

# Palaeobiogeography of the genus *Latochara* (fossil Charophyta) in the Upper Jurassic of Southern Europe. New data from Oléron Island (France)



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### ABSTRACT

*A charophyte assemblage including Latochara tenuicostata (PECK 1937) and Mesochara gr. voluta (PECK 1937) was found in the Lower Tithonian bone-bed 148 of the stratigraphic section at the Pointe de Chassiron, Oléron Island (Charente-Maritime, Southwestern France). This bed, which is well known for its rich and diverse fauna of tetrapods, was deposited in a margino-littoral environment of Purbeckian facies in the Late Jurassic Charente palaeogulf. The occurrence of Latochara at Oléron Island is the most southern location known in the distribution of this genus during the Late Jurassic. This suggests that the boundary between the charophyte Boreal and Tethyan provinces, defined on the basis of this distribution, is not solely determined by latitudinal (i.e. thermal) factors. Ecological factors such as salinity and competition with other charophyte families are hypothesized as alternative explanations.*

**Keywords:** Charophytes, ostracods, vertebrates, Tithonian, France, bioprovinces

### 1. INTRODUCTION

Palaeobiogeography of Late Jurassic and Early Cretaceous charophytes is a relatively new and poorly understood subject in charophyte research. The pioneer studies of SIRNA (1968) and PALAMAREV (1971) on Early Cretaceous clavatoraceans, showed for the first time that large palaeogeographic regions shared a similar charophyte flora, which was useful not only for characterising them biogeographically, but also for large-scale biostratigraphic correlation. Late Jurassic charophyte biogeography of the Northern Hemisphere, (Europe

and North America), was characterized by SCHUDACK (1996) and SCHUDACK et al. (1998). These studies were significant in showing that floras from North America and Northern Europe were much more like each other than like floras of the Tethyan domain. Thus, without calling them bioprovinces, SCHUDACK et al. (1998) characterized two different regions on the basis of Late Jurassic charophyte assemblages. A Northern or Boreal region was determined with characean-porocharacean floras in opposition to a Southern or Tethyan region, dominated at that time by clavatoracean floras. The genus

*Latochara* was considered as a key taxon of the Northern Region. Furthermore, the boundary between both regions was set at the 20°C isotherm of mean winter temperature. Later studies showed that even in the Northern part of the Iberian palaeoisland, Tithonian charophyte assemblages lacked this genus and were instead dominated by clavatoracean genera such as *Globator* and *Clavator* (HERNÁNDEZ et al., 1999; MARTÍN-CLO-SAS, 2000). This suggested that the 20°C isotherm could be a real Late Jurassic bioprovincial boundary. Now, the occurrence of the marker of the northern province, (the genus *Latochara*), south of the boundary, raises the question of whether factors other than thermal boundaries should be taken into account if we are to understand charophyte palaeobiogeography.

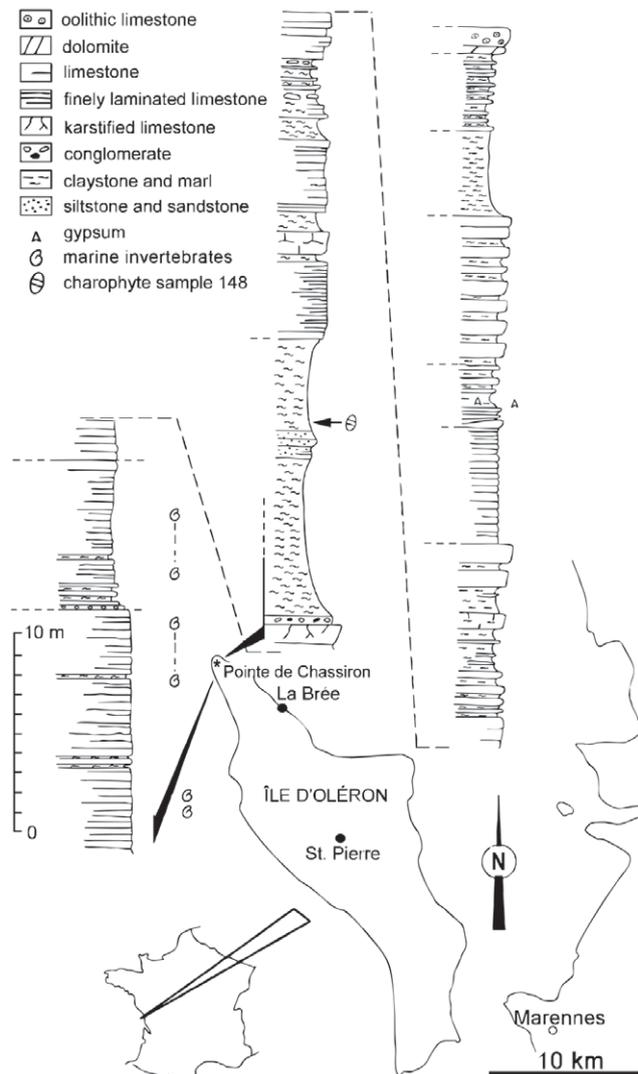
## 2. GEOLOGICAL AND PALAEONTOLOGICAL SETTING

### 2.1. GEOLOGICAL BACKGROUND

The beginning of the uppermost Jurassic is generally represented in Western Europe by a major drop in relative sea level. Thus, the epicontinental marine deposits of the lowermost Upper Jurassic are covered by lagoonal to non-marine facies, including evaporites that develop well into the Lower Cretaceous (JACQUIN et al., 1998; RUSCIADELLI, 1999). These facies are generally referred to as “Purbeckian”, through comparison with reference-sections in England. In France, the Charente Basin is one such Purbeckian basin that is rich in evaporites. The palaeogeography of this basin shows a narrow gulf opening to the West according to DELFAUD & GOTTIS (1966) and HANTZPERGUE & LAFAURIE (1994). This hypothesis has been challenged by a recent palaeogeographic reconstruction by THIERRY (2000), showing a connection southward and eastward between the Aquitanian Basin and the Mediterranean Tethys. The outcrops are located in the northern part of Oléron Island, along the cliffs of the Pointe de Chassiron, near the Chassiron lighthouse (Fig. 1). This section represents the most complete stratigraphic record of the Purbeckian basin of the Charentes. In particular, it is an excellent outcrop of the boundary between the underlying Upper Jurassic marine rocks and the Purbeckian non-marine facies. The stratigraphy and biostratigraphy of the section were studied in detail by LANTZ (1958), DONZE (1960), MALZ (1958, 1966) and BOUSQUET (1967), who provided a detailed sedimentological study and BOURGUEIL et al. (1976). More recently, HANTZPERGUE (1989) and HANTZPERGUE et al. (2004) reported new biostratigraphic data and SCHNYDER (2003) proposed a new palaeoclimatic interpretation based on palynological and mineralogical evidence.

### 2.2. DESCRIPTION OF THE STRATIGRAPHIC SECTION AT POINTE DE CHASSIRON

The base of the section consists of grey-beige limestones (mudstone to bioclastic packstone), showing poorly stratified or irregular, nodular bedding, alternating with marls (Fig. 1). In sedimentological and palaeontological terms, the facies correspond to a shallow, open platform of normal salinity, with ammonites, echinoderms and dinoflagellates (BOUSQUET, 1967; SCHNYDER, 2003). This succession which is up to 24



**Figure 1:** The studied locality and stratigraphic section at the Pointe de Chassiron (Oléron Island, Southwestern France) with the charophyte bearing bed (Bed 148) indicated.

m thick, is Late Kimmeridgian (biozone *Autissiodorensis*) to Early Tithonian (biozone *Gigas*) in age (HANTZPERGUE, 1989; HANTZPERGUE et al., 2004).

A sequence boundary associated with a drop in sea-level is found at the top of the previous limestone-dominated succession and is marked by a conglomerate 50 cm thick, showing at the top, an accumulation of large woody remains (Fig. 1). Upon this boundary bed, a Purbeckian succession, 56 m thick, developed with non-marine lutites dominating in the lower and upper members, whilst marine carbonates are characteristic of the central member. Bioclasts accumulated in particular horizons. The top of the section includes one gypsum layer. Sedimentological evidence and the occurrence of layers with marine fossils, such as benthic foraminifera, marine ostracods, echinoderm debris and brachiopod-rich horizons, alternating with other layers rich in charophytes and non-marine ostracods, indicate that this succession was formed in a shallow marine, littoral context influenced by freshwater discharges (BOUSQUET, 1967; SCHNYDER, 2003). The age of the

Purbeckian succession is not easy to establish in the absence of ammonites. However, an Early to Late Tithonian age was suggested on the basis of ostracods, brachiopods (HANTZ-PERGUE et al., 2004), calcareous nannofossils and dinoflagellates (SCHNYDER, 2003).

Bed 148, which provided the fossils that are the subject of this study, is a marl with small carbonaceous nodules, located in the lower part of the Purbeckian succession, upon a greenish marly-silty layer (Fig. 1). It shows an accumulation of woody remains at the base, charophyte gyrogonites and vertebrate remains. The member of the section containing this layer was attributed to the Early to Middle Tithonian. This member is formed by dark blue marly claystones interlayered with siltstones and silty, finely bedded limestone. These rocks are thought to have been deposited in a littoral or estuarine bay with abundant freshwater discharges. The lack of fauna indicating normal marine salinity such as echinoderms is of particular interest and, in contrast, the presence of rare ostracods of the “*Cypris*” type, indicates brackish to freshwater conditions, together with charophytes (BOUSQUET, 1967; SCHNYDER, 2003).

### 2.3. THE FAUNA ASSOCIATED WITH CHAROPHYTES

Two main groups of fossils were found associated with the charophytes studied: ostracods and vertebrates. Ostracods are represented by about 20 species. The euryaline form *Fabanel-la boloniensis ornata* (STEGHAUS, 1953) and the limnic genus *Mantelliana* cf. *perlata* WIENHOLZ, 1968 are dominant. The remaining fauna consists mainly of non-marine species: *Cetacella armata* MARTIN, 1958, *Darwinula oblonga* (ROMER, 1839), *Alicenula leguminella* (FORBES in LYELL 1855) *Theriosynoecum* aff. *forbesii* (JONES, 1885), *Theriosynoecum* cf. *albertense* (PINTO & SANGUINETTI, 1962), *Cypridea* spp., *Eoparacypris* sp., *Stenestroemia* sp., *Damonella pygmaea* (ANDERSON, 1941), *Damonella ellipsoidea* (WOLBURG, 1962), “*Bisulcocypris*” *dilatata* ANDERSON, 1971, and *Rhinocypris jurassica* (MARTIN, 1940). Marine genera are rare and represented by a few specimens of *Dicrorhygma*, *Asciocythere?* and *Cytheroptera*.

The vertebrate fauna from the Pointe de Chassiron consists of chondrichthyans, osteichthyans and tetrapods. Tetrapods have been reported in 14 beds from the Purbeckian succession (beds B104 to B203a from BOUSQUET, 1967). They include remains from a lissamphibian, turtles, a lepidosaurian, crocodilians, pterosaurs and dinosaurs (LAPPARENT & OULMI, 1964; RIEPPEL, 1980; BILLON-BRUYAT et al., 2001; BILLON-BRUYAT, 2003). A detailed list and a description of these tetrapods is given in BILLON-BRUYAT (2003).

Bed 148 (B148 from BOUSQUET, 1967) was termed a bone-bed and is considered the horizon with the most diverse vertebrate fauna in the section. A preliminary study of chondrichthyans and osteichthyans from this bed was carried out by VULLO (2001), who reported a number of families living in marine or margino-littoral environments. A recent isotopic geochemical study showed that Semionotidae remains from bed B148 are of marine origin (BILLON-BRUYAT et al., 2005).

Tetrapod remains from the same bed include a lissamphibian (*Urodela incertae sedis*), turtles (Plesiochelyidae), crocodilians (Teleosauridae, Atoposauridae, Goniopholididae, Bernissartiidae), pterosaurs (Pterodactyloidea indet, Pterosauria indet.) and dinosaurs (Theropoda indet.). Most of these taxa were identified on the basis of microremains, mainly isolated teeth. Only the plesiochelyids, teleosaurids, goniopholidids and a theropod are represented by larger remains. The stratigraphic distribution of these tetrapod families is consistent with a latest Jurassic age. They were known from the Jurassic and Cretaceous with the exception of plesiochelyids, which disappeared in the Tithonian, and teleosaurids, which are only represented in the Cretaceous by a single questionable specimen (CORNÉE & BUFFETAUT, 1979; BENTON, 1993; BARDET, 1995). A margino-littoral depositional environment is consistent with the composition of the tetrapod fauna. Plesiochelyids and teleosaurids in particular are considered as coastal marine reptiles (BUFFETAUT, 1982; BROIN, 1994; BARDET, 1995). In addition, BILLON-BRUYAT et al. (2005) reported that samples from these families in bed B148 indicate a marine isotopic signal. Their remains were abundant and include some connected bones. All the other tetrapod families were non-marine, either freshwater/terrestrial (lissamphibians), freshwater/brackish (goniopholidid, bernissartiid crocodilians), terrestrial (atoposaurid crocodilians, theropod dinosaurs) and aerial elements (pterosaurs). The occurrence of these continental families in the margino-littoral depositional environment clearly reflects a freshwater inflow.

### 3. SYSTEMATIC PALAEOLOGY

**Division Charophyta MIGULA, 1897**

**Class Charophyceae SMITH, 1938**

**Order Charales LINDLEY, 1836**

**Family Nitellaceae von LEONHARDI, 1864**

**emend. MARTÍN-CLOSAS & SCHUDACK, 1991**

**Genus *Latochara* MÄDLER 1955 emend.**

**FEIST in FEIST & CUBAYNES, 1984**

***Latochara latitruncata* (PECK, 1937) MÄDLER, 1955**

(Figs. 2.1–2.4)

1937 *Aclistochara latitruncata* PECK, n. sp. – PECK, p. 89, pl. 14, figs 1–4

1955 *Latochara latitruncata* (PECK) nov. comb. – MÄDLER, p. 271

1957 *Latochara latitruncata* (PECK) – PECK, p. 32–33, pl. 5, figs. 7, 21–33

1957 *Latochara concinna* PECK, n. sp. – PECK, p. 34, pl. 5, figs. 5–6, 8–9

1990 *Latochara latitruncata* (PECK 1937) MÄDLER 1955 – SCHUDACK, p. 219, pl. 2, figs. 1–4

1993 *Latochara latitruncata* (PECK 1937) MÄDLER 1955 – SCHUDACK, p. 56, pl. 4, figs. 1–4

Material: About 200 gyrogonites from sample 148b.

Description: Medium-sized gyrogonites, in shape subspherical to ellipsoidal. Length ranges 351–432  $\mu\text{m}$  (average 404  $\mu\text{m}$ ), including the neck. Width ranges 270–351  $\mu\text{m}$  (average 312  $\mu\text{m}$ ). Isopolarity index 123–136 (average ISI 129).

Spiral cells are flat or slightly concave with carinated sutures. The number of convolutions visible in frontal view ranges from 10 to 13. Apex generally pointed. Apical neck generally short and pyramidal but in isolated specimens may be almost prismatic, similar to the neck of *Stellatochara*. When approaching the neck, spiral cells become first wider and then narrow suddenly up to the summit. In this area the spiral cells are strongly concave. A periapical depression is present in some specimens. The apical pore is small and hardly visible. Base rounded or truncated. Basal plate not observed, but probably multipartite, as in other species of the genus.



**Figure 2:** Early Tithonian charophytes from bed 148 at the Pointe de Chassiron. 1, 2: *Latochara latitruncata*. Lateral view of two gyrogonites showing globulosity and pointed apex. 3: Lateral view of gyrogonite showing an elongated shape and an apical neck. 4: Lateral view of a well-calcified gyrogonite showing a conical apex. 5: *Mesochara* gr. *voluta*. Lateral view of gyrogonite showing drop shape and prominent sutures.

**Discussion:** The population studied belongs to medium-sized Jurassic and Lower Cretaceous *Latochara* species. These are *L. latitruncata*, *L. collina* PECK, 1957, *L. concinna* PECK, 1957, *L. tenuicostata* (PECK, 1937) and *L. maedleri* SCHUDACK, 1996. Other species are smaller, i.e. about 300  $\mu\text{m}$  average length (*L. mensinki* SCHUDACK, 1990 and *L. bellatula* PECK, 1957) or larger, i.e. more than 500  $\mu\text{m}$  average length (*L. sphaerica* PECK, 1957 and *L. durand-delgai* FEIST 1984) and will not be considered for comparison.

The population studied is similar in size and shape to *L. latitruncata* (PECK, 1937) from the Tithonian and Kimmeridgian of the Morrison Formation (USA), with the difference that this population is more ellipsoidal and has more numerous and thinner spiral cells. The specimen shown by PECK (1957, pl. 5, fig. 22) is very close to this population in its number of convolutions and general shape. Apart from the Morrison Formation, this species was reported from the Lower Kimmeridgian of the Saxony Basin (NW Germany), by SCHUDACK (1993) and from the Tithonian of the Dnieper-Donets basin (Ukraine) by SHADKIN (1967). The German material shown by SCHUDACK (1990, 1993) differs from the population studied here in the stronger calcification of spiral cells. The number of convolutions is somewhat smaller but overlaps with the range of the French population.

*Latochara collina* PECK 1957 is very close to the previous species and PECK (1957) suggested that they may be distinct only at the sub-species level. The only noticeable difference between the two species is the shape of the intercellular sutures which is wavy in *L. collina*. This may give a knotty aspect to spiral cells. This characteristic is not present in this material. SCHUDACK (1993) points to the larger width (sub-lat shape) and the truncated summit of gyrogonites to distinguish this species; however these characters are also present in *Latochara latitruncata*, as clearly indicated in its species description.

*Latochara concinna* PECK 1957 is considered in the original description as being very similar to *L. latitruncata* and SCHUDACK (1993) concludes that both species are synonymous, a point of view to which we adhere.

*Latochara tenuicostata* PECK 1957 from the Aptian of Wyoming is somewhat smaller than the material here, but is similar in the number of convolutions. However, the apical pore of this species is large and rose-shaped, unlike the apical pores of other *Latochara*. This pore is reminiscent of the apical pores of Clavatoraceae. Also the overall aspect of the gyrogonite, including its pointed base, is similar to internal casts of the fructification of genus *Atopochara*. PECK (1957) noticed the presence of clavatoracean remains associated with *Latochara tenuicostata*. In consequence, it appears that this species should not be ascribed to the genus *Latochara* but rather to an internal cast of a clavatoracean oosporangium.

*Latochara maedleri* SCHUDACK, 1996 from the Berriasian of NW Germany is distinct from other species in its extremely truncated apex, which results in a very wide gyrogonite. This form does not occur in the material described here.

**Family Characeae (R. ex C. AGARDH, 1824) emend.****MARTÍN-CLOSAS and SCHUDACK, 1991****Genus *Mesochara* GRAMBAST, 1962*****Mesochara* gr. *voluta* (PECK, 1937) emend. PECK, 1957****nov. comb. GRAMBAST, 1965**

(Fig. 2.5)

1937 *Chara voluta* PECK, n. sp. – PECK, p. 85–86, pl. 14, figs. 16–191957 *Praechara voluta* (PECK) – PECK, p. 39, pl. 7, figs. 7, 22–271965 *Mesochara voluta* (PECK) nov. comb. – GRAMBAST, p. 581

Material: Six gyrogonites from sample 148b.

Description: The gyrogonite is small, 270–350  $\mu\text{m}$  in high and 240–300  $\mu\text{m}$  wide. Isopolarity index ranges between 100 and 120. The gyrogonite is normally drop-shaped with a flat apex and a pointed base. Some specimens also show a pointed apex. The maximum width is above the middle point. In profile, 7–8 convolutions are visible, separated by prominent ridges. In the equatorial zone, spiral cells are between 25–60  $\mu\text{m}$  high. Apex closed by simple junction of spiral cells. Base shows a pentagonal pore with a maximum diameter of about 50  $\mu\text{m}$ . Basal plate not observed.

Discussion: The group *voluta* has a wide chronostratigraphic range, from the Kimmeridgian to the Barremian (SCHUDACK, 1993; MARTÍN-CLOSAS, 2000).

**4. PALAEOBIOGEOGRAPHY**

Whilst *Latochara* from the Lower Jurassic is known from southern France, (FEIST and CUBAYNES, 1984), in the Upper Jurassic and Lower Cretaceous, the genus was exclusively known from the Boreal domain, i.e. regions north of the Tethyan Sea. PECK (1957) and SCHUDACK et al. (1998) reported the genus in the Kimmeridgian and Berriasian of the Morrison Formation (Western United States), FEIST et al. (1995) in the Upper Tithonian–Lower Berriasian from the Purbeck facies in England, SCHUDACK (1993) from the Kimmeridgian, Tithonian and Berriasian in the North-western German basins, and SHAĎKIN (1967), from the Tithonian of the Dnieper-Donetz basin (Fig. 3). However, the genus is completely unknown in the Tithonian–Berriasian basins of Central Tethys, i.e. in the Iberian Peninsula, Sardinian High, Provence and Northern Africa, where charophyte associations were generally dominated by clavatoraceans during that period (SCHUDACK et al., 1998; MARTÍN-CLOSAS, 2003). In consequence, the *Latochara* genus was considered by SCHUDACK (1996) as one of the most characteristic genera of the Northern charophyte biogeographic province during the Kimmeridgian–Tithonian and Berriasian. He hypothesized that a thermal barrier at 20°C of mean winter temperature would account for the biogeographic boundary (Fig. 3).

The occurrence of *Latochara temuicostata* at Oléron Island, Southwestern France, during the Late Jurassic, allows us to shift the known biogeographic distribution of this genus 570 km southwards, to touch the northern margins of the Mesogea, in Central Tethys.



**Figure 3:** Global distribution of Tithonian *Latochara* with its southernmost location on Oléron Island, beyond the winter isotherm of 20°C (modified from SCHUDACK et al., 1998). Legend: 1–5 localities in the Morrison Fm (United States), 1. Montana, 2. South Dakota, 3. Central and Eastern Wyoming, 4. East-Central Utah, 5. Colorado, 6. Purbeck basin, S. England, 7. Saxony basin, N. Germany, 8. Oléron Island, Charente basin, France.

The new distribution suggests that the biogeography of the genus was not just controlled by temperature as proposed by SCHUDACK (1996). Other factors, in addition to temperature, may have hindered the expansion of the genus into the central Tethyan islands (Iberian Peninsula, Sardinian high and Morocco Meseta). The next Upper Jurassic–Lower Cretaceous charophyte locality south of Oléron Island occurs in the Lower Berriasian lacustrine limestone of the Aguilar de Campoo Fm, Cantabrian Chain, where charophyte assemblages are dominated by *Globator maillardii praecursor* and *Clavator reidii* (HERNÁNDEZ et al., 1999). This formation is attributed to deposition in large, permanent, alkaline and freshwater lakes without any marine influence. Also the other localities from Iberia (SCHUDACK, 1993), the Sardinian High (COLIN et al., 1985) and the Morocco Meseta (MOJON, 2002) correspond to lacustrine limestone belonging to freshwater alkaline lakes, whilst localities dominated by *Latochara*, such as the new occurrence described here, correspond to brackish or littoral marshes. In conclusion, palaeoecology also appears to play a significant role in the distribution of *Latochara* in addition to climate. It is known that Late Jurassic and Early Cretaceous charophyte assemblages dominated by porocharaceans, (the family to which *Latochara* belongs), are characteristic of brackish environments (MARTÍN-CLOSAS & GRAMBAST-FESSARD, 1986; MOJON, 1989). Palaeoenvironmental factors, such as water alkalinity or salinity, may be an important factor in the palaeogeographic distribution of Mesozoic charophytes. Also, the conjoint or disjoint disposition of gametangia has to be taken into account when drawing the biogeography of fossil species. PROCTOR (1980) showed that monoecious species of extant *Chara* were cosmopolitan whilst dioecious ones were restricted to single land masses. This was found to be significant in at least one Early Cretaceous species, *Atopochara trivolis* according to MARTÍN-CLOSAS & WANG (2008).

## 5. CONCLUSION

Bone bed 148 of the Pointe de Chassiron section on Oléron Island, (Charente-Maritime, France) contains a Tithonian assemblage of *Latochara tenuicostata* and *Mesochara* gr. *voluta* that represents the southernmost occurrence of the genus *Latochara* in the Latest Jurassic-Earliest Cretaceous of Europe. This genus, which was considered by SCHUDACK et al. (1998) to be characteristic of a Boreal charophyte region, occurs beyond the southern boundary (as set by these authors at the 20°C isotherm of winter temperature) of this Boreal Region. Since all the Latest Jurassic to Earliest Cretaceous localities without *Latochara*, occur south of Oléron Island and were deposited in freshwater alkaline lakes we suggest that palaeoenvironmental factors as well as thermal boundaries were involved in the biogeographic distribution of the genus.

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## REFERENCES

- AGARDH, C.A. (1824): *Systema Algarum*. – Lundae Literis Berlingianis, Lund, 312 p.
- ANDERSON, F.W. (1941): Ostracoda from the Portland and Purbeck beds at Swindon. – *P. Geologists Assoc.*, 41, 373–384.
- ANDERSON, F.W. (1971): The sequence of ostracod faunas in the Wealden and Purbeck of the Warrlingham borehole. – In: WORSSAM, B.C. & IVIMEY-COOK, H.C.: *The stratigraphy of the Geological Survey Borehole at Warrlingham, Surrey*. Bulletin of the Geological Survey of Great-Britain, 36, 122–138.
- BARDET, N. (1995): Evolution et extinction des reptiles marins au cours du Mésozoïque. – *Paleovertebrata*, 24, 177–283.
- BENTON, M. J. (1993): *The Fossil Record 2*. – Chapman & Hall, London, 845 p.
- BILLON-BRUYAT, J.-P. (2003): Les écosystèmes margino-littoraux du Jurassique terminal et du Crétacé basal d'Europe occidentale: biodiversité, biogéochimie et l'événement biotique Jurassique/Crétacé. – Unpublished PhD thesis, University of Poitiers (France), 254 p.
- BILLON-BRUYAT, J.-P., BUFFETAUT, E. & ABIT, D. (2001): New occurrence of pterosaur remains in the latest Jurassic of Western France. – *Strata*, 1, 20–22.
- BILLON-BRUYAT, J.-P., LÉCUYER, C., MARTINEAU, F. & MAZIN, J.-M. (2005): Oxygen isotope compositions of Late Jurassic vertebrate remains from lithographic limestones of western Europe: implications for the ecology of fish, turtles and crocodylians. – *Palaeogeogr., Palaeoclim., Palaeoecol.*, 216, 359–375.
- BOURGUEIL, B., MOREAU, P., DUBREUILH, J. & VOUVÉ, J. (1976): Notice de la carte géologique de la France au 1/50 000 n°657, Île d'Oléron. – Bureau des Recherches Géologiques et Minières, Paris, 23 p.
- BOUSQUET, P. (1967): Contribution à l'étude stratigraphique et micro-paléontologique du Jurassique et du Crétacé de l'île d'Oléron (Charentes-Maritime). – Thèse de la Faculté des Sciences, Université de Paris, 180 p.
- BROIN, F. de (1994): Données préliminaires sur les chéloniens du Tithonien inférieur des calcaires lithographiques de Canjuers (Var, France). – *Geobios Mém. Spéc.*, 16, 167–175.
- BUFFETAUT, E. (1982): Radiation évolutive, paléoécologie et biogéographie des crocodyliens mésosuchiens. – *Mém. Soc. Géol. France*, 142, 1–88.
- COLIN, J.P., FEIST, M., GRAMBAST-FESSARD, N., CHERCHI, A. & SCHROEDER, R. (1985): Charophytes and ostracods from the Berriasian (Purbeckian facies) of Cala d'Inferno (Nurra Region, NW Sardinia). – *Boll. Soc. Paleontol. Ital.*, 23, 345–354.
- CORNÉE, J.-J. & BUFFETAUT, E. (1979): Découverte d'un Téléosauridé (Crocodylia Mesosuchia) dans le Valanginien supérieur du massif d'Allauch (sud-est de la France). – *C. R. Acad. Sci., Paris*, 288, 1151–1154.
- DELFAUD, J. & GOTTIS, M. (1966): Sur quelques figures de sédimentation dans le Portlandien du Lot et sur leur cadre paléogéographique en Aquitaine septentrionale. – *Actes de la Société Linnéenne de Bordeaux B7*, 103, 3–9.
- DONZE, P. (1960): Les formations du Jurassique terminal de la partie NW de l'île d'Oléron, Charente Maritime. – *Travaux du Laboratoire de Géologie de la Faculté des Sciences de Lyon*, num. spec., 5, 1–30.
- FEIST, M. & CUBAYNES, R. (1984): Découverte de Charophytes dans le Lias du Sud de la France. Implications paléoécologiques et phylogénétiques. – *C. R. Acad. Sci., Paris*, 299, ser. II, 593–596.
- FEIST, M., LAKE, R.D. & WOOD, C. J. (1995): Charophyte biostratigraphy of the Purbeck and Wealden of Southern England. – *Palaeontology*, 38, 407–442.
- GRAMBAST, L. (1962): Classification de l'embranchement des charophytes. – *Naturalia Monspeliensia, Série botanique*, 14, 63–86.
- GRAMBAST, L. (1965): État des connaissances acquises sur les charophytes du Crétacé inférieur. – *Mémoires du Bureau des Recherches Géologiques et Minières*, 34, 577–582.
- HANTZPERGUE, P. (1989): Les ammonites kimméridgiennes du haut-fond d'Europe occidentale: biochronologie, systématique, évolution, paléobiogéographie. – *Cahiers de Paléontologie, Éditions du CNRS*, 428 p.
- HANTZPERGUE, P., BOULLIER, A., COLIN, J.-P. & ABIT, D. (2004): Nouveaux repères biostratigraphiques à Terebratulidés (Brachiopodes) dans le Tithonien inférieur ouest-européen. – *Geobios*, 37, 361–375.
- HANTZPERGUE, P. & LAFaurie, G. (1994): Les calcaires lithographiques du Tithonien quercynois: stratigraphie, paléogéographie et contexte biosédimentaire. – In: BERNIER, P. & GAILLARD, C. (eds.): *Les calcaires lithographiques: sédimentologie, paléontologie, taphonomie*. *Geobios*, MS, 16, 237–243.
- HERNÁNDEZ, J.M., PUJALTE, V., ROBLES, S. & MARTÍN-CLOSAS, C. (1999): División estratigráfica genética del grupo Campoo (Malm-Cretácico inferior, SO Cuenca Vascoantabrica). – *Revista de la Sociedad Geológica de España*, 12, 277–296.
- JACQUIN, T., DARDEAU, G., DURLET, C., GRACIANSKY, P.-C. de & HANTZPERGUE, P. (1998): The North-Sea cycle: an overview of 2nd-order transgressive/regressive facies cycles in western Europe. – *SEPM Spec. Publi.*, 60, 445–466.

- JONES, T.R. (1885): On the ostracoda of the Purbeck Formation with notes on the Wealden species. – *Quarterly Journal of the Geological Society of London*, 41, 311–353.
- LANTZ, J. (1958): Étude des spores et pollens d'un échantillon purbeckien de l'île d'Oléron. – *Rev. Micropal.*, 1, 33–37.
- LAPPARENT, A.F. de & OULMI, M. (1964): Une empreinte de pas de Dinosaurien dans le Portlandien de Chassiron (île d'Oléron). – *Comptes Rendus Sommaires de la Société Géologique de France*, 61, 232–233.
- LEONHARDI, H. von (1864): Die bisher bekannten österreichischen Armleuchter-Gewächse besprochen von morphogenetischen Standpunkte. – *Verhandlungen der Naturforschende Vereins zu Brünn*, 2, 122–224.
- LINDLEY, J. (1836): *A natural system of Botany*. 2<sup>nd</sup> edition. – Longman, London, 526 p.
- LYELL, C. (1855): *Manual of Elementary Geology*. 5<sup>th</sup> edition. – Little, Brown and Co., Boston, 655 p.
- MALZ, H. (1958): Die Gattung *Macrodentina* und einige andere Ostracoden-Arten aus dem Oberen Jura von NW-Deutschland, England und Frankreich. – *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft*, 497, 1–67.
- MALZ, H. (1966): *Rectocythere rugosa*, eine neue Ostracoden-Art aus dem französischen Portlandian. – *Senckenbergiana Lethaea*, 47, 405–409.
- MÄDLER, K. (1955): Zur Taxinomie der tertiären Charophyten. – *Geologisches Jahrbuch*, 70, 265–328.
- MARTIN, G.P.R. (1940): Ostracoden des norddeutschen Purbeck und Wealden. – *Senckenbergiana*, 22, 275–402.
- MARTIN, G.P.R. (1958): *Cetacella*, eine neue Ostracoden-Gattung aus dem Kimmeridge Nordwestdeutschlands. – *Paläontologische Zeitschrift*, 32, 190–196.
- MARTÍN-CLOSAS, C. (2000): Els caròfits del Juràssic superior i Cretaci inferior de la Península Ibèrica [*Charophytes from the Upper Jurassic and Lower Cretaceous of the Iberian Peninsula* – in Catalan]. – *Arxius de les Seccions de Ciències, Institut d'Estudis Catalans*, 125, 1–304.
- MARTÍN-CLOSAS, C. (2003): The fossil record and evolution of freshwater plants. A review. – *Geologica Acta*, 1, 315–338.
- MARTÍN-CLOSAS, C. & GRAMBAST-FESSARD, N. (1986): Les charophytes du Crétacé inférieur de la région du Maestrat (Chaîne Ibérique, Catalanides, Espagne). – *Paléobiologie Continentale*, 15, 1–66.
- MARTÍN-CLOSAS, C. & SCHUDACK, M.E. (1991): Phylogenetic analysis and systematisation of post-palaeozoic charophytes. – *Revue de la Société Botanique de France*, 138, Actualités Botaniques, 1, 53–71.
- MARTÍN-CLOSAS, C. & WANG, Q. (2008): Historical biogeography of lineage *Atopochara trivolvris* PECK 1941 (Cretaceous Charophyta). – *Palaeogeography, Palaeoclimatology, Palaeoecology*, 260/3, 435–451.
- MIGULA, W. (1897): Die Characeen Deutschlands, Österreich und der Schweiz [*The Characeans of Germany, Austria and Switzerland* – in German]. – In: RABENHORST, X. (ed.): *Kryptogamic Flora*, Vol. 5. E. Kummer, Leipzig, 1–765.
- MOJON, P.O. (1989): Polymorphisme ecophénotypique et paléocécologie des Porocharacées (Charophytes) du Crétacé Basal (Berrisien) du Jura Franco Suisse. – *Rev. Paléobiol.*, 2, 505–524.
- MOJON, P.O. (2002): La lignée phylogénétique des *Hemiglobator* nov. gen – *Globator* (Clavatoracées, Charophytes) du Jurassique terminal – Crétacé inférieur de l'Europe et de l'Afrique nord-occidentale. – *Archives des Sciences Genève*, 55, 33–45.
- PALAMAREV, E. (1971): Fossile Charophyten aus der Unterkreide Nordbulgarischens. – *Mitteilungen des Botanischen Instituts*, 21, 145–159.
- PECK, R.E. (1937): Morrison Charophyta from Wyoming. – *J. Paleontol.*, 11, 83–90.
- PECK, R.E. (1957): North American Charophyta. – *Geol. Surv. Prof. Paper*, 294 A, 44 p.
- PINTO, I. & SANGUINETTI, Y. (1962): A complete revision of the genera *Bisulcocypris* and *Theriosynoecum* (ostracoda) with the world geographical and stratigraphical distribution. – *Escola de Geologia de Porto Alegre, Publ. Esp.*, 4, 1–165.
- PROCTOR, V.W. (1980): Historical biogeography of *Chara* (Charophyta) an appraisal of the Braun-Wood classification plus a falsifiable alternative for future consideration. – *J. Phycol.*, 16, 218–233.
- RIEPEL, O. (1980): The skull of the Upper Jurassic cryptodire turtle *Thalassemys*, with a reconsideration of the chelonian braincase. – *Palaeontographica Abt. A*, 171, 105–140.
- ROEMER, F.A. (1839): Die Versteinerungen des norddeutschen Oolithengebirges. – Hahn, Hannover.
- RUSCIADELLI, G. (1999): Stratigraphie séquentielle et analyse de l'espace disponible du Jurassique supérieur et du Crétacé inférieur du Bassin de Paris. – *Atti Ticinensi di Scienze della Terra, Serie Speciale* 8, 3–83.
- SCHNYDER, J. (2003): Le passage Jurassique/Crétacé: événements instantanés, variations climatiques enregistrées dans les faciès turbécien français (Boulonnais, Charentes) et anglais (Dorset). Comparaison avec le domaine téthysien. – Thèse de 3<sup>me</sup> cycle, Universités de Lille 1 et Paris 6, 389 p.
- SCHUDACK, M. (1990): Bestandsaufnahme und Lokalisation der Charophyten aus dem Oberjura und Unterkreide des Nordwestdeutschen Beckens. – *Berliner Geowissenschaftliche Abhandlungen (A)*, 124, 209–245.
- SCHUDACK, M.E. (1993): Die Charophyten im Oberjura und Unterkreide Westeuropas. Mit einer phylogenetischen Analyse der Gesamtgruppe. – *Berliner Geowissenschaftliche Abhandlungen (A)*, 8, 209 p.
- SCHUDACK, M.E. (1996): Ostracode and charophyte biogeography in the continental Upper Jurassic of Europe and North America as influenced by Plate Tectonics and paleoclimate. – In: M. MORALES (ed.): *The Continental Jurassic*. Museum of Northern Arizona Bulletin, 60, 333–341.
- SCHUDACK, M.E., TURNER, C.E. & PETERSON, F. (1998): Biostratigraphy, paleoecology and biogeography of charophytes and ostracodes from the Upper Jurassic Morrison Formation, Western interior, USA. – *Modern Geology*, 22, 379–414.
- SHADKIN, I.M. (1967): *Fossil Charophyta of Upper Jurassic Deposits of the Dnieper-Donetz Depression*. – In: *Fossil Algae of the USSR*. IZDAT Nauk SSSR, 43–47 [in Russian].
- SIRNA, G. (1968): The Lower Cretaceous Charophyta and the Paleogeography of Mediterranean basin. – *Atti Accademia Nazionali Lincei (Rendiconti della classe di Scienza fisiche, matematiche e naturali)*, Serie 8, 44, 566–573.
- SMITH, G.M. (1938): *Botany*. Vol. I, Algae and Fungi. Charophyceae. – McGraw Hill, New York, 127 p.
- STEGHAUS, H. (1953): Über die Möglichkeit einer Gliederung des Weiss-Jura von Dalum. – *Berliner Naturforschung Gesellschaft*, 42, 39–46.
- THIERRY, J. (2000): Early Tithonian (141–139 Ma). – In: CRASQUIN, S. (ed.): *Atlas Peri-Tethys, Palaeogeographical Maps-Explanatory Notes*. CCGM/CGMW, Paris, 99–110.

- VULLO, R. (2001): Étude d'un niveau de type „bone-bed“ dans le Tithonien (faciès purbeckien) de Chassiron (île d'Oléron, Charente-Maritime, France. – Mémoire de Maîtrise, Université de Poitiers (France), 20 p.
- WIENHOLZ, E. (1968): Ostracodenfaunen der Jura/Kreide-Grenzschichten im Norden der Deutschen Demokratischen Republik. – Berichte der Deutschen Gessellschaft für Geologische Wissenschaften, A, 13, 233–238.
- WOLBURG, J. (1962): Die leitenden Ostracoden des nordwestdeutschen Wealden. – In: SIMON, W. & BARTENSTEIN, H.L. (eds): Leitfossilien der Mikropaläontologie. Gebrüder Borntraeger, Berlin, 204–224.

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