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8. Palaeontology – in memoriam of Jean-Pierre Berger

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**UNIVERSITÄT
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8. Palaeontology – in memoriam of Jean-Pierre Berger

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Schweizerische Paläontologische Gesellschaft

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8.1

Pore morphometrics applied to Oligocene planktonic foraminifera : a method to disentangle phylogeny ?

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The Late Eocene is a time of general warm conditions. During this time planktonic foraminiferal assemblages are dominated by strongly specialized species (K-strategists) such as hantkeninids, morozovellids and acarinids. The Eocene-Oligocene transition marks the passage from « greenhouse » to « icehouse » conditions in the Paleogene (Coccioni et al. 2000) and witnesses the establishment of the Antarctic ice sheet (Coxall and Pearson 2007).

The entire Oligocene underwent a period of cool conditions (Zone P19 to P21) during which the warm and specialized K-strategist Eocene species were replaced by the cold simple r-strategist planktonic foraminifera possessing a high evolutionary potential. This climatic trend culminated in a strong climatic instability at its end corresponding to the Oligocene/Miocene boundary (equated to the major period's boundary Paleogene/Neogene).

It is only with the warm pulse from Zone P21b to the end of Zone P22 that the tendency reverses and K-strategists planktonic foraminifera re-appear in the world oceans. In particular, a new genus of planktonic foraminifera, the genus *Globigerinoides* first occurs during this time of climatic instability (Spezzaferri 1995). Species of this genus radiate and evolve starting from the Oligocene-Miocene boundary. They are still among the most important and abundant species in modern oceans.

Despite their present diversification, the early appearance and development of this lineage is still poorly known. The evolution of the early *Globigerinoides* represents the passage from r- to K-strategists by the appearance of supplementary apertures on the spiral side. However, their general morphologies are still not well defined, species cannot be clearly distinguished and therefore their lineage is difficult to trace.

We suggest here that pore density and diameters can be linked to different species and we propose to apply to the Late Oligocene and Early Miocene *Globigerinoides* a morphometric method previously applied to recent genera by Bé et al. (1969).

It consists in accurately measuring the diameter of pores from the internal wall texture and plot them versus the number of pores counted in a given shell surface.

We apply a statistical approach to test the method. As a result, we expect to link different species in a coherent lineage according to size and density of pores.

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8.2

The pachypleurosaurs from the Ducan area, southeastern Switzerland – validation of the species *Neusticosaurus staubi*?

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The Ducan region near Davos in southeastern Switzerland (Austroalpine Silvretta nappe in Canton Graubünden) provides an important site for Middle Triassic vertebrate fossils, excavated systematically since 1996. Beside numerous fish fossils only a few marine and terrestrial reptiles were discovered in the early Ladinian Prosanto Formation: pachypleurosaurs, nothosaurs, a placodont, two protorosaurs, and a rauisuchian (Furrer 2009). The first postcranial skeletal fragment of a pachypleurosaur was formerly classified as *Neusticosaurus staubi* (Kuhn-Schnyder 1959), however it was considered to be non-diagnostic at the species level (Sander 1989; Rieppel 2000). New findings of six nearly complete specimens allow a detailed reinvestigation of the pachypleurosaurs from the Ducan area.

Based on morphological and morphometric analyses, a species level classification is attempted. The specimens from the Ducan area are compared to the four species occurring in the classical section at Monte San Giorgio in southern Switzerland (late Anisian – early Ladinian). A review of the pachypleurosaurs from the Middle Triassic in Germany and the Netherlands gives insight into the temporal and geographical distribution of these animals.

The specimens from the Ducan area combine several characteristics of *Serpianosaurus mirigiolensis* and *Neusticosaurus pusillus* known from Monte San Giorgio. However, classification is complicated due to differences related to sex and age of the individuals. A preliminary parsimony analysis including all European pachypleurosaurs places the Ducan material between *Serpianosaurus mirigiolensis* and *Neusticosaurus pusillus*, within the clade of the Monte San Giorgio species.

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8.3

Unusually diverse bivalve assemblages from the Early Triassic (Griesbachian) of South China

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Early Triassic (Griesbachian) microbial limestone commonly overlays the latest Permian thick-bedded peri-reefal/shallow water limestone in the Guangxi part of the Nanpanjiang Basin (South China). Several fossiliferous lenses were discovered within the microbial limestone during two field campaigns.

These shelly accumulations form distinct intercalations between domes of microbial limestone. Such coquinoid lenses are interpreted as material washed in and trapped between the domes. They contain bivalves, gastropods, brachiopods and occasional ammonoids and ostracodes. Lenses from the new Wuzhuan section are dominated by bivalves; however the subordinate fauna contains gastropods, brachiopods and ostracodes.

Thirteen species of bivalves were recovered from the Wuzhuan lenses. *Towapteria schyhtica* is one of the dominant species. Other bivalves include *Bakevellia* sp., *Claraia* cf. *liuqiaoensis*, *Astartella* sp., and *Streblopteria* sp. nov., among others. At the genus level, five are long-ranging survivors, four are late Permian holdovers and four first appear in the Griesbachian.

From Shanggan, an unusually diverse mollusc fauna of Griesbachian age with high evenness of species abundances was first described by Kaim et al. 2010 and Hautmann et al. 2011. There, eleven bivalve species were obtained from a single lens.

Among the thirteen bivalve species from Wuzhuan, only a single one is shared with the Shanggan fauna, thus yielding a total of 24 species of bivalves for the benthic faunas of the microbial limestone in this area. This reflects a high diversity and evenness of the benthic fauna from the microbial limestone in China already in the Griesbachian. Sediments enclosed within the basal Triassic microbial limestone documents the first recovery episode of benthic ecosystems in the immediate aftermath of the end-Permian mass extinction.

8.4

Phylogenetic and ecological impact of Eocene climatic events on European artiodactyls

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We present here the objectives and first results of a project launched by the late Professor Jean-Pierre Berger. Aim of the project is to test if there is a causal link between the evolution of European artiodactyls and Eocene climatic events.

Numerous significant climatic events were recorded during the Eocene including the Paleocene-Eocene Thermal Maximum (PETM), the Eocene Thermal Maximum (ETM), the Early Eocene Climatic Optimum (EECO), the Middle Eocene Climatic Optimum (MECO), and finally the Terminal Eocene Event (TEE) (Berger 2011). Extinctions and apparitions of land mammal communities, and in particular of the European artiodactyls, occurred during those climatic events (e.g. Erfurt and Métais 2007). The first European Diacodexids appeared during the PETM. Most of the representatives of this group disappeared during the EECO. This time also witnesses the appearance of European Dichobunidae and probably of Xiphodontidae. A strong turnover can be noticed at the MECO in almost all the families. At the TEE, most of the species disappeared, replaced by taxa with major components of Asian origin. Additionally, in the middle Lutetian several families such as Anoplotheriidae, Choeropotamidae and Dichobunidae diversified. Likewise, the family Anoplotheriidae endured drastic changes around the Bartonian-Priabonian boundary: almost all Dacrytheriinae disappeared and the Anoplotheriinae diversified. Analogous turnovers happened in the other families in the same time.

The enhancement of knowledge about the phylogeny of Eocene artiodactyls, which is still controversial, is an essential requirement to better understand the effect of the climatic changes on their evolution. The genus *Robiacina*, for example, is sometimes considered as the oldest Cainotheriidae and sometimes as a primitive Anoplotheriidae (Erfurt and Métais 2007). Within the Anoplotheriidae, the phylogenetic link between the subfamily Dacrytheriinae and the more recent subfamily Anoplotheriinae is unknown. Also, tracing the relationships between the families Cainotheriidae, Anoplotheriidae, Xiphodontidae and Mixtotheriidae is essential to understand the evolution of the classic group of Tylopoda.

Referring the ecology, the progressive emergence of some particular adaptations within several families such as the selenodontology and the elongation of limbs occurred also during Eocene climatic events. Therefore, a better description of the ecological adaptations of the Eocene artiodactyls can bring significant insight about the European terrestrial palaeoecosystems. In particular, the cranial and mandibular morphologies, the teeth shape and an analysis of teeth meso-wears may give relevant information about their diet (e.g. Fortelius and Solounias 2000). An analysis of dental cementum may relate to seasonality (Lieberman 1994) and the analysis of postcranial remains allows identifying some strategies of locomotion and of adaptations to environments (e.g. Christensen 2002).

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8.5

Soft-part preservation in heteromorph ammonites from the Cenomanian-Turonian Boundary Event (OAE 2) in the Teutoburger Wald (Germany)

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Excellent preservation of ammonites in Cretaceous rocks has been documented several times already. For instance, Lebanese Plattenkalke have yielded heteromorph ammonites with phosphatised soft tissue (Wippich & Lehmann 2004) and, more recently, US-American baculitids (also heteromorphs) were published showing a perfectly preserved radula *in situ* (Kruta et al. 2011).

Several decades ago, WR extracted 17 flattened individuals of baculitid ammonoids with carbonised and partially also phosphatised soft parts from thin laminated marlstones belonging to the OAE 2 of the Late Cenomanian Hesseltal Formation of Lengerich in the Teutoburger Wald mountains (Westphalia, Northwestern Germany). The advantage of these specimens is that the shell is dissolved. However, it appears like the shell has been deposited with the soft parts because the shell outline is still visible as well as such shell structures that were not carbonatic like the siphuncle and melanin-rich parts of the shell (megastriae, aperture).

Several of these ammonites preserve remains of the buccal mass including jaws (more or less articulated) and radulae. Additional remains which were not mineralised *in vivo* have been found. Most of which are much more difficult to homologue with organs of their Recent coleoid or nautilid counterparts. For example, behind the mouth parts, two specimens display two lateral, symmetrically arranged more or less oval structures. In one of the two specimens, these two are linked with each other and this connection covers the supposed oesophagus. According to this arrangement, these oval structures have been interpreted as remains of the cephalic cartilage with the eye capsules, which were previously unknown from ammonoids. Further soft-parts include structures, which we interpret as digestive tract including oesophagus, crop, stomach and (?) the caecum as well as remains of what might have been the oviduct.

In the same horizon, patchy occurrences of numerous isolated upper and (less abundant) lower jaws (probably also from baculitids) as well as radulae occur (Wippich 2005). These jaw-accumulations may represent regurgitates or droppings of larger predators. According to the facies and associated microfossils, the here portrayed cephalopod remains were probably deposited in an epicontinental setting, perhaps at a palaeodepth between 200 and 600 metres. In this Late Cretaceous fossilagerstätte, ammonite upper jaws and anaptychi are among the most abundant fossils.

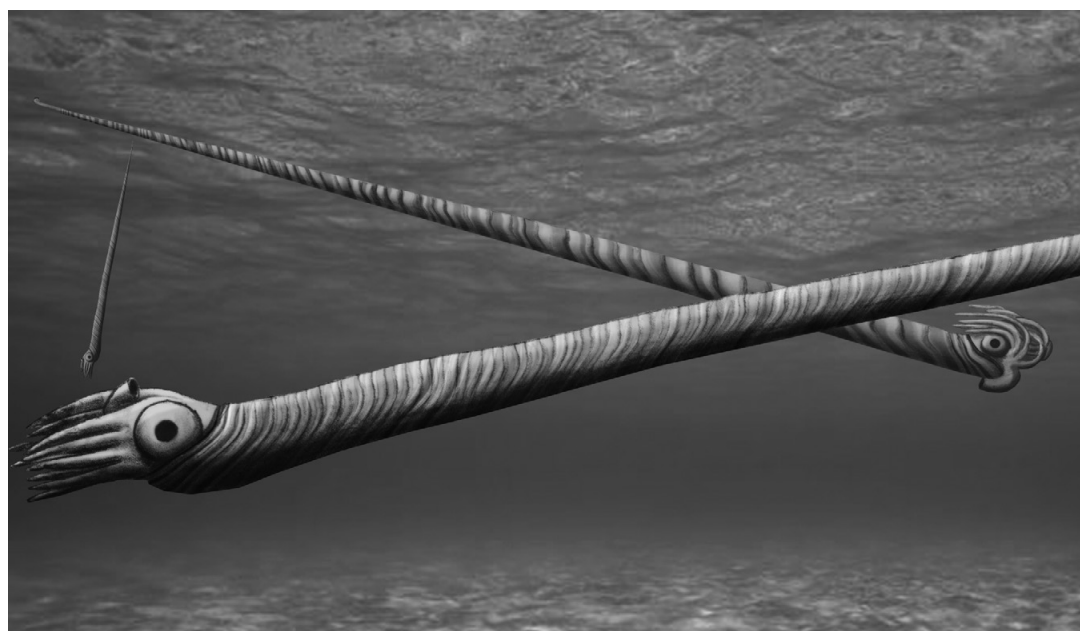


Figure 1. Reconstruction of the baculitid from northern Germany. Note the large eyes. Their swimming orientation is according to Hauschke et al. (2011), but a more or less vertical shell orientation is also conceivable, at least when the distribution of shell mass and phragmocone-gas is taken into account. The arm morphology and positions are speculative.

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8.6

Morphological evolution of *Globorotalia menardii* and related forms during the past 8 million years at ODP Site 925B (Ceara Rise, western tropical Atlantic)

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“Evolutionary prospection” was initiated with the goal to investigate the morphological evolution of Neogene menardi-form globorotalids from selected time-slices and key-locations in the world ocean as a case study for morpho-logical speciation in calcareous plankton (Knappertsbusch, 2011). For this purpose downcore studies of changes of menardi-form globorotalid shells during the past 8 million years was carried out at the western tropical Atlantic ODP Site 925B. A total of 5976 specimens from 33 isochronous time-levels to previous studies at DSDP Sites 502 and 503 were measured. Taxa include lineages of *G. menardii-limbata-multicamerata*, *G. menardii-pertenuis-exilis*, the *G. miocenica*-“pseudo-miocenica” group and the *G. menardii-G. tumida* morpho-plexus. Using our robot AMOR (Knappertsbusch et al, 2009) and MorphCol software shell parameters from digitized outlines were obtained. Special attention was given to the evolution of spiral width (Dx) versus axial length (Dy) of tests in keel position, but other parameters were collected as well. Results show a dominating gradual increase of shell size in *G. menardii*, but a prominent expansion to large forms after 2.72 Ma (normalized time of -0.34 in Figure 1), which is surprisingly similar to trends observed at remote Caribbean DSDP Site 502 (Knappertsbusch, 2007).

In Figure 1 shell variability of *G. menardii*, transitional *G. limbata* and *G. multicamerata* is shown in form of surfaces of equal specimen frequency in the bivariate morphospace of Dx versus Dy and ranging from 0 through 8 Ma. These iso-surfaces enclose specimens of equal frequency throughout the Dx, Dy morphospace across the studied time span. The philosophy behind is, that populations belonging to a particular taxon would appear as clusters, that through time connect together to form a “phylophenetic” tree. Such trends were visualized with Voxler software from Golden Software, Inc. (Knappertsbusch and Mary (2012).

The combination of visual taxonomy and morphometric measurements from ODP Site 925B allowed to visualize the transition from ancestral, extant *G. menardii* to the extinct *G. limbata-G. multicamerata*. Without resolving along the time-axis, these three morphological groups would strongly overlap and distinction would not be possible without extra information.

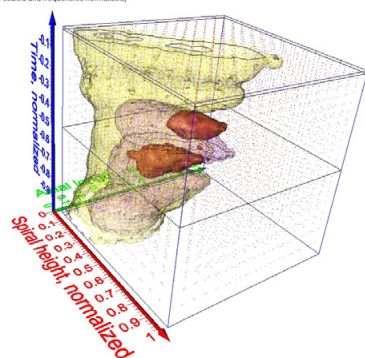
In these volume-density representations high iso-values indicate frequent specimens (occurring in the central part of bivariate frequency contour diagrams). In contrast, low iso-values indicate rare specimens and form the outermost “skin” of a distribution through time. Because innovative specimens are usually rare at their first appearance, low-frequency iso-surfaces (arbitrary iso-values of 0.4665 of sample normalized frequencies) were chosen to illustrate evolutionary progress in *G. menardii*, *G. limbata* and *G. multicamerata*.

G. menardii (4 to 6 chambers in the final whorl) slowly increases in size until about 2.7 Ma, when it suddenly expanded to large shells in the Dx versus Dy plane. *G. limbata* (which was recognized by 7 chambers in the final whorl and by a somewhat shiny surface texture) falls almost completely inside the distribution of *G. menardii* but shows a slow increase in size. *G. multicamerata* (8 or more chambers in the final whorl) appears as two clusters within the Pliocene and morphologically shows strong overlap with 5 to 6 chambered *G. menardii* from after 2.7 Ma.

Further statistical analysis must be carried out including all the remaining measurements in order to develop a numerical classification, that is independent from visual species identification.

Evolution of menardiform globorotalids

Red: *G. multicamerata* from ODP Site 925B (Ceara Rise)
Purple: *G. limbata* from ODP Site 925B (Ceara Rise)
Yellow: *G. menardii* from ODP Site 925B (Ceara Rise)
(Axes scaled and frequencies normalized)



Evolution of menardiform globorotalids

Red: *G. multicamerata* from ODP Site 925B (Ceara Rise)
Purple: *G. limbata* from ODP Site 925B (Ceara Rise)
Yellow: *G. menardii* from ODP Site 925B (Ceara Rise)
(Axes scaled and frequencies normalized)

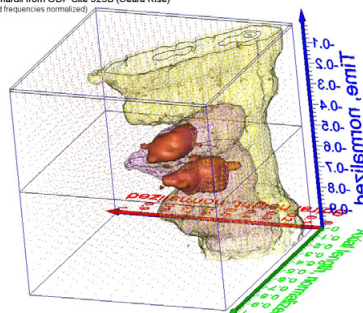


Figure 1. Volume-density diagrams of the variation of Dx (spiral height, red axis) versus Dy (length in keel view, green axis) through time (blue axis) for *G. menardii* (yellow), *G. limbata* (purple), and *G. multicamerata* (red) at ODP Site 925B (Ceara Rise) during the past 8 million years. Left figure in front view, right figure in back-view. Axes are normalized to values between 0 and 1, while the time axis ranges from 0 (Recent) to -1 (8 Ma).

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8.7

Paleontology and stratigraphy of the North- Middle Upper Rhine Graben (N-Middle URG): relationships between rift system, alpine orogeny and paleoclimate

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Located between Strasbourg (France) in the south and Landau (Germany) in the north, the North- Middle Upper Rhine Graben (N-Middle URG) was the site of an intense lacustrine, brackish and marine sedimentation from the middle Eocene to the Late Oligocen

The traditional stratigraphic succession (Schnaebale 1948) is, in stratigraphic order : the Transition zone, in contact with the underlying Jurassic limestone, the Dolomitic zone, the Red Bed, the Lower- Middle- and Upper Pechelbronn Beds, and the “Série Grise”.

There are very few outcrops in this area, mainly the old quarry of Bouxwiller, consisting in lutetian marls and limestones, marls from the Upper Pechelbronn Beds, as well as the Série Grise (Isselbaechel), but many boreholes and seismic lines exist because of the oil industry, especially GPK4 Soultz-sous-Forêts, covering the whole series, and the borehole of Preuschdorf 01983X2854, which is a complete cored drilling corresponding to the Upper Pechelbronn Beds with a small part of the Middle Pechelbronn Beds at the base. These localities provided heavy minerals, lithological, micro- macro- and nanopaleontological data.

Using these data and the previous publications, a stratigraphic correlation will be exposed, with a datation of the Red Bed based on charophytes, showing that these layer are different from the Red Bed found in the South Upper Rhine Graben (Schwartz1997), and a datation of the Upper Pechelbronn Beds based on nanofossils in contradiction with Martini and Reichenbacher (2007).

The previous paleogeographical and paleoclimatic reconstitutions (Berger et al. 2005 a, Pirkenseer 2007) will also be discussed, with a focus on the predominance, in the North- Middle Upper Rhine Graben, of local tectonic on global sea level changes.

This study is financed by the SNF Project 200020-118025 “Paleontology and Stratigraphy of the Rhine graben during the Paleogene”. We thank Marion Kimmel (Geoderis) for giving access to the core Preuschdorf, Philippe Elsass (BRGM) for access to the Soultz samples and for fruitful discussions.

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8.8

Micro-dissection reveals inner structure and ontogenetic growth of Pliocene menardellids (planktonic foraminifera)

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Planktonic foraminifera are marine protists that build a calcareous shell. They are widely used as biostratigraphic markers and as tools for paleoceanographic reconstructions. Recently, molecular approaches have targeted critical aspects of their classification, revealing the existence of genetically distinct cryptic species within the traditionally established morphospecies (Darling and Wade, 2008), calling for extra morphological studies of extant and fossil foraminifera.

Discrimination between species by shell morphology remains, however, still difficult, many planktonic foraminiferal species showing convergent morphologies and clinal intergradation. Morphological plasticity is strongly influenced by ontogeny (Hemleben et al., 1985; Brummer et al., 1987), which has important implications for the morphological characterization on the population level and in the preserved assemblages. The present work investigates the possibility of distinction between morphologically convergent morphospecies by the study of their ontogenetic growth.

Although micro-CT techniques nowadays allow for studying foraminiferal shell growth of individuals, this novel technique is still at infancy for routine application in larger amounts of specimens, which draws us back to traditional shell dissection techniques. Such techniques, however, are difficult, very labor intensive, and documented studies were limited to a few of largest individuals (Huber, 1994). We have developed microdissolution as an alternative and more efficient protocol to study ontogenetic shell growth of foraminifera on a statistically significant number of specimens (up to 350 individuals). For this we use concentrated hydrochloric acid to dissolve the umbilical side of the test under the binocular, while the dorsal side of the test is mounted on multicellular faunal slides using a mixture of water soluble glue and sodium hydroxide to protect the spiral side from dissolution. This method proofed very fast and allowed the study of ontogenetic growth and internal ultrastructural features.

Using SEM pictures of microdissected specimens, we could measure the ontogenetic growth of Pliocene menardellid foraminifera. We show the relationship between shell morphology and growth rate within three morphological convergent groups, e.g. - *Globorotalia menardii*, *Globorotalia limbata* and *Globorotalia multicamerata*. Our study confirms the occurrence of a strong size dependent variation caused by differences of maturation between species within this genus (Schmidt et al. 2006). In addition, we identified several internal structures, that serve as primary taxonomical criteria to discriminate the different Pliocene menardellid morphospecies.

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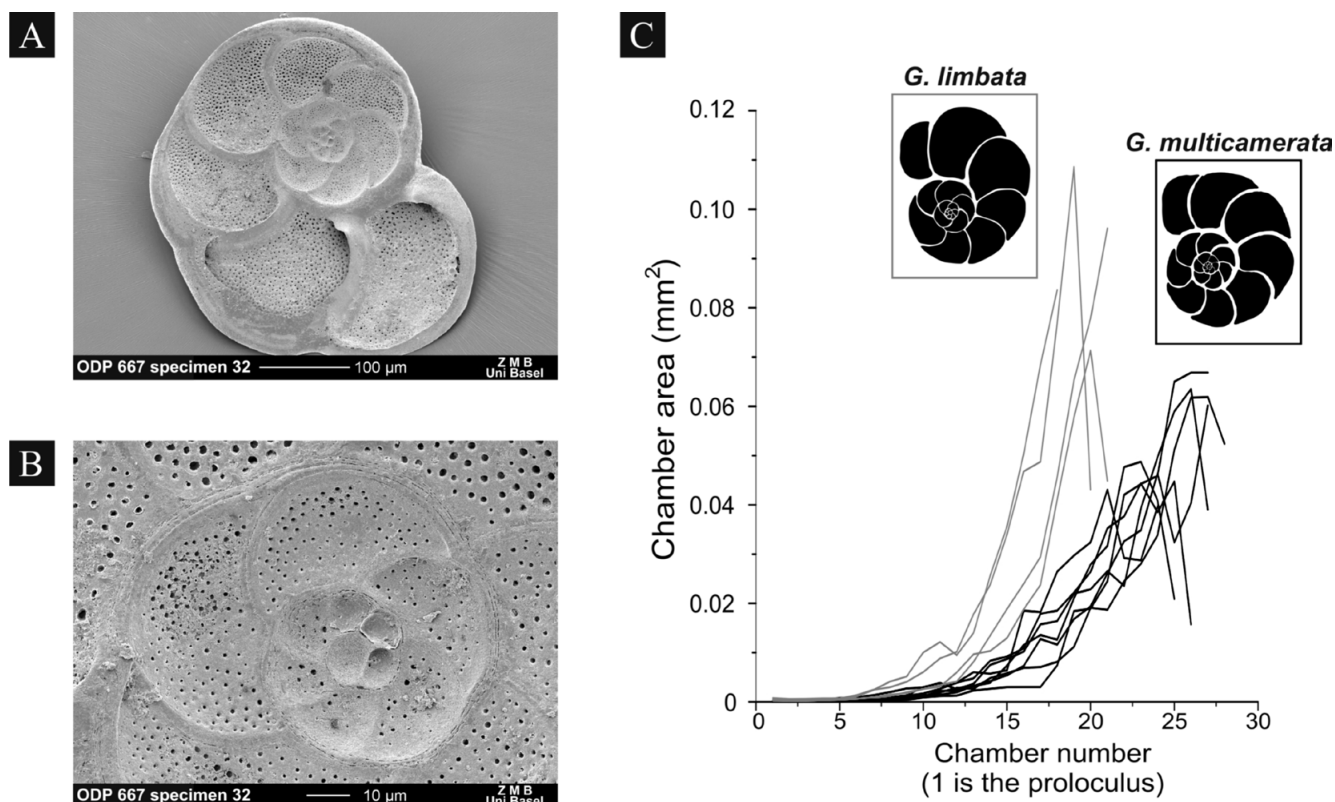


Figure 1: Examples of a microdissected menardellids : A: Specimen overview B: Magnification of the first whorl exhibiting the proloculus. C: Differences in growth rate between specimens of *G. limbata* and *G. multicamerata*.

8.9

Ruminantia ecomorphology and the complexity of the phylogenetic signal

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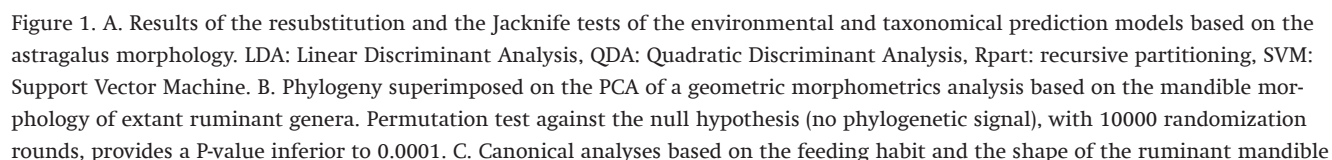
The covariation of an organism's morphology (or a part of it) and its ecology corresponds to the ecomorphology. The shape of a bone is strongly influenced by its function and the physical requirement of this function. In the present study, two specific bones of ruminants (the astragalus used for locomotion and the mandible used for mastication) have been analyzed in order to define ecological pressures and phylogenetic trends.

Nowadays, the ruminants are the most diversified group of large mammals in having more than 200 extant species. They occupy numerous ecological niches covering many different types of environment such as deserts, grasslands, savannas, forested areas, and mountains. Their feeding habits vary from selective browsing to pure grazing. Their evolution is deeply anchored in the Paleogene of Laurasia (Mid to Late Eocene). However, extant families only appeared during the Mid-Miocene.

Numerous ecomorphological studies on postcranial bones have recently demonstrated that the ruminants, especially Bovidae, that cover the largest range of ecological variability among the ungulates, are good ecological proxies. Using the Support Vector Machine (SVM) method, associated with a Principal Component Analysis (PCA), we greatly improved the

The Geometric Morphometrics analysis based on the shape of the mandible provided good results on the phylogeny and ecology of fossil (until the Burdigalian) and extant ruminants. Within extant Pecora, Giraffidae differ by having an extremely elongated *diastema*. Cervidae are generally more slender than Bovidae, but an overlapping area between these two families groups together the most massive Cervidae and the most slender Bovidae (Mennecart et al. 2011, in press). Superimposing the phylogeny on the plots of the analysis permits us to prove (with a permutation test) that the phylogeny is supported by the graph, and the mandible shape possesses a strong phylogenetic signal (Fig. 1B).

			Environment				Taxonomy	
			Bovidae		Ruminantia		without PCA	with PCA
			without PCA	with PCA	without PCA	with PCA		
Resolution	LDA		65.5	65.6	47.8	47.8	70.9	70.9
	QDA		75.7	75.7	61.2	61.2	79.4	79.4
	rpart		79.8	76.6	69.4	72.7	85.7	87.8
	SVM		73.4	83.0	55.0	72.7	77.8	87.3
Resolution @ 100% overlap	LDA		62.9 (6.6)	62.1 (6.4)	39.1 (4.2)	39.0 (4.4)	66.8 (2.8)	66.9 (2.7)
	QDA		60.6 (5.7)	57.9 (5.2)	44.0 (4.8)	43.8 (4.9)	68.1 (3.3)	68.2 (3.6)
	rpart		57.7 (5.3)	57.9 (6.0)	33.2 (4.1)	38.1 (4.4)	76.3 (3.1)	69.5 (4.9)
	SVM		64.1 (5.4)	66.1 (6.2)	45.4 (3.6)	50.1 (4.4)	75.5 (2.0)	74.1 (3.3)



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8.10

From beachboys to river rafters – The sedimentary environment of the vertebrate tracksites of the autochthonous Triassic of the Aiguilles Rouges Massif (SW Switzerland)

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The autochthonous Triassic sediments of the Aiguilles Rouges Massif in SW Switzerland were last extensively studied by Amberger (1960). On the basis of lithological sections he concluded that the siliciclastic sequence unconformably overlying the Carboniferous/Permian basement was part of the Alpine Buntsandstein and were deposited in a shallow marine/sandy beach environment. Later on, Demathieu & Weidmann (1982) concluded that this unit was of Carnian age because of the presence of dinosaur footprints. This age and track assignment was challenged by several authors (e.g. Lockley & Meyer 2000). Most tracks, if not all, belong to indeterminate chirotheriids and dinosaur footprints are absent.

Reinterpretation of the main site at Vieux Emosson and the analysis of nearby newly discovered trackways reveal the presence of the ichnotaxa *Isochirotherium soergeli* and *Chirotherium barthi*. These ichnotaxa represent a “Chirothere assemblage” and indicate an older, Late Olenekian to Early Ladinian, age (Cavin et al. 2012) confirming earlier interpretations (Lockley and Meyer, 2000; Meyer & Thüring, 2002).

The present study focuses on detailed analysis of the sedimentary sequence of the Triassic between the Col du Jorat in the North to the Col de la Terrasse in the South.

The sequence consists of a basal conglomerate that fines upward to medium- and coarse-grained sandstones with trough cross bedding, and capped by rippled surfaces with thin mudstones beds with mudcracks. The rippled surface at the top of the sandstone-dominated sequence is the main track level, as seen at the Vieux Emosson and Cascade d'Emaney localities. It is overlain by red and green mudstones interbedded with thin rippled sandstones. The latter show two additional trackbearing levels near the base. Consequent prospection have led to the discovery of eight new track localities between the Col du Jorat and the Col de la Terrasse during the field season 2012 confirming a recurrent track association that forms a megatracksite.

Fining upward sequences, truncated by channel-fills, texturally immature conglomerates, and unimodal paleocurrents indicate deposition in shallow bedload-dominated streams. Fine-grained facies are interpreted as floodplain and possibly playa lake deposits. The northwest paleoslope supports drainage into the Germanic Basin, and not to the Tethyan realm as postulated by others. Consequently the original idea of Amberger (1960) that these deposit form part of the “Buntsandstein” is corroborated by the present study, however the archosaurs were not beach boys but river rafters.

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8.11

Empirical 3D-models of Palaeozoic ammonoids and the ontogeny of septum- and chamber-volumes of three major ammonoid-clades

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Ammonoids belong to the cephalopods and are of a great importance in stratigraphy. Although they are well studied, some aspects of their palaeobiology and evolution are still unexplored. For example, empirical studies of changes in shell and chamber volume through ontogeny of the major clades have never been carried out. 3D-modelling offers new perspectives to provide new insights in their shell properties. The aims of our present work consist in documenting (1) volumetric growth of septa and phragmocone chambers in detail and (2) ontogenetic changes between major ammonoid-clades from the Palaeozoic.

This is achieved by 3D-reconstructions (see figure 1) based on actual specimens, which were subjected to grinding tomography. For those specimens, CT-scans cannot be used because of the insufficient contrast between the calcitic replacement shell and the carbonatic sediment matrix. Therefore, three specimens of three major clades have been investigated using grinding tomography: the Middle Devonian agoniatitid *Agoniatites clariondi*, the Middle Devonian anarcestid *Diallagites lenticulifer*, and the Early Carboniferous goniatitid *Goniatites multiratus*. The sections were then traced manually for each fourth slice, and lastly processed for the 3D-reconstruction using VGstudiomax® 2.1, which allows direct volume calculations. The chamber volumes are plotted *versus* shell diameter, which is used as a proxy for growth while the septum volumes are plotted *versus* aperture height through the ontogeny of the respective specimen.

The obtained volume data allow both intra-specimen comparisons through ontogeny and inter-clade comparisons, i.e. through phylogeny. Further specimens from both older and younger ammonoid clades are planned to be investigated to provide more information on volumetric changes through ontogeny and phylogeny. Additionally, these first volumetric data provide the possibility to empirically test the existing mathematical models for neutral buoyancy of ammonoids.

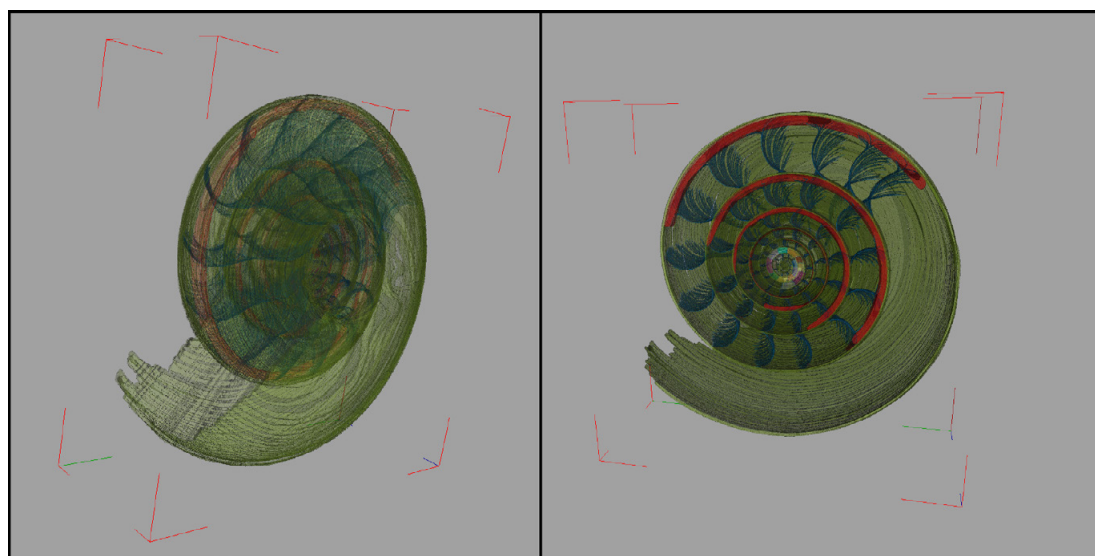


Figure 1. 3D reconstructions of *Agoniatites clariondi*: complete (left) and clipped (right)

8.12

Comparative skull anatomy of placodonts (Diapsida: Sauropterygia) using μ CT scanning - implications for palaeobiogeography and palaeoecology

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Placodontia are a basal group of durophagous and often heavily armoured sauropterygian marine reptiles that inhabited shallow marine environments of the Tethys Ocean from the early Middle to the Late Triassic (e.g. Rieppel 2000). They are well known from Europe, especially Switzerland, Germany and Italy, and have recently been discovered in southern China, with four new taxa being described in the last twelve years (Li 2000; Li & Rieppel 2002; Jiang et al. 2008; Zhao et al. 2008). However, detailed phylogenetic and palaeoecologic analyses that go beyond the primary osteological descriptions have not yet been conducted for all of these new taxa.

As part of an on-going project to create a comprehensive phylogeny of the Placodontia, placodont skulls from both Europe and China were scanned using micro-computed tomography (μ CT). This exposed many important details that were previously obscured or unclear in previous descriptive works, such as braincase anatomy, as well as allowing the reconstruction of structures such as the endocranium and inner ear (e.g. Neenan & Scheyer in press; Fig. 1). The inclusion of a new skull from the middle Triassic of the Netherlands also sheds light on the origins of the clade, with implications for their dispersal and subsequent diversification throughout the Tethys.

These results are not only significant for the understanding of placodont relationships and dispersal but, due to the plesiomorphic position of Placodontia within Sauropterygia, also have implications for our understanding of sauropterygian palaeobiogeography as a whole.

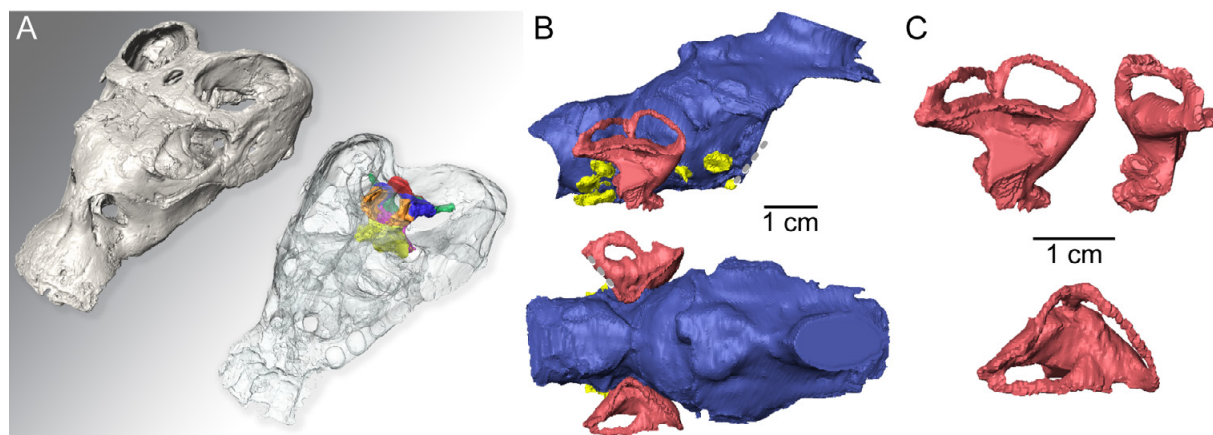


Figure 1. Reconstructions from a skull of the placodont *Placodus gigas* as an example of what can be achieved with the use of μ CT scanning. A, Braincase reconstruction, highlighting how elements that are usually obscured can be modeled. B, Virtual model of the endocranium (blue), inner ear (pink) and cranial nerves (yellow) in right lateral (top) and dorsal (bottom) views. C, Virtual model of the inner ear in right lateral (top left), caudal (top right) and dorsal (bottom) views. Modified from Neenan & Scheyer (in press).

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8.13

Stratigraphic Studies In The Sivas Basin (Central Anatolia, Turkey). 1- The Role Of The Charophytes.

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The Sivas Basin is one of the Central Anatolian Basins in Turkey which developed after the closure of the North Neotethys ocean in Late Cretaceous times. This basin mainly Cenozoic records the geodynamics of the collisional and post-collisional history of the Alpine belt in Central Anatolia. It covers the eastern and southeastern parts of the Kirsehir Massif to the North and the northern part of the Taurus belt to the South. It can be subdivided in several sub-basins which present rather different lithostratigraphic successions. However all include an alternation of marine and continental formations (with evaporites in some sub-basins) which interfinger together. Synsedimentary tectonic (especially the salt tectonics) and magmatic events led to a very complex tectono-lithostratigraphic successions. In such a context the precise knowledge of the chronology is of prime importance for the reconstitution of the imbricated paleogeographies and paleoenvironments. If the marine sequences (Paleocene-Eocene; Upper Oligocene-Lower Miocene) are rather well dated due to their fossiliferous facies it is not the case for the continental series in which only a few number of sites have been previously dated by different methods such as vertebrates in lacustrine layers (Uppermost Oligocene; Mid and Upper Miocene; Pliocene); spores and pollens in lignites (Middle Miocene); K/Ar in basaltic lavas (13 to 15 Ma). Despite these punctual well dated sites the main part of the thick (one to three km thick), continental sequences (including the evaporites) remained undated until the discovery of charophytes in lenses of lacustrine marls and limestones intercalated in the red clastics, or above the evaporites, in several sites over the western half of the basin. We present here preliminary results of a study of these charophytes.

The following assemblages have been found in several sites located in the Western part of the basin (Malak, Kabasakal, Apa), or in the central part (the others):

Malak: *Rhabdochara praelangeri-major*, *Rh. stockmansii-major*, *Chara microcera*, *Sphaerochara hirmeri?*, *Nitellopsis* sp., *Gyrogonia* sp. (Rupelian-Chattian)

Kabasakal: *Charites minutissima*, *Tolypella* sp., *Chara* sp., *Rhabdochara major?*. (Lower Oligocene: Rupelian)

Apa: *Chara notata*, *Sphaerochara hirmeri* gr., *Lychnothamnus* sp., *Rectangulochara* sp. (Lower to Middle Miocene according to the other data such as K/Ar age at 13Ma)

Egribucak: *Lychnothamnus (Stephanochara) ungeri-rochettiana* gr., *Rhabdochara* sp. (Upper Oligocene)

Emirhan: *Nitellopsis (Tectochara) meriani* gr., *Lychnothamnus (Stephanochara) cavaleri*, *Chara notata*, *Sphaerochara hirmeri* (Upper Oligocene-Lower Miocene)

Karayün-1: *Lychnothamnus (Stephanochara) cavaleri*, *Chara notata*, *Sphaerochara hirmeri* gr., *Lychnothamnus (Stephanochara) ungeri-rochettiana* gr. (Upper Oligocene-Lower Miocene)

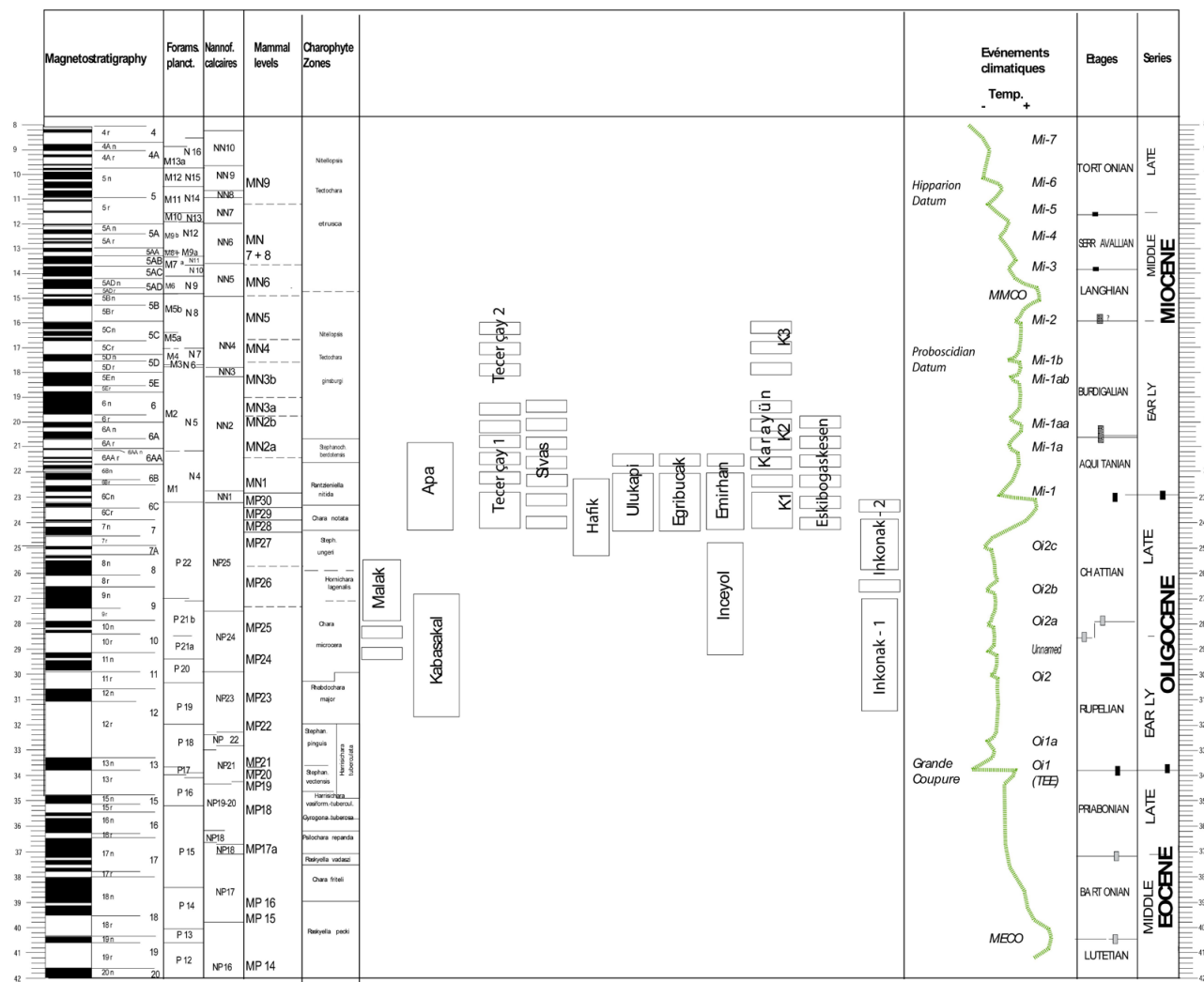
Karayün-2: *Charites minutissima*, *Lychnothamnus (Stephanochara) cavaleri*, *Nitellopsis (Tectochara) meriani* gr., *Chara notata*, *Sphaerochara hirmeri* gr., *Lychnothamnus (Stephanochara) ungeri-rochettiana* gr. (Upper Oligocene-Lower Miocene)

Karayün-3: *Chara notata*, *Ch. praeberdotensis-berdotensis*. (Burdigalian)

Inkonak-1: *Chara microcera-notata* gr., *Sphaerochara hirmeri* gr., *Tolypella* sp., *Rabdochara major* (Lower Oligocene)

Inkonak-2: *Nitellopsis meriani*, *Lychnothamnus ungeri* ?.

Discussion. In the absence of a Tertiary calibrated reference section for Central Anatolia the ages are tentatively attributed here on the basis of the western European zonation for the charophytes. These ages are generally in more or less good agreement with other chronological data (K/Ar ages and biochronology), but an uncertainty subsists in some cases. For instance the Notata zone covers the uppermost Oligocene and the Lower Miocene (perhaps up to Langhian). This is not precise enough for dating the synsedimentary events such as the tectonic events (salt tectonics), nevertheless these data show that an important period of deformation occurred before the Notata zone, which mean during the Upper Oligocene.



Magneto-Bio-Chronostratigraphie

Corrélations modifiées d'après Berger & al. 2005, Kálin & Kempf 2009, Berger 20

11

Evénements climatiques:

MMCO: Middle Miocene Climatic Optimum

TEE: Terminal Eocene Event

MECO: Middle Eocene Climatic Optimum

JPB version 2 dec 2011

(modifié d'après Zachos et al. 2001, Pälike & Hilgen 2009)

8.14

Taxonomy and phylogeny of the turtle *Tropidemys langii* Rütimeyer, 1873 based on new specimens from the Kimmeridgian of the Swiss Jura Mountains

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The fossil turtle *Tropidemys langii* is a representative of Plesiochelyidae, a traditionally recognized group of Late Jurassic turtles (Joyce 2007) diagnosed by the presence of three cervical scutes (Fig. 1) and adapted to life in the sea. *Tropidemys langii* was only known from fossilized carapaces and, possibly, plastra from Europe, most notably the famous 'Solothurn Turtle Limestone' of Switzerland (Rütimeyer 1873; Bräm 1965; Meyer 1994). Due to the sparse fossil record of *Tropidemys langii*, several questions concerning its taxonomy and phylogeny have remained unanswered.

Here, new material of *Tropidemys langii* is reported from the Kimmeridgian of the region of Porrentruy, Canton Jura, Switzerland. In addition to three well-preserved carapaces (Fig. 1), associated plastra and limb bones (humerus and femur) are described for the first time. The type specimen of '*Tropidemys valanginiensis*' and '*Pelobatochelys blakii*' lack diagnostic characters, but can nevertheless be referred to *Tropidemys* (Püntener et al., submitted). A potential extension of the lineage into the Early Cretaceous is uncertain, however, as the type locality of '*Tropidemys valanginiensis*' is dubious. A cladistic analysis shows that *Tropidemys langii* is sister to *Plesiochelys solodurensis*, thereby tentatively confirming for the first time the monophyly of Plesiochelyidae using cladistic arguments (Püntener et al., submitted).

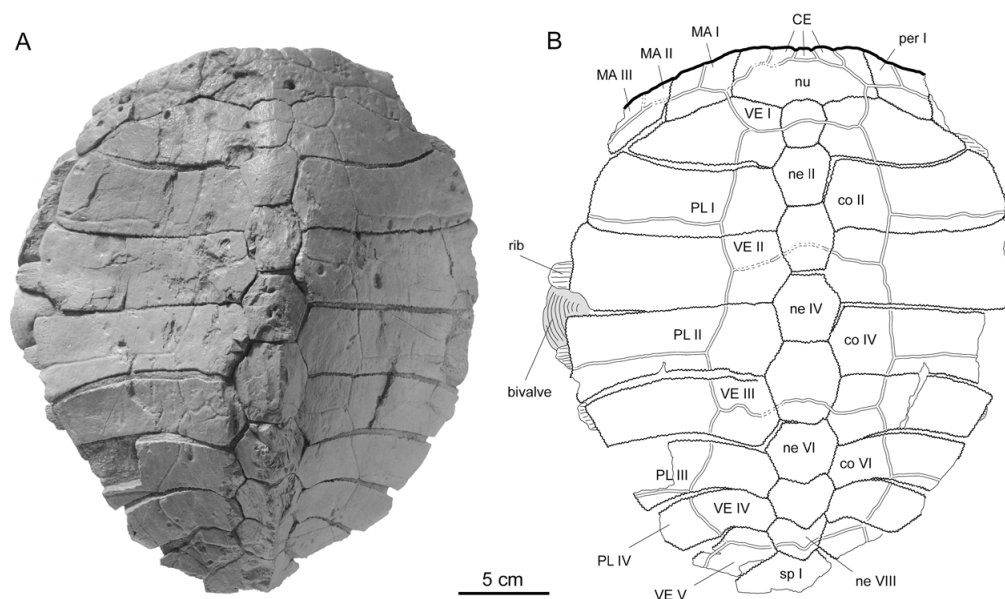


Figure 1. Specimen CRE985-1 of *Tropidemys langii* (Kimmeridgian, Porrentruy, Switzerland). Carapace in dorsal view. A, photograph; B, illustrative drawing showing bone sutures (zigzag line); scute sulci (double line); the preserved outline of the carapace (thick line); and fractures (thin line). Abbreviations: co, costal; ne, neural; nu, nuchal; per, peripheral; sp, suprapygal; CE, cervical; MA, marginal; PL, pleural; VE, vertebral. Photograph by Palaeontology A16.

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8.15

New insights on the stratigraphic distribution and phylogeny of foraminifers from the study of a Panthalassan terrane

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On account of their abundance, diversity, rapid evolution, wide distribution, and ease of use and recovery in both modern and fossil environments, foraminifers are routinely used to reconstruct environmental changes. Excellent markers of decline and diversification through time, they are also widely used as biostratigraphic indicators. Multiple unknowns, however, still remain as far as their phylogeny, global distribution over time, and ability to survive and recover from major biological crises is concerned.

During the Triassic, the earth was divided into two distinct marine worlds, namely the Tethyan and the Panthalassan domains, which connections were limited. Whereas the foraminiferal distribution has been thoroughly studied in the Tethys, only few investigations have been lead in the Panthalassa, where several million years of the foraminiferal evolution are unknown. Our study of the Late Triassic Wallowa carbonate platform (Wallowa Terrane, NW USA) of Panthalassan affinity has provided significant contributions to the understanding of the global diversity, distribution, and evolution of foraminifers.

In the Panthalassa, the stratigraphic distribution of foraminifers differs significantly from that of the Tethys. As indicated by a stratigraphic shift of several million years, Late Triassic foraminifers were not able to disperse easily across the open sea and have evolved independently in the two domains. The finding of numerous missing links reveals that a large part of the foraminiferal evolution occurred in this disregarded oceanic domain and greatly improves previous phylogenetic frames. As suggested by the strong similarities existing between Late Triassic Panthalassan foraminifers and complex Early Jurassic Tethyan foraminifers, the Panthalassa was probably a refuge for foraminifers during the Triassic-Jurassic biotic crisis.

These discoveries have important implications for the use of foraminifers in biostratigraphy, paleobiogeography, taxonomy, and molecular phylogeny. Further studies of the spatial and temporal evolution of Panthalassan foraminifers should provide a solid basis to understand processes controlling the foraminiferal speciation, diversification, extinction, dispersal, and recovery before, during, and after major extinction events.

8.16

Palaeogeography and evolution of the Triassic basal ray-finned fish *Saurichthys*

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Saurichthys was a Triassic lower actinopterygian (ray-finned fish) with a global distribution. It is distinguished from contemporaneous fishes by its garfish-like body shape – in fact, *Saurichthys* was the first actinopterygian that developed such a highly derived bauplan. Its elongated rostrum and body and specialised squamation pattern enabled *Saurichthys* to become one of the top predators among Triassic fishes, both in marine and freshwater environments. The specialized morphology of *Saurichthys* makes even fragmentary material easily identifiable at least at the genus level, thereby reducing the risk of being overlooked in the field and in collections. Hence, the fossil record of *Saurichthys* can be considered as well-known. We review the global fossil record of *Saurichthys* and use it for a case study of trends in morphological adaptations as well as changes in palaeogeographic distribution and diversity dynamics of Triassic fishes. The results are compared to patterns observed among other osteichthyans (bony fishes) during the Triassic, especially in the context of recovery after the end-Permian mass extinction.

8.17

Embryos in Deep Time - Palaeontology and the Study of the Evolution of Biological DevelopmentMarcelo R. Sánchez-Villagra¹¹ *Palaeontological Institute and Museum, University of Zurich, Karl Schmid-Straße 4, CH-8006 Zurich (m.sanchez@pim.uzh.ch)*

If the expanded evolutionary synthesis places development as a key subject, then the role of palaeontology to address developmental evolution becomes a central issue. Palaeohistology and the occasional embryos or growth series provide means of examination of what is otherwise rare: the direct study of development in fossil vertebrates. A web-database provides a bibliographic listing covering all major groups of vertebrates (www.developmental-palaeontology.net). Fossil phenotypes provide an indirect but rich source of data for developmental evolution. Collaborative works in my lab provide examples of different approaches. The resolution of the homologies of the interparietal bone and its dual embryonic tissue origin would not be possible without early synapsid (stem-mammals) data. The study of palaeohistology in fossil deer demonstrates how gigantic and dwarf forms grew. Fossils can expand the morphospace of a clade which otherwise would be considered to be biased negatively by some developmental pattern of that clade. Examples can be found in the size and dental morphological range of fossil marsupials. Studies of development also provide models and predictions which serve to interpret the fossil record. This is exemplified by the study of the potential molecular bases for the morphological diversification of a ray-finned fish from the middle Triassic of Switzerland. Another example is the application of the 'inhibitory cascade model' to predict molar proportions and its examination in a large radiation of extinct and endemic ungulate mammals from South America. Finally, palaeontology together with comparative morphology can provide the questions that developmental studies should address. This is exemplified by the investigation of the apparent extra-digit in talpid moles among mammals. The partial preservation of fossils and the impossibility of performing experiments on them put major limits on what can be achieved in developmental palaeontology. But the direct evidence fossils provide of development in geological time make them a central subject of an expanded evolutionary synthesis.

8.18

Taphonomy and palaeoecology of the green pentamerid Devonian brachiopods from the Aferdou el Mrakib, eastern Anti-Atlas, Morocco

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On the large reef mound Aferdou El Mrakib in the Maïder Basin (Anti-Atlas, Morocco), thick-shelled pentamerids occur in a locally high abundance. Like *Stringocephalus* from shallow water limestones of Germany, these Moroccan brachiopods of the genera *Devonogypa* and *Ivdelinia* often display greenish shells. By EDX analyses of the shells, it turned out that the colour was caused by impurities of Fe²⁺-ions. Their concentration varies strongly between the samples, indicating that the colour is less dependent on the iron-concentration than on shell thickness. Indeed, only the thickest parts of the shells appear green. There is also some indication that the Fe-content increases towards a deeper shell layer (further away from the surface).

Additionally, we examined the quality and spatial distribution of sublethal injuries in over 200 specimens of *Devonogypa* and *Ivdelinia* in order to find indications for their origin. The results support the hypotheses that (1) the injuries had several causes, (2) some of which were inflicted by predators, probably cephalopods, and (3) many fractures might have been caused by the brachiopod shells hitting each other in dense populations in agitated water. Numerous such dense clusters of these pentamerid brachiopods were examined in the field. They consisted of the association of members of both brachiopod genera or of only one taxon, occasionally accompanied by other brachiopods, some trilobites, corals and a few other groups.

P 8.1

Alpha diversity and palaeoecology of invertebrate associations of the Early Devonian in the Moroccan Anti-Atlas

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The Moroccan Anti-Atlas is famous for its highly fossiliferous and well-exposed Palaeozoic rocks. These include Lower Devonian outcrops in the Maider and the Tafilalt of the eastern Anti-Atlas. The superb exposures, local abundance of fossils and their sometimes excellent preservation provide the possibility of studying Early Devonian faunal associations in their stratigraphical context.

A rich fauna with well-preserved macrofossils of Pragian age (411- 407 Ma) and five more faunas of different Early Devonian ages (Lochkovian-Early Emsian) are under investigation and will be included in a study on alpha-diversity. The fossils were collected from the south-west of Jebel Ouaoufilal in the Tafilalt.

The taxonomic composition of every fauna has been examined and all taxa grouped according to their habitat and feeding behaviour. In combination with abundance data, this information will be evaluated with respect to palaeoecology. First analyses of the data show an increase in alpha diversity from the Silurian/ Devonian boundary to the early Emsian.

Orthoconic nautiloids are abundant in all faunas included in this study, but they become more diverse during the Pragian. The diversity of bivalves gradually increases during the Lochkovian and is highest during the Early Emsian. Other benthic organisms such as gastropods and brachiopods appear during the Lochkovian and have high diversities in the Pragian and Lower Emsian. Tabulate and rugose corals first occur in the Pragian and Emsian sediments. Sclerobionts colonizing the nautiloid shells include auloporid corals, cornulitids and a new hederelloid (?phoronid) genus.

The increase in species diversity and the change in species composition reflect a regional environmental change during the Early Devonian. In particular, the increase in benthic species leads to the supposition that a steady rise of oxygen content near the seafloor occurred in combination with a sea-level fall. This is in accordance with existing Devonian sea level curves (Kaufmann 1998). Further investigations may reveal relationships with the end-*pesavis* Event at the Lochkovian/ Pragian boundary, and the corresponding regional regression evident in eastern Australia (Talent *et al.* 1993).

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P 8.2

Comparing intraspecific variability of ammonoids

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Heritable phenotypic variation is usually thought to be the raw material for evolution and natural selection. Knowledge of the intraspecific variability of any taxon is therefore essential for systematics and diversity studies. Heritable variation is, however, hard to separate from morphological variation resulting from a plastic response to the environment, especially in extinct groups. For instance, a large part of the intraspecific variability in shelled molluscs could be caused by differences in growth rates, which could also explain certain recurrent patterns in intraspecific variability in the shells of coiled mollusc shells. Probably because of a low amount of specimens, poor preservation of study materials and/ or the lack of time and/ or motivation, intraspecific morphological variability has been poorly studied in ammonoids (as it is the case in most other groups of fossil and extant organisms). In ammonoids, this might lead to biases and problems such as, e.g., overlooking the influence of coiling on the intraspecific variability, oversplitting of taxa, and insufficient knowledge of taxa.

We have finished first studies on variability in relation to coiling with loosely coiled ammonoids of the genera *Anetoceras* and *Erbenoceras* from the early Emsian (Early Devonian) of Morocco and could demonstrate high degrees of intraspecific variability in both genera. We compared the morphometric data of the Moroccan material with published specimens of the same age worldwide. This led to the conclusion that the current amount of valid ammonoid species of the studied interval (> 20) is not supported by differences in the classical dimensional shell characters. Since the suture lines of these ammonoids are extremely simple, they are insufficient to base species exclusively on their suture line courses. This led to the conclusion that the existing wealth of species with loosely coiled shells has originated from oversplitting and has no profound scientific base. Estimates of ammonoid diversity are thus probably too high for the early Emsian.

In the past decade, we have collected and measured many Palaeozoic ammonoids, predominantly of Early and Middle Devonian age, but also of Late Devonian and Carboniferous age. These included species that have the advantages that several of which originated more or less close to the origin of the respective clade and that several show traces of ancestral characters especially in the early parts of ontogeny. An important plesiomorphic trait is the loose coiling, which is seen in several early Emsian ammonoid species. Our material of these very early forms led to the hypotheses that (1) intraspecific variability (at least of some characters) is intimately linked with coiling and therefore, (2) earlier forms are more variable than more derived forms with more tightly coiled shells.

To test the relation of the degree of intraspecific variability of conch parameters with coiling, we measured additional datasets of ammonoids from the late Emsian, the Eifelian, and the Carboniferous; the representatives of which have more or less tightly coiled shells. We used the coefficient of variation as a measure of the range of variability. Preliminary tests appear to support the two hypotheses, but further tests are needed before drawing a conclusion.

P 8.3

New coastline morphology in Western France during the Miocene

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Classically, no Miocene deposits are recorded in the Poitou-Charentes region (Central Western France). Previous authors suggested the existence of a hill forming a peninsula during high sea level periods (Aquitainian, Burdigalian, Langhian and Serravallian) in this area. This relief seems to be highly linked to the general Alpin orogen and the formation of the “Seuil du Poitou”. However, the absence of such sediments could also be linked to secondary erosion of them due to a late uplift between the Paris Basin and the Aquitaine Basin.

A first outcrop lies directly on a Cenomanian reefs, it is small and 6 meters thick. It is located in the Aix island (Charente Maritime, France). Sediments composing the outcrop are layered and slightly tilted following Cretaceous deposits. A long-ranging unconformity separates the Cretaceous from the Tertiary layers, the Cretaceous being highly karstified. The base of the Tertiary deposits is mainly composed of sandstones with some thin marly layers (probably paleosoils). On the top of the outcrop, a very dark marly layer finely litified, contains marine fossils: calcareous dinocysts and foraminifera. The dinocysts are not described in the literature and probably belong to a new species of *Alasphaera*. A preliminary analysis of the foraminifera (possibly a *Dentoglobigerina langhiana*) gives a Miocene age to these deposits.

A second outcrop consists of several fissure fillings documented in a Coniacian and Santonian quarry from Grezac (Charente Maritime, France). The fossiliferous assemblage from these pockets is peculiar: it comprises Cretaceous varanid and shark teeth, Miocene shark teeth (such as *Megalosuchus megalodon*, *Cosmopolitodus hastalis*, and *Hexanchus primigenius*), marine (dolphin and manatee) and terrestrial Miocene mammals (*Micromeryx* sp., *Suoidea*, *Proboscidea*, *Carnivora*, etc.). Our present hypothesis is that these fissures were Miocene coastal caves where terrestrial and marine fauna was mixed by various taphonomic processes; the Cretaceous fauna deriving from the dissolution of the karsts (similarly to the Burdigalian deposits in Jurassic limestone from La petite Morée in Glovelier, Switzerland). The presence of *Micromeryx* in this locality gives an age comprise between MN5 and MN11. These deposits could correspond to the Serravallian transgression.

The description of these new outcrops could change the datation of a late uplift of the “Seuil du Poitou” during the Late Miocene and the French Miocene coastline shape. On both localities, further investigations will be done to precise the age and the environment based on micro-, nannofossils, and the sedimentology.

P 8.4

Variability of the dental morphology in marine crocodilians (Thalattosuchia) from the Kimmeridgian of Ajoie (Jura, Switzerland)

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Discoveries of Thalattosuchia (Crocodylia, Mesosuchia) are common in the Mesozoic, notably in the Late Jurassic of Europe. During the nineteenth and the beginning of the twentieth centuries, many species or genera were erected. Due to the dental renewal in crocodilians, the most frequent remains are isolated teeth. For example, *Machimosaurus hugii* (Teleosauridae) was originally based solely upon isolated teeth. In the nineties, Vignaud (1995, 1997) established a synthesis of thalattosuchian dental morphotypes and associated them to known species. Between 2000 and 2009, more than 500 isolated teeth and about 10 jaw remains of Thalattosuchia were discovered in the Kimmeridgian of Ajoie (Canton Jura, Switzerland). They have been excavated during controlled excavations on the future path of the A16 motorway (Transjurane). Those remains have been initially ascribed to two genera of Teleosauridae (*Steneosaurus* and *Machimosaurus*) and to one genus of Metriorhynchidae (*Dakosaurus*).

In this work, dental morphotypes were defined based upon morphology, ornamentation and size of teeth, in order to identify the thalattosuchian fauna from Ajoie. In order to complete the dataset, additional material of thalattosuchians from the Kimmeridgian of Swiss and German localities was included. Four dental morphotypes, one including two sub-morphotypes, were defined. By comparison with the literature, especially Vignaud's morphotypes (1995, 1997), they were ascribed to four genera represented by five species: two genera of Teleosauridae (*Steneosaurus*, including two species, and *Machimosaurus*) and two of Metriorhynchidae (*Metriorhynchus* and *Dakosaurus*) (Table 1). Furthermore, a bivariate synthesis diagram “height/diameter” grouping all the taxa was compared to the dental morphotypes defined by Massare (1987). It indicates that the dental morphotypes from Ajoie correspond to five feeding guilds with five types of preferred prey. This shows that coexistence of the five species (*Steneosaurus* cf. *jugleri*, *S.* cf. *bouchardi*, *Machimosaurus* sp., *Metriorhynchus* sp., *Dakosaurus maximus*) in an open coastal marine environment was possible. In addition, there is a correlation between the distribution of thalattosuchian teeth and sea level variations, the metriorhynchids matching with transgression phases.

Isolated teeth of *Thalattosuchia* are useful to estimate the palaeobiodiversity of these marine crocodilians in a deposit. They are numerous and have more discriminant characters than postcranial elements for the identification at the genus level. However, it is tricky to assign isolated teeth to particular species. Results gained by this work may be used as reference for the identification of future discoveries of thalattosuchian teeth in the Kimmeridgian of Europe. Finally, an assemblage of isolated thalattosuchian teeth can contribute to the reconstruction of marine palaeoenvironments.

	Morphotype 1		Morphotype 2	Morphotype 3	Morphotype 4
	Sub-morphotype 1A	Sub-morphotype 1B			
Family	Teleosauridae		Metriorhynchidae		
Genera	<i>Steneosaurus</i>	<i>Steneosaurus</i>	<i>Machimosaurus</i>	<i>Metriorhynchus</i>	<i>Dakosaurus</i>
Species	cf. <i>jugleri</i>	cf. <i>bouchardi</i>	sp.	sp.	<i>maximus</i>
Number of isolated teeth	355		74	24	1
Percent of isolated teeth	78.19%		16.30%	5.29%	0.22%
Nature of the presence in Ajoie	Autochthonous	Autochthonous	Autochthonous	Parautochthonous Autochthonous?	Allochthonous?
Habitat	Coastal	Coastal	Coastal Pelagic?	Pelagic Coastal?	Pelagic
Type of prehension	Piercing	General	Crushing	Piercing/Cutting	Cutting
Estimated size	~ 3 meters	4 - 5 meters	Up to 9 meters	~ 4 meters	> 4 meters

Table 1: Synthesis of the thalattosuchian dental morphotypes from the Kimmeridgian of Ajoie (Jura): systematics, distribution and palaeoecology.

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