The potential of vertebrate microfossils for marine to non-marine correlation in the Late Jurassic*

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Abstract Fish (cartilaginous: elasmobranch and bony: osteichthyan actinopterygian) and reptile (crocodile) microfossils comprising scales and teeth have been examined from a series of limestone samples in the Upper Jurassic of France and Germany to gauge the possibilities of using them for correlation between fully marine and hypo- or hyper-saline (non-marine) deposits.

Keywords: Upper Jurassic, Kimmeridgian, chondrichthyans, actinopterygians, crocodilians, microfossils, biostratigraphy.

The most frequent remains of fossil vertebrates in aquatic sediments are the scales, teeth, and otoliths of chondrichthyans and actinopterygians. Most of these remains are very small and are therefore called microvertebrate remains. Such fish remains have long been considered as useful tools for the stratigraphical and palaeoecological interpretation of Paleozoic sediments. This is reflected by numerous publications on Paleozoic microvertebrates (e. g., Blieck and Turner[1]). Microvertebrate remains are present not only in sediments of Paleozoic age. They occur in similar frequency in deposits of all time. However, microvertebrate remains from the Mesozoic have been studied rarely to date, although they were found frequently in washing residues of Mesozoic sediments. This is documented by micropaleontological studies such as those of Arbeitskreis Deutscher Mikropaläontologen[2], Martin and Weiler[3], and Zihrul[4] in which actinopterygian teeth are figured interspersed in samples of foraminifera. The sparse knowledge of Mesozoic microvertbrate remains have clearly prevented the taxonomic identification of these teeth in the past, because they were regularely listed as "fish tooth gen. et spec. indet.".

In the Late Jurassic rocks of northwestern (NW) Germany microvertebrate remains are most common in strata of Kimmeridgian age. These rocks are included in the regional lithostratigraphical unit "Kimmeridge". Paleoecological interpretation and stratigraphical correlation of the NW German Kimmeridge strata is still under debate, mostly because of the lack of ammonites and the endemic character of the invertebrate faunas of these strata[5]. A major problem concerns the depositional environment of the Kimmeridge strata. Publications dealing with this problem cover a wide spectrum of opinions ranging from brackish to hypersaline to characterize the salinity of the depositional environment of the NW German Kimmeridge marls[6,7]. Facing this controversy we wondered if a study of Kimmeridgian microvertebrate remains could contribute to the solution of the problems posed by the Kimmeridge rocks of NW Germany. At first the research program was focussed only on the investigation of microvertebrate remains of the NW German Kimmeridge, but this was subsequently expanded to cover also the study of miroverte-brate remains of other Late Jurassic formations of NW Germany and of the Late Jurassic rock succession exposed at the cliff section NE of Boulogne-sur-Mer on the south coast of the English-French Channel.

In a preliminary analysis of microvertebrate remains as a basis for correlation between Upper Jurassic normal marine strata of northern France and non-marine strata of north Germany and, in addition, between two localities with non-marine Upper Jurassic strata in north Germany, we reached some results

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which are presented here. This study has not previously been published; the results were part of a wider report submitted to the DFG in 1999[1)].

1 Localities and methodology

1.1 NW Germany localities

The northwest German material analyzed here comes from two localities (Fig. 1):

(1) Uppen: southward facing wall of a cutting made for the passage of Autobahn A2 between km 183+200 m and 183+700 m near the village of Achtum-Uppen, 4 km east of the city of Hildesheim (Korallen-Oolith-Lower Kimmeridge, joKO-joKI (u), Upper Oxfordian-Lower Kimmeridgian). Grid reference: topographical map of Germany 1∶25.000, sheet no. 3826 Dingelbe, R 35 69 300, H 57 78 700. Lit.: Gramann and Luppold[8], Weiß[9].

(2) Oker: working quarry for cement and road aggregate, located on the southern slope of the Langenberg, 5 km east of the city of Goslar (Kimmeridge, joKI, Kimmeridgian). Grid reference: topographical map of Germany 1∶25.000, sheet no. 4029 Vienenburg, R 36 03 175, H 57 53 075. Lit.: Fischer[10].

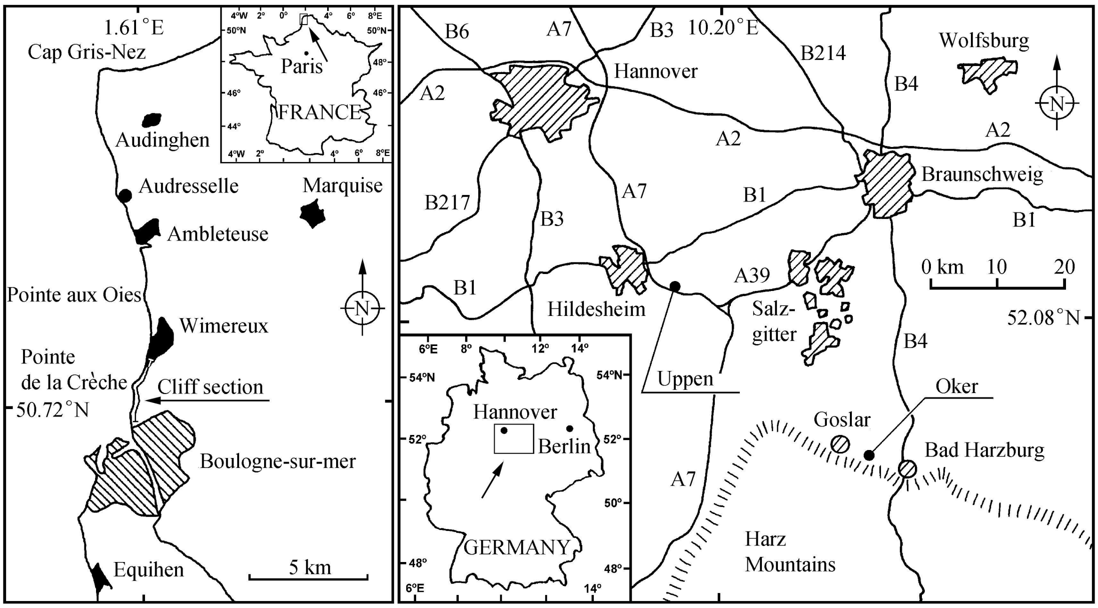

Fig. 1. Geographical maps to show the localities where samples were taken from the cliff section at Boulonnais, northern France (left), and sections at Oker and Uppen in northwestern Germany (right).

1.2 North France (Boulonnais) locality

For comparative purpose we sampled a section of Late Jurassic rocks exposed on the N French channel coast between the towns of Boulogne-sur-Mer and Wimereux (Boulonnais, Dep. Nord/Pas-de-Calais; Fig. 1). The deposits here are known to be laid down essentially in a normal marine environment. Descriptions of this section were given by Oschmann[11] and Proust et al.[12].

Fig. 2 shows the two localities in a Late Jurassic palaeogeographical context.

1.3 Material

Technical details of sampling and sample processing will be published elsewhere[2)]. The material recovered from the samples consists almost exclusively of elasmobranch and osteichthyan oral teeth, scales and bone fragments. Additionally, a few teeth of an atoposaurid crocodile were discovered. Altogether the material comprises ca. 20000 teeth and scales of fishes, half of which came from the German and half from the French samples, respectively.

1) Thies D and Mudroch A. Microvertebrate remains from the northwest European Upper Jurassic Systematics, Palaeoecology and Stratigraphy, 1999, Hannover (unpublished DFG-report, in German).

2) Mudroch A and Thies D. in preparation.

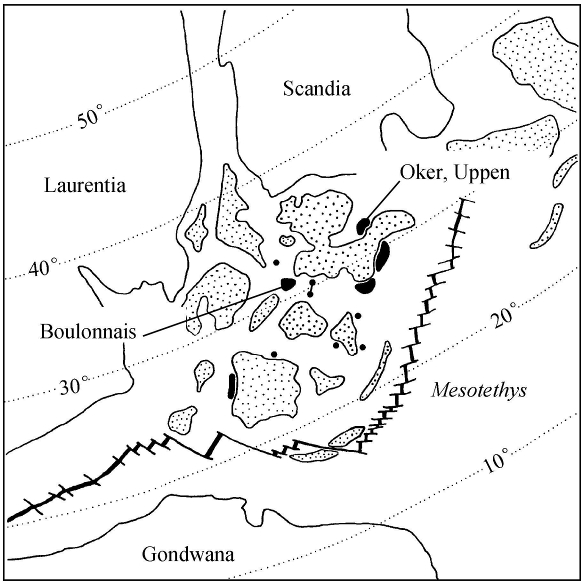

Fig. 2. Palaeogeography of the European archipelago in the Late Jurassic (Kimmeridgian) with the situation of the sampled localities indicated (map based on the result of the working group "Late Jurassic Vertebrate Palaeogeography" at the 5th European Workshop on Vertebrate Palaeontology (EWVP), Karlsruhe, 2000).

1.4 Identification of microvertebrate remains

The study of fish microfossils, especially in the Mesozoic is in its infancy. However, the relationship of fish microremains to their respective articulated fish is as old as the formal scientific study of fishes (cf. the pioneer work of Agassiz[13]). Microfossils of actinopterygians (bony fishes) were the most common fossils in all of our Upper Jurassic samples. However, there are almost no published data for the identification of Mesozoic teeth and scales of bony fishes. Whereas line illustrations have been done in the past, for detailed views and identification scanning electron microscopy now provides the best option. Frequently found Upper Jurassic actinopterygian teeth are illustrated in Fig. 3(a)—(h).

As to chondrichthyans (cartilaginous fishes), the situation is only slightly better. Even though there are some previous studies on Jurassic chondrichthyan oral teeth (e.g., Thies[14], Underwood and Ward[15]) the dental morphology of the famous articulated specimens from the south German and French Upper Jurassic plattenkalke is still widely unknown. Excepting a preliminary report (Leidner and Thies[16]) and an unpublished manuscript1) the same holds true for Upper Jurassic chondrichthyan scales that in many of our samples were more frequent than teeth. Fig. 3(i)—(t) provide examples of common tooth and scale forms found.

Mesozoic reptiles are dominated by dinosaurs. Studies on reptilian especially non-dinosaurian microremains are extremely rare but lizards and others have been described. Recently, Kosma2) has studied jaws and dentitions of living and fossil lacertilians (lizards). Our samples contained very rare teeth of dwarf crocodiles (Fig. 3(u)—(v)).

Therefore, in general we have identified our microvertebrate remains mainly by comparison with articulated and already-systematically identified specimens of chondrichthyans, actinopterygians and reptilians from the Upper Jurassic (Kimmeridgian-Tithonian) plattenkalks of south Germany and south France. The specimens are housed in numerous European museum collections. Results of these identification attempts have been published[16—25].

2 Biostratigraphical results

Depending on their systematic affinity, Upper Jurassic microvertebrate remains appear to be of different significance for biostratigraphical purposes.

2.1 Actinopterygians

2.1.1 Teeth Upper Jurassic actinopterygians are represented by different groups such as the semionotiforms, pycnodontiforms, caturids, pachycormids, pholidophoriforms, basal teleosts and others. Among the teeth of these actinopterygians, which occur most frequently in our samples we did not trace any forms of biostratigraphical significance. For example, teeth of *Caturus* (Fig. 3(a)—(c)) showing identical morphologies were found in the Kimmeridge (Kimmeridgian) and in the Münder Mergel (Upper Tithonian) of north Germany[26] as well as in the plattenkalks (lithograpic limestones) of Solnhofen (Upper Tithonian, south Germany), Cerin (Upper Kimmeridgian, south France), and the Boulonnais (Kimmeridgian/Tithonian, north France). The low biostratigraphical significance of actinopter-

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2) Kosma R. The dentitions of recent and fossil scincomorphan lizards (Lacertilia, Squamata): systematics, functional morphology, paleoecology. Dissertation, Hannover Univ., Fachbereich Geowissenschaften und Geographie, 2003 [URN (NBN): urn: nbn: de: gbv: 089-37698354X2] http://www.tib.uni-hannover.de/spezialsammlungen/dissertationen/diss-ev-04.p

ygian microremains can be explained as follows:

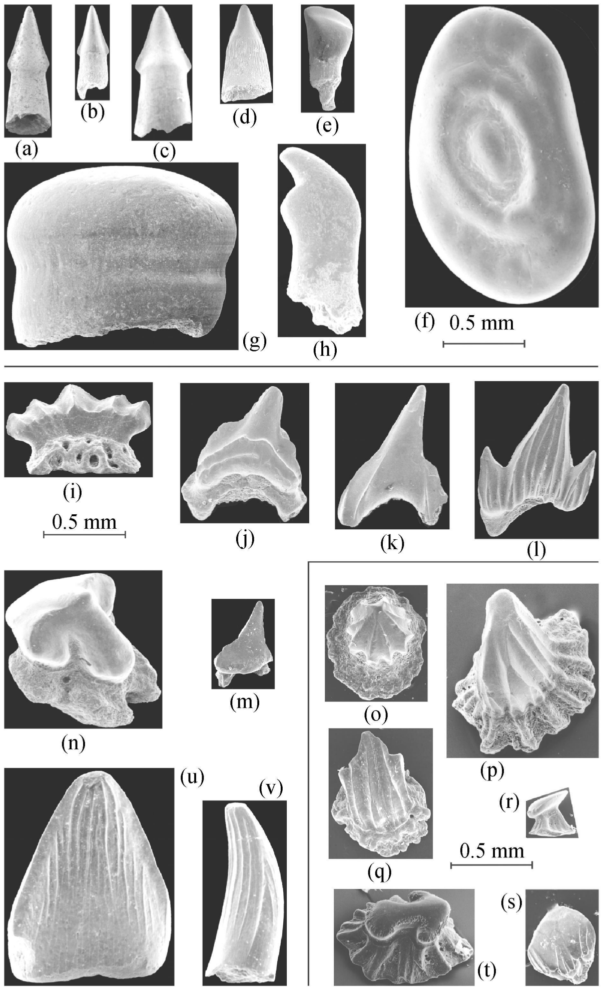

Fig. 3. Microvertebrate remains from the Upper Jurassic of N Europe (repositories: GPH-Institut für Geologie und Paläontologie, Universität Hannover, Germany; TUCLP-Geologisches Institut der Technischen Universität Clausthal, Germany; details of the NW German localities Varrigsen, Hirschkopf and Holzen II given by Mudroch[1)]).

(a)—(h) Oral teeth of bony fishes (actinopterygians). (a) *Caturus* sp., Oker (bed 47), Kimmeridgian, lingual view, GPH cat. no. 2000-II-69; (b) *Caturus* sp., Oker (bed 27), Kimmeridgian, labial view, GPH cat. no. 1996-I-47; (c) *Caturus* sp., Boulonnais (Calcaire de Moulin Wibert, sample 4), Kimmeridgian, labial view, GPH cat. no. 2000-II-71; (d) *Ionoscopus* cf. *desori* (Thiollière 1858), Oker (bed 56), Kimmeridgian, lingual view, GPH cat. no. 2000-II-55; (e) *Coelodus* cf. *mantelli* (Agassiz 1843), Varrigsen (bed 8), Tithonium, lingual view, GPH cat. no. 2000-II-46; (f) *Gyrodus* sp. (enamel cap), Boulonnais (Argiles de Chatillon, sample 1), Kimmeridgian, apical view, GPH cat. no. 2000-II-40; (g) *Lepidotes* sp., Oker (bed 27), Kimmeridgian, lateral view, GPH cat. no. 1996-I-1; (h) *Lepidotes* sp., Oker (bed 49), Kimmeridgian, lateral view, GPH cat. no. 1996-I-11.

(i)—(n) Oral teeth of cartilagenous fishes (selachians). (i) *Lissodus curvidens* Duffin & Thies 1997 (hybodontoid shark), Oker (bed 153), Kimmeridgian, lingual view, GPH cat. no. 1994-I-8 (paratype); (j) *Corysodon* sp. (neoselachian shark), Oker (bed 128), Kimmeridgian, labial view, TUCLP cat. no. VB224; (k) *Bavariscyllium tischlingeri* Thies 2006 (neoselachian shark), Oker (bed 70), Kimmeridgian, labial view, GPH cat. no. 2000-II-26; (l) *Palaeoscyllium formosum* Wagner 1857 (neoselachian shark), Hirschkopf, Oxfordian, labial view, GPH cat. no. 2000-II-25; (m) *Phorcynis* cf. *catulina* Thiollière 1854 (neoselachian shark), Holzen II (P. 3), Tithonian, labial view, GPH cat. no. 2000-II-17; (n) *Spathobatis* sp. (guitar fish), Boulonnais (Argiles de la Crèche (above the Grès de la Crèche), sample 5), Tithonian, apicolingual view, GPH cat. no. 2000-II-32.

Placoid scales (dermal denticles) of cartilagenous fishes (selachians). (o) Unidentified hybodontoid, Oker (bed 153), Kimmeridgian, apical view, GPH cat. no. 93-I-1; (p) unidentified hybodontoid, Oker (bed 84), Kimmeridgian, anterolateral view, GPH cat. no. 93-I-5; (q) unidentified hybodontoid, Oker (bed 70), Kimmeridgian, anteroapical view, GPH cat. no. 93-I-12; (r) unidentified neoselachian shark (galeomorph or squatinomorph), Oker (bed 49), Kimmeridgian, lateral view, GPH cat. no. 93-I-31; (s) *Synechodus* sp. (neoselachian shark), Oker (bed 27), Kimmeridgian, apical view, GPH cat. no. 93-I-31; (t) *Asterodermus* sp. (guitar fish), Oker (bed 84), Kimmeridgian, lateral view, GPH cat. no. 93-I-40.

Teeth of reptilians (crocodilians). (u) cf. *Theriosuchus* sp., Uppen (bed 6/2), Kimmeridgian, lingual view, GPH cat. no. 1996-III-4; (v) cf. *Theriosuchus* sp., Oker (bed 83), Kimmeridgian, lateral view, GPH cat. no. 1996-III-3.

1) Mudroch A. Fischzähne aus dem Oberjura Nordwesteuropas. Systematik, Biogeochemie und Paläokologie. PhD Thesis, University of Hannover, 2001.

(1) Species of studied Upper Jurassic actinopterygian genera show identical or very similar dental morphologies, which do not allow identification of isolated teeth at the species level;

(2) systematic treatment of Upper Jurassic actinopterygians is still mostly artificial, and many "genera" therefore have a wide stratigraphical range.

2.1.2 Scales With the exception of *Lepidotes*, the scales of most Upper Jurassic actinopterygians are thin and fragile. They are usually preserved as fragments only, which cannot be identified further. The scale armour of *Lepidotes* is poorly known and needs to be studied in detail in all the species of this genus.

2.2 Cartilagenous fishes

2.2.1 Placoid scales In contrast to the actinopterygian teeth, the placoid scales of chondrichthyan fishes have developed specific morphologies, which are characteristic for many species. For recent sharks this was demonstrated well by Reif[27]. However, in the Upper Jurassic specimens of articulated chondrichthyans studied by us the potential of scale morphology for the identification of species is less evident. Specimens used for sampling often belonged to monotypic genera, such as *Corysodon* or *Phorcynis*. Therefore, it remains uncertain whether possible additional but yet unknown species of these genera would differ in scale morphology from the already known taxa. However, easily recognizable differences in scale morphology exist between the genera[1)]. Also, published records show that in terms of stratigraphical range at least some Upper Jurassic selachian genera or species are more restricted than contemporaneous actinopterygian taxa. Accordingly, placoid scales are presumed at present to be of greater potential biostratigraphical significance than bony fish teeth. Unfortunately, placoid scales cannot be used as biostratigraphical index fossils as yet. At present, the scales of only ca. 20 specimens of sharks and rays from the south German Tithonian plattenkalke and elsewhere are studied. For a proper evaluation of the biostratigraphical potential of Upper Jurassic placoid scales additional sampling from sediments other than the plattenkalke is needed. Examples of isolated placoid scales from the Upper Jurassic samples of northwest Germany are shown in Fig. 3(o)—(t).

2.2.2 Oral teeth The oral teeth of chondrichthyans do appear be useful for biostratigraphical purposes[14, 15]. Their scarcity in many horizons of the northwest German Mesozoic sections, however, makes it impossible at present to subdivide these sections using chondrichthyan teeth. Nevertheless, they seem to be suited for long distance correlation of Kimmeridge horizons of northwest Germany with those of the Boulonnais coastal section in northern France and thus for an approximate correlation of the northwest German Kimmeridge with Upper Jurassic boreal ammonite subdivision. This is demonstrated by the teeth of two sharks: *Lissodus* and *Palaeoscyllium*.

Bed 153 at the top of the Oker section (Fig. 4) has yielded numerous teeth of the hybodontiform shark *Lissodus curvidens* DUFFIN and THIES, 1997[21] (Fig. 3(i)). This is the only occurrence of this taxon at Oker. The teeth of this shark were, however, also found in the coastal section of the Boulonnais (north France). Here they occur exclusively in the Argiles de Moulin Wibert. These beds extend over the upper part of the *Aulacostephanoides* (= *Rasenia*) *mutabilis* ammonite Zone and the lower part of the *eudoxus* ammonite Zone (*orthocera* Subzone, Proust et al.[12]). *L. curvidens* teeth were collected from the lower part of the Argiles de Moulin Wibert close to the boundary of the *mutabilis* and *eudoxus* zones. We therefore tentatively correlate that part of the French Argiles de Moulin Wibert lying at the *mutabilis/eudoxus* zone boundary with bed 153 of the German Oker section. The occurrence of *L. curvidens* at Oker indicates that the boundary of the boreal *mutabilis/eudoxus* Zone might be present in the Oker section close to bed 153 and a little above the boundary of the regional lithostratigraphical units Middle/Upper Kimmeridge. Such a correlation agrees with Schweigert[28] who identified the *eudoxus* Zone in the Oberer Kimmeridge strata of the Porta Westfalica section (north Germany) on the basis of historical ammonite findings.

The lower boundary of *mutabilis* Zone is uncertain in the Oker section. However, a second shark species - *Palaeoscyllium formosum* WAGNER 1857 (Fig. 3(l))-may be helpful to find this boundary. Teeth of this species were described from the Kimmeridgian "Argiles d' Octeville" at the base of the *mutabilis* Zone of Normandy, north France (as

1) See footnote 1 on page 657

Parasymbolus octœvillensis, CANDONI[29]). In the Oker section, teeth of *P. formosum* occur in bed 36 (Fig. 4); so far, in other horizons teeth of this shark seem to be absent. We therefore suppose that the lower boundary of the *mutabilis* Zone lies at bed 36 or in its vicinity. This agrees with the occurrence of a fragmentary *Rasenia* sp. in bed 38 of the Oker section. A fragmentary *Lithacoceras* cf. *subachilles* from bed 24 also indicates an earliest Kimmeridgian age of these horizons[10]. *Lithacœras subachilles* is part of the ammonite fauna characterizing the *platynota* Zone, which is the basal ammonite zone of the Lower Kimmeridgian biostratigraphical subdivision in the Tethyan realm applied in south Germany.

Altogether, this could mean that the local lithostratigraphical units, Lower, Middle and Upper Kimmeridge in the Oker section mostly fit into the *mutabilis* Zone. In this case the *mutabilis* Zone reaches 75 metres in thickness at Oker (Fig. 4). Zeiss[30] and Weiß[9] placed the Oxfordian/Kimmeridgian stage boundary into the upper part of the north German lithostratigraphical unit Korallenoolith, which is immediately below the Kimmeridge (Fig. 4). This would leave in the Oker section only a few metres of thickness for the *cymodoce* and *baylei* ammonite zones below the *mutabilis* Zone of the Boreal lowermost Kimmeridgian ammonite subdivision. However, because of the almost complete lack of ammonites it remains obscure at present if the *cymodoce* and *baylei* zones are developed in the Oker section[1)]. Comparison with the Upper Jurassic coastal section of the Boulonnais (north France) does not help to solve this problem. Here, the lower boundary of the *mutabilis* Zone is also uncertain and the presence or absence of the *cymodoce* and *baylei* zones is unclear (Fig. 4). Also, the lowermost part of the Boulonnais section including the base of the Argiles de Moulin Wibert, Calcaires de Brecquerecque, Caillasses d' Hesdigneul and the Oolite d' Hesdin l' Abbé (Fig. 4) was not available for sampling. A tentative correlation of the Oker and Boulonnais sections on the basis of shark teeth is shown in Fig. 4.

3 Higher vertebrate microfossils

In the Jurassic there is potential to find amphibian, reptile, bird, and mammalian microfossils, teeth and bones, even scales. Richter, later Broschinski, and others[24, 31—34] have published descriptions of lizard-like forms and crocodilians from Europe (including Germany) and Africa. In this study of northern France and Germany we found distinctive crocodilian teeth.

Reptile teeth: Microvertebrate remains also seem to be suited for regional correlations between individual horizons in the northwest German Kimmeridge. This is demonstrated by certain horizons of the Kimmeridge sections of Oker (beds 56 and 83) and Uppen (bed 6/2) in which the teeth of the dwarf crocodile cf. *Theriosuchus* have been found (Fig. 3 (u)—(v)). These teeth are unknown from other beds. Strontium isotope studies of the teeth of cf. *Theriosuchus* from bed 83 indicate a marginal marine palaeoenvironment[22]. We suppose that there is a relationship between the limited distribution in time and space of the teeth and of the marginal marine conditions represented in the teeth-bearing beds which might indicate a short lived palaeoecological and/or palaeogeographic event of unknown character. Otherwise the Kimmeridge deposits are interpreted as being deposited under conditions of more reduced salinity. Based on ostracode faunas, Weiß[9] identified the strata in the Uppen section as Upper Korallenoolith and Lower Kimmeridge and also observed repetition of lithology with the same ostracode assemblages. At Uppen the cf. *Theriosuchus* teeth only occur in bed 6/2 and therefore this bed has been correlated with the lower bed (56) at Oker, which also belongs to the Lower Kimmeridge. The higher bed (83) at Oker is placed in the Middle Kimmeridge[34] (Fig. 4).

Given that this hypothesis is substantiated then for the first time a biostratigraphical correlation is possible for Kimmeridge beds between distant localities in north Germany and even further afield.

4 Results

Upper Jurassic microvertebrate remains include taxa of biostratigraphical significance. However, compared to the frequency of microvertebrate remains these potential zone fossils are rare.

(1) The cartilaginous fish teeth support the earlier supposition of Fischer[10] based on a fragmentary ammonite (now lost), that the lithological stratigraphical units of Lower, Middle and Upper Kimmeridge in the Oker section should all be placed in the Lower Kimmeridgian.

1) Personal communication, Dr. Gramann F. Bundesanstalt für Geowissenschaften und Rohstoffe, Hannover.

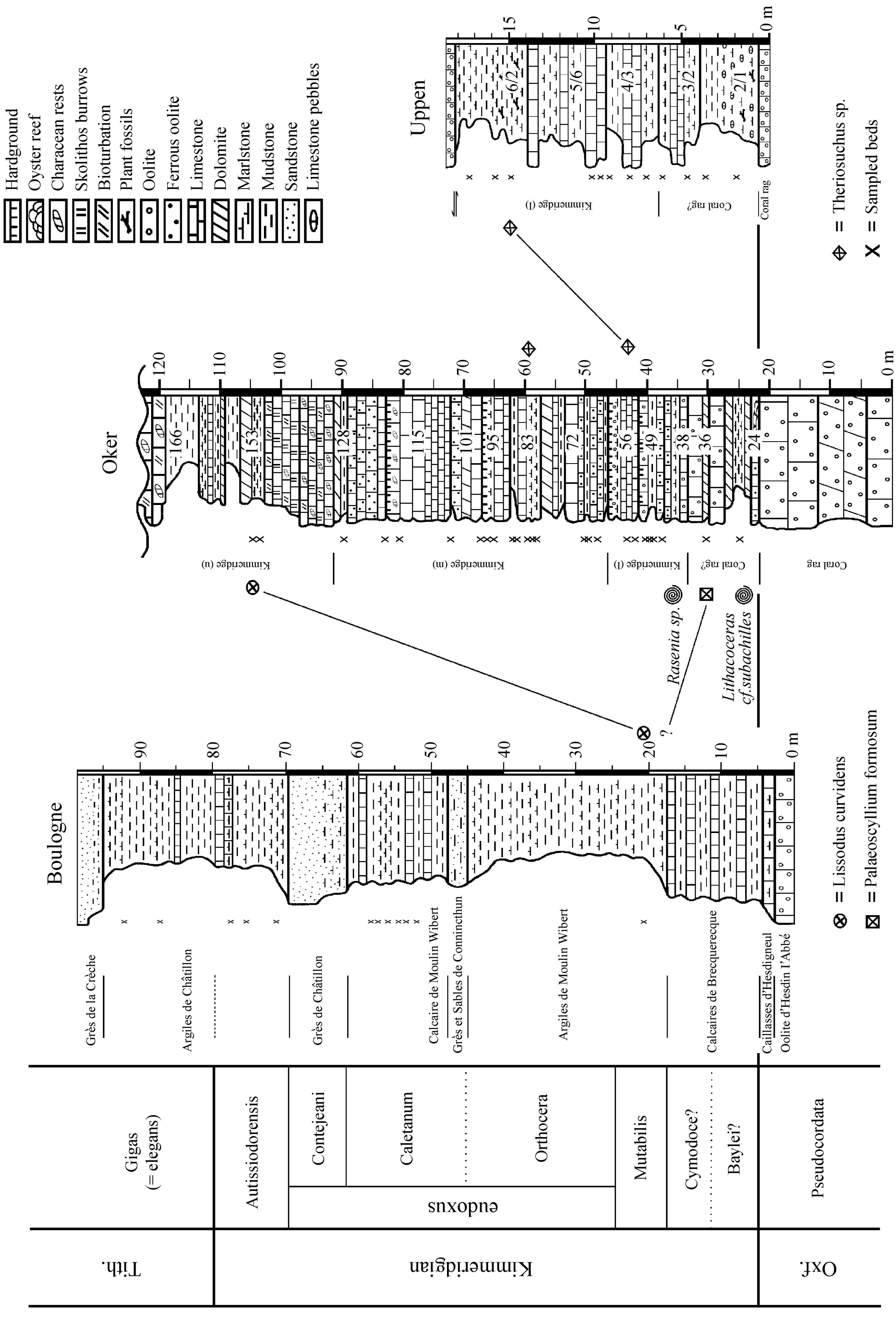

Fig. 4. Correlated stratigraphical sections of the Boulonnais, Oker and Uppen. Baseline is the Oxfordian-Kimmeridgian boundary. Ammonite zones and subzones for the Boulonnais section after Proust et al.[12]. Stratigraphical information for the Oker section after Fischer[10] and for the Uppen section after Weiß[9]. Sampled horizons are marked with "x"; crossed circles represent records of *Lissodus curvidens* Duffin & Thies, 1997; crossed square represents records of *Palaeoscyllium formosum* Wagner, 1857; crossed diamonds represent records of small atoposaurid crocodile teeth (cf. *Theriosuchus* sp.[22]).

(2) Also, the chondrichthyan teeth indicate that most of the Oker section belongs in the *mutabilis* ammonite Zone.

The resulting charts (Fig. 4) relate the fish and reptile evidence gleaned thus far to that of the standard classic ammonite zonation in Europe.

5 Conclusions

Our knowledge of Upper Jurassic (even the whole Mesozoic) microvertebrate remains is still very fragmentary and so our correlations can only be considered as tentative. Further studies on the taxonomy and stratigraphical distribution of Upper Jurassic microvertebrate remains are needed.

As with use of fish microvertebrate remains in the Palaeozoic, the preliminary results of our research indicate that of the fish it is currently mainly selachian remains that have the most potential for stratigraphic control and correlation purposes. This study shows that reptilian teeth can also provide solutions to stratigraphical problems that were previously intractible.

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