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Source: Acta Palaeontologica Polonica, 55(3) : 471-478

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: https://doi.org/10.4202/app.2009.0100

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Palaeoecology of Late Triassic conodonts: Constraints from oxygen isotopes in biogenic apatite

MANUEL RIGO and MICHAEL M. JOACHIMSKI

Rigo, M. and Joachimski M.M. 2010. Palaeoecology of Late Triassic conodonts: Constraints from oxygen isotopes in biogenic apatite. *Acta Palaeontologica Polonica* 55 (3): 471–478.

The oxygen isotopic composition of conodont apatite derived from the Late Triassic (Carnian to lower Norian), Pignola 2 and Sasso di Castalda sections in the Lagonegro Basin (Southern Apennines, Italy) was studied in order to constrain the habitat of Late Triassic conodont animals. Oxygen isotope ratios of conodonts range from 18.5 to 20.8‰ V-SMOW, which translate to palaeotemperatures ranging from 22 to 31°C, assuming a $\delta^{18}O$ of Triassic subtropical sea water of -0.12‰ V-SMOW. These warm temperatures, which are well comparable to those of modern subtropical-tropical oceans, along with the body features of the conodont animal suggest that conodont $\delta^{18}O$ values reflect surface water temperatures, that the studied conodont taxa lived in near-surface waters, and that $\delta^{18}O$ values of Late Triassic conodonts can be used for palaeoclimatic reconstructions.

Key words: Conodonta, palaeoecology, oxygen isotope, palaeotemperatures, Late Triassic, Tethys.

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Received 23 October 2009, accepted 8 March 2010, available online 16 March 2010.

Introduction

Palaeozoic and Triassic conodonts are found in a variety of sedimentary rocks, which represent different depositional environments. Whereas some conodont species were cosmopolitan, others had a somewhat more restricted geographic distribution. In particular, most Late Permian to Triassic conodonts were cosmopolitan within low latitudes, but most of the low latitude genera are absent in high latitudes of northern Siberia and New Zealand (e.g., Late Triassic *Carnepigondolella*, *Epigondolella*, *Mockina*, *Parvigondolella*, sculptured *Metapolygnathus*, *Orchardella*, *Neocavitella*, and *Misikella*). However, some conodonts show a distinct provincialism within the low latitudes during the Middle Triassic (Kozur 1980; Charpentier 1984). Since conodonts became extinct within the earliest Jurassic (e.g., Kozur 1993; Pálfy et al. 2007), the palaeoecology of the conodont animal can only be deduced from indirect information, e.g., faunal associations in different settings or sedimentological features indicating distinct environments.

Several ecologic models have been proposed to explain the distribution of conodonts in sedimentary marine deposits: (i) the depth-stratification model by Seddon and Sweet (1971), (ii) the lateral-segregation model by Barnes and Fåhraeus (1975), and (iii) a combination of these two models considering also the principles of modern oceanic biogeography proposed by Zhen and Percival (2003). The depth-stratification model suggests that different conodont species lived at different water depths. If a conodont species lived at a particular depth within the water column, this species could be recovered from sediments deposited at equal or greater water depths. For instance, a species living in near-surface waters could hypothetically be found in different sediments: in shallow-water sediments it would represent the whole conodont assemblage, while in deeper-water sediments it would co-occur with other conodont species. This model is well applicable for cosmopolitan and widespread conodont taxa.

The lateral-segregation model explains the discontinuities in the lateral conodont distribution considering conodonts as bottom dwellers, either benthic or nektobenthic and only some cone-shaped genera as pelagic forms. Most Triassic conodonts do not generally occur in anoxic sediments. Late Triassic anoxic sediments are characterised by monospecific faunas, from which only three species are known, *Pseudofurnishius murcianus* in the early Carnian (e.g., Ramovš 1977, 1978), *Nicoraella*? *budaensis* (e.g., Kozur and Mock 1991; Kolar-Jurkovšek et al. 2005) in the middle Carnian, and *Mockina slovakensis* in the late Norian (e.g., Budai and Kovács 1986; Roghi et al. 1995; Rigo et al. 2009). The recovery of these conodonts from either dysoxic to anoxic Triassic sediments (e.g., Ramovš 1977, 1978; Budai and Kovács 1986; Kozur and Mock 1991; Roghi et al. 1995; Kolar-Jurkovšek et al. 2005) excludes a benthic or nektobenthic lifestyle.

Zhen and Percival (2003) proposed a hierarchical scheme to explain the distribution of pelagic, benthic, or nektobenthic conodonts in marine deposits. The authors recognised first-order (realms) and second-order (domains) divisions defined by

doi:10.4202/app.2009.0100

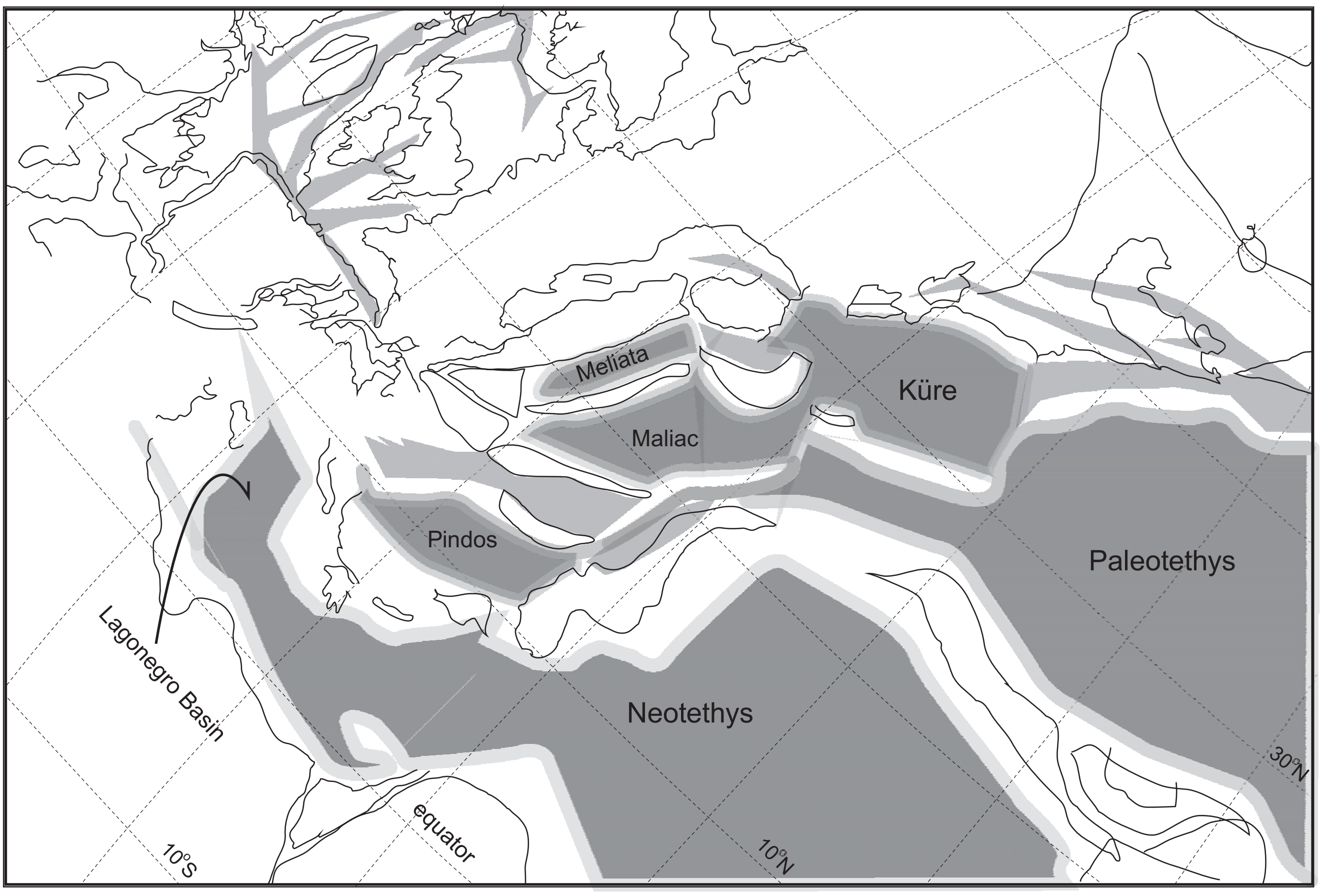

Fig. 1. Reconstruction of the Western Tethys and position of the Lagonegro Basin (Southern Apennines, Italy) for the Carnian (Late Triassic), modified after Stampfli and Kozur (2006). White, landmass; dark grey, basins; light grey, rift zones; hazel grey, continent margins.

climatic and oceanographic factors and a third-order division (provinces), which is identified by endemic faunas. Late Triassic conodonts are preferentially found in pelagic deep-water sediments but sometimes also occur in shallow-water deposits (e.g., Liebermann 1980; Carey 1984; Jadoul et al. 2002; Hounslow et al. 2004; Kolar-Jurkovšek et al. 2005) or within euxinic intraplatform basins, such as that of the Dolomia di Forni (Roghi et al. 1995) within the Dolomia Principale, characterised by dysoxic-anoxic bottom conditions. Moreover, a few conodonts have been recently collected from the peritidal-subtidal cycles of the Dolomia Principale of the Pasubio Massif (Vicenza, Italy) (Belvedere et al. 2008), which clearly represent a shallow-water environment. However, the life habitat of Triassic conodont animals is unknown and has never been constrained. Unfortunately, taking into account the published studies on Triassic conodonts, it is not yet possible to apply any of the previous models, in particular the new hierarchical scheme proposed by Zhen and Percival (2003), to the Late Triassic, because Late Triassic conodont studies have focused preferentially on conodonts from basinal deposits and only few sections representing shallow-water conditions have been investigated. As a consequence, only a few endemic taxa have been described, such as the genera *Gladigondolella* and *Pseudofurnishius*, limited to the lower latitudes of the Tethyan gulf, or the species *Nicoraella*? *budaensis*, a form restricted to shallow-water conditions (Kozur and Mock 1991; Kolar-Jurkovšek et al. 2005).

In this paper, we present oxygen isotope data measured on conodont elements from the Lagonegro Basin (Potenza, Southern Apennines, Southern Italy) in order to provide information about the palaeoecology of Late Triassic conodonts.

Abbreviations.—CAI, colour alteration index; CCD, Calcite Compensation Depth; FO, first occurrence.

Geological setting

During Late Triassic, the western Neotethys was dissected into several ocean basins, named from S to N the Lagonegro-Sicani, Pindos, Maliac, and Meliata Oceans (Scandone 1967; Channell and Kozur 1997; Stampfli and Borel 2002; Stampfli et al. 2003; Stampfli and Kozur 2006). According to Stampfli and Borel (2002), Stampfli et al. (2003), and Stampfli and Kozur (2006), during the Late Triassic the Lagonegro Basin was situated at the northern margin of the Neotethys, south of the Palaeotethys, in tropical latitudes around 10°N (Fig. 1). The Lagonegro Basin has been interpreted as a strictly oceanic setting since oceanic crust has been identified in seismic lines of the Ionian Sea below the sedimentary cover of the Lagonegro succession (e.g., Finetti 1982; Finetti et al. 1996; Catalano et al. 2001; Argnani 2005; Passeri et al. 2005). Reliable palaeodepth estimates for the Lagonegro Basin are not available, but sediments were deposited below the Calcite Compensation Depth (CCD) at least twice during the Triassic, in the Carnian and Rhaetian (Scandone 1967; Bazzucchi et al. 2005; Bertinelli et al. 2005; Reggiani et al. 2005; Rigo et al. 2007). We studied the late Julian to Tuvalian (Carnian) interval in the Pignola 2 section, which is characterised by hemipelagic to pelagic, bioturbated, grey cherty limestones of the Calcari con Selce Formation yielding abundant conodonts (often > 100 platform specimens per 5 kg of rock; Rigo et al. 2007). Previously, Rigo et al. (2007) recognised the Carnian–Norian boundary, as defined by the first occurrence (FO) of *Metapolygnathus primitius*, at the Pignola 2 section. Nicora et al. (2007) described the Pizzo Mondello section (Sicily, Italy) as a candidate section for the Norian GSSP (Global boundary Stratotype Section and Point) and proposed that the base of the Norian Stage should be at the FO of the conodont *Epigondolella quadrata.* Based on the conodont distribution in the Pizzo Mondello, the FO of *Epigondolella quadrata* is clearly younger than the top of the Pignola 2 section where *E. quadrata* does not occur. Consequently, the upper part of the Pignola 2 section is attributed to the Tuvalian (late Carnian) rather than to the Lacian (early Norian), as assumed by Rigo et al. (2007) and in agreement with the re-classification of *Metapolygnathus communisti* sensu Rigo et al. (2007) as *Metapolygnathus praecommunisti* after Mazza et al. (2010). The conodont colour alteration index (CAI) is 1–1.5 and indicates maximum burial temperatures of ca. 90°C (Epstein et al. 1977).

A conodont sample from the Sasso di Castalda section produced a low diversity conodont fauna, which is assigned to the middle Norian (Bertinelli et al. 2005; Rigo et al. 2005). The conodont CAI at Sasso di Castalda is 3, implying maximum burial temperatures of 200°C (Epstein et al. 1977).

Detailed descriptions of the Pignola 2 section were published by Rigo et al. (2007) and of the Sasso di Castalda section by Bertinelli et al. (2005) and Rigo et al. (2005).

Material and methods

Conodont elements were extracted using standard techniques (in 10% acetic or formic acid) from thirty-four carbonate samples (33 from the Pignola 2 section and 1 from the Sasso di Castalda section), with an average weight of 8 kg. Conodonts from the Pignola 2 section belong mainly to the genera *Gladigondolella* and *Paragondolella* in the lower part of the section, while *Paragondolella*, *Metapolygnathus*, *Carnepigondolella*, and *Norigondolella* characterise the upper part (Rigo et al. 2007). Conodonts from the Sasso di Castalda section belong only to the genus *Epigondolella*.

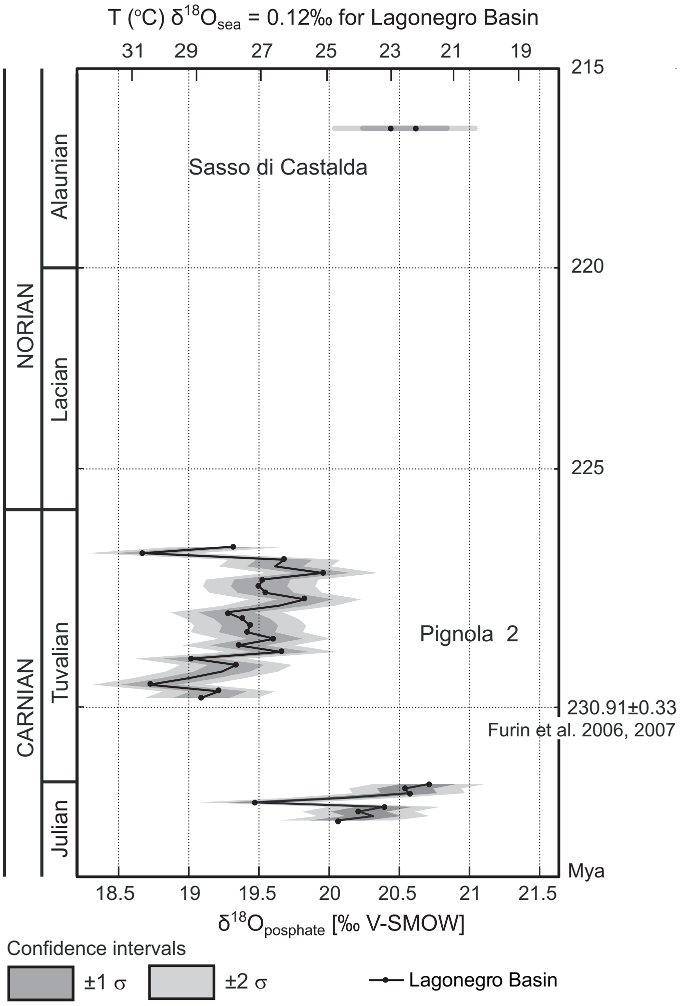

Fig. 2. Oxygen isotope curves of conodont apatite from the Sasso di Castalda and Pignola 2 sections, Lagonegro Basin (Southern Apennines, Italy). Dark gray and light gray contours give, respectively, analytical reproducibility of 1 σ and 2 σ for $\delta^{18}O$. Radiometric age of 230.91 ± 0.33 Mya from Furin et al. (2006, 2007). Time scale after Brack et al. (2005).

Oxygen isotope analyses of conodont apatite (0.5 to 1.3 mg of conodont apatite, which corresponds to hundreds of pectiniform and ramiform conodont elements) were performed on trisilverphosphate after dissolving conodont apatite in nitric acid and precipitating the phosphate group as Ag_3PO_4 (O'Neil et al. 1994; Joachimski et al. 2009). Isotope analyses were performed using a high-temperature conversion-elemental analyzer (TC-EA) connected on-line to a ThermoFinnigan Delta Plus mass spectrometer. All samples were measured in triplicate. Accuracy and reproducibility were monitored by multiple analyses of trisilverphosphate from NBS120c and using several trisilverphosphate standards (TUI-1, TUI-2, YR-2; Vennemann et al. 2002). The average oxygen isotope composition of TUI-1, TUI-2, and YR-2 standards was 21.3, 5.5, and 13.2‰ V-SMOW, respectively. The mean $\delta^{18}O$ value of NBS120c was 22.7‰ V-SMOW, which is relatively close to the value of 22.6‰ V-SMOW determined by Vennemann et al. (2002). The overall reproducibility determined by replicate analyses of trisilverphosphate standards as well as replicate sample analysis was better than ±0.2‰ (1 σ). All values are reported in the standard delta notation in per mil relative to

Table 1. $\delta^{18}O$ of conodont apatite from Pignola 2 (P) and Sasso di Castalda (KZ). Palaeotemperatures calculated using the equation given by Kolodny et al. (1983). $\delta^{18}O$ value of Late Triassic surface sea water ($\delta^{18}O_{sea}$) in the Lagonegro Basin is assumed to have been -0.12‰ V-SMOW.

Sample	Section	Biostratigraphic age		$\delta^{18}O$ (‰ V-SMOW)	T (°C) $\delta^{18}O$ sea = -0.12 ‰
KZ 6A (polyspecific)	Sasso di Castalda	Norian	Alaunian	20.7	21.9
KZ 6B (monospecific)	Sasso di Castalda	Norian	Alaunian	20.5	22.9
P 38	Pignola 2	Carnian	Tuvalian	19.4	28.0
P 37	Pignola 2	Carnian	Tuvalian	18.7	30.7
P 36	Pignola 2	Carnian	Tuvalian	19.7	26.3
P 35	Pignola 2	Carnian	Tuvalian	19.7	26.6
P 34	Pignola 2	Carnian	Tuvalian	20.0	25.1
P 33	Pignola 2	Carnian	Tuvalian	19.6	27.0
P 32	Pignola 2	Carnian	Tuvalian	19.6	27.1
P 31	Pignola 2	Carnian	Tuvalian	19.6	26.9
P 30	Pignola 2	Carnian	Tuvalian	19.9	25.7
P 29	Pignola 2	Carnian	Tuvalian	19.7	26.5
P 28	Pignola 2	Carnian	Tuvalian	19.3	28.1
P 27	Pignola 2	Carnian	Tuvalian	19.4	27.6
P 26	Pignola 2	Carnian	Tuvalian	19.5	27.4
P 25	Pignola 2	Carnian	Tuvalian	19.5	27.5
P 24	Pignola 2	Carnian	Tuvalian	19.7	26.6
P 23	Pignola 2	Carnian	Tuvalian	19.4	27.7
P 21	Pignola 2	Carnian	Tuvalian	19.7	26.4
P 20	Pignola 2	Carnian	Tuvalian	19.1	29.2
P 19	Pignola 2	Carnian	Tuvalian	19.4	27.8
P 18	Pignola 2	Carnian	Tuvalian	19.3	28.2
P 17	Pignola 2	Carnian	Tuvalian	19.1	29.3
P 14	Pignola 2	Carnian	Tuvalian	18.8	30.5
P 13	Pignola 2	Carnian	Tuvalian	19.3	28.3
P 12	Pignola 2	Carnian	Tuvalian	19.2	28.9
P 8	Pignola 2	Carnian	Julian	20.8	21.8
P 7	Pignola 2	Carnian	Julian	20.6	22.5
P 6	Pignola 2	Carnian	Julian	20.6	22.4
P 4	Pignola 2	Carnian	Julian	20.2	24.3
P 3c	Pignola 2	Carnian	Julian	19.5	27.2
P 3b	Pignola 2	Carnian	Julian	20.5	23.2
P 3a	Pignola 2	Carnian	Julian	20.3	24.0
P 2	Pignola 2	Carnian	Julian	20.4	23.5
P 1	Pignola 2	Carnian	Julian	20.8	24.7

V-SMOW (Table 1). Palaeotemperatures were calculated using the equation given by Kolodny et al. (1983) and are given in Table 1 and Fig. 2.

Results

Oxygen isotope ratios of apatite phosphate ($\delta^{18}O_{phos}$) in Carnian and Norian conodonts range from 18.7 to 20.8‰ in the Pignola 2 and Sasso di Castalda sections (Fig. 2, Table 1). Conodonts from the Julian substage (early Carnian) show $\delta^{18}O$ values between 19.5 and 20.8‰ and are enriched in ^{18}O compared to Tuvalian (late Carnian) conodonts having values ranging from 18.7 to 20.0‰ (Fig. 2). A gradual upward increase in $\delta^{18}O$ is observed in the Tuvalian strata. Highest values around 20‰ are observed in the upper part of the section; $\delta^{18}O$ values tend to decrease again at the top (Fig. 2).

A monospecific pectiniform conodont sample (KZ 6 B), composed exclusively of elements of *Epigondolella triangularis*, and a polyspecific assemblage (KZ 6A), composed of pectiniform and ramiform gondolellids such as *Epigondolella quadrata*, *E. abneptis*, *E. spatulata*, *E. rigoi*, and *E. spiculata* in addition to *E. triangularis*, were extracted from the same rock sample (KZ 6) of the Sasso di Castalda section (Norian) and analysed separately. The $\delta^{18}O$ value of the monospecific sample (KZ 6B) is 20.5‰ and compares well to the value of 20.7‰ measured for the polyspecific conodont sample (KZ 6A) (Table 1).

These analyses were carried out in order to compare the δ^{18}O values of conodonts from the Pignola 2 section to the value measured for the monospecific sample of *E. triangularis*, which is interpreted as a surface dweller as it was described from shallow-water sediments from Nevada (Carey 1984). Since the polyspecific assemblage from the same bed yields a similar isotopic composition, species composing this assemblage are interpreted to have lived in similar water depths and at comparable water temperatures.

Discussion

Triassic palaeotemperature reconstructions based on conodont δ^{18}O.—Oxygen isotopes of conodont apatite have been used for sea water palaeotemperature reconstructions (e.g., Joachimski and Buggisch 2002; Joachimski et al. 2004, 2006, 2009; Buggisch et al. 2008; Trotter et al. 2008; Elrick et al. 2009). The δ^{18}O of marine biogenic apatite is a function of temperature during precipitation of apatite and of the δ^{18}O of sea water (Kolodny et al. 1983). The latter depends on ice volume, fresh water input, and evaporation. Fresh water input and evaporation are locally traced by salinity (S), and a robust linear relationship can be established between salinity and δ^{18}O at the regional scale (LeGrande and Schmidt 2006). Adopting the δ^{18}O-S relationship proposed by LeGrande and Schmidt (2006) for the Tropical Pacific, Mediterranean, or Red Sea/Persian Gulf, a 1‰ difference in δ^{18}O of conodont apatite corresponds to a ~4°C temperature change, or a ~3.5 psu (= practical salinity units) shift in salinity, or a combination of both. Any temperature reconstruction based on δ^{18}O of conodont apatite requires an estimate of δ^{18}O of ambient sea water, which as shown above is dependent on freshwater input or evaporation, and thus on salinity.

Veizer et al. (1999) suggested that the oxygen isotope composition of sea water may have changed through time. However, a recent study on the oxygen isotope composition of Late Triassic bivalve shells (Nützel et al. 2009) preserved as pristine aragonite does not indicate that Triassic sea water was significantly different in δ^{18}O in comparison to modern oceans. Consequently, we assumed a δ^{18}O value of -1‰ V-SMOW for the ice-free Triassic time period (Shackelton and Kennett 1975). Using the δ^{18}O-latitude relationship proposed by Zachos et al. (1994) and a palaeolatitude of 10°N (e.g., Stampfli and Kozur 2006; Fig. 1), a sea water δ^{18}O of -0.12‰ was calculated for the Lagonegro Basin. With this estimate and assuming constant salinity, palaeotemperatures reconstructed for the early Carnian (Julian) in the Pignola 2 section and for the middle Norian at the Sasso di Castalda section are mostly 22 to 23°C. Palaeotemperatures from the Pignola 2 section range between 25 and 31°C for the Tuvalian part of the succession (Fig. 2, Table 1). These temperatures are observed today only in tropical and subtropical waters above the thermocline and are compatible with modern tropical surface water temperatures ranging from 23 to 30°C (http://www.noaa.gov).

The decrease in δ ^{18}O recorded between the Julian and Tuvalian in the Pignola 2 section can neither be attributed to a change in the depositional depth and thus water temperature (Rigo et al. 2007) nor to different life habitats of Julian and Tuvalian conodonts since all Tuvalian conodonts are interpreted to be descendents from the Julian conodont *Paragondolella polygnathiformis* (Rigo et al. 2007; Mazza et al. 2010). Most importantly, the change in δ^{18}O coincides with the Carnial Pluvial Event (CPE; e.g., Simms and Ruffell 1989, Simms et al. 1995; Rigo et al. 2007; Preto et al. 2010) that is seen in context with a major change in climate resulting in more humid conditions and increased rainfall (e.g., Roghi 2004; Rigo et al. 2007). Accordingly, the generally lower δ^{18}O values of Tuvalian conodonts are interpreted to reflect higher water temperatures and/or slightly lower salinities (Hornung et al. 2007).

Constraints on the life habitat of Triassic conodont animals.—Geochemical constraints add to several lines of evidence supporting a life habitat of Late Triassic conodont animals in surface waters. Following Donoghue et al. (2000), the conodont animals represent early vertebrates (Sansom et al. 1992) with an eel-like body characterised by a finned tail. The anatomy of the described conodont animals was well adapted to fast swimming and a predatory mode of life. It was argued that the conodont animal was an active swimmer (Sweet 1988). Eye movements of the conodont animal were controlled by extrinsic eye muscles (Gabbott et al. 1995), which suggest that the conodont animal was well adapted to the photic zone. Otherwise, the extrinsic eye musculature would have been atrophied by the non-use of the eye as observed for animals living in environments devoid of light. Even though the conodont animal has been reconstructed based on findings in Palaeozoic sediments, we assume that this reconstruction can be adapted to Triassic representatives.

It might be argued that while some conodont animals lived in surface waters, others may have thrived in deeper and cooler waters. A mixed palaeotemperature signal would be obtained if it was the case that both surface and deep-water conodonts contributed in varying proportions to the oxygen isotope composition of a mixed sample. A monospecific sample from the middle Norian of the Sasso di Castalda section (Lagonegro Basin) gave a δ^{18}O value of 20.5‰, which compares very well to the δ^{18}O value of 20.7‰ of the polyspecific conodont sample from the same bed (Table 1). The monospecific sample was composed of pectiniform elements of *Epigondolella triangularis*, which corresponds to *E. abneptis* subsp. B of Orchard (1983). Since this species was found both in shallow- and deep-water sediments of the northwestern Nevada terrane, Carey (1984) concluded that *E. triangularis* lived in surface waters. The comparable δ^{18}O values of the mono- and polyspecific assemblages indicate that all conodont taxa in this sample live in waters with comparable δ^{18}O and temperature. This implies that all taxa composing the polyspecific assemblage (*Epigondolella*

doi:10.4202/app.2009.0100

quadrata, *E. abneptis*, *E. spatulata*, *E. rigoi*, *E. spiculata*, and *E. triangularis*) should be considered as well as surface water dwellers. Consequently, we interpret the oxygen isotope ratios of the studied Late Triassic conodonts to reflect temperature and δ^{18}O of surface sea water.

Cladistic analyses show that conodont animals are phylogenetically related to (even if more derived than) animals belonging to Infraphylum (or superclass) Agnatha, which are represented today by hagfishes and lampreys (Donoghue et al. 2000). Lampreys are parasitic and live mostly in coastal and fresh waters. In contrast, hagfish (*Myxine*) are marine demersal fishes (living at or near to the sea floor), preferring muddy environments. Usually, hagfish feed on bristleworms (polychaete marine worms) but often can disembowel dead or dying marine animals, behaving as active predators. Most hagfish taxa live in cold or temperate seas of both hemispheres, preferentially in water depth of at least 20 m with some representatives thriving in water depths around 100–300 m (e.g., *Myxine glutinosa*).

In the Pignola 2 section, a short episode with a rise in the CCD was suggested to have occurred at the Julian/Tuvalian boundary (early/late Carnian boundary; Rigo et al. 2007). At present, the CCD in the tropics is located on average at water depth of 4500–5000 m (e.g., Brown et al. 2005), so we assume a similar depth for the oceanic floor of the studied section even if a higher position of the CCD cannot be ruled out. At such water depths, temperatures ranging between 25 and 31°C are very unlikely. Instead, these palaeotemperatures are more comparable to present-day surface waters of the tropical ocean. Therefore, a comparable life habitat of the Triassic conodont animals and modern, cold water-dwelling Agnatha seems unlikely.

The studied Late Triassic conodont assemblages include several common and mostly cosmopolitan, low- to mid-latitude species that are considered typical representatives of the Late Triassic conodont fauna (Rigo et al. 2007). A more detailed understanding of the palaeoecology of the Late Triassic conodont animal would require isotopic analyses on a species-by-species and basin-by-basin basis, which is only possible for samples with abundant conodont elements that are relatively scarce in Tethyan Triassic successions.

Conclusions

Palaeotemperatures calculated from oxygen isotopes of biogenic apatite of Late Triassic conodonts from the Lagonegro Basin have been used to constrain the life habitat of the Late Triassic conodont animal. Based on this dataset and considering the anatomical characteristics of the conodont animal and its phylogenetic relationships, Late Triassic conodonts are interpreted as surface dwellers with a nektonic lifestyle, within the euphotic zone. The oxygen isotopic composition of Late Triassic conodonts can be used to reconstruct palaeotemperature and δ^{18}O of surface sea waters.

Acknowledgements

We would like to acknowledge Dieter Lutz (University of Erlangen-Nürnberg, Erlangen, Germany) for conodont apatite δ^{18}O analyses. Additional thanks go to Heinz Kozur (Budapest, Hungary) for discussion and suggestions to support our idea on Triassic conodont palaeocology during "The Triassic climate" congress in Bolzano (Italy, 2008) and for a pre-revision of the manuscript. The first version of the manuscript benefited from useful comments of Alda Nicora (University of Milan, Milan, Italy) and Svend Stouge (Natural History Museum of Denmark, University of Copenhagen, Copenhagen, Denmark). Financial support for this work was provided by the M.I.U.R., grant 2004048302_002 to Paolo Mietto (University of Padova, Padova, Italy). MR is grateful to the "Fondazione Ing. Aldo Gini" for financial support of his research stay at the University of Erlangen-Nürnberg. We acknowledge comments and suggestions by Jared R. Morrow (San Diego State University, San Diego, California, USA) and Krzysztof Małkowski ((Instytut Paleobiologii PAN, Warszawa, Poland) as well as by the editor Jarosław Stolarski (Instytut Paleobiologii PAN, Warszawa, Poland).

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