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Ostracoda (marine/nonmarine) and palaeoclimate history in the Upper Jurassic of Central Europe and North America

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Abstract

The role of Ostracoda in determining climate developments in the Upper Jurassic of Central Europe and North America is reviewed, based upon two different studies. The Late Jurassic is a period of time for which a change from a humid to a more arid climate has been suggested for several parts of the world. However, a correlation, though almost logical, between the arid phase in the middle and late Tithonian and a generally cooler climate, combined with a sea-level lowstand and lower water temperatures, has only been demonstrated in very few papers. This study intends to seeks palaeoclimatic evidence for the Late Jurassic by the use of Ostracoda. Development of marine ostracod palaeobiogeography in Central and Western Europe parallels a suggested cooling trend. During the Oxfordian, Kimmeridgian, Tithonian, and Berriasian, a growing diversification of marine ostracod biogeography and an increase in the degree of endemism can be observed. In addition, there is a gradual southward migration of many species from the subboreally influenced areas in the northwest towards the margin of the Tethys in the southeast, mainly from the Kimmeridgian into the Tithonian. Moreover, the genus *Cytherelloidea*, which has a long tradition (despite some recent contradictions) as an indicator for relatively warm water temperatures, shifts its northern boundary of occurrence towards the south during the Kimmeridgian, Tithonian, and Berriasian. This occurs independently from the general change of facies, because conditions principally suitable for *Cytherelloidea* (salinity, water depth) have at times also existed in some northern basins during the Tithonian/Berriasian. These data are in correspondence with a suggested increase in the influx of cold boreal waters into central Europe with the beginning of the Tithonian, leading to slightly colder water temperatures in the shallow seas, reduced atmospheric moisture, cool-arid conditions on the neighbouring continents, and also to the diversification of biogeographic regions as a reaction to the conflicting boreal (increased) and Tethyan (still steady) influences. For the Kimmeridgian/Tithonian nonmarine Morrison Formation in the Western Interior Basin, USA, both temporal and latitudinal trends from warm climates in the south and near the base of the formation to slightly cooler climates in the north and in the upper parts of the sections have been detected on the basis of the charophyte floras. Monospecific δ^{18}O isotope data from charophytes and ostracods have revealed a trend towards lighter compositions towards the top of the formation. This might be interpreted as a general cooling, but other interpretations must also be discussed. From preserved vital effects and δ^{18}O/δ^{13}C plots of charophyte/ostracod associations showing coherent groupings similar to those from modern lakes, it is likely that the calcite shells have preserved a high degree of isotopic fidelity. Different scenarios to explain the observed patterns are

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discussed. A global change towards colder temperatures and arid conditions near the end of the Jurassic period is in good correspondence with all the results. More local factors, however, would also be able to explain the data.

Keywords: Ostracoda; Upper Jurassic; palaeoclimate; palaeobiogeography; isotope geochemistry; North America; Central Europe

1. Introduction

The Late Jurassic is a period of time for which very different trends in palaeoclimate have been suggested in the last decades. The former general consensus that the climates of the Jurassic were more equable than today, without polar ice caps and with cold-intolerant organisms extending over a wider range of latitudes (Hallam, 1985), however, has more recently been called into question (Crowley and North, 1991; Hallam, 1994). Concerning the two major climatic parameters, temperature and precipitation, the following conflicting views have been published: Vakhrameev (1991) detected a northward shift of Eurasian latitudinal floral provinces from the mid- to the Late Jurassic. Continuation of this trend would mean a slight warming through the Late Jurassic. Faunal distributions, as summarized by Hallam (1994) provide a more uniform distribution for many vertebrate groups, whereas others such as ammonites, belemnites, hermatypic corals, dasycladaceans etc. show the well known subdivision into the Boreal and Tethyan realms. Their interpretation as a palaeoclimatic differentiation (boreal = cold, tethyan = warm), however, is still under discussion (Doyle, 1987; Hallam, 1984a, 1994). The southward shift of the boundary between the two realms from the Bathonian to the Tithonian, interpreted as a reaction to climate change, would correlate with a general trend towards cooler water temperatures during the Late Jurassic as suggested in this paper. A slight cooling trend would obviously oppose the one observed by the palaeobotanists (Vakhrameev, 1991), but the idea is supported by a marked fall of estimated CO_2 from around four times the present value at the beginning of the Late Jurassic to about three times that value at the Jurassic–Cretaceous boundary (Berner, 1991). The slight lowering of the greenhouse effect caused by lowering concentrations of carbon dioxide in the atmosphere would correlate with the suggested cooling trend.

Aridity was reported to be higher in the Late Jurassic than during the earlier periods of the Jurassic on the basis of the palaeobotanical and sedimentary record. In Europe, Early and Middle Jurassic climates have largely been interpreted as humid (Hallam, 1984b). The onset of arid conditions, as detected by clay mineralogy, was diachronous, beginning earlier in Southern Europe (Oxfordian–Kimmeridgian), and later in northwestern Europe (early Tithonian; Wignall and Ruffell, 1990; Wignall and Pickering, 1993; Ruffell and Rawson, 1994), with a maximum in the early Berriasian (Hallam et al., 1991). Hallam (1984b, 1994) interpreted the Late Jurassic spread of arid conditions as an orographic effect, caused by the Cimmeride mountain collision with Eurasia. This would account for the aridity further east, but leaves the question open, why “western European landmasses enveloped by the sea should be similarly affected” (Hallam, 1994). A correlation, though almost logical, between the arid phase in the middle and late Tithonian and a generally cooler climate, combined with a sea-level lowstand and lower water temperatures, has only been demonstrated in very few papers (Ruffell and Rawson, 1994). It is the first of two major objectives of this paper to examine this idea by use of ostracod palaeobiogeography.

The second main objective of this paper is an examination of whether, and to what degree a change of climate occurred in the Late Jurassic of the U.S. Western Interior Basin, and to assess the utility of fossil ostracods for that purpose. In this continental basin, the nonmarine Morrison Formation, famous for its rich dinosaur fauna, was deposited during the Kimmeridgian and early Tithonian (Fig. 5; Schudack et al., 1998; Litwin et al., 1998). The formation represents, according to the latest argon isotope data, a time span of about 7–8 million years (Kowallis et al., 1998). Climatic interpretations for the Morrison ecosystem range from wet to dry, depending on the indications used and the area and stratigraphic unit under study (see Dodson et al., 1980, for a review). The point is that there is not just one climate for the Morrison, as some earlier workers have claimed, but rather a variety of very different climates depending on the time level (7–8 million years!) and local area (2000 km south-to-north!) at issue. Therefore, more recent interpretations have mostly dealt with limited depositional times, but results are still conflicting: The climate during deposition of the Brushy Basin Member (upper Morrison) was arid according to Turner and Fishman (1991), but humid according to Fiorillo and McCarty (1996). Aridity/humidity trends in time have only rarely been suggested and vary from a trend towards more humid conditions to a trend towards more arid conditions in the upper part (see Dodson et al., 1980, for a review). Schudack (1995), by examination of the percentages of cold water vs. warm water charophyte genera, has detected both a N–S gradient, in the sense of a latitudinal climatic zonation within the basin, and a trend in time towards slightly colder lake waters and therefore also colder air temperatures in later Morrison depositional times (i.e. Tithonian). Such a cooling trend would parallel the suggested development in Europe. The oxygen isotopes of ostracod shells from long-ranging species and out of complete sections of the Morrison Formation have been studied in order to provide more information for these questions.

2. Areas, methods and material studied

This paper is based on two independent studies: (1) an analysis of the diversification of palaeobiogeography of marine Ostracoda during the Late Jurassic (Oxfordian, Kimmeridgian, and Tithonian) in Central and Western Europe (Fig. 3); and (2) stable oxygen isotope analyses of calcite shells of nonmarine Ostracoda from the Morrison Formation (Kimmeridgian and early Tithonian) in the U.S. Western Interior (Fig. 4).

The palaeobiogeographic analyses (see Section 3) uses two different approaches: (1) phenetic biogeography, which emphasizes use of similarity coefficients or other quantitative techniques as applied to whole-fauna comparisons (Newton, 1990); and (2) a taxonomic and functional approach which uses ecologies known from modern relatives or derived from functional morphology. Palaeobiogeographic distributions of Late Jurassic marine Ostracoda in Central and Western Europe have been studied by Glashoff (1964) for the Oxfordian and by Christensen and Kilenyi (1970) for the Kimmeridgian and Tithonian (p.p.) stages. More detailed and comprehensive studies for the complete Late Jurassic sequences have been published by Schudack and Schudack (1995). Recent revisions of Late Jurassic ostracod faunas from the Aquitaine Basin, southern, northwestern und northeastern Germany and Moravia by Schudack (1994, 1997 and papers in prep.) have allowed even more refined biogeographic analyses on the basis of a largely updated database. It contains all published and self-detected occurrences of marine Ostracoda in 15 separate European areas (see Fig. 3) for the four successive stages Oxfordian, Kimmeridgian, Tithonian, and Berriasian and can be used for computerized calculations and graphic output (Schudack and Schudack, 1997). The biogeographic summary (Fig. 1) is currently based on the calculations of five similarity indices (Jaccard, Johnson, Simpson, Sörenson and a new one, see Newton, 1990; Schudack and Schudack, 1997) between the 15 areas and the occurrences of 122 Oxfordian, 174 Kimmeridgian, and 121 Tithonian species.

Oxygen stable isotopes ($^{16}O/^{18}O$) have been analysed from the calcite shells of two stratigraphically long-ranging ostracod species from two measured sections in the Morrison Formation of Utah (Dinosaur National Monument) and Colorado (Owl Canyon). For location and subdivision of the sections and the biostratigraphy of the Morrison Formation see Schudack et al. (1998). The samples may represent about 5–6 million years, which is from well in the Kimmeridgian into the Tithonian (Fig. 5). They have been processed by K. Conrad at the U.S.G.S. micropalaeontological laboratory by the standard method used there, mainly dry-freeze and glauber salt, which largely avoids the use of hydrogen peroxide and its dubious influence on the calcite oxygen isotope composition. Picked ostracod valves have been mechanically cleaned from sedimentary residues and sparite fillings. Stable isotope measurements were carried out at the Alfred Wegener Institute (AWI) Stable Isotope Laboratory, Bremerhaven, by A. Mackensen and his team using a Finnigan MAT 251 mass spectrometer coupled to an

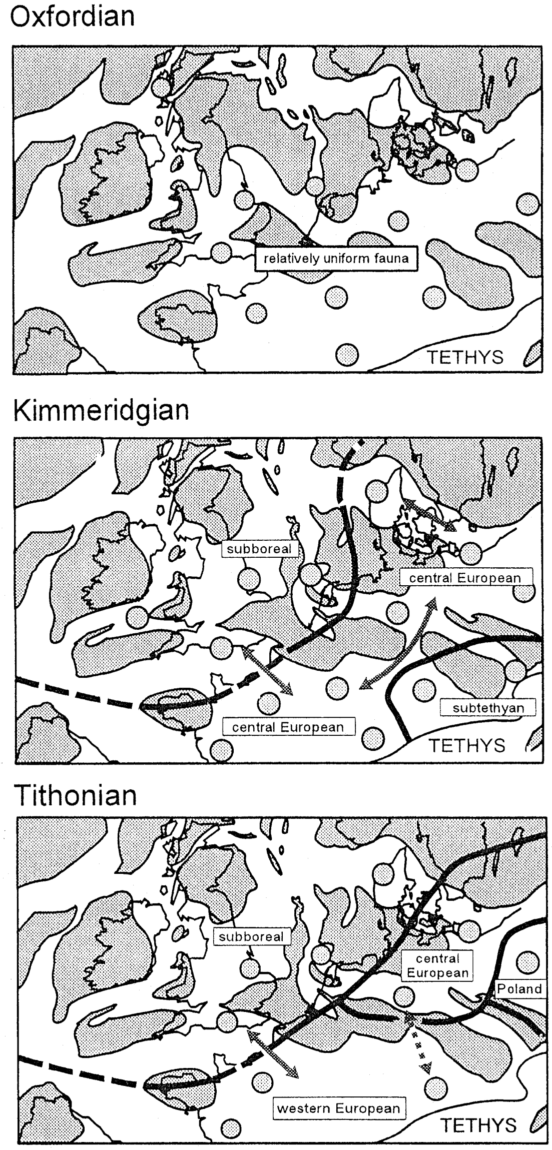

Fig. 1. The differentiation of marine ostracod palaeobiogeography during the Late Jurassic in Central and Western Europe. Black lines = subprovince boundaries; grey arrows = intensive faunal exchange. For an explanation of the areas compared in this study (grey circles) see Fig. 3. Palaeogeography modified after Ziegler (1990).

automatic carbonate preparation. Data were related to the PDB standard (Pee Dee Belemnite).

Kimmeridgian in this report follows international usage in which the Kimmeridgian stage is succeeded by the Tithonian Stage. The Kimmeridgian of international terminology does not include the upper Kimmeridgian of British terminology, which has the Kimmeridgian stage succeeded by the Portlandian Stage.

3. Palaeoclimate changes in the Late Jurassic–earliest Cretaceous of Central and Western Europe

3.1. The palaeobiogeography of Late Jurassic and Berriasian marine Ostracoda

During the Late Jurassic, a growing diversification of marine ostracod biogeography and an increase in the degree of endemism can be observed, from a rather uniform fauna in the Oxfordian to a differentiation into three subprovinces in the Kimmeridgian, however, still allowing intensive faunal exchange, up to the four distinctive subprovinces in the Tithonian (Fig. 1). In the general development, there is an increase in provincialism and a decrease in overall faunal similarities between the 15 separate basins under study (Fig. 3). The average of all the similarity indices calculated between all the 15 areas is 0.194 for the Oxfordian, 0.155 for the Kimmeridgian, and 0.133 for the Tithonian, which clearly underlines the increasing diversification. Moreover, in areas with an almost complete marine succession, such as southern Germany, the observed differentiation correlates with: (1) an increase in simple species diversity (i.e. number of species per stage; (2) an increase in the number of endemic species; and (3) an increase in the number of short-living species. In southern Germany, for instance, we have described 17 Oxfordian species, 20 Kimmeridgian species, and 23 Tithonian species (Schudack and Schudack, 1997).

In addition, there is a gradual southward migration of many shallow-water ostracod species from the subboreally influenced areas in the northwest towards the margin of the Tethys in the southeast, mainly from the Kimmeridgian into the Tithonian. This phenomenon can best be studied by direct comparison of the stratigraphic ranges of species in northwest and southern Germany. Of the 15 species occurring in both areas, 12 appear earlier (FAD) and/or disappear earlier (LAD) in the Lower Saxony Basin than in southern Germany (Schudack and

Schudack, 1997). This fact, among others, refers to all the species of the warm water genus *Cytherelloidea* (see Section 3.2). Stratigraphic control on these correlations is by ammonite biostratigraphy (Zeiss, 1977; Ziegler, 1977; Gramann et al., 1997). Similar trends can be observed in comparisons with other basins such as the Paris Basin or the Baltic Sea area p.p. (i.e. northeastern Germany).

3.2. The genus Cytherelloidea as an indicator for relatively warm water temperatures

The ostracod genus *Cytherelloidea* has a long tradition as an indicator for relatively warm water temperatures. According to Sohn (1962, 1964), the distribution of living species of *Cytherelloidea* is bounded roughly by the latitudes 40°S and 37°N, which is the oceanic zone where surface and shallow waters never cool down to monthly mean temperatures of below 10°C. This author has also provided arguments for the use of the genus as an indicator for warm water temperatures in the Late Cretaceous, from taxonomic (association with certain Foraminifera), oxygen stable isotope, and biogeographic studies (see below). The genus has since then widely and successfully been used for that purpose (see, for instance, Whatley, 1996).

Recently, however, there has been some contradiction of his biogeographic conclusions (e.g. unpublished talk by N. Johnson at the 12th Int. Symp. Ostr. in Prague, 1994), with arguments mainly from the spatial distribution of the genus during the Late Cretaceous. In the Late Jurassic and earliest Cretaceous of Europe, however, *Cytherelloidea* appears to work well as a warm-water indicator. The genus shifts its northern boundary of occurrence towards the south during this period of time (Fig. 2), paralleling the trend towards cooler waters suggested by several authors (see Section 1) and supported by other arguments within this paper. This occurs independently from the general change of facies, because ecological conditions principally suitable for *Cytherelloidea* have in times also existed in some northern basins during the Tithonian and Berriasian.

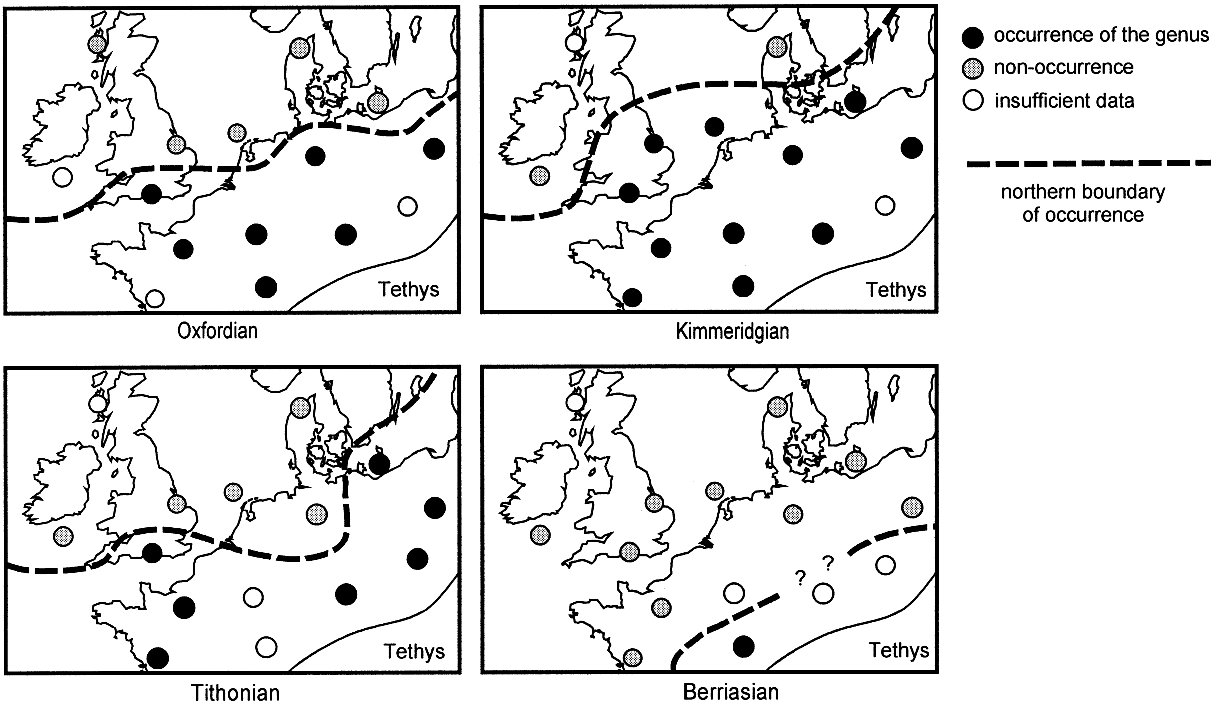

Fig. 2. The southward migration of the thermophilic genus *Cytherelloidea* during the Late Jurassic and earliest Cretaceous. For an explanation of the areas compared in this study (circles) see Fig. 3.

However, *Cytherelloidea* has not been observed so far to the north during these stages, a fact which confirms the preference of the genus for relatively higher water temperatures.

In addition to the spatial distribution, there are also some arguments from functional morphology. *Cytherelloidea* belongs to the filter-feeding Platycopida which have a survival advantage in times of reduced oxygen (Whatley, 1995). This is because ostracods with this feeding strategy pass more water over their respiratory surfaces than those with other alimentary strategies (Whatley, 1996). According to the rules of physics, there is less oxygen in warmer than in colder water, in the very simplified case. Therefore, *Cytherelloidea* should be more competitive in warmer waters. In nature, however, things are much more complicated, because increased oxygen production due to photosynthesis of marine plants in the upper 10–20 m of warm seas also has to be considered (Pickard and Emery, 1996). Below this zone, however, but still on the shelf and thus within a depth where many *Cytherelloidea* have lived (down to about 100 m after Sohn, 1962), but well above the Oxygen Minimum Zone (OMZ), dissolved oxygen is negatively correlated with water temperature. This correlation roughly parallels the distribution of modern *Cytherelloidea* species. Therefore, oxygen dissolution rather than water temperature might be one out of several true controlling factors for their distribution.

Cytherella, another genus of the filter-feeding Platycopida, is much more cold-water tolerant than *Cytherelloidea*. Species of this genus dominate the OMZ in modern oceans at a depth of about 1000 m, which consists of water masses considerably colder than those in the upper 100–200 m, and they also dominate the sediments (black shales and others) deposited during fossil kenoxic events (Whatley, 1995, 1996). This fact does not necessarily contradict the thermophylly of *Cytherelloidea* because (1) the oxygen minimum is not yet fully understood and still requires a full explanation (Pickard and Emery, 1996), and (2) independently from the temperature of the water *Cytherella* and *Cytherelloidea* live in, low oxygen conditions are one of the main controlling factors for the distribution of both filter-feeding platycopids. The point is that *Cytherelloidea* only lives in warm shallow seas where dissolved oxygen and water temperature are negatively correlated (except for the upper 10–20 m, see above), whereas *Cytherella* also tolerates colder water temperatures, but has the same survival advantage in times of reduced oxygen typical for the whole group.

The above-summarized arguments and observations support further use of *Cytherelloidea* as a thermophilic genus and interpretation of their southward migration during the Late Jurassic as an indication for a trend towards cooler water temperatures.

3.3. Interpretation of the palaeobiogeographic patterns: palaeoclimate and ocean currents

The data and trends described in the last paragraphs can principally be explained by very different controlling factors such as plate tectonics, sea-level changes (eustatic or regional), changes in the system of ocean currents, climate change and differentiation, regional tectonics, combined with the closure of marine corridors, the rise of physical barriers, and a drastic change in sedimentary facies and ecology. All these factors may be combined in different ways. In the following, I will confine myself to the relationships with palaeoclimate, though this is, of course, only one possible explanation and only one aspect of a very complex story.

The biogeographic differentiation and southward migration of many species are in correspondence with an increase in the influx of cold boreal waters into Central Europe with the beginning of the Tithonian suggested in this paper. A possible reason for this suggested change in the ocean current system is that, during the Late Jurassic, the Proto-North Atlantic slowly began to open (Fig. 3; Ziegler, 1988). Deep-water sedimentation started in the Bay of Biscay and its northward prolongations through the Rockall Rift (west of Scotland) up to the area west of Norway (Ziegler, 1988, 1990). Tithonian calpionellid limestones, as part of these sequences, indicate the influence of warm Tethyan surface waters in the Bay of Biscay (Boillot et al., 1971, 1979). Perhaps, a northward current of warm Tethyan (surface?) waters through the Proto-North Atlantic was established, at least in the Tithonian (Fig. 3). Such a palaeocurrent, however, would appear to give a water mass balance problem in the area between Norway and Greenland.

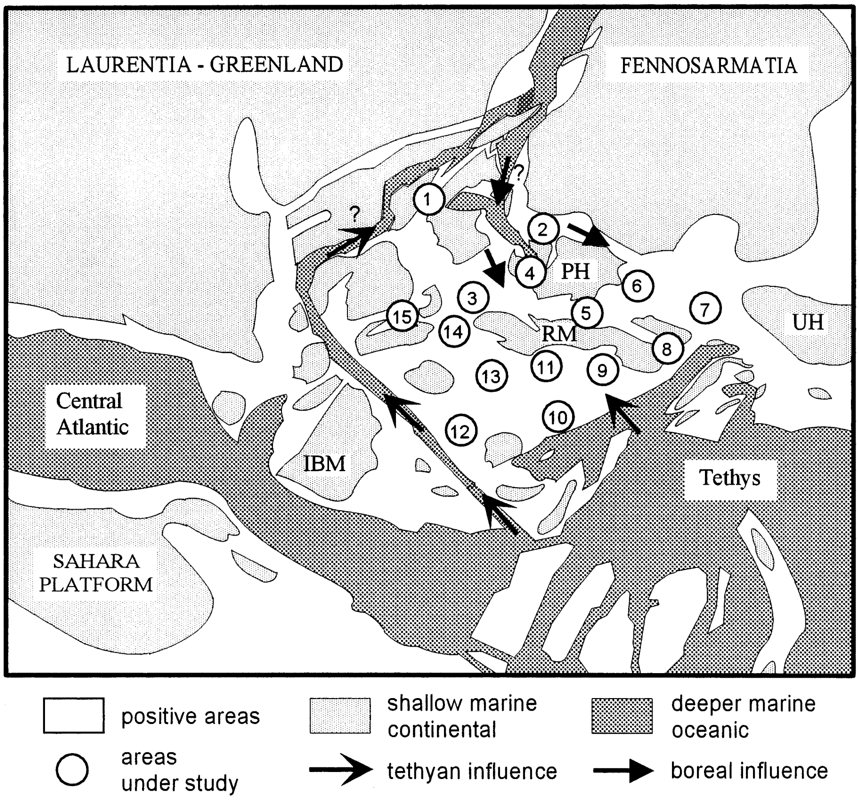

Fig. 3. Palaeogeographic and plate tectonical setting of Central and Western Europe between the conflicting boreal and tethyan influences (based upon the Oxfordian–Tithonian map of Ziegler, 1988). The areas compared in this study are: Scotland (*1*), Danish Embayment (*2*), eastern England (*3*), Dutch Central Graben (*4*), Lower Saxony Basin (*5*), Baltic Sea Basin (*6*), central Poland (*7*), Moravia (*8*), southern Germany (*9*), French and Swiss Jura (*10*), Lorraine (*11*), Aquitaine Basin (*12*), Paris Basin (*13*), southern England (*14*), Celtic and Fastnet basins (*15*). *IM* = Irish Massif; *IBM* = Iberian Meseta; *PH* = Pompeckj High; *RM* = Rhenish Massif; *UH* = Ukrainian High.

A possible reaction to that problem was an increased influx of cold boreal surface waters from the north into Central Europe, which would have caused slightly cooler water temperatures in the shallow seas of the northern part of the area under study (Fig. 3, North Sea area, England, Baltic Sea area, also Central Europe later in the Tithonian). This, possibly amongst other reasons, led both to the higher palaeobiogeographic diversification and provincialism (Fig. 1), due to the increased temperature gradient between the conflicting boreal (increased) and tethyan (still steady) influences, and the southward migration of many species (Fig. 2).

The proposed change of ocean currents is in good correspondence not only with the observed differentiation of marine ostracod palaeobiogeography and the southward migration of many species, but also with a climate change from humid (Oxfordian, Kimmeridgian, and early Tithonian) to arid (late Tithonian and Berriasian) in Central and northwestern Europe (Wignall and Ruffell, 1990; Wignall and Pickering, 1993; Ruffell and Rawson, 1994), based upon the weathering regime and runoff on the landmasses, clay mineralogy, and architecture of sedimentary sequences. The slightly colder water of the late Tithonian and Berriasian, as compared to the earlier stages, gave rise to reduced atmospheric moisture, both by reduced evaporation from the sea and the fact, that cold air holds less atmospheric moisture. Cool-arid conditions on the neighbouring continents, as observed by the above-mentioned authors, are the logical consequence of such a scenario. Climate and ocean current change is most probably not the only reason for the described biogeographic developments, but they are certainly among the main factors in a complex story.

4. Palaeoclimate changes in the Kimmeridgian/Tithonian of the U.S. Western Interior (Morrison Formation)

The Kimmeridgian/Tithonian Morrison Formation represents one of the best preserved Mesozoic nonmarine ecosystems. It is distributed throughout much of the Western Interior physiographic province of the United States (Fig. 4). The "Morrison Formation Extinct Ecoystems Project", coordinated by C.E. Turner and F. Peterson (U.S. Geol. Surv., Denver), is a multidisciplinary effort to interpret this ancient ecosystem, of which climate, of course, is an important factor. During recent decades, the nature of Morrison climates have been very controversial (see Section 1). A change of clay mineralogy, which has been shown to occur throughout most of the sedimentary basin, has recently pointed to a more arid climate in the upper part than presumed so far (Turner and Fishman, 1991; Schudack et al., 1998). These data are in coincidence with the Late Jurassic trend from humid to arid conditions observed in Europe (see Section 3.3), but there were no publications yet suggesting that this development would also parallel a slight cooling of the air and lake water temperatures in the Morrison depositional basin. To find indications for these questions, besides the biostratigraphic subdivision, age determination, and ecological (i.e. salinity) interpretation, I have studied nonmarine Ostracoda and charophyte algae from 22 measured sections in 7 US states (detailed locations in Schudack et al., 1998).

4.1. The taxonomic approach

Statistical analysis of 132 associations of ostracods and charophytes from the Morrison Formation was undertaken to contribute to the questions, if there was evidence (1) for the observed development towards more arid conditions, and/or (2) for a cooling trend, both in time (7–8 million years) and space (2000 km north-to-south). For the first purpose, Morrison ostracod and charophyte genera have been classified according to their relative salinity tolerance (for a summary of these see Schudack, 1993), and their relative percentages calculated for the five successive local biozones of Schudack et al. (1998) and for three latitudinal belts (Schudack, 1995). The idea was that the more arid the climate was, the more often lakes in which these organisms lived would evaporate a greater amount of their water, which would possibly lead to increased salinities in the course of a year or other periods of time. Unfortunately, no clear trend was apparent with this approach, both in time and space.

The stratigraphic distribution of (relatively) cold

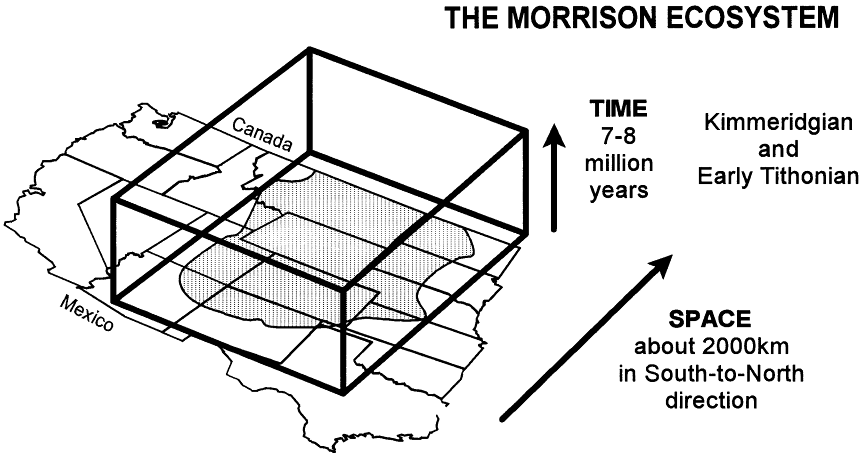

Fig. 4. Position of the Morrison ecosystem in time (7–8 million years) and space (about 2000 km in S–N direction. Present outcrop distribution of the Morrison Formation (dashed area) in 12 U.S. states.

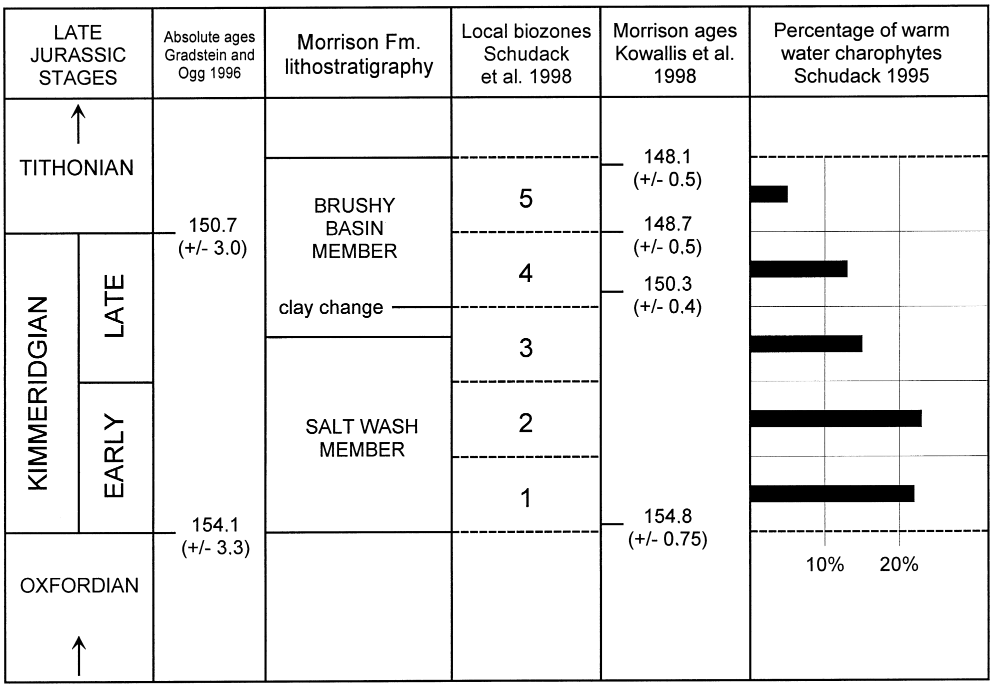

Fig. 5. Decrease in the percentages of (relatively) warm water tolerant charophyte genera within Morrison depositional times (from Schudack, 1995). Local biozones and correlation with Late Jurassic stages from Schudack et al. (1998). Late Jurassic time scale from Gradstein and Ogg (1996). New absolute ages of Kowallis et al. (1998) would possibly (if the boundary ages of Gradstein and Ogg are exact) allow latest Oxfordian ages for the base of the formation and earliest Tithonian ages for local biozone *4*.

water tolerant towards (relatively) warm water tolerant charophyte genera, however, shows a clear trend from warmer waters in the lower part to colder waters in the upper part of the formation (Fig. 5). This can be interpreted as a general trend towards colder atmospheric temperatures because water temperatures in the shallow ponds and littoral zones of lakes in which these plants have lived have certainly been in close correspondence with air temperatures. Such an attempt was not made with nonmarine ostracods because there is yet insufficient knowledge about their temperature tolerance. Among charophytes, a N–S trend, in the sense of a latitudinal climatic zonation within the basin, is even more evident (Fig. 6) and supports the use of the relevant charophyte genera as 'cold' or 'warm' water tolerant.

Biogeographic patterns of ostracod and charophyte species in the continental Upper Jurassic of North America and Europe are significantly different (Schudack, 1996). Distribution of the two ostracod superfamilies Cypridacea and Cytheracea corresponds well with the possibilities allowed by their respective dispersal strategies (see Whatley, 1990, 1992, for a summary) and the palaeogeographic and plate tectonic situation (Ziegler, 1988).

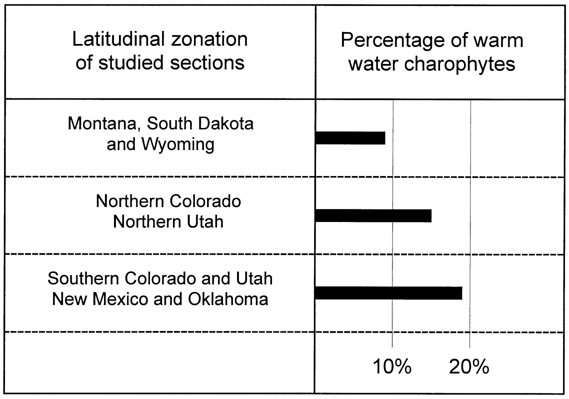

Fig. 6. Decrease in the percentages of (relatively) warm water tolerant charophyte genera from south to north within the Morrison depositional basin (data from Schudack, 1995).

Many cypridacean species crossed the faunal barrier of the Bay of Biscay Rift and the Proto-North Atlantic into Central Europe due to their favourable dispersal strategies (e.g. desiccation- and freeze-resistant wind-blown eggs), whereas among nonmarine Cytheracea, having less favourable dispersal strategies, Morrison species only occurred on the Iberian Peninsula (Schudack, 1996). Iberia was close to North America, only separated by shallow seas, but separated from Western and Central Europe by a more open extent of the deep sea. Migration of nonmarine cytheracean species by means of non-flying animals was hindered by the Bay of Biscay Rift and Proto-North Atlantic. In addition, there is a minor correlation of the general nonmarine ostracod distributional pattern with the simulated winter total precipitation for the Kimmeridgian (Valdes, 1994): the closely related Morrison and Iberian ostracod faunas lived in areas with low winter precipitation rates, the northwestern and Central European ostracod faunas in areas with high winter precipitation rates and thus fewer ephemeral lakes.

In contrast, Morrison charophyte floras, as a whole, are part of a northern flora preferring relatively cold waters when compared with floras of the European continent. However, palaeolatitudinal correlation between Europe and the Western Interior cannot fully explain these similarities. Due to its continental setting, winter temperatures in the Western Interior Basin were lower than in western European areas of the same palaeolatitude (Moore et al., 1992a,b; Valdes and Sellwood, 1992; Valdes, 1994), and therefore, charophytes even from the southern parts of the Western Interior are closely related to European counterparts of higher palaeolatitudes.

4.2. The oxygen stable isotope approach

In order to test the assumption of a general decrease of atmospheric temperatures during the 7–8 million years duration of the Morrison ecosystem, oxygen stable isotope geochemistry ($^{16}O/^{18}O$) has been applied to the calcite of ostracod valves and charophyte gyrogonites. Ostracods are generally considered to calcify near to equilibrium with the lake water chemistry and thus can serve as sensitive palaeoenvironmental tracers (Lister, 1988). Application of the method to charophyte gyrogonites has only been carried out in very few pioneer projects so far (Berger, 1989, 1990; Forester and Whelan, 1999).

Two monospecific series from the Dinosaur National Monument section (Utah), analyzing the ostracod species *Bisulcocypris pahasapensis* and *Cetacella* sp. (Fig. 7), and two monospecific series from the Owl Canyon Section, analyzing the ostracod species *Bisulcocypris pahasapensis* and the charophyte species *Aclistochara bransoni*, have all shown a general trend towards lighter oxygen isotope compositions towards the top of the formation (for position of the sections see Schudack et al., 1998). A fifth set of samples, using just charophyte gyrogonites from very different species and genera, shows no clear trend at all.

4.2.1. On the fidelity of the isotope signals from Morrison samples

In formations as old as the Jurassic, possible alteration of the original isotope signal by subsequent diagenesis is always an important question. Therefore, fidelity and originality of the signal has to be evaluated prior to an interpretation of the isotope data. Among the various methods used for this purpose, four have been applied to the material:

(1) Preservation of the original ultrastructure of calcite shells is one of the major points. In the Morrison material, preservation is of varying quality, but mostly very good. In particular the charophyte gyrogonites show the whole variety of ultrastructures known from their modern counterparts (Schudack, 1993).

(2) Vital effects are demonstrated by the described phenomenon that all the monospecific sample series show the same trend towards lighter oxygen compositions (e.g. Fig. 7), whereas the series consisting of different genera shows no trend at all. It must be suggested that if major diagenesis had affected the material, the isotope signal would have been adjusted to such a similar level that this difference would have been obscured.

(3) The same refers to ecological effects on the isotope signals of shells of different groups of organisms. Though this is a relatively new field of research in palaeolimnology, first published $\delta^{18}O/\delta^{13}C$ plots of data from different ostracod species and charophytes have revealed coherent groupings of (i) *Chara* oogonia (relatively heavy in carbon isotopes,

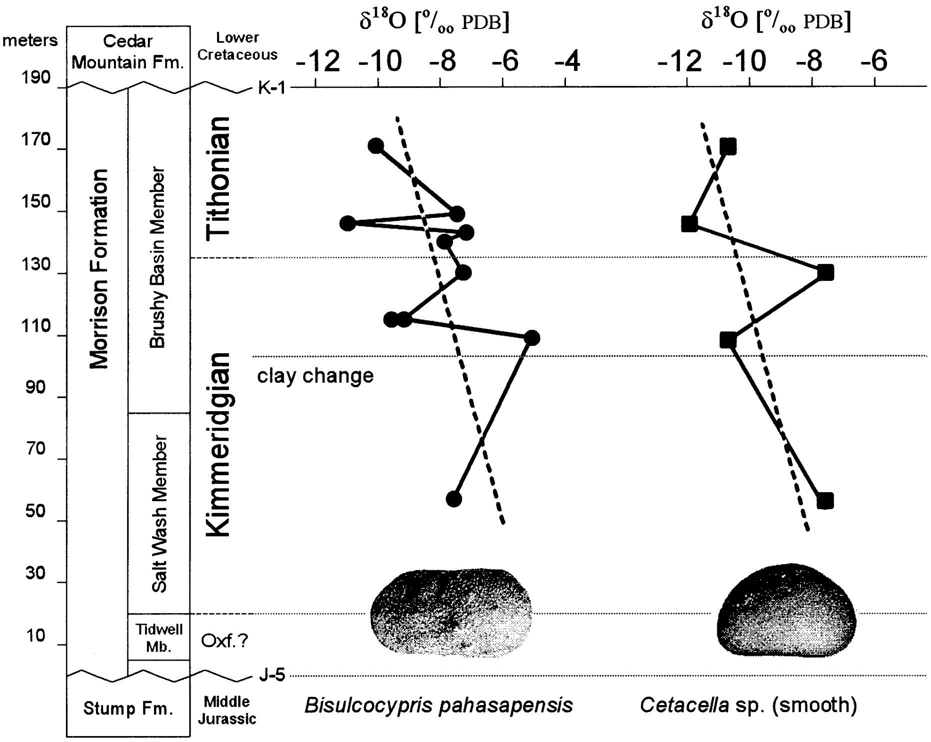

Fig. 7. $\delta^{18}O$ (‰ PDB) plots for two stratigraphically long-ranging ostracod species in Dinosaur National Monument (Utah). Measured section and position of the 'clay change' from Schudack et al. (1998). Both series show a clear trend towards lighter oxygen isotope compositions towards the top of the formation.

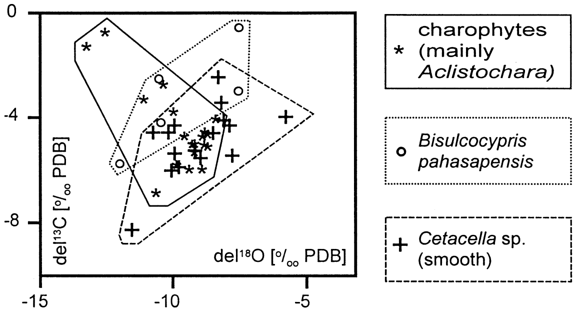

Fig. 8. $\delta^{18}O/\delta^{13}C$ (‰ PDB) plot for charophyte gyrogonites and ostracod valves from various levels in the Morrison Formation (Dinosaur National Monument and Owl Canyon sections, Utah and Colorado). Coherent groupings for charophytes, limnocytherids and cypridaceans are similar to examples from modern lakes.

but light in oxygen isotopes), (ii) limnocytherids (*Limnocythere*, relatively light both in carbon and oxygen isotopes), and (iii) cypridaceans (*Candona*, relatively heavy both in carbon and oxygen isotopes), data by Forester and Whelan (1999). Photosynthetic depletion explains the heavy carbon in charophyte gyrogonites, because the light carbon (^{12}C) goes to organic matter leaving enriched carbon in the vicinity of the plant to make a heavy carbon calcite.

The same type of cross plot for samples from the Morrison Formation provides a similar pattern, as far as the coherent groupings are concerned (Fig. 8): carbon isotopes in charophyte oogonia (*Aclistochara*) are heavier than in limnocytherid valves (*Bisulcocypris*), whereas cypridaceans (*Cetacella*) are similar in carbon isotopes, but heavier in oxygen isotopes as compared to charophyte oogonia. Though these groupings are not as clearly distinct as in published recent examples (Forester and Whelan, 1999) and may be somewhat obscured due to a limited degree of diagenesis — an almost inevitable consequence of the 150 million years age of the samples — their principal relationships are the same and may therefore serve as another indication for the relatively high isotopic fidelity of the Morrison calcite.

(4) On a higher ecologic level, taking the whole ecosystem instead of just the biotope “shallow lake or pond with calcareous production” (see above), other members of the “Morrison Extinct Ecosystems Project” have performed isotopic analyses on many other materials such as pedogenic and lacustrine carbonates, matrices, diagenetic calcite, vertebrate teeth, wood, eggshells, and molluscs. Plotted on $\delta^{18}O/\delta^{13}C$ graphs, the distribution of the material also shows coherent groupings with the relative proportions of the materials similar to those from modern ecosystems (Ekhart and Cerling, 1996). This fact also indicates that the materials have undergone relatively minor diagenesis and have preserved a high degree of isotopic fidelity.

4.2.2. Interpretation of the general trend towards lighter oxygen isotope compositions

In the continental realm, such as the Morrison depositional basin, trends from heavier to lighter oxygen stable isotope compositions can be explained in at least five independent ways (Lister, 1988). Of course, interpretation of changes in stable isotope composition in calcite shells from lakes is even more complicated than in the marine environment, but it must be emphasized here that the following interpretations strictly refer to a very general long-term trend, thus neglecting all the short-term changes with all the possible factors in single-lake histories such as evaporation events, freshwater influxes, mixing of different groundwaters etc. On the contrary, the rock successions of the Morrison Formation represent 7–8 million years with repeated intercalations of several single lake horizons. At the present state of sampling density and — even more — of the density of isotope measurements, single Morrison lake histories cannot be interpreted. The isotopic trend demonstrated here rather represents the average development in the isotope composition of atmospheric waters brought into the basin. The individual measurements (see Fig. 7) are each from a yet unknown phase of a single-lake history, which may modify the oxygen isotope value to a much higher degree than the general long-term trend (see for instance Lister et al., 1991, for a summary). Therefore, it is almost logical that the variability of negative values (the ‘zigzagging’ of the curve in Fig. 7) is even more pronounced than in examples from the marine environment or from single lake histories (e.g. Lister et al., 1991; Schwalb et al., 1994; Last et al., 1994).

(1) The first possible reason for the observed trend is a general supraregional cooling of the atmosphere which would lead to a decrease in evaporation of the heavy oxygen isotope from the Proto-Pacific Ocean and thus a decrease of the ^{18}O contents in the vapour transported with the prevailing westwind into the Morrison depositional basin. This interpretation would correlate both to the cooling trend observed in the Western Interior on the basis of charophyte taxonomic composition Section 4.1) and to the suggested cooling trend in Central and Western Europe (Section 3).

(2) A development from more arid conditions near the base to more humid conditions near the top of the formation, as suggested by several authors (Section 1), would also explain the observed pattern due to an increase of the input of isotopically light atmospheric water into the basin (see Lister et al., 1991, for the discussion of a Pleistocene example). However, most of the more recent data from sedimentology rather indicate a more arid climate during later Morrison depositional times. Such a trend, however, if eventually combined with increased evaporation and salinities of the lake water at least at certain times of the year, would contradict the observed trend because evaporation would also increase the percentage of the heavy oxygen isotope in the water. It must be argued that these effects which mainly refer to single lake histories are not strong enough to really influence the observed long-term development (Fig. 7).

(3) The substantial south-to-north wandering of the North-American plate during the Late Jurassic (Steiner and Helsley, 1975) and the resulting effects of the global equator to pole rain water isotopic gradient would also, at least partly, explain the observed trend.

(4) Increase in the degree of continentality, another possible explanation due to the overall increase in the ocean-to-basin distance and the correlated increase in highly depleted atmospheric water, is another possible explanation. The observed development within the Morrison depositional basin would parallel the accelerated retreat of the Jurassic seas

from the American continent during the general regressive phase near the end of the Jurassic period.

(5) The local tectonic development, i.e. the rise of the Proto-Cordillera to the west of the Western Interior Basin during later Morrison times (Turner and Fishman, 1991; Peterson, 1988, 1994), has possibly lead to increased rainfall on the west slope of the Cordillera, associated with a pronounced depletion in heavy oxygen isotopes in the remaining atmospheric vapour. The isotopic composition of the atmospheric water which finally reached the Morrison Basin with the prevailing westwinds was therefore lighter than in previous periods with no considerably high mountains to the west. As Ekhart and Cerling (1996) pointed out, oxygen isotope results from various materials of the Morrison suggest that the palaeometeoric waters were as highly depleted as in modern ecosystems in areas downwind of topographic highs.

5. Discussion of palaeoclimate changes

The results of palaeobiogeographical, taxonomic, and stable isotope geochemical analyses of calcareous microfossils in Europe and North America, as applied to palaeoclimatic interpretations, are in correspondence with different scenarios:

(1) A global cooling trend during the latest Jurassic and earliest Cretaceous would explain both the biogeographic differentiation and southward migration of thermophile marine ostracods in Europe (Section 3), and the change in taxonomic composition of the charophyte floras as well as the long-term depletion in heavy oxygen isotopes in calcareous shells from several successive lake horizons in the U.S. Western Interior (Section 4). The same would correlate well with a general trend from more humid to more cool-arid climates as observed by sedimentological criteria in Europe and North America. In this case, more regional explanations such as a change in ocean currents (Europe) or an increase in continentality and in the rise of the Proto-Cordillera (North America) are not needed to understand the observed patterns. One could argue that a global climate change towards generally more cool and arid conditions might have played a major role in the decrease of the very big sauropod dinosaurs for which the Late Jurassic has become so popular. A global cooling would correlate with the observed slight decrease of atmospheric CO_2 near the end of the Jurassic (Berner, 1991) and of the combined greenhouse effect, but contradict the suggested climate change towards warmer temperatures suggested by other authors (Vakhrameev, 1991).

(2) Independently of any global palaeoclimatic developments, more regional factors can also explain each of the observed phenomena.

- The biogeographic development of the marine faunas and the trend towards more arid climates on the landmasses in Europe (Section 3) would correlate well with the suggested increase of the influx of relatively cold boreal waters into central Europe, caused by the opening of the Proto-North Atlantic and the change in ocean current systems. Such an explanation would also answer the question expressed by Hallam (1994), why the Cimmeride mountain collision with Eurasia, responsible for the general spread of aridity, would also have affected the climate in Western Europe (see Section 1).
- The change in the taxonomic composition of charophyte floras in the Morrison Formation (Section 4.1) indicates generally colder atmospheric temperatures in the Tithonian, as compared to the Kimmeridgian, but this fact can — in principle — also be explained by two more regional factors: (i) the relatively fast northward movement of North America during this period of time (7–8 million years of Morrison deposition), which would also explain the isotopic trend (see below) if interpreted as to reflect gradual cooling; and (ii) a dramatic increase of volcanic activities in the Proto-Cordillera to the west of the basin (Turner and Fishman, 1991) and the combined frequent shadowing of the Morrison ecosystem by volcanic ash clouds over a period of several million years. This phenomenon should not be underestimated, because the sedimentary succession in the upper part of the Morrison Formation (Brushy Basin Member) holds a great number of tuff horizons, and even the general clay mineralogy indicates strong volcanic influence over a long period of time (Turner and Fishman, 1991).
- The general long-term trend towards lighter oxygen isotope compositions in the lake waters of the Morrison Formation (Section 4.2), if not in-

terpreted to reflect a global cooling or (at least) a relative cooling of the Proto-Pacific ocean which was the primary source of atmospheric vapour to the west of the basin, could also be explained by (i) the substantial south-to-north wandering of the North-American plate, (ii) a rise of continentality (retreat of the Jurassic seas from the North American continent), or (iii) the local tectonic development, i.e. the rise of the Proto-Cordillera to the west of the Western Interior Basin during later Morrison times. A combination of these factors would easily explain the observed isotopic trend, without the necessity of a global cooling, but such a global cooling would also correlate with rather than contradict the observations. However, a local trend towards colder atmospheric temperatures, only in the Morrison depositional basin, would not be able to explain the isotopic trend because evaporation of moisture from colder lake waters would lead to heavier oxygen isotope compositions. In this context, the possible effect of increased volcanic activity on the isotopic composition of lake waters in the Morrison ecosystem is yet unknown.

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References

Berger, J.-P., 1989. Stable isotopes (^{18}O, ^{13}O) on charophyte gyrogonites: examples from the Swiss molasse (Oligo–Miocene). 1st Int. Symp. Extant and Fossil Charophytes, Montpellier, p. 1 (abstract).

Berger, J.-P., 1990 Floral changes in the Molasse of western Switzerland (Oligo-Miocene). Paleoclimatic implications. Proc. Symp. on Paleofloristic and paleoclimatic changes in the Cretaceous and Tertiary, Prague, 1989, pp. 189–194.

Berner, R.A., 1991. A model for atmospheric CO_2 over Phanerozoic time. Am. J. Sci. 291, 339–376.

Boillot, G., Dupeuble, P.-A., Durand-Delga, L., D'Ozouville, L., 1971. Age minimal de l'Atlantique Nord d'après la découverte de calcaire tithonique à Calpionelles dans le Golfe de Gascogne. C. R. Acad. Sci. Paris D 273, 671–674.

Boillot, G., Dupeuble, P.A., Malod, J., 1979. Subduction and tectonics on the continental margin off Northern Spain. Mar. Geol. 32, 53–70.

Christensen, O.B., Kilenyi, T.I., 1970. Ostracod biostratigraphy of the Kimmeridgian in northern and western Europe. Dan. Geol. Unders. II 95, 1–65.

Crowley, T.J., North, G.R., 1991. Paleoclimatology. Clarendon Press, Oxford.

Dodson, P.A., Behrensmeyer, R.T., Bakker, R.T., McIntosh, J.S., 1980. Taphonomy and paleoecology of the dinosaur beds of the Jurassic Morrison Formation. Paleobiology 6, 208–232.

Doyle, P., 1987. Lower Jurassic–Lower Cretaceous belemnite biogeography and the development of the Mesozoic boreal realm. Palaeogeogr., Palaeoclimatol., Palaeoecol. 61, 237–254.

Ekhart, D.D., Cerling, T.E., 1996. P_{CO_2} during deposition of the Late Jurassic Morrison Formation and other paleoclimatic/ecologic data as inferred by stable carbon and oxygen isotope analyses. Annu. G.S.A. Meeting 1996, Denver, 50381 (abstract).

Fiorillo, A.R., McCarty, D.K., 1996. Paleopedological evidence for a humid paleoenvironment in the lower part of the Brushy Basin Member, Morrison Formation, of Curecanti National Recreation Area, Colorado. In: Morales, M. (Ed.), The Continental Jurassic. Mus. North. Ariz. Bull. 60, 575–580.

Forester, R.M., Whelan, J.F., 1999. Ostracodes and stable carbon and oxygen isotopes. Proxies for paleohydrology and paleoclimate: The past as a key to the Present. In: Kendall, C., McDonnell, J.J. (Eds.), Isotope Tracers in Catchment Hydrology. Elsevier, Amsterdam, chapter 23 (in press).

Glashoff, H., 1964. Ostrakoden-Faunen und Paläogeographie im Oxford NW-Europas. Paläontol. Z. 38, 28–65.

Gradstein, F.M., Ogg, J., 1996. A Phanerozoic time scale. Episodes 19, 3–4.

Gramann, F., Heunisch, C., Klassen, H., Kockel, F., Dulce, G., Harms, F.-J., Katschorek, T., Mönnig, E., Schudack, M., Schudack, U., Thies, D., Weiss, M., 1997. In: Hinze, C. (Coord.), Das Niedersächsische Oberjura-Becken — Ergebnisse interdisziplinärer Zusammenarbeit. Z. Dtsch. Geol. Ges. 148, 165–236.

Hallam, A., 1984a. Distribution of fossil marine invertebrates in relation to climate. In: Brenchley, P.J. (Ed.), Fossils and Climate. Wiley, London, pp. 107–125.

Hallam, A., 1984b. Continental humid and arid zones during the Jurassic and Cretaceous. Palaeogeogr., Palaeoclimatol., Palaeoecol. 47, 195–223.

Hallam, A., 1985. A review of Mesozoic climates. J. Geol. Soc. London 142, 433–445.

Hallam, A., 1994. Jurassic climates as inferred from the sedimentary and fossil record. In: Allen, J.R.L., Hoskins, B.J., Sellwood, B.W., Spicer, R.A., Valdes, P.J. (Eds.), Palaeoclimates and their Modelling. Chapman and Hall, London, pp. 79–88.

Hallam, A., Grose, J.A., Ruffell, A.H., 1991. Palaeoclimatic significance of changes in clay mineralogy across the Jurassic–Cretaceous in England and France. Palaeogeogr., Palaeoclimatol., Palaeoecol. 81, 173–187.

Kowallis, B.J., Christiansen, E.H., Deino, A.L., Peterson, F., Turner, C.E., Kunk, M.J., Obradovich, J.D., 1998. The age of the Morrison Formation. Mod. Geol. 22, 235–260.

Last, W.M., Teller, J.T., Forester, R.M., 1994. Paleohydrology and paleochemistry of Lake Manitoba, Canada: the isotope and ostracode records. J. Paleolimnol. 12, 269–282.

Lister, G.S., 1988. Stable isotopes from lacustrine Ostracoda as tracers for continental palaeoenvironments. In: DeDeckker, P., Colin, J.-P., Peypouquet, J.-P. (Eds.), Ostracoda in the Earth Sciences. Elsevier, Amsterdam, pp. 201–218.

Lister, G.S., Kelts, K., Zao, C.K., Yu, J.Q., Niessen, F., 1991. Lake Quinghai, China: Closed-basin lake levels and oxygen isotope record for ostracoda since the latest Pleistocene. Palaeogeogr., Palaeoclimatol., Palaeoecol. 84, 141–162.

Litwin, R.J., Turner, C.E., Peterson, F., 1998. Palynological evidence on the age of the Morrison Formation: Dinosaur National Monument (Utah and Colorado) and Western Interior, U.S.A. Mod. Geol. 22, 297–319.

Moore, G.T., Hayashida, D.N., Ross, C.A., Jacobson, S.R., 1992a. Paleoclimate of the Kimmeridgian/Tithonian (Late Jurassic) world: I, Results using a general circulation model. Palaeogeogr., Palaeoclimatol., Palaeoecol. 93, 113–150.

Moore, G.T., Sloan, L.C., Hayashida, D.N., Umrigar, N.P., 1992b. Paleoclimate of the Kimmeridgian/Tithonian (Late Jurassic) world: II, Sensitivity tests comparing three different paleotopographic settings. Palaeogeogr., Palaeoclimatol., Palaeoecol. 95, 229–252.

Newton, C.R., 1990. Palaeobiogeography. In: Briggs, D.E.G., Crowther, P.R. (Eds.), Palaeobiology, a Synthesis. Blackwell, Oxford, pp. 452–460.

Peterson, F., 1988. Pennsylvanian to Jurassic eolian transportation systems in the western United States. Sediment. Geol. 56, 207–260.

Peterson, F., 1994. Sand dunes, sabkhas, streams, and shallow seas: Jurassic paleogeography in the southern part of the Western Interior Basin. In: Caputo, M.V., Peterson, J.A., Franczyk, K.J. (Eds.), Mesozoic Systems of the Rocky Mountain Region, USA. Rocky Mountain Section SEPM (Soc. Sediment. Geol.), pp. 233–272.

Pickard, G.L., Emery, W.J., 1996. Descriptive Physical Oceanography, 5th ed. Butterworth–Heinemann, Oxford.

Ruffell, A.H., Rawson, P.F., 1994. Palaeoclimate control on sequence stratigraphic patterns in the Late Jurassic to mid-Cretaceous, with a case study from Eastern England. Palaeogeogr., Palaeoclimatol., Palaeoecol. 110, 43–54.

Schudack, M., 1993. Die Charophyten aus Oberjura und Unterkreide von Westeuropa. Mit einer phylogenetischen Analyse der Gesamtgruppe. Berliner Geowiss. Abh. E 8.

Schudack, M., 1995. Neue mikropaläontologische Beiträge (Ostracoda, Charophyta) zum Morrison-Ökosystem (Oberjura des Western Interior, USA). Berl. Geowiss. Abh. E 16, 389–407.

Schudack, M., 1996. Ostracode and charophyte biogeography in the continental Upper Jurassic of Europe and North America as influenced by plate tectonics and paleoclimate. In: Morales, M. (Ed.), The Continental Jurassic. Mus. North. Ariz. Bull. 60, 333–342.

Schudack, M., Schudack, U., 1995. Late Jurassic and Berriasian ostracod biogeography in northwestern and Central Europe. In: Riha, J. (Ed.), Ostracoda and Biostratigraphy, Proc. 12th Int. Symp. on Ostracoda. Balkema, Rotterdam, pp. 99–109.

Schudack, M., Schudack, U., 1997. Biostratigraphische und biogeographische Beziehungen der süddeutschen Oberjura-Ostracoden: Parallelen zu paläogeographischen und paläoklimatischen Entwicklungen. Geol. Blätter NO-Bayern 47, 99–116.

Schudack, M., Turner, C., Peterson, F., 1998. Biostratigraphy, paleoecology, and biogeography of charophytes and ostracodes from the Upper Jurassic Morrison Formation, Western Interior, U.S.A. Mod. Geol. 22, 379–414.

Schudack, U., 1994. Revision, Dokumentation und Stratigraphie der Ostracoden des nordwestdeutschen Oberjura und Unter-Berriasium. Berl. Geowiss. Abh. E 11.

Schudack, U., 1997. *Palaeocytheridea groissi* n.sp. (Ostracoda) aus den Mörnsheimer Schichten (Tithonium) von Oberhartheim bei Vohburg (Donau). Geol. Blätter NO-Bayern 47, 17–24.

Schwalb, A., Lister, G.S., Kelts, K., 1994. Ostracoda $\delta^{18}O$ and $\delta^{13}C$ signatures of hydrological and climatic changes affecting Lake Neuchatel (Switzerland). J. Paleolimnol. 11, 3–17.

Sohn, I.G., 1962. The ostracode genus *Cytherelloidea*, a possible indicator of paleotemperature. U.S.G.S. Prof. Pap. 450-D, 144–147.

Sohn, I.G., 1964. The ostracode genus *Cytherelloidea*, a possible indicator of paleotemperature. Publ. Staz. Zool. Napoli 33 (Suppl.), 529–534.

Steiner, M.B., Helsley, C.E., 1975. Reversal pattern and apparent polar wander for the Late Jurassic. Geol. Soc. Am. Bull. 86, 1537–1543.

Turner, C.E., Fishman, N.S., 1991. Jurassic Lake T'oo'dichi': A large alkaline, saline lake, Morrison Formation, eastern Colorado Plateau. Geol. Soc. Am. Bull. 103, 538–558.

Vakhrameev, V.A., 1991. Jurassic and Cretaceaous Floras and Climates of the Earth. Cambridge Univ. Press.

Valdes, P.J., 1994. Atmospheric general circulation models of the Jurassic. In: Allen, J.R.L., Hoskins, B.J., Sellwood, B.W., Spicer, R.A., Valdes, P.J. (Eds.), Palaeoclimates and their Modelling. Chapman and Hall, London, pp. 109–118.

Valdes, P.J., Sellwood, B.W., 1992. A palaeoclimate model for the Kimmeridgian. Palaeogeogr., Palaeoclimatol., Palaeoecol. 95, 47–72.

Whatley, R., 1990. The relationship between extrinsic and intrinsic events in the evolution of Mesozoic non-marine Ostracoda. In: Kaufmann, E.G., Walliser, O.H. (Eds.), Extinction Events in Earth History. Lect. Notes Earth Sci. 30, 253–263.

Whatley, R., 1992. The reproductive and dispersal strategies of Cretaceous nonmarine Ostracoda: the key to pandemism. In: Mateer, N.J., Chen, P.-J. (Eds.), Aspects of Nonmarine Cretaceous Geology. Proc. First Int. Symp. on Nonmarine Cretaceous Correlations, Urumqui, China, 1987, pp. 177–192.

Whatley, R., 1995. Ostracoda and oceanic palaeoxygen levels. Mitt. Hamb. Zool. Mus. Inst. 92, 337–353.

Whatley, R., 1996. The bonds unloosed: The contribution of Ostracoda to our understanding of deep sea events and processes. In: Moguilevsky, A., Whatley, R. (Eds.), Microfossils and Oceanic Environments. Aberystwyth Press, Univ. Wales, pp. 6–25.

Wignall, P.B., Pickering, K.T., 1993. A palaeoecological and sedimentological analysis of fault-controlled deposition in the Kimmeridgian (Late Jurassic) of N.E. Scotland. J. Geol. Soc. London 150, 323–340.

Wignall, P.B., Ruffell, A.H., 1990. The influence of a sudden climatic change on marine deposition in the Kimmeridgian of northwest Europe. J. Geol. Soc. London 147, 365–371.

Zeiss, A., 1977. Jurassic Stratigraphy of Franconia. Stuttgarter Beitr. Naturkd. B 31.

Ziegler, B., 1977. The 'White' (Upper) Jurassic in Southern Germany. Stuttgarter Beitr. Naturkd. B 26.

Ziegler, P.A., 1988. Evolution of the Arctic-North Atlantic and the Western Tethys. Am. Assoc. Pet. Geol. Mem 43.

Ziegler, P.A., 1990. Geological Atlas of Western and Central Europe. Shell, The Hague.