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* (HERNANDEZ et al., 1999; MARTÍN-CLOSSAS, 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 PALAEOONTOLOGICAL 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 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 (HANZ- 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 Cypris forbesii (JONES, 1885), Theriosynocym aff. forbesii (JONES, 1885), Theriosynocym 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 Dicryoptygma, Aciocythera? and Cytheropterina.

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, chondrichthyans and osteichthyans from this bed was carried out by CORNÉE & BUFFETAUT, 1979; BENTON, 1993; BARDET, 1995). A margino-littoral depositional environment is consistent with the composition of the tetrapod fauna. Pleurochelyids and telesaurids 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 crocodylians), terrestrial (atoposaurid crocodylians, 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 PALAEONTOLOGY

Division Charophyta Migula, 1897
Class Charophyceae Smith, 1938
Order Charales LINDLEY, 1836
Family Nitellaceae von LEONHARDI, 1864
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 sub-spherical to ellipsoidal. Length ranges 351–432 μm (average 404 μm), including the neck. Width ranges 270–351 μm (average 312 μm). 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.

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 mm average length (*L. mensinki* SCHUDACK, 1990 and *L. bel-latula* PECK, 1957) or larger, i.e. more than 500 mm average length (*L. sphaerica* PECK, 1957 and *L. durand-delgai* FEIST 1984) and will be 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 SHAĐKIN (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 (sublat 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.

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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.
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. 16–19
1957 Praechara voluta (PECK) – PECK, p. 39, pl. 7, figs. 7, 22–27
1965 Mesochara voluta (PECK) nov. comb. – GRAMBAST, p. 581
Material: Six gyrogonites from sample 148b.
Description: The gyrogonite is small, 270–350 μm in high and 240–300 μm 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 μm high. Apex closed by simple junction of spiral cells. Base shows a pentagonal pore with a maximum diameter of about 50 μm. 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 SHAĐKIN (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.

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 metangia 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 trivolvis 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 *Mesochora* 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 SCHUDDACK 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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