

Revision of Late Tithonian charophytes from Lisbon and Sintra-Cascais (Portugal): taxonomy, biostratigraphy and palaeobiogeographical significance

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ABSTRACT – The re-evaluation of the charophyte content of ‘Purbeckian’ sediments from several sections around Lisbon (Olelas and Brouco) and Sintra-Cascais (Murches, Atrozela and Malveira-Guincho) revealed new palaeofloral associations from the Late Tithonian of the South Lusitanian Basin (Portugal). These sections contain *Globator rectispirella*, *G. aff. nurrensis*, *Nodosoclavator bradleyi*, *Clavator reidi*, *Clypeator cf. discordis*, *Porochara maxima*, and newly described occurrences of *P. jaccardi*, *Mesochara harrisi* and nodosoclavatoide utricles. These revised data reinforce the evidence for assigning most of the studied deposits to a Late Tithonian age, instead of the formerly accepted wider interval Tithonian to Early Berriasian (‘Purbeckian’). Population analysis and statistics were applied in order to better assess population variation of the different species.

The results of this study are relevant as they contribute to improve the biostratigraphical definition of the ‘Purbeckian’ formations of Portugal and allow more accurate palaeobiogeographical interpretations within the central Tethyan domain, by comparison of the identified charophyte assemblages with documented Jurassic–Cretaceous transition charophytes from other regions. *J. Micropalaeontol.* 29(1): 37–49, May 2010.

KEYWORDS: *charophytes, biostratigraphy, palaeobiogeography, Late Tithonian, Portugal*

INTRODUCTION

The present work presents and discusses the results of a re-evaluation study of the charophyte content of several sections (Murches, Malveira-Guincho, Atrozela, Brouco and Olelas; Fig. 1). These belong to the classical sections covering the Jurassic–Cretaceous transition (‘Purbeckian’ facies) of the Lisbon and Sintra-Cascais regions (southern Lusitanian Basin, west Portugal; Fig. 1), formerly described by Ramalho (1971) and Rey (1972). These floral assemblages were only partially identified and incompletely studied in previous works, which aimed at broader stratigraphical analysis. The charophytes of the Brouco section were partially revised by Feist *et al.* (1995). Consequently, a comprehensive description of the charophytes occurring in these successions is used to establish a comparison with other regions and biozones. The systematic study of the charophytes presented herein is reinforced by statistical analysis, aiming at a better characterization of the intraspecific population variation. This methodology gives the best results when applied to a population of charophytes with few distinguishing features, such as *Characeae* and *Porocharaceae*.

The present study used, with permission of the owners, samples from the Ramalho and Grambast collections, from the archives of the Instituto Geológico e Mineiro (Portugal) and from the University of Montpellier II (France), respectively. Fourteen samples from marly beds of the five selected sections (Murches, Malveira-Guincho, Atrozela, Brouco and Olelas) were studied and described with regard to charophyte content. At the Murches section, a new field survey and sampling of the few exposed marly layers revealed rare and poorly preserved charophytes. However, the overall content of the sample residues was also analysed, including foraminifers (A. Azerêdo) and

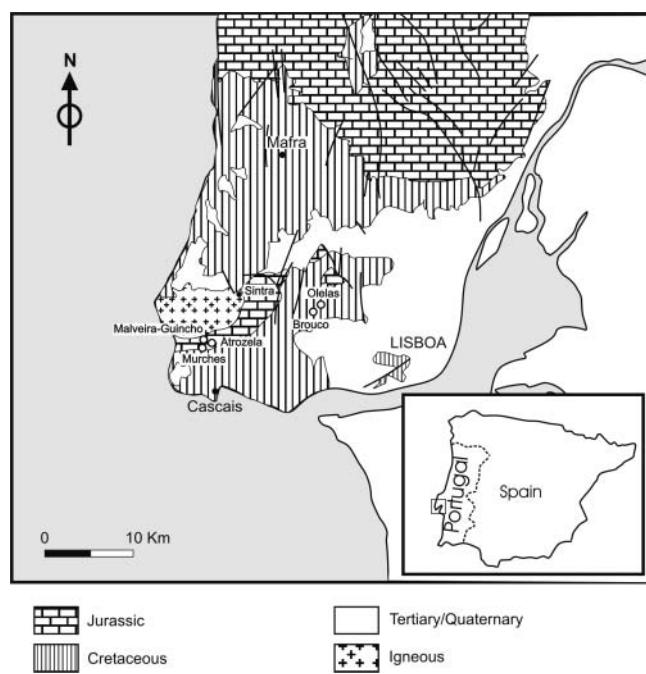


Fig. 1. Schematic location of the studied sections and simplified geological map of the Lisbon and Sintra-Cascais regions (after Pereira & Cabral, 2005).

ostracods (M. C. Cabral, pers. comm.). This has helped to establish a correlation with the units described by Ramalho (1971) (see below). The Murches section, together with the Malveira-Guincho section, can still be followed approximately

Choffat, 1901	Ramalho, 1971		Rey, 1972, 1979		Rey, 1992	
Chronostratigraphy	Chronostratigraphy		Chronostratigraphy	Lithostratigraphy	Chronostratigraphy	Lithostratigraphy
Hauterivian	Hauterivian p.p.	B	Hauterivian	Calcários recifais inferiores	Hauterivian	Cabo Raso Fm.
Valanginian			upper Valanginian	Margas com <i>Toxaster</i>		Maceira Fm.
Infravalanginian	Valanginian	A	Lower Valanginian to Berriasian p.p.	Calcários vermelhos	Valanginian	Guia Fm.
Freixialian			"Purbeckian"	Margo-calcários com <i>Ampulina leviathan</i>		Serradão Fm.
Pterocerian	Portlandian	B	"Purbeckian"	Calcários e margas com <i>Trocholinas e Achispirocyclina</i>	Berriasian	Farta Pão Fm.
		A		Margas com <i>Anchispirocyclina</i>	Tithonian	
				Margo-calcários com <i>Mantelliana purbeckensis</i>		

Fig. 2. Comparative chart of the chronostratigraphical and lithostratigraphical units of the Jurassic–Cretaceous transition in the study region, according to the principal previous works (Choffat, 1901; Ramalho, 1971; Rey, 1972, 1979, 1992).

in the field, but with a few gaps. The other three sections are no longer exposed or are very poorly preserved.

In all of the five sections limestone dominates over marl; therefore, the number of levels likely to yield material suitable for charophyte study is restricted. However, the complete Late Jurassic–Early Cretaceous succession is very well documented and clearly established in the study region and at other locations in the basin. Therefore, the interval corresponding to the ‘Purbeckian’ facies is very well constrained, as addressed below (see Rey *et al.*, 1968; Ramalho, 1971; Rey, 1972, 1992; Ramalho & Rey, 1975; Ramalho *et al.*, 1981, 1993).

BRIEF GEOLOGICAL SETTING

The Late Jurassic–Early Cretaceous successions from Lisbon and the Sintra–Cascais regions are part of the sedimentary fill of the Mesozoic Lusitanian Basin of west-central Portugal (Fig. 1), which is one of the marginal basins associated with the opening of the North Atlantic Ocean (e.g. Ribeiro *et al.*, 1979; Wilson *et al.*, 1989). Most of the basin fill is Jurassic in age, but sediments from the Upper Triassic to the Upper Cretaceous occur, with a Tertiary cover. The basin is bounded to the east by uplifted Hercynian basement and to the west (offshore) by small basement horsts. Initial rifting took place during the Late Triassic, followed by mostly non-rift conditions during the Early and Middle Jurassic; the main rifting phase, leading to ocean spreading between Iberia and Newfoundland, led to major subsidence and extension from the Late Jurassic to Early Cretaceous (e.g. Ribeiro *et al.* 1979; Wilson *et al.* 1989).

The lithostratigraphical succession of the Lusitanian Basin is bounded at the base by the unconformity between pre-Mesozoic and Triassic formations. The latter correspond to alluvial-fluvial deposits, which are succeeded by Lower and Middle Jurassic marine carbonates. The Upper Jurassic and the Cretaceous are composed of diverse marine, terrigenous and mixed

facies, reflecting the frequent changes of depositional and tectonic conditions (e.g. Ramalho *et al.*, 1993; Rey *et al.*, 2006).

STRATIGRAPHICAL SETTING

The charophyte-bearing deposits are part of wider successions that range from the Upper Oxfordian to the Valanginian, comprising a broad range of marine (pelagic/hemipelagic, reefal and lagoonal) and terrestrial-influenced facies.

The uppermost Jurassic–lowermost Cretaceous deposits reflect a regressive trend, evolving from outer-marine to shallow-marine and then to lagoonal-lacustrine settings, with some terrigenous influence. The formations are locally affected by contact metamorphism related to the intrusion of the granitic Sintra Massif. For detailed descriptions of these formations the reader is referred to Ramalho (1971), Rey (1972, 1992), Ramalho & Rey (1975) and Ramalho *et al.* (1981, 1993).

Since the pioneering works on the region, the latest Upper Jurassic units have been informally subdivided into ‘Calcários com *L. pseudoalternicosta*’, ‘Pterocerian’ and ‘Freixialian’ (Choffat, 1901), ‘Portlandian A’ and ‘Portlandian B’ (Ramalho, 1971) or Portlandian (Rey, 1972) (Fig. 2). The earliest Cretaceous units were referred to as ‘Infravalanginian’ (Choffat, 1901), ‘Purbeckian’ (Ramalho, 1971) or ‘Margo-calcários com *Mantelliana purbeckensis*’ (Rey, 1972). Nowadays, these units are formally grouped in the Farta Pão Formation (Rey, 1992; Rey *et al.*, 2006) (Fig. 2).

The present work covers only the lagoonal-lacustrine deposits of the Jurassic–Cretaceous transition, mostly from the interval traditionally known as the ‘Purbeckian’ (Ramalho, 1971; Rey, 1972; Ramalho & Rey, 1975). This terminology can be misleading for biostratigraphical purposes and has been adopted differently by several authors. In the study area, this interval has been well constrained by Ramalho (1971), as follows:

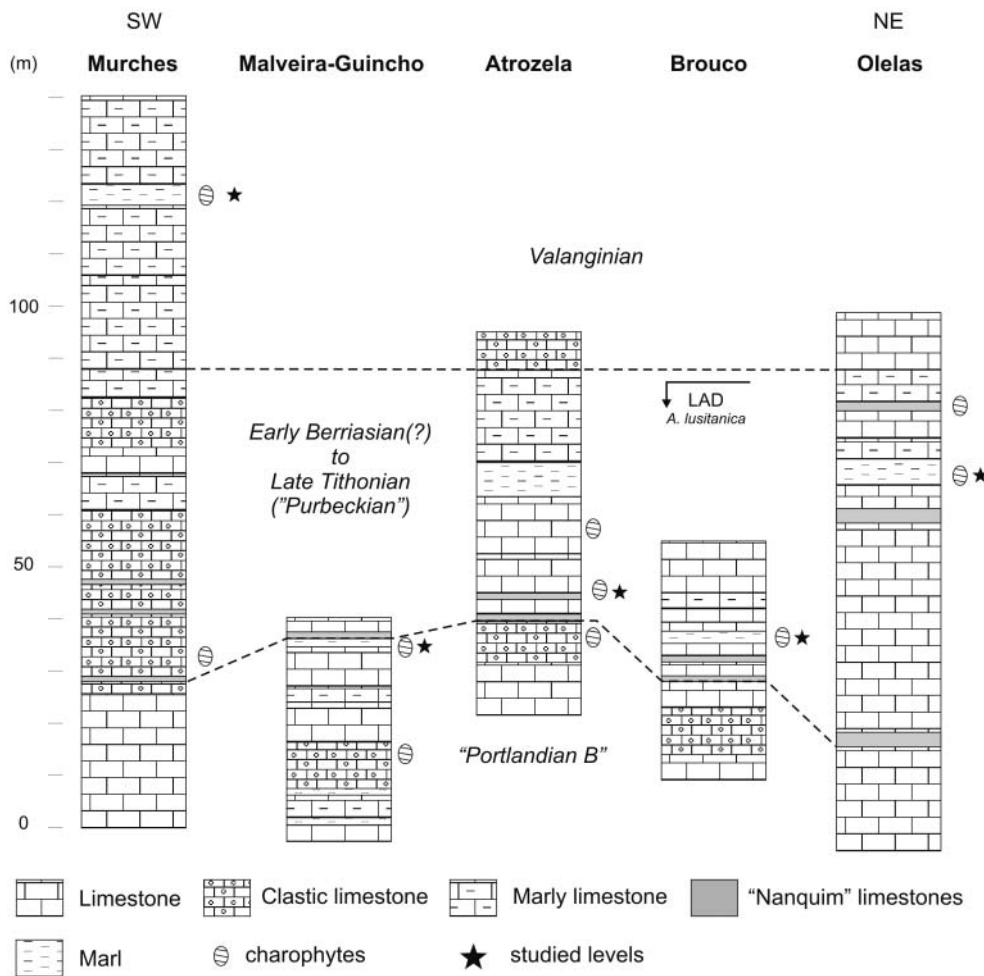


Fig. 3. Simplified lithostratigraphical columns and correlation of the interval at the five studied sections (based on Ramalho, 1971, simplified).

- The top of the Upper Jurassic is characterized by alternation of restricted, lagoonal marine deposits with abundant *Anchispirocyclina lusitanica* (Egger), other foraminifers and dasyclads (see description of sections) with terrestrially influenced deposits rich in charophytes and ostracods.
- For correlation purposes, Ramalho (1971) considered the base of the 'Purbeckian' interval marked by the first bed of a distinct local lithotype – a yellow, ferruginous clastic limestone traditionally known as 'Calcário amarelo-nanquim' (Choffat, 1901), which only occurs at the lowermost part of this interval. These yellow limestones are rich in charophytes (stems and gyrogonites) and ostracods.
- The upper limit of the same interval is marked by the disappearance of *Anchispirocyclina lusitanica* whose individuals, in addition, show consistently very high numbers and aberrant growth-types towards the top of the interval. Other differences within the foraminiferal fauna as compared to that in the Valanginian above were also clearly identified by Ramalho (1971). *A. lusitanica* has a high biostratigraphical value because it is documented to disappear at the Jurassic-Cretaceous transition (basal Berriasiian at the most) in the entire western peri-Tethyan realm (Bassoulet, 1997).

DESCRIPTION OF THE STUDIED SECTIONS

A brief description of the sections from which the studied charophyte material was obtained is presented below, covering only the part of the successions relevant for this study (uppermost Jurassic-lowermost Cretaceous). Figure 3 presents the schematic lithostratigraphical columns of the considered sections, with a correlation of the studied interval at the five locations.

Murches

As fully described by Ramalho (1971), the latest Tithonian (uppermost Portlandian B) of this section is approximately 28 m thick, being composed of micritic limestones, clastic towards the top (Fig. 3), with a few molluscs, foraminifers and dasyclads (Ramalho, 1971). The foraminifers include *Nauiloculina oolithica* (Mohler), *Pseudocyclammina lituus* (Yokoyama), *Anchispirocyclina lusitanica* (Egger), *Trocholina gr. alpina-elongata*, miliolids; the dasyclads, *Salpingoporella annulata* (Carozzi).

The 'Purbeckian' of this section shows, from the base towards the top, a 60 m thick succession comprising yellow limestones (the 'Calcários amarelo-nanquim' or 'Calcários Inferiores' *sensu*

Choffat, in Ramalho, 1971), rich in charophytes and ostracods, overlain by alternating marls and limestones grading upwards into most common limestones. In the marly levels, the foraminifera assemblage is restricted to *Anchispirocyclina lusitanica* (with very abundant individuals), but it is of much higher diversity in the limestones, comprising *Nautiloculina oolithica*, *Feurtillia frequens* (Maync), *Pseudocyammina lituus*, *Anchispirocyclina lusitanica*, *Rectocyammina chouberti* (Hottinger), *Trocholina gr. alpina-elongata*, miliolids and verneulinids (Ramalho, 1971). Also significant is the occurrence of dasyclads, such as *Salpingoporella annulata* and *Cylindroporella cf. arabica* (Elliot) (Ramalho, 1971), and of ostracods, such as *Stenestroemia* sp., *Schuleridea* sp., *Paracypris* sp. and *Asciocythere* sp. (M. C. Cabral identification).

Charophytes occur in Valanginian level 50 of Ramalho (1971), a yellow to greenish marly bed bearing *Pseudocyammina lituus*, with the ostracods *Cypridea gr. valdensis*, *Mantelliana purbeckensis*, *Darwinilla leguminella*, *Schuleridea* sp., *Cytheropteron* sp. and *Cytherella turgida*. Charophyte association includes *Globator maillardii* nurrensis Pecorini, 1969 previously reported as *G. maillardii* var. (e.g. Schudack, 1993a), *Nodosoclavator bradleyi* (Harris, 1961) Grambast, 1966, and a new description of *Clypeator cf. discordis* Shaikin, 1976 and *Porochara jaccardi* (Heer, 1865) Mojón, 1989.

Malveira-Guincho

This section, described by Ramalho (1971) as Corte nº1, ranges throughout the Late Tithonian (Portlandian B according to this author) into the ‘Purbeckian’. The Late Tithonian interval (about 42 m thick) corresponds to massive limestones (often clastic), marly limestones and marls (Fig. 3), bearing diverse foraminifera, *Anchispirocyclina lusitanica*, *Rectocyammina chouberti*, *Pseudocyammina lituus*, *Everticyammina virguliana* (Koechlin), *Nautiloculina oolithica*, *Trocholina gr. alpina-elongata* and miliolids; ostracods (*Paracypris* sp., *Cytheropteron* sp.); dasyclads and charophytes; shell remains and coprolites (Ramalho, 1971). The present work, using samples from three different levels (Fig. 3), confirms the occurrence of *Nodosoclavator bradleyi* (already identified by Ramalho, 1971) and highlights the new occurrence of *Porochara jaccardi* (Heer, 1865) Mojón, 1989.

The ‘Purbeckian’ (4 m) is recognized by a basal bed of the typical yellow ferruginous limestone (‘Calcários amarelo-nanquim’), overlain by grey massive limestones, interbedded with a thin yellow marl layer; only miliolids occur in the grey limestones (Ramalho, 1971; Rey, 1972).

Atrozela

This section (Fig. 3), described by Ramalho (1971) as Corte nº2, displays Late Tithonian (Portlandian B *pro parte*) limestones (often clastic and nodular) and marls (over 18 m), bearing: foraminifera (*Feurtillia frequens*, *Pseudocyammina lituus*, *Anchispirocyclina lusitanica* and other lituolids, *Trocholina gr. alpina-elongata*, miliolids); ostracods (*Fabanella polita polita* Martin); dasyclads; charophyte stems and oogonia of *Nodosoclavator bradleyi* and *Porochara* sp. (Ramalho, 1971; Rey, 1972).

The ‘Purbeckian’ (48 m) grades from yellow ferruginous limestones (the ‘Calcários amarelo-nanquim’) at the base, to grey limestones and marly limestones, massive, nodular and

clastic limestones and marls with gastropod fragments, *Anchispirocyclina lusitanica*, *Everticyammina virguliana*, *Rectocyammina chouberti*, other lituolids, miliolids, dasyclads (*Salpingoporella annulata*, *Clypeina inopinata* (Favre), *Permocalculus* sp.).

The previously recorded charophyte association includes *Porochara* sp., *Nodosoclavator bradleyi*, *Clavator cf. reidi* Groves, 1924, *Globator maillardii* (Saporta, 1891) Grambast, 1966 and *Dictyoclavator cf. fieri* (Donze, 1955) Grambast, 1966 (Ramalho, 1971; Rey, 1972). The new evaluation of four samples from levels 1, 2 and 3 of Ramalho (1971) and two samples from J. Rey (Grambast collection) yielded *Nodosoclavator bradleyi* and *Clavator reidi*, and further indicated the new occurrences of *Porochara jaccardi*, *Mesochara harrisi* and *Globator rectispireale* (a revision of *G. maillardii*). This association points to a Late Tithonian to Early Berriasian (?) age.

Brouco

The Brouco section is a sequence (over 60 m thick) of Late Tithonian (Portlandian B *pro parte*) massive and nodular limestones, interbedded with thin marl layers (Fig. 3), with diverse foraminifera (e.g. *Nautiloculina oolithica*, *Freixialina planispiralis* (Ramalho), *Anchispirocyclina lusitanica*, *Pseudocyammina lituus*, miliolids) and dasyclads (Ramalho, 1971). Above, the ‘Purbeckian’ (equivalent to the Berriasian of Rey, 1972; Fig. 2) yellow limestones interbedded with grey limestones, overlain by >20 m of thinner-bedded limestones and marly limestones, bear *Feurtillia frequens*, *Anchispirocyclina lusitanica* (which, in a few marly levels, is the single species, with many individuals), *Pseudocyammina lituus*, *Trocholina gr. alpina-elongata*, *Permocalculus* sp., *Clypeina cf. inopinata* and ostracods, such as *Cypridea tumescens praecursor* (Oertli), *Theriosynoecum forbesii* (Jones) and *Fabanella polita polita* (Ramalho, 1971; Rey, 1972).

The charophyte assemblage, as revealed from the study of five samples from unit 4 of Rey (1972), comprises *Globator rectispireale*, *Nodosoclavator bradleyi*, *Clypeator cf. discordis* (species already reported by Ramalho, 1971 and Rey, 1972), *Porochara jaccardi*, *Aclistochara* sp., *Mesochara harrisi* and *nodosoclavatoroides* utricles (*sensu* Schudack, 1993a) with new occurrences now identified in this section. This association suggests a Late Tithonian to Early Berriasian (?) age.

Olelas

The Olelas section ranges from the Tithonian (Portlandian A and Portlandian B of Ramalho, 1971) to the Valanginian, with a succession of nodular limestones (sometimes clastic) and limestones (Fig. 3). The uppermost part of the Late Tithonian was described by Ramalho (1971) as more than 70 m of grey, massive or clastic limestones, commonly with irregular yellowish spots and, locally, a bivalve coquina. The fossil content includes molluscs, echinoids, *Nautiloculina oolithica*, *Anchispirocyclina lusitanica*, *Everticyammina virguliana*, *Rectocyammina chouberti*, *Trocholina gr. alpina-elongata*, miliolids, *Salpingoporella annulata* and *Cylindroporella cf. arabica*, among other taxa.

The ‘Purbeckian’ (60–80 m) presents massive, yellow and grey limestones with marly intercalations, bearing mollusc remains, crustaceans, coprolites, sponge spicules, *Nautiloculina oolithica*, *Anchispirocyclina lusitanica*, *Everticyammina virguliana*, miliolids, *Permocalculus* sp., dasyclads and ostracods,

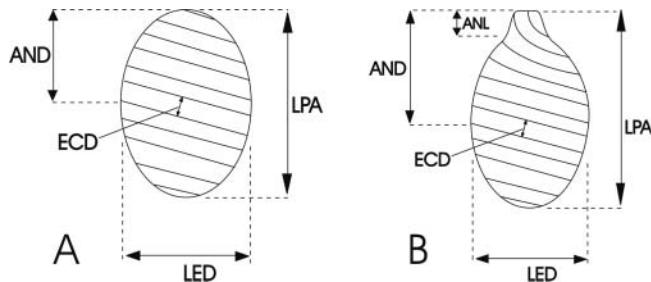


Fig. 4. Simplified scheme of some of the measured parameters in a gyrogonite (see text for description of parameters): (A) forms without apical neck; (B) forms with apical neck.

such as *Fabarella polita polita* (Ramalho, 1971). Charophytes occur in a marly bed, which bears *Globator rectispirale*, *Nodosoclavator bradleyi*, *Porochara jaccardi*, *Mesochara harrisii*, nodosoclavatoredi utricles and *Porochara* sp., of Late Tithonian–Early Berriasian(?) age. Above, in deposits assigned by Rey (1972) to the ‘Margo-calcários com *Mantelliana purbeckensis*’ unit, this author mentions the occurrence of *Porochara cf. maxima* (Donze, 1955) Donze, 1958 emend. Mojon and *Clavator reidi*.

POPULATION ANALYSIS

Analysis of charophyte populations was made measuring distinct morphological parameters (Fig. 4), from which morphometric ratios were derived, following several reference works (Peck, 1937; Mädler, 1952; Horn & Rantzien, 1956; Bonnet & Soulié-Märsche, 1971; Soulié-Märsche *et al.*, 1991; Soulié-Märsche & Joseph, 1991; Schudack, 1993a): LPA, length of polar axis (μm); LED, length of equatorial distance (μm); NC, number of convolutions; ECD, equatorial cell diameter (μm); AND, anisopolarity distance (μm); APD, apical pore diameter (μm); and BPD, basal pore diameter (μm).

In an attempt to better describe the morphological variation in those forms that show a particular character, such as *Clavatoraceae* forms with apical necking (Fig. 4), additional parameters were applied: ANL, apical neck length (μm); and AACD, apical annular cell diameter (μm) – applied to the cells of the ‘Ringstruktur’ (Schudack, 1993a).

ANL allows the characterization of the dimension of the apical neck and, therefore, reduces the effect of this character in the sphericity and asymmetry ratios. Using these parameters, the form of the gyrogonite can then be described for the sphericity index (ISI) and anisopolarity index (ANI). The ISI, isopolarity index (sphericity), for gyrogonites without apical necking is

$$\text{ISI} = \frac{\text{LPA}}{\text{LED}} \times 100$$

	LPA	LED	NC	AND	ISI	ANI	APD	BPD	ANL	AACD
Average	575	391	9	307	134	48	69	39	53	26
Median	569	392	10	304	132	48	69	39	59	29
Minimum	402	304	8	225	110	29	20	10	0	20
Maximum	765	510	11	431	185	76	118	78	176	39
<i>n</i>	204	201	12	191	201	189	175	99	200	11

Table 3. Statistics for morphometric parameters (Fig. 4) of the studied populations of *Nodosoclavator bradleyi*.

	LPA	LED	NC	AND	ISI	ANI	ECD	BPD
Average	294	246	7	137	119	47	40	21
Median	294	245	7	137	119	47	39	20
Minimum	216	206	6	98	100	36	20	20
Maximum	353	294	10	176	141	57	59	29
<i>n</i>	103	103	103	103	103	103	59	43

Table 1. Statistics for morphometric parameters (Fig. 4) of the studied populations of *Mesochara harrisii*.

	LPA	LED	NB	AND	ISI	ANI	APD	BPD
Average	1068	851	14	583	126	54	137	78
Median	1049	843	15	588	127	53	137	78
Minimum	902	706	11	490	101	49	118	78
Maximum	1275	1000	15	765	151	60	157	78
<i>n</i>	21	21	7	18	20	17	4	1

Table 2. Statistics for morphometric parameters (Fig. 4) of the studied populations of *Globator rectispirale*.

or without apical necking is

$$\text{ISI} = \frac{\text{LPA} - \text{ANL}}{\text{LED}} \times 100$$

The ANI, anisopolarity index (asymmetry), for gyrogonites without apical necking is

$$\text{ANI} = \frac{\text{AND}}{\text{LPA}} \times 100$$

or with apical necking is

$$\text{ANI} = \frac{\text{AND} - \text{ANL}}{\text{LPA} - \text{ANL}} \times 100$$

Statistical analysis was applied to the parameters measured from every specimen in order to calculate average, median, minimum and maximum. Results from each species are compiled in Tables 1–7. The parameter *n* refers to the number of specimens measured within a population.

The use of the morphometric parameters in population analysis is of significant importance for species definition, mainly in the case of *Porocharaceae* and *Characeae*, as confirmed in previous studies on a large population of Oxfordian charophytes from the Lusitanian Basin (Pereira *et al.*, 2003). In addition, this kind of approach is also relevant for some forms of *Clavatoraceae* devoid of utricle calcification (e.g. Pereira & Cabral, 2005), for which population analysis is often required for a thorough evaluation and systematics.

	LPA	LED	AND	ISI	ANI	APD	BPD	ANL
Average	612	460	312	122	45	77	53	69
Median	608	451	314	121	47	78	44	78
Minimum	431	353	167	88	19	39	20	0
Maximum	784	598	431	156	65	118	118	157
n	114	105	85	105	85	43	18	97

Table 4. Statistics for morphometric parameters (Fig. 4) of the studied populations of *Clavator reidi*.

The methodology applied in the present work is an attempt to fully depict problematic taxa and to provide their complete description, as with *Porochara jaccardi* and *Mesochara harrisi*. Due to the complex systematics of these forms, several different methods were applied: (1) traditional population analysis using statistical parameters as average, median, mode, minimum and maximum; (2) graphical plots such as LPA vs. LED; and (3) Box and Whisker plots. The latter set of plots displays the range of data from a population where the whiskers reflect the total dispersion of a particular parameter; the box reflects the amount of data that fits into the interval which contains 50% of the measured values. This is helpful to assess the scattering of measurements that fall out of the box, reflecting population variation regarding a similar character.

Figure 5 is a projection of the population of *Porochara jaccardi* using all the values from the different studied sections. Dashed areas indicate the population variation from reference values of Mädler (1952), Mojón (1989) and Schudack (1993a).

	LPA	LED	NC	AND	ISI	ANI	APD	ECD	BPD	ANL
Average	573	338	8	296	146	44	65	55	34	82
Median	569	333	8	294	143	44	59	49	39	78
Minimum	490	294	7	206	118	25	49	39	20	0
Maximum	725	412	10	412	184	53	78	78	59	157
n	32	32	32	32	32	32	25	25	17	32

Table 5. Statistics for morphometric parameters (Fig. 4) of the studied populations of nodosoclavatoide utricle.

	LPA	LED	NC	AND	ISI	ANI	APD	ECD	BPD
Average	524	403	10	270	130	52	52	61	34
Median	539	412	10	275	129	51	49	59	39
Minimum	373	294	8	196	108	46	20	39	20
Maximum	647	520	12	363	157	71	108	88	59
n	129	129	128	126	129	126	87	39	65

Table 6. Statistics for morphometric parameters (Fig. 4) of the studied populations of *Porochara jaccardi*.

	LPA	LED	NC	AND	ISI	ANI	APD	ECD	BPD
Average	771	614	10	397	126	51	102	90	53
Median	765	608	10	402	126	51	98	88	59
Minimum	608	490	8	314	114	49	78	59	39
Maximum	941	824	12	480	147	59	137	118	78
n	71	71	71	71	71	71	52	51	30

Table 7. Statistics for morphometric parameters (Fig. 4) of the populations of *Porochara maxima*.

SYSTEMATIC PALAEONTOLOGY (R. PEREIRA AND M. FEIST)

Phylum Charophyta Migula, 1897

Class Charophyceae Smith, 1938

Order Charales Lindley, 1836

Family Characeae Agardh, 1824

Genus *Mesochara* Grambast, 1962

Mesochara harrisi (Mädler, 1952) Shaikin, 1967

(Pl. 1, figs 7–10)

1952 *Tolypella harrisi* Mädler: 31, pl. B, figs 31–35.

1967 *Mesochara harrisi* (Mädler); Shaikin: 47.

1986 *Tolypella harrisi* (Mädler); Martín-Closas & Grambast-Fessard: 49, pl. X, figs 9–12.

1989 *Mesochara amoena* (Mädler) Shaikin; Schudack: 424, pl. 5, figs 5–7.

1996a *Mesochara harrisi* (Mädler) Shaikin; Schudack: 160, pl. 2, figs 5–7.

1999 *Mesochara harrisi* (Mädler) Shaikin; Schudack: 203, pl. 1, figs 5–8.

Locality. Olelas, Atrozela and Brouco.

Age. Late Tithonian to Early Berriasian(?)

Description. Gyrogonites ranging from 216 to 353 µm in length (Table 1), 206 to 294 µm in width. Spherical to ovoid shape, with

	LPA	LED	NC	AND	ISI	ANI	APD	ECD	BPD	ANL
Average	573	338	8	296	146	44	65	55	34	82
Median	569	333	8	294	143	44	59	49	39	78
Minimum	490	294	7	206	118	25	49	39	20	0
Maximum	725	412	10	412	184	53	78	78	59	157
n	32	32	32	32	32	32	25	25	17	32

Table 5. Statistics for morphometric parameters (Fig. 4) of the studied populations of nodosoclavatoide utricle.

	LPA	LED	NC	AND	ISI	ANI	APD	ECD	BPD
Average	524	403	10	270	130	52	52	61	34
Median	539	412	10	275	129	51	49	59	39
Minimum	373	294	8	196	108	46	20	39	20
Maximum	647	520	12	363	157	71	108	88	59
n	129	129	128	126	129	126	87	39	65

Table 6. Statistics for morphometric parameters (Fig. 4) of the studied populations of *Porochara jaccardi*.

	LPA	LED	NC	AND	ISI	ANI	APD	ECD	BPD
Average	771	614	10	397	126	51	102	90	53
Median	765	608	10	402	126	51	98	88	59
Minimum	608	490	8	314	114	49	78	59	39
Maximum	941	824	12	480	147	59	137	118	78
n	71	71	71	71	71	71	52	51	30

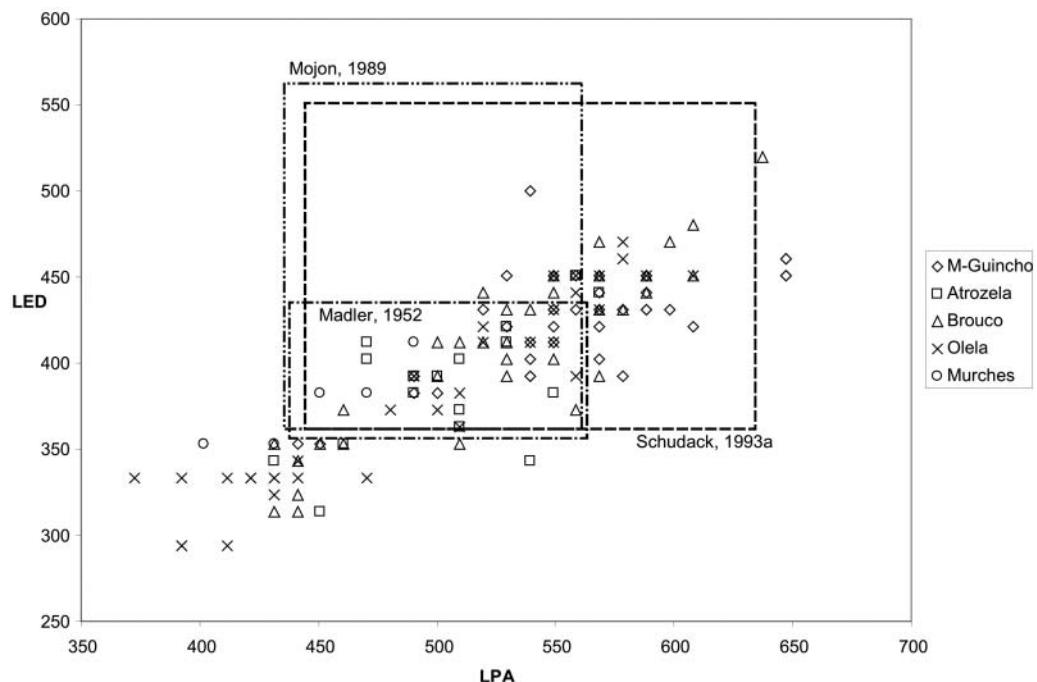


Fig. 5. Graphical projection of the populations of *Porochara jaccardi* for the studied sections. Dashed areas represent the reference values (Mädler, 1952; Mojon, 1989; Schudack, 1993a) for this form.

larger apical half (ANI averages 47), presenting ISI ratios of 100 to 141, but common values average 119. With 6–10 concave to convex spiral cells, averaging 40 µm in width. Basal pore diameter small, (on average 21 µm), at the end of a conical half. Basal plate could not be isolated or identified. Apical pore closed, usually of conical to rounded shape.

Occurrence. Similar forms have been described from the Kimmeridgian to Berriasian of Germany (Schudack, 1993a; 1996a), the Kimmeridgian of Spain (Schudack, 1993a) and the Berriasian of Spain and France (Martín-Closas & Grambast-Fessard, 1986; Schudack, 1989), also from the Kimmeridgian/Tithonian of the former USSR (Shaikin, 1967), the Lower Cretaceous of China (Schudack, 1993a) and the Upper Jurassic of Tanzania (Schudack, 1999).

Remarks. The systematics of *Mesochara* is, at present, still under discussion (Schudack, 1993a; Martín-Closas, 2000) due to the great similarities between the different species originally described mainly by Mädler (1952). When comparing the studied samples of *Mesochara*, several possible species could be accepted. In the case of *M. harrisi*, graphical analysis (Fig. 6) shows that populations are strongly variable, although the majority of the data (LPA and LED) are plotted within the interval defined by the original description of Mädler (1952). Figures 7 and 8 are box and whisker plots for LPA, LED and ISI for the studied populations.

In addition, when considering the overall shape and morphological parameters, i.e. its population dimensions, sphericity, symmetry and number of spiral cells, the closest form accepted is *Mesochara harrisi*. *Mesochara voluta* (Peck, 1937) Grambast, 1965 is larger in size, whereas in *M. minuta* (Mädler, 1952)

Shaikin, 1955 and *M. canellata* (Mädler, 1952) Shaikin, 1967, the studied population is larger (Schudack, 1996a).

Family Clavatoraceae Pia, 1927

Subfamily Atopocharoideae (Peck, 1957) Grambast, 1969

Genus *Globator* Grambast, 1966

Globator rectispirale (Feist *et al.*, 1995)
(Pl. 1, figs 20–21)

1971 *Globator maillardi* (Saporta); Ramalho: 181, pl. 33, fig 7.

1972 *Globator maillardi* (Saporta); Rey: 38, 43, 50.

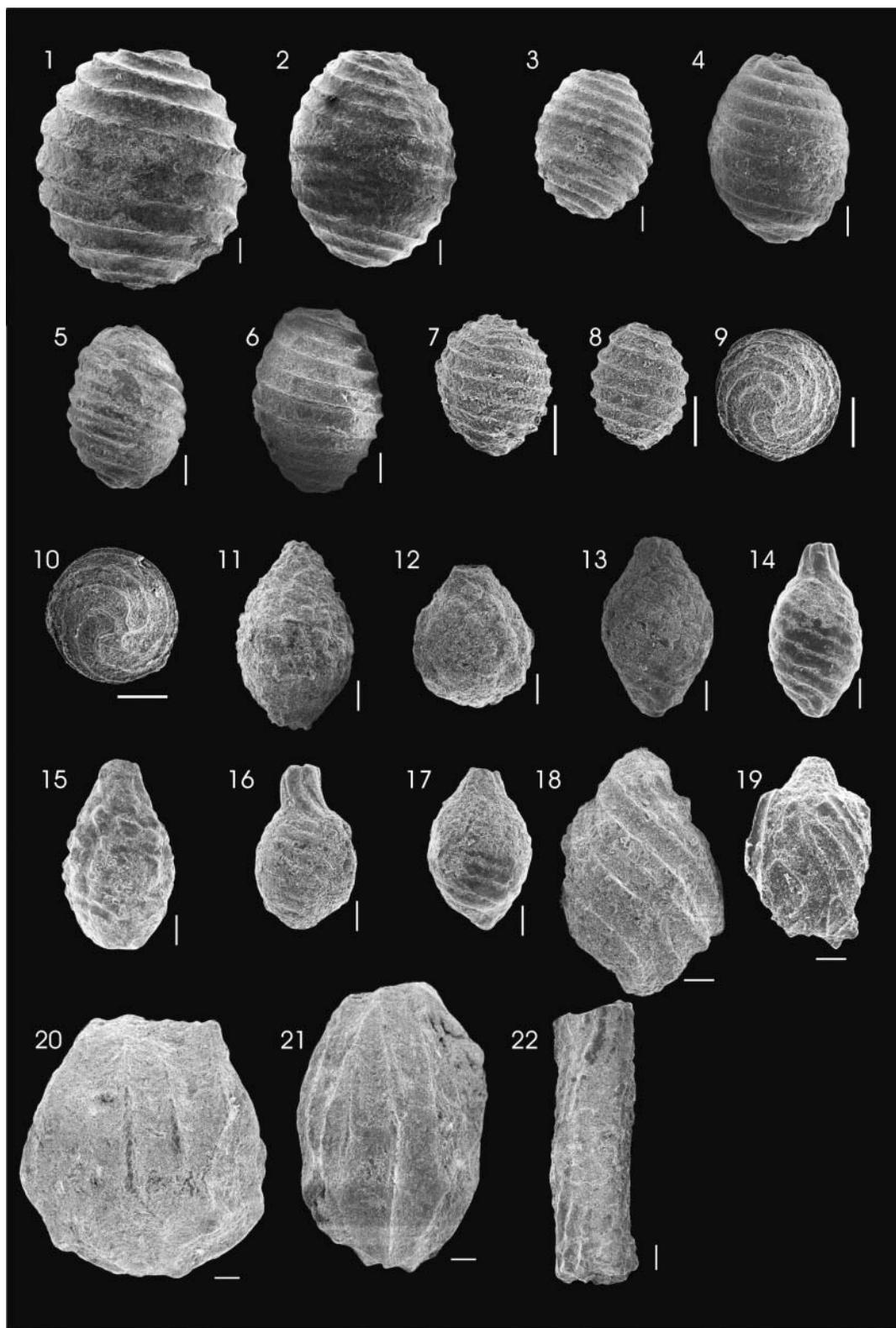
1995 *Globator rectispirale* Feist; Feist *et al.*: 412, pl. 1, figs 1, 5.

Locality. Brouco, Atrozela and Olelas.

Age. Late Tithonian.

Description. Utricle of *Globator*, with three groups of cells vertically aligned. Each group comprises one basal cell and three upper cells. General shape is globular to ovoid with asymmetrical halves in longitudinal view, of which the basal half is larger. In apical view, the shape is roughly triangular. Large-sized utricle (average length 1068 µm and 851 µm in width) with sphericity index and asymmetry averaging 126 and 54, respectively (Table 2). With 11–15 bract cells (NB) vertically aligned from the basal half.

Occurrence. In Portugal this form has been described from Brouco (Ramalho, 1971; Feist *et al.*, 1995); in England, from the Late Tithonian of the Lulworth Formation (key correlation Zone 1) and from the Tithonian of Algeria (Feist *et al.*, 1995).



Explanation of Plate 1.

figs 1–3. *Porochara maxima* (Donze) Donze; Mojon; lateral view; Olelas. **figs 4–6.** *Porochara jaccardi* (Heer) Mojon; lateral view: **4, 5**, Brouco; **6**, Olelas. **figs 7–10.** *Mesochara harrisi* (Mädler) Shaikin: **7, 8**, lateral view, Olelas; **9**, apical view, Olelas; **10**, basal view, Olelas. **figs 11–13.** *Nodosoclavator bradleyi* (Harris) Grambast; lateral view: **11, 12**, Atrozela; **13**, Olelas. **figs 14–17.** *nodosoclavatoroide utricle* Schudack; lateral view; Olelas. **figs 18, 19.** *Clavator reidi* Groves; lateral view: **18**, Atrozela; **19**, Olelas. **figs 20, 21.** *Globator rectispirale* Feist; lateral view; Brouco. **fig. 22.** *Charaxis* sp. Harris; Olelas. White rule is 100 µm.

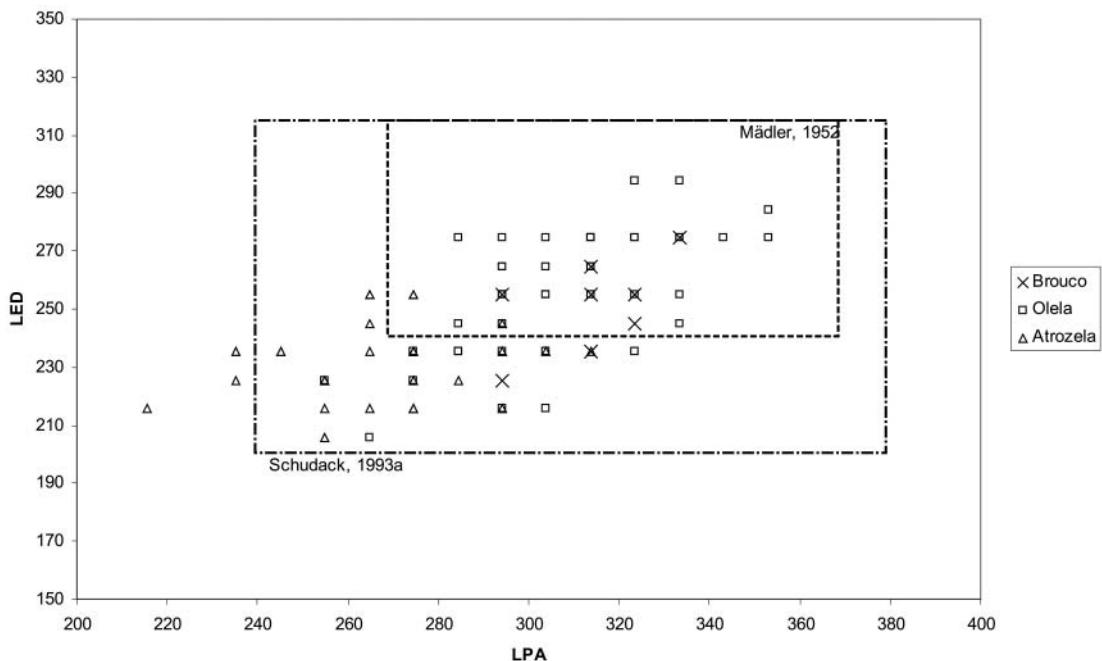


Fig. 6. Graphical projection of the populations of *Mesochara harrisi* for the studied sections. Dashed area represents the reference values (Mädler, 1952; Schudack, 1993a) for this form.

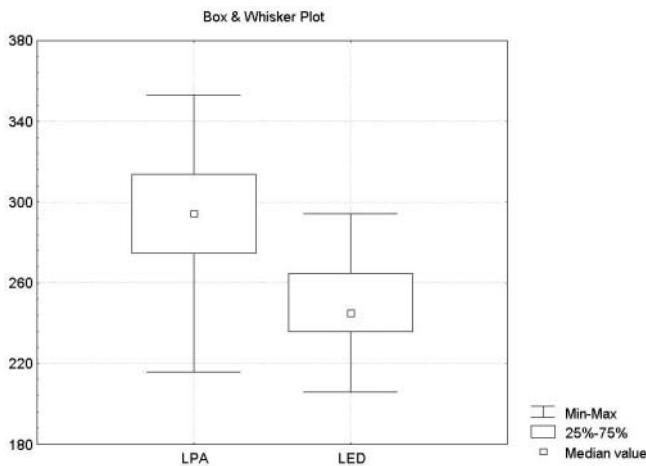


Fig. 7. Box and whisker plot of LPA and LED for the studied populations of *Mesochara harrisi*.

Remarks: The evolutionary trend of the *Globator* utricle is characterized by the progressive spiralization of the long upper cells and the reduction of the short basal ones. The studied specimens show vertical long cells, which give these samples a primitive feature.

Subfamily **Clavatormidae** Pia, 1927, emend. Grambast, 1969

Genus *Nodosoclavator* (Maslov, 1961) Grambast, 1966

Nodosoclavator bradleyi (Harris, 1961) Grambast, 1969
(Pl. 1, figs 11–13)

1939 *Clavator bradleyi* Harris: 53–54, pl. XVI, figs 1, 3–5, 7.

1957 *Clavator nodosus* Peck: 8, figs 3–18.

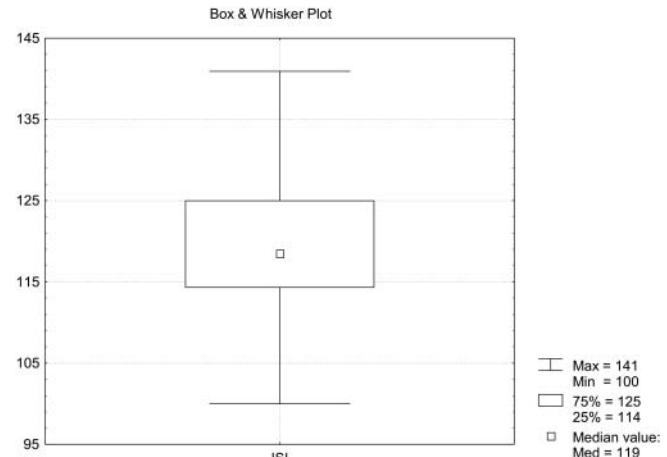


Fig. 8. Box and whisker plot of ISI ratio for the studied populations of *Mesochara harrisi*.

1969 *Nodosoclavator bradleyi* (Harris); Grambast: 878.

1971 *Nodosoclavator bradleyi* (Harris) Grambast; Ramalho: 182, pl. 33, fig. 5.

1972 *Nodosoclavator bradleyi* (Harris) Grambast; Rey: 38, 43, 50.

1987 *Nodosoclavator bradleyi* (Harris) Grambast; Mojón & Strasser: 45, pl. 9, P.

2000 *Nodosoclavator bradleyi* (Harris) Grambast; Martín-Closas: 121, pl. 12, figs 1–2.

Locality. Malveira-Guincho, Olelas, Atrozela and Brouco.

Age. Late Tithonian to Early Berriasian(?)

Description. Utricle with ellipsoidal bottle shape, with larger basal half. Apical half with a well-defined apical neck, but forms without this feature are also present. Utricle often showing bracteal impressions at the basal half and revealing the nodular layer, which covers totally or partially the gyrogonite. Five circular cells ('Ringstruktur') at the apical pore, ranging from 20 to 39 µm (Table 3); apical pore diameter averaging 69 µm. Medium-sized utricle, with 402–765 µm in length, and width from 304–510 µm. When visible, 8–12 (usually 9) concave spiral cells can be seen laterally. Sphericity index of the 'body' of the utricle averages 134, but for the whole specimen including the apical projection, ISI averages 148. Apical neck length is variable and, when present, can reach up to 176 µm, but average values are of 53 µm.

Occurrence. In Portugal, this form is known from the 'Purbeckian' of the Algarve and Sintra-Cascais (Ramalho, 1971; Rey, 1972; Ramalho & Rey, 1975); it is also reported from the Goldberg Formation of the Swiss Jura (Mojon & Strasser, 1987), the Berriasian of Spain (Martín-Closas & Salas, 1998; Martín-Closas, 2000) and northern Germany (Schudack, 1993a), the Lower Cretaceous of England (Harris, 1939), Odessa and Moldavia (Shaikin, 1976), from the Kimmeridgian to Tithonian of the USA (Peck, 1957) and China (Martín-Closas, 2000).

Genus *Clavator* Reid & Groves, 1916

Clavator reidi Groves, 1924 (Pl. 1, figs 18–19)

- 1924 *Clavator reidi* Groves: 116.
 1971 *Clavator* cf. *reidi* Groves; Ramalho: 182
 1972 *Clavator* cf. *reidi* Groves; Rey: 43.
 1993a *Clavator reidi reidi* (Groves) Martín-Closas; Schudack: 75, pl. 9, figs 1–7.
 1993b *Clavator reidi reidi* (Groves) Martín-Closas; Schudack: 53, pl. 2, fig. 2.
 1995 *Clavator reidi* Groves; Feist *et al.*: 415, pl. 1, figs 9–13.
 1996a *Clavator reidi reidi* (Groves) Martín-Closas; Schudack: 162, pl. 2, figs 11–12.
 1996b *Clavator reidi reidi* (Groves) Martín-Closas; Schudack: 38, fig. 18.
 2000 *Clavator reidi reidi* (Groves) Martín-Closas; Martín-Closas: 128, pl. 13, figs 1–3.

Locality. Brouco, Olelas and Atrozela.

Age. Late Tithonian to Early Berriasian(?).

Occurrence. In Portugal this form was found in the Lower Cretaceous (Rey *et al.*, 1968 in Feist *et al.*, 1995; Ramalho, 1971). It is known from the Berriasian of Spain (Feist *et al.*, 1995), the Lower Berriasian of Switzerland (Mojon & Strasser, 1987) and the Berriasian of Germany (Feist *et al.*, 1995; Schudack, 1993a, b, 1996a, b).

Description. Bottle-shaped utricle, formed by five sinistrogyrous spiralled cells, rounded basal half and short apical neck. Utri-

cular cells ranging from the base to the top, but sometimes covering only the basal half. Medium-sized utricle averaging 612 µm in length and 460 µm in width, with an average sphericity of 122, usually with larger apical half (Table 4). Apical pore medium to large and basal pore averaging 53 µm. Necking of apical region when present can be as high as 157 µm. Calcified utricle sometimes incomplete, showing nodular layer.

Genus *Clypeator* (Grambast, 1962) Grambast, 1970

Clypeator cf. *discordis* Shaikin, 1976

- 1970 *Clypeator* sp. Grambast: 1965, b, pl. I, fig. 3.
 1971 *Flabellochara grovesi* (Harris) Grambast; Ramalho: 83, pl. 33, fig. 6.
 1972 *Flabellochara grovesi* (Harris) Grambast; Rey: 38, fig. 50.
 1974 *Clypeator* sp. Grambast: 475, fig. 7.2.
 1976 *Clypeator discordis* Shaikin: 82, figs 9–11.
 1989 *Clypeator discordis* Shaikin; Schudack: 421, pl. 4, figs 9–13.
 1993a *Clavator grovesii* var. *discordis* (Shaikin) nov. comb.; Schudack: 77–78, pl. 9, figs 15–18.
 1995 *Clypeator discordis* Shaikin; Feist *et al.*: 418, pl. 2, figs 5–6.
 2000 *Clavator grovesii* var. *discordis* (Shaikin) Schudack; Martín-Closas: 136–139, pl. 14, fig. 2.

Locality. Brouco.

Age. Late Tithonian.

Description. Poorly preserved medium-sized diamond-shaped utricle (larger at basal half), with bilateral symmetry. Vegetative cells form two groups of utricular coatings around the lateral pores.

Occurrence. In Portugal this form was described from the Brouco section (Ramalho, 1971; Feist *et al.*, 1995). In Spain, Martín-Closas (2000) refers to its occurrence at the Lower Berriasian of the Cameros basin and at the Basque-Cantabrian basin. Similar forms are also described from the Late Tithonian of the Lulworth beds in England, the Berriasian of Germany (Schudack, 1993a), the Valanginian of China (Feist *et al.*, 1995) and from the Hauterivian to Barremian of the Ukraine (Shaikin, 1976).

nodosoclavatoroide utricle Schudack, 1993a

Clavatoroidea indet. (Pl. 1, figs 14–17)

- 1993a *nodosoclavatoroide* Schudack: 90, pl. 12, figs 9–15.
 1993b *nodosoclavatoroide*; Schudack: 53, pl. 2, fig. 9.
 1996a *nodosoclavatoroide*; Schudack: 163, pl. 2, fig. 13.

Locality. Brouco and Olelas.

Age. Late Tithonian.

Description. *Clavatoraceae* gyrogonite usually devoid of utricle calcification, with bottle shape and long apical neck. Presents 7–10 (usually 8) convex to flat spirals visible laterally, aligned

vertically at the apex (Table 5). The utricle cover, when present, shows portions of the nodular layer and/or of bracteal impressions at the base. Length 490–725 µm and width 294–412 µm. The gyrogonite, excluding the apical neck, is markedly ellipsoidal (average ISI of 146), whilst the gyrogonite can range from 145 to 212 (average of 171). Marked apical necking (82 µm average length), often with vertical cells. Apical pore ranging from 49 to 78 µm, and basal pore averages 34 µm.

Occurrence. Apart from Portugal, similar specimens are known from the Berriasian of Germany (Schudack, 1993a, 1996a).

Remarks. Utricles similar to *Nodosoclavator*, but with incomplete or absent utricle cover. When comparing the apical neck, *nodosoclavatoroide* utricle usually has larger dimensions than *Nodosoclavator bradleyi*; the same applies to the overall dimensions and sphericity ratio (more elliptical).

Family **Porocharaceae** Grambast, 1962

Genus **Porochara** Mädler, 1955 emend. Schudack, 1986

Porochara jaccardi (Heer, 1865) Mojon, 1989

(Pl. 1, figs 4–6)

1865 *Chara jaccardi* n. sp. Heer: 218, fig. 134.

1952 *Aclistochara hildesiensis* n. sp.; Mädler: 18–19, pl. A, figs 17–21.

1955 *Porochara hildesiensis* (Mädler); Mädler: 271.

1971 *Porochara* sp., Ramalho: 50, 51, 59, 66, 67, 80, 83.

1972 *Porochara* sp., Rey: 38, 43, 49, 50.

1985 *Musacchiella sardinae* Feist & Grambast-Fessard; Colin *et al.*: 348–350, pl. 1, figs 6–13.

1987 *Porochara* cf. *hildesiensis* (Mädler) Mädler; Mojon & Strasser: figs 9F–J.

1989 *Porochara jaccardi* (Heer); Mojon: 509–512, pl. VI, figs A1–7, B1–15, C1–12.

1993a *Porochara jaccardi* (Heer) Mojon; Schudack: 53, pl. 3, figs 7–8.

Locality. Atrozela, Malveira-Guincho, Olelas, Murches and Brouco.

Age. Late Tithonian to Early Berriasian(?)

Description. Medium-sized gyrogonite, with oval shape and larger basal half. In lateral view, usually 9–10 spiral concave to convex cells can be observed (Table 6), but specimens with 8–12 spiral cells are also present. Equatorial cell diameter averages 62 µm, apical pore small averaging 52 µm and the basal pore diameter averages 34 µm. Truncated to rounded apex and rounded base are the most common features.

Occurrence. *Porochara jaccardi* has been described from the Kimmeridgian to Lower Tithonian(?) of Germany (Schudack, 1993a), the Berriasian of France and Switzerland (Heer, 1865; Mojon & Strasser, 1987; Mojon, 1989) and Sardinia, Italy (Colin *et al.*, 1985) and the Berriasian to Barremian of Spain (Martín-Closas & Grambast-Fessard, 1986).

Porochara maxima (Donze, 1955) Donze, 1958
(Pl. 1, figs 1–3)

1955 *Aclistochara maxima* Donze: 289, pl. 13, figs 6–7.

1958 *Porochara maxima* Donze: 180.

1972 *Porochara* cf. *maxima* (Donze) Donze; Rey: 49.

1989 *Porochara maxima* (Donze) Donze; Mojon: 508, pl. 3, figs A–P, pl. 4, A1–7, B1–6, C1–15, pl. 5, B1–33.

1993a *Porochara maxima* (Donze) Donze; Schudack: 55, pl. 3, figs 18–21.

1995 *Porochara maxima* (Donze) Donze; Feist *et al.*: 410, pl. 2, fig. 21.

Locality. Olelas.

Age. Late Tithonian.

Description. Gyrogonite of *Porochara* of large size with ellipsoidal form, with rounded larger apical half. Spiral cells concave, often well marked. Gyrogonite with large apical pore (102 µm average) and truncated apex. 8–12 (commonly 10) concave spiral cells visible in lateral view. Basal pore averaging 53 µm. Equatorial cell diameter ranges from 59 to 118 µm.

Occurrence. This form is present in the Lower Berriasian of the French–Swiss Jura mountains (Donze, 1955; Mojon, 1989); in the Lower Berriasian of the Lulworth Formation, England (Feist *et al.*, 1995), northwest Germany, Sardinia and Spain (Schudack, 1993a; Feist *et al.*, 1995).

Charaxis Harris, 1939
(Pl. 1, fig. 22)

Locality. Olelas.

Description. Charophyte thalli with nodes and internodes showing longitudinal cortical cells spiralled along the main axis. In section, 12 cortical cells can be observed.

DISCUSSION AND CONCLUSIONS

The ‘Purbeckian’ facies of the Sintra-Cascais and Lisbon area (Portugal) are characterized by the occurrence of charophytes typical of the Late Tithonian–Early Berriasian interval. These deposits were formed in a lagoonal to lacustrine environment (e.g. Ramalho & Rey, 1975), which allowed several species of charophytes to flourish under suitable oligo-haline to mesohaline conditions (*sensu* Schudack, 1993a).

Comparing the studied Portuguese charophyte floral assemblage with those described from other regions, namely those identified by Feist *et al.* (1995) from the Late Tithonian of the Lulworth Formation in England and from the Tithonian of the Mahjouba Formation in Algeria, allows better constraint on the stratigraphic positioning of the studied successions. The Lulworth succession presents, for Zone 1 (Late Tithonian; Feist *et al.*, 1995), the occurrence of *Globator rectispirale* and *Clypearator discordis*, forms similar to those of the Sintra-Cascais and Lisbon region. Similarly, Feist *et al.* (1995) describe the occurrence of the former in the Mahjouba Formation of Algeria. Thus, the studied interval in all sections but Murches should

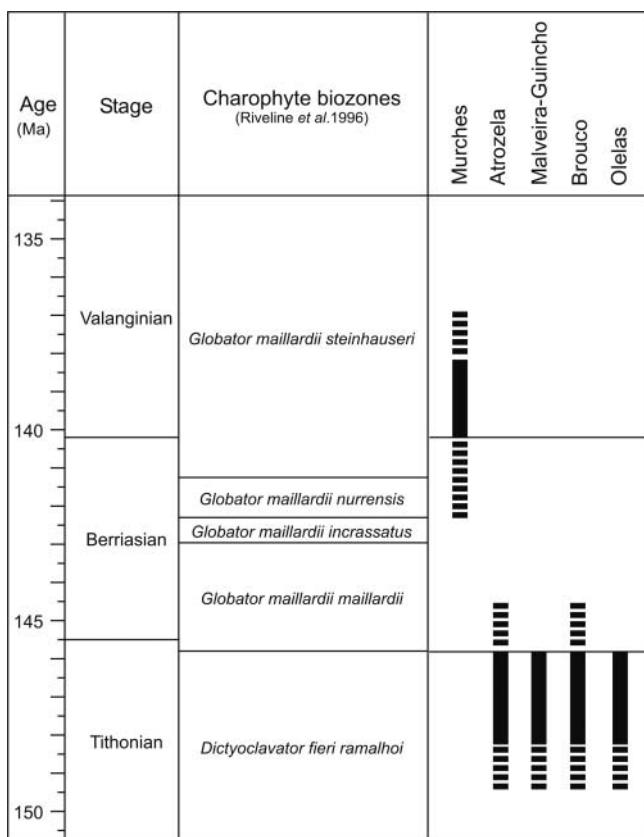


Fig. 9. Stratigraphical positioning of the studied charophytes and comparison with the biozones of Riveline *et al.* (1996). Dashed columns represent possible age extension.

now be considered to most likely represent a Late Tithonian age. This is in accordance with the fact stated by Feist *et al.* (1995) that *Mantelliana purbeckensis*, which used to be taken as indicating a Berriasian age, is now accepted to exist from the Late Jurassic.

This stratigraphical positioning in the Late Tithonian interval is reinforced by the fact that, whereas these Portuguese assemblages do not correlate with clear Cretaceous assemblages described elsewhere, they are broadly similar to those found in known European ‘Purbeckian’ successions, such as those from Spain (Martín-Closas & Salas, 1998), Italy (Colin *et al.*, 1985) and Switzerland (Mojon & Strasser, 1987), even though exact age correlations cannot be made.

When comparing the assemblages presented herein to the biozones defined by Riveline *et al.* (1996), it is not possible to make a direct correlation to those formally defined biostratigraphical units of the Tithonian, as *Globator maillardii maillardii* was not reported. Therefore, a greater age is accepted, so that the studied sections are likely to belong to the Late Tithonian interval (Fig. 9), instead of the previously accepted wider ‘Purbeckian’ interval, i.e. Tithonian to Early Berriasian age.

The occurrence of these Late Tithonian forms in Portugal is important for palaeobiogeographical interpretations, considering the intermediate geographical position of Portugal relative to England and Algeria where similar assemblages were previously reported.

The Murches charophyte beds (Fig. 9) are considered to be Late Berriasian(?) to Valanginian, as evidenced by the occurrence of the association bearing *Globator aff. nurrensis*, a revision of *G. maillardii* var.

Statistical analysis applied to the studied charophytes has allowed better characterization of the population variation within each species. This methodology presents the best results when applied to families of charophytes with few distinguishing features, mainly to *Characeae* and *Porocharaceae*, forms without utricle covers. However, even for *Clavatoraceae* this approach is useful, since it allows enhancing the descriptive features with a more objective quantitative contribution to systematics.

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