

## Endemic Sinemurian (Early Jurassic) ammonites from the Lusitanian Basin (Portugal)

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### Abstract

This paper studies the very first Lusitanian ammonites. These late Sinemurian (Obtusum Zone) forms are found in two distinctly marly layers within the mainly calcareous "Coimbra Beds s.s." which crop out north of São Pedro de Muel (Portugal). These ammonites are endemic taxa belonging to the groups *Ptycharietites ptychogenos* (ПОМРЕККІ) and *Ptycharietites muellense* nov. sp. They exhibit such highly derived morphologies that they cannot be likened to any other genus of the related Asterooceratinae subfamily. Paedomorphic spreading of smooth, involute, platycone morphologies is a very unusual process within the Asterooceratinae in particular and within the Arietitidae in general. Until now the groups of *P. ptychogenos* (ПОМРЕККІ) and of *P. muellense* nov. sp. have only been reported in the northern part of the Lusitanian basin and do not seem to have any palaeogeographical affinities with the adjacent NW European or Tethyan faunas. The first appearance of the genus *Ptycharietites* in the Lusitanian basin was a sudden event. It could be interpreted as a punctuated evolutionary event or as a faunal ingression from some undetermined origin. In fact, as the Lusitanian basin has the only onshore outcrops for the whole Central North Atlantic area, origination in one or more undocumented neighbouring offshore basins is the more plausible hypothesis.

### Key words

Ammonites, Early Jurassic, Sinemurian, Portugal, Taxonomy, Evolution, Palaeobiogeography.

### INTRODUCTION

With the exception of the Lusitanian basin, all the Central North Atlantic Mesozoic deposits are confined at the present time to some ten offshore basins. A wealth of academic investigation and hydrocarbon exploration over the last three decades has yielded huge quantities of geological and geophysical data significantly improving our understanding of the pre-drift history of the Central North Atlantic (CNA). Unfortunately there is a total absence of data on macro fauna and especially ammonites for all the offshore basins. Thus, despite the invaluable Lusitanian source of macro-palaeontological data, the entire CNA remains one of the least known regions of the peri-Tethyan domain (s.l.). This would be of minor palaeobiogeographical importance if the Lusitanian macro-faunas were little different from the neighbouring NW European or Tethyan faunas. If this were so, simple extrapolation from the Lusitanian data would be an acceptable proxy for the undocumented basins. However, at least during the late Sinemurian and

the early Pliensbachian, the initial phases of colonisation of the Lusitanian basin by pelagic taxa are characterised by an unusual abundance of endemic species and/or lineages (DOMMERGUES & MOUTERDE, 1987; DOMMERGUES & EL HARIRI, 2002). This being so, the CNA as a whole may form a complex and prolific palaeobiogeographical network of possible nurseries and/or refuges for numerous endemic taxa. Such a hypothesis implicitly enhances the importance of studies of endemic Lusitanian taxa for palaeobiogeography and phyletics alike. This paper, which analyses the so far little known very first Lusitanian endemic lineage, is entirely consistent with this line of enquiry.

### GEOLOGICAL SETTING

The Hettangian and Sinemurian deposits of the Lusitanian basin are mostly marls and sandstones (e.g. "Dagorda Marls" and "Pereiros Beds") overlain by dolomitic limestone and dolomites (e.g. "Coimbra Beds s.s.") yielding

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only poorly diversified faunas of lamellibranchia and gastropods (MOUTERDE & RUGET, 1975; MOUTERDE & ROCHA, 1981). Ammonites do not appear before the base of the upper Sinemurian (Obtusum zone) and then only in a limited area in the vicinity of the present-day coastline from São Pedro de Muel (Penedo da Saudade outcrops) in the south to Figueira da Foz (Verride borehole) in the North. In the uppermost Sinemurian (Oxynotum Zone and mainly Raricostatum Zone), the ammonite-bearing deposits extend progressively southwards to Peniche and eastwards to the Coimbra area (Fig. 1). This paper studies the very earliest Lusitanian ammonites, which are roughly associated with a few argillaceous strata (marls, bituminous shales) interbedded within the essentially carbonate succession of the “Coimbra Beds s.s.” (e.g. neritic limestones often with numerous lamellibranchia and gastropods) (Fig. 2). These ammonite faunas are found mainly in the coastal outcrops of São Pedro de Muel but also occur in subsurface deposits at Verride about 12 km East of Figueira da Foz (Fig. 1). The fos-

siliferous Sinemurian outcrops of São Pedro de Muel and their associated ammonite faunas were chiefly studied in the late 19th (POMPECKJ, 1897, 1898) and early 20th centuries (CHOFFAT, 1903). More recent stratigraphic and palaeontological discussion of the fossils initially studied by POMPECKJ (1897, 1898) only came with the publication of the first part of a monographic “Atlas” by MOUTERDE & ROCHA (1981) illustrating the main typical Liassic fossils of Portugal. Even so, the precise stratigraphic context of the earliest Lusitanian Sinemurian ammonites and their intra-species variations or the composition of the faunal assemblages (e.g. diversity and disparity) have remained obscure until now.

All of the ammonites analysed here were collected recently bed-by-bed from the fossiliferous outcrops to the North of the small seaside town of São Pedro de Muel (Fig. 1). These outcrops are a more or less interconnected complex of cliffs and reefs listed as “Penedo da Saudade” or sometimes formerly as “Penedo do Cabo” in the literature and in the collections (MOUTERDE & ROCHA,

Fig. 1: Left frame – Map showing the location of São Pedro de Muel and Verride (Portugal). Right frame – Detailed map of the rocky coast just North of the village of São Pedro de Muel (these outcrops are usually indicated as Penedo da Saudade). 1: location of the main costal outcrops (cliffs, reefs, etc.) (after an aerial photograph dating from 1989). Letters A to E indicate different parts of the Sinemurian succession (see Fig. 2 for explanation).

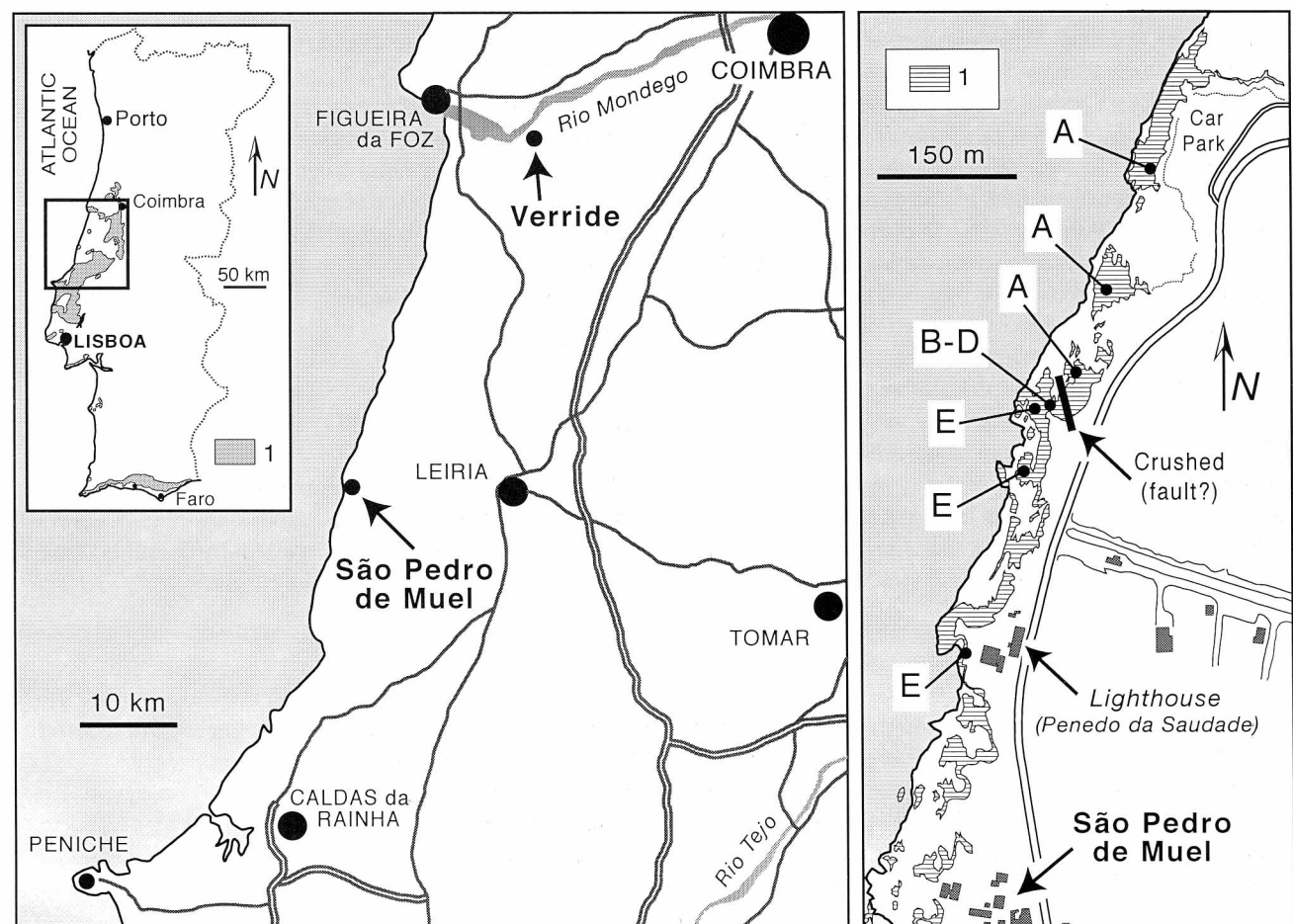
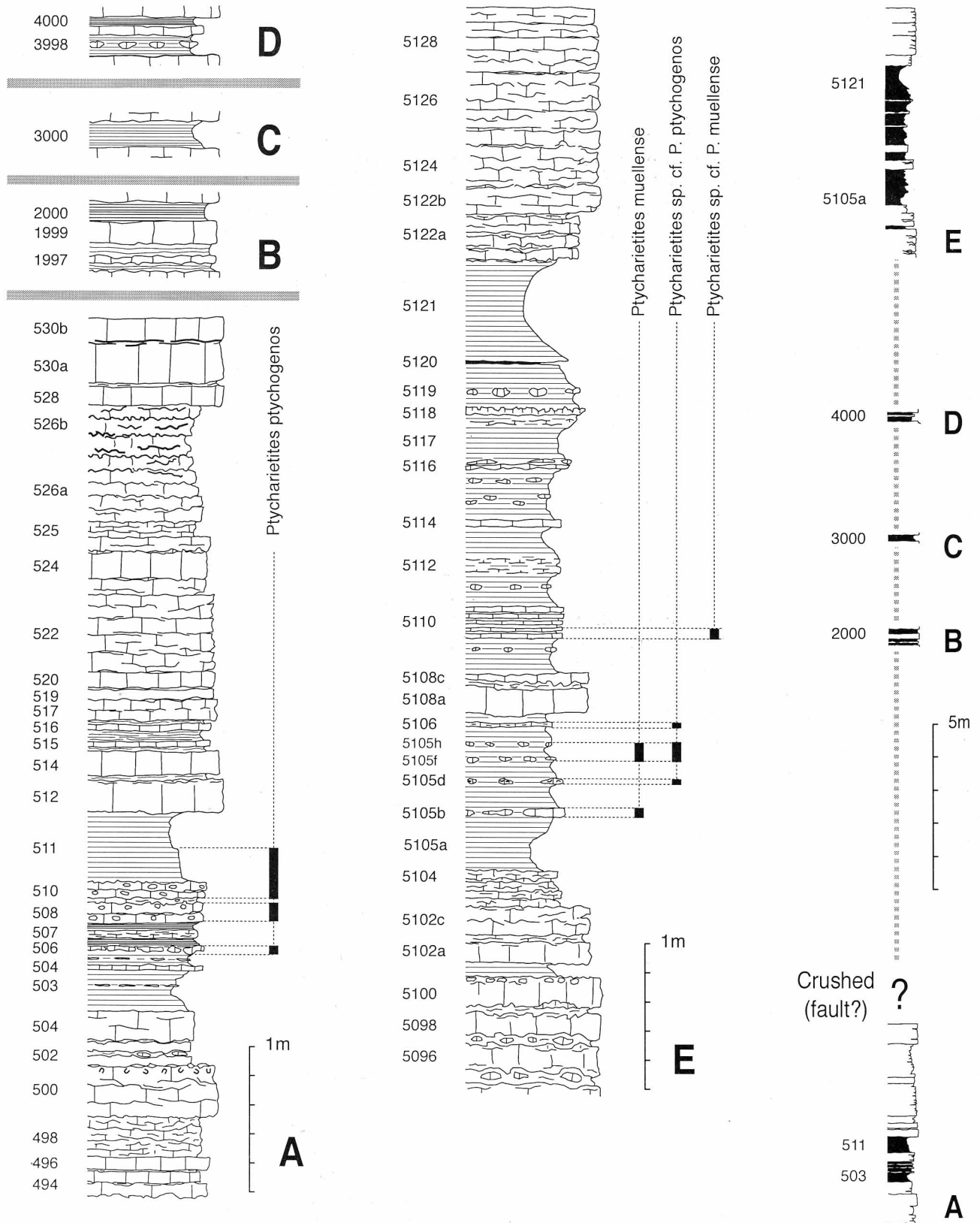


Fig. 2: Left and inner columns illustrate in detail the lithologic context of the main fossiliferous layers (Upper Sinemurian, ? Obutum zone) outcropping to the North of São Pedro de Muel (Penedo da Saudade). The distribution of the ammonite species is given in parallel to the lithologic logs. Right column gives a reconstitution of the whole succession. This reconstruction is a hypothesis because a crushed zone (fault?) separates the suspected lower part of the series (A) from the assumed upper part of the succession (B to E) (see Fig. 1 for the location of the different parts of the succession).



1981). These fossiliferous outcrops extend along about 600 m of coastline from the lighthouse of Penedo da Saudade in the South to the car park of "Praia Dourada" in the North (Fig. 1). The series dips steeply towards the ocean and the fossiliferous levels can be easily traced roughly parallel to the coastline. As a result of slight variations in orientation of the coastline, what is very probably the lower part of the series outcrops in the North (Fig. 1, A) and the upper part in the South (Fig. 1, B-E). Figure 2 shows partial and detailed lithological logs of the main argillaceous and possibly fossiliferous episodes plus a hypothetical reconstruction for the entire series. The continuity of the sequence from about 10 m below B to the top of E is proved and can be traced bed-by-bed. Conversely, the supposed basal position of episode A, while very probable remains questionable. A crushed zone (Figs 1 and 2), perhaps a fault, interrupts the series preventing continuous observation.

## AGE AND CORRELATION

All of the ammonites newly collected at Penedo da Saudade come from two clearly distinct fossiliferous layers (A and E) and a probable stratigraphical succession can be proposed with A below E (Fig 2). For both episodes, the newly collected material is constituted entirely by restricted Lusitanian taxa and it would therefore be hazardous to propose any putative correlations with either the NW European or the Mediterranean biostratigraphical framework. Nevertheless, besides the prevalent endemic components, the material previously collected at Penedo da Saudade includes a specimen attributed first by POMPECKJ (1897, 1898, fig. A) and subsequently by MOUTERDE & ROCHA (1981, pl. 1, fig. 12) to the NW European species *Asteroceras obtusum* (SOWERBY, 1817). This attribution was rejected by DONOVAN (1994, p. 392) who proposed to include this rare Portuguese ammonite within an informal "New Tethyan genus". This group should be characterised by its quadrate to compressed whorl section, its bisulcate venter with prominent keel and its straight, sharp, prominent ribs. It differs from *Asteroceras* [e.g. *A. obtusum* (SOWERBY, 1817)] in that the ribs curve little if at all towards the venter. DONOVAN (1994) includes in his provisional grouping some forms, mainly from the Apennines or the Austro-Alpine area, at first attributed to *Asteroceras*. All these forms are, in fact, very close to classical NW European *Asteroceras* and the relevance of a taxonomic formalisation remains questionable. Regardless of the conclusion of this problem, the Portuguese specimen displays moderately curved ribs on the last half whorl and is probably closely related to the NW European *Asteroceras* [e.g. *A. obtusum* (SOWERBY, 1817)] of the Obtusum subzone (late Sinemurian, Obtusum zone). Despite the many shortcomings (e.g. questionable species attribution, lack of accurate stratigraphic data) this ammonite provides

the only available starting point for a discussion of biostratigraphy. Nevertheless and since evolute species of *Asteroceras* such as *A. blakei* SPATH (1925) are known to range upwards through the Stellare subzone and into the Denotatus subzone (HOWARTH, 2002) correlation of the Lusitanian assemblages with the Obtusum subzone is less convincing.

## SYSTEMATIC PALAEOLOGY

**Remarks:** The name Psiloceratida is used at the order rank according to the revised meaning proposed by DOMMERGUES (2000) following the earlier proposal of GUÉX (1987) and TAYLOR (1998). In this way Psiloceratida approximately includes all the species classically allotted to the suborders Lytoceratinae HYATT (1889) and Ammonitina HYATT (1889). DOMMERGUES (2000) discusses this issue. In this paper, the suborder rank is not used.

### Class Cephalopoda CUVIER, 1797

#### Subclass Ammonoidea ZITTEL, 1884

#### Order Psiloceratida HOUSA, 1965

#### Superfamily Psiloceratoidea HYATT, 1867

#### Family Arietitidae HYATT, 1875

#### Subfamily Asteroceratinae SPATH, 1946

#### Genus *Ptycharietites* SPATH, 1925

**Type species:** *Arietites (Asteroceras) ptychogenos* POMPECKJ, 1897, "Coimbra beds s.s.", São Pedro de Muel, Portugal.

**Remarks:** POMPECKJ (1897) described an "*Arietites*" fauna from Penedo da Saudade (São Pedro de Muel, Portugal) with several new species. These forms are obviously distinct from the familiar northern European species and SPATH (1925) divided them into two new genera, *Ptycharietites* (SPATH, 1925, p. 267) and *Pompeckioceras* (SPATH, 1925, p. 268). New field data suggest that all these Lusitanian ammonites came from the same fossiliferous beds and doubtless belong to a single variable biological entity. In this paper, the Linnaean binomial *Ptycharietites ptychogenos* (POMPECKJ, 1897) is used to designate this species and implicitly *Pompeckioceras* is considered synonymous with *Ptycharietites*.

As the POMPECKJ study was first published in Germany (1897) and then the following year in Portugal (1898), two references are given in this paper.

#### *Ptycharietites ptychogenos* (POMPECKJ, 1897)

#### Pl. I, figs 1-8; Pl. II, figs 1-7; Pl. III, figs 1-6

1897. *Arietites (Asteroceras) ptychogenos* POMPECKJ, pl. 23, figs 1-3. [= 1898 *Arietites (Asteroceras) ptychogenos* POMPECKJ, pl. 1, figs 1-3].

#### Synonymous species

1897. *Arietites (Asteroceras) amblyptychus* POMPECKJ,

pl. 23, figs 4-5. [= 1898 *Arietites (Asterocheras) amblyptychus* POMPECKJ, pl. 1, figs 4-5].

1897. *Arietites (Arnioceras?) oncocephalus* POMPECKJ, pl. 23, fig. 7. [= 1898 *Arietites (Arnioceras?) oncocephalus* POMPECKJ, pl. 1, fig. 7].

#### Other citations

1897. *Arietites (Asterocheras)* sp. POMPECKJ, pl. 23, fig. 6. [= 1898 *Arietites (Asterocheras)* sp. POMPECKJ, pl. 1, fig. 6].
1981. *Asterocheras (Ptycharietites) ptychogenos* (POMPECKJ).- MOUTERDE & ROCHA, pl. 1, figs 11, 14.
1981. *Asterocheras? (Pompeckioceras) oncocephalus* (POMPECKJ).- MOUTERDE & ROCHA, pl. 2, fig. 3.

**Lectotype:** Three specimens were illustrated by POMPECKJ (1897, pl. 23, figs 1-3) to support the initial description of the species but none of them was designated as the holotype. Later, SPATH (1925) indicated the specimen illustrated (pl. 23, fig. 3) as representative of the species but he designated the one illustrated (pl. 23, fig. 2) as the “genotype” of his new genus *Ptycharietites*. To resolve this ambiguity the first of these specimens POMPECKJ (1897, pl. 23, fig. 3) is here designated as lectotype. This specimen was also illustrated by MOUTERDE & ROCHA (1981, pl. 1, fig. 11) and is housed in the “Portuguese Mining and Geological Institute” (PMGI) (n° SGP 371-3).

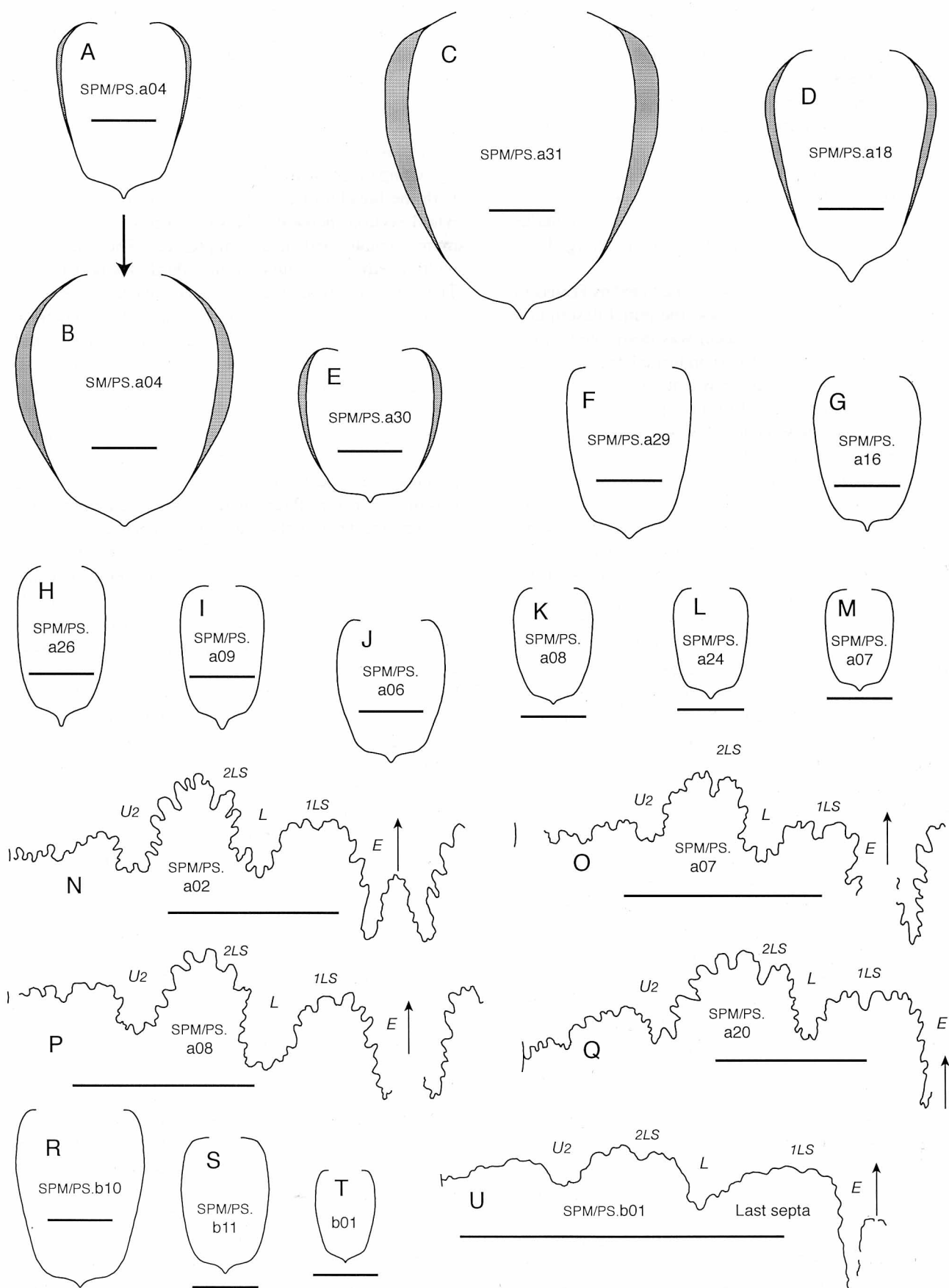
**Material:** In addition to the material illustrated by POMPECKJ (1897) and partly more recently figured by MOUTERDE & ROCHA (1981), the new find consists of 32 specimens, 22 of which are illustrated (Pl. I-V).

**Description:** *Ptycharietites ptychogenos* (POMPECKJ) is a species characterised by considerable morphological changes during shell growth and by its obvious intraspecific variation. To take into account such a complex morphological pattern the consecutive ontogenetic stages must be successively described. The innermost whorls of the shell (less than 1.5 cm in diameter) are not usually preserved. A single specimen (Pl. II, fig. 6), attributed with some doubt to *P. ptychogenos* (POMPECKJ), exhibits a confusedly ribbed nucleus which is already characterised by a rather compressed whorl section and by a ventral area bearing an obvious keel flanked by two visible grooves. Depending on the specimen examined, the next stage extends from 4 to 8 cm in diameter. During this subsequent, transitional phase of the growth, shell coiling is compressed, involute and planulate. Umbilical width ranges from 27% to 38% of the diameter. The transition from the umbilical area to the side is marked by an abrupt curvature. The rather flat (or hardly arched), subparallel (or hardly convergent) sides of the whorl occupy four-fifths or more of the whorl height (Fig. 3, A-M). Ribbing is entirely or almost entirely absent although some striae are sometimes visible. Such smooth inner whorls are partly visible in the lectotype. The ventral area is keeled-shouldered with a prominent keel flanked by more or less inclined flat strips or shallow grooves. This smooth compressed habitus, characteristic of the juvenile stages

(inner whorls) of *P. ptychogenos* (POMPECKJ), is likened by some authors (SPATH, 1925; MOUTERDE & ROCHA, 1981) to the late stages (e.g. body chamber) of *Eparietes*. Nevertheless, unlike in *Eparietes*, the outer whorls of *P. ptychogenos* (POMPECKJ) display a distinctive, strongly ribbed, broad habitus. This subadult and/or adult stage usually includes the last part of the phragmocone (e.g. the holotype) and/or the body chamber of the large specimens of *P. ptychogenos* (POMPECKJ) (Pl. II, fig. 1). By comparison with the previous ontogenetic stage, both the breadth of the umbilicus and the width of the whorl section increase. The shell becomes appreciably more evolute and less compressed. The maximum width is situated around the first third of whorl height. The transition from the umbilical area to the side is regularly arched and difficult to situate. The somewhat arched sides of the whorl converge towards the ventral area. The whorl section, which is rather subrectangular in the juvenile, becomes more and more subtriangular during the final part of growth (Fig. 3). Moreover, this subtriangular feature is reinforced by the concomitant development of strong, swollen ribs which are most prominent around the first third of whorl height. These ribs die out before three-quarters of whorl height. Thus the uppermost part of the side and the ventral area are free of any radial ornamentation (e.g. Pl. I, fig. 6). Although it undeniably becomes fainter during development, the keel remains distinct until the end of growth and extends as a short rostrum in the adult aperture. Likewise, two rather broad flat and convergent strips flank the keel as far as the aperture (Pl. II, fig. 1; Pl. V, fig. 1). The forms designated by the authors as *Pompeckioceras oncocephalus* POMPECKJ are situated at the fringe of the wide intraspecific variation of *Ptycharietites ptychogenos* (POMPECKJ) and are nothing more than an extreme peramorphic expression of the late subtriangular habitus. A broad subtriangular whorl section with swollen ribs is a rather uncommon morphological pattern. It is usually restricted to the outer whorls of some large shells. Among the Psiloceratoidea this type of morphology is found for instance on the body chamber of some *Paracoroniceras* or *Agassicerias* [e.g. *P. crossi* (WRIGHT, 1879), *A. superbium* GUERIN-FRANCIATTE, 1966]. A further good example among the Lusitanian fauna in a separate superfamily, the Eoderoceratoidea, is the early Carixian endemic *Epideroceras trigonale* MOUTERDE, DOMMERMUES & ROCHA (1983).

The suture line is usually poorly preserved on the ammonites collected at Penedo da Saudade (São Pedro de Muel). Nevertheless, the lateral and ventral parts of the suture could be drawn and studied on four of the newly collected specimens (Fig. 3, N-Q). The suture lines illustrated by POMPECKJ (1898, figs D, E) corresponding to two specimens of one of his new species, *Arietites amblyptychus* POMPECKJ, also yield valuable information corroborating the new observations. Considering the whole of these data: 1) the suture line of *Ptycharietites*

Fig. 3: Illustration of the variation of the whorl sections and suture lines among the genus *Ptycharietites*. A-Q, *Ptycharietites ptychogenos* (POMPECKJ, 1897). R-U, *Ptycharietites muellense* nov. sp. Horizontal bars indicate one centimetre.



*ptychogenos* (POMPECKI) seems to be a less variable trait than the other shell features, 2) for the main points, it fits in well with the basic features of the subfamily (Asteroceratinae) such as a notable forward projection of the second lateral saddle or a crude differentiation of the line close to the umbilicus. This late trait is especially obvious in the species which like *P. ptychogenos* (POMPECKI) have a weakly denticulate suture line. In fact, the lobules as well as the folioles of *P. ptychogenos* (POMPECKI) are remarkably poorly incised for a suture related to the “ammonitic” type.

**Remarks:** As previously suggested by SPATH (1925) and/or by DONOVAN (1994), the ammonites designated here as *Ptycharietites* and especially as *P. ptychogenos* (POMPECKI) display some features which, at first sight anyway, call to mind certain species belonging to the genera *Aegasteroceras*, *Arctoasteroceras*, *Eparietites*, *Parasteroceras* and probably also *Euerbenites*. These resemblances mainly concern a) the fading during growth of the tricarinate-bisulcate ventral pattern for *Aegasteroceras*, *Arctoasteroceras* and *Parasteroceras*, and b) the presence of a platycone, involute and ribless, or at least poorly ribbed, ontogenetic stage for *Eparietites*. All these similarities are believed to be homoplasies: parallelisms in the cases of the fading of the tricarinate-bisulcate pattern, or convergence in the case of the formation of a platycone involute shell. Even with these resemblances 1) *Aegasteroceras* can be easily identified by its obvious, simple and straight ribbing in the inner-medium whorls (versus ribless or almost ribless in *Ptycharietites*) and by its uninterrupted or at least hardly interrupted ribs on the ventral area of the outer whorl (versus always interrupted before the latero-ventral rim in *Ptycharietites*); 2) *Arctoasteroceras* can also be identified by its moderately ribbed inner-medium whorls (versus smooth in *Ptycharietites*) and by its regularly arched and practically keelless broad ventral area in large diameter specimens (versus slightly angular and invariably keeled in *Ptycharietites*); 3) *Parasteroceras* can be identified by its peculiar flexuous and delicately polyfurcated ribbing in the inner-medium whorls (versus smooth in *Ptycharietites*) and by its sharply bent and keelless or nearly keelless narrow ventral area (versus broader, slightly angular and always keeled in *Ptycharietites*); 4) *Eparietites* can be easily distinguished by the peramorphic significance (= late ontogenetic occurrence) of its platycone, involute and ribless pattern (versus paedomorphic in *Ptycharietites*). Thus, careful observations indicate that *Ptycharietites* is an isolated peculiar “excurrent” branch with no obvious close relatives among the Asteroceratinae subfamily.

**Distribution and biostratigraphical range:** In addition to the type locality of São Pedro de Muel where *P. ptychogenos* (POMPECKI) is fairly numerous, the presence of species is also attested by some indistinct specimens in a borehole at Verride (Verride-2, -540 m, about 12 km East of Figueira da Foz). *P. ptychogenos*

(POMPECKI) is a restricted taxon only reported in the “Coimbra Beds s.s.” of the Lusitanian basin and it occurs in the lowest fossiliferous interval of the Penedo da Saudade succession (beds 506-511) (late Sinemurian, Obtusum zone). In the higher levels the species is substituted by a close but probably distinct form, *Ptycharietites* sp. cf. *P. ptychogenos* (POMPECKI).

***Ptycharietites* sp. cf. *P. ptychogenos* (POMPECKI, 1897)**

**Pl. IV, fig. 6; Pl. V, figs 1-5**

**Remarks:** The ammonites designated here are the large, unfortunately always crushed, *Ptycharietites* collected in the following higher fossiliferous interval of the Penedo da Saudade succession (beds 5105d-5106) (late Sinemurian, Obtusum zone). Although imperfectly preserved these forms seem to be subtly different from the former *P. ptychogenos* (POMPECKI) (cf. supra) in having larger adult diameters and more marked contrasts between the completely smooth inner whorls and the more coarsely ribbed outer whorls with noteworthy swollen primaries. A working hypothesis is that these large *Ptycharietites* are possible macroconchs of the smaller but mature concomitant *P. muellense* nov. sp. See hereinafter for a discussion about this problem.

***Ptycharietites muellense* nov. sp.**

**Pl. IV, figs 2-4**

**Derivation of the name:** Refers to the type locality, São Pedro de Muel.

**Type locality:** Penedo da Saudade, North of São Pedro de Muel, Beira Litoral, Portugal. “Coimbra Beds s.s.”, beds 5105b and 5105f-h, Early Jurassic, Late Sinemurian, ? Obtusum zone.

**Type specimens:** A finely preserved specimen (SPM/PS.b01) is selected as holotype. It is illustrated in Pl. IV, fig. 3. Although the thin shell is only partly conserved, the inner cast allows some subtle ornamental traits to be observed. The final suture lines of the phragmocone can be observed. The inner whorls as well as the body chamber are visible. The peristome is preserved. Two additional incompletely preserved specimens (SPM/PS.b10 and b11) are designated as paratypes.

**Material:** Additionally to the holotype and the two paratypes, another specimen (SPM/PS.b06) can be tentatively attributed to this new species.

**Diagnosis:** Small, platycone, compressed *Ptycharietites* characterised by a hardly perceptible and confusedly structured radial ornamentation composed of striae, slender ribs and/or undulations. The umbilicus widens noticeably towards the end of growth and the aperture may be constricted.

**Description:** The adult diameter of *Ptycharietites muellense* nov. sp. ranges from 50 mm to 90 mm. On the final whorl (mainly the body chamber) at least, the shell is platycone and well-compressed. The breadth

of the whorl section is about 23% of the diameter for the holotype and the umbilical width varies from about 30% to 40% of the diameter. The subrectangular to subogival whorl section is rather compressed ( $b/a \approx 0.64$  for the holotype). The shallow umbilical area is poorly differentiated and the umbilical rim is a simple accentuation of the curvature between the umbilicus and the sides of the whorls. The latter are gently curved and subparallel to slightly convergent. Maximum breadth occurs around the first-third of whorl height. The more or less marked latero-ventral rim corresponds to an sharpening of the bend between the sides and the ventral area. The venter bears a keel flanked by two obvious flat or slightly depressed oblique strips. Although moderately raised (at least on the internal cast) the keel remains an obvious trait until the end of growth where it extends as a short rostrum on the adult aperture. Unlike the obvious longitudinal ventral structures, the radial ornamentation is only perceptible under suitable lighting and consists of a confused combination of striae, slender ribs and/or vague undulations. In addition, the holotype has some tiny, barely visible bullae close to the latero-ventral rim (Pl. IV, fig. 3). This degenerated appearance of the radial ornamentation is consistent with its probable paedomorphic origin. Likewise, the barely denticulate suture line has a remarkable hardly structured appearance with broad, low saddles separated by narrow, shallow lobes (Fig. 3, U).

**Remarks:** The new species can be convincingly attributed to the genus *Ptycharietites* on the grounds of the morphology of the ventral area and the faint ornament of the sides, which are similar to some of the more characteristic traits of the inner whorls of *P. ptychogenos* (POMPECKJ). Despite these similarities, *P. muellense* nov. sp. has a truly unusual habitus for an Asteroceratinae. In fact, with its nearly smooth sides until the end of growth, its rather compressed platycone shell, the appreciable gradual widening of the umbilicus on the body chamber and its possibly constricted aperture, *P. muellense* nov. sp. possesses a singular set of features for a Sinemurian ammonite. The relatively small size of the shell associated with certain mature features such as the approximation of the last suture lines of the phragmocone, the belated widening

of the umbilicus, the complex pattern of the aperture with rostrum and marginal constriction might suggest a dimorphic pair with *P. muellense* nov. sp. as microconch and *Ptycharietites* sp. cf. *P. ptychogenos* (POMPECKJ) as macroconch. Nevertheless, the hypothesis of a distinct paedomorphic species is preferred here for *P. muellense* nov. sp. to the hypothesis of a dimorphic pattern because 1) small adult forms (possible microconch) are not found in the lower fossiliferous layers containing *Ptycharietites* (bed 506-511), 2) "a priori" it is a more neutral conjecture in terms of palaeobiology to assume this is a distinct species or lineage than to speculate dimorphism.

The Sinemurian Lusitanian faunas include another keeled and barely ribbed to practically smooth species. This form initially described as *Oxynoticeras choffati* by POMPECKJ (1906) is believed to have first appeared in the middle-late Sinemurian (Oxynotum zone) (MOUTERDE & ROCHA, 1981). Nevertheless, given its small umbilicus and its oxycone habitus this form can be easily differentiated from the evolute platycone *Ptycharietites muellense* nov. sp. *Oxynoticeras choffati* POMPECKJ was variously attributed to the genera *Oxynoticeras* (Oxynoticeratinae) (POMPECKJ, 1906; MOUTERDE & ROCHA, 1981), *Eparietites* (Asteroceratinae) (SPATH, 1925) or, tentatively, to the genus *Ptycharietites* (Asteroceratinae) (DOMMERGUES & MOUTERDE, 1987). For SPATH (1925) and DOMMERGUES & MOUTERDE (1987), *O. choffati* POMPECKJ is considered a younger relative of *Ptycharietites ptychogenos* (POMPECKJ) and the genus *Ptycharietites* as a whole as a lineage leading from coarsely ribbed, planulate to smooth, oxycone shells. This hypothesis remains plausible but is conjectural because of the lack of any data about the inner whorls of *O. choffati* POMPECKJ. Indeed, it would be necessary to demonstrate the paedomorphic origin of the smooth oxycone pattern to prove any close relationship between *P. ptychogenos* (POMPECKJ) and *O. choffati* POMPECKJ. For instance, the presence of a ribbed and possibly more or less tricarinate-bisulcate stage in the innermost whorls of *O. choffati* POMPECKJ would be sufficient evidence to exclude this species from the *Ptycharietites* lineage.

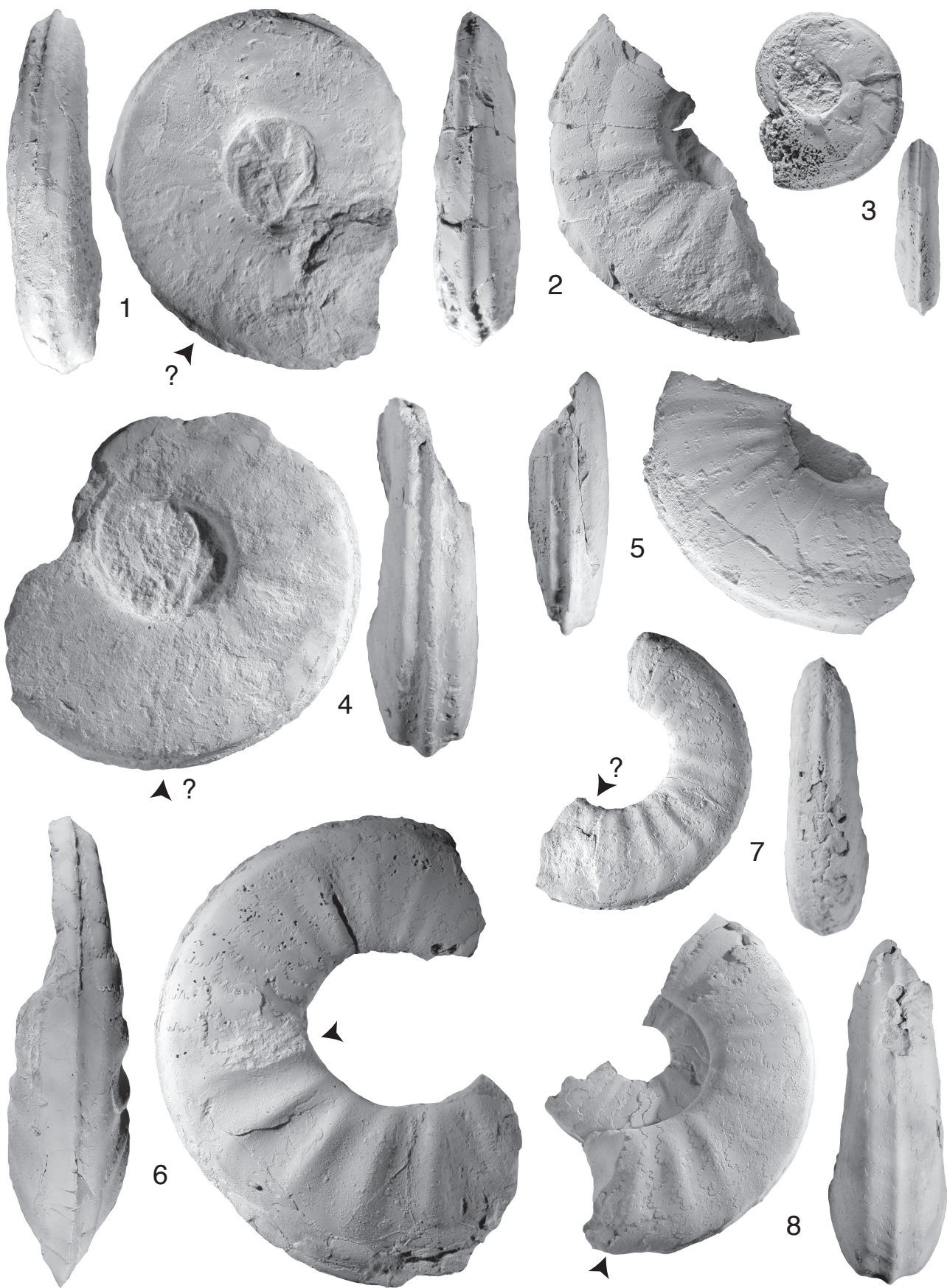
**Distribution and biostratigraphical range:** Until now *Ptycharietites muellense* nov. sp. has only been reported in the type locality of São Pedro de Muel in

#### Plate I

Figs 1-8: *Ptycharietites ptychogenos* (POMPECKJ, 1897), São Pedro de Muel, Penedo da Saudade. 1-3, SPM/PS.a26, x1, SPM/PS.a27, x1, SPM/PS.a21, x1, bed 510 sup.; 4, SPM/PS.a29, x1, bed 511; 5-6, SPM/PS.a25, x1, SPM/PS.a20, x1, bed 510 sup.; 7, SPM/PS.a08, x1, bed 506; 8, SPM/PS.a30, x1, bed 511.

All the specimens were whitened with ammonium chloride before being photographed. The arrow indicates the end of the phragmocone. The specimens are housed in the collections of the "Centre des Sciences de la Terre de l'Université de Bourgogne".





the “Coimbra Beds s.s.”. Its presence is restricted to the highest fossiliferous interval of the Penedo da Saudade succession (bed 5105b-5105g) (Late Sinemurian, Obtusum zone, ? Obtusum subzone).

***Ptycharietites* sp. cf. *P. muellense* nov. sp.**

**Pl. V, fig. 6**

**Remarks:** The specimen considered here is the youngest ammonite newly collected in the Penedo da Saudade succession. It came from the lower part of a set of small beds numbered 5110 on the section and situated about 2.5 m above the main levels containing *P. muellense* nov. sp. (Fig. 2). Although only partially preserved this crushed specimen displays the main characteristics of *P. muellense* nov. sp. as a small platycone shell bearing rather faint radial ornamentation. Nevertheless, there is a subtle but definite contrast between the faintly ribbed inner part of the preserved whorl and the delicately striated outer part of this whorl. This trait, unknown in the typical *P. muellense* nov. sp., must be emphasised.

**RELATIONSHIPS, ONTOGENY AND VARIATION**

Among the Early Jurassic ammonites many of the species attributed to the Asterooceratinae, Oxynoticeratidae and Echioceratidae can be assumed to form a clade (= monophyletic group). This clade will be designated by the abbreviation AOEG (for Asterooceratinae, Oxynoticeratidae and Echioceratidae group). The earliest members of the genus *Caenisites*, *C. costariformis* (SPATH, 1926) or *C. obtusifomis* (SPATH, 1926) (Early Sinemurian, Turneri Zone), provide an image of the probably more primitive forms of AOEG. Highly derived serpenticone forms (Echioceratidae) or, conversely, oxycone forms (Oxynoticeratidae) evolved in a dramatic radiation from the fairly evolute, subserpenticone and tricarinate-bisulcate earliest *Caenisites*. AOEG have been studied in detail at least since the days of HYATT (1889). HYATT concludes that there may be several independent branches and, for example, arranges *Eparietites*, *Oxynoticerias* and *Gleviceras* in three different lineages (HYATT, 1889, pl. 13). Subsequently, PIA (1914) proposed another synthesis but unlike HYATT, admitted the existence of a predominant branch leading from *Asteroceras* to *Oxynoticerias* via *Gleviceras*. No modern synthesis was available until the revisions proposed by DONOVAN (1987,

1994). In these works and mainly in the latter, DONOVAN (1994) offers a valuable synthetic view covering both morphology and stratigraphy. DONOVAN'S hypothesis strongly rejects the idea that a single lineage might lead to the whole of the involute taxa (e.g. *Oxynoticerias*, *Gleviceras*, *Radstockicerias*) traditionally included in the Oxynoticeratidae family. Indeed, DONOVAN (1994) proposes the existence of two distinct major lineages. The first (lineage A *sensu* DONOVAN, 1994) roots with *Caenisites turneri* (J. DE C. SOWERBY, 1824) and ends during the Carixian with discoid forms like *Carixicerias wiltshirei* (WRIGHT, 1881). For DONOVAN (1994) this lineage includes as transitional steps the genera *Eparietites*, *Oxynoticerias* and also encompasses as minor branches *Cheltonia* and *Paracymbites*. According to DONOVAN (1994, fig. 3) the second clade (lineage B) originated with *Caenisites obtusifomis* (SPATH, 1926) and became extinct during the Pliensbachian with *Radstockicerias* or even perhaps later with *Fanninoceras*. Again according to DONOVAN, the transitional genera of the “main line” of lineage B should be *Asteroceras* then *Gleviceras*. Beside that main line but still within lineage B, DONOVAN (1994) assumes that several planulate or suboxycone groups (*Aegasteroceras*, *Arctoasteroceras*, *Parasteroceras*, *Pompeckioceras* and a new Tethyan genus) evolved separately from the genus *Asteroceras*.

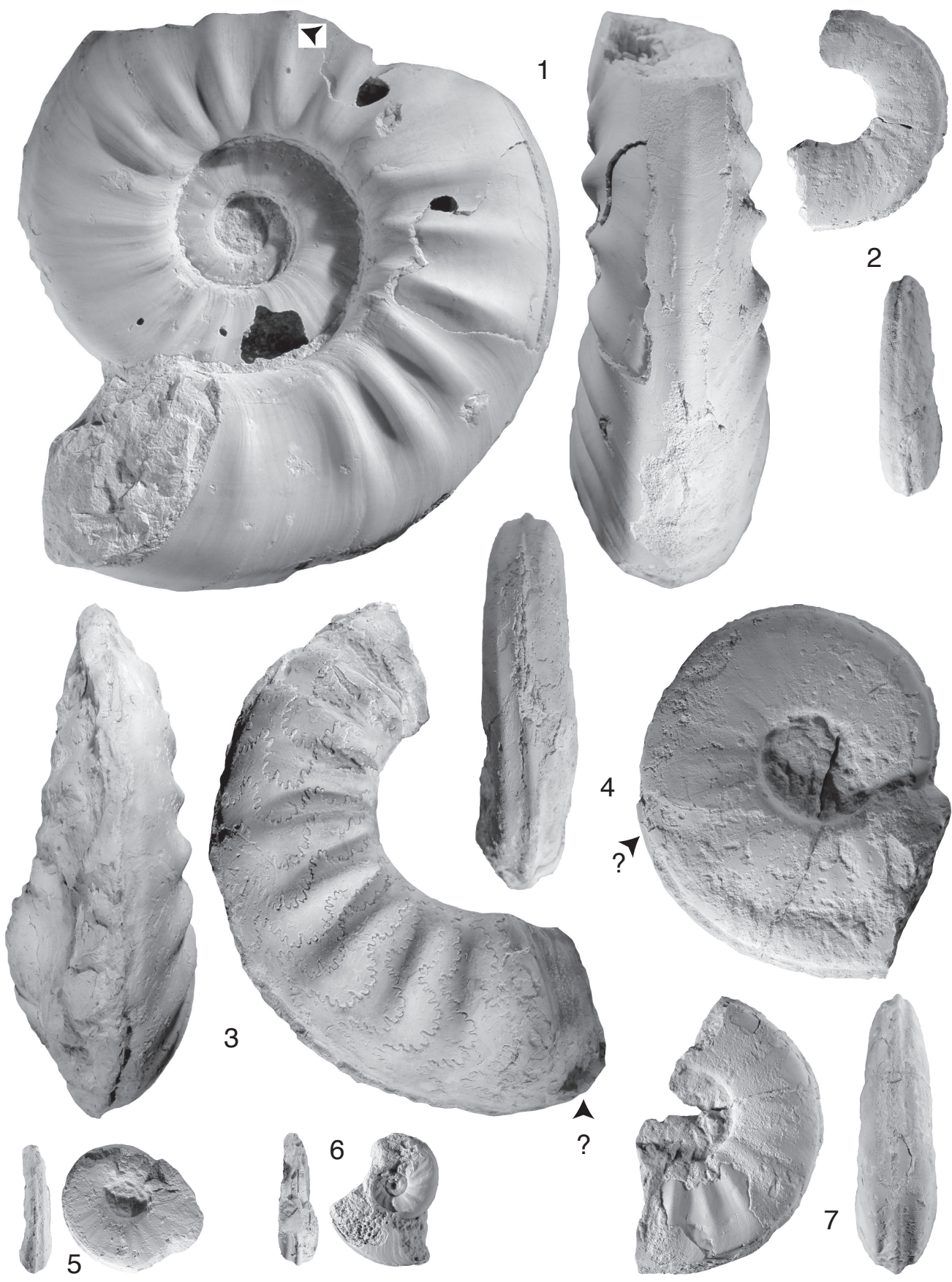
DONOVAN'S work provides the only possible reference for the present discussion about the Lusitanian endemic Asterooceratinae (= LEA). For DONOVAN (1994, fig. 4) the LEA form one of the minor excurrent branches belonging to lineage B. This short-lived branch evolved from *Asteroceras obtusum* (J. SOWERBY, 1817) in the early Obtusum zone and ended during the middle part of this zone (DONOVAN, 1994, fig. 4). More generally, DONOVAN (1994) classifies LEA with the genera *Aegasteroceras*, *Arctoasteroceras* and *Parasteroceras* in a group of planulate forms characterised by “degeneration” or loss of ventral ornament (e.g. keel, sulci). Nevertheless, a careful analysis of these similar patterns suggests convergences. For example, and even if only the late ontogenetic stages (apart from the apertural patterns) of the large specimens are considered:

1) *Aegasteroceras* differs from the LEA by its propensity to lose all longitudinal ventral structures (keel, furrows, sulci) in favour of greater radial ornament (ribs). In the extreme, this trend ends up giving rather “capricorn” morphologies (e.g. *Aegasteroceras simile* SPATH, 1925), which are virtually keelless and with subradial, coarse

Plate II

Figs 1-7: *Ptycharietites ptychogenos* (POMPECKJ, 1897), São Pedro de Muel, Penedo da Saudade. 1-2, SPM/PS.a04, x1, SPM/PS.a07, bed 506; 3, SPM/PS.a31, x0.75, bed 511; 4, SPM/PS.a16, x1, bed 510 inf.; 5-6, SPM/PS.a22, x1, SPM/PS.a00, x1.2, bed 510 sup.; 7, SPM/PS.a12, x1, bed 510 inf.

Plate II



and distant ribs running without interruption across the ventral area.

2) *Arctoasteroceras* also differs from the LEA by its propensity to lose all longitudinal ventral patterns but unlike *Aegasteroceras*, the radial ornamentation too is significantly affected by this phenomenon. Thus, ribs die out about two-thirds of the way across the whorl side and the rather broad ventral area of the largest derived forms (e.g. *A. jeletzkyi* FREBOLD, 1960) is often evenly arched with either a scarcely perceptible keel or no keel at all. In this case, longitudinal grooves or flat strips are also usually missing.

3) At least on the body chamber of the largest specimens (macroconchs?) (e.g. *P. rakusi* DOMMERGUES, FAURE & PEYBERNES, 1986), *Parasteroceras* displays a narrow, evenly arched and keelless, smooth ventral area which excludes any close relationship with either the LEA or with *Arctoasteroceras*. Indeed, in this late genus, which also has a smooth keelless ventral area, the whorl section is definitely broader and the shells look very different.

To resume in the late ontogenetic stages of the large specimens, LEA differs from all the other roughly similar genera (*Aegasteroceras*, *Arctoasteroceras* and *Parasteroceras*) in that some longitudinal ornament persists albeit more faintly. Indeed, the keel, and very often the flat or slightly depressed, smooth flanking strips, invariably persist until the aperture (Pl. II, fig. 1). Moreover, even at the largest diameters, the ribs are strictly limited to the inner two-thirds of the sides but have a curious inflated (turgescens) appearance, contrasting sharply with the fairly smooth outer part of the sides (Pl. II, fig. 3; Pl. V, figs 1, 4).

If the entire shell ontogeny is considered and not just its late stages, the peculiarity of the LEA lineage among AOEG becomes more obvious. Excluding the serpenticone forms (lineage C *sensu* DONOVAN, 1994), and the suspected first members of AOEG, all the other species included in AOEG display some more or less obvious morphological changes during ontogenesis. To simplify, two opposing patterns are roughly recognisable. The first, of plesiomorphic significance, corresponds to a rather evolute shell with little overlap of the whorls. The whorl section is hardly compressed. The ribs are usually sharp, more or less straight on the whorl side, and then often curve forwards and run into the raised lateral margins of the ventral grooves. These grooves are broad and semicircular in cross section. The keel is roughly as high as the lateral margins and the ventral areas seem

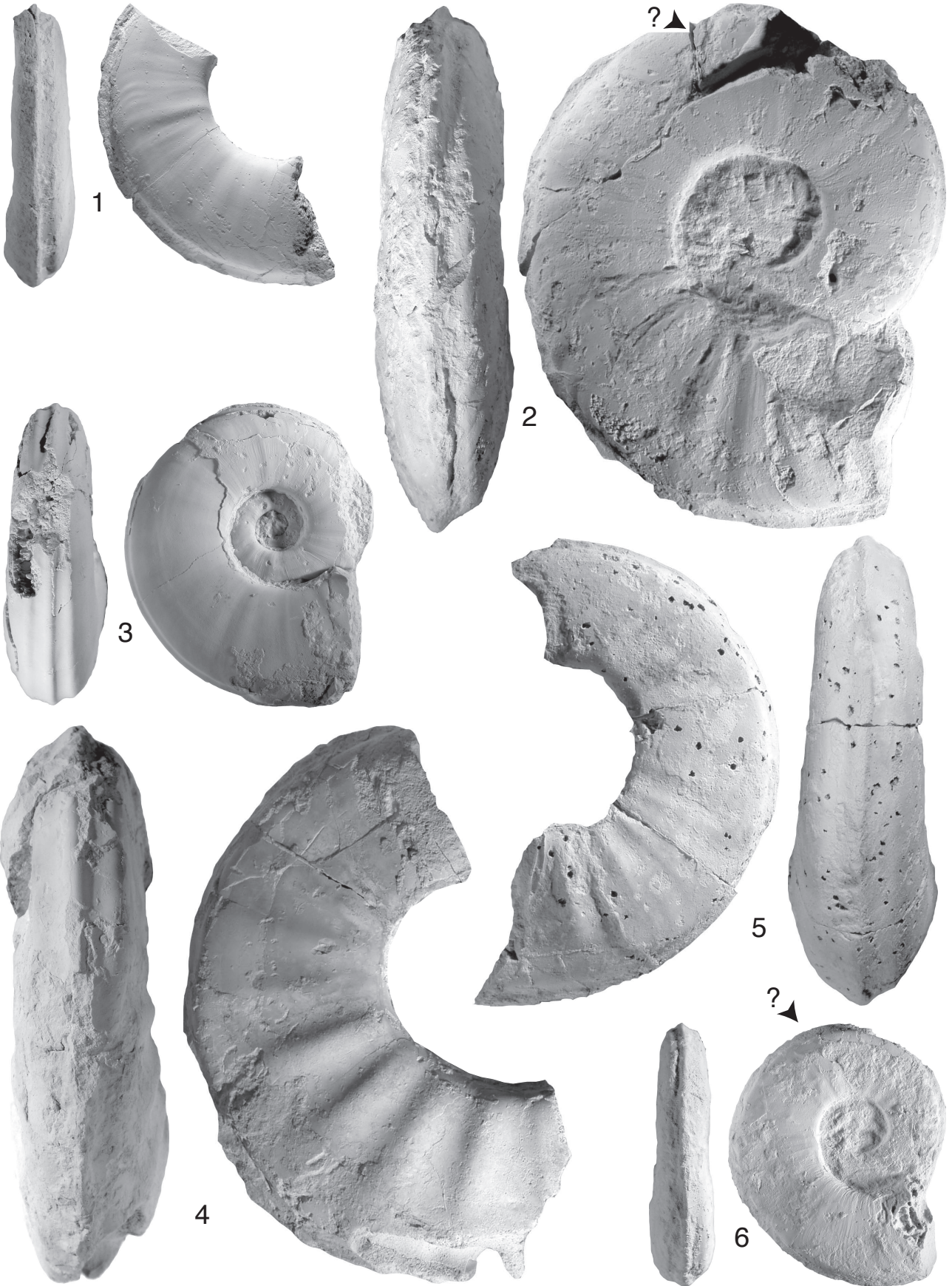
flat. The second pattern, of apomorphic significance, is of an involute shell with strongly overlapping whorls and a small umbilicus. The whorl section is clearly compressed. Apart from the usually sharp keel, all the ornamental structures are missing. In the extreme, the shell can look like a smooth disc with a sharp edge.

Of course, all the intermediate stages can occur and a wide array of combinations is possible. The body chamber of *Eparietites denotatus* (SIMPSON, 1855) is an example of such a morphological transitional morphology (Fig. 4, A). Around the end of growth, *E. denotatus* (SIMPSON) has a fairly involute shell with significantly overlapping whorls. The whorl section is compressed. The ribs are missing or reduced to faint undulations. Two flat, more or less oblique strips flank the sharp and prominent keel.

At this stage of the study these patterns are only of descriptive value and are devoid of any phyletic presupposition. In almost all cases ontogeny unfolds from a relatively evolute, ribbed and tricarinate-bisulcate shell with a rather broad whorl section (symbolised in dark grey in Fig. 4) towards a relatively involute, ribless and monocarinate shell with a compressed whorl section (symbolised in white in Fig. 4). This is especially true for the main lines of the two major lineages A and B (*sensu* DONOVAN, 1994) of AOEG. In the course of these two assumed evolutionary lines, the species follow peramorphoclines *sensu* McNAMARA (1982) and the evolute ribbed juvenile stage tends to be restricted to the innermost whorls or may sometimes virtually disappear. As underlined by SPATH (1925), some specimens belonging to *Ptycharietites* may exhibit a striking likeness to *Eparietites* and especially to the outer whorl of this latter genus. The fairly involute, compressed and smooth specimens of *Ptycharietites ptychogenos* (POMPECKI, 1897) illustrated here (Pl. I, figs 1, 4; Pl. II, fig. 4; Pl. III, fig. 3) are good examples of such resemblances. SPATH (1925) considers these similarities are of phyletic significance and he assumes close relationships between *Ptycharietites* and *Eparietites*. On the basis of ontogeny, though, this hypothesis must be rejected. Indeed, while in *Eparietites* an involute and ribless stage with a compressed whorl section succeeds an evolute and ribbed stage with a rather broad whorl section, the opposite polarity characterises the LEA and is obvious in *Ptycharietites ptychogenos* (POMPECKI) (Pl. I, fig. 6; Pl. II, fig. 1; Pl. III, figs 2, 4, 5; Pl. V, fig. 4; Fig. 4). Thus, if in *Eparietites* and in the main part of AOEG the involute ribless stage spreads and becomes predominant within

### Plate III

Figs 1-6: *Ptycharietites ptychogenos* (POMPECKI, 1897), São Pedro de Muel, Penedo da Saudade. 1, SPM/PS.a09,  $\times 1$ , bed 506 inf.; 2, SPM/PS.a18,  $\times 1$ , bed 510 sup.; 3, SPM/PS.a06,  $\times 1$ , bed 506; 4, SPM/PS.a10,  $\times 0.75$ , bed 508; 5, SPM/PS.a28,  $\times 1$ , bed 511 inf.; 6, SPM/PS.a24,  $\times 1$ , bed 510 sup.



a peramorphic context, the opposite (paedomorphosis) occurs in the LEA. In fact, the discoid and ribless habitus is not a homology at the scale of the whole AOEG: 1) the similarities between the smooth oxycone derived forms belonging to lineages A and B (*sensu* DONOVAN, 1994) result from parallelisms, 2) the resemblances between *Eparietites* and *Ptycharietites* are convergencies. The paedomorphic significance of the platycone and ribless stage in LEA explains the significant intra-specific variation as well as the extensive disparity within the group. Indeed mere modifications of growth rates and/or mere shifts in the timing of ontogenetic events (e.g. sexual maturity, end of growth) can bring out obvious morphological changes. For instance, in *Ptycharietites ptychogenos* (POMPECKI), the transition from the rather involute, compressed and ribless “juvenile” stage to the more evolute, broad and ribbed “late” stage occurs at various diameters. Some specimens (Pl. I, figs 7, 8; Pl. II, fig. 7) illustrate precocious transition (ribs appear about 4 to 5 cm in diameter) while others (Pl. II, fig. 1; Pl. III, figs 2, 4, 5) display late transition (ribs appear about 6 to 9 cm in diameter). In addition, the transition ranges from abrupt (Pl. II, fig. 7) to gradual (Pl. III, fig. 2). Taking into account the difficulty of observing features indicating the end of growth within *P. ptychogenos* (POMPECKI) it can, at the very most, be suspected that in some specimens growth may end before the appearance of the ribbed stage (e.g. Pl. I, fig 1; Pl. III, figs 1, 6). With *Ptycharietites muellense* nov. sp. a younger representative of LEA, the extension and the prominence of the ribless stage increase and some evidently adult specimens remain smooth until the end of growth at about 10 cm diameter (Pl. IV, fig 2; Fig. 4, C). In the same levels but expressing a clearly distinct trend, the large *Ptycharietites* sp. cf. *P. ptychogenos* (POMPECKI) display an obvious and predominant coarsely ribbed stage. However, in these forms and until about 8 cm in diameter, the inner whorls are usually perfectly smooth and there is a striking contrast between the inner and outer whorls (Pl. V, fig. 4). In fact, the heterochronic

evolution of LEA leads to an increase in the magnitude and heterogeneity of disparity.

## PALAEOBIOGEOGRAPHIC DISCUSSION

With three endemic genera, *Ptycharietites* (late Sinemurian), *Pseudophricodoceras* (early Carixian), *Dayiceras* (middle Carixian) and about five early or middle Carixian endemic species, the Lusitanian basin is definitely a major centre of endemism (DOMMERGUES & MOUTERDE, 1987; DOMMERGUES & EL HARIRI, 2002). This endemic phenomenon persists through five ammonites zones ( $\approx 7$  Ma).

In cases of such recurrent endemic patterns within a given region, the possibility of a palaeogeographical constraint capable of inducing faunal confinement must be explored first. To this end, Figures 5 and 6 are given to illustrate the geological and palaeogeographical setting of the Lusitanian basin. Figure 5 shows the distribution of the predrift Mesozoic basins on the CNA margins.

Predrift basins without doubt yield a truncated image of the full extent of the Jurassic seas and of their associated deposits. Consequently any palaeogeographic reconstruction is unavoidably tentative in part. For example, despite the lack of any objective data, ZIEGLER's maps (1988) indicate that deep water conditions were established by the end of the Early Jurassic on the Tagus-Iberia abyssal plains and Newfoundland basin (Fig. 6, A). Thus, for that author the present Lusitanian basin is merely viewed as the Eastern border of a wider pre-Atlantic basin. In a different way and more in accordance with the geological and geophysical constraints, the reconstructions proposed by THIERRY *et al.* (2000) (Fig. 6, B) and by STAMFLI & BOREL (2001) show the Lusitanian and Alentejo basins as forming a fairly narrow furrow between the Flemish cap and the Grand Banks to the West and the Iberian landmass to the East.

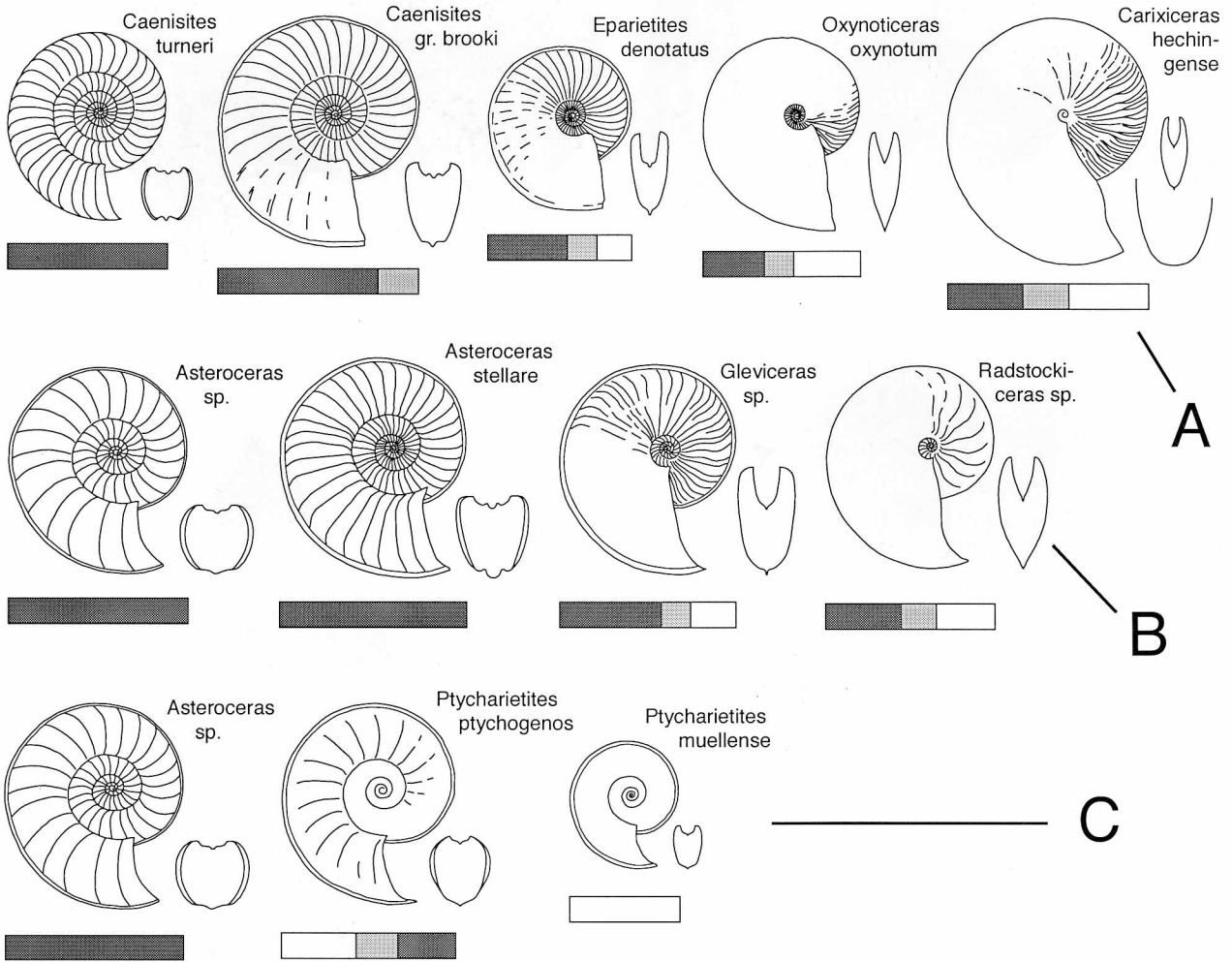
Nevertheless, above and beyond these differences all the available palaeobiogeographical models are largely

## Plate IV

- Fig. 1: *Ptycharietites* sp., possibly a body chamber of *P. muellense* nov. sp., São Pedro de Muel, Penedo da Saudade; SPM/PS.b06, x1, bed 5105f.
- Fig. 2: *Ptycharietites muellense* nov. sp., Paratype, São Pedro de Muel, Penedo da Saudade; SPM/PS.b10, x1, bed 5105f-g.
- Fig. 3: *Ptycharietites muellense* nov. sp., Holotype, São Pedro de Muel, Penedo da Saudade; SPM/PS.b01, x1, bed 5105b.
- Fig. 4: *Ptycharietites muellense* nov. sp., Paratype, São Pedro de Muel, Penedo da Saudade; SPM/PS.b11, x1, bed 5105g-h.
- Fig. 5: *Ptycharietites* sp., São Pedro de Muel, Penedo da Saudade; SPM/PS.b12, x1, bed 5105 g-h.
- Fig. 6: *Ptycharietites* sp. cf. *P. ptychogenos* (POMPECKI, 1897), crushed specimens, São Pedro de Muel, Penedo da Saudade; SPM/PS.b16, x1, bed 5106.



Fig. 4: Habitus and ontogeny within three closely related lineages of upper Sinemurian to lower Pliensbachian Psilocerataceae. A, *Caenisites* to *Carixiceras* via *Eparietites* and *Oxynoticeras* (DOMMERMUES, 1990; DONOVAN, 1994). B, *Asteroceras* to *Radstockiceras* via *Gleviceras* (DONOVAN, 1994). C, *Asteroceras* to *Ptycharietites*. Within each lineage, the evolution unfolds from left to right. Ontogeny is suggested by symbolic cartouches below each illustrated species. Cartouche length is proportional to adult diameter. Ontogeny must be read from left (juvenile stage) to right (adult stage). The dark grey rectangle symbolises stout ribs, clear furrows by the side of the keel and usually a fairly broad whorl section. The white rectangle symbolise smooth sides, lack of furrows by the side of the keel (if any) and usually fairly compressed whorl section. The light grey suggests an intermediate morphology.



Morphological sequence (from plesiomorphy to apomorphy)

Plate V

Figs 1-5: *Ptycharietites* sp. cf. *P. ptychogenos* (POMPECKI, 1897), crushed specimens, São Pedro de Muel, Penedo da Saudade. 1, SPM/PS.b14, x1, bed 5105g-h; 2, SPM/PS.b00, x1.5, bed 5105; 3, SPM/PS.b04, x1, bed 5105d; 4, SPM/PS.b08, x1, bed 5105f; 5, SPM/PS.b03, x1, bed 5105d;

Fig. 6: *Ptycharietites* sp. cf. *P. muellense* nov. sp., São Pedro de Muel, Penedo da Saudade; SPM/PS.b17, x1, bed 5110 inf.



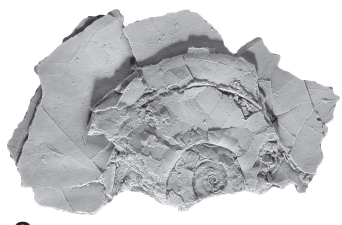
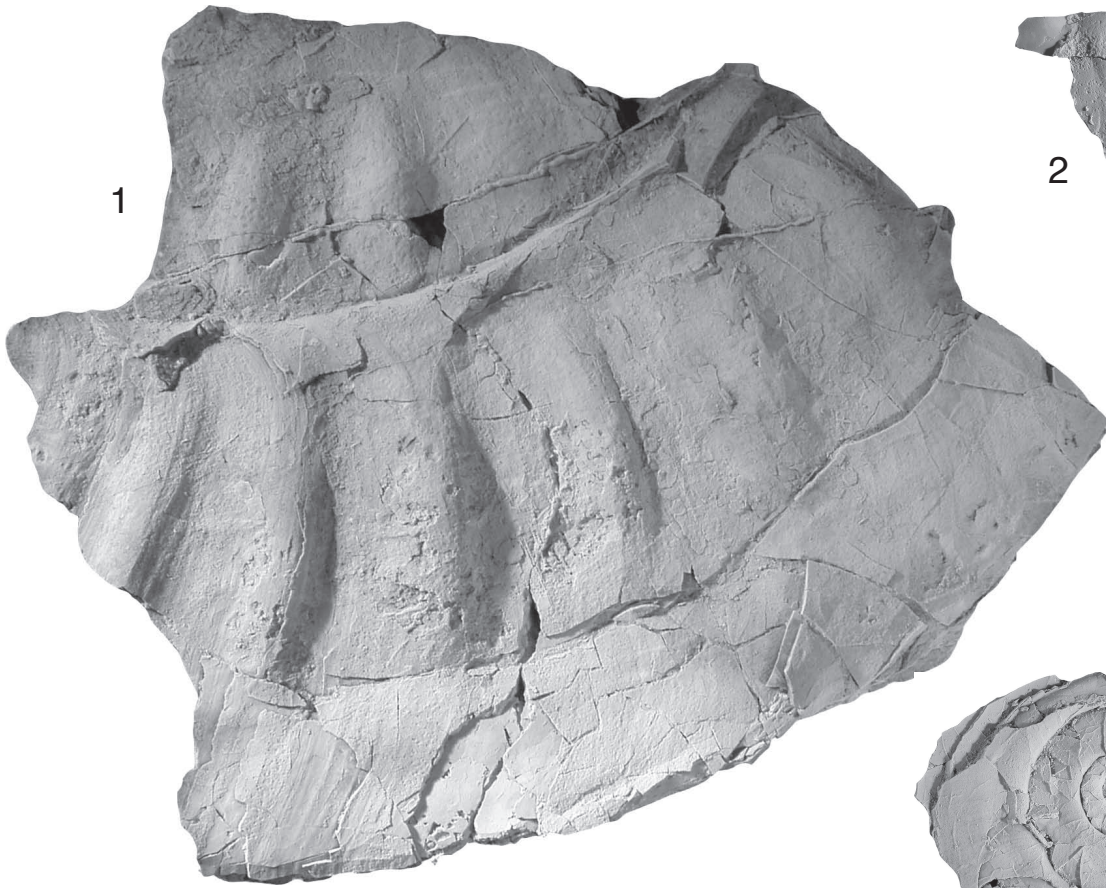
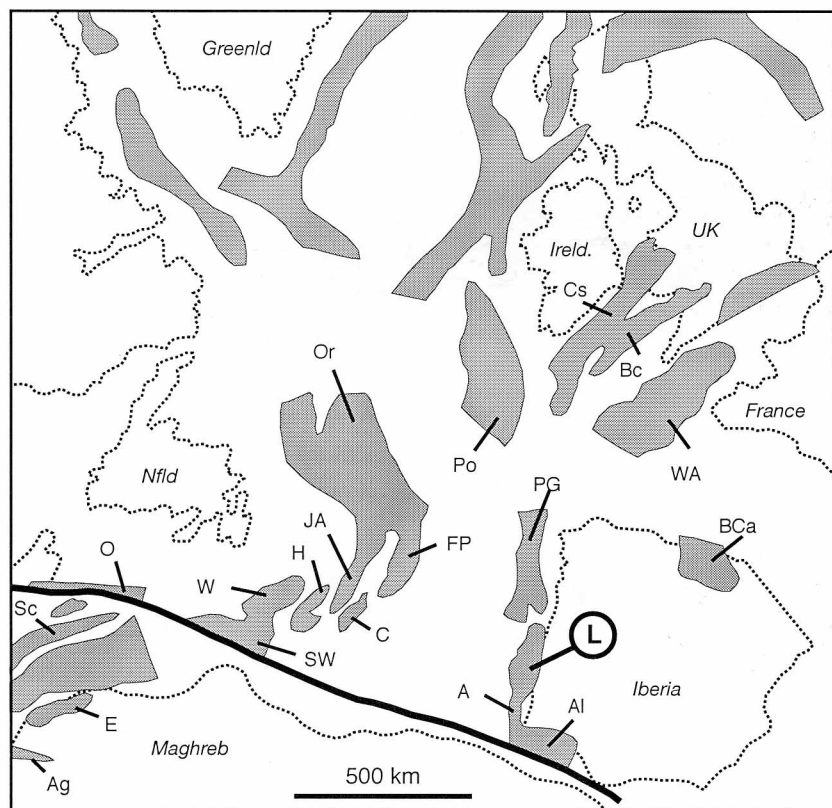


Fig. 5: Predrift basins of the Central North Atlantic margins (Modified and simplified after TANKARD & BALKWILL, 1989). Landmass distribution is not in predrift position but is given at magnetic anomaly M-0 (118 Ma, Aptian) hence about 38 Ma after the initiation of the opening at probably M-25 (156 Ma, Kimmeridgian). The thick black line indicates the "Azores fracture zone".



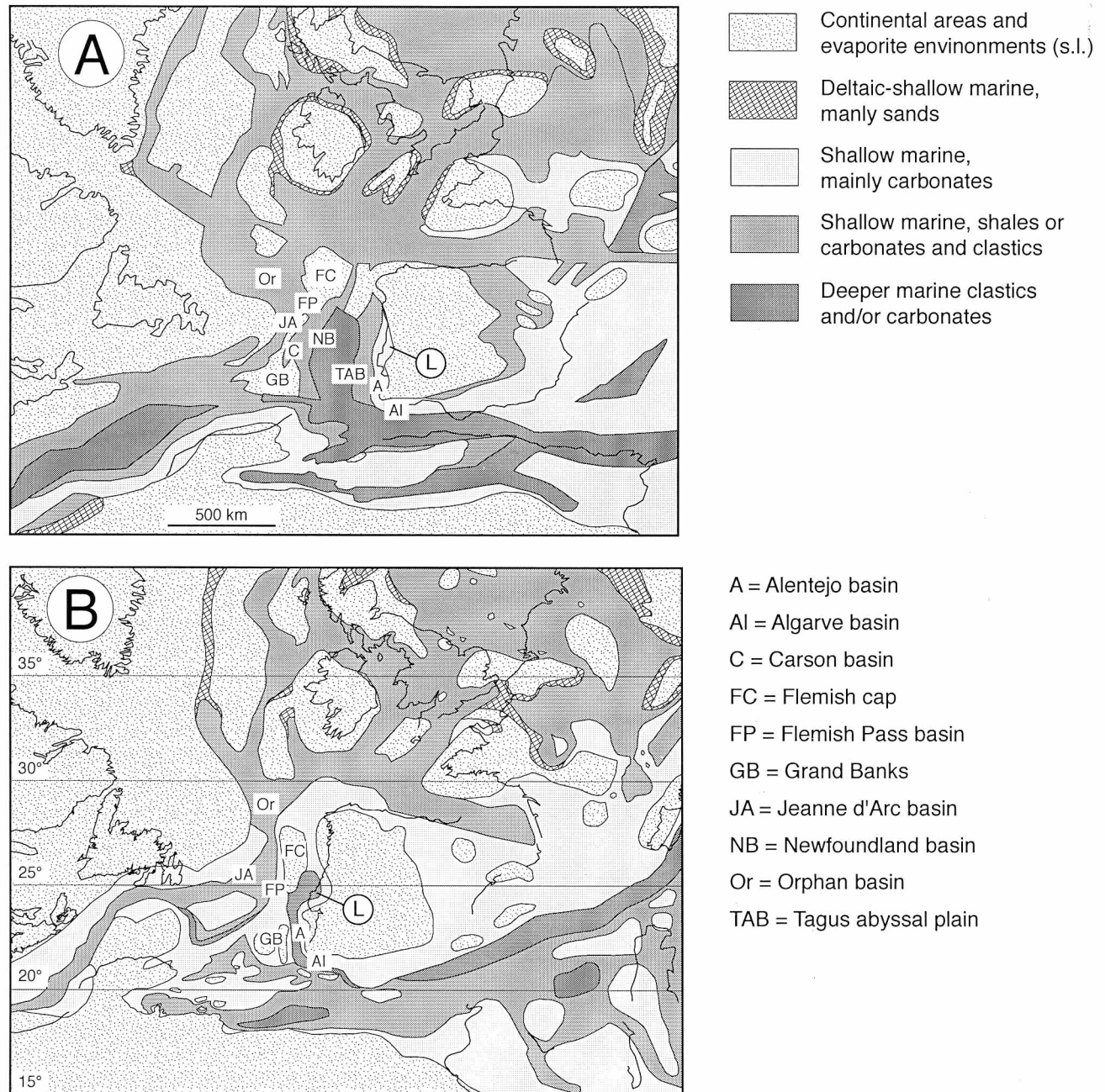
- A = Alentejo basin
- Ag = Agadir basin
- Al = Algarve basin
- Bc = Bristol Channel basin
- Bca = Basque-Cantabrian basin
- C = Carson basin
- Cs = Celtic Sea basin
- E = Essaouira basin
- FP = Flemish Pass basin
- H = Horseshoe basin
- JA = Jeanne d'Arc basin
- L = Lusitanian basin
- O = Orpheus basin
- Or = Orphan basin
- PG = Porto-Galicia basin
- Po = Porcupine basin
- Sc = Scotian basin
- SW = South Whale basin
- W = Whale basin
- WA = Western Approaches basin

equivalent: 1) The Lusitanian-Alentejo basins [and also for ZIEGLER (1988) the Tagus abyssal plain and the Newfoundland basin] made up a roughly South-North rift basin. 2) This basin opened towards the Mediterranean areas (e.g. Algarve basin, North Africa, etc.) and can be thought of as a peri-Tethyan appendix. 3) The connections towards the northern seas were limited to just a few narrow and probably shallow seaways. 4) The Lusitanian basin is part of the maze of the westernmost confines of the peri-Tethyan seas. 5) The Lusitanian basin was situated in nearly tropical latitudes ( $\approx 25^\circ$  N).

Of all the characteristics of the Lusitanian basin, 1) the remoteness from the main peri-Tethyan North-West European and Mediterranean seas and 2) the maze of basins and seaways between Iberia and Laurentia may have been favourable factors for the emergence and the survival of endemic species and/or lineages. From many points of view the Lusitanian endemic ammonites and more generally the Lusitanian ammonite faunas, are a palaeobiogeographic enigma during the late Sinemurian and the Carixian. Indeed, despite geological and geophysical indications strongly supporting easier southwards than northwards marine connections, the

taxa, including the endemic ones, have usually clear North-West European relationships (DOMMERGUES & EL HARIRI, 2002). Elucidation of this apparent paradox is perhaps to be sought in the study of marine currents and of related environmental parameters. Anyway, the palaeogeographical and palaeoecological contexts still raise too many unresolved questions to propose an unambiguous, convincing and mainly falsifiable palaeobiogeographical scenario about the endemic Lusitanian *Ptychariatites* lineage. Nevertheless, four facts can be underlined: 1) the appearance of the first representatives of the endemic *Ptychariatites* lineage [*P. ptychogenos* (POMPECKJ)] is synchronous with the first clearly pelagic episode in the São Pedro de Muel section (Penedo da Saudade, levels 506-511). 2) From the time it first appears in the Lusitanian fossil record with the species *P. ptychogenos* (POMPECKJ), *Ptychariatites* is a fairly plentiful genus. 3) With *Ptychariatites ptychogenos* (POMPECKJ), the lineage immediately shows an advanced pedomorphic habitus. 4) The very low diversities of Lusitanian Late Sinemurian faunas with *Ptychariatites* are surprising in view of the usually high diversity of tropical or subtropical faunas.

Fig. 6: The Lusitanian basin in its palaeogeographical context. Comparison of two palaeogeographic reconstructions including the North-Central Atlantic region. A, map for the Sinemurian-Toarcian interval after ZIEGLER (1988, modified and simplified). B, map for the Sinemurian after THIERRY *et al.* (2000, modified and simplified). Notice that different cartographic projections are used for maps A and B.



Thus unless a punctuated origination (e.g. punctuated equilibrium *sensu* ELDREDGE & GOULD, 1972) of the *Ptychrietites* lineage is envisaged, it must be admitted that the first steps in the group history are unknown. Indeed, given our ignorance of CNA macro-faunas, it is tempting to assume an origination in a undocumented part of the Lusitanian deposits and/or in a completely different sector of the CNA seas. In this case, the

appearance of *Ptychrietites* in the mainly neritic series of São Pedro de Muel should be just the distal result of faunal intrusions associated with relative sea level rises. It should be interesting to discuss if the cause of such sea level variations was primarily eustatic or local tectonic but recent synthesis (e.g. HARDENBOLD *et al.*, 1998) as well as regional studies for north-west European or Mediterranean areas (e.g. DONOVAN *et al.*,

1979; SOUHEL *et al.*, 1998) are often clashing and hardly relevant to the CNA context.

## ACKNOWLEDGEMENTS

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