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Parallel Biozonation in the Upper Callovian and the Lower Oxfordian Based on the Peltoceratinae Subfamily (Ammonitina, Aspidoceratidae)

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Callovian
Oxfordian
Ammonoidea
Peltoceratinae
Biozonation

Contents

Parallele Biozonierung im Oberen Callovium und Unteren Oxfordium basierend auf der Subfamilie Peltoceratinae (Ammonitina, Aspidoceratidae)

Zusammenfassung

Die frühesten Peltoceratinae, Perisphinctaceae aus dem Tethysbereich, werden in der submediterranen Provinz im untersten Obercallovium gefunden. Sie sind relativ häufig durch das ganze obere Callovium und das untere Oxfordium und treten praktisch weltweit auf. Ihre Ontogenie und ihr Sexualdimorphismus sind gut definiert. Vier Eigenschaften ergeben zuverlässige Bestimmungsmerkmale:

1) die adulte Größe der Makro- und Mikrokonche,
2) die Lage des Rippengabelungspunktes auf der Flanke, der bei Mikro- und Makrokonchen etwa gleich ist,
3) das Vorhandensein oder Fehlen eines "Zwischenstadiums" zwischen den berippten und den tuberkulaten Stadien der Makrokonche und
4) die Morphologie der Ventrolateraltuberkeln der Makrokonche.

Diese Eigenschaften wurden zur Definition oder Redefinition von elf Arten in einer Folge von vier Ammonitenzonen verwendet. Diese Arten zeichnen sich entweder durch ihre kurze stratigraphische Reichweite oder ihr plötzliches Auftreten aus. Die Peltoceratinae stellen demzufolge gute Leitfossilien für die Standard-Biozonierung in den submediterranen (Oberes Callovium) und mediterranen (Unteres Oxfordium) Provinzen dar, parallel zur Biozonierung, die auf borealen Taxa beruht.

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Abstract

The earliest Peltoceratinae, Perisphinctaceae of Tethyan origin, are found in the Submediterranean province at the very bottom of the Upper Callovian. They are relatively abundant throughout the Upper Callovian and Lower Oxfordian and occur virtually worldwide. Their ontogeny and sexual dimorphism are well defined. Four characters constitute reliable criteria for identification:

1) the mature size of macroconchs and microconchs,
2) the average position of the rib bifurcation point on the shell flanks, which is similar in macro- and microconchs,
3) the presence or absence of an "intermediate stage" between the ribbed and tuberculate stages in the macroconchs, and
4) the morphology of the macroconch ventrolateral tubercles.

These characters have been used to define or re-define eleven palaeospecies in a succession of four ammonite zones. These palaeospecies are characterised by either their short stratigraphic range or their sudden appearance. The Peltoceratinae are therefore good candidates to serve as index species for standard biozonation in the Submediterranean (Upper Callovian) and Mediterranean (Lower Oxfordian) provinces alongside the biozonation based on taxa of Boreal origin.

Biozonation parallèle au Callovien supérieur et à l'Oxfordien inférieur basée sur la sous-famille des Peltoceratinae (Ammonitina, Aspidoceratidae)

Resumé

Les Peltoceratinae, Perisphinctaceae d'origine téthysienne, apparaissent dans la province subméditerranéenne à l'extrême base du Callovien supérieur. Ils sont relativement abondants dans tous les niveaux du Callovien supérieur et de l'Oxfordien inférieur et ont une répartition géographique quasi mondiale. Ils sont bien définis par leur ontogenèse et par leur dimorphisme sexuel. Quatre caractères constituent des critères de reconnaissance fiables:

1) la taille adulte des macroconques et des microconques,
2) la position moyenne du point de bifurcation des côtes sur les flancs, similaire chez les macroconques et les microconques,
3) l'absence ou la présence d'un stade intermédiaire entre les stades costulé et tuberculé des seuls macroconques et
4) la morphologie des tubercules latéro-ventraux des macroconques.

Ces caractères ont permis la définition ou la redéfinition de onze paléoespèces qui se succèdent sur quatre zones d'ammonites et qui sont caractérisées, soit par leur brève extension stratigraphique, soit par leur apparition brutale. Les Peltoceratinae sont donc de bons candidats pour servir d'espèces-indices pour la biozonation standard des provinces subméditerranéenne (Callovien supérieur) et méditerranéenne (Oxfordien inférieur), en parallèle avec celle construite à partir des taxons d'origine boréale.

1. Introduction

The ammonite biozonation for the Submediterranean province in the Upper Callovian and the Mediterranean province in the Lower Oxfordian (Table 1) is composite; it is based on taxa of Tethyan origin (the Pseudoperisphinctinae, Hecticoceratinae, Reineckeiinae, and Pelto-

	Zone	Subzone	Horizon
Lower Oxfordian	CORDATUM[1]	Cordatum[1]	
		Costicardia[2]	
		Claromontanus[3]	**Mazuricus**[3]
			Claromontanus[3]
	MARIAE[4] (= ***ATHLETOIDES***[5])	Præcordatum[6]	Præcordatum[6]
			Alphacordatum[7]
			Præmartini[7]
		Scarburgense[8] (= ***Athletoides***[9])	Woodhamense[7]
			Scarburgense[8] (= ***Athletoides***[9])
			Thuouxensis[7]
Upper Callovian	LAMBERTI[10]	Lamberti[11]	Paucicostatum[12]
			Lamberti[13]
			Prælamberti[14]
		Poculum[15]	***Athletoides***[16] (= ***Schroederi***[9])
			Subtense[16]
			Nodulosum[15]
	ATHLETA[17]	**Collotiformis**[18]	**Collotiformis**[18]
			Piveteaui[15]
		Trezeense[19]	***Athleta***[20]
			Leckenbyi[18]

1 d'Orbigny 1852
2 Arkell 1941
3 Brochwicz-Lewinski 1981
4 Douvillé 1881
5 Sapunov 1976
6 Morley-Davièss 1916
7 Fortwengler & Marchand 1994
8 Buckman 1913
9 Bonnot & Cariou 1999
10 Hébert 1857
11 Callomon & Sykes 1980
12 Marchand 1979, *emend* Fortwengler & Marchand 1994
13 Callomon 1964
14 Marchand 1986
15 Cariou 1974, 1980, 1984
16 Cariou 1980, 1984
17 d'Orbigny 1852 ; Oppel 1857
18 Bourquin & Contini 1968
19 Cariou 1969
20 Cariou 1969, 1980, 1984

boreal origin taxa **tethyan origin taxa** ***Peltoceratinae***

Table 1.
Ammonites biozonation of the Submediterranean province (Upper Callovian [THIERRY et al., 1997]) and Mediterranean province (Lower Oxfordian [CARIOU et al., 1997]).

ceratinae subfamilies) and on a taxon of Boreal origin (the Cardioceratinae subfamily) which is also widely used for biozonation in the Subboreal province. For large scale correlations it is therefore essential to propose new index fossils of Tethyan origin but found in association with Boreal forms.

The earliest Peltoceratinae, Aspidoceratidae of Tethyan origin, in Western Europe are found at the very bottom of the Athleta zone. They occur – and sometimes quite abundantly – throughout the Upper Callovian and Lower Oxfordian (four ammonite zones in all). They are very widely distributed geographically (from Portugal to the Middle East). Revision of this subfamily has been underway for a decade now (BONNOT, 1990, 1993, 1995; BONNOT et al., 1997; COURVILLE & BONNOT, 1998) and has furthered our understanding of

1) their ontogeny,
2) their sexual dimorphism and
3) their modes of evolution, thereby allowing their use in biostratigraphy.

Three taxa are already used as index fossils:

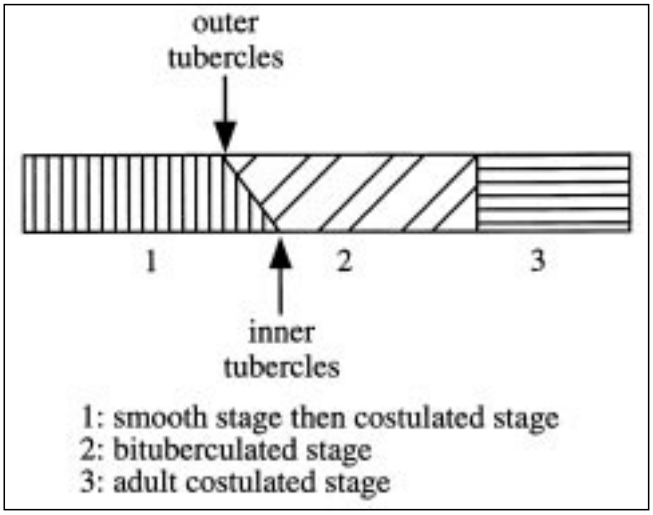
1) *Peltoceras athleta* (PHILLIPS) for the first zone of the Upper Callovian (D'ORBIGNY, 1852 and OPPEL, 1857) and as an alternative to *Orbignyceras trezeense* GERARD & CONTAUT for the second horizon of the zone;
2) *Peltoceras subtense* (LECKENBY) for the second horizon of the Lamberti zone (CARIOU, 1980);
3) *Peltoceratoides athletoides* (LAHUSEN), as recently re-interpreted, is proposed as an index fossil for the first subzone and second horizon of the Lower Oxfordian (BONNOT & CARIOU, 1999).

2. The Peltoceratinae Subfamily

2.1. Ontogeny of Ornamentation

Macroconch ornamentation comprises a series of three stages (Text-Fig. 1):

1) Ribbed stage (simple or forked ribs).
2) Bituberculate stage with two rows of tubercles: outer (ventrolateral) and inner (umbilical). The inner tubercles arise after the outer ones or sometimes at the same time, but never before.
3) Mature ribbed stage with strong simple ribs crossing the venter.



Text-Fig. 1.
Ornamental stages of Peltoceratinae.

2.2. Sexual Dimorphism

The different-sized specimens invariably found at all sites are interpreted as sexual dimorphs (Table 2).

1) The microconchs have apertures with lateral lappets. They never bear tubercles (save very rare exceptions). They range in size from 30 to 130 mm. Their ribs are successively radial, retroverse and convex ahead of the aperture.
2) The macroconchs have simple apertures and range from 200 to 600 mm in size depending on species. They exhibit ornamental stages 1–3 above.

Table 2.
Sexual dimorphism in Peltoceratinae.

Character	Microconch	Macroconch
Adult size	Small (30->130 mm)	Large (200->600 mm)
Peristome	With lappets	Simple
Ornamentation	Stage 1	Stages 1, 2 & 3

2.3. Evolutionary Mode

Three events punctuate the subfamily's evolution. One is the gradual shift in the average position of the point of bifurcation of the ribs on the flanks over time. The other two are sudden changes: the appearance and then disappearance of an intermediate ornamental stage in the macroconchs between ornamental stages 1 and 2, and the duplication of each ventrolateral tubercle.

2.3.1. Position of the Rib Bifurcation Point on the Shell Flanks

This varies with

1) individual,
2) populational and
3) temporal parameters.

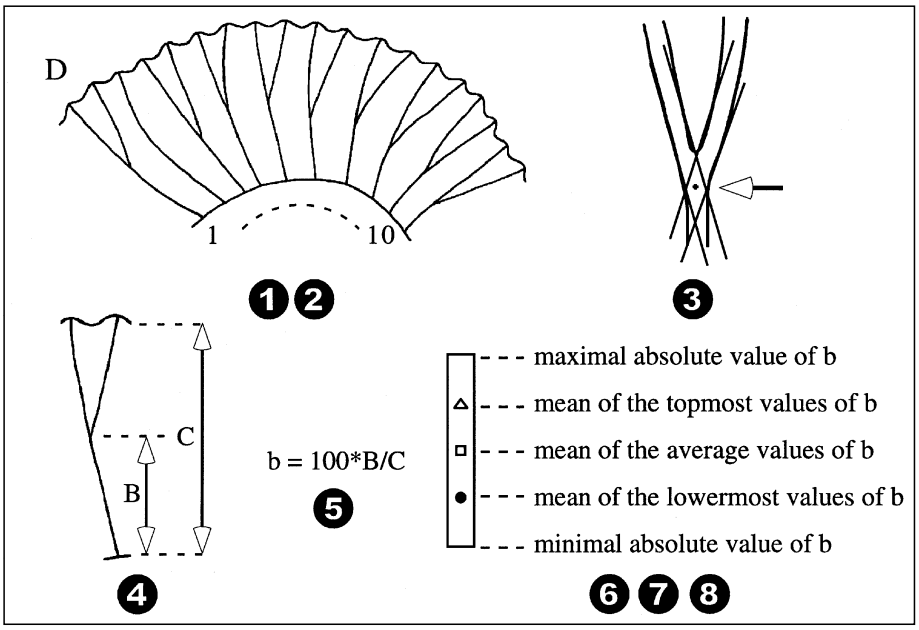
If we consider together the influence of parameters 1. and 2., the position of the bifurcation point can be used as an indicator of time.

Method (Text-Fig. 2)

The procedure for measuring the bifurcation point position has been standardised as follows:

1) Count the 10 ribs preceding diameter D.
2) Make a camera lucida drawing of the part of the whorl containing these 10 ribs at the greatest possible magnification.
3) Locate the point of bifurcation, always in the same way.
4) Measure the position of the bifurcation point relative to the base of the rib (B) and the apparent rib length (C) working from the umbilical suture towards the venter.
5) Calculate the ratio B/C for each bifurcated rib and express it as a percentage relative to the base of the rib: b = 100B/C.
6) Calculate the mean values of b for the specimen considered at diameter D to allow for individual variability. We then have minimum, maximum and mean values of b for diameter D for each specimen.
7) Repeat the procedure at the same diameter D on a sample of N specimens from the same population.

Text-Fig. 2.
Position of the rib bifurcation point in Peltoceratinae: method.



8) Find the average of the minimum, maximum and mean values to allow for populational variability.
   We then have the absolute maximum value, the average highest values, the average mean values, the average lowest values and the absolute minimum value for each sample.
9) Compare the values of b obtained for samples of different ages.

Results (Text-Fig. 3)

The downward shift in the average position of the point of bifurcation is clearly continuous from the bottom of the Upper Callovian to the top of the Lower Oxfordian. The point is located on the upper two-thirds of the shell flank in *Peltoceras athleta* (PHILLIPS), as opposed to the lower quarter in *Peltoceratoides williamsoni* (PHILLIPS). Similar variability can be found for all species.

There are two exceptions though. In *Peltoceras retrospinatum* GERARD & CONTAUT, the bifurcation point is both very low on the flank (for the stratigraphic level) and highly variable. In *Peltoceratoides interruptum* (NEUMANN), the last recorded species before the Peltoceratinae became extinct, the bifurcation point shifted upwards to about a third of the way up the flank.

2.3.2. Intermediate Stage Between Stages 1 and 2 in Macroconchs

This is characterised by (Text-Fig. 4):

1) the very variable position of the point of rib bifurcation on the shell flanks (between the umbilical margin and the ventrolateral shoulder);
2) variable spacing between primary ribs leaving smooth areas of varying width on the flanks and the ventral region;
3) recurrence of a few non tuberculate ribs after the appearance of the first tubercles.

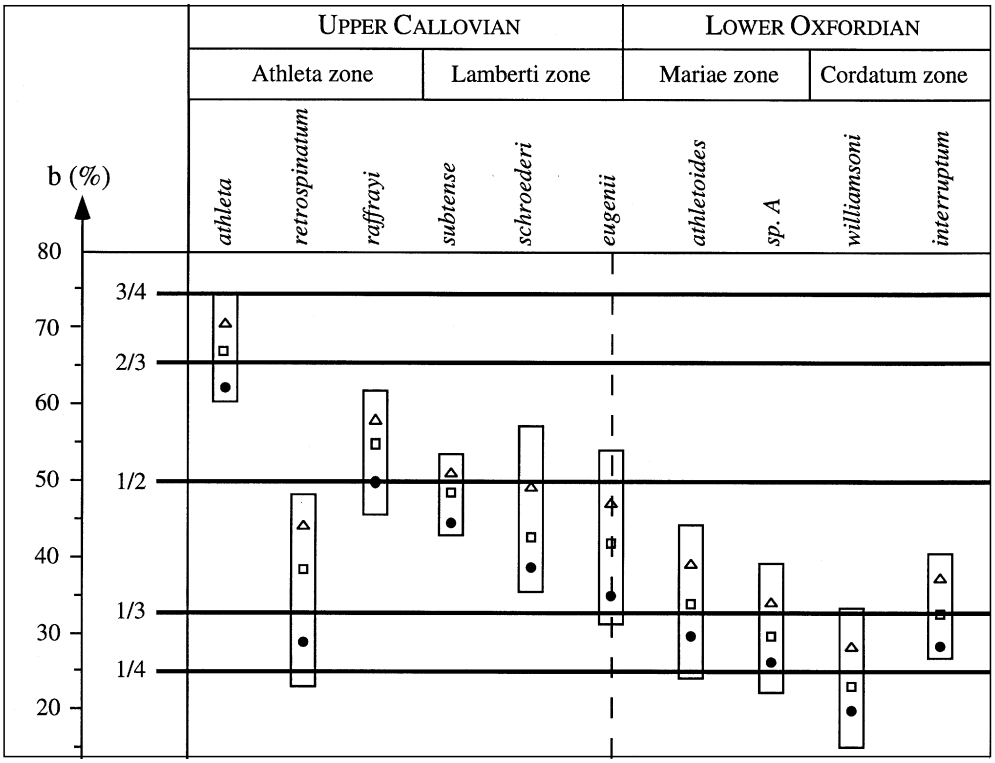
The intermediate stage is found in all macroconchs from the bottom of the Collotiformis subzone to the middle of the Praecordatum subzone.

2.3.4. Duplication of the Ventrolateral Tubercles in Macroconchs

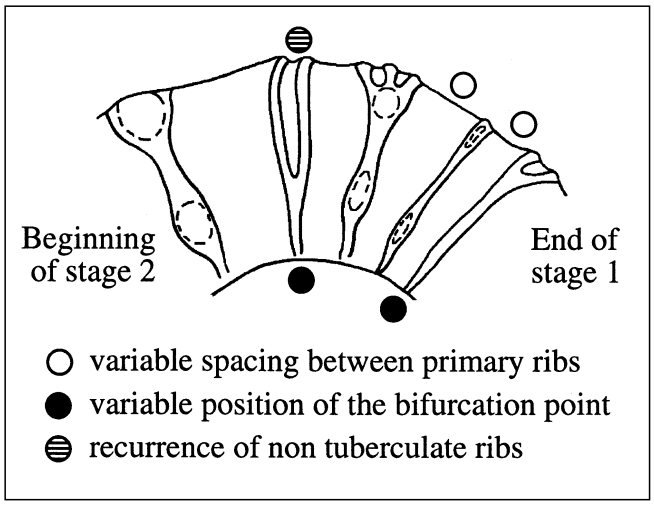
Duplication of the ventrolateral tubercles (Text-Fig. 5) occurs in all macroconchs in the uppermost Lamberti subzone (middle of the Paucicostatum horizon) and continues until the subfamily becomes extinct at the top of the Cordatum subzone. Duplication invariably occurs with the onset of stage 2. The duration of duplication varies within a population but also with species.

This easily recognisable character occurs very suddenly. We believe this vindicates maintaining the two classically recognised successive genera *Peltoceras* WAAGEN, 1871 (non duplicated ventrolateral tubercles) and *Peltoceratoides* SPATH, 1924 (duplicated ventrolateral tubercles).

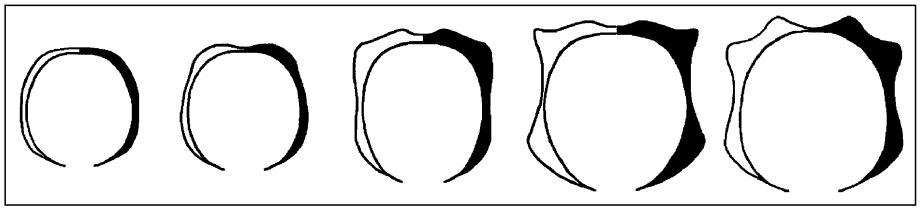
These three "evolutionary" characters associated with the mature size character (usable mainly in microconchs and stage 2 for macroconchs only) and with the other



Text-Fig. 3.
Variation of the position of the rib bifurcation point in Peltoceratinae: results.



Text-Fig. 4.
Intermediate ornamental stage in Peltoceratinae.



Text-Fig. 5.
Successive sections showing the duplication of the ventrolateral tubercles in Peltoceratinae macroconchs (Example in *Peltoceratoides eugenii* (RASPAIL), top of the Paucicostatum horizon).

morphological characters (coiling, cross-section) form a set of criteria for reliable species identification. This method has allowed us to recognise 11 taxa interpreted as 11 palaeospecies (Table 3).

3. Comparison with the Standard Biozonation Scale Based on the Peltoceratinae Subfamily

The different palaeospecies of Peltoceratinae have variable stratigraphic ranges: some are characteristic of a horizon, others of a subzone. Despite this disparity they can be used as index fossils at a scale that can be set alongside the composite standard scale (Table 4).

1) *Peltoceras athleta* (PHILLIPS) first appears at the bottom of the Athleta zone (Leckenbyi horizon) and reaches its high point in the next horizon (Trezeense horizon = Athleta horizon).
2) *Peltoceras dischizocostatum* BONNOT & COURVILLE is characteristic of the Piveteaui horizon. This is the first species to display an intermediate ornamental stage. It also possesses a few double forked ribs.
3) *Peltoceras retrospinatum* GERARD & CONTAUT is easily recognisable as the macroconchs and microconchs have a stage 1 with very markedly retroverse ribs. It is indicative of the Collotiformis horizon.
4) *Peltoceras raffrayi* BONNOT & COURVILLE is a contemporary of *Peltoceras retrospinatum* exhibiting a very long stage 1 with proverse ribs. Since there is no morphologically intermediate form between the two they are treated as separate species.
5) *Peltoceras subtense* (LECKENBY) is a comparatively little known species (scarce material at the bottom of the Lamberti zone).
6) *Peltoceras schroederi* PRIESER is a very widespread species whose morphology remains unchanged throughout the Lamberti subzone. This is the first large species with concomitant "lengthening" of the ornamental stages.

   At the top of the Lamberti zone, just before forms with duplicated tubercles first appear, the Peltoceratinae are scarce and poorly known.
7) *Peltoceratoides eugenii* (RASPAIL) is the first species to display both the intermediate stage, which is usually clearly defined, and duplicated outer tubercles.

   It first appears at the top of the Paucicostatum horizon and reaches the Athletoides subzone. Its first appearance immediately precedes that of the first members of the genus *Cardioceras*.

Table 3.
Criteria for identification of the Peltoceratinae palaeospecies.

Paleospecies	(M) size	(m) size	Intermediate stage (M)	Duplic. ventrolat. tubercles	b at 30 mm (%)
interruptum	-> 250 mm	70-100 mm	-	x	33
williamsoni	-> 600 mm	70 à 135 mm	-	x	23
sp. A	?	?	x	x	30
athletoides	-> 300 mm	-> 100 mm	x	x	35
eugenii	-> 250 mm	40 –70 mm	x	x	42
schroederi	-> 400 mm	-> 110 mm	x	-	43
subtense	-> ? 250 mm	60 à 90 mm	x	-	48
raffrayi	-> ? 200 mm	80 à 120 mm	x	-	55
retrospinatum	-> 200 mm	40 à 70 mm	x	-	38
dischizocostatum	?	?	appearance	-	(no valid)
athleta	-> 300 mm	30 à 105 mm	-	-	67

Table 4.
Parallel biozonation based on the Peltoceratinae subfamily.

	Zone	Subzone	Horizon	Horizon	Subzone	Zone
Lower Oxfordian	CORDATUM	Cordatum		Interruptum	Interruptum	WILLIAMSONI
		Costicardia		?		
		Claromontanus	Mazuricus		Williamsoni	
			Claromontanus	Williamsoni		
	ATHLETOIDES	Præcordatum	Præcordatum			ATHLETOIDES
			Alphacordatum	sp. A	sp. A	
			Præmartini			
		Athletoides	Woodhamense		Athletoides	
			Athletoides			
			Thuouxensis	Eugenii		
Upper Callovian	LAMBERTI	Lamberti	Paucicostatum	Schroederi β	Schroederi	SCHROEDERI
			Lamberti			
			Prælamberti	Schroederi α		
		Poculum	Schroederi			
			Subtense	Subtense	Subtense	
			Nodulosum			
	ATHLETA	Collotiformis	Collotiformis	Retrospinatum Raffrayi	Retrospinatum	ATHLETA
			Piveteaui	Dischizocostatum		
		Trezeense	Athleta	Athleta	Athleta	
			Leckenbyi			

8) *Peltoceras athletoides* (LAHUSEN) has recently been proposed (BONNOT & CARIOU, 1999) as a subzone and horizon index species for the bottom of the Lower Oxfordian (Mariae zone = Athletoides zone [SAPUNOV, 1976]). The intermediate stage is discrete and the ventral region narrow.
9) *Peltoceratoides* sp A. The Peltoceratinae are poorly known in most of the Praecordatum subzone (no deposits and/or intrinsic scarcity). They display clear affinities with *Peltoceras athletoides* but are distinguishable by the lower position of the bifurcation point on the flanks. The only samples dated with certainty from the Praemartini horizon and the Alphacordatum horizon are from the *Creniceras renggeri*-bearing marls of the Jura. These deposits contain no large specimens. Their ontogeny and sexual dimorphism are therefore inadequately known. This putative species will only be defined after collection and study of more abundant and more complete material.
10) *Peltoceratoides williamsoni* (PHILLIPS) is a highly variable species that reached its acme throughout Europe in the Praecordatum subzone. It is also found in the Bukowskii subzone.
11) *Peltoceratoides interruptum* (NEUMANN) is the final species of the Lower Oxfordian (Cordatum subzone). It is characterised by a comparatively high point of rib bifurcation.

4. Conclusion

The Peltoceratinae first appear in the Submediterranean province at the bottom of the Upper Callovian. Reliable criteria are used to define or re-define eleven taxa, considered to be palaeospecies, forming a largely uninterrupted lineage from the bottom of the Upper Callovian to the top of the Lower Oxfordian and with a wide geographical distribution.

Several of them are characterised by their short stratigraphic range (the horizon) and/or by their sudden appearance. They may therefore be ranked as index species on the current standard scale for the Submediterranean (Upper Callovian) and Mediterranean (Lower Oxfordian) provinces, either in support of index species of Tethyan origin or as surrogates for species of Boreal origin. These species are *Peltoceras dischizocostatum* found with *Orionoides piveteaui*, *Peltoceras retrospinatum* and *Peltoceras raffrayi* confined to the Collotiformis horizon, *Peltoceratoides eugenii* marking the Callovian/Oxfordian boundary, *Peltoceratoides williamsoni* which first appears in the Praecordatum horizon and *Peltoceratoides interruptum* which is confined to the Cordatum subzone.

It also appears that the Peltoceratinae are one of the rare groups that can be used for correlations worldwide during the period in question. Two examples:

1) In Chile, HILLEBRANDT & GRÖSCHKE (1995) use a biochronological scale based on Peltoceratinae at the

Callovian/Oxfordian boundary. This scale comprises a Primus zone that is assumed to be the equivalent of the Lamberti zone for the Upper Callovian and the Dimorphosus and Eugenii zones which are assumed to be equivalent to the Mariae (= Athletoides zone) and Cordatum zones for the Lower Oxfordian. Now, if we rule out the hypothesis of pronounced endemism, the identification procedure shows that the Chilean forms depicted by HILLEBRANDT & GRÖSCHKE (1995) can all be ascribed either to *Peltoceratoides eugenii* (D'ORB.) or to *Peltoceratoides athletoides* (LAHUSEN) species. It follows that their Eugenii zone must be correlated with the Athletoides subzone of the Mediterranean province and not with the Cordatum zone. This casts doubt on the equivalence proposed. In addition, our conclusions throw new light on the rate of sedimentation and therefore on the rate of subsidence of the region, which may be controlled by synsedimentary tectonism.

2) At the top of the Praecordatum subzone and in the lower part of the Cordatum zone (Bukowskii subzone) *Peltoceratoides williamsoni* (PHILLIPS) and allied species, are found almost worldwide. Correlations can therefore be envisaged between Western Europe and the Indo-Madagascan domain (SPATH, 1931; COLLIGNON, 1959), or with Indonesia (BOEHM, 1907) and Japan (SATO, 1960, 1985; BONNOT & MARCHAND, work in progress).

Finally it should be reported that a revision of the subfamily of the Euaspidoceratinae, in parallel with that of the Peltoceratinae, is currently underway. It already appears that some taxa are stratigraphically valuable (BONNOT et al., work in progress). The Aspidoceratidae are therefore an essential family for establishing a standard biochronological scale in the Tethyan domain, which can be readily correlated with existing scales for the Boreal and Subboreal domains.

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