Ammonites from the *Apoderoceras* beds (Early Pliensbachian) in São Pedro de Muel (Lusitanian Basin, Portugal)

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The lowermost Portuguese Pliensbachian is characterized by the association of *Apoderoceras dunrobinense* Spath, *Tragophylloceras numismale* (Quenstedt) and *Vicininodiceras* aff. *mouterdei* Donovan. This ammonite fauna indicates the lower part of the *Jamesoni* Chronozone (lower to middle *Taylori* Subchronozone). Thanks to the numerous specimens collected, the ontogeny and variability of *A. dunrobinense* Spath, could also be investigated. The paleogeographical distribution of these ammonites underlines the close connections between the Lusitanian Basin and the Euroboreal seas during the Early Pliensbachian. • Key words: Lower Jurassic, ammonites, taxonomy, biostratigraphy, paleogeography, Lusitanian Basin.

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São Pedro de Muel is a classical locality for the Lias of the Lusitanian Basin. The Liassic series outcrop along the coast and form thick, continuous succession quite near the more subsiding part of the basin (Fig. 1A–C). The Lusitanian Basin belongs to the Central North Atlantic domain, which at this time formed a pre-oceanic corridor with several basins more or less interconnected. It was situated between Iberica to the East and the Newfoundland area to the West (see Dommergues *et al.* 2010, fig. 12).

The Lias of São Pedro de Muel has been known since the works of Choffat (1880, 1885, 1903–1904) and Pompeckj (1897, 1898). Subsequently, Mouterde (1947, 1951, 1967a, b, 1970), Mouterde *et al.* (1981, 1983), Dommergues & Mouterde (1980, 1981), Phelps (1985), Dommergues (1987) and, more recently, Dommergues *et al.* (2004a, 2004b) and Mouterde *et al.* (2007) have discussed the stratigraphy and systematics of the ammonite faunas from this area.

The present work focuses on the ammonites from the Sinemurian–Pliensbachian boundary beds. The aim is to describe this stage boundary, to provide new ammonite data and to complete the study of Antunes *et al.* (1981) and of the 'Atlas des fossiles caractéristiques du Lias portugais I et II' by Mouterde *et al.* (1981, 1983).

The Liassic sediments of São Pedro de Muel belongs to the Hettangian–Toarcian. In Agua de Madeiros the Upper Sinemurian series outcrops in the northern part and the Pliensbachian starts near the steps and continues to the south (Fig. 2A).

The lithological profile of Água de Madeiros is situated just under the houses of Pedra Lisa on both sides of the steps leading to the beach (praia da Pedra Lisa). The material comes from thick marly limestone and marl alternations (Fig. 2B) and includes 40 more or less well preserved ammonites. It corresponds to beds 19c, d to 19e of Antunes *et al.* (1981, fig. 1). These sediments belong to the Pedra Lisa Member of the upper part of the Água de Madeiros Formation (Duarte *et al.* 2010; Fig. 3).

Following Duarte *et al.* (2010) the thin bedded limestones (unit A in Fig. 3) indicate rather shallow marine environments corresponding to the end of a 2nd order transgressive-regressive facies cycle, and the overlying limestone–marl alternations with ammonites corresponding to the beginning of a 2nd order transgressive-regressive facies cycle.

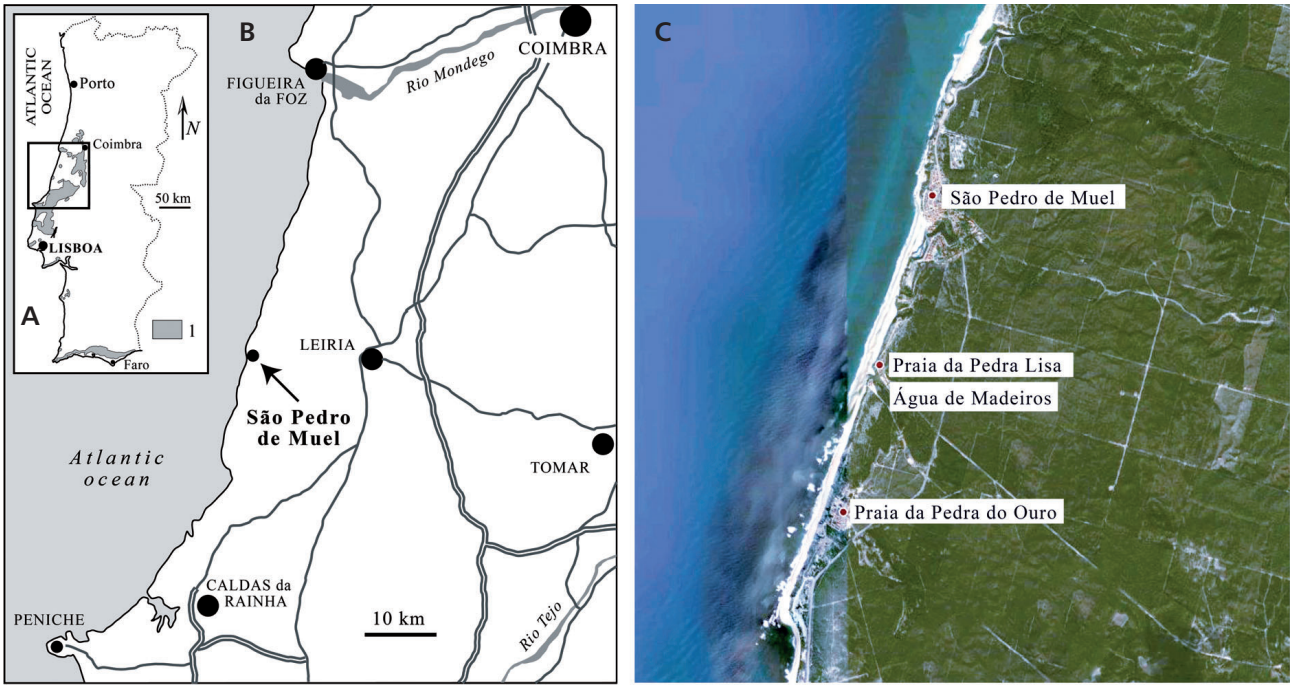


Figure 1. Maps (A, B) and satellite photograph modified from Google Earth (C) showing the studied area and the location of Água de Madeiros.

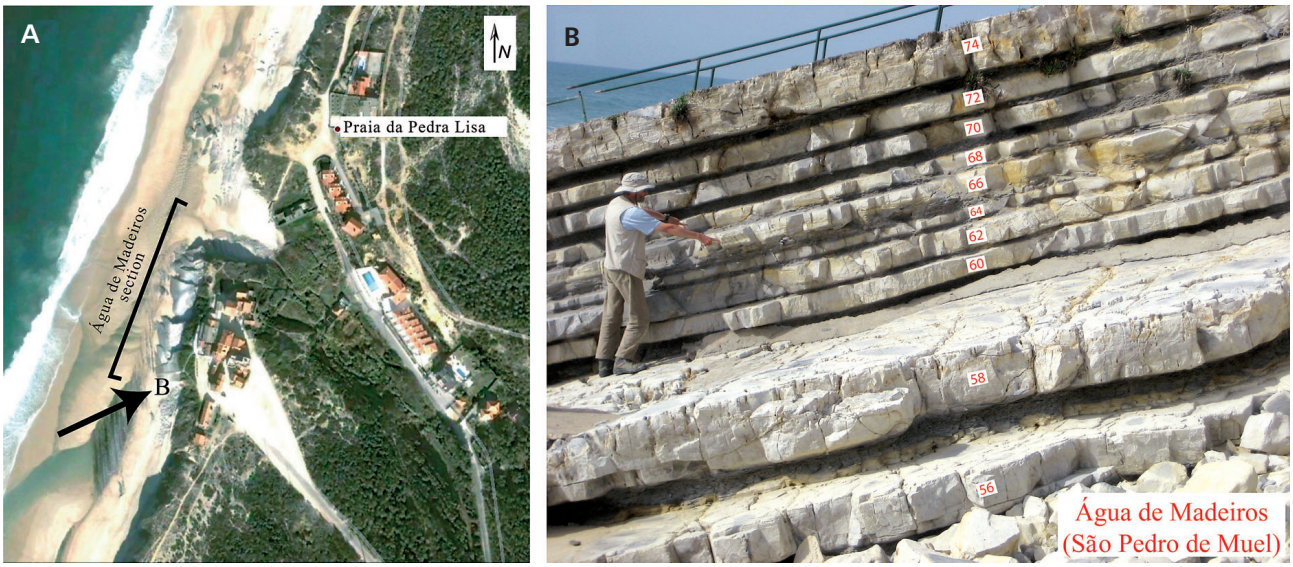


Figure 2. Location of Água de Madeiros section (A – modified from Google Earth) and detail of the upper *Apoderoceras* beds (B).

Systematic part

Class Cephalopoda Cuvier, 1798
Subclass Ammonoidea Zittel, 1884
Order Phylloceratida Arkell, 1950
Superfamily Phylloceratoidea Zittel, 1884
Family Juraphyllitidae Arkell, 1950

Genus *Tragophylloceras* Hyatt, 1900

Type species. – *Ammonites numismalis* Quenstedt, 1845.

Tragophylloceras numismale (Quenstedt, 1845)

Figure 4C–F

1845–49 *Ammonites heterophyllus nunismalis*; Quenstedt, pl. 6, figs 4a, b, 5a, b, non 3a, b et 5c.
1964 *Tragophylloceras numismale* (Quenstedt). – Howarth & Donovan, pl. 48, fig. 5 with synonymy.
1980 *Tragophylloceras numismale* (Quenstedt). – Schlatter, pl. 1, fig. 1.
1982 *Tragophylloceras numismale* (Quenstedt). – Hoffmann, pl. 1, figs 1–3.

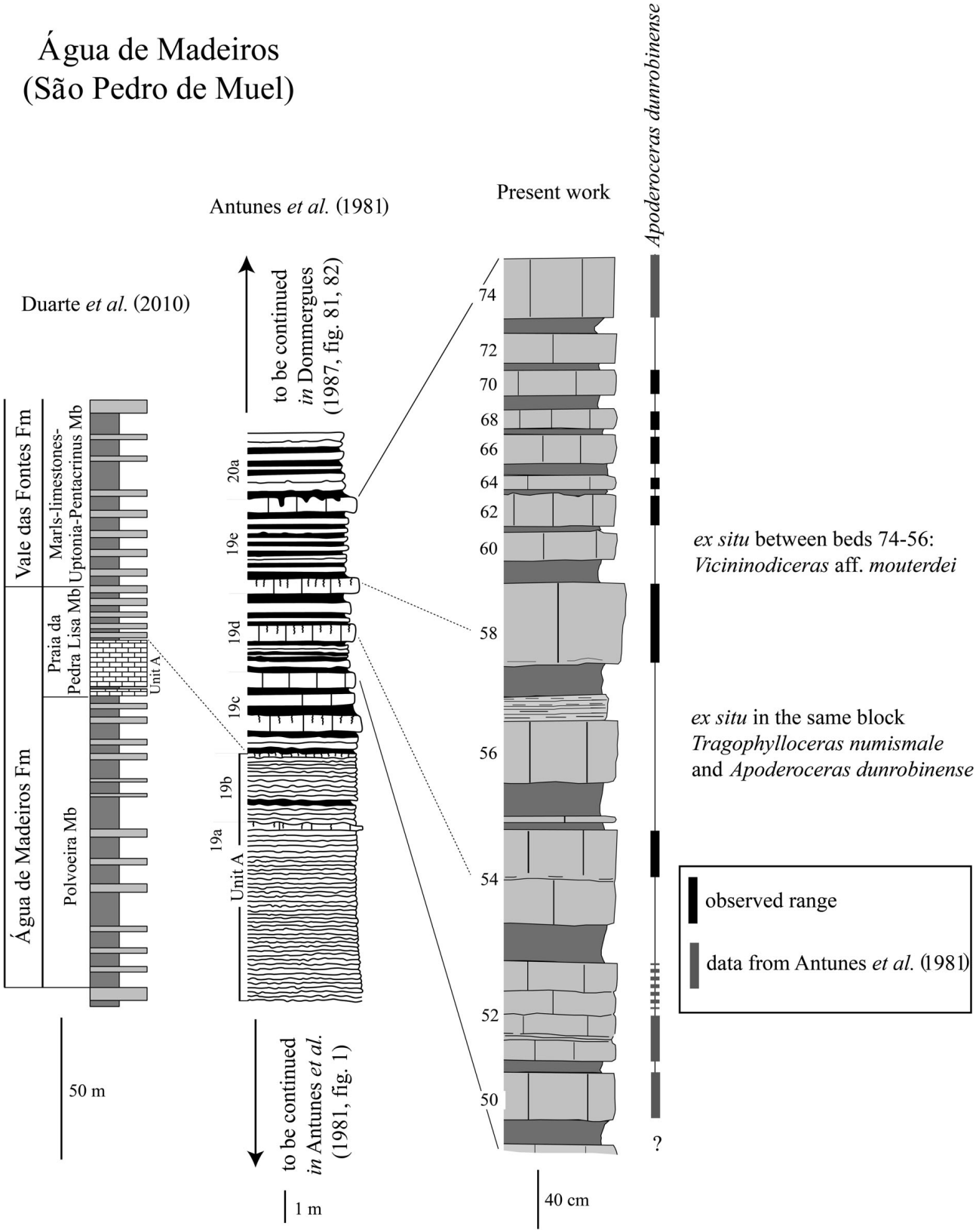


Figure 3. Água de Madeiros profile with different scales (Antunes *et al.* 1981, Duarte *et al.* 2010 and present work) with *Apoderoceras* range.

1982 *Tragophylloceras* cf. *numismale* (Quenstedt). – Hoffmann, p. 129, text-fig. 18.
1986 *Tragophylloceras numismale* (Quenstedt). – Meister, pl. 1, fig. 5.
1991 *Tragophylloceras numismale* (Quenstedt). – Schlatter, pl. 1, figs 1, 2.
non 1991 *Tragophylloceras numismale* (Quenstedt). – Cope, pl. 1, fig. 4; pl. 2, fig. 6.
1992 *Tragophylloceras numismale* (Quenstedt). – Schlegelmilch, pl. 2, figs 1, 2.
1998 *Tragophylloceras numismale* (Quenstedt). – Rulleau, pl. 21, fig. 6.
2000 *Tragophylloceras numismale* (Quenstedt). – Joly, pl. 2, fig. 7, 9; pl. 3, fig. 1.
2002 *Tragophylloceras numismale* (Quenstedt). – Howarth, pl. 1, fig. 1.
2003 *Tragophylloceras numismale* (Quenstedt). – Donovan & Surlyk, p. 561, fig. B.
2003 *Tragophylloceras* cf. *numismale* (Quenstedt). – Donovan & Surlyk, p. 573, figs 1–6.
2007 *Tragophylloceras numismale* (Quenstedt). – Schubert, pl. 1, fig. 5.

Remarks. – Four small crushed Juraphyllitidae (D = 27 mm) were found in the *Apoderoceras* beds. These are compressed suboxycones with a narrow umbilicus (O/D = 0.12) and fine, sinuous ribs, hardly noticeable on the flanks and more clearly expressed on the external part of the whorl where they cross the venter (Fig. 4C, E). In this species ribs on the outer part are already well expressed in the inner whorls as shown by Schlatter (1980, fig. 1). One specimen (Fig. 4D) bears some constrictions.

T. loscombi (Sowerby) is the closest form to *T. numismale* (Quenstedt), probably a directly derived form (Meister 1993). Sowerby's species differs by a narrower umbilicus (*ibid.* 1993, p. 127, fig. 4), a wider whorl section on the lower part of the flanks (more suboval) and finer ribbing, less strongly expressed on the outer part. In *T. undulatum* (Smith) the ribs are more developed on the flanks and rather sinuous.

Age and distribution. – *T. numismale* (Quenstedt) is characteristic of the Early Pliensbachian, more precisely to the Taylori Subchronozone – Valdani Subchronozone (base of Jamesoni Chronozone – base of Ibex Chronozone; see Meister 1993, Joly 2000). This species is confined to the Euroboreal regions: UK (Yorkshire, Somerset, Hebrides, Leicestershire, Gloucestershire), Denmark (Bornholm), NW and SW Germany, France (Causses, Cher, Burgundy) and Portugal (Lusitanian Basin).

Order Psiloceratida Houša, 1965
Superfamily Eoderoceratoidea Spath, 1929
Family Coeloceratidae Haug, 1910 emended Dommergues & Meister, 1999

Genus *Apoderoceras* S.S. Buckman, 1921

Type species. – *Apoderoceras lobulatum* S.S. Buckman, 1921.

Description. – The genus *Apoderoceras* belongs to the family Coeloceratidae emended Dommergues & Meister (1999). This classification has been followed by Howarth (2002), Edmunds *et al.* (2003) and Edmunds (2009). Previously this genus was placed in the Polymorphitidae by Schlatter (1980) and later in the Eoderoceratidae by the same author (*ibid.* 1991).

In the diagnosis of the Treatise (Arkell *et al.* 1957) *Apoderoceras* contains large forms, on the one hand with coeloceratomorph inner whorls becoming smooth in the adult morphology and, on the other hand more clearly ribbed forms developing spiny tubercles on the external edge. Both groups show divergent flanks and a ventral area rounded and rather flat.

The Portuguese specimens, a rather homogeneous population, belong to the second group characterized by well expressed ornamentation including the outer whorls.

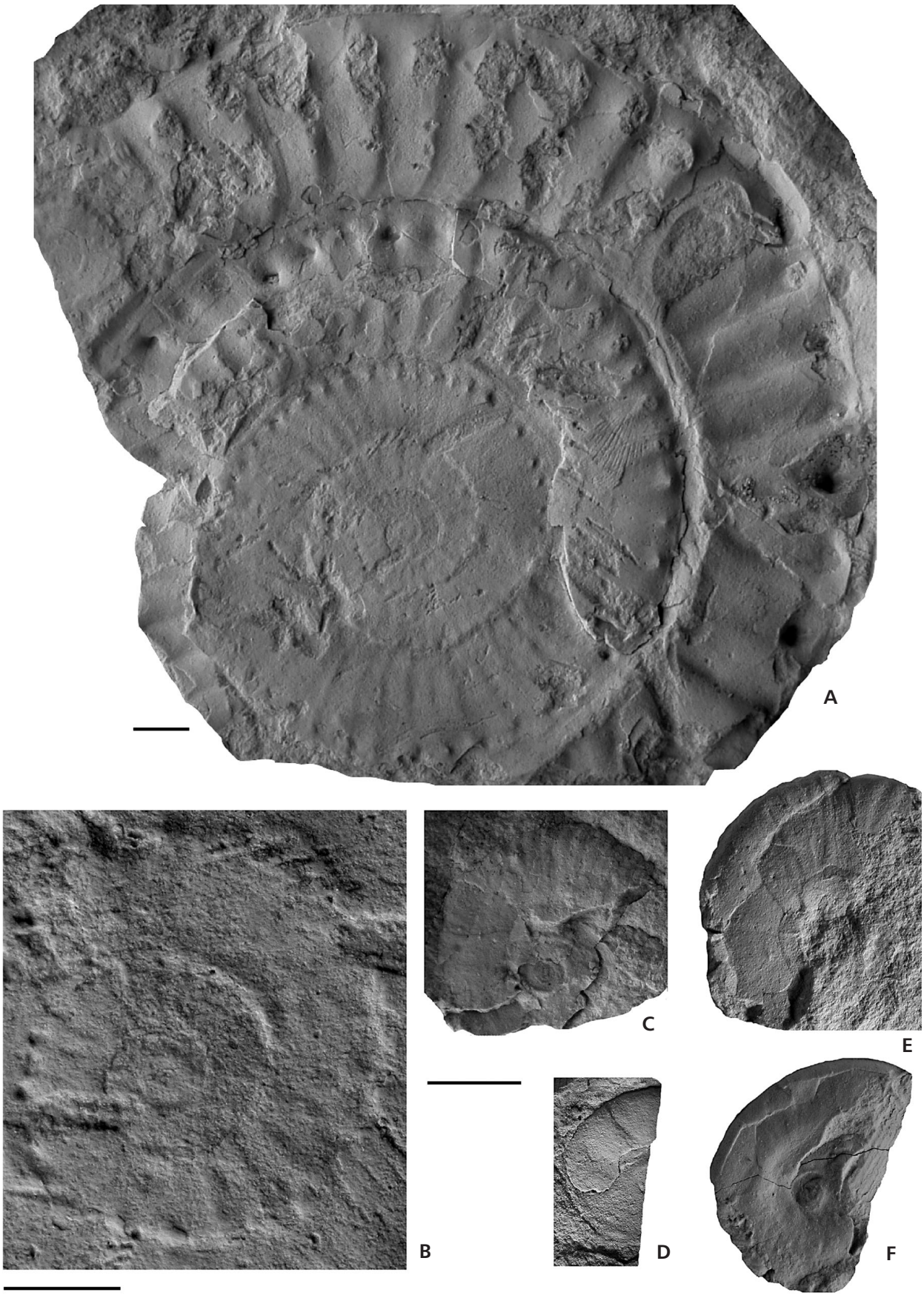
Age and distribution of the genus. – UK (Yorkshire, Somerset, Dorset), Denmark (Bornholm), NW and SW Germany (Hannover area, Bade, Jura of Souabe, Württemberg), Switzerland (Jura), France [Calvados, Lyonnais (Mt d'Or) Burgundy, Gard, SW France (Aude, Quercy)], Portugal (Lusitanian Basin), Hungary (Villany, Bakony), Turkey (Pontids), USA (Alaska). This genus characterizes the lowermost part of the Pliensbachian.

Remarks. – The South American forms illustrated by Hillebrandt (1987) as *Apoderoceras* (*Miltoceras*) are true *Miltoceras* (Coeloceratidae) and do not belong to the genus *Apoderoceras*. The same is true of the Italian specimens from the Central Apennines (Venturi *et al.* 2005).

***Apoderoceras dunrobinense* Spath, 1926**
Figures 4A, B, 5–14, 16A, B

1882–85 *Ammonites* cf. *armatus nodogigas* Quenstedt, pl. 25, fig. 6.

Figure 4. Early Pliensbachian ammonites (*A. dunrobinense* biohorizon) from Água de Madeiros. • A, B – *Apoderoceras dunrobinense* Spath, 1926, form 'b' (?). B – enlargement of the innerwhorls 2×. • C, D, E, F – *Tragophylloceras numismale* (Quenstedt). Scale bar = 10 mm.


A
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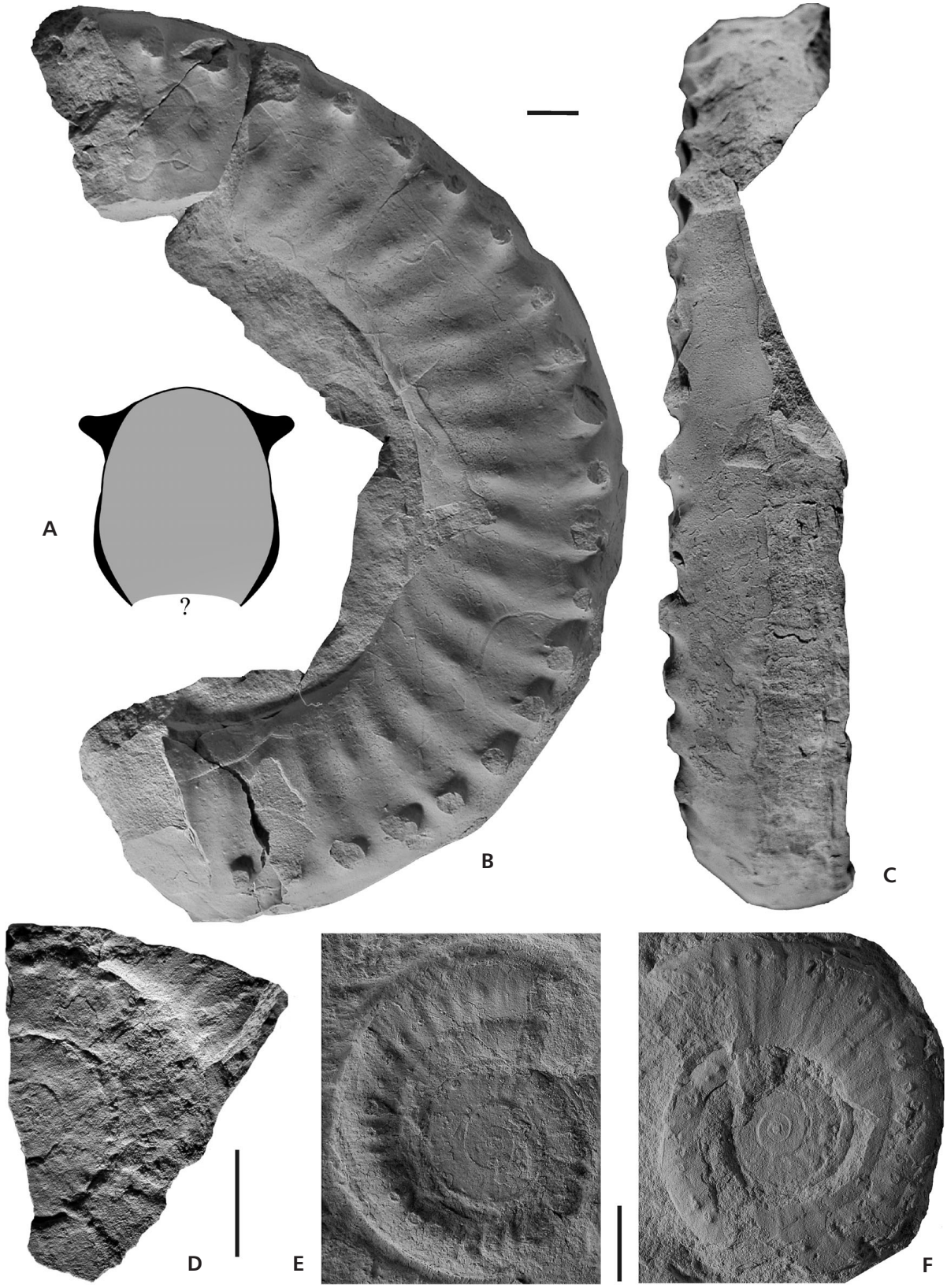


Figure 5. Early Pliensbachian ammonites (*A. dunrobinense* biohorizon) from Água de Madeiros. • A–C – *Apoderoceras dunrobinense* Spath, 1926. A, B – part of the body chamber with C the whorl section (diameter = 170 mm). • D–F – *Apoderoceras dunrobinense* Spath, 1926. D – form 'b' inner whorls; E, F – forms 'a' inner whorls. Scale bar = 10 mm.

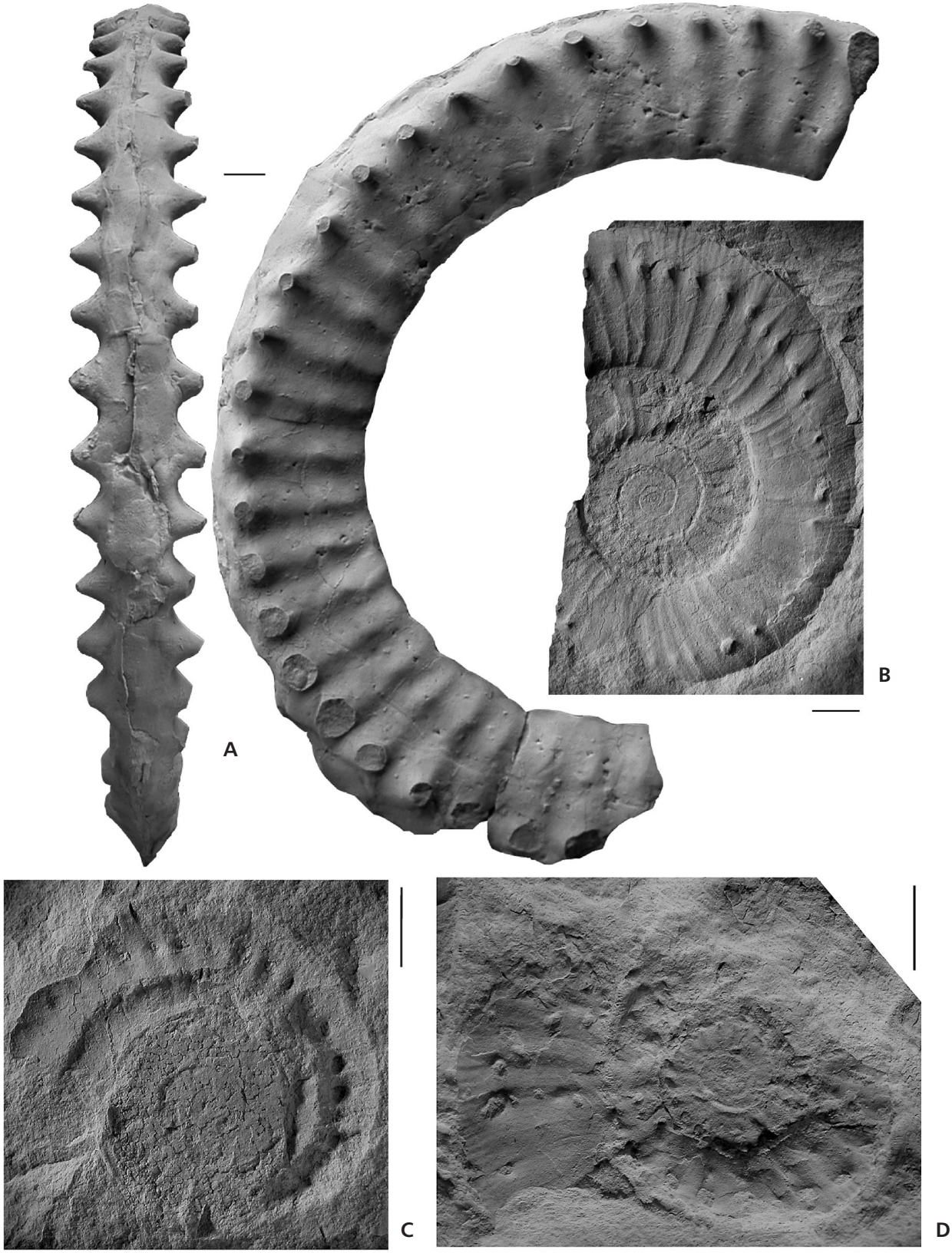


Figure 6. Early Pliensbachian ammonites (*A. dunrobinense* biohorizon) from Água de Madeiros. • A, B – *Apoderoceras dunrobinense* Spath, 1926. A – part of the body chamber (diameter = 215 mm); B – form 'a' inner whorls. • C, D – *Apoderoceras dunrobinense* Spath, 1926. C – form 'a' inner whorls; D – form 'b' inner whorls. Scale bar = 10 mm.

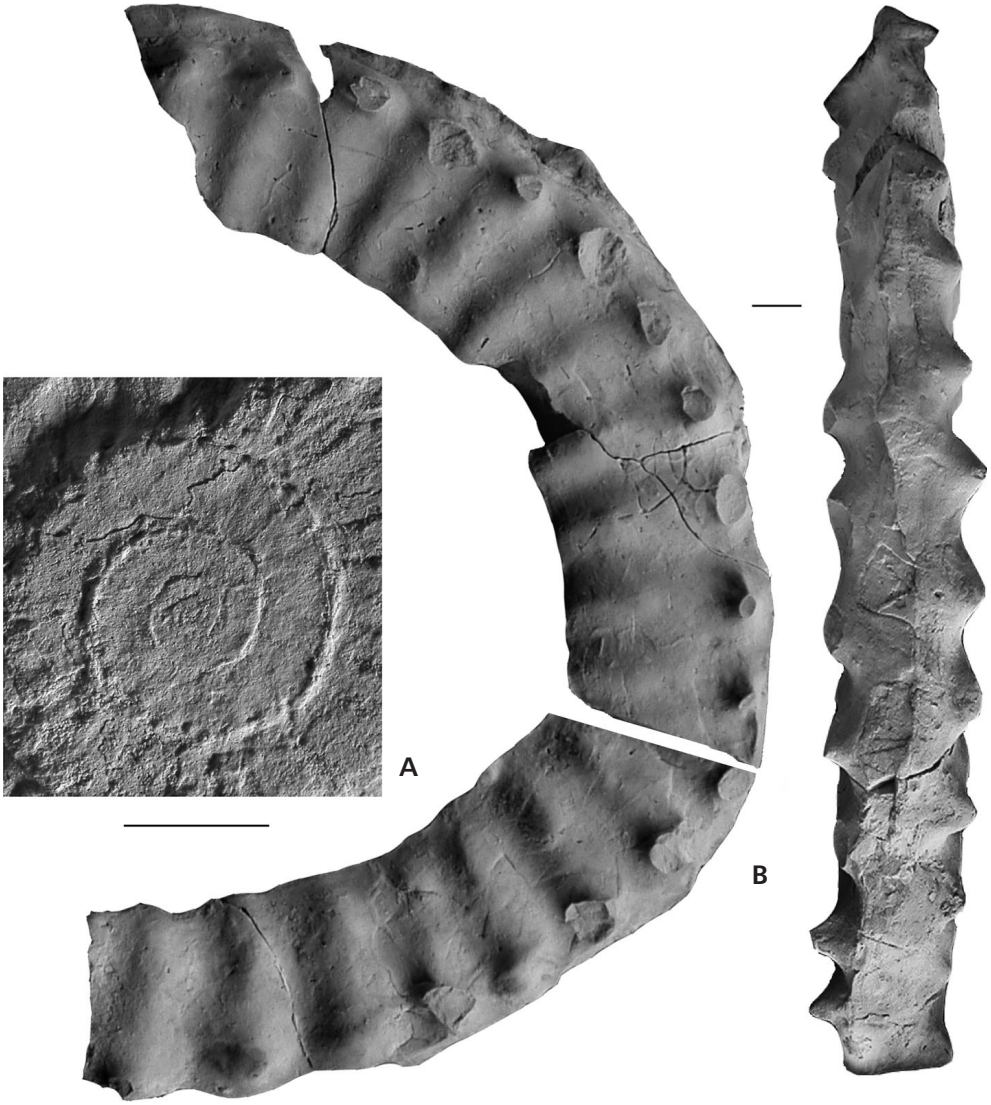


Figure 7. Early Pliensbachian ammonites (*A. dunrobinense* biohorizon) from Água de Madeiros. *Apoderoceras dunrobinense* Spath, 1926. • A – form 'a', enlargement of the inner whorls of the same specimen illustrated in Fig. 6B. • B – part of the body chamber (diameter = 220 mm). Scale bar = 10 mm.

1926 *Apoderoceras dunrobinense* Spath, p. 47, footnote 1.
?1967a *Apoderoceras leckenbyi* (Wright). – Mouterde, p. 190.
?1967a *Eoderoceras* cf. *miles* (Simpson). – Mouterde, p. 190.
?1967a *Eoderoceras* aff. *armatum* (Sowerby). – Mouterde, p. 190.
?1967a *Eoderoceras* sp. – Mouterde, p. 190.
?1967b *Eoderoceras* gr. *armatum.* – Mouterde, p. 212.
?1967b *Eoderoceras leckenbyi.* – Mouterde, p. 212.
1976 *Apoderoceras dunrobinense* Spath. – Géczy, pl. 5, fig. 2.
1978 *Apoderoceras* sp. *voisin* de *A. dunrobiense* Spath. – Mouterde, Rocha & Ruget, p. 88.
1978 *Apoderoceras* sp. – Mouterde, Rocha & Ruget, p. 88.
1981 *Apoderoceras* sp. cf. *dunrobinense* Spath. – Mouterde, Rocha & Delance, pl. 4, fig. 5.
2003 *Apoderoceras* cf. *dunrobinense* Spath. – Edmunds, Varah & Bentley, pl. 9, fig. 3.

Remarks. – Several taxa cited by Mouterde (1967a, p. 190 and 1967b, p. 212) under the names *Apoderoceras leckenbyi* (Wright), *Eoderoceras* cf. *miles* (Simpson), *Eoderoceras* aff. *armatum* (Sowerby) and *Eoderoceras* sp. are recorded from levels 19e of Água de Madeiros profile. They probably belong to the *Apoderoceras dunrobinense* Spath, but this fauna is not illustrated and was not found in the Mouterde's collection. A doubt remains concerning their systematic position and is indicated with a question mark in the synonymy list.

In Portugal, the first citation of *A. dunrobinense* Spath is made by Mouterde *et al*. (1978, p. 88) for the Quiaios profile in Mondego area.

Material. – 24 specimens including 13 large ones with crushed inner and intermediary whorls and 11 small samples showing more or less well preserved inner and intermediate whorls.

Figure 8. Early Pliensbachian ammonites (*A. dunrobinense* biohorizon) from Água de Madeiros. *Apoderoceras dunrobinense* Spath, 1926 (diameter = 253 mm). Scale bar = 10 mm.

Description. – These forms are characterized by a serpenticone coiling and by their size, the largest exceeds 250 mm in diameter.

In some specimens the innermost whorls exhibit a finely ribbed stage, almost smooth until *ca* 12 à 18 mm diameter (*e.g.* Fig. 6B), while for others, this 'smooth' stage is reduced to *ca* 6 mm diameter (*e.g.* Fig. 16B). The cadicone habitus of the inner whorls is not very developed, indeed

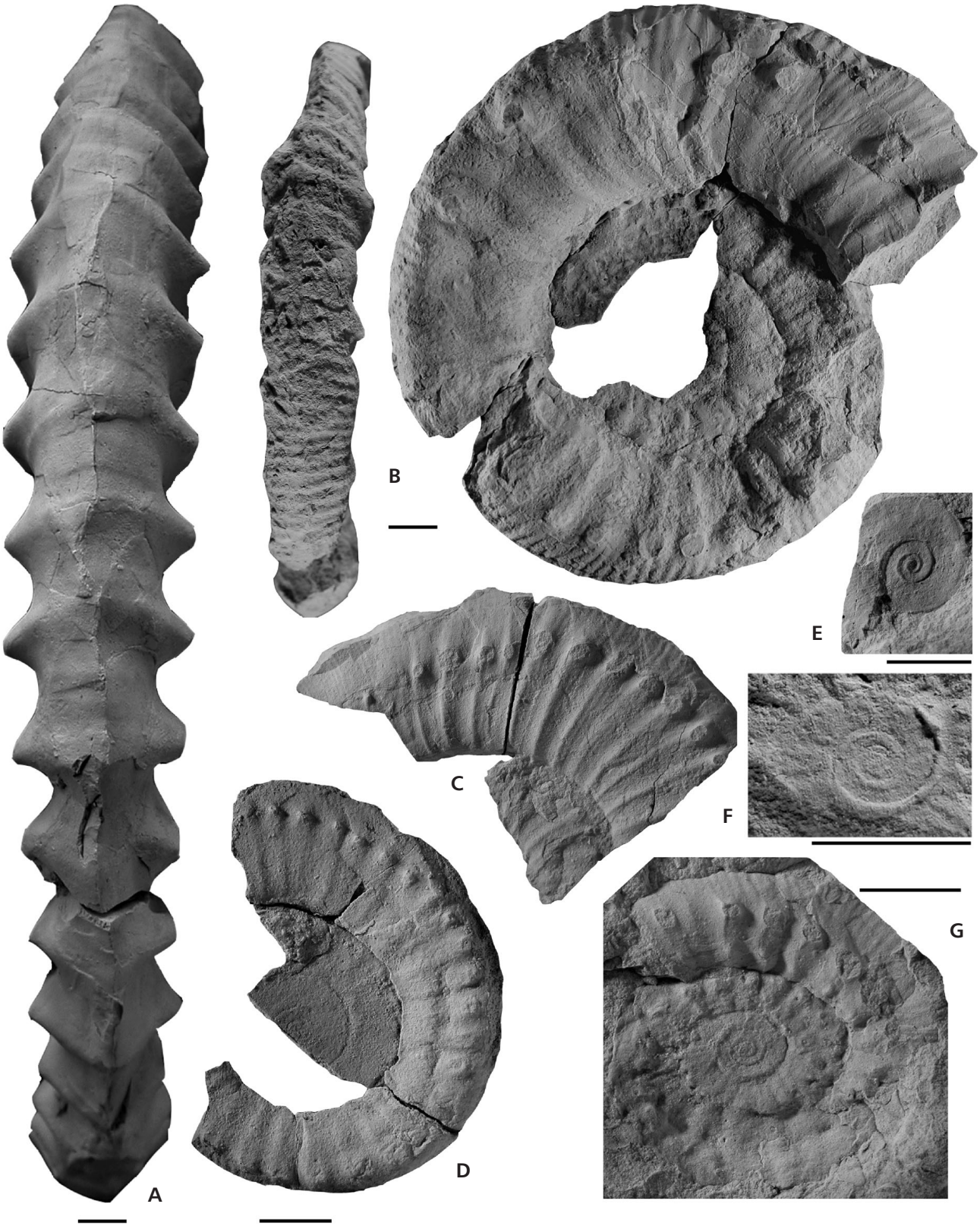


Figure 9. Early Pliensbachian ammonites (*A. dunrobinense* biohorizon) from Água de Madeiros. *Apoderoceras dunrobinense* Spath, 1926. • A – a part of the body chamber (diameter = 253 mm), ventral part of specimen illustrated in Fig. 8. • B, C, D – form 'a' (?). • E, F, G – inner whorls, notice the small bullae in specimen G (bullae are accentuated by the crushing). Scale bar = 10 mm.

Figure 10. Early Pliensbachian ammonites (*A. dunrobinense* biohorizon) from Água de Madeiros. *Apoderoceras dunrobinense* Spath, 1926 (diameter = 238 mm). Scale bar = 10 mm.

almost non-existent. This can lead to confusion with the inner whorls of Eoderoceratidae like *Eteoderoceras.*

Then in all the specimens, a strong ornamentation appears that is composed of ribs, slightly rursiradiate on the umbilical edge, becoming subradiate and strong on the flank and bearing a bullae-like reinforcement on the lower part of the flank, then continuing and thickening on the upper part of the flank until the spiny tubercles and ending just after them on the ventrolateral part (*e.g.* Fig. 9B).

For the coarser specimens (*e.g.* Figs 6D, 9G) the nodosity on the lower part of the flanks is well developed conferring a bituberculation-like habitus. This reinforcement is weakly expressed in some specimens but always obvious in the adult.

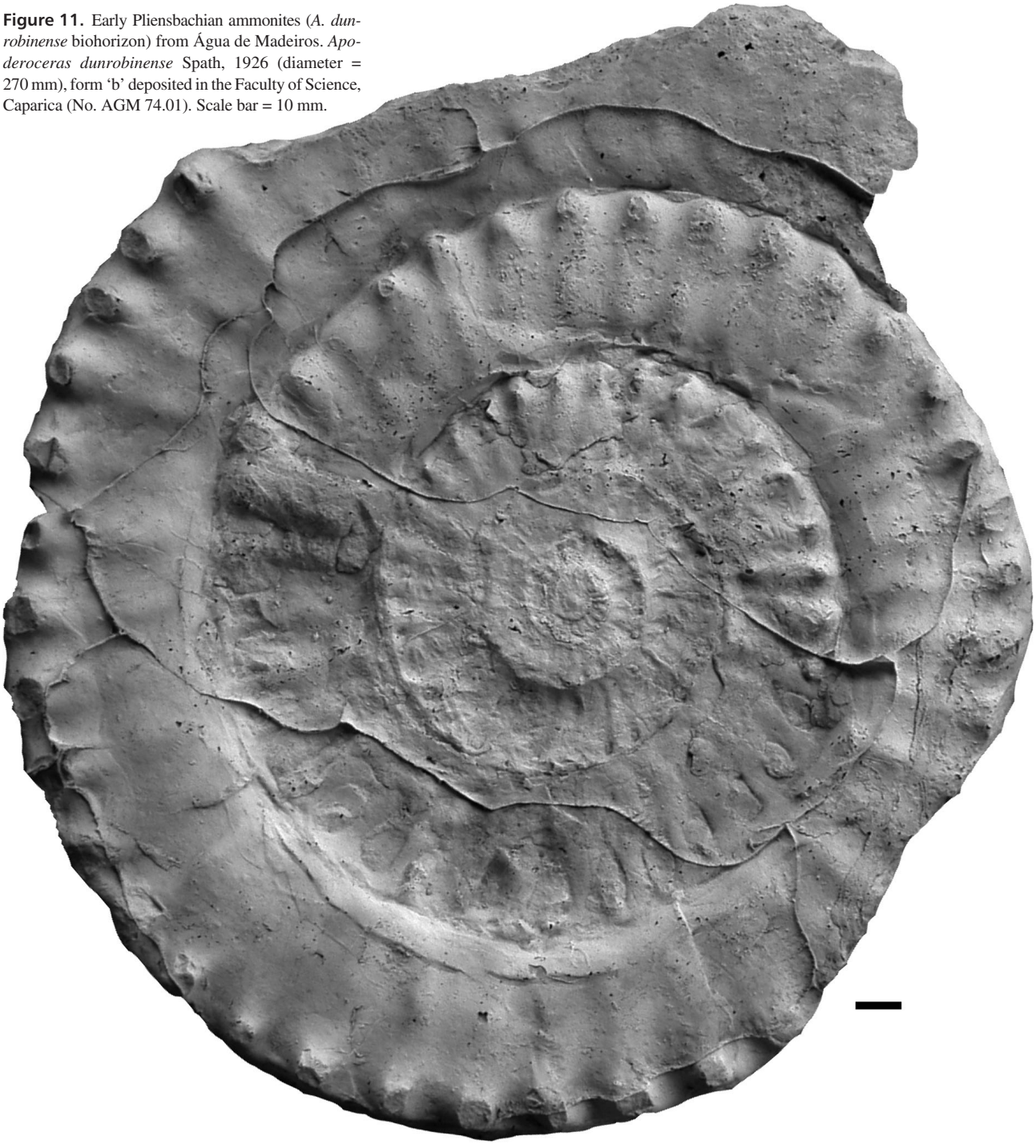


Figure 11. Early Pliensbachian ammonites (*A. dunrobinense* biohorizon) from Água de Madeiros. *Apoderoceras dunrobinense* Spath, 1926 (diameter = 270 mm), form 'b' deposited in the Faculty of Science, Caparica (No. AGM 74.01). Scale bar = 10 mm.

On the rather high convex ventral part, a fine and close secondary ribbing is developed and is obvious at least as far as 100 mm diameter (inner – intermediate whorls; *e.g.* Fig. 6B). On some specimens, fine secondary ribs cover the primary ribbing (*e.g.* Fig. 9B). This character superficially resembles the ornamentation of *Apoderoceras aculeatum* (Simpson 1855).

In the adults, the ribs remain well developed on the lower part of the flanks and the tubercles become true spines (*e.g.* Fig. 5B). The monotony of the ornamentation throughout the ontogeny is notable. Only some rare specimens show a tendency for the ribs to fade on the lower part of the flanks, maybe an artefact of preservation. The ventral part becomes smooth (*e.g.* Fig. 13A).

The thickness of the whorls is preserved in two specimens only, showing a thick subelleptic whorl section

Figure 12. Early Pliensbachian ammonites (*A. dunrobinense* biohorizon) from Água de Madeiros. *Apoderoceras dunrobinense* Spath, 1926 (diameter = 254 mm) form 'a'. Scale bar = 10 mm.

(Ww/Wh = 0.78–0.83) with slightly convex flanks and flat rounded venter (Figs 5C, 13A). These specimens clearly show a very original character for an *Apoderoceras*, with the developement of weak regular nodosities on the lower part of the flanks precisely on the 2/5 of the flank, the outer row of spines being situated on the 4/5 of the flank (Figs 5A–C, 13B).

Our population has a weak morphological variability for the ornamentation and for the coiling, even if some specimens (*e.g.* Figs 10, 12) show a more or less coarse and close ornamentation in the adult stage. In fact the variability is only significant in the innermost whorls. So two morphs of *A. dunrobinense* Spath: form 'a' corresponding to the 'long' smooth stages and form 'b' corresponding to the 'short' smooth stage associated with a precocious coarse 'bi-' tuberculated development can be distinguished. These two

kinds of morphologies can be observed in other *Apoderoceras*. In that way, *A. nodogigas* (Quenstedt) illustrated by Quenstedt (1882–1885, pl. 27, fig. 9) shows a serpenticone stage, smooth in the very inner whorls. We observe the same habitus in one specimen from the Yorkshire Coast (Meister *et al.* 2003, pl. 2, fig. 27). A. (?) *marshallani* (Simpson) also has rather smooth serpenticone innermost whorls. Conversely, in *A. aculeatum* (Simpson) (Howarth 2002, pl. 6, fig. 2; Hoffmann 1982, pl. 17, fig. 1) or in *A. subtriangulare* (Young & Bird) (Howarth 2002, pl. 6, fig. 4a; Edmunds 2009, pl. 28, fig. 3) the ribbing of the very inner whorls and the cadicone habitus are clearly expressed.

An original feature of the population studied is the serpenticone coiling associated with a regular strong ornamentation throughout ontogeny, in particular the persistence of the ribs on the lower part of the flanks and the presence of a row of weak nodosities on the lower part of the flanks. They also have a rather more slender habitus than the other *Apoderoceras*. This combination of traits defines *Apoderoceras dunrobinense* Spath.

A. dunrobinense Spath is characterized by well developed ribbing from the umbilicus to the ventrolateral edge throughout the ontogeny. The whorls are quite massive with a slow growth rate (Ww/Wh ~ 1). Our specimens are close to the type species illustrated by Quenstedt (1882–1885, pl. 25, fig. 6).

A. cf. *dunrobinense* Spath *in* Edmunds *et al.* (2003, fig. 9.3) perhaps shows a slightly denser ribbing and is situated in the variability of the strong rib density group. The Portugese form illustrated by Mouterde *et al.* (1981, pl. 4, fig. 5) shows a medium rib density, only the last third of the whorl is more finely and densely ribbed. Notice the presence of nodosities at the lower part of the flank.

In the Portuguese population, the rib density (N/2) very slowly increases during the ontogeny with a slight stagnation phasis (decrease) near 170–180 mm diameter at least for the specimen illustrated in Fig. 10 (Fig. 17). The rib spacing is standardized using the SRS parameter (Standardized Rib Spacing: D / N/2) established by Dommergues & Bonnot (2007). The clustering of the points shows a weak variability for this character as far as 170–180 mm diameter, then the point scattering becomes wider, probably corresponding to the adult morphology. The SRS varies from about 9–10 mm to 15–16 mm, showing a relative pre-adult and adult variability in ribbing. For SRS there is no correlation with the ratio N/2 which on the contrary shows a weak increase of the rib density. Notice that the Portuguese form illustrated by Mouterde *et al.* (1981, pl. 4, fig. 5) from another locality (Vale das Fontes) is well integrated in the variability range of our specimens.

If we compare the Portuguese population with some NW European *Apoderoceras* characterized with well developed and persistent ribs throughout the ontogeny, we observe the same evolution of N/2 and SRS for the whole *Apoderoceras* (Fig. 18). There is not much difference, for these two parameters, between the Portuguese fauna and the NW European *Apoderoceras*. Their evolution remains quite homogeneous. Nevertheless, the points are now more scattered because of a comparison between several species. After 170–180 mm diameter, the point dispersion is wider but the SRS remains between 9–10 mm and 15–16 mm. We must bear in mind that several 'species' of *Apoderoceras* are very close, and sometimes only known from fragments, and that the number of valid species is probably lower than the number of nominal species.

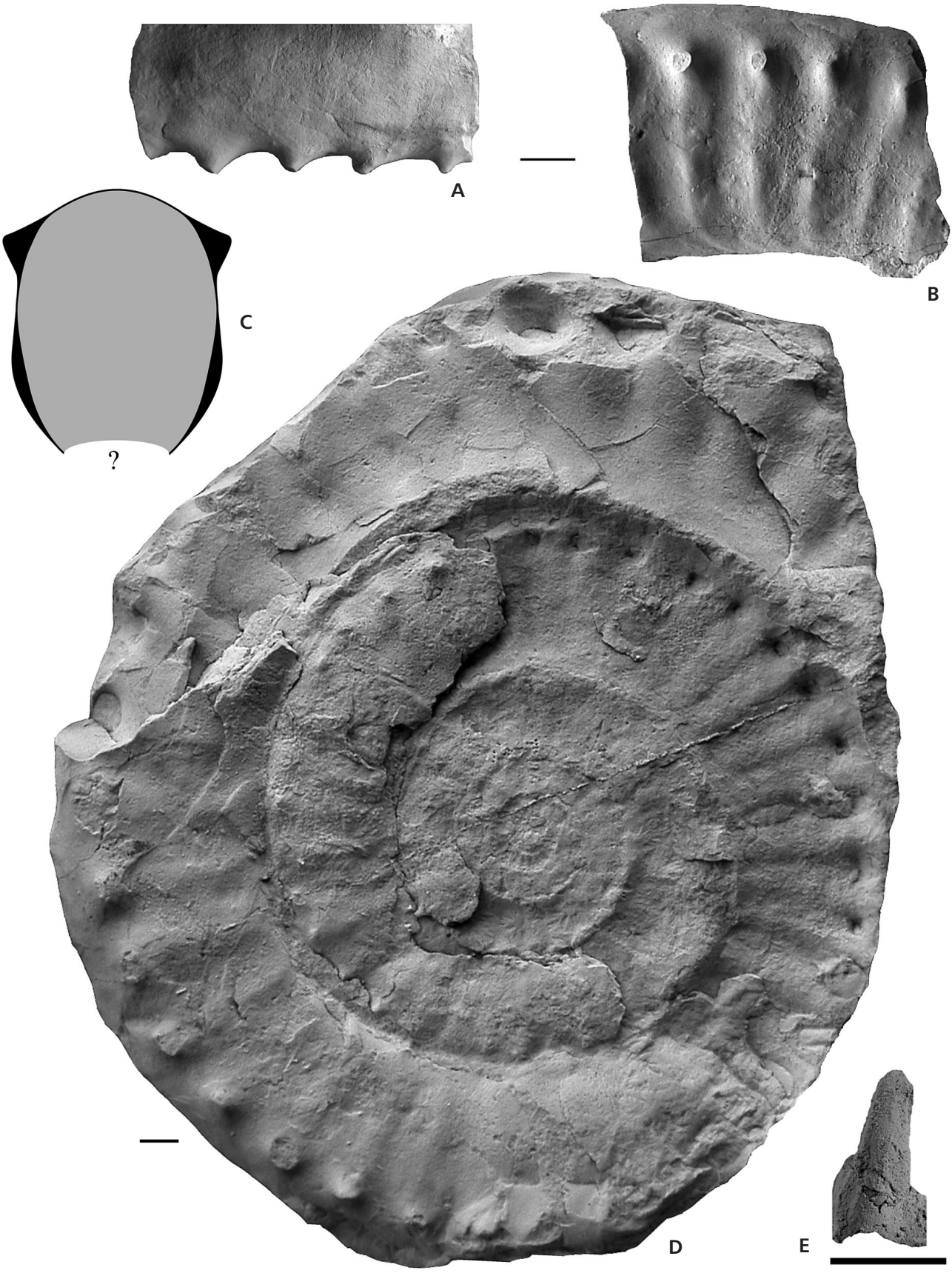
Comparison. – *A. aculeatum* (Simpson) includes *A. antiquum* Lóczy, *A. decussum* (Simpson) and *A. leckenbyi* (Wright). In this species, a less serpenticone coiling associated with more massive whorls, mainly in the adult morphology, distinguishes it from the Portugese specimens (see Géczy 1998, pl. 12, figs 1–3; Howarth 2002, pl. 7, fig. 1; Meister *et al.* 2003, pl. 2, fig. 23). Moreover, in the intermediate whorls, the ribbing is finer, and irregular in intensity and spacing (see Donovan & Surlyk 2003, p. 575, fig. 4). At a similar diameter our specimens seem to have an attenuated '*aculeatum* ornamented stage', but the adult ornamentation remains totaly different in Simpson's species with only the preservation of a spaced spiny row (see Buckman 1913, pl. 72B).

A. dubari Géczy is a form with broad and massive, rather rounded, whorls and with less expressed tubercles. It is close to *A. aculeatum* (Simpson) but with slower growth in whorl height.

A. ferox Buckman, a very large specimen (500 mm diameter), has a very slow whorl growth rate and marginal tubercles associated with a barely convex ventral part. Its ribbing is spaced and very coarse, hardly developed and fading on the lower part of the flanks. Whorls are clearly broader than high.

A. hamiltoni (Simpson) is a form with a slow growth rate and its size exceeds 400 mm diameter. The whorls are close to those of *A. aculeatum* (Simpson) but the rib density is very low at comparable diameters (N/2 = 13 for a diameter of 290 mm). It superficially resembles the Portuguese specimens.

Figure 13. Early Pliensbachian ammonites (*A. dunrobinense* biohorizon) from Água de Madeiros. • A, B, C, D, E – *Apoderoceras dunrobinense* Spath, 1926. A, B – part of the body chamber with C the whorl section. D – form 'b' (diameter = 184 mm). E – complete ventro-lateral spine. Scale bar = 10 mm.


A
B
C
?
D
E

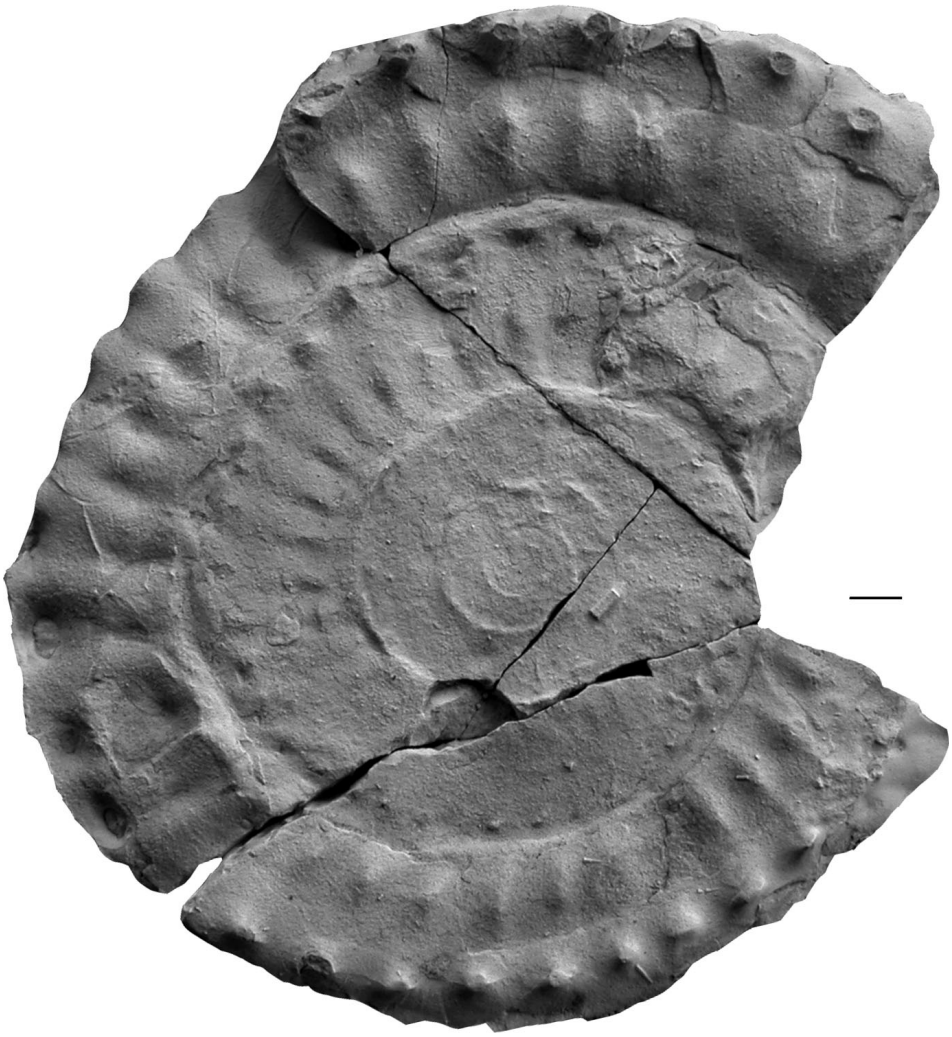


Figure 14. Early Pliensbachian ammonites (*A. dunrobinense* biohorizon) from Água de Madeiros. *Apoderoceras dunrobinense* Spath, 1926 (diameter = 200 mm). Scale bar = 10 mm.

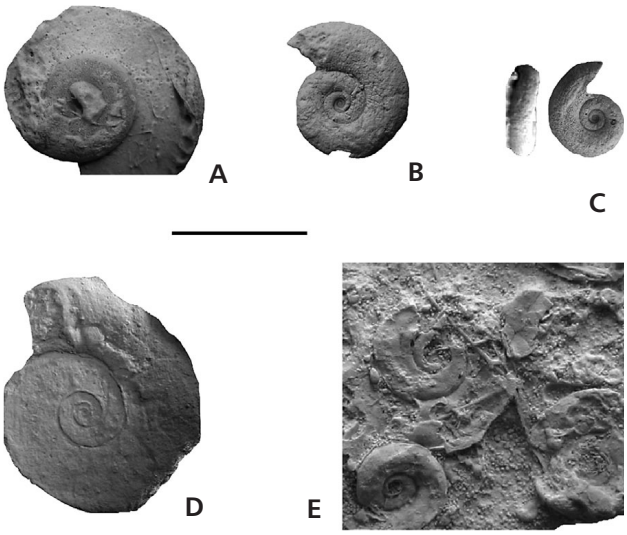


Figure 15. Early Pliensbachian gasteropods (*A. dunrobinense* biohorizon) from Água de Madeiros. • A–E – small undetermined gasteropods (= *Gemmellaroceras* sp. *sensu* Antunes *et al.*, 1981). Scale bar = 10 mm.

'*A*' *limatum* Pompeckj is close to A. *lobulatum* Buckman with rounded whorls; both lack ornament at a small diameter (D = 100 mm). Moreover A. *lobulatum* Buckman is a massive form with rounded, broader than high, whorls.

A. nodogigas (Quenstedt) with its smooth inner whorls followed by a well expressed ribbed stage shows a quite high rib density. The ribbing seems to persist during the whole ontogeny. Tuberculation is present but little developed in the inner and middle whorls, becoming spiny in the outer whorls. This ornament habitus also closely related to the Portuguese forms.

A. sparsinodosum (Quenstedt) shows a convex ventral area, a very coarse ornament with blunt, thickened ribs on the upper part of the flanks and very thick, strong tubercles. Whorls are very massive and broader than they are high.

A. spicatum (Simpson) has a slow growth and bears strong spines and poorly developed ribs on the lower part of the flanks in the adult. This species is only known from fragments of large specimens.

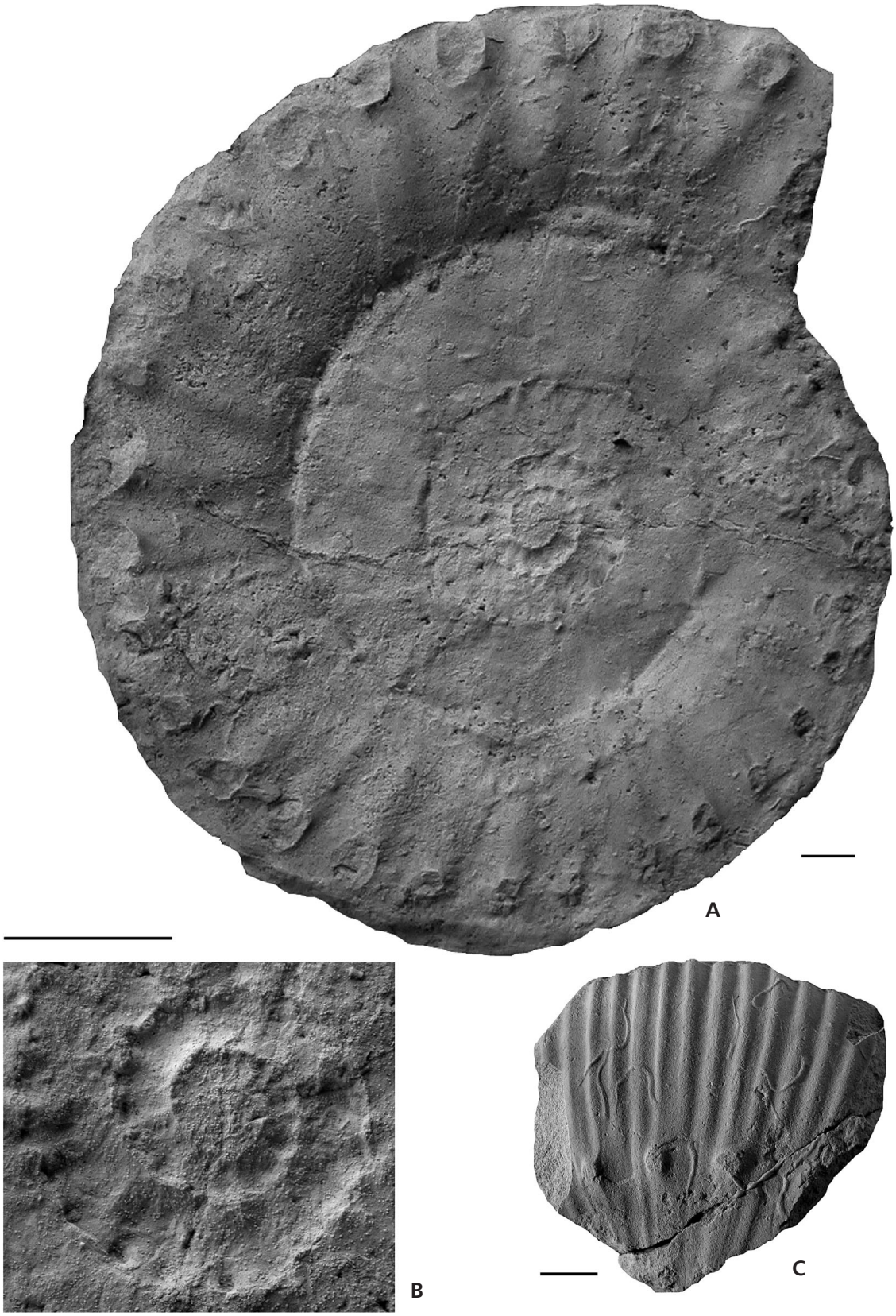


Figure 16. Early Pliensbachian ammonites (*A. dunrobinense* biohorizon) from Água de Madeiros. • A, B – *Apoderoceras dunrobinense* Spath, 1926. A – form 'b' (diameter = 178 mm); B – enlargement of the inner whorls of A. • C – *Vicininodiceras* aff. *mouterdei* Donovan, 1990. Scale bar = 10 mm.

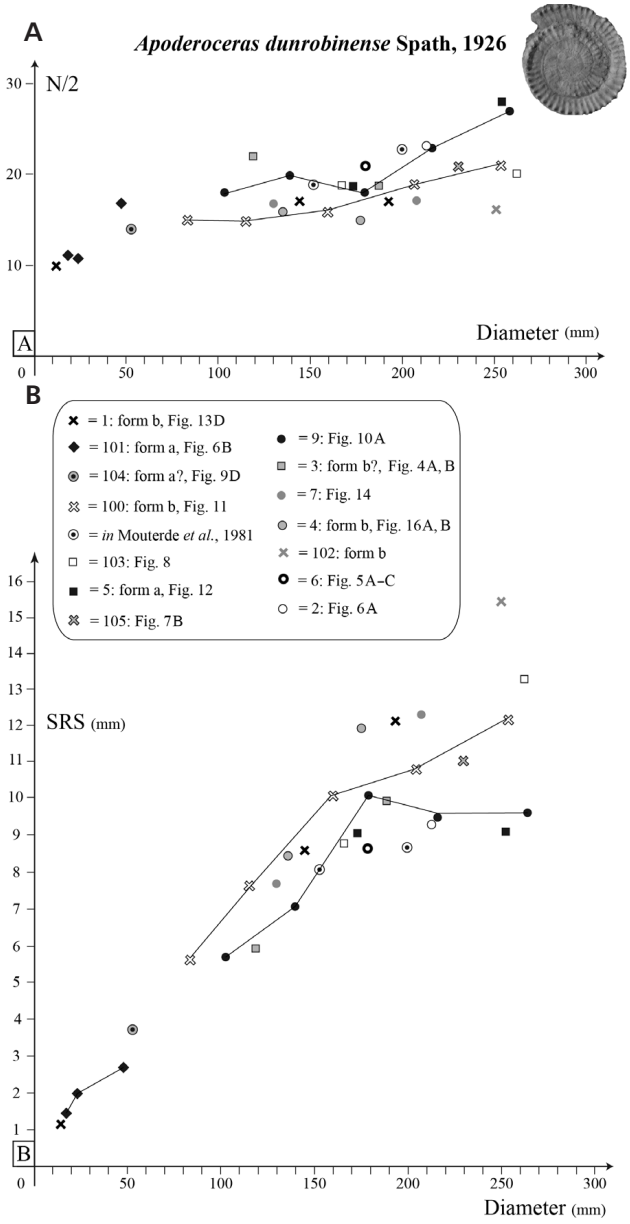


Figure 17. A – illustration of the ontogenetic variations of the rib number per half whorl (N/2) versus the diameter (D) for the Portuguese *Apoderoceras dunrobinense* Spath. • B – variations of their inter-rib spacement (SRS) per half whorl versus diameter for the same specimens.

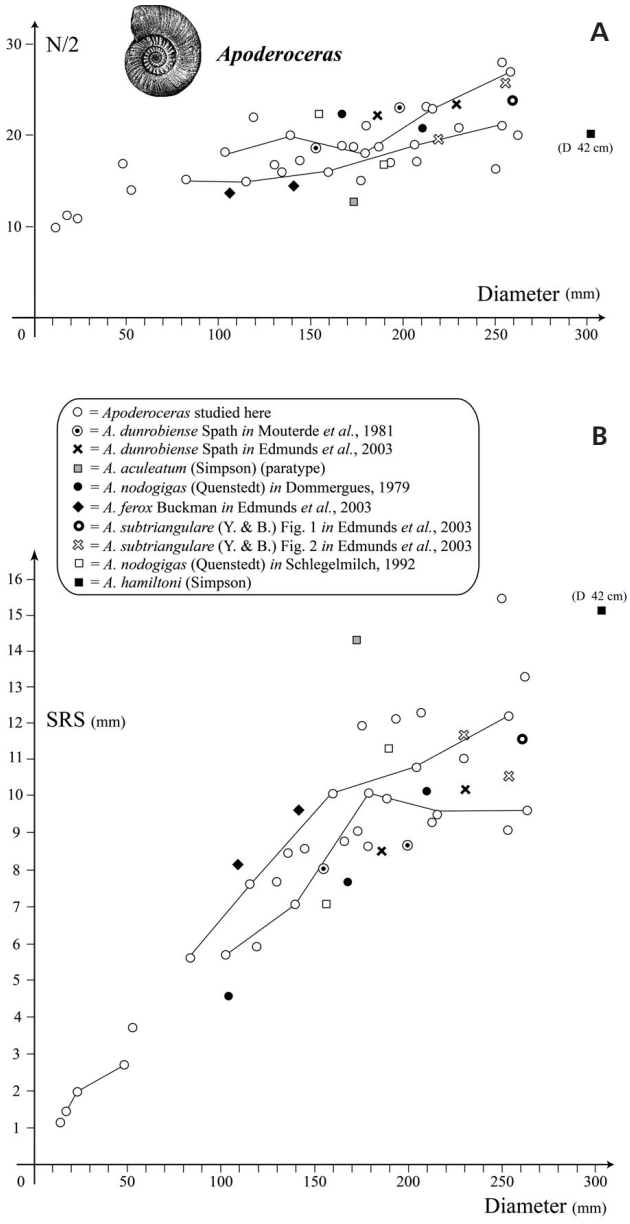


Figure 18. A – illustration of the ontogenetic variations of the rib number per half whorl (N/2) versus the diameter (D) for different species of *Apoderoceras*. • B – variations of their inter-rib spacement (SRS) per half whorl versus diameter for the same specimens.

A. subtriangulare (Young & Bird) is described from one small fragment. This has a subtrapezoidal whorl section, clearly broader than high. The forms illustrated by Howarth (2002, pl. 6, figs 4a, 5a) show cadicone stages in their inner whorls.

The *A. subtriangulare* (Young & Bird) *sensu* Edmunds *et al.* (2003, fig. 9.1, 2; fig. 11.1, 2) contains massive whorl forms some of which are serpenticone similar to the type (*ibid.*, fig. 9.1, 2) with a more finely ornamented stage (N/2 = 20) becoming coarser but still closely ornamented in the adult (N/2 = 25). At the same time these authors include forms with more rapid coiling, clearly different from true *A. subtriangulare* (Young & Bird) (*ibid.*, fig. 11.1, 2) suggesting a large variability.

A. tardarmatum Buckman belongs to the large forms with massive whorls like *A. subtriangulare* (Young & Bird) or *A. sparsinodosum* (Quenstedt). Its ventral part is broad and convex.

A. triornatum Buckman shows a strong irregularity of the ornament in the inner whorls where the secondary

Figure 19. Biohorizon succession near the Sinemurian–Pliensbachian boundary for NW Europe and Lusitanian Basin with the position of the new *A. dunrobinense* biohorizon and its associate fauna.

ribbing obliterates the primary tuberculate ribs as for some *Apoderoceras* [*A. aculeatum* (Simpson), *A. subtriangulare* (Young & Bird) or *A. tardarmatum* Buckman]. Its whorl section is higher than it is broad, quite close to the one of the Portuguese specimens (Figs 5A, 13C); nevertheless the whorl growth is faster (less serpenticone whorls).

Two doubful *Apoderoceras* [(?) *A. sinuatum* (Simpson) illustrated by Buckman (1914, pl. 94) and (?) *A. armiger* (Simpson) according to Simpson's description (1855, p. 66)] do not show close morphological affinities with the Portuguese specimens.

The serpenticone coiling and the persistance of the ribbing with a tendency towards a 'bituberculate' habitus of *A. dunrobinense* Spath superficially also resemble some bituberculate Eoderoceratidae like *Microderoceras* s.l. or *Bakonyceras,* which are, among others, clearly bituberculate.

Age and distribution. – The stratigraphic repartition of the different species of *Apoderoceras* in the Jamesoni Chronozone remains poorly known. Nevertheless, the first *Apoderoceras* are pratically present at the base of the Pliensbachian, like *A. aculeatum* (Simpson) in the stratotype of the Pliensbachian in Wine Haven (Yorshire, UK) (see Dommergues & Meister 1992; Meister *et al.* 2003, 2006).

A. dunrobinense Spath is recorded from SW Germany, ?Hungary (Upper Austroalpine unit), UK (Somerset) and Portugal. The new data from Portugal, with the association of *T. numismale* (Quenstedt), Spath's species and *V.* aff. *mouterdei* Donovan, allow us to situate it in the lower part of the Jamesoni Chronozone (lower to middle Taylori Subchronozone), which is correlated with the *Apoderoceras* ssp. and *partim* with the *P. taylori* standard biohorizons (Fig. 19).

Remarks. – São Pedro de Muel is situated in a rather basinal position where the ammonite succession is clear with an Upper Sinemurian ammonite fauna (with true *Eteoderoceras*) that is located far below the *Apoderoceras* beds. Conversly in Mondego (Quiaios) the stratigraphical context still remains unclear. This area is situated closier to the border of the basin and the ammonite association given by

Mouterde *et al.* (1978) suggest a condensed serie with *Apoderoceras*, *Tragophylloceras* of Pliensbachian age and with Sinenurian ones like *Eteoderoceras*. This fauna must be examined again.

Family Liparoceratidae Hyatt, 1867
emend. Dommergues & Meister, 1999

Genus *Vicininodiceras* Trueman, 1919

Type species. – *Vicininodiceras simplicicosta* Trueman, 1919.

***Vicininodiceras* aff. *mouterdei* Donovan, 1990**
Figure 16C

1970 *Liparoceras* (*Vicininodiceras*?) sp. – Mouterde, pl. 6, fig. 2.
1990 *Vicininodiceras mouterdei.* – Donovan, p. 33.
?1990 *Liparoceras* (*Vicininodiceras*) sp. – Dommergues & Meister, pl. 2, fig. 5.

Discussion. – A fragment of a Liparoceratidae was found in association with the *Apoderoceras*. Such ammonites, which also comes from São Pedro de Muel, were illustrated by Mouterde (1970, pl. 6, fig. 2). It is characterized by a subsphaerocone habitus and a liparoceratomorph-like ornanentation. Because of the preservation, only the upper row of lateral tubercles is observable. Almost every tubercle gives rise to two secondary ribs intercalated with a primary one, so increasing the rib density on the ventral part. The ventro-lateral and ventral ribs are thick, subradiate and regular. Lower on the flanks, primary ribs are more irregular in intensity and spacing.

On the basis of these observations, and because of a similar stratigraphical position, we place our specimen near the *Vicininodiceras* illustrated by Mouterde and reinterpretated by Donovan (1990) as *V. mouterdei*.

Our specimen also resembles other Liparoceratidae like the *Becheiceras.* However, this genus differs from *Vicininodiceras* in having a larger distance between the two rows of tubercles. *Becheiceras* is a younger genus first known from the Ibex Chrozozone.

The Portuguese forms (also including a *Vicininodiceras* illustrated by Dommergues & Meister 1990, pl. 2, fig. 5) show an intermediate morphology between *V. simplicicosta* Trueman (with a more open umbilicus) and the first *Becheiceras* (smaller umbilicus). *Becheiceras* probably originated in the *Vicininodiceras* during the Lower Pliensbachian (top of Jamesoni Chronozone – base Ibex Chronozone) even if some old and recent hypotheses propose origins in the *Parinodiceras* (a Polymorphitidae) (see Spath 1938, Edmunds 2009).

V. gollingense (Rosenberg) has finer ornamentation, while *V. tomfryi* Donovan exhibits a coarser ornamentation, mainly on the flanks.

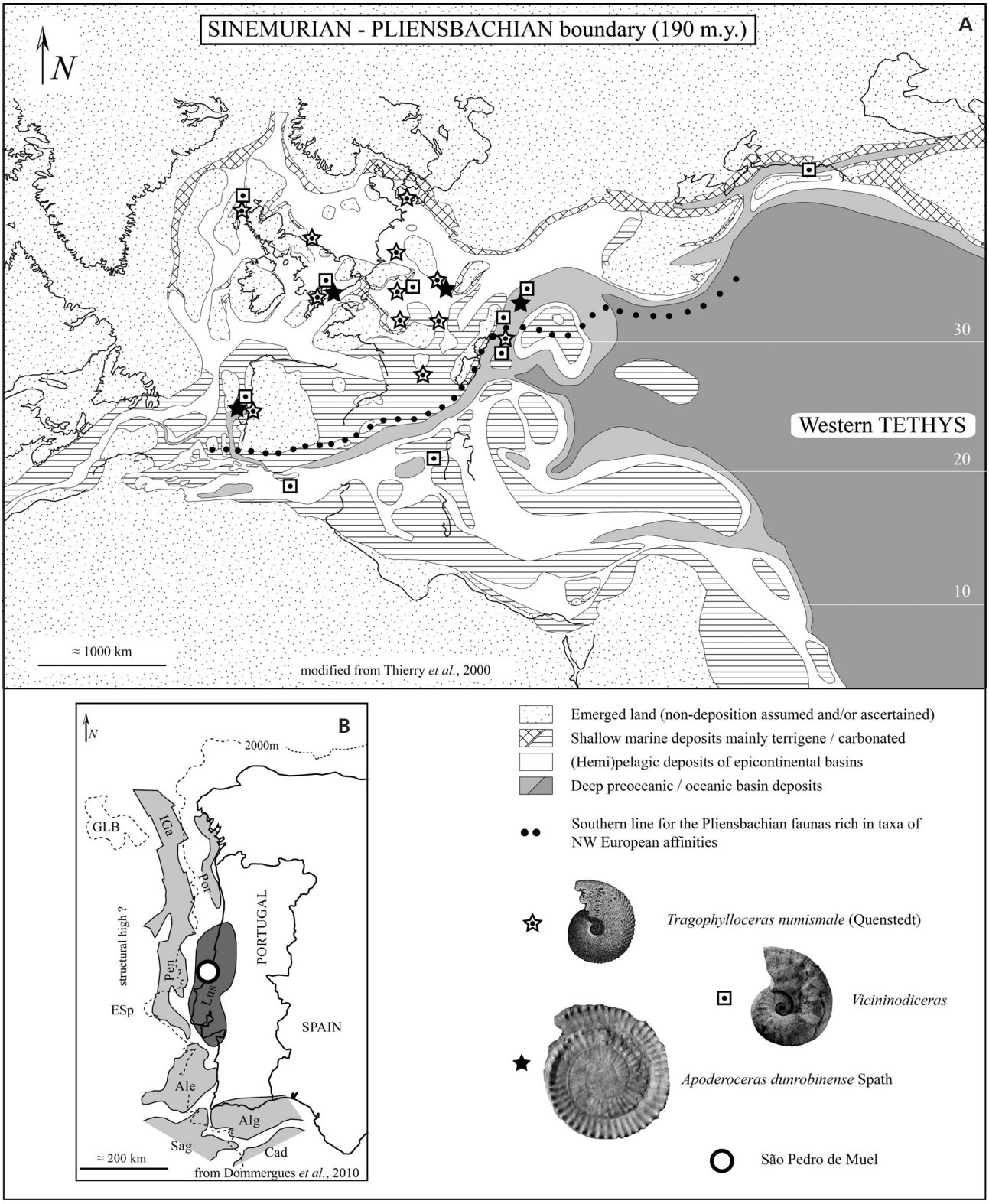
Age and distribution. – The range of *Vicininodiceras* is rather restricted and covers a part of the Raricostatum and Jamesoni Chronozones. Most of the *Vicininodiceras* in the literature are of Upper Sinemurian age (Raricostatum Chronozone) and some more precise indications give a Tardecrescens Subchronozone age. The Portuguese specimens allow us to confirm the Pliensbachian age of this genus. The form mentioned by Mouterde (1970, p. 56) is situated 5 m above the '*Deroceras*' (= *Apoderoceras*) beds [niv. 20a *in* Antunes *et al.* 1981 = above bed 74 of the present work] and consequently is a little younger than our specimen. However these two *Vicininodiceras* are of Lower Pliensbachian age (Jamesoni Chronozone).

The genus *Vicininodiceras* also present in the Upper Sinemurian, it is distributed in the both NW European domain (UK, Luxembourg, Portugal) and the Tethyan domain [Middle Austroalpine of the Italian Rhetic Alps, Upper Austroalpine of Austria and Hungary, Pontides (Turkey), Apennines and Algeria (Grande Kabylie)]. *V.* aff. *mouterdei* Donovan is known only from the Lusitanian Basin and doubtfully from the Alps (Fig. 20).

Remarks. – Antunes *et al.* (1981) cited several *Gemmellaroceras* sp. (never illustrated) from the 'laminite bed' (unit A *in* Fig. 3); this information is restated in the most recent literature where authors state that these beds are of decimetre to centimetre thick microspar limestone (rich in ostracods and radiolarians) with planar laminations, Rhizocorallium, Thalassinoides and *Gemmellaroceras* (*e.g.* Duarte & Soares 2002; Duarte *et al.* 2010, p. 327). Having carefully collected macrofossils in these beds we have found only small gastropods (Fig. 15). These gastropods are very similar in form to *Gemmellaroceras* and can be confused with this ammonite, but they are not strictly planispirale and no suture line is obvious.

This observation in the 'laminite bed' does not exclude the presence of *Gemmellaroceras*-like micromorphs in Portugal as attested by the presence of *Leptonotoceras leptonotum* Spath in Quiaios profile (Mondego area) (Mouterde & Rocha 1981).

Figure 20. A – paleogeographical reconstruction for the Upper Sinemurian–Lower Pliensbachian period of the Western Tethys and adjacent areas with distribution of *T. numismale* (Quenstedt), *Vicininodiceras* and *A. dunrobinense* Spath. • B – pre-drift sketch maps of the "Iberia-Newfoundland" conju-



gate margins with location of the main basin. 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 & Verfoef (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. Abbreviations: GLB – Galicia Bank; Esp – Estremadura spur; Iga – Inner Galicia Basin; Por – Porto Basin; Pen – Peniche Basin; Lus – Lusitanian Basin; Ale – Alentejo Basin; Alg – Algarve Basin; Sag – Sagres Basin; Cad – Cadiz Basin.

Concluding remarks

(i) The Portuguese population of *A. dunrobinense* Spath is rather homogeneous. These ammonites are characterized by serpenticone coiling associated with a regular strong ornamentation throughout the ontogeny and in the presence of a row of weak nodosities on the lower part of the flanks.

(ii) The *A. dunrobinense* biohorizon, including beds 50 to 74, is characterized by the association of the index species with *T. numismale* (Quenstedt) and *V.* aff. *mouterdei* Donovan and is easily correlated with the standard biohorizons of NW Europe. It corresponds to the lower part of the Jamesoni Chronozone (lower to middle Taylori Subchronozone). This unit can also be precisely correlated with other regions like Yorkshire, Dorset and New Hebrides (UK), NW and SW Germany and Burgundy, Causses, Alps and Pyrénées (France), where equivalent faunas are recorded [*e.g. Apoderoceras* ssp., *Tetraspidoceras quadrarmatum* (Dumortier)]. Correlations with Tethyan regions are less precise because of the difference in the composition of the faunas (see Meister 2010). For example, some *Microderoceras* (*Eoderoceras*) of North Africa or *Catriceras* from Hungary of Lowermost Pliensbachian age could be equivalent in age with our faunas.

(iii) In the section of Água de Madeiros, the Sinemurian–Pliensbachian boundary cannot be precisely determined by ammonites (the primary marker to define this boundary) due to the presence of about 10 meters of laminite deposits without ammonites between the Sinemurian Echioceratidae beds and the Pliensbachian *Apoderoceras* beds.

(iv) *T. numismale* (Quenstedt) and *A. dunrobinense* Spath have a paleogeographical distribution restricted mainly to the Euroboreal domain, maybe including the northern margin of the Tethys for Spath's species. This underlines the close connections of the Lusitanian Basin and the Euroboreal seas during the earliest Pliensbachian. The rare genus *Vicininodiceras* has a rather more ubiquitous paleogeographical distribution, being present in the Euroboreal domain as well as in the Mediterranean Tethys domain.

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