

The Sinemurian ammonites of the Lusitanian Basin (Portugal): an example of complex endemic evolution

JEAN-LOUIS DOMMERGUES, CHRISTIAN MEISTER & ROGÉRIO B. ROCHA

Abstract

This work synthesizes all of the observations since the late nineteenth century of the highly endemic Late Sinemurian (Obtusum Chronozone) ammonite faunas of the Lusitanian Basin. It is based mainly on recent abundant collections from the Penedo da Saudade section near São Pedro de Muel (Leiria, Portugal). This rich material (some eight species and four genera), collected bed by bed, allows us to propose an initial biostratigraphic, palaeobiogeographic, evolutionary and taxonomic synthesis of these mostly endemic faunas. The genus *Epophioceroides* n. gen. is new and three new species are identified: *Epophioceroides apertus* n. gen. n. sp., *Ptycharietites* (Subgen. indet. A) *asteroceroides* n. sp. and *Ptycharietites* (*Ptycharietites*) *heterogenus* n. sp. So far they have been found at São Pedro de Muel only. The only non-endemic ammonite, *Asteroceras* sp. indet., collected from the base of the fossiliferous sequence, suggests an age in the Obtusum Chronozone for the subsequent taxa. Most probably faunas belong to the Stellare Subchronozone but taxa from the highest fossiliferous levels may also belong to the Denotatus Subchronozone. The newly collected material requires the morphological range of the genus *Ptycharietites* to be extended to include late forms that become either clearly evolute (subserpenticone) such as *Ptycharietites* (*Pompeckioceras*) cf. *onchocephalus* or clearly involute (suboxycone) such as *Ptycharietites* (? Subgen. indet. B) sp. indet. A. In terms of ontogeny, pedomorphosis – a rare “size-based” heterochronic process among the Asteroceratinae subfamily – is shown to be of major importance throughout the evolution of the genus *Ptycharietites*. In palaeobiogeographic terms all endemic Late Sinemurian (Obtusum Chronozone) ammonite faunas (*Ptycharietites* and *Epophioceroides* n. gen.) of the Lusitanian Basin remain poorly understood. While they suggest marked isolation of the Lusitanian Basin and perhaps also constraining environmental conditions during the Obtusum Chronozone, there is nothing to indicate whether other basins of the “Iberia-Newfoundland” conjugate margins experienced the same endemic trend. Nor is it clear whether the Late Sinemurian endemic faunas are closely related to NW European or to W Tethyan (Mediterranean) faunas. However, the earliest ammonite collected from the São Pedro de Muel section (i. e., *Asteroceras* sp. indet., bed 500b) suggests a possible NW European affinity.

Key words: Ammonites, Early Jurassic, Lusitanian Basin, Portugal, evolution, endemism, palaeobiogeography.

Zusammenfassung

In der vorliegenden Arbeit synthetisieren wir die Ergebnisse aller seit dem späten 19. Jahrhundert erschienenen Arbeiten über die Ammoniten-Faunen des späten Sinemurium (Obtusum Chronozone) des Lusitanischen Beckens. Die Datenbasis bilden hauptsächlich Neuaufsammlungen in dem Profil Penedo da Saudade bei São Pedro de Muel (Leiria, Portugal). Das reiche Material (ca. acht Arten aus vier Gattungen) wurde bankweise entnommen und erlaubt eine erste biostratigraphische, paläobiogeographische, evolutionäre und taxonomische Synthese der hoch-endemischen Faunen. Die Gattung *Epophioceroides* n. gen. sowie die drei Arten *Epophioceroides apertus* n. gen., n. sp., *Ptycharietites* (Subgen. indet. A) *asteroceroides* n. sp. und *Ptycharietites* (*Ptycharietites*) *heterogenus* n. sp. werden erstbeschrieben. Diese sind bislang nur von São Pedro de Muel bekannt. Eine einzige Form – *Asteroceras* sp. indet. von der Basis des fossilführenden Profilschnittes – scheint nicht endemisch zu sein und legt die Obtusum Chronozone als Alter der Fauna nahe. Höchstwahrscheinlich gehört die Fauna zu der Stellare Subchronozone aber die Taxa aus den jüngsten fossilführenden Schichten können auch Denotatus Subchronozone anzeigen. Das neu gesammelte Material erlaubt es, die morphologische Variabilität der Gattung *Ptycharietites* zu erweitern: zeitlich späte Formen sind entweder deutlich evolut (subserpenticone) wie *Ptycharietites* cf. *onchocephalus* oder deutlich involut (suboxycon) wie bei *Ptycharietites* (? Subgen. indet. B) sp. indet. A. Auf die Ontogenie bezogen ist Pädomorphose ein sehr wichtiger Prozess in der Evolution der Gattung *Ptycharietites*. Pädomorphose ist sonst selten in der Unterfamilie Asteroceratinae. Die Paläobiogeographie der endemischen Ammoniten-Faunen (*Ptycharietites* und *Epophioceroides* n. gen.) des Lusitanischen Beckens ist weiterhin unklar. Die Faunen legen eine deutlich isolierte geographische Position des Lusitanischen Beckens und vielleicht restriktive Umweltbedingungen in der Obtusum Chronozone nahe. Es gibt aber keine Hinweise, ob andere Becken des konjugierten „Iberia-Newfoundland“-Randes in Bezug auf ihre Faunen einen ähnlichen endemischen Trend haben. Zusätzlich bleibt die Beziehung der endemischen Spätsinemur-Faunen entweder zu NW-europäischen Faunenentwicklung oder zur der der W-Tethys (Mediterran) unklar. Der früheste im Profil São Pedro de Muel gefundene Ammonit (*Asteroceras* sp. indet., Schicht 500b) deutet jedoch wahrscheinlich auf NW-Europa hin.

Contents

1. Introduction.....	60
2. Geographical, geological and historical settings.....	61
3. Systematic palaeontology.....	63
4. Evolution and ontogeny.....	75
5. Palaeogeography and palaeobiogeography.....	77
6. Conclusions.....	79
7. References.....	79

1. Introduction

Endemism, whether neo-endemism (endemism by novation) or palaeo-endemism (relic endemism), is a fascinating (palaeo)biogeographic phenomenon immediately suggesting close relationships between the evolution of life forms and that of the Earth itself. Endemism is a fairly common phenomenon among taxa that disperse little (e. g., flightless island birds, various cavernicolous taxa). However, it is usually less common and/or less obvious among more or less dispersive taxa. Ammonites belong to this latter category and so the faunal palaeobiogeographical patterning of ammonites usually implies large or very large areas or biochores (i. e., realms or provinces). Widespread (e. g., ubiquitous and pantropical) ammonite taxa are fairly common even. It is exceptional, then, to observe a persistent and obvious endemic trend affecting all or at any rate a significant proportion of the ammonite faunas within a restricted area such as a single limited basin (CARIOU et al. 1985; WESTERMANN 2000; BRAYARD et al. 2006, 2007; CECCA 2002). The sustained endemic trend that affected the ammonite faunas of the Lusitanian Basin during the Late Sinemurian and the Early Pliensbachian is a remarkable palaeobiogeographical phenomenon suggesting a similarly uncommon palaeogeographical context (MOUTERDE & ROCHA 1981; MOUTERDE et al. 1983; DOMMERMUES 1987, DOMMERMUES & MOUTERDE 1987; DOMMERMUES & EL HARRI 2002; DOMMERMUES et al. 2004). The present study addresses the first phase of this phenomenon that occurred during the Late Sinemurian (Obtusum Chronozone). The duration of this first phase of Lusitanian endemism is difficult to estimate but it probably lasted for close to the length of a subchronozone (about 0.4 Myr). The Late Sinemurian palaeobiogeographical Lusitanian episode studied here is characterized by at least six endemic species belonging to two similarly endemic genera. Consequently, the faunal importance of this first episode of endemism is analogous to or even more significant than those of the Early Pliensbachian episodes characterized by the occurrences of the genera *Pseudophricodoceras* or *Dayiceras*, for example. Sound knowledge of the Late Sinemurian (Obtusum Chronozone) first episode of Lusitanian faunal differentiation is an unavoidable preliminary to a proper understanding of the Lusitanian endemic trend as a whole.

The aim of the present publication is to produce a synthesis of what is currently known about the earliest, mostly endemic ammonite faunas of the Lusitanian Basin. This synthesis considers the ammonites with no accurate stratigraphic attributions collected around the end of the nineteenth century (POMPECKJ 1897, 1898, 1906; CHOFFAT 1903–1904), but it is chiefly based on plentiful new material collected extensively, bed by bed, from the Penedo da Saudade section (São Pedro de Muel, Portugal). A first part of this new material (collected in 2003) has already been published (DOMMERMUES et al. 2004) but the second significant part of the material (collected in 2008) is published here.

Because it is based on accurate but insufficiently extensive data, the preliminary paper (DOMMERMUES et al. 2004) leaves several major questions unanswered. In that earlier work, the lowermost and the uppermost fossiliferous levels (chiefly below bed 508 and above level 5106) are not documented or only poorly so and only discontinuous fossiliferous outcrops were examined. As a result, the stratigraphic arrangement of the main fossiliferous episodes is uncertain and the whole succession remains doubtful (DOMMERMUES et al. 2004, fig. 2). Subsequent complementary observations and collections made in 2008 have filled all the gaps. The lowest and highest fossiliferous beds are now fairly well documented and a convincing biostratigraphic synthesis can be proposed for the whole of the ammonite succession recorded at Penedo da Saudade. Consequently, a credible spatio-temporal framework for the first Lusitanian endemic episode can now be proposed. The aim of this publication is to illustrate and describe the newly collected material and to propose a synthesis taking into account all of the biostratigraphical, palaeobiogeographical, taxonomical and evolutionary aspects of the faunal phenomenon recorded in the Penedo da Saudade deposits. The proposed synthesis is based as far as possible on quantitative (morphometrical) analyses of the variation (disparity) expressed in the various fossiliferous beds.

The newly collected ammonites are housed in the collections of the “Centre des Sciences de la Terre de l’Université de Bourgogne” (code: UBGD).

Acknowledgements

This paper is a contribution by the FED “Forme, Evolution, Diversité” team of the “Biogéosciences” research unit (UMR 5561, CNRS/uB). We thank CHRISTOPHER SUTCLIFFE for help with

the English version and JOACHIM BLAU for the “Zusammenfassung”. We are grateful to the “Nucleo de Espeleologia de Leiria” for help in collecting ammonites from the steeper cliffs of Penedo da Saudade and to CYRIL HUGUES DOMMERMUES for his fine photographic work.

2. Geographical, geological and historical settings

In the entire Lusitanian Basin, beds bearing ammonites of the Obtusum Chronozone crop out only in the Penedo da Saudade section N and N-W of São Pedro de Muel (Leiria, Portugal) (Figs. 1–2). These coastal outcrops

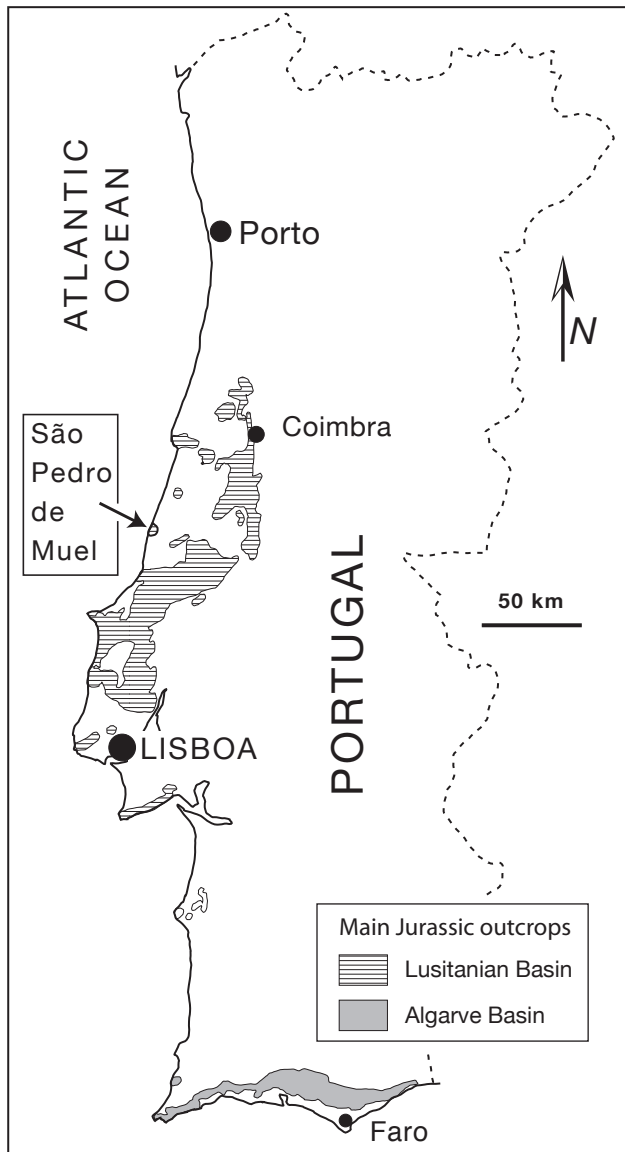


Fig. 1. Sketch map showing the location of the studied fossiliferous section: São Pedro de Muel, Portugal. The main Jurassic outcrops in Portugal (mainly the Lusitanian and Algarve Basins) are indicated.

belong to the Coimbra Formation, which is chiefly constituted by series of more or less amalgamated calcareous beds that are largely devoid of ammonites. Apart

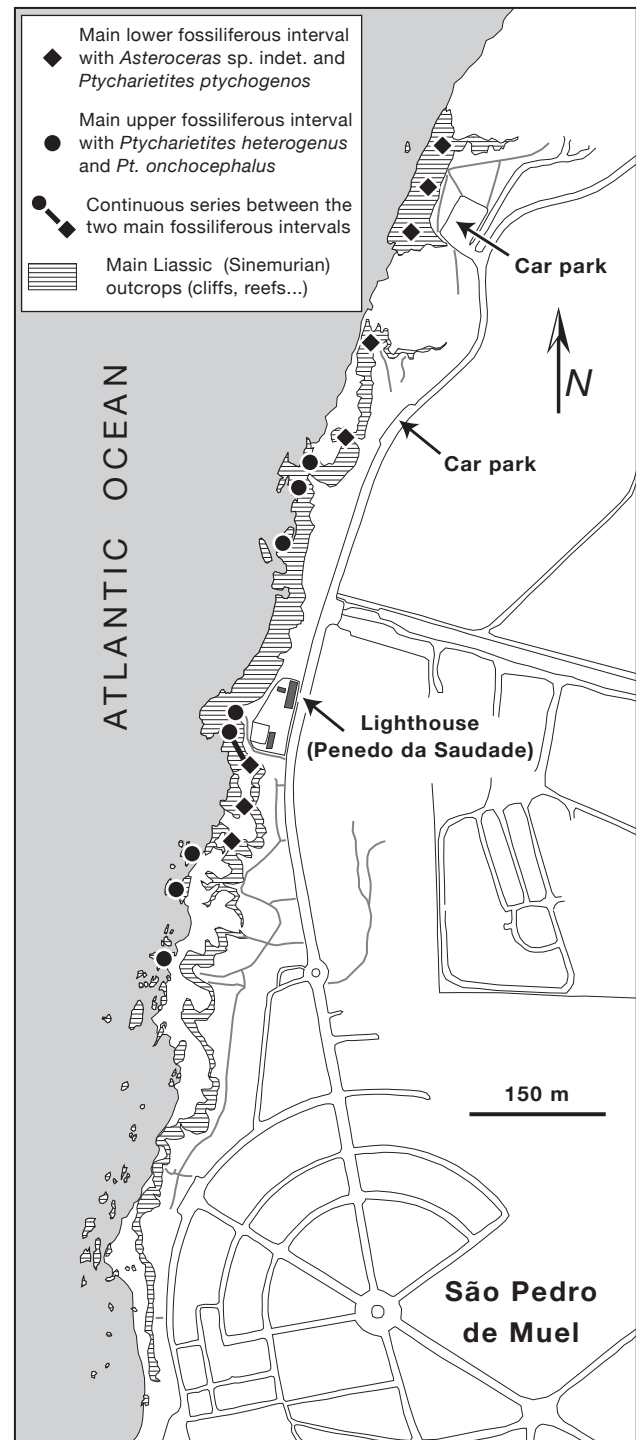


Fig. 2. Detailed map of the rocky coast (cliffs, reefs, etc.) just N-W and N of the village of São Pedro de Muel. These outcrops are usually indicated in the geological literature as “Penedo da Saudade”. The fossiliferous outcrops are pinpointed.

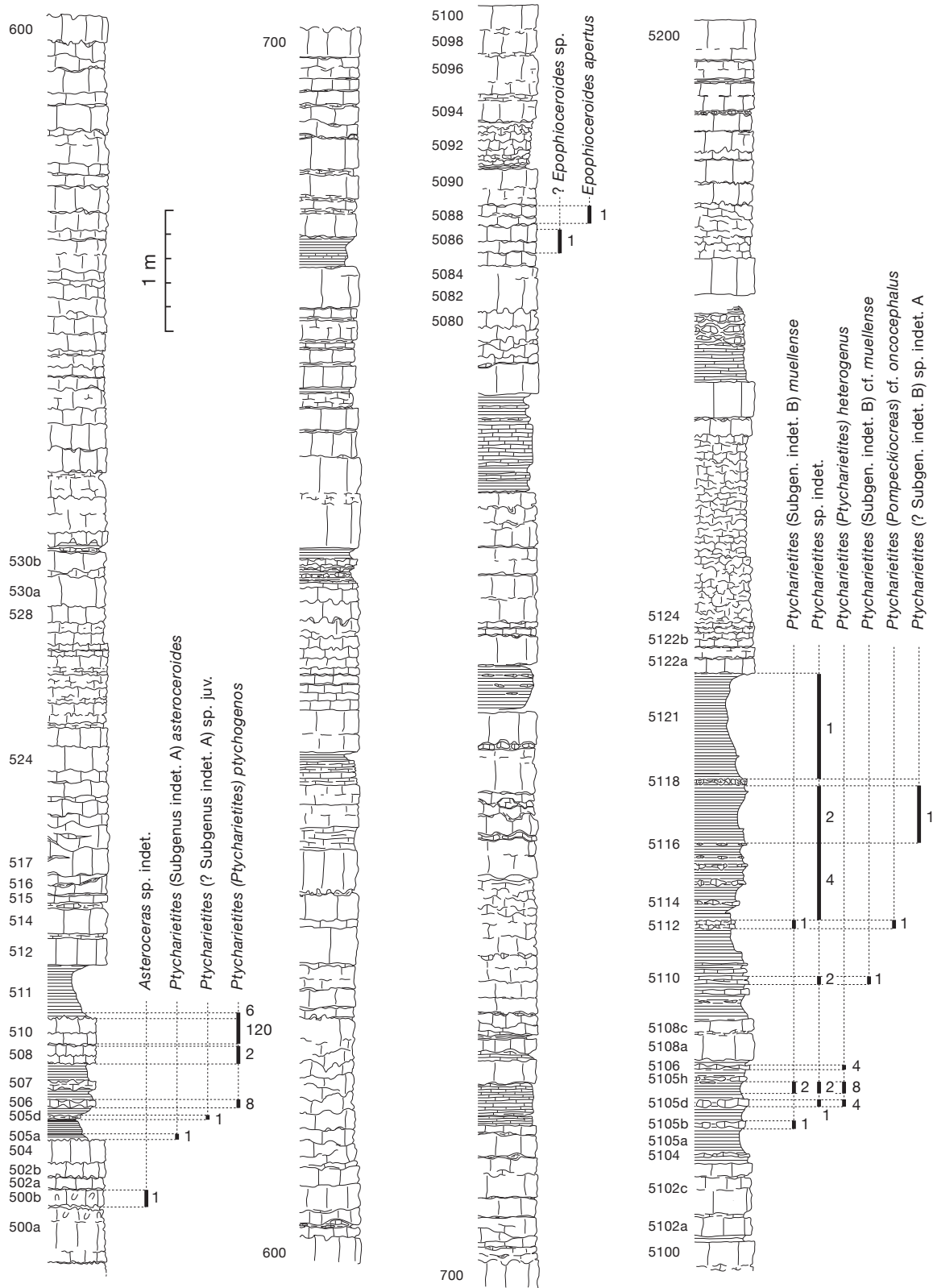


Fig. 3. Lithological pattern (erosion) and faunal succession of the Penedo da Saudade section (São Pedro de Muel, Portugal). A near-continuous section crops out on the shore just below (SSW) the lighthouse (Fig. 2). The number of specimens collected is given for each taxon and each level.

from some usually poorly preserved ammonites collected from the subsurface at Verride and from a quarry at Montemore-o-Velho E of Figueira da Foz (DOMMERGUES et al. 2004: 530, fig. 1) all the ammonites of the Obtusum Chronozone collected in the Lusitanian Basin are from the Penedo da Saudade section. In fact, this section offers a unique opportunity to gather, doubtless partial, but nevertheless plentiful data about the Lusitanian ammonite faunas of the Obtusum Chronozone.

This section and the significant related ammonite faunas have been known since the late nineteenth century (POMPECKJ 1897, 1898, 1906; CHOFFAT 1903–1904). Later MOUTERDE & RUGET (1975), MOUTERDE & ROCHA (1981) and DOMMERGUES & MOUTERDE (1987) reconsidered these valuable but limited and partial old data in various stratigraphic, palaeogeographic, taxonomical and/or palaeobiogeographical syntheses. By contrast, this publication, which completes an earlier preliminary study (DOMMERGUES et al. 2004), is chiefly grounded on plentiful new material collected extensively, bed by bed, from all the accessible fossiliferous levels of the Penedo da Saudade section (Figs. 2–3). The historical context of the studies of the Lusitanian Sinemurian as well as the geographical, palaeogeographical, stratigraphical and sedimentological settings are extensively developed in the introductory paper (DOMMERGUES et al. 2004: 529–532, fig. 1). To avoid repetition they are only briefly summarized in the present work.

3. Systematic palaeontology

Class Cephalopoda CUVIER, 1797
Subclass Ammonoidea ZITTEL, 1884

Order Psiloceratida HOUSA, 1965

Remarks. – The taxon Psiloceratida HOUSA, 1965 is used here as an order. This systematic option is inspired by the phylogenetic hypothesis proposed by GUEX (1987) and by TAYLOR (1998). It corresponds to the emended definition proposed by DOMMERGUES (2002). This taxon is understood as a monophyletic group including almost all the species classically included within *Lytoceratina* HYATT, 1889 and *Ammonitina* ZITTEL, 1884 suborders.

Superfamily Psiloceratoidea HYATT, 1867
Family Arietitidae HYATT, 1874
Subfamily Asterooceratinae SPATH, 1946

Genus *Asteroceras* HYATT, 1867

Type species: *Ammonites stellaris* SOWERBY, 1815, Lyme Regis, Dorset, England. Subsequent designation by BUCKMAN (1911).

Asteroceras sp. indet.

Fig. 4A, Pl. 1, Fig. 1

Material: A single specimen (UBGD 277084), a cast in compact limestone, displaying the end of the phragmocone and a significant part of the body chamber. The inner and medium whorls are not preserved.

Description. – The adult diameter of this somewhat evolute platycone ammonite is probably about 15 mm. The measurable geometric parameters of the shell are given in Fig. 10A–B. The subrectangular whorl section is moderately compressed for an Asterooceratinae (Fig. 4A). The transition between the convex umbilical wall and the base of the flanks is gradual. The umbilical shoulders are indistinct. The flanks, which are initially slightly rounded and roughly parallel (if the ribs are ignored), end by gently converging towards the rather broad and confusedly carinate-bisulcate ventral area. The ventrolateral shoulders are dull and hardly raised but distinct. They visibly limit the ventral area. The venter bears a relatively narrow, low keel which looks blunt (at least on the inner cast). This keel is bordered by two slightly oblique rather broad shallow grooves. With some 13 to 14 ribs per half-whorl, the lateral ribbing is rather dense for a Lusitanian Asterooceratinae (Fig. 5B). The single ribs arise at the umbilical seam. They are distinct on the umbilical wall where they bend slightly backwards before crossing the umbilical margin without fading. The prominent, broad, rounded and subradial flank ribs are slightly concave to nearly straight. They project faintly forwards and fade only beyond the upper two thirds of the flanks before disappearing at the ventrolateral margins. The ribs are most prominent a little below mid-flank.

The suture line is not preserved.

Discussion. – The habitus of this ammonite clearly designates an Asterooceratinae and particularly an *Asteroceras*. Comparisons are possible, for example, with *Asteroceras confusum* SPATH, 1925, which bears resemblances to the Portuguese ammonite although the adult size of this mainly NW European species is obviously greater, its ventral area is broader and its keel is clearly coarser. In fact, with its rather narrow keel flanked by slightly concave oblique grooves, the ventral area of the Lusitanian ammonite may suggest possible relationships with the supervening and possibly descendant *Ptycharietites ptychogenos* (POMPECKJ, 1897). Indeed, these latter ammonites usually display a rather subtle ventral pattern with notably a fairly narrow and unobtrusive keel.

Stratigraphic and geographic range: *Asteroceras* sp. indet. comes from bed 500b of Penedo da Saudade section (São Pedro de Muel, Portugal). It is the lowest ammonite collected in situ at this locality (Fig. 3). The difficulty in proposing a specific attribution for this, perhaps endemic, Lusitanian *Asteroceras* and more gener-

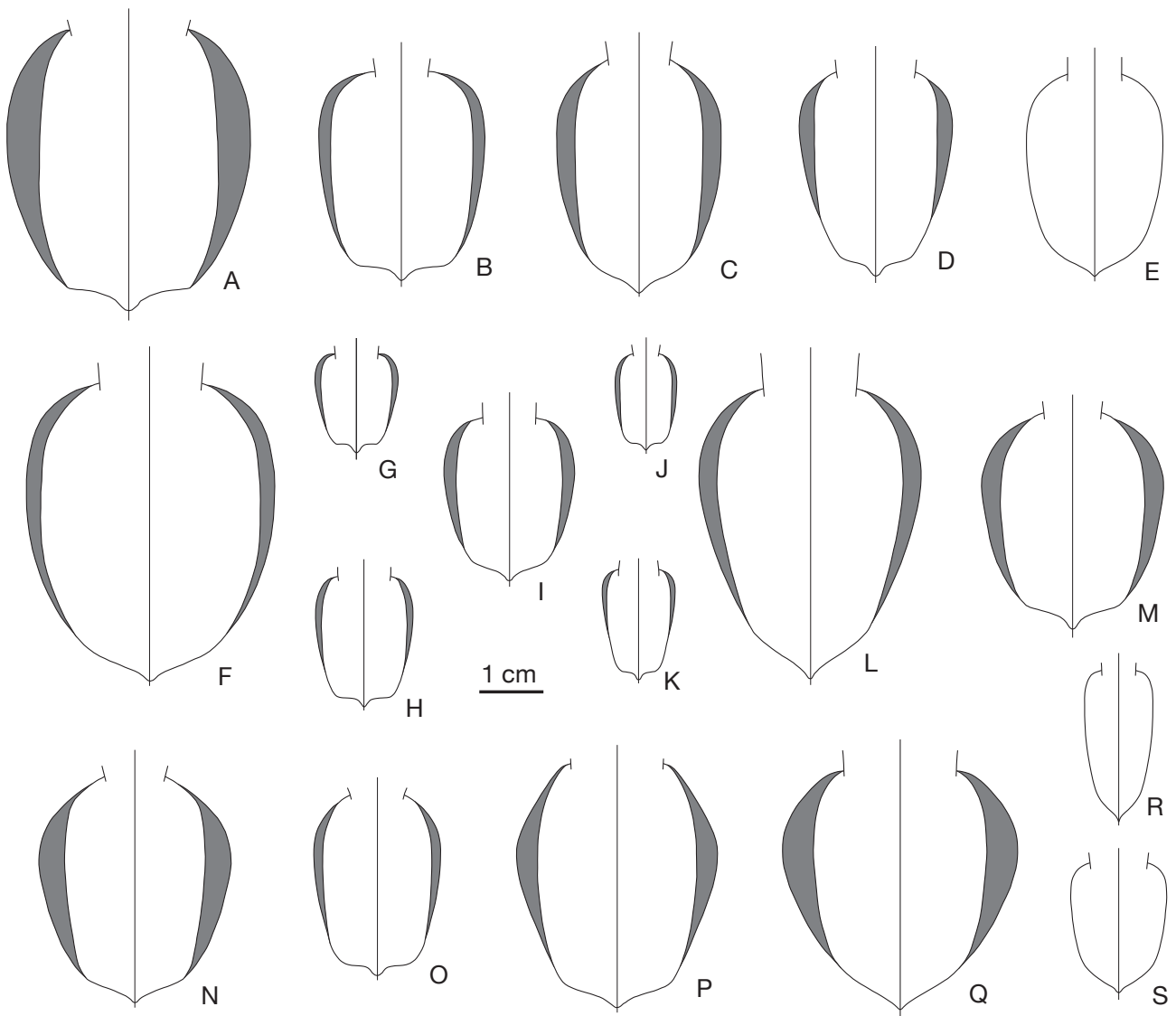


Fig. 4. Whorl sections of ammonites from the Coimbra Formation, Penedo da Saudade section (São Pedro de Muel, Portugal). All these ammonites are illustrated in Figs. 6–7 and Pls. 1–3. – **A.** *Asteroceras* sp. indet., level 500b, UBGD 277084 (Pl. 1, Fig.1). **B.** *Ptycharietites* (Subgenus indet. A) *asteroceroides* n. sp., holotype, level 505a, UBGD 277086 (Pl. 1, Fig. 3). **C.** *Ptycharietites* (*Ptycharietites*) *ptychogenos* (POMPECKJ, 1897), Lectotype (Fig. 7A). **D–F, H–N.** *Ptycharietites* (*Ptycharietites*) *ptychogenos* (POMPECKJ, 1897), level 510. **D.** UBGD 277087 (Pl. 1, Fig. 4). **E.** UBGD 277088 (Pl. 1, Fig. 5). **F.** UBGD 277089 (Pl. 2, Fig.1). **H.** UBGD 277099 (Pl. 3, Fig. 5). **I.** UBGD 277090 (Pl. 2, Fig. 2). **J.** UBGD 277092 (Pl. 2, Fig. 4). **K.** UBGD 277098 (Pl. 3, Fig. 4). **L.** UBGD 277093 (Pl. 2, Fig. 5). **M.** UBGD 277094 (Pl. 2, Fig. 6). **N.** UBGD 277095 (Pl. 3, Fig. 1). **G.** *Ptycharietites* (? Subgenus indet. A) sp. juv., level 505d, UBGD 277085 (Pl. 1, Fig. 2). **O.** *Epophioceroides apertus* n. gen. n. sp., holotype, level 5088, UBGD 277102 (Fig. 6A). **P.** *Ptycharietites* (*Ptycharietites*) *heterogenus* n. sp., holotype, level 5106, UBGD 277096 (Pl. 3, Fig. 2). **Q.** *Ptycharietites* (*Pompeckioceras*) cf. *oncocephalus* (POMPECKJ, 1897), level 5112, UBGD 277101 (Pl. 3, Fig. 7). **R.** *Ptycharietites* (? Subgen. indet. B) sp. indet. A, level 5117, UBGD 277103 (Fig. 6B). **S.** *Ptycharietites* (Subgen. indet. B) *muellense* DOMMERGUES, MEISTER, NEIGE & ROCHA, 2004, level 5112, UBGD 277104 (Fig. 6C).

ally, the marked endemic pattern of the Portuguese Sinemurian faunas precludes us from proposing a convincingly accurate chronostratigraphic attribution. Nevertheless, it is reasonable to suspect an age close to the boundary between the lower and the middle part of the Obtusum Chronozone.

Genus *Epophioceroides* n. gen.

Type species: *Epophioceroides apertus* n. gen. n. sp.
 Derivation of the name: The root “Epophio” evokes the morphological resemblance (within the Asteroceratinae) between the new Lusitanian taxon and the genus *Epophi-*

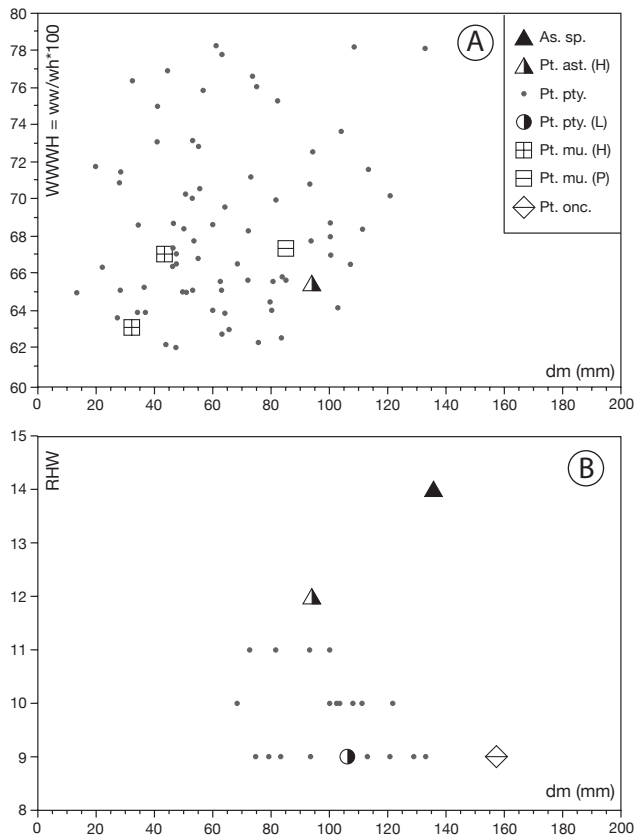


Fig. 5. Plots of the ratio (%) of whorl width (ww) to whorl height (wh) = WWWW (A) and of rib density = RHW (B) vs. shell diameter (dm). Rib density is the number of ribs per half-whorl. All specimens are from the Penedo da Saudade section (São Pedro de Muel, Portugal). As. sp. = *Asteroceras* sp. indet. (level 500b); Pt. ast. (H) = *Ptycharietites* (Subgenus indet. A) *asterocerooides* (holotype) (level 505a); Pt. pty. = *P. ptychogenos* (levels 506–510); Pt. pty. (L) = *P. ptychogenos* (lectotype); Pt. mu. (H) = *P. muellense* (holotype) (level 5105b); Pt. mu. (P) = *P. muellense* (paratype) (level 5105 F–G); Pt. onc. = *P. oncocephalus* (level 5112). All available measurable specimens are plotted.

oceras. The suffix “oides” indicates that this resemblance (mainly the evolute platycone shell) is understood as resulting from convergence.

Discussion. – See the discussion for the type species of the new genus: *Epophioceroides apertus* n. gen. n. sp.

Epophioceroides apertus n. sp.
Figs. 4O, 6A.

Type material: The holotype is an incompletely preserved but undeformed limestone cast (UBGD 277102; Fig. 6A). About half a whorl – probably mainly the first part of the body chamber – is preserved. The inner and medium whorls are missing. The suture line is unknown. The coiling pattern, the outline

of the whorl cross-section and the ornamentation can be unambiguously studied.

Type horizon: Coimbra Formation, Upper Sinemurian, Obtusum Chronozone, Penedo da Saudade section bed 5088 (Fig. 3).

Type locality: Penedo da Saudade section, outcrop located about 170 m N of the lighthouse at Penedo da Saudade, São Pedro de Muel, Portugal (Figs. 1, 2).

Derivation of the name: To suggest the wide-open umbilicus of this atypical evolute *Asteroceratinae*.

Material: The holotype from bed 5088 of Penedo da Saudade section (São Pedro de Muel, Portugal) is the only known specimen of the new species. Nevertheless, a poorly evolute preserved ammonite collected from a nearby stratigraphic location (bed 5086) (Fig. 3) is tentatively attributed to the genus *Epophioceroides* n. gen.

Diagnosis. – The subplatycone evolute shell exhibits a wide-open umbilicus. The clearly compressed whorl section is subrectangular (Fig. 4O). The high, slightly convex flanks look almost flat and subparallel, especially if the ribs are ignored. The rather wide, keeled ventral area is perceptibly carinate-bisulcate. The obvious but low, blunt keel is flanked by two oblique, shallow, smooth grooves. The ribs are most prominent close to the flank base. They fade rapidly towards the venter before disappearing on the upper flanks (well before reaching the ventrolateral shoulders).

Description. – The only preserved half-whorl (about 11 cm in diameter) probably corresponds mostly to the first part of the body chamber. Early and medium growth stages are unknown. With a possible adult diameter of about 13 to 15 cm this form is somewhat small for an *Asteroceratinae*. The subplatycone shell is clearly evolute with a wide umbilicus and a slight overlap between whorls. The clearly compressed whorl section is rounded-rectangular in outline. The fairly shallow, sloping umbilical wall is rounded. The umbilical shoulders are indistinct if the ribs are ignored. The whorl is widest close to the base of the flanks. These are gently rounded at first but quickly become almost flat to barely curved, ending, on the upper flanks, by converging slightly towards the ventral area. This is rather broad and bears an obvious blunt keel flanked by two smooth, shallow, oblique grooves. The ventrolateral shoulders are blunt but distinct and gently raised. The lateral ornamentation is constituted by unobtrusive subradial, straight to slightly concave, simple ribs. They arise on the umbilical wall but are most prominent on the lower part of the flanks before quickly fading and then vanishing before they reach the ventrolateral shoulders.

Discussion. – If one considers the morphology of the ventral area – particularly the blunted appearance of the keel and ventrolateral shoulders – and the ribbing pattern – chiefly the fading of the ribs towards the venter – *Epophioceroides apertus* n. gen. n. sp. might be convincingly attributed to the *Asteroceratinae*. Indeed, and, at least if one considers the Late Sinemurian faunas, such features are found among this subfamily only [e. g., *Asteroceras* gr.

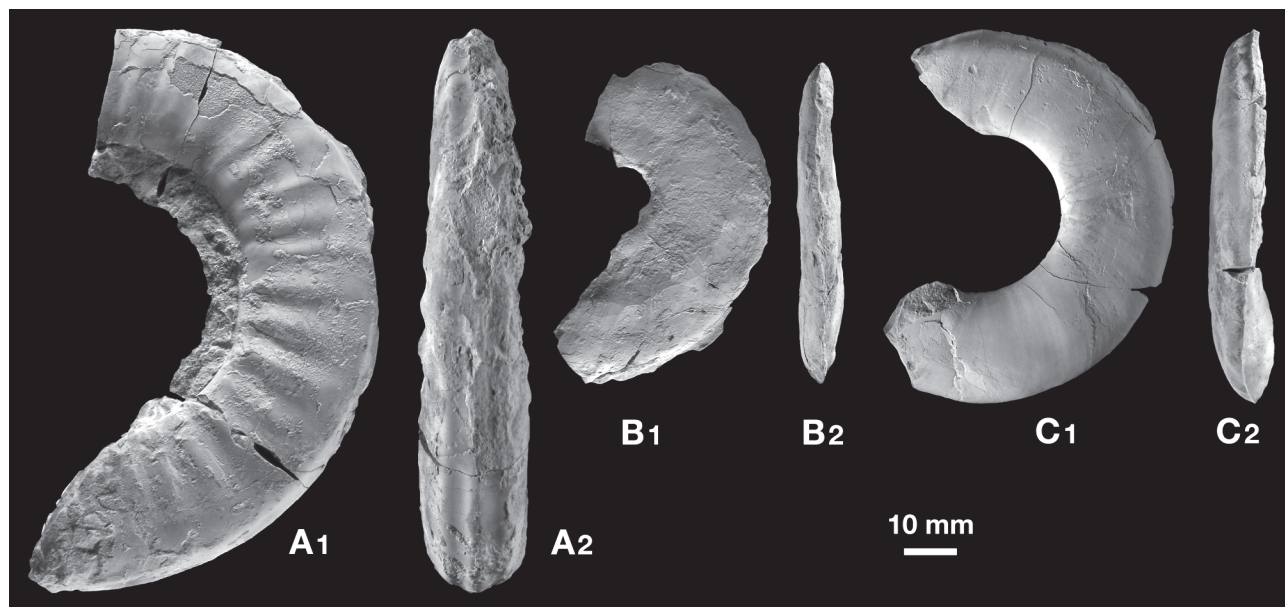


Fig. 6. Sinemurian ammonites from the Coimbra Formation, Penedo da Saudade section (São Pedro de Muel, Portugal). – **A.** *Epophioceroides apertus* n. gen. n. sp., holotype, level 5088, UBGD 277102. **B.** *Ptycharietites* (? Subgen. indet. B) sp. indet. A, level 5117, UBGD 277103. **C.** *Ptycharietites* (Subgen. indet. B) *muellense* DOMMERMUES, MEISTER, NEIGE & ROCHA, 2004, level 5112, UBGD 277104.

varians FUCINI, 1903, *Aegasteroceras blakei* SPATH, 1925 and *Ptycharietites ptychogenos* (POMPECKJ, 1897)]. The full expression of these traits in the new species allows us to exclude close relationships with, for example, the Upper Sinemurian *Arnioceras* in which adult ornamentation (e. g., ribs, keel, ventrolateral shoulders) never looks weakened and/or blunted.

Species with subplatycone evolute or subserpenticone shells are rather rare among the Asteroceratinae. They are classically attributed to the genus *Epophioceras*. However, such a generic assignment is unacceptable for the new Lusitanian species. The obviously compressed subrectangular whorl section and the rapid fading of the ribs on the outer parts of the flanks do not match the traits usually expressed by *Epophioceras*. The new Lusitanian ammonite is clearly a form apart that deserves to be designated as a new genus.

While the evolute coiling pattern of *Epophioceroides apertus* n. gen. n. sp. can be convincingly understood as a homoplasy (convergence or parallelism) within the Asteroceratinae, the phyletic meanings of the other diagnostic traits are more difficult to interpret. The relationships of *Epophioceroides apertus* n. gen. n. sp. within the subfamily remain unclear. At most it can be pointed out that the ornamental and ventral patterns of the new species are similar to those expressed by other Late Sinemurian Lusitanian ammonites [e. g., *Ptycharietites* (Subgen. indet. A) *asteroceroides* n. sp., *P. ptychogenos* (POMPECKJ, 1897) and *P. heterogenus* n. sp.].

Stratigraphic and geographic range: *Epophioceroides apertus* n. gen. n. sp. is for the moment known only in the type locality (bed 5088 of Penedo da Saudade section (Coimbra Formation), São Pedro de Muel, Portugal). Given the endemic pattern of the Sinemurian faunas of this locality, it is impossible to propose a convincing, accurate chronostratigraphic attribution but an occurrence in the middle part of Obtusum Chronozone (Stellare Subchronozone) may be suspected.

Genus *Ptycharietites* SPATH, 1925

Type species: *Arietites (Asteroceras) ptychogenos* POMPECKJ, 1897, Coimbra Formation, São Pedro de Muel, Portugal. Original designation by SPATH (1925).

Remarks. – For morphological reasons (peculiar features suspected as apomorphies) and because of stratigraphical constraints (a coherent sequence of closely-related species in the fossiliferous succession) the genus *Ptycharietites* is understood here to very probably be a monophyletic group (clade). The most obvious apomorphy of *Ptycharietites* is the long (for an Asteroceratinae) smooth, ribless, juvenile stage. However, and to consider the complexity within the clade, we propose to informally use four distinct subgenera to designate three noticeable steps occurring throughout the main evolutionary line and also to identify a presumed late minor diverging line.

Most of the *Ptycharietites* collected from the Penedo da Saudade section correspond to the subgenus (*Ptycharietites*). These forms belong to two closely-related but distinct subplatycone species, namely the type species of the genus, *Ptycharietites (Ptycharietites) ptychogenos* (POMPECKJ, 1897), and a new species, *Ptycharietites (Ptycharietites) heterogenus*. These two taxa are common. They form the core of the main evolutionary line of the genus. They are followed in the fossiliferous successions by *Ptycharietites (Pompeckioceras) cf. oncocephalus* (POMPECKJ, 1897), a rare and morphologically idiosyncratic subserpenticone form. The use of the subgenus (*Pompeckioceras*) underlines the significant morphological gap between this late *Ptycharietites* and the immediately preceding *Ptycharietites (Ptycharietites) heterogenus* n. sp. Anyway, *P. (Ptycharietites) ptychogenos* (POMPECKJ, 1897), *P. (Ptycharietites) heterogenus* n. sp. and *P. (Pompeckioceras) cf. oncocephalus* (POMPECKJ, 1897) are large or medium-sized forms that all exhibit a distinctive complex ontogeny characterized by a long, smooth, juvenile stage that is quickly superseded by a contrasting, coarsely-ribbed, late stage. A roughly similar type of ontogeny is credible but unfortunately partly hypothetical for *Ptycharietites* (Subgen. indet. A) *asteroceroides* n. sp., a new species, known by a single specimen with no preserved inner whorls. It was collected from bed 505a roughly between beds 500b and 506, which yielded *Asteroceras* sp. indet. and the first *P. (Ptycharietites) ptychogenos* (POMPECKJ, 1897), respectively. In this context, the use of an informal subgenus (i. e., Subgen. indet. A) underlines the intermediate stratigraphical position and the transitional habitus of the new species between *Asteroceras* s. l. and *P. (Ptycharietites) ptychogenos* (POMPECKJ, 1897).

Outside of the main evolutionary line, two smallish (adult diameters probably do not exceed 10 mm), late species are characterized by incomplete ontogeny interrupted before the end of the smooth, ribless, juvenile stage. These entirely smooth forms, *Ptycharietites* (Subgen. indet. B) *muellense* DOMMERMUES, MEISTER, NEIGE & ROCHA, 2004 and *Ptycharietites* (? Subgen. indet. B) sp. indet. A, may constitute a late minor diverging evolutionary line or are microconchs. They are identified by the informal subgeneric designation: (Subgen. indet. B).

Subgenus *Ptycharietites* SPATH, 1925

Type species: *Arietites (Asteroceras) ptychogenos* POMPECKJ, 1897, Coimbra Formation, São Pedro de Muel, Portugal. Original designation by SPATH (1925).

Discussion. – See the discussion for the genus *Ptycharietites*.

Ptycharietites (Ptycharietites) ptychogenos (POMPECKJ, 1897)

Figs. 4C–F, H–N, 7A, 8B–O, Pl. 1, Figs. 4–5, Pl. 2, Figs. 1–6, Pl. 3, Figs. 1, 3–6

- * 1897 *Arietites (Asteroceras) ptychogenos*. – POMPECKJ, pl. 23, figs. 1–3.
- 1897 *Arietites (Asteroceras) amblyptychus*. – POMPECKJ, pl. 23, figs. 4, 5.
- 1897 *Arietites (Asteroceras)* sp. – POMPECKJ, pl. 23, fig. 6.
- 1898 *Arietites (Asteroceras) ptychogenos* POMPECKJ. – POMPECKJ, pl. 1, figs. 1–3.
- 1898 *Arietites (Asteroceras) amblyptychus* POMPECKJ. – POMPECKJ, pl. 1, figs. 4–5.

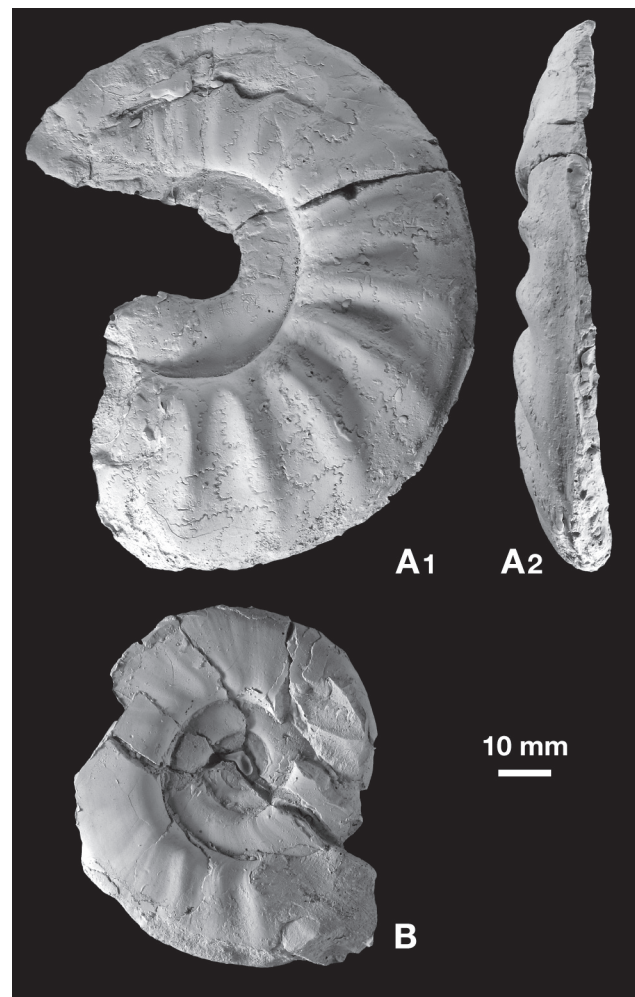


Fig. 7. Sinemurian ammonites from the Coimbra Formation, Penedo da Saudade section (São Pedro de Muel, Portugal). – A. *Ptycharietites (Ptycharietites) ptychogenos* (POMPECKJ, 1897), Lectotype designated by DOMMERMUES et al. (2004: 533). This specimen was initially illustrated by POMPECKJ (1897, pl. 23, fig. 3). B. *Ptycharietites (Pompeckioceras) oncocephalus* (POMPECKJ, 1897). This specimen was initially illustrated by POMPECKJ (1897, pl. 23, fig. 7). Ammonites are coated with ammonium chloride.

- 1898 *Arietites (Asterocheras)* sp. – POMPECKI, pl. 1, fig. 6.
 1981 *Asterocheras (Ptycharietites) ptychogenos* (POMPECKI).
 – MOUTERDE & ROCHA, pl. 1, figs. 11, 14.
 2004 *Ptycharietites ptychogenos* (POMPECKI). – DOMMERGUES et al., pl. 1, figs. 1–8, pl. 2, figs. 1–7, pl. 3, figs. 1–6.

Material: *Ptycharietites (Ptycharietites) ptychogenos* (POMPECKI, 1897) is a spatially very restricted but locally plentiful species. Some 120, often fairly well preserved specimens were collected from beds 506, 508, 511 (base) and chiefly 510 of the Penedo da Saudade section (São Pedro de Muel, Portugal). Six specimens, including the lectotype and the two paralectotypes, illustrated by POMPECKI (1897), also come from this section.

Description. – Size is fairly variable as indicated by the variation in phragmocone diameter (Fig. 9A). The distribution is skewed but there is no indication of signifi-

cant bimodality and consequently no suggestion of dimorphism. A complete adult diameter of 150 mm is probably rarely achieved and the mean is credibly included between 80 and 120 mm. Such an average adult size is relatively small for a member of the Asterocheratinae subfamily. The body chamber occupies about two thirds of the whorl. Large-diameter shells are clearly subplatycone but smaller-diameter shells (chiefly juvenile shells) are often obviously more involute and therefore platycone/oxycone (sensu OLORIZ et al. 2002) (Fig. 10A–B). The moderately to clearly compressed whorl cross-section varies from subrectangular (mainly for small diameters) (Fig. 4H, J) to subtrapezoidal (Fig. 4D, N) or even subtriangular (Fig. 4L) (mainly for large diameters). The subtrapezoidal form is prevalent. In this case and if the ribs are ignored, the moderately sloping umbilical wall is arched and the umbilical

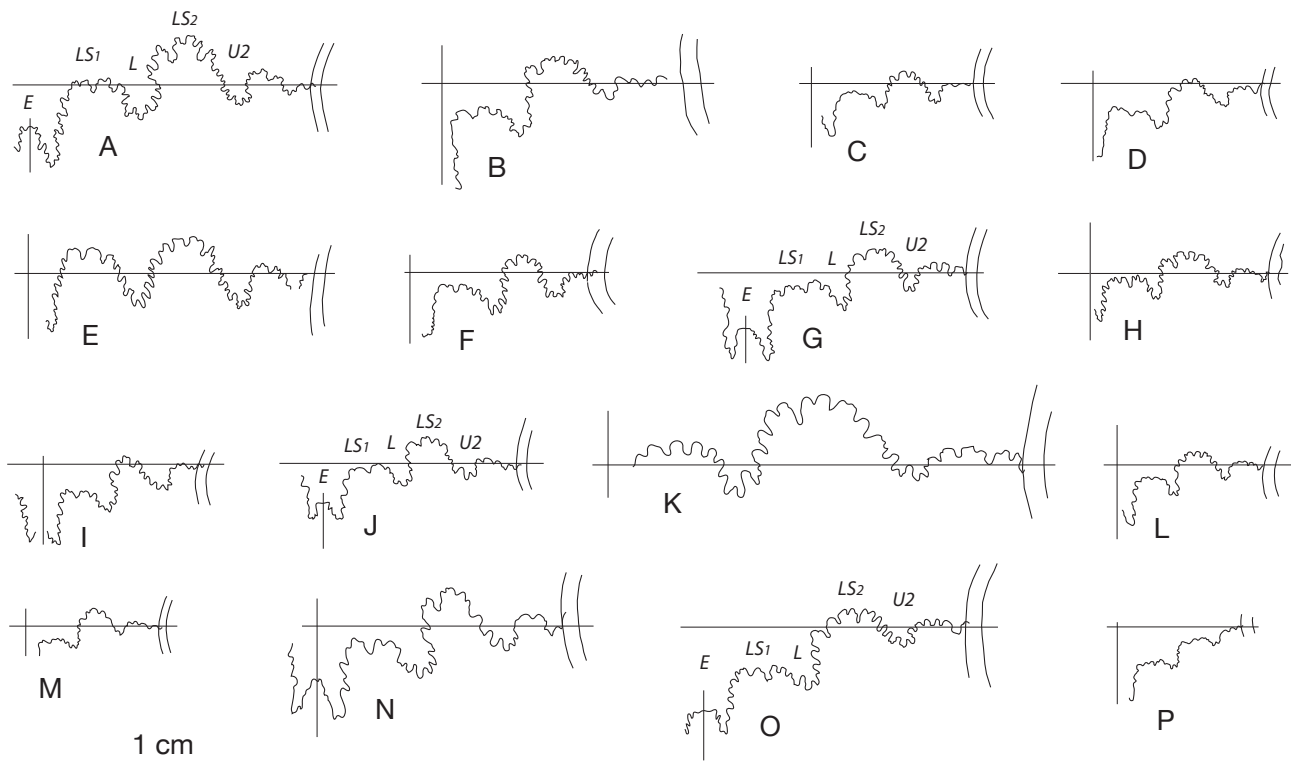


Fig. 8. Suture lines of ammonites from the Coimbra Formation, Penedo da Saudade section (São Pedro de Muel, Portugal). Some of these ammonites (A–G) are illustrated in Fig. 7 and Pls. 1–3, others (H–K, P) in DOMMERGUES et al. (2004), and others (L–O) still are not illustrated. – **A.** *Ptycharietites* (subgenus indet. A) *asteroceroides* n. sp., holotype, level 505a, UBGD 277086 (Pl. 1, Fig. 3). **B.** *Ptycharietites (Pt.) ptychogenos* (POMPECKI, 1897), Lectotype, (Fig. 7A). **C–O.** *Ptycharietites (Pt.) ptychogenos* (POMPECKI, 1897), level 510. **C.** UBGD 277088 (Pl. 1, Fig. 5). **D.** UBGD 277090 (Pl. 2, Fig. 2). **E.** UBGD 277093 (Pl. 2, Fig. 5). **F.** UBGD 277094 (Pl. 2, Fig. 6). **G.** UBGD 277095 (Pl. 3, Fig. 1). **H.** UBGD SPM/PS.a20 (DOMMERGUES et al. 2004, pl. 1, fig. 6). **I.** UBGD SPM/PS.a08 (DOMMERGUES et al. 2004, pl. 1, fig. 7). **J.** UBGD SPM/PS.a30 (DOMMERGUES et al. 2004, pl. 1, fig. 8). **K.** UBGD SPM/PS.a31 (DOMMERGUES et al. 2004, pl. 2, fig. 3). **L.** UBGD 277105. **M.** UBGD 277106. **N.** UBGD 277107. **O.** UBGD 277108. **P.** *Ptycharietites* (Subgen. indet. B) *muellense* DOMMERGUES, MEISTER, NEIGE & ROCHA, 2004, holotype, level 5105b, SPM/PS.b01 (DOMMERGUES et al. 2004, pl. 4, fig. 3). – The main sutural elements are indicated for the suture lines A, G, J and O: *E* = external (or ventral) lobe, *LS*₁ = first lateral saddle, *L* = lateral lobe, *LS*₂ = second lateral saddle, *U*₂ = second umbilical lobe. The locations of the venter and of the umbilical seam and edge are indicated. A radial line is drawn for each suture line.

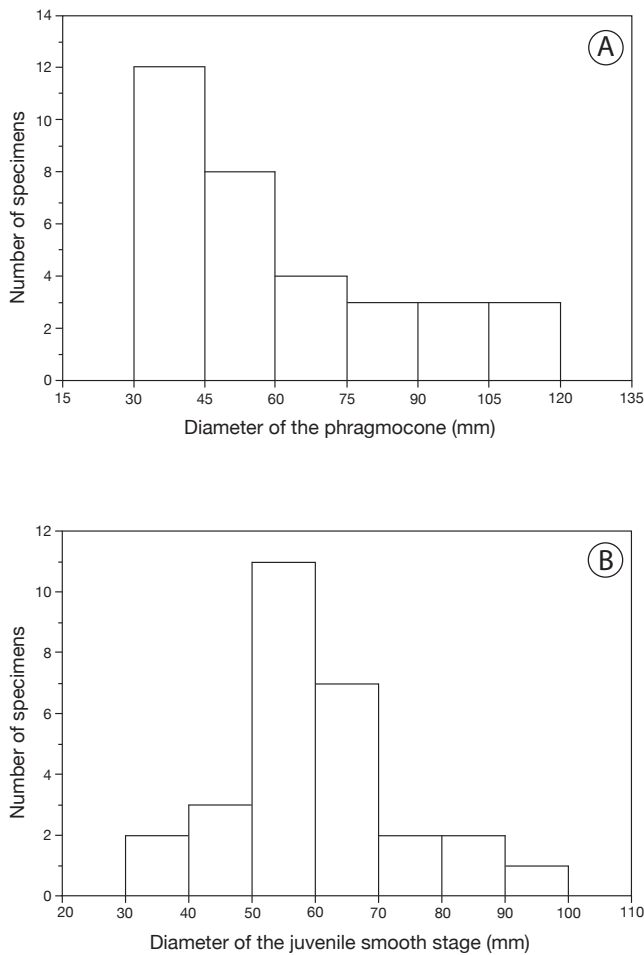


Fig. 9. Histograms illustrating the distribution of phragmocone diameters (A) and the distribution of the diameters of the juvenile smooth stage (B) among all the measurable *Ptycharietites* (*Pt.*) *ptychogenos* (POMPECKI, 1897) collected from the Penedo da Saudade section (São Pedro de Muel, Portugal). The mode of the distribution of phragmocone diameters is obviously smaller than that of the juvenile smooth stage diameters.

shoulders are indistinct or incipient. The whorl section is thickest between the lower quarter and the lower third of the whorl height. The flanks are at first moderately rounded but quickly become slightly arched and converge gently towards the quite broad ventral area. This is bounded by often unobtrusive but always distinct ventrolateral shoulders. The venter bears a rather modest keel which is moderately broad, high and sharp. This keel is flanked by two rather broad, almost plane to faintly concave bands that are often clearly sloping and converge towards the venter. Lateral ornamentation changes considerably during growth. The comparatively involute inner whorls and often also part of the medium whorls are smooth or almost smooth. Ribbing is then missing or else reduced to incipient folds. The smooth stage is highly variable in

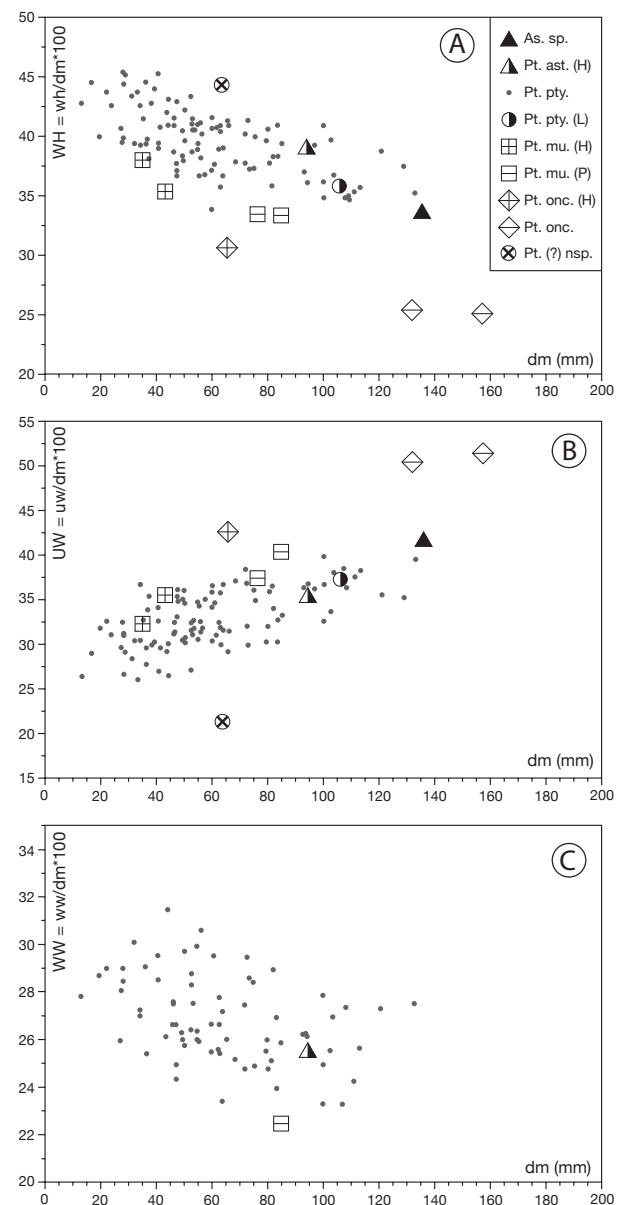


Fig. 10. Plots of whorl height = WH (A), umbilical width = UW (B) and whorl width = WW (C) as ratios (%) of shell diameter vs. shell diameter. The parameters used for calculating these ratios are: dm = shell (or conch) diameter, wh = whorl height, uw = umbilical width (or umbilical diameter) and ww = whorl width. See KORN & KLUG (2007, fig. 3.5) or LONGRIDGE et al. (2008) for illustrations and/or use of such parameters and ratios. Symbols indicate species and/or significant specimens; *As. sp.* = *Asteroceras* sp. indet. (level 500b); *Pt. ast. (H)* = *Ptycharietites* (Subgenus indet. A) *asteroceroideus* (holotype) (level 505a); *Pt. pty.* = *P. ptychogenos* (levels 506–510); *Pt. pty. (L)* = *P. ptychogenos* (lectotype); *Pt. mu. (H)* = *P. muellense* (holotype) (level 5105b); *Pt. mu. (P)* = *P. muellense* (paraholotype) (level 5105 F–G); *Pt. onc. (H)* = *P. oncocephalus* (holotype); *Pt. onc.* = *P. oncocephalus* (level 5112); *Pt. (?) nsp.* = *P. (?)* Subgen. indet. B) n. sp. (level 5117). All the specimens are from the Penedo da Saudade section (São Pedro de Muel, Portugal). All measurable specimens are plotted.

length (e. g., Fig. 9B). It can spread over all or part of the phragmocone and even extend to the first part of the body chamber. By contrast, the late stages of growth are characterized by usually prominent, lateral, relatively widely-spaced ribbing (e. g., Fig. 5B). The ribs arise on the umbilical wall where they are faint and slightly rursiradiate. They bend forward at the umbilical margin and become subradial on the flanks where they are straight to barely curved. The ribs are most prominent close to (usually a little below) the lower third of the whorl height. Beyond this, they weaken rapidly and disappear just before reaching the ventrolateral margins (e. g., Fig. 4N, Pl. 3, Fig. 1) or upper flanks (e. g., Fig. 4D, Pl. 1, Fig 4).

Septal suture lines are often preserved. They are somewhat variable (Fig. 8B–O) in detail but show similar major characteristics. Suture lines are, on the whole, rather simple, weakly incised and faintly frilled (e. g., Fig. 8H, O). Broad and thickset lateral and umbilical saddles contrast noticeably with the shallow and narrow (sometime tiny) lateral and umbilical lobes (e. g., Fig. 8C, G, O). In some cases, the suture lines look to be formed mostly by a succession of broad, barely incised saddles. If compared with a radius crossing the intersection between the suture line and the umbilical margin, the barely incised umbilical segment of the suture line (between U_2 and the umbilical margin) looks slightly arched but subradial (Fig. 8). The second lateral saddle (LS_2) is frequently prominent but the lateral lobe and above all the first lateral saddle and the external lobe are usually significantly retracted.

Discussion. – *Ptycharietites ptychogenos* (POMPECKJ, 1897) displays traits such as the subtrapezoidal whorl section, the weak ventrolateral shoulders and the rapidly fading ribs on the mid and upper flanks that may suggest some relationship among the Asteroceratinae with the genera *Aegasteroceras*, *Arctoasteroceras*, *Eparietites*, *Parasteroceras* or possibly also *Euerbenites*. Nevertheless, the special (for a member of the Asteroceratinae subfamily) ontogeny of *P. ptychogenos* (POMPECKJ, 1897) excludes any close relationship with these genera and marks out this Lusitanian species in particular and the *Ptycharietites* genus in general as very peculiar taxa. The occurrence of a remarkable smooth, ribless, paedomorphic stage in the inner and medium whorls is a unique phenomenon within the Asteroceratinae and more widely within the Arietitidae (DOMMERMUES et al. 2004, fig. 4). Actually, relevant comparisons are mostly possible with the other Lusitanian species attributed to the genus *Ptycharietites*.

Many characteristics of the septal pattern of *Ptycharietites ptychogenos* (POMPECKJ, 1897), notably the prominent second lateral saddle (LS_2) contrasting with the retracted first lateral saddle (LS_1) and external lobe (L), are general traits of the Asteroceratinae (e. g., *Asteroceras* and *Aegasteroceras*). However, the sometimes tiny lateral and umbilical lobes as well as the marked weakening of in-

cisions and frilling are typical of *Ptycharietites ptychogenos* (POMPECKJ, 1897) and probably also, by extension, of many if not all *Ptycharietites*. Such simplified suture lines suggest probable, but still poorly understood, environmental constraints.

Stratigraphic and geographic range: *Ptycharietites ptychogenos* (POMPECKJ, 1897) is currently known only for sure in beds 506, 508, 510 and 511 (base) of Penedo da Saudade section (Coimbra Formation, São Pedro de Muel, Portugal) but some poorly preserved and doubtful specimens are also reported from a borehole at Verride (E of Figueira da Foz), another Lusitanian locality (DOMMERMUES et al. 2004, fig. 1). Hence, *P. ptychogenos* (POMPECKJ, 1897) is a strictly restricted Lusitanian ammonite. The stratigraphic context of the Penedo da Saudade section and especially the presence of *Asteroceras* sp. indet. in bed 500b attest to an age within the middle part of Obtusum Chronozone (Stellare Subchronozone). Unfortunately the markedly endemic pattern of the Sinemurian Lusitanian faunas significantly reduces the possibilities of correlation.

Ptycharietites (Ptycharietites) heterogenus n. sp.

Fig. 4P, Pl. 3, Fig. 2

2004 *Ptycharietites* sp. cf. *P. ptychogenos* (POMPECKJ, 1897). – DOMMERMUES et al., pl. 4, fig. 6, pl. 5, figs. 1–5.

Type material: The holotype is an incomplete specimen that is slightly deformed but apparently only just or not crushed (UBGD 277096; Pl. 3, Fig. 2). This specimen is a internal cast in compact, grey limestone bearing no trace of the shell. It corresponds to about a half whorl of what is probably the body chamber. The paratypes are six incomplete, crushed specimens with shells preserved as calcitic pseudomorph. They are illustrated by DOMMERMUES et al. 2004, pl. 4, fig. 6 (SPM/PS.b16); pl. 5, figs. 1–5 (SPM/PS.b14, b00, b04, b08, b03). The early growth stages can be observed on four of these paratypes (DOMMERMUES et al. 2004, pl. 5, figs. 2–5).

Type horizon: The holotype (Pl. 3, Fig. 2) and one paratype (DOMMERMUES et al. 2004, pl. 4, fig. 6) have been collected from bed 5106 of the Penedo da Saudade section (Coimbra Formation, Upper Sinemurian, Obtusum Chronozone). The other paratypes (DOMMERMUES et al. 2004, pl. 5, figs. 1–5) come from beds 5105d, f, g–h.

Type locality: Penedo da Saudade section, São Pedro de Muel, Portugal (Figs. 1, 2). The holotype was collected from a small outcrop isolated on the shore, about 320 m SSW of the lighthouse at Penedo da Saudade, São Pedro de Muel, Portugal. All the paratypes come from the outcrops situated about 250 m N of the lighthouse.

Derivation of the name: To suggest the obvious changes in morphology and chiefly ornamentation occurring during the ontogeny of this especially large *Ptycharietites*.

Material: In addition to the holotype and to the six paratypes about 15 specimens of the new species come from beds 5105b, d, f, g–h. The new species is rather common in these beds but the large crushed specimens are unfortunately usually difficult to extract.

Diagnosis. – By comparison with the other *Ptycharietites* this new species is characterized by its obviously larger adult size. The largest specimens probably

reach about 30 cm in diameter (e. g., DOMMERMUES et al. 2004, pl. 5, fig. 1). At least in the medium and late stages of growth, the umbilicus is wide open and the shell is platycone and evolute (Pl. 3, Fig. 2). In the inner whorls (as far as 8 to 10 cm diameter) the shell is ribless and the crushed specimens look perfectly smooth. In contrast with the juvenile stages, the intermediate and outer whorls exhibit coarse lateral ornamentation which is constituted by simple subradial or slightly prorsiradiate swollen ribs. They protrude close to (usually a little below) midflank only, but noticeably so. They fade rapidly and ostensibly towards both the umbilicus and the venter.

Description. – Except for the holotype (Pl. 3, Fig. 2), which is an incomplete but barely deformed inner cast, all the available specimens are intensely flattened. The shells, still unfilled or nearly unfilled before their probably rapid burial, were broken during the compaction process. The calcitic pseudomorphs of the shells often look cracked (e. g., DOMMERMUES et al. 2004, pl. 4, fig. 6, pl. 5, fig. 4). Their curious state of preservation precludes any morphometric analysis and many geometrical or ornamental traits can be only reconstructed and/or surmised.

Ptycharietites (Ptycharietites) heterogenus n. sp. is a species whose largest specimens can probably attain or even exceed 30 cm in diameter. With a rather wide umbilicus, a slight overlap between whorls and more or less compressed whorls cross-section, the medium and late stages of growth are platycone and evolute. By contrast, the inner whorls, at least up to 8 to 10 mm, look more involute but, unfortunately the juvenile coiling pattern is difficult to appraise from the intensely crushed phragmocone. These fairly involute juvenile stages are devoid of any lateral ornamentation and the surface of the shell pseudomorphs looks perfectly smooth. In contradistinction, the following more evolute stages of growth display coarse lateral ribbing. The stout, swollen, subradial to weakly prorsiradiate, simple ribs reach their greatest height close to (often a little below) midflank. These prominent but curiously stubby ribs quickly fade towards both the umbilicus and the venter. The ribs arise but remain faint on the umbilical wall where they are slightly rursiradiate. They quickly weaken on the upper flanks before disappearing shortly before reaching the unobtrusive ventrolateral margins. In addition to the stout lateral ribbing, the surface of the shell pseudomorphs displays a very dense striation which is obvious, for example, on the large specimens illustrated by DOMMERMUES et al. (2004, pl. 4, fig. 6, pl. 5, fig. 1). These striae, which are parallel to the rib trajectories, are chiefly apparent on the flanks and the ventral area. The striae also occur on and between ribs.

The whorl cross-section cannot be directly observed on the flattened ammonites but the barely deformed holotype (Pl. 3, Fig. 2) yields many data which help us to understand most of the initial features of the crushed speci-

mens. Chiefly, if the ribs are ignored, the whorl section is compressed and subrectangular to suboval in outline, being thickest a little below midflank (Fig. 4P). The moderately high, sloping umbilical wall is rounded. If the ribs are ignored, the gently curved umbilical shoulders are indistinct and the moderately rounded flanks are subparallel and converge slightly towards the ventrolateral margins. On the holotype at least, the latter are blunt but distinct. They probably tend to fade at larger diameters where it becomes difficult to pinpoint the dividing line between the smooth upper flanks and the ventral area (e. g., DOMMERMUES et al. 2004, pl. 5, fig. 1). The venter of the holotype bears a narrow blunt (at least on the inner cast) keel which is flanked by two rather wide, sloping, plane bands. By contrast, the significance of the keel is difficult to appraise on the crushed material.

Discussion. – The new species was initially illustrated and described as *Ptycharietites* sp. cf. *P. ptychogenos* (POMPECKI, 1897) by DOMMERMUES et al. (2004: 535, pl. 4, fig. 6, pl. 5, fig. 1–5). Meanwhile, the newly collected material including the barely deformed holotype (Pl. 3, Fig. 2) allows us to justify the formalization of a new taxon that is clearly distinct from *P. ptychogenos* (POMPECKI, 1897). *Ptycharietites (Ptycharietites) heterogenus* n. sp. can be separated from the POMPECKI (1897) species by i) a statistically larger (about twofold) adult diameter, ii) a more evolute shell (at least in the intermediate and late stages of growth), iii) stout lateral ribbing which tends to protrude close to midflank, and iv) faint ribbing on the nearly smooth lowermost flanks and umbilical wall.

On the other hand, *Ptycharietites (Ptycharietites) heterogenus* n. sp. may also be compared with *Ptycharietites (Pompekioceras) cf. oncocephalus* (SPATH, 1925). Nevertheless, this latter taxon can be differentiated from the new species by i) its probably appreciably smaller adult size, ii) a more evolute coiling pattern which occurs as early as the juvenile stages and leads to a subserpenticone shell by the medium and chiefly outer whorls, and iii) an adult habitus that roughly evokes certain coarsely ribbed, evolute Hettangian ammonites (e. g., *Caloceras*).

In fact, *Ptycharietites (Ptycharietites) heterogenus* n. sp. is, for many of its traits, a transitional taxon between *P. (Ptycharietites) ptychogenos* (POMPECKI, 1897) and the subsequent *P. (Pompekioceras) cf. oncocephalus* (SPATH, 1925). Therefore, the choice of the subgenus *P. (Ptycharietites)* or *P. (Pompekioceras)* is debateable.

Stratigraphic and geographic range: *Ptycharietites (Ptycharietites) heterogenus* n. sp. is known in the type locality only (bed 5105d to 5106, of the Penado da Saudade section, São Pedro de Muel, Portugal). These Sinemurian levels probably correspond to an interval occurring during the middle part of Obtusum Chronozone (Stellare Subchronozone) but a more accurate chronostratigraphical attribution is impossible.

Subgenus *Pompekioceras* SPATH, 1925

Type species: *Arietites* (*Arnioceras*?) *oncocephalus* POMPECKJ, 1897, Coimbra Formation, São Pedro de Muel, Portugal. Original designation by SPATH (1925).

Discussion. – See the discussion for the genus *Ptycharietites*.

Ptycharietites (*Pompekioceras*) cf. *oncocephalus*
(POMPECKJ, 1897)

Figs. 4Q, 7B, Pl. 3, Fig. 7.

- cf. 1897 *Arietites* (*Arnioceras*?) *oncocephalus*. – POMPECKJ, pl. 23, fig. 7.
cf. 1898 cf. *Arietites* (*Arnioceras*?) *oncocephalus* POMPECKJ. – POMPECKJ, pl. 1, fig. 7.
cf. 1981 cf. *Asteroceras*? (*Pompekioceras*) *onchocephalus* (POMPECKJ). – MOUTERDE & ROCHA, pl. 2, fig. 3.

Material: A large specimen (UBGD 277101) collected from bed 5112 of the Penedo da Saudade section (São Pedro de Muel, Portugal) (Pl. 3, Fig. 7). The shell is preserved as calcitic pseudomorph and is partly broken on the outer whorl. The septal suture line is not visible.

Description. – The adult diameter of the fine specimen illustrated Fig. 4Q and Pl. 3, Fig. 7, and preserved with a body chamber of almost one whorl, measures about 150 mm. The adult shell is platycone/serpenticone sensu OLORIZ et al. (2002). The measurable geometric parameters of the shell are given in Fig. 10A–B. On the last whorl and if the ribs are ignored, the compressed whorl cross-section is subogival (Fig. 4Q). The greatest whorl width occurs perceptibly below mid flank. The upright, moderately high umbilical wall and the umbilical margin are rounded with no distinct umbilical shoulder. The gently curved flanks are subparallel to fairly converging towards the rounded ventrolateral margins. On the body chamber at least, the ventrolateral shoulders are barely distinct and the venter bears a rather modest, fairly broad, high keel. It is flanked by two wide, smooth, sloping bands which give the ventral area a subtectiform appearance.

The ribbing pattern is probably the most salient aspect of this ammonite. In the inner whorls, as far as about a diameter of 50 mm, the lateral ornamentation is either missing or is restricted to some incipient, low, broad folds. Apart from fine striae, the shell surface looks almost smooth. Beyond 50 mm the ornamentation quickly changes with the beginning of coarse and spaced ribbing. The initially gently rursiradiate ribs arise close to the umbilical seam but remain inconspicuous on the umbilical wall. At the umbilical margin they bend slightly forward and quickly become more prominent. The greatest rib height is achieved a little below midflank. Beyond this point, rib strength quickly fades and vanishes before reaching the ventrolateral margin. The contrast is outstanding between

the stout, swollen ribs around midflank and their inconspicuous extensions towards both the ventrolateral margin and the umbilicus. Given its platycone/serpenticone shell and its strange, swollen lateral ribbing, this ammonite evokes the habitus of certain Hettangian ammonites belonging to the genus *Caloceras*.

Discussion. – Even if this ammonite shares numerous traits with the holotype of *Ptycharietites* (*Pompekioceras*) *oncocephalus* (POMPECKJ, 1897) (Fig. 7B), a identification is impossible. The holotype is a small, imperfectly preserved specimen probably corresponding to the juvenile stages only of a larger shell. Direct comparisons are therefore only possible with the inner whorls of the large specimen illustrated in Pl. 3, Fig. 7. The most significant similarity is probably the evolute coiling of the ribless whorls preceding the beginning of the lateral ornamentation. Such a feature is unknown in all the other ribbed *Ptycharietites*. It is perhaps the most distinctive feature of the subgenus *P.* (*Pompekioceras*). For instance, the inner whorls of *P.* (*Ptycharietites*) *heterogenus* n. sp., doubtless a closely related predecessor, clearly exhibit more involute smooth inner whorls.

Stratigraphic and geographic range: The ammonite here identified as *Ptycharietites* (*Pompekioceras*) cf. *oncocephalus* (POMPECKJ, 1897) comes from bed 5112 of the Penedo da Saudade section (São Pedro de Muel, Portugal). It is one of the most outstanding endemic forms of the Lusitanian Sinemurian endemic episode. It may be suspected that this ammonite occurred during the middle or upper parts of the Obtusum Chronozone (Stellare or Denotatus Subchronozones).

Subgenus indet. A

Discussion. – See the discussion for the genus *Ptycharietites*.

Ptycharietites (Subgen. indet. A) *asterocerooides* n. sp.
Fig. 4B, Pl. 1, Fig. 3

Type material: The holotype (UBGD 277086) is a limestone internal cast exhibiting the last whorl of the phragmocone and a large part (about half a whorl) of the body chamber (UBGD 277086; Pl. 1, Fig. 3). The juvenile stages are missing. The phragmocone is undeformed but the body chamber is crushed. The suture line is visible.

Type horizon: Coimbra Formation, Upper Sinemurian, Obtusum Chronozone, Penedo da Saudade section, bed 505a (Fig. 3).

Type locality: Penedo da Saudade section, outcrop located about 400 m N of the lighthouse at Penedo da Saudade, São Pedro de Muel, Portugal (Figs. 1, 2).

Derivation of the name: To suggest the intermediate morphology and ornamentation between the genera *Asteroceras* and *Ptycharietites*.

Material: The new species is known only by its holotype from bed 505a of the Penedo da Saudade section (São Pedro de Muel, Portugal).

Diagnosis. – *Platycone involute Asteroceratinae* with a compressed whorl section. The measurable geometric parameters of the shell are given in Figs. 5A and 10A–C. This form is characterized by a broad ventral area bearing a rather sharp, narrow keel flanked by two wide, plane bands that are almost perpendicular to the plane of symmetry. The ventral area is bounded by blunt but distinct latero-ventral shoulders. The straight to slightly concave subradial ribs are raised, narrow and almost sharp on the lower flank. Beyond, they fade and broaden towards the ventrolateral margin before vanishing just before the ventrolateral shoulder.

Description. – The adult diameter of the only available specimen (holotype) can be evaluated at about 140 mm. With an umbilicus of about 35 % of the diameter (Fig. 10B) close to the end of the phragmocone, this subplatycone ammonite expresses a fairly involute coiling for an *Asteroceratinae*. The subrectangular whorl cross-section is compressed (Fig. 5A). The rather high, sloping umbilical wall and the umbilical margin are rounded. The umbilical shoulders are indistinct, especially if the ribs are ignored. The whorl section is widest close to the flank base. The barely arched flanks converge slightly towards the ventrolateral margin. The broad ventral area is clearly bounded by two blunt but distinct ventrolateral shoulders (Pl. 1, Fig. 3). The venter bears an obvious, fairly narrow, sharp keel which is flanked by two marked, smooth, flat, broad bands. They are almost perpendicular to the plane of symmetry to slightly sloping and confer a distinctive appearance on the ventral area.

The ribbing is relatively dense for a Lusitanian *Asteroceratinae* (Fig. 5B).

The ribs arise at or close to the umbilical seam and are moderately rursiradiate on the umbilical wall. They bend gently forwards on the umbilical margin and become subradial on the flanks where they are almost straight to slightly concave. The ribs are highest close to the flank base, where they look sharp as if pinched. Beyond, and chiefly past the low flank, they fade steadily before disappearing slightly before the ventrolateral shoulder.

The finely preserved septal suture line is illustrated in Fig. 8A. It displays all the major features characteristic of the *Asteroceratinae* subfamily and for instance: i) relatively broad lateral saddles if compared with the rather narrow lateral (*L*) and umbilical (*U2*) lobes, ii) a clearly projected second lateral saddle (*LS*₂), iii) a rather broad and deep but moderately incised external lobe and 4) uniformly fairly modest frilling. Meanwhile, the simplified aspect of the line is more obvious in the new species than is usual within the genus *Asteroceras*. In fact, and if the sutural features are considered, *Ptycharietites* (Subgen. indet. A) *asteroceroides* n. sp. can be understood as a transitional step between the moderately simple suture lines of *Asteroceras* and the much simpler lines of the unequivocal

Ptycharietites, such as *Ptycharietites* (*Pt.*) *ptychogenos* (POMPECKJ, 1897).

Discussion. – *Ptycharietites* (Subgen. indet. A) *asteroceroides* n. sp. is for many of its traits (e. g., the subplatycone compressed shell, the rather dense and simple ribbing) close to certain species classically assigned to the genus *Asteroceras* (e. g., *A. stellare* (J. SOWERBY, 1815) and *A. gr. varians* FUCINI, 1903). Nevertheless, other features, such as the original aspect of the broad ventral area (e. g., a rather narrow and moderately high keel flanked by two obvious, flat and smooth, broad bands), the rapid weakening of the ribs towards the ventrolateral shoulder and the considerable breadth of the first and second lateral saddles compared to the relatively small and narrow lateral and second umbilical lobes, suggest some affinity with *Ptycharietites* (*Pt.*) *ptychogenos* (POMPECKJ, 1897), the next species in the geological succession (Fig. 3). In fact, *P. asteroceroides* n. sp. can be reasonably suspected to be a transitional form between the genera *Asteroceras* and *Ptycharietites*. In an attempt to confer a preferential phyletic meaning on the taxonomic framework of the Sinemurian Lusitanian ammonites, the new species is here provisionally assigned to the endemic genus *Ptycharietites* and not to *Asteroceras*. Nevertheless, we suggest the informal use of a subgenus to underline the plausible transitional significance of this form.

Stratigraphic and geographic range: *Ptycharietites* (Subgen. indet. A) *asteroceroides* n. sp. is known in the type locality only (bed 505a of the Penedo da Saudade section, São Pedro de Muel, Portugal). Allowing for the difficulties in correlating all the Sinemurian endemic faunas, it is hard to propose a precise chronostratigraphic ascription. Nevertheless, an interval in the middle part of Obtusum Chronozone (Stellare Subchronozone) may be suggested. An age in the lower part of this subchronozone can be hypothesized.

Subgenus indet. B

Discussion. – See the discussion for the genus *Ptycharietites*.

Ptycharietites (Subgen. indet. B) *muellense*
DOMMERMUES, MEISTER, NEIGE & ROCHA, 2004
Figs. 4S, 6C

- * 2004 *Ptycharietites muellense*. – DOMMERMUES et al., pl. 4, figs. 2–4.
- 2004 ? *Ptycharietites* sp. cf. *muellense*. – DOMMERMUES et al., pl. 5, fig. 6.

Material: Four specimens of this rare Lusitanian species, including the holotype and the paratypes illustrated by DOMMERMUES et al. (2004), were collected from beds 5105b, 5105f–h and 5112 of the Penedo da Saudade section (São Pedro de Muel, Portugal). These ammonites are internal casts of fine grey lime-

stone. Some recrystallized small parts of shells may be preserved. The holotype and the paratype display the entire body chamber and the aperture. The suture line is visible on the holotype.

Description. – The adult diameter of this small *Ptycharietites* varies from five (holotype) to nine (paratype) centimetres. The body chamber perceptibly occupies more than three-quarters of the whorl. The concave and prorsiradiate aperture – possibly preceded by a moderate uncoiling of the umbilical seam and bordered by a vague constriction – is prolonged by a short ventral rostrum. The evolute to moderately involute subplatycone shell is compressed (= platycone/discocone sensu OLORIZ et al. 2002). The measurable geometric parameters of the shell are given in Figs. 5A and 10A–C. The subogival to subtrapezoidal whorl cross-section is compressed. The whorl is widest close to the flank base. The moderately high, sloping umbilical wall is slightly curved and the umbilical shoulder is rounded and barely distinct. The scarcely rounded flanks taper gently towards the inconspicuous ventrolateral shoulders. The venter bears a keel which, at least on the internal cast, is blunt and moderately high and broad. This keel is flanked by two sloping, plane to slightly concave bands that are bounded by rounded ventrolateral shoulders.

The lateral ornamentation is missing or incipient. In this latter case one can observe, at least on the internal cast, barely distinct, slightly concave to almost straight, very fine riblets arising in a short, faint bulla close to the ventrolateral margin (DOMMERGUES et al. 2004, pl. 4, fig. 3).

If compared with *Ptycharietites* (*Pt.*) *ptychogenos* (POMPECKJ, 1897) (Fig. 8B–O) the septal suture line is, at equivalent whorl height, particularly simple (Fig. 8P) with slight incisions and inconspicuous frilling. Moreover the second lateral saddle (*LS*₂) is not projected and the saddles look flattened.

Discussion. – The holotype and chiefly the paratype of this small smooth *Ptycharietites* show signs of maturity including uncoiling of the umbilical seam, possession of an apertural constriction and of a ventral rostrum (DOMMERGUES et al. 2004, pl. 4, fig. 2). Such features are frequently interpreted as indicative of microconch sexual morphotypes. If such a hypothesis is retained, *Ptycharietites muellense* DOMMERGUES, MEISTER, NEIGE & ROCHA, 2004 can be understood as a microconch associated with *Ptycharietites* (*Ptycharietites*) *heterogenus* n. sp. and possibly also with *Ptycharietites* (*Pompeckioceras*) cf. *oncocephalus* (POMPECKJ, 1897), as macroconchs. Indeed *P. muellense* DOMMERGUES, MEISTER, NEIGE & ROCHA, 2004 occurs in the same beds as these two large *Ptycharietites*. However, another possibility is to interpret *P. muellense* DOMMERGUES, MEISTER, NEIGE & ROCHA, 2004 as a small, perhaps paedomorphic (hypomorphosis sensu REILLEY et al. 1997) species probably closely related to but definitely separate from *Ptycharietites* (*Pt.*) *heterogenus* n. sp. Such

an assumption is tentatively considered here as a possible working hypothesis, but available data are obviously too scant to exclude the possibility of dimorphism. Prudently, and since it is the most neutral taxonomic option, the group of small forms including *Ptycharietites* (Subgen. indet. B) *muellense* DOMMERGUES, MEISTER, NEIGE & ROCHA, 2004 is designated by a distinctive subgenus. This group brings together small species whose complete ontogeny is limited to the ribless stage of growth, which is restricted in the inner whorls of the large species (e. g., *Ptycharietites* (*Pt.*) *ptychogenos* (POMPECKJ, 1897) and *Ptycharietites* (*Pt.*) *heterogenus* n. sp.).

Stratigraphic and geographic range: *Ptycharietites* (Subgen. indet. B) *muellense* DOMMERGUES, MEISTER, NEIGE & ROCHA, 2004 is restricted to beds 5105b, 5105f–h and 5112 in the upper fossiliferous episode of the Penedo da Saudade section (São Pedro de Muel, Portugal). This species and the coeval *Ptycharietites* (*Pt.*) *heterogenus* n. sp. and *Ptycharietites* (*Pompeckioceras*) cf. *oncocephalus* (POMPECKJ, 1897) are strictly endemic taxa, which are known only in this Lusitanian locality. These ammonites can be assumed to occur during the middle or upper parts of Obtusum Chronozone (Stellare or Denotatus Subchronozones).

Ptycharietites (? Subgen. indet. B) sp. indet. A
Figs. 4R, 6B

Material: This possibly new species is known only from one somewhat flattened specimen collected from bed 5117 of the Penedo da Saudade section (São Pedro de Muel, Portugal). The specimen is about half a whorl. The suture line is not visible.

Description. – The only preserved half whorl is perhaps a part of the body chamber and the adult diameter probably does not exceed 10 mm. Because the shell has been visibly although probably only slightly flattened, the whorl width cannot be accurately measured. The involute compressed shell can be assumed to be suboxycone or oxycone/discocone (sensu OLORIZ et al. 2002) with a small umbilicus and a narrow, high, ogival whorl section (Fig. 4R). The flanks probably taper gently towards the venter. The umbilical wall looks low and rounded and the umbilical shoulder is probably distinct but blunt. The ventrolateral margin is gently rounded with indistinct ventrolateral shoulders. The venter bears a narrow but high and sharp keel. Except for faint growth lines, the ribless shell looks perfectly smooth.

Discussion. – This small involute ammonite is unfortunately poorly preserved and difficult to interpret but given the strongly endemic context of the Lusitanian Late Sinemurian it is tempting to suspect close relationships with the genus *Ptycharietites* and more particularly with the equally small and smooth *Ptycharietites muellense* DOMMERGUES, MEISTER, NEIGE & ROCHA, 2004. It may be assumed that *Ptycharietites* (? Subgen. indet. B) sp. indet. A is a late, especially involute (suboxycone) represent-

ative of the paedomorphic lineage initiated by *P.* (Subgen. indet. B) *muellense* DOMMERMUES, MEISTER, NEIGE & ROCHA, 2004. The reserved attribution to subgenus indet. B suggests this phyletic hypothesis.

Comparisons are also possible, but less convincing, with "*Oxynoticeras*" *hoffati* POMPECKJ, 1906 another smooth suboxycone to subdiscocone Lusitanian ammonite which is characterized by a subvertical, barely rounded umbilical wall, an obvious umbilical shoulder and a rounded but distinct ventrolateral shoulder. The age and relationships of "*Oxynoticeras*" *hoffati* POMPECKJ, 1906 are largely undefined but close relationships with the genus *Ptycharietites* are credible. "*Oxynoticeras*" *hoffati* POMPECKJ, 1906 bears many similarities for example with some rather involute, smooth inner whorls of *Ptycharietites* (*Pt.*) *ptychogenos* (POMPECKJ, 1897). By contrast, the Lusitanian ammonite illustrated by POMPECKJ (1906, pl. 1, fig. 1) as "*Oxynoticeras* cf. *oxynotum* Dum. sp." is probably an involute but true *Oxynoticeras* and clearly distinct from the *Ptycharietites* s. l.

Stratigraphic and geographic range: *Ptycharietites* (? Subgen. indet. B) sp. indet. A was collected from bed 5117 of the Penedo da Saudade section (São Pedro de Muel, Portugal). It is one of the youngest ammonites collected in this section. The age of this poorly defined ammonite can be assumed to be in the middle or upper parts of Obtusum Chronozone (Stellare or Denotatus Subchronozones) but this hypothesis is highly tentative.

4. Evolution and ontogeny

All of the ammonites collected from the Penedo da Saudade section belong to the Asterooceratinae, a subfamily within the Arietitidae. Apart from *Asteroceras* sp. indet. – the oldest ammonite collected in a clear stratigraphical context (bed 500b) – all the other ammonites recently collected are strictly endemic Lusitanian taxa. Moreover, except for *Ptycharietites* (*Pt.*) *ptychogenos* (POMPECKJ, 1897), they are only known in a single locality of the Lusitanian Basin. But for *Ptycharietites* (Subgen. indet. A) *asteroceroides* n. sp. and *Epophioceroides apertus* n. gen. n. sp. whose inner and medium whorls are unknown, all of the species collected from the Penedo da Saudade section exhibit a remarkably long, smooth, ribless juvenile stage. This usually precedes a stage of coarse ribbing that often arises quickly on the intermediate whorls (phragmocone) and persists as far as the end of the body chamber. This remarkable changing and contrasted ontogeny is a singular feature within the Asterooceratinae. The smooth juvenile stage is distinctive. It unequivocally designates, among the subfamily, members of a homogenous group that is clearly individualized and easily identifiable. This lineage is here designated by the generic name *Ptycharietites*. It probably corresponds to a monophyletic group (clade) of

which the long, smooth, juvenile stage is the most obvious apomorphy. Moreover, as discussed and illustrated by DOMMERMUES et al. (2004, fig. 4) the smooth juvenile stage of *Ptycharietites* is involved in a paedomorphic dynamic that is a rare "size-based" heterochronic polarity within the Asterooceratinae subfamily and more generally, within the Arietitidae family which are dominated by peramorphic processes. In the case of ammonites, the concept of "size-based" heterochrony (or "allometric" heterochrony) rather than that of "age-based" heterochrony is necessary. Heterochronic processes s. s. refer to the timing of developmental events throughout the evolutionary changes within lineages. However, the timing of these developmental events cannot be addressed in ammonites since the knowledge of growth rates is very limited. Consequently "size" and not "age" must be used as the standard for growth in ammonites (McNAMARA 1986; MCKINNEY 1988; MCKINNEY & McNAMARA 1991).

Although, the inner and medium whorls of *Ptycharietites* (Subgen. indet. A) *asteroceroides* n. sp. are missing, this new species, which in many aspects looks to be transitional between *Asteroceras* sp. indet. and *Ptycharietites* (*Pt.*) *ptychogenos* (POMPECKJ, 1897), is here tentatively understood as a primitive *Ptycharietites*. In fact, *Ptycharietites* (Subgen. indet. A) *asteroceroides* n. sp. is probably situated at, or close to, the root of the genus. Consequently and as hypothesis, the inner whorls of *Ptycharietites* (Subgen. indet. A) *asteroceroides* n. sp. can be expected to possess a fairly obvious smooth and ribless juvenile stage.

On this interpretation, the genus *Ptycharietites* includes almost all of the ammonites collected from the Penedo da Saudade section. Within this genus, *Ptycharietites* (Subgen. indet. A) *asteroceroides* n. sp., *P. (Ptycharietites) ptychogenos* (POMPECKJ, 1897), *P. (Ptycharietites) heterogenus* n. sp. and *P. (Pompeckioceras) cf. oncocephalus* (POMPECKJ, 1897), which are all large or rather large species with complex and contrasted ontogenies, can be understood as a sequence of successive taxa constituting a main evolutionary line within the genus (Fig. 11). Of course, there is no proof that they are a true series of successive ancestors and descendants. Moreover, the main fossiliferous beds are separated by thick series of limestone devoid of ammonites (Fig. 3) and some significant evolutionary episodes are certainly not documented in the Penedo da Saudade section.

Besides this main evolutionary line, *Ptycharietites* (Subgen. indet. B) *muellense* DOMMERMUES, MEISTER, NEIGE & ROCHA, 2004 and *Ptycharietites* (? Subgen. indet. B) sp. indet. A are tentatively interpreted as members of a late excurrent minor line within the genus. These rather small forms are entirely smooth. They probably attained sexual maturity quickly thus interrupting growth early before the onset of the late stage with the coarse ribbing characteristic of the outer whorls of the large *Ptycharietites*. If

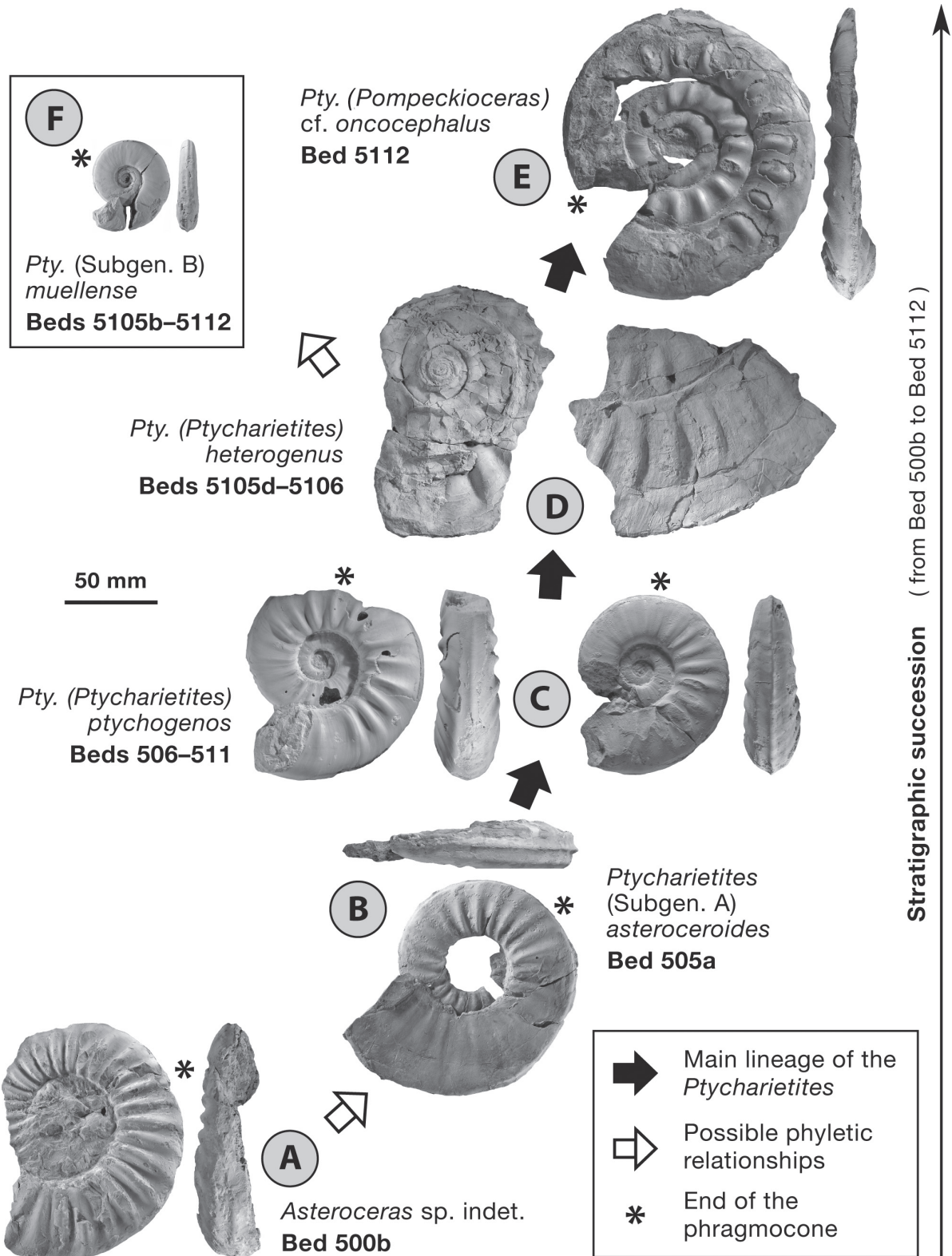


Fig. 11. Schematic illustration of the assumed main lineage of the genus *Ptycharietites* (B–E) in the stratigraphical context of the Penedo da Saudade section (São Pedro de Muel, Portugal). *Asteroceras* sp. indet. (A), which is a possible ancestor of *Ptycharietites*, and *P.* (subgenus B) *muellense* (F), which is a possible microconch or a late excurrent minor line within the genus, are also illustrated for comparison. All the ammonites are illustrated at the same scale and (if possible) with the same orientation.

the possibility of an excurrent minor line is considered, at least as a working hypothesis, the “size-based” heterochronic process involved is “progenesis” or “hypomorphosis” (sensu REILLEY et al. 1997). An alternative hypothesis would be to consider *Ptycharietites* (Subgen. indet. B) *muellense* DOMMERMUES, MEISTER, NEIGE & ROCHA, 2004 as a possible microconch associated with the late representative of the main line, *P. (Ptycharietites) heterogenus* n. sp. and *P. (Pompeckioceras)* cf. *oncocephalus* (POMPECKJ, 1897).

In addition to *Asteroceras* sp. indet. and to the plentiful and diversified *Ptycharietites*, the Late Sinemurian faunas of the Penedo da Saudade section also include the rare *Epophioceroides apertus* n. gen. n. sp. This unfortunately poorly known and curiously evolute Asterooceratinae is almost certainly a strictly endemic Lusitanian ammonite, but its relationships among the subfamily and especially with the genus *Ptycharietites* remain obscure. Similar comments are valid for “*Oxynoticeras*” *choffati* POMPECKJ, 1906, another poorly known but rather involute Lusitanian ammonite collected by CHOFFAT (1903) from Monte-de-Vera elsewhere in the Lusitanian Basin.

To recapitulate, the late Sinemurian Lusitanian faunas of the Obtusum Chronozone are on the whole highly endemic and mainly constituted by the plentiful and prevalent *Ptycharietites* but they also include some rare taxa with enigmatic relationships (e. g., “*Oxynoticeras*” *choffati* POMPECKJ, 1906 and *Epophioceroides apertus* n. gen. n. sp.). It is worth pointing out that the distinctive habitus of *Ptycharietites*, the prevalent Late Sinemurian Lusitanian taxon, is associated with an atypical simplified septal suture line. A trait often taken to be an adaptation to a rather shallow environment and more or less isolated basin. Nevertheless, the most obvious characteristics of the Late Sinemurian endemic genus *Ptycharietites* (i. e., the long smooth inner whorls and the simplified suture line) are exclusive features if compared with the other (Early Pliensbachian) endemic Lusitanian lineages (e. g., *Pseudophriconoceras* and *Dayiceras*). As a result, it is difficult to propose a single and univocal hypothesis to explain the various Late Sinemurian and Early Pliensbachian episodes of endemism within the Lusitanian Basin.

5. Palaeogeography and palaeobiogeography

If, as is usually thought, endemism is a phenomenon associated with more or less isolated areas (e. g., islands s.l. and isolated basins) it can be assumed that, during the Late Sinemurian (Obtusum Chronozone) and episodically later, during the Early Pliensbachian, the Lusitanian Basin was an often isolated palaeogeographical entity or a part of an isolated region possibly featuring several interconnected basins. The Late Sinemurian

and Early Pliensbachian ammonite faunas of the Lusitanian Basin display a succession of several distinct episodes of often obvious endemism (MOUTERDE & RUGET 1975; DOMMERMUES 1987; DOMMERMUES & MOUTERDE 1987; DOMMERMUES & EL HARIRI 2002). The case of the Early Pliensbachian genus *Dayiceras* is probably one of the most remarkable and best known episodes of Lusitanian endemism. The genus *Dayiceras* includes five to six species which are usually plentiful during the Ibex Chronozone (Valdani Subchronozone) in the Lusitanian Basin. Only one of these species is also known outside of this basin: *Dayiceras polymorphoides* (SPATH, 1920) briefly became established in SW England (SPATH 1920; PHELPS 1985). In many ways (e. g., number of species concerned, duration of the endemic episode, idiosyncrasy of the main diagnostic traits, and extremely restricted Lusitanian occurrence), the case of the Late Sinemurian *Ptycharietites* is comparable with that of *Dayiceras*.

The Late Sinemurian (probably chiefly Obtusum Chronozone) ammonites studied here belonging to the genus *Asteroceras*, *Ptycharietites* and *Epophioceroides* n. gen. correspond to both the first ammonite-bearing beds in the basin and to the first episode of Lusitanian endemism. Moreover, the phenomenon of endemism is patent in the lowermost fossiliferous levels (i. e., beds 505a, 506, 508 and 510) following the very first ammonite-bearing bed (i. e. bed 500b) in the fossiliferous succession of Penedo da Saudade (Fig. 3). If the Lusitanian ammonites of the Obtusum Chronozone alone are concerned it is difficult to propose a palaeobiogeographical polarity for the Lusitanian faunas. By contrast, the Early Pliensbachian Lusitanian faunas (endemic or non endemic taxa) are clearly connected with the NW European palaeobiogeographical province and not with the Mediterranean (= western Tethyan) faunas (DOMMERMUES 1987; DOMMERMUES & MOUTERDE 1987; DOMMERMUES & EL HARIRI 2002). This NW European polarity is outwardly difficult to explain in palaeobiogeographic and or palaeoecological terms because all of the palaeobiogeographic reconstructions currently available (ZIEGLER 1988; THIERRY et al. 2000; DOMMERMUES et al. 2004, fig. 6A–B) suggest that the Lusitanian Basin was, more or less directly, connected with the westernmost Tethyan basins and hence with Mediterranean faunas. This clash between faunal facts and palaeobiogeographic synthetic maps, was termed the “Lusitanian paradox” by DOMMERMUES & EL HARIRI (2002).

In fact, this paradox may be merely an artefact. While faunal data are robust, palaeobiogeographical hypotheses are highly speculative and poorly constrained by facts. Fig. 12A–B show sketch maps summarizing what is really known about the palaeogeographical context of the Lusitanian Basin in the pre-drift framework of the “Iberia-Newfoundland” conjugate margins. All the Mesozoic pre-drift basins are schematically delimited (Fig. 12A) and their

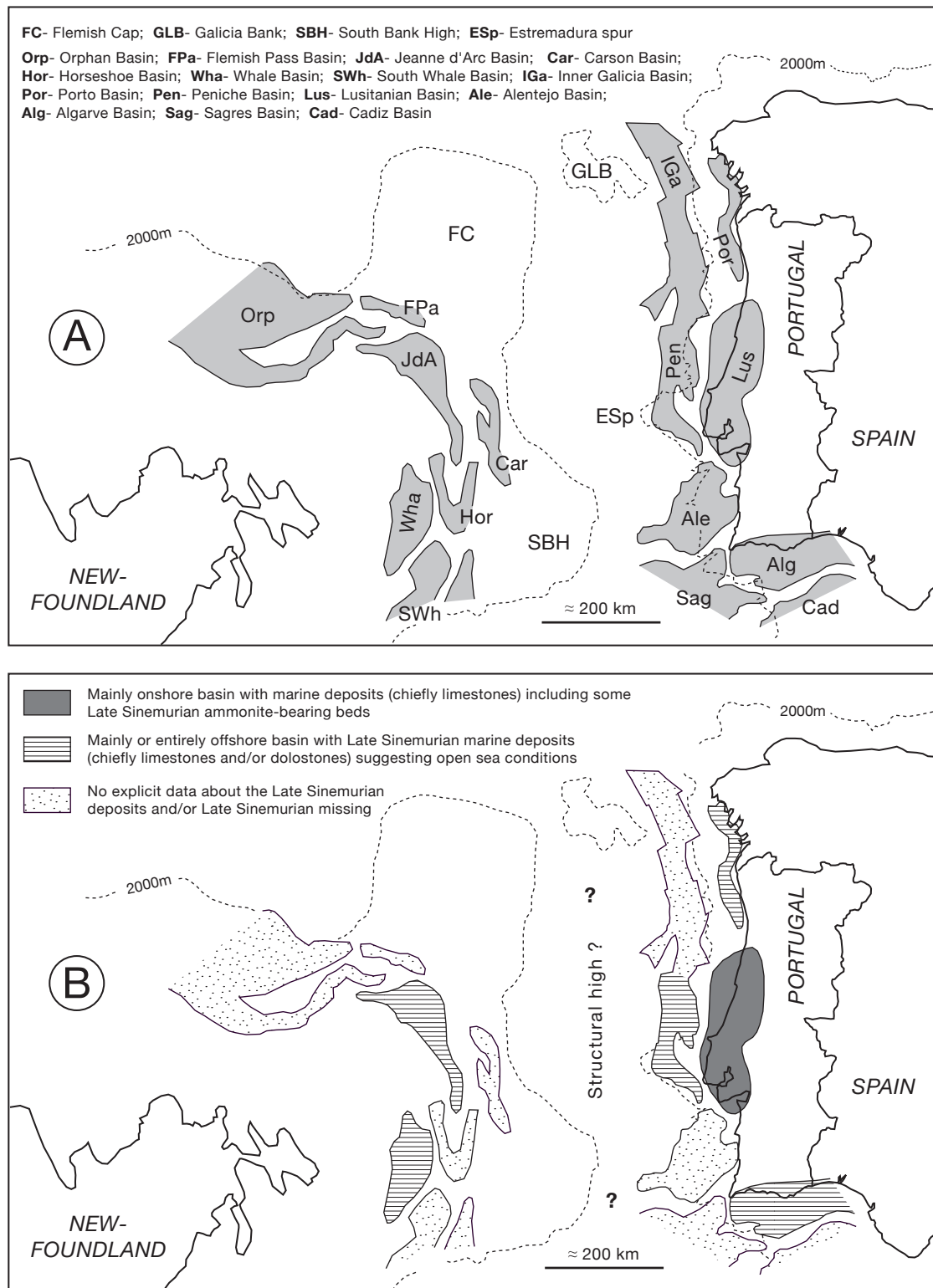


Fig. 12. Pre-drift sketch maps of the “Iberia-Newfoundland” conjugate margins. The Iberian landmass is outlined in its present-day configuration as a landmark. The location and extent of Mesozoic pre-drift basins (shaded regions) are approximate only (modified from SRIVASTAVA & VERHOEF 1992 and SANDNESS & PACHECO 2002). The 2000 m isobath is suggested by dotted lines to approximate the offshore outlines of the Newfoundland and Iberian landmasses. Plate boundaries cannot be pinpointed. – **A.** Pre-drift palaeogeographical framework and denominations of the main Mesozoic basins. **B.** Facies and palaeoecological framework for the Late Sinemurian.

main sedimentological and palaeoecological characteristics are suggested (Fig. 12B). The paucity of data available for the offshore and chiefly offshore basins is confounding. The Lusitanian Basin is definitely the only properly investigated basin of the entire “Iberia-Newfoundland” conjugate margins. Moreover, while some published data exist for other offshore or chiefly offshore basins (e. g., Algarve, Peniche, Porto, Whale and Jeanne d'Arc Basins), they are partial, heterogeneous and difficult to include in a synthesis on the “Iberia-Newfoundland” scale. Thus, while connections between the Lusitanian and neighbouring basins are conceivable, they are all highly speculative and poorly documented. In fact, and at least in palaeogeographic terms and if faunal data are ignored, nothing allows us to prefer a southward (towards the Mediterranean basins) rather than a northward polarity (towards the NW European basins) for the Lusitanian Basin. As a result, the clear NW European affinities of the Early Pliensbachian Lusitanian faunas do not really contradict the still insufficiently documented palaeogeographical framework. In any event, the Late Sinemurian and Early Pliensbachian Lusitanian endemic trend is a well documented, remarkable palaeobiogeographical phenomenon whose palaeogeographical and palaeoecological causes remain poorly understood. This is a real challenge for further palaeobiogeographical research.

6. Conclusions

Unlike all earlier publications (POMPECKJ 1897, 1898, 1906; CHOFFAT 1903–1904; MOUTERDE & ROCHA 1981; DOMMERMUES & MOUTERDE 1987; DOMMERMUES et al. 2004) on the Late Sinemurian ammonites of the Lusitanian Basin, the present work, based on extensive, bed by bed collection from the Penedo da Saudade section (São Pedro de Muel), demonstrates that the earliest episode of Liassic Lusitanian endemism was a complex and long-lasting phenomenon and not, as previously supposed, a single, brief, anecdotal event. In many ways this first Sinemurian episode can be compared with the familiar and remarkable Early Pliensbachian reign of the genus *Dayiceras* during the Valdani Subchronozone. Each of these two instances of endemism is characterized by a more or less continuous sequence of several (five to six) related but clearly distinct species constituting, in each case, a dominant monophyletic group or clade (i. e., *Ptycharietites* and *Dayiceras*). The Pliensbachian *Dayiceras* are accompanied by certain partly- or non-endemic taxa (e. g., *Acanthopleuroceras* and *Metaderoceras*) that are clearly related to NW European faunas, making accurate chronostratigraphic datings possible. However, the dominant endemic genus of the Sinemurian endemic episode (i. e., *Ptycharietites*) is accompanied exclusively by similarly endemic taxa (i. e.,

Epophioceroides n. gen.). Consequently there is no sound basis for chronostratigraphic correlations for this period.

In fact, the first episode of Liassic Lusitanian endemism studied here is definitely one of the most marked phases of faunal differentiation of the entire period (Late Sinemurian and Early Pliensbachian).

Many questions about the first (Late Sinemurian) Lusitanian ammonite faunas remain unresolved while our now significantly improved understanding of them has given rise to many more. Some of the most puzzling of these questions are about the poorly resolved age of the faunas. While the first two endemic species, *Ptycharietites asteroceroides* and *P. ptychogenos*, which occur with *Asteroceras* sp. indet. in the lower fossiliferous interval of the Penedo da Saudade section (beds 500b to 511), can be credibly suspected of occurring during the Stellare Subchronozone, all of the other species, which were collected from significantly higher levels, are difficult to date within a period encompassing the Stellare and the Denotatus Subchronozones. This problem cannot be resolved without observation of barely- or non-endemic taxa in clear stratigraphic association with the Lusitanian endemic species. Given the high endemicity of these faunas, the questions about the ages of *Ptycharietites* and *Epophioceroides* n. gen. may long remain unresolved.

Other significant but still poorly resolved questions concern the palaeogeographical framework and the causes of Lusitanian endemism. Firstly, it is important to understand why the Lusitanian faunas are, at least during the Early Pliensbachian and possibly also as early as the Late Sinemurian, clearly related to NW European rather than western Tethyan (= Mediterranean) faunas. Secondly, it is important to find out whether the remarkable “Lusitanian” endemic phenomenon is restricted to the Lusitanian Basin alone or if it also affects other neighbouring offshore or chiefly offshore basins of “Iberia-Newfoundland”. Given the difficulty in obtaining data about macro-faunas in offshore basins, these questions may long remain enigmatic. Accordingly Liassic Lusitanian endemism may well remain for some time yet a fascinating, well described but paradoxically poorly understood palaeobiogeographic phenomenon.

7. References

- BRAYARD, A., BUCHER, H., ESCARGUEL, G., FLUTEAU, F., BOURQUIN, S. & GOLFETTI, T. (2006): The Early Triassic ammonoid recovery: paleoclimatic significance of diversity gradients. – *Palaeogeography, Palaeoclimatology, Palaeoecology*, **239**: 374–395.
- BRAYARD, A., ESCARGUEL, G. & BUCHER, H. (2007): The biogeography of Early Triassic ammonoid faunas: clusters, gradients, and networks. – *Geobios*, **40**: 749–765.
- BUCKMAN, S. S. (1909–1930): *Yorkshire Type Ammonites* (volumes 1–2), *Type Ammonites* (volumes 3–7). 709 pls.; London (Wheldon & Wesley).

- CARIOU, E., CONTINI, D., DOMMERMUES, J.-L., ENAY, R., GEYSSAN, J. R., MANGOLD, C. & THIERRY, J. (1985): Biogéographie des ammonites et évolution structurale de la Téthys au cours du Jurassique. – *Bulletin de la Société Géologique de France*, série 8, **1**: 679–697.
- CECCA, F. (2002): *Palaeobiogeography of Marine Fossil Invertebrates. Concepts and Methods*. 272pp.; London, New York (Taylor & Francis).
- CHOFFAT, P. (1903–1904): L'Infralias et le Sinémurien du Portugal. – *Comunicações da Comissão do Serviço geológico de Portugal*, **5**: 4–114.
- DOMMERMUES, J.-L. (1987): L'évolution chez les Ammonitina du Lias moyen (Carixien, Domérien basal) en Europe occidentale. – *Documents des Laboratoires de Géologie Lyon*, **98**: 87 pp.
- DOMMERMUES, J.-L. (2002): Les premiers Lytoceratoidea du Nord-Ouest de l'Europe (Ammonoidea, Sinémurien inférieur, France). Exemple de convergence évolutive vers les morphologies "capricornes". – *Revue de Paléobiologie*, **21**: 257–277.
- DOMMERMUES, J.-L. & EL HARIRI, K. (2002): Endemism as a palaeobiogeographic parameter of basin history illustrated by early- and mid-Liassic peri-Tethyan ammonite faunas. – *Palaeogeography, Palaeoclimatology, Palaeoecology*, **184**: 407–418.
- DOMMERMUES, J.-L. & MOUTERDE, R. (1981): Les Acanthopleurocératinés portugais et leurs relations avec les formes subboréales. – *Ciências da Terra*, **6**: 77–100.
- DOMMERMUES, J.-L. & MOUTERDE, R. (1987): The endemic trends of the Liassic ammonite faunas of Portugal as the result of the opening up of a narrow epicontinental basin. – *Palaeogeography, Palaeoclimatology, Palaeoecology*, **58**: 129–137.
- DOMMERMUES, J.-L., MEISTER, C., NEIGE, P. & ROCHA, R. B. (2004): Endemic Sinemurian (Early Jurassic) ammonites from the Lusitanian Basin (Portugal). – *Revue de Paléobiologie*, **23**: 529–549.
- GUÉX, J. (1987): Sur la phylogénèse des ammonites du Lias inférieur. – *Bulletin de Géologie Lausanne*, **292**: 455–469.
- KORN, D. & KLUG, C. (2007): Conch Form Analysis, Variability, Morphological Disparity, and Mode of Life of the Frasnian (Late Devonian) Ammonoid Manticoceras from Coumiac (Montagne Noire, France). – In: LANDMAN, N. H., DAVIS, R. A. & MAPES, R. H. (eds.): *Cephalopods Present and Past: New Insights and Fresh Perspectives*: 57–85; Dordrecht (Springer).
- LONGRIDGE, L. M., SMITH, P. L., PALFY, J. & TIPPER, H. W. (2008): Three new species of the Hettangian (Early Jurassic) ammonite *Sunrisites* from British Columbia, Canada. – *Journal of Paleontology*, **82**: 128–139.
- McKINNEY, M. L. (1988): Classifying heterochrony: allometry, size and time. – In: McKINNEY, M. L. (ed.): *Heterochrony in evolution: a multidisciplinary approach*: 17–34; New York (Plenum Publishing Corporation).
- McKINNEY, M. L. & McNAMARA, K. J. (1991): *Heterochrony: the evolution of ontogeny*. 437 pp.; New York (Plenum Publishing Corporation).
- McNAMARA, K. J. (1986): A guide to the nomenclature of heterochrony. – *Journal of Paleontology*, **60**: 4–13.
- MOUTERDE, R. & ROCHA, R. B. (1981): Atlas des fossiles caractéristiques du Lias portugais, 1 – Lias inférieur. – *Ciências da Terra*, **6**: 49–76.
- MOUTERDE, R., & RUGET, C. (1975): Esquisse de la paléogéographie du Jurassique inférieur et moyen au Portugal. – *Bulletin de la Société géologique de France*, 7^e Série, **17**: 779–786.
- MOUTERDE, R., DOMMERMUES, J.-L. & ROCHA, R. B. (1983): Atlas des fossiles caractéristiques du Lias portugais, 2 – Carixien. – *Ciências da Terra*, **7**: 187–254.
- OLORIZ, F., PALMQVIST, P. & RÉREZ-CLAROS, J. A. (2002): Morphostructural constraints and phylogenetic overprint on sutural frilling in Late Jurassic ammonites. – *Lethaia*, **35**: 158–168.
- PHELPS, M. (1985): A refined ammonite biostratigraphy for the Middle and Upper Carixian (ibex and davoei zones, Lower Jurassic) in North-West Europe and stratigraphical details of the Carixian-Domerian boundary. – *Geobios*, **18**: 321–362.
- POMPECKJ, J. F. (1897): Neue Ammoniten aus dem unteren Lias von Portugal. – *Zeitschrift der Deutschen Geologischen Gesellschaft*, **49**: 636–661.
- POMPECKJ, J. F. (1898): Notes sur quelques ammonites du Sinémurien du Portugal. – *Comunicações de Direcção de Trabalhos Geológicos de Portugal*, **3**: 210–238.
- POMPECKJ, J. F. (1906): Notes sur les *Oxynoticeras* du Sinémurien supérieur du Portugal et remarques sur le genre *Oxynoticeras*. – *Comunicações da Comissão do Serviço Geológico de Portugal*, **6**: 214–338.
- REILLEY, S. M., WILEY E. O. & MEINHARDT, D. J. (1997): An integrative approach to heterochrony: the distinction between interspecific and intraspecific phenomena. – *Biological Journal of the Linnean Society*, **60**: 119–143.
- SANDNESS, F. & PACHECO, J. (2002): Portuguese deepwater basins show potential. – *Offshore*, **62** (8): 1–3.
- SPATH, L. F. (1920): On a new genus *Dayiceras* from the Lias of Charmouth. – *Geological Magazine*, **57**: 538–543.
- SPATH, L. F. (1925): Notes on Yorkshire ammonites. V. *Arietites*, *Asiteroceras* and allied genera. – *The Naturalist*, **September 1**: 263–269.
- SRIVASTAVA, S. P. & VERHOEF, J. (1992): Evolution of Mesozoic sedimentary basins around the North Central Atlantic: a preliminary plate kinematic solution. – In: PARNELL, J. (ed.): *Basins of the Atlantic Seaboard: Petroleum Geology, Sedimentology and Basin Evolution*. – Geological Society (London) Special Publication, **62**: 397–420.
- TAYLOR, D. G. (1998): Late Hettangian–Early Sinemurian (Jurassic) ammonite biochronology of the Western Cordillera, United States. – *Geobios*, **31**: 467–497.
- THIERRY, J. et al. (40 co-authors) (2000): Late Sinemurian (193–191 Ma). In: DERCOURT, J., GAETANI, M., VRIELINCK, B., BARRIER, E., BIJU-DUVAL, B., BRUNER, M. F., CADET, J. P., CRASQUIN, S. & SANDULESCU, M. (eds.): *Atlas Peri-Tethys, Palaeogeographical maps*. Map n° 7; Paris (CCGM/CGMW).
- WESTERMANN, G. E. G. (2000): Marine faunal realms of the Mesozoic: review and revision under the new guidelines for biogeographic classification and nomenclature. – *Palaeogeography, Palaeoclimatology, Palaeoecology*, **163**: 49–68.
- ZIEGLER, P. A. (1988): Evolution of the Arctic-North Atlantic and the western Tethys. – *American Association of Petroleum Geologists, Memoir*, **43**: 1–198.

Addresses of the authors:

JEAN-LOUIS DOMMERMUES, Université de Bourgogne, Biogeosciences, UMR CNRS 5561, 6 Boulevard Gabriel, 21000 Dijon, France
E-mail: Jean-Louis.Dommergues@u-bourgogne.fr

CHRISTIAN MEISTER, Muséum d'Histoire naturelle de Genève, Département de Géologie et de Paléontologie,
1 route de Malagnou, c.p. 6434, 1211 Geneva, Switzerland
E-mail: Christian.Meister@ville-ge.ch

ROGÉRIO BORDALO DA ROCHA, CICEGe & Earth Sciences Department, Faculty of Sciences and Technology,
Universidade Nova Lisboa, Campus de Caparica, 2829-516 Caparica, Portugal
E-mail: rbr@fct.unl.pt

Manuscript received: 2 July 2009, accepted: 4 November 2009.

Plate 1

Late Sinemurian ammonites from the Coimbra Formation, Penedo da Saudade section (São Pedro de Muel, Portugal).

Fig. 1. *Asteroceras* sp. indet., level 500b, UBGD 277084.

Fig. 2. *Ptycharietites* (? Subgenus indet. A) sp. juv., level 505d, UBGD 277085.

Fig. 3. *Ptycharietites* (Subgenus indet. A) *asterocerooides* n. sp., holotype, level 505a, UBGD 277086.

Figs. 4–5. *Ptycharietites* (*Pt.*) *ptychogenos* (POMPECKJ, 1897), level 510.

Fig. 4. UBGD 277087.

Fig. 5. UBGD 277088.

Arrow on lateral view indicate onset of body chamber at the last septum. Ammonites are coated with ammonium chloride.

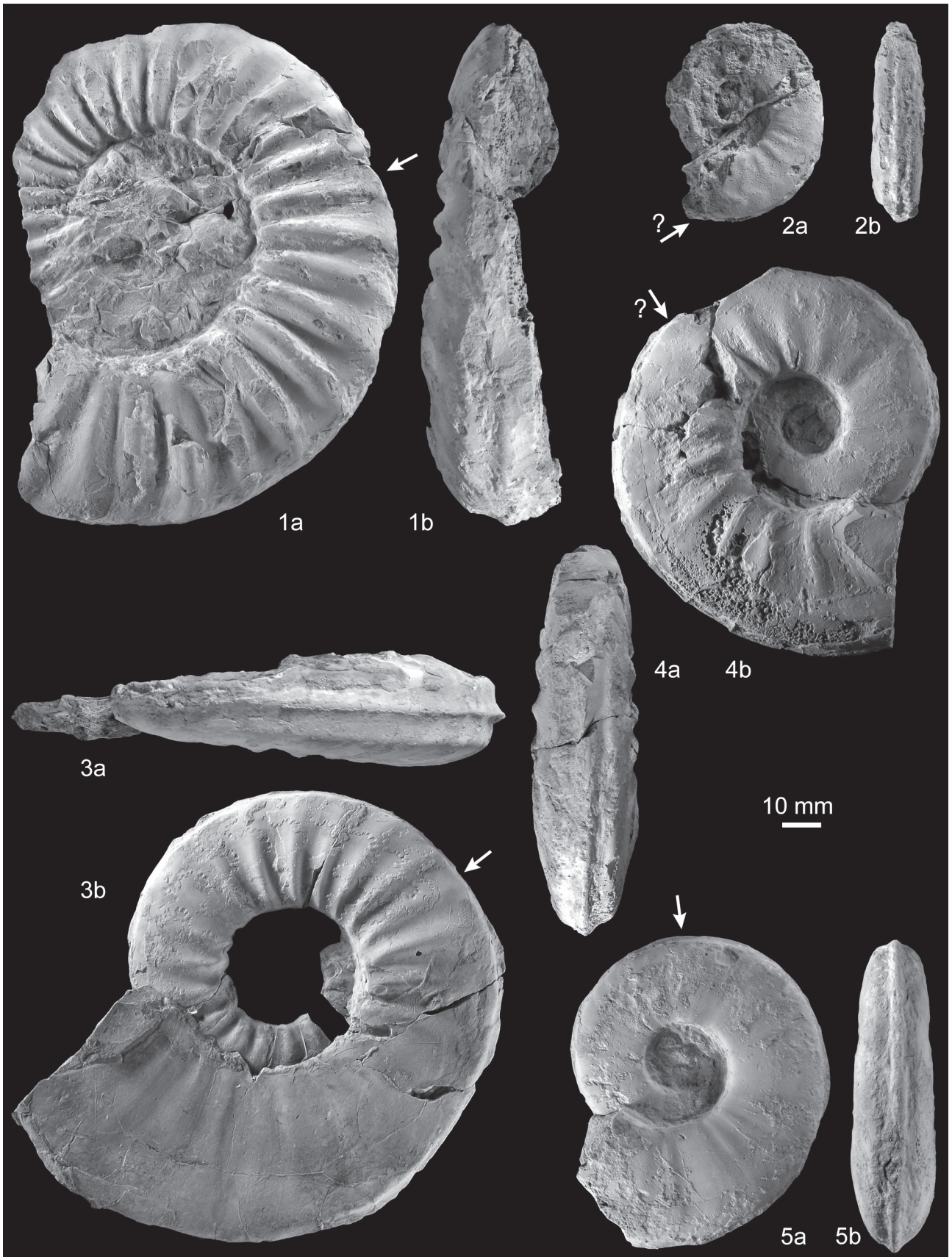


Plate 2

Ptycharietites (Pt.) ptychogenos (POMPECKI, 1897), level 510; Late Sinemurian, Coimbra Formation, Penedo da Saudade section (São Pedro de Muel, Portugal).

Fig. 1. UBGD 277089.

Fig. 2. UBGD 277090.

Fig. 3. UBGD 277091.

Fig. 4. UBGD 277092.

Fig. 5. UBGD 277093.

Fig. 6. UBGD 277094.

Arrow on lateral view indicate onset of body chamber at the last septum. Ammonites are coated with ammonium chloride.

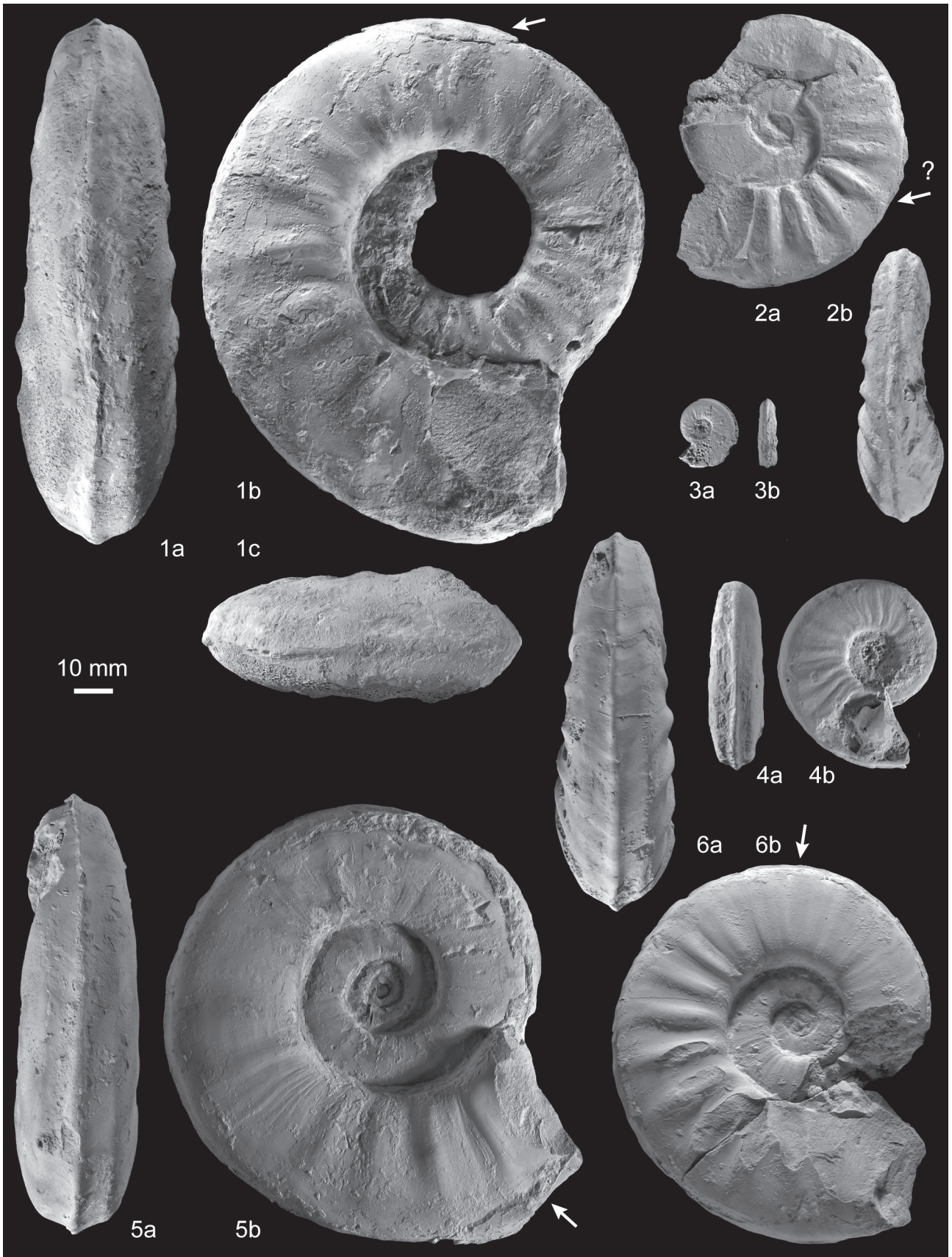


Plate 3

Late Sinemurian ammonites from the Coimbra Formation, Penedo da Saudade section (São Pedro de Muel, Portugal).

Figs. 1, 3–6. *Ptycharietites (Ptycharietites) ptychogenos* (POMPECKJ, 1897), level 510.

Fig. 1. UBGD 277095.

Fig. 3. UBGD 277097.

Fig. 4. UBGD 277098.

Fig. 5. UBGD 277099.

Fig. 6. UBGD 277100.

Fig. 2. *Ptycharietites (Ptycharietites) heterogenus* n. sp., holotype, level 5106, UBGD 277096.

Fig. 7. *Ptycharietites (Pompeckioceras) cf. oncocephalus* (POMPECKJ, 1897), level 5112, UBGD 277101.

Arrow on lateral view indicate onset of body chamber at the last septum. Ammonites are coated with ammonium chloride.

