner whorls given that they are present on the last whorl as soon as it begins. The branching points are a little higher than mid-whorl until the last quarter whorl where gerontic ornamentation begins. The lappet is short and rounded at about mid-side.

Specimen K 1581 shows a faster increase of the whorl height, but this may be the result of crushing. When a spherical distortion is applied to the image to remove some of the effects of crushing, the increase in whorl height and coiling is slower, but this may not be a true representation of the undistorted shape. The ribbing remains unchanged as soon the ribs become obvious (as far as 20/30 mm). It is made up of radiate coarse and strong bifurcate primaries, with some single ribs occurring occasionally. The branching points are not obvious on the inner whorls, and are thus probably high, but a little lower than the whorl mid-side on the last preserved whorl.

Discussion: The suggestion by Gallois & Etches (2010) that K 1581 and K 1757 might be “the oldest recorded *Gravesia*” was based on general morphology not on any additional supporting evidence. The corresponding beds have to date only yielded *Aulacostephanus* and *Subdichotomoceras*. K 1757 looks similar to some *Crussoliceras* microconchs except for the rib number of the inner whorls which is lower and closer to that of some *Subdichotomoceras*. The rib-curves of both specimens are similar, the rib numbers increasing to about 13-15 ribs per half whorl at a diameter of about 70-80 mm, then decreasing to 12 ribs per half whorl. Thus, neither K 1581 nor K 1757 can be determined as

Subdichotomoceras because all the described species and subspecies of that genus exhibit a regular increase in rib density. When compared with the rib-curves of the genera and species described in this account, the rib-curves of K1581 and K1757 are in closest agreement with those of “*Tolvericeras*” *murogense* which is here referred to the genus *Pseudogravesia*.

The microconch specimen K 1757 differs from the species of Hantzpergue in its larger size and an unusual last quarter whorl that is similar to some *Crussoliceras*. All the small number of known *Subdichotomoceras*-like microconchs of *P. murogense* are incomplete and the adult morphology unknown. K 1757 is, therefore, best described as *Pseudogravesia* n. sp. ind. The same is true for K 1581 which has a similar rib-curve and whose spherically distorted image looks very near to the inner whorls of the macroconch of *P. murogense* in Hantzpergue (1989, pl. 12, fig. a).

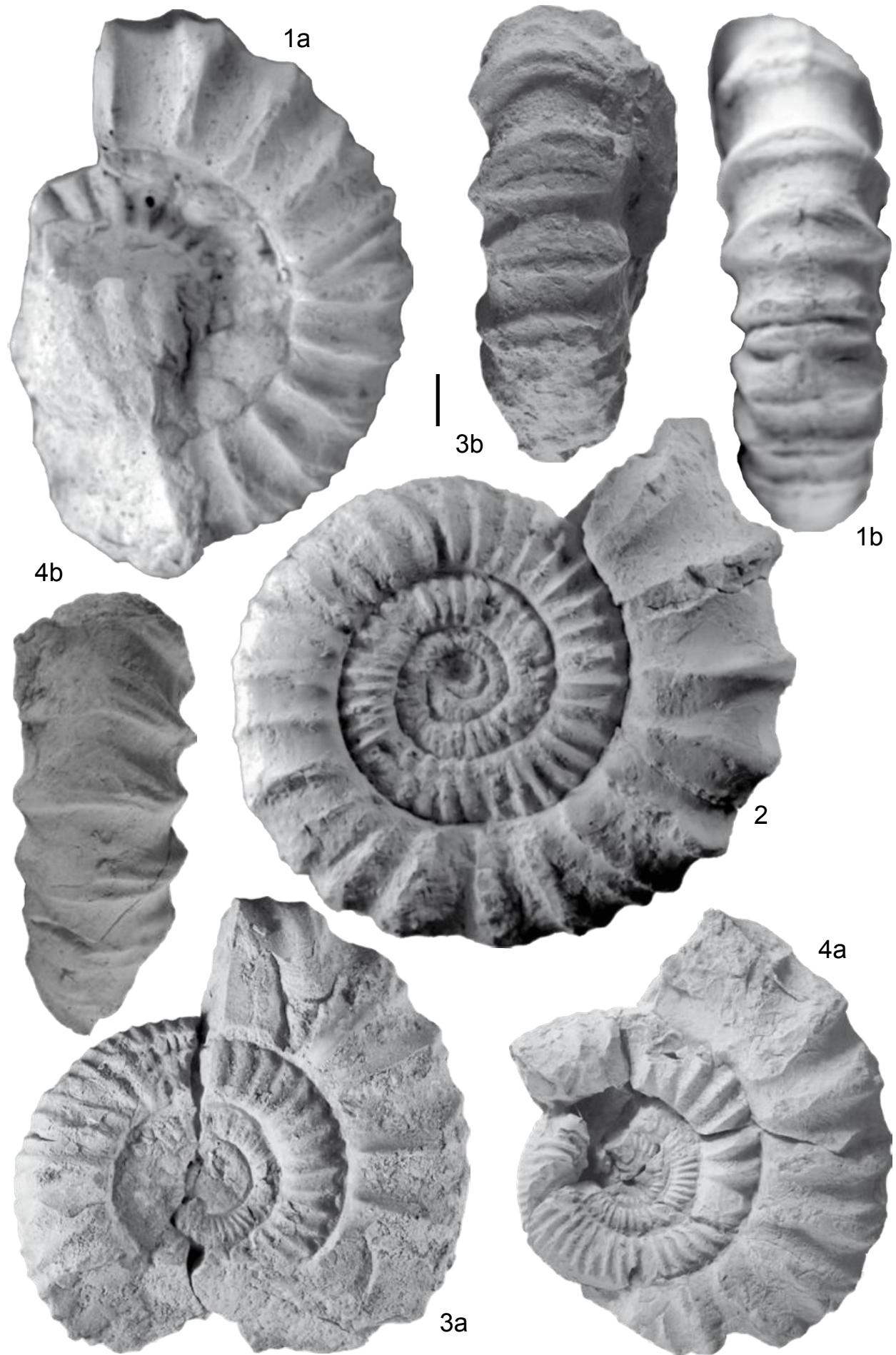
Distribution: Kimmeridge Clay, Autissiodorensis Zone, Chronosubzone KC 34, Brandy Bay and Kimmeridge Bay, Dorset.

5. ORIGIN OF THE SUBBOREAL PERISPINCTIDS

Kimmeridgian perispinctid faunas from England and France have been studied to clarify the relationships between those of the Subboreal Province, whose forerunners have not been recognised in that province, and their possible ancestors in the Submediterranean Province. Almost all the specimens from the English Kimmeridge Clay are preserved as crushed impressions, but their positions are accurately located within a well-defined stratigraphical succession. In contrast, most of the material from France comprises uncrushed museum specimens whose stratigraphical relationships are uncertain. From Late Oxfordian times onward central France was occupied by the Western European Swell, a shallow water area with laterally more variable environments that stretched from Aquitaine to Poland, which acted as a transitional faunal region between the Subboreal and Submediterranean Provinces.

Plate I

- Fig. 1 a, b: *Crussoliceras crusoliense* (Font.) holotype of “*Badenia*” *wegelei* Enay, 1959 (= *Perispinctes acerrimus* Wegele, non Siemiradzki, 1891; Wegele, 1929, p. 62, pl. 5, fig. 4); microconch. 1a, lateral view and 1b, ventral view. Photos R. Énay.
- Fig. 2: *Crussoliceras crusoliense* (Font.). Microconch, nearly complete adult specimen; lateral view. Early Kimmeridgian, Divisum Zone; Mount Crussol, Ardèche; Boselli Collection. Photo R. Énay.
- Fig. 3a, b: *Crussoliceras crusoliense* (Font.). Microconch, adult incomplete specimen; 3a, lateral view and 3b, ventral view. Early Kimmeridgian, Divisum Zone; Mount Crussol, Ardèche; Martin Collection, FSL 35110. Photos R. Énay.
- Fig. 4a, b: *Crussoliceras crusoliense* (Font.). Microconch, adult incomplete specimen; 4a, lateral view and 4b, ventral view. Early Kimmeridgian, Divisum Zone; Mount Crussol, Ardèche; Martin Collection, FSL 35114. Photos R. Énay.
- Scale bar represents 10 mm.



5.1. Distribution of the Kimmeridgian perisphinctid

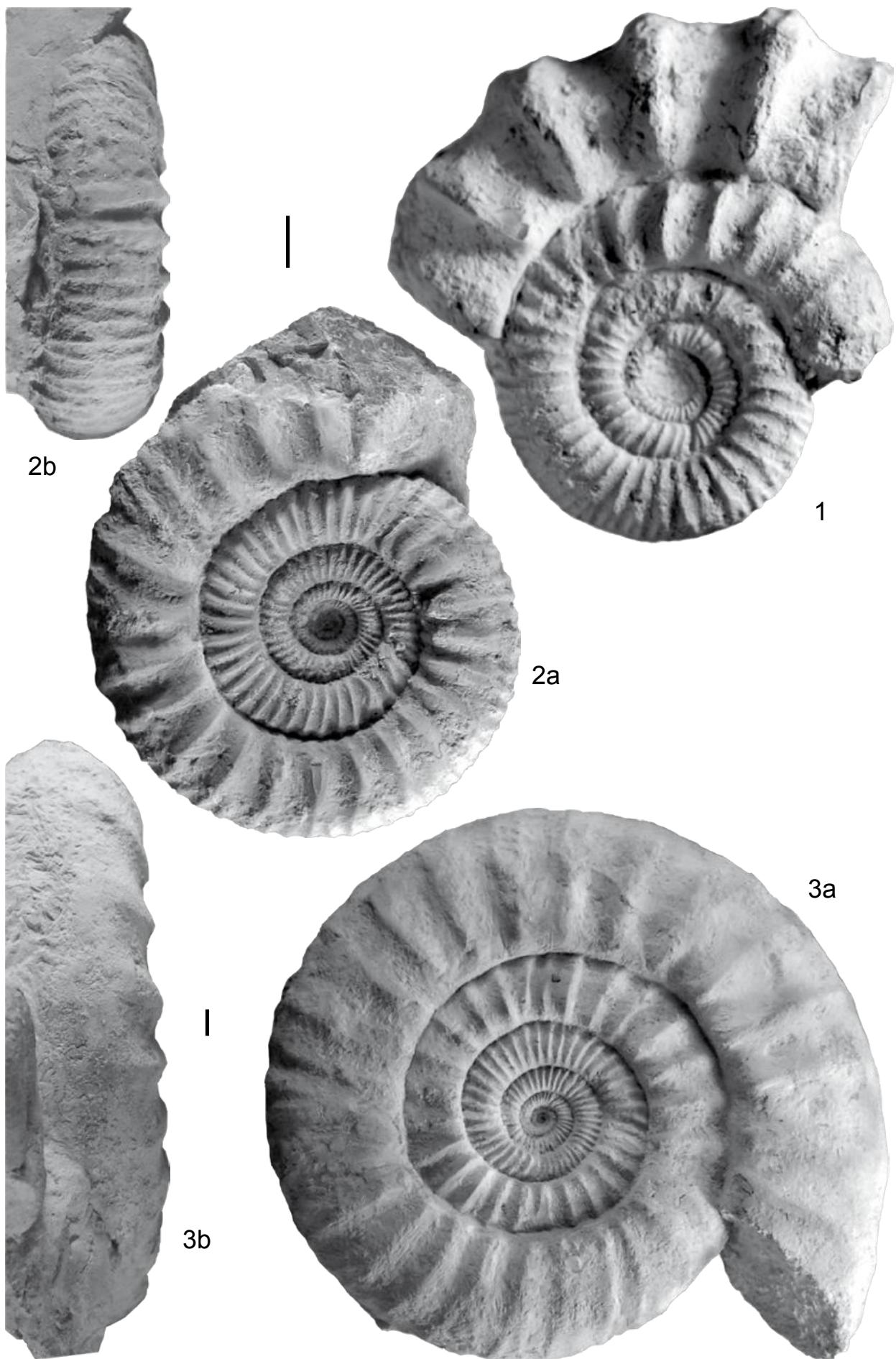
The perisphinctids recorded to date from the English and northern French Kimmeridgian can be grouped into six genera. These are, in ascending and overlapping stratigraphical order, *Garnierisphinctes*, *Crussoliceras*, *Tolvericeras*, *Pseudogravesia*, *Subdichotomoceras* and *Gravesia*. The stratigraphical and geographical distributions of the first five of these are described in the present work and their relationships discussed. *Gravesia*, which is only present in the youngest part of the Kimmeridgian and in the overlying Tithonian, did not form part of the present study. The perisphinctid faunas of the Western European Swell are represented by *Crussoliceras*, *Tolvericeras* and *Pseudogravesia*. Specimens from the eastern and southern parts of the Paris Basin, the French Jura and Haute-Saône and the Côte d'Or have been examined and revised. *Subdichotomoceras* is revised on the basis of museum specimens and new material from the Kimmeridge Clay.

The ammonite assemblages in the areas studied include forms with Subboreal and Submediterranean affinities. *Crussoliceras* is a Submediterranean genus that has been recorded at numerous stratigraphical levels in the Western European Swell area and at a few in the Subboreal Province. In the Divisum Zone, *Crussoliceras* was the only Submediterranean genus to have colonised the shallow platform environments of the Western European Swell. In the deeper-water environments of the Subalpine ranges, the Cévennes and the southeastern (French) Jura, *Crussoliceras* occurs with representatives of the Oppeliidae and Aspidoceratidae. When traced northwards and westwards into the swell area only the perisphinctids, particularly the *C. crusoliense* group, and aspidoceratids remain. In the Tethyan region, *Garnierisphinctes* ranges from the Hypselocyclum to Divisum Zones and *Crussoliceras* from the Hypselocyclum to Acanthicum and Eudoxus Zones. A pronounced decrease in abundance of *Crussoliceras* in the Acanthicum Zone coincides with a major change in the ammonite assemblages to one with an abundance of the typically Tethyan taxa *Nebrodites*, *Taramelliceras* and *Aspidoceras*. The characterization

of *Crussoliceras* is revised based on specimens from the type-locality of the type species at Mount Crussol (Ardèche), the Cévennes and the French Jura. The genus has been shown to be dimorphic. The microconchiate form is typified by the holotype of the type-species *C. crusoliense*. The macroconch dimorph is described and illustrated here for the first time. *Crussoliceras* has been recorded in thin (0.1 m thick) ammonite-rich marker beds, one in the Mutabilis Zone and one in the Eudoxus Zone, in the Kimmeridge Clay. The younger of these contains *C. sevogodense*. The geographical distribution and variety of forms of *Tolvericeras* and *Pseudogravesia* suggest that they were also indigenous genera of the Western Europe Swell that migrated from time to time into the adjacent provinces. *Tolvericeras* spp. and *Pseudogravesia* have been recorded from the Eudoxus Zone and Autissiodorensis Zone respectively in England, and *Tolvericeras* from the Autissiodorensis Zone on the Boulonnais coast (Geyssant *et al.*, 1993). *Subdichotomoceras* is a Subboreal form that is common (albeit poorly preserved) at some stratigraphical levels in the upper Eudoxus Zone in the Kimmeridge Clay, and is abundant at some levels in the Autissiodorensis Zone throughout the English outcrop and subcrop of the formation. *S. lamplughi*, *S. speetonensis* and *S. websteri* have to date only been recorded from the Autissiodorensis Zone. Two subspecies, *S. lamplughi lamplughi* and *S. lamplughi dorsetense*, have been recognized in the present study. Both are known from only a few specimens, *S. lamplughi lamplughi* from Yorkshire and *S. lamplughi dorsetense* from Dorset, so their geographical distribution is poorly understood. The genus has not been recorded from the Kimmeridgian outcrops of the Boulonnais coast, but this is probably due to a combination of collection failure and poor exposure at the relevant stratigraphical levels. If the assumed generic determination is correct, *S.? praecursor* n. sp. from the Haute-Saône (Early or Early Late Kimmeridgian, precise age not known) is the only species recorded from the Western European Swell.

Plate II

- Fig. 1: *Crussoliceras crusoliense* (Font.). Holotype, microconch, adult but incomplete specimen; lateral view. Early Kimmeridgian, Divisum Zone; Mount Crussol, Ardèche; Huguenin Collection, FSL 12631. Photos R. Énay.
- Fig. 2a, b: *Crussoliceras crusoliense* (Font.). Microconch, inner whorls with more regular ribbing than it is in the holotype; 2a, lateral view and 2b, ventral view. Early Kimmeridgian, Divisum Zone; Mount Crussol, Ardèche; Boselli Collection. Photos R. Énay.
- Fig. 3a, b: *Crussoliceras crusoliense* (Font.). Macroconch, adult complete specimen but without the aperture and the ribbing a little worn; 3a, lateral view and 3b, ventral view. Early Kimmeridgian, Divisum Zone; Mount Crussol, Ardèche; Boselli Collection. Photos R. Énay.
- Scale bars represent 10 mm.



5.2. Origin of the Subboreal perisphinctids

The present work has shown that the Subboreal perisphinctid faunas are the result of an evolutionary process that was related to the development of the Western Europe Swell in the Early Kimmeridgian. Énay (1985) suggested that the probable origin of the Subboreal dorsoplanitids was to be found in the Submediterranean perisphinctids, in particular via the genus *Crussoliceras*. This has been confirmed by the present work, but an alternative evolutionary path via *Tolvericeras* (Hantzpergue, 1989) has not been confirmed. In the present study *Tolvericeras* is restricted to the type species *T. tolverense*, and some new species including *Tolvericeras* sp. (Gygi, 2003), *T. popeyense*, *T. anglicum* and *T. robertianum* which are presumed here to be derived from *Garnierisphinctes* from the uppermost Divisum Zone. '*T.*' *murogense* is now considered to be the first known species of the *Pseudogravesia-Gravesia* lineage which, based on the *Subdichotomoceras*-like morphologies of the microconchs, is assumed to be a separate off-shoot from *Crussoliceras*.

The principal reason for suggesting that the Kimmeridgian Subboreal perisphinctids were originated from Submediterranean migrants is that there are no known earlier Subboreal forms. The last representatives of the Pictoniinae and Aulacostephaninae, which have evolved from Submediterranean forms in the Oxfordian, were too differentiated and specialized to give rise to the succeeding perisphinctids. However, no form has been recorded that might be transitional between the Kimmeridgian Submediterranean and Subboreal faunas. Perisphinctid ammonites with simple bifurcate ribbing are common at some levels and abundant at others in the latest Eudoxus Zone, and in much of the Autissiodorensis Zone. In Dorset, those in the Autissiodorensis Zone up to a level close below Blake's (1875) Bed 42 include typical *Subdichotomoceras* macroconch and microconch forms with lappets. But those in the uppermost Eudoxus Zone and the lowermost Autissiodorensis Zone, between the upper *Crussoliceras* Bed (Fig. 3) up to the earliest well characterized *Subdichotomoceras* spp. in Chronosubzone KC 34, are too poorly preserved to be assigned either to *Subdichotomoceras* or *Crussoliceras* with confidence, and none of them preserves the aperture. These

constraints make any suggested phyletic relationship questionable. However, comparison of the ontogenetic changes (or modifications) of presumed ancestral and derived groups can enable their interpretation in the light of the concepts on the relationships between ontogenesis and phylogenesis (Gould, 1977; Mayr, 1942) and the evolutionary patterns and process (Mayr, 1942).

5.3. *Lithacosphinctes*, *Crussoliceras* and *Subdichotomoceras*

The Kimmeridgian *Crussoliceras* have been shown to have evolved from the Oxfordian *Lithacosphinctes* in the Submediterranean Province (Atrops, 1982 and Hantzpergue, 1989). In an alternative hypothesis, Pavia *et al.* (1987) suggested that *Crussoliceras* is closer to *Pseudosimoceras* [a Simoceratinae according to Arkell (in Arkell *et al.*, 1957)] and that the genus had a Mediterranean origin where it evolved from Late Oxfordian Passendorferiinae via a palingenetic process. However, the specimens identified as *Crussoliceras* sp. ind. from condensed beds dated as Platynota and Strombecki (= Hypselocyclus) Zone age (Pavia *et al.*, 1987, p. 84, pl. 5, fig. 2, 4) are not *Crussoliceras*. It is noteworthy that in northern Italy *Orthosphinctes* (m) is known up to the lower Strombecki Zone (*Orthosphinctes* Subzone). *Orthosphinctes* (m) and large *O.* (*Lithacosphinctes*) (M) of about the same age (e.g. Hantzpergue's Achilles Subzone, equivalent of the Submediterranean Hypselocyclus Zone), are also known in northern Aquitaine (Hantzpergue, 1989, p. 147).

According to Hantzpergue (1989), the principal differences between *Crussoliceras* and *Lithacosphinctes* are:

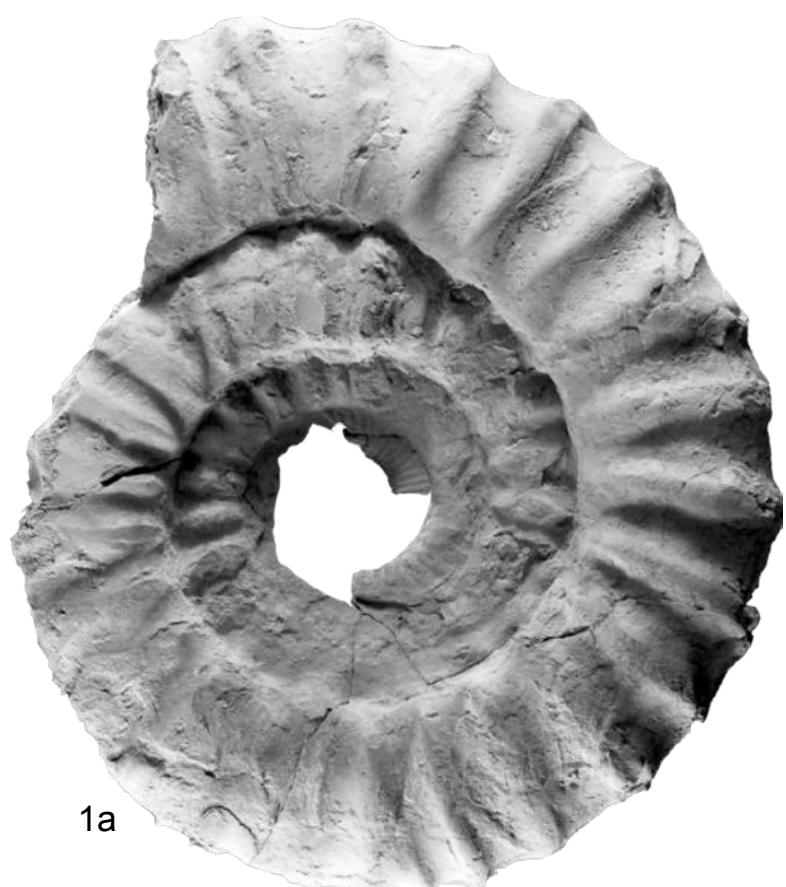
- 1) *Crussoliceras* is much reduced in adult size;
- 2) *Crussoliceras* has a simplified ornament which, according to Hantzpergue (1989), is the result of a centrifugal extension of the bifurcate initial stage towards outer whorls with respect to the older *Lithacosphinctes*;
- 3) *Crussoliceras* lacks polyfurcate or palmate ribs at the end of the middle stage, and has a depressed whorl section until a late ontogenetic stage. This last corresponds to a centrifugal extension of the juvenile

Plate III

Fig. 1 a, b: *Crussoliceras crusoliense* (Font.). Macroconch, well preserved adult complete specimen without the aperture, and strong adult ribbing; 1a, lateral view and 1b, ventral view. Early Kimmeridgian, Divisum Zone; Couches à Céphalopodes, Arête de la Roche, Saint-Jean-de-Gonville, Ain; Énay Collection, FSL 101153. Photos R. Énay.

Fig. 2: *Crussoliceras sayni* Camus & Thieuloy. Microconch, complete adult specimen, the living chamber slightly crushed a whorl long and the aperture preserved. Lateral view. Early Kimmeridgian, Divisum Zone; Couches à Céphalopodes, Saint-André-Val-de-Fier, Savoie; Hirtz collection, FSL 101124. Photo R. Énay.

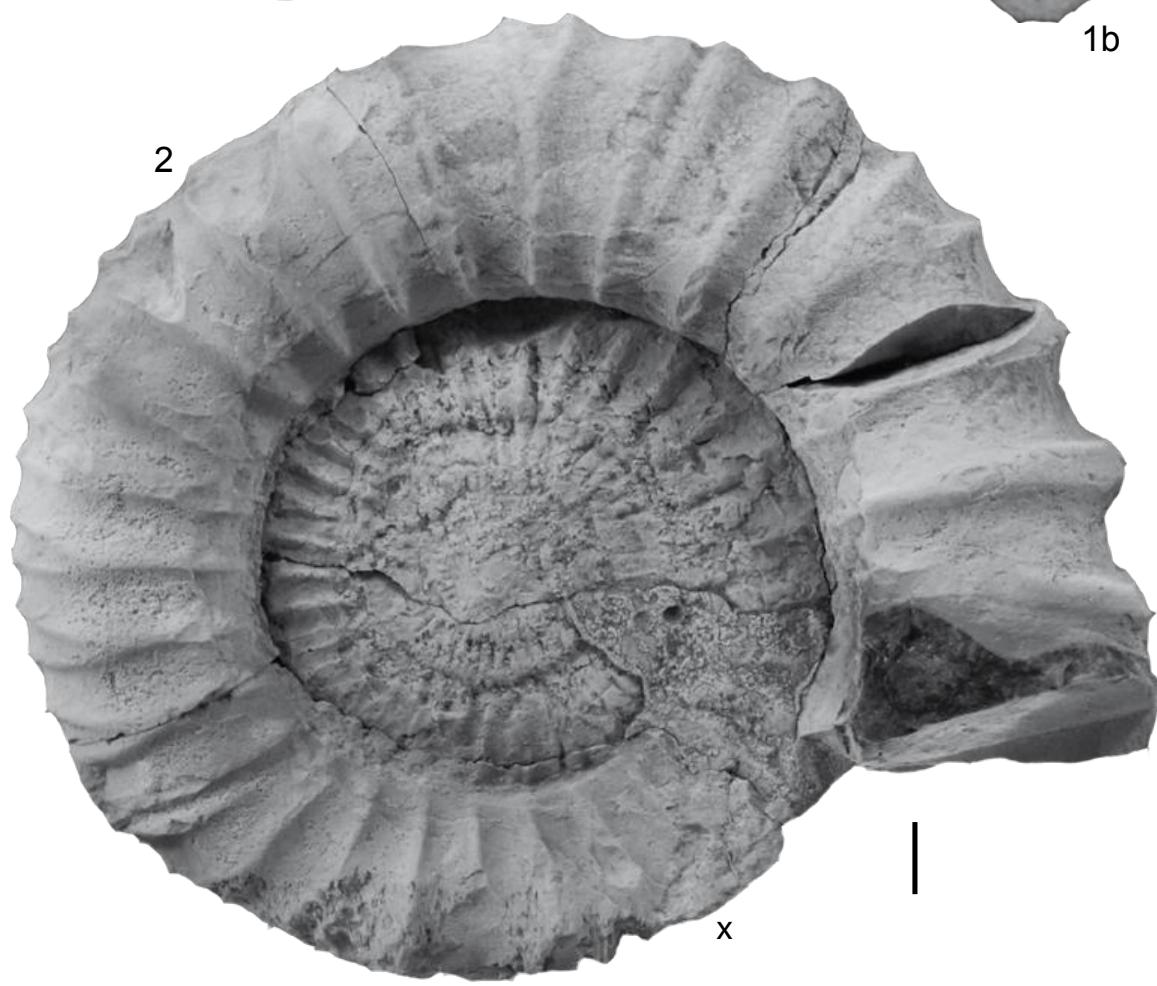
Scale bars represent 10 mm.



1a



1b



2

x

morphology that is commonly limited to the early ontogeny. The initial stage of *Crussoliceras* shows rectiradiate and regularly bifurcate primary ribs. Bifurcate ribs continue with strengthening of the ribbing and the occurrence of intercalatory ribs to form pseudoschizotomous trifurcations of polygyrate type ('false virgatome' of Énay, 1959) during the middle stage. The final stage shows strong ribs, the ventral end thickened, sometimes cuneiform; simple or the secondary ribs are less well developed.

These changes in the adult shape and sculpture are interpreted as the result of different developmental heterochronic processes. These processes include growth heterochrony such as progenesis and neoteny (Hantzpergue, 1989) that resulted in an adult size reduction and centrifugal extension of the bifurcate ribbing and the depressed whorl section, respectively; and acceleration would have produced the development of bulky primary in early ontogeny.

A similar combination of processes can be evoked to explain the main morphological changes in the evolution of *Subdichotomoceras* from *Crussoliceras*. The principal differences between *Subdichotomoceras* and *Crussoliceras* are:

- 1) A decrease in adult size depending on the species;
- 2) Depressed to very depressed whorl section throughout the ontogeny;
- 3) Simplified ornamentation with rectiradiate primary ribs that bifurcate uniformly until the end of the adult body chamber, in both the microconchs and the macroconchs and very few intercalatory ribs;
- 4) Suppression of part of the middle ('false trifurcate') ribbing stage and the final stage with strongly thickened ribs.

As seen in the evolution of *Crussoliceras* from *Lithacosphinctes*, heterochronic development by progenesis and neoteny can account for the adult size reduction, and the centrifugal extension of the depressed whorl section with the prolongation of the bifurcate ribbing into the mature stage.

These evolutionary changes could have occurred in populations of differing sizes in different environments

(Mayr, 1942). The ontogeny of *Subdichotomoceras* shows a shift in the ontogenetic stages without innovation combined with an earlier onset of sexual maturation, respect to the ancestor, that resulted in an adult size reduction (progenesis) and a centrifugal shift (neoteny) of the shape of the whorl section and the ornaments at different ontogenetic stages. The apparently mutually exclusive geographical distribution of *Subdichotomoceras* and *Crussoliceras*, with the possible exception of *S. praecursor* n. sp. means that it is not possible to propose any of the possible evolutionary models that have been proposed for such evolutionary changes (e.g. peripatric speciation or bottleneck speciation of Stanley, 1979).

5.4. *Crussoliceras*, *Tolvericeras* and *Subdichotomoceras*

The morphology of the microconch dimorph of the type species of *Tolvericeras* (*T. tolverense*) is similar to that of the microconchs of *Progeronia*, and the microconch of '*T.*' *murogense* is similar to that of *Subdichotomoceras*. The occurrence of microconchs with either *Progeronia*-like or *Subdichotomoceras*-like morphologies is consistent with the view of Atrops (1982) and Hantzpergue (1989) that *Progeronia* and *Crussoliceras* evolved from *Lithacosphinctes*. Hantzpergue (1989, p. 70) assumed that the last representatives of the *Tolvericeras* lineage have morphological features that foreshadow the Boreal Dorsoplanitidae. Under this interpretation the Dorsoplanitidae were derived from the *Pseudogravesia*-lineage. However, the *Tolvericeras* s. s. and the new species described in the present account, are thought to have evolved from species of *Garnierisphinctes*, and '*Tolvericeras*' *murogense* and the subgenus *Pseudogravesia* from *Crussoliceras*. These lineages follow markedly different evolutionary paths. Both increase their adult size, but the terminal adult stages are different. *Tolvericeras* s. s. develops a subquadratic to subcircular whorl section with cuneiform-shaped ribs, some of which are flared at their distal end. '*T.*' *murogense* and *Pseudogravesia* show a rapid increase in whorl width and a depressed final-stage

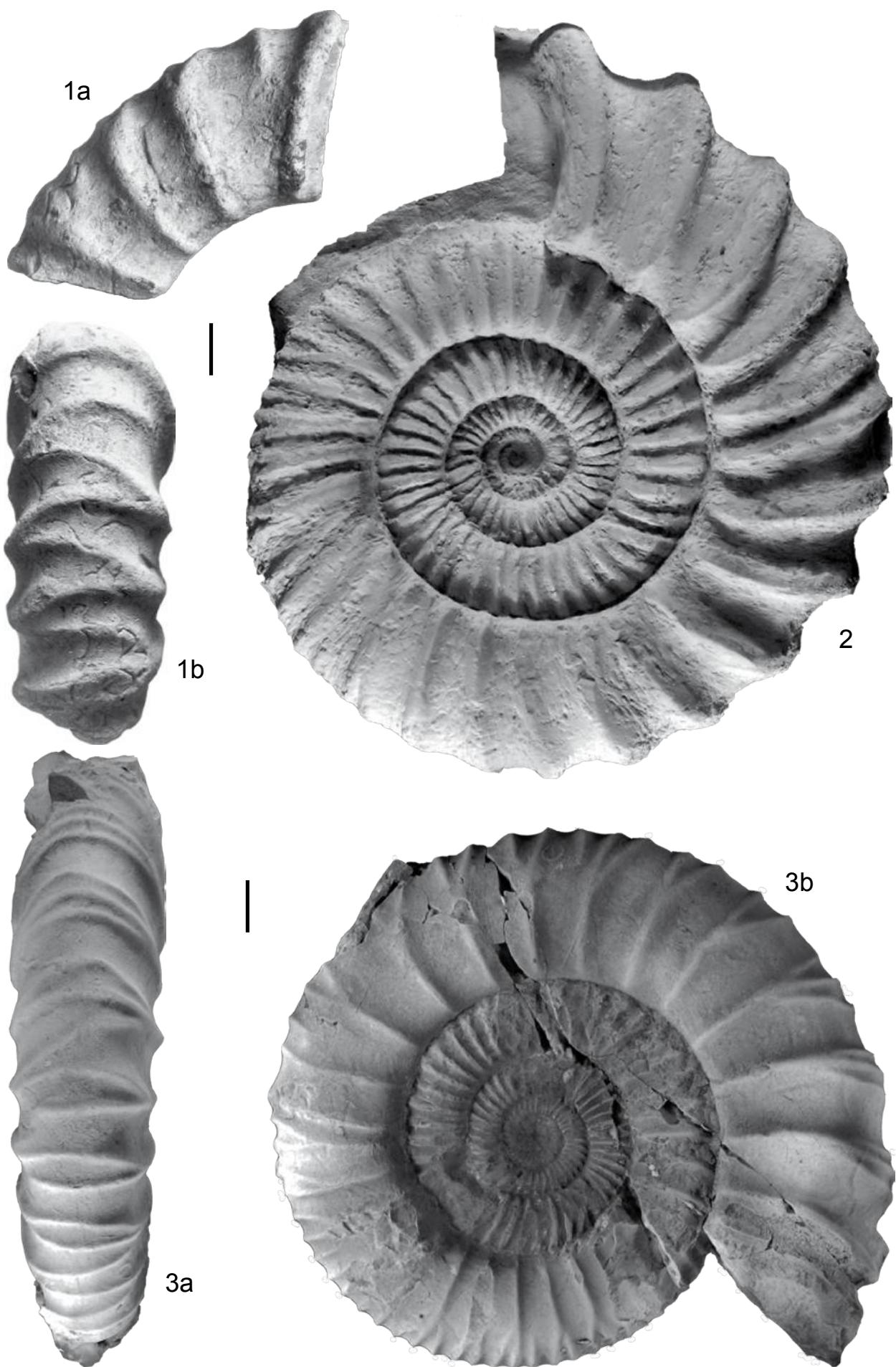
Plate IV

Fig. 1a, b: *Crussoliceras divisum* (Quenstedt) - *tenuicostatum* Geyer. Fragment of the living chamber; 1a, lateral view and 1b, ventral view, x 1,00. Kimmeridgian possibly derived, either from the "Marnes à Exogyres inférieures" which would begin with the Divisum Zone, or perhaps (?) from the underlying beds, Bar-le-Duc (Meuse), Durand collection, N° 17, ENSG Nancy, MAN (no Collection number). Photos R. Énay.

Fig. 2: *Crussoliceras divisum* (Quenstedt). Microconch, adult complete or nearly complete specimen. Lateral view. Early Kimmeridgian, Divisum Zone; Mount Crussol, Ardèche; Boselli Collection. Photo R. Énay.

Fig. 3a, b: *Crussoliceras divisum* (Quenstedt). Microconch, probably a young specimen with the living chamber a whorl long; 3a lateral view and 3b, ventral view showing the zig-zag arrangement of the secondary ribs. Early Kimmeridgian, Divisum Zone; Le Bois Noir, Conqueyrac, Gard; Atrops collection, FSL 185014. Photos R. Énay.

Scale bars represent 10 mm.



whorl section with strongly thickened ribs of a type that is not known in *Subdichotomoceras*. The ancestors of *Subdichotomoceras* and the Dorsoplanitidae would not, therefore, be *Tolvericeras* s. s. or *Pseudogravesia*.

5.5. *Subdichotomoceras* and the Dorsoplanitidae

Arkell (in Arkell *et al.*, 1957, p. L328) noted that *Subdichotomoceras* Spath, 1925 is closely similar to the Boreal dorsoplanitid genus *Pavlovia* Illovaisky, 1917 (and 1924) and suggested that the Boreal genus *Sphinctoceras* Neaverson, 1925 might be a junior synonym. He proposed (in Arkell *et al.*, 1957, p. L332) that the Dorsoplanitinae Arkell, 1950 were probably derived from *Subdichotomoceras*. The Dorsoplanitidae comprises three sub-families, the Pectinatitinae Zeiss, 1968 from which the Pavloviinae Spath, 1931 and the Dorsoplanitinae are derived (Callomon in Donovan *et al.*, 1981).

5.6. *Subdichotomoceras* and Pectinatites

Cope (1968) suggested that his proposed new genus *Propectinatites* from the middle part of the Autissiodorensis Zone, a junior synonym of *Subdichotomoceras* from the same beds, was ancestral to *Pectinatites*. A large number of photographs of *in situ* perisphinctids in Kimmeridge Bay and Brandy Bay in the upper part of the Autissiodorensis Zone, between the highest *Subdichotomoceras websteri* with a well-developed lappet and the base of the Elegans Zone, were examined. None of the microconchs showed the peristome, a feature that is commonly preserved in *Subdichotomoceras* in the middle part of the Autissiodorensis Zone. One of the macroconchs (from M11b) is somewhat similar to *P. (Arkellites) primitivus* Cope (1967, pl. 2, fig. 2) but is markedly different in sculpture by having less primary ribs. Two later macroconchs (from M14b and M15a) are close to *S. lamplughii*

dorsetense, but they are incomplete and difficult to differentiate from *S. websteri*.

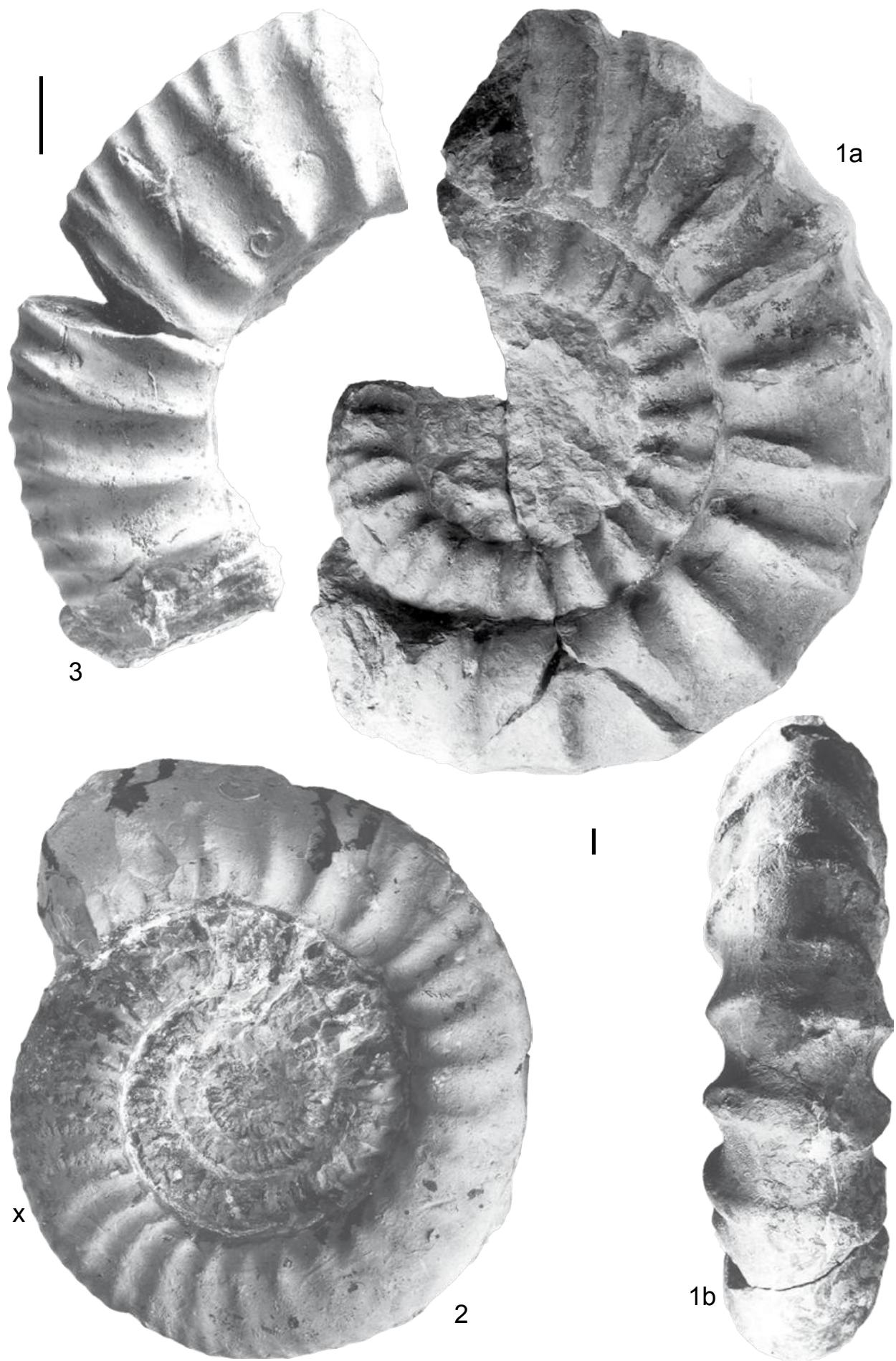
Typical *Subdichotomoceras* macroconchs and microconch with lappets occur in much of the Autissiodorensis Zone up to a level close below the Bed 42 of Blake (1875). The lowermost occurrence of a *Pectinatites* microconch with a horn, a distinguishing feature of the genus, 3 m below the Yellow Ledge Stone Band and the uppermost *Pectinatites* (*Arkellites*) with horn in Etches collection is about 5 m above the Bed 42 of Blake (1875) and older than the oldest of the Cope specimen. The beds where could be observed the change from *Subdichotomoceras* to *Pectinatites* are only about 5-6 m thick (e.g. Bed 42 of Blake (1875) up to HC5 and perhaps a little part of the bed M15 just below), from the latest *Subdichotomoceras* sp. (e.g. KFMP 15) from M15b up to the earliest *Pectinatites* (*Arkellites*) *primitivus* (Cope, 1967, pl. 1, fig. 2) from HC6, according to our information. In the present state of knowledge there is no sufficient evidence to confirm or otherwise the suggestion of Cope (1968) that *Subdichotomoceras* gave rise to *Pectinatites* via progressive changes of the apertural structure whereby lappets were replaced by horns. Here, a quantum evolution is needed of the type proposed for the evolution of *Subdichotomoceras* from *Crussoliceras*. At Kimmeridge Bay, c. 8 m of continuously exposed marine mudstones with only a few minor sedimentary breaks separate the youngest recorded *Subdichotomoceras* in this account from the oldest record of *Pectinatites* [*P. (Arkellites) primitivus*] (Cope, 1967). The macroconch of the latter species shows features which Cope (1967) interpreted as primitive characters of *Pectinatites*. These include a wide angle of furcation, abundant unbranched primary ribs, the relative absence of trifurcate (polygyrate) ribs, and microconchs that lack a horn but which have a feeble ventral inflation of the peristome. The principal differences between *Pectinatites* (*Arkellites*) and *Subdichotomoceras* are:

- 1) An important adult size reduction in *Pectinatites* (*Arkellites*);

Plate V

- Fig. 1a, b: *Crussoliceras lamberti* n. sp. Holotype (= *Ammonites eupalus* D'Orbigny, Lambert *in de Loriol & Lambert*, 1893, p. 209. Adult complete specimen with the aperture preserved and half a whorl long living chamber. 1a, lateral view and 1b, ventral view. "Argiles bleues de Fontaine", Kimmeridgian B, Early Kimmeridgian, Divisum/Chatelaillonensis Zone; Fontaine, Aube. Lambert Collection, P. and M. Curie-Paris 6 University, UPMC 151. Photos N. Podevigne, University of Lyon.
- Fig. 2: *Crussoliceras* cf. *aceroides* Geyer. Macroconch. Nearly complete adult specimen without the peristome; lateral view. ? Lower Late Kimmeridgian; ?"Marnes à Exogyres" Formation; Tronville, Meuse; Durand collection, ENSG Nancy, MAN (no collection number). Photo N. Podevigne, University of Lyon.
- Fig. 3: *Crussoliceras* cf. *aceroides* Geyer. Whorl fragment corresponding to the beginning of the living chamber; lateral view. "Pterocerian" but more probably derived from the "Marnes à Exogyres" Formation, ? lower Late Kimmeridgian; Bar-le-Duc, Meuse, Durand collection n° 19, ENSG Nancy, MAN (no collection number). Photo N. Podevigne, University of Lyon.

Scale bars represent 10 mm.



- 2) A more involute coiling of the *Pectinatites* (*Arkellites*) macroconch;
- 3) A large increase in the rib density of *Pectinatites* from the innermost whorls.

These are major morphological changes that are interpreted here as the result of developmental heterochronies and innovation. The pattern of proterogenesis is accompanied by innovation that, associated with an adult size reduction, produced a complete renewal of the ribbing style, and the change in the apertural structure whereby lappets were initially replaced by a feeble ventral inflation and later by a ventral horn.

Unlike the evolution of *Subdichotomoceras* from *Crussoliceras*, the supposed derivation of *Pectinatites* from *Subdichotomoceras* did not occur in different areas or different environments. In this case a peripatric speciation model is not applicable but speciation via bottleneck effects could be proposed. Such a pronounced change in the shell morphology could be the result of a genetic revolution related to an environmental crisis, but there is no evidence that this was the case in the Kimmeridge Clay as seen in the outcrops on the Dorset coast. In contrast to the major sedimentary breaks at the bases of the Baylei to Eudoxus Zones (Fig. 3), the sequence boundary (Km 6 of Taylor *et al.*, 2002) at the end of the Autissiodorensis Zone is a correlative conformity at Kimmeridge that is not marked by a sedimentary break or change in facies.

6. CONCLUSIONS

Kimmeridgian perisphinctids from southern England and north-eastern France are studied. New specimens in solid preservation from Dorset and Speeton, Yorkshire confirm the synonymy between *Propectinatites* Cope and *Subdichotomoceras* Spath. Together with *in situ* and non-collected crushed specimens they show that *Subdichotomoceras* is the prevailing perisphinctid genus in the upper Autissiodorensis Zone, but there is some evidence that it occurs in the underlying beds of the lower Autissiorensis Zone and even below in the uppermost Eudoxus Zone, but new and better evidence

is needed. Other very scarce perisphinctids are a species of *Crussoliceras* and a new species of *Tolvericeras* in the upper Eudoxus Zone, *Pseudogravesia* sp. in the upper Autissiodorensis Zone, here described for the first time. Studied specimens from north-eastern France belong mainly to the Submediterranean *Crussoliceras*; other perisphinctids are *Pseudogravesia* described (as *Tolvericeras*) by Hantzpergue (1989), a new species of *Tolvericeras* and a possible *Subdichotomoceras*. *Crussoliceras* is a characteristic genus (together with *Ataxioceras* and *Progeronia*, missing in the study area) of the upper Lower Kimmeridgian (e.g. Divisum–upper Chatelaillonensis Zones). There is evidence that *Crussoliceras* still occurs in the upper Kimmeridgian beds (Acanthicum and Eudoxus Zones) and the species *C. sevogodense* is here considered as a member of the genus. New undescribed specimens from the type locality (Mount Crussol) and from other areas allow confirming *Crussoliceras* as a dimorphic genus. Both dimorphs, but especially the microconchs (e.g. *C. divisum* and *C. sayni*), display several features reminiscent of *Subdichotomoceras*.

The probable origin of the Subboreal dorsoplanitids from the genus *Crussoliceras* (Enay, 1985) is here adopted since the alternative evolutionary path via *Tolvericeras* (Hantzpergue, 1989) has not been confirmed. Moreover this genus is restricted to the type species (*T. tolverense*) and some new species described in the present paper which are presumed to be derived from *Garnierisphinctes* of the Divisum Zone. Therefore, on the basis of its *Subdichotomoceras*-like morphology of the microconch, "*T.*" *murogense* is considered as the oldest species of *Pseudogravesia*, which is here considered a genus and a separate off-shot of *Crussoliceras*. As no transitional forms between the Kimmeridgian Submediterranean and Subboreal forms have been recorded, the phyletic relationships are suggested from the comparison of the ontogenies of presumed ancestral groups. Thus the genera are discussed accordingly, first the *Lithacosphinctes*, *Crussoliceras* and *Subdichotomoceras*; then the *Crussoliceras*, *Tolvericeras* and *Subdichotomoceras*; finally the relationships between *Subdichotomoceras* and the Dorsoplanitidae. The supposed derivation of

Plate VI

Fig. 1: *Crussoliceras dubisense* n. sp. Holotype, macroconch; nearly complete adult specimen, a little more than half a whorl of the living chamber preserved; lateral view. Lower "Calcaires à Corbis" Formation, Early Kimmeridgian, Divisum Zone; La Baume quarry, Audincourt, Doubs, Besançon University, Town Museum, Besançon. Plaster cast FSL 175915. Photo N. Podevigne, University of Lyon.

Fig. 2-3: *Crussoliceras atavum* (Schneid.). Macroconch. Two incomplete specimens, the smaller restricted to the inner whorls (2a, b), the larger corresponding to the living chamber of an adult individual without the aperture (3a, b). 2a, normal lateral view; 2b, reversed lateral view associated to 3a, the living chamber of the larger specimen; 3b, ventral view of the living chamber. "Calcaires à Aspidoceras" Formation, Late Kimmeridgian, Acanthicum Zone; La Gorge, Creys-Pusignieu, Isère. Énay collection, FSL 175 913 (3a, b) and 175 914 (2a, b). Photos N. Podevigne, University of Lyon.

Scale bars represent 10 mm.

