No dicynodont in the Keuper – a reconsideration of the occurrence of aff. *Dinodontosaurus* in the Middle Triassic of Southern Germany

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Abstract

An isolated humerus, attributed to a dicynodont therapsid and identified as aff. *Dinodontosaurus*, from the Lower Keuper (Middle Ladinian, Middle Triassic) of southwestern Germany is redescribed. An additional but smaller humerus that is similar in morphology might pertain to the same taxon. Several morphological features preclude an identification of the material as either aff. *Dinodontosaurus*, a dicynodont, or even a synapsid. The deltopectoral crest shows a number of tubercles, probably for muscle attachment. The supinator process is strongly developed and clearly offset from the rest of the bone. The distal articulation facet is very narrow transversely. There is no foramen entepicondyloideum. The ectepicondyle has a deeply concave distal surface, at least in the large and presumably adult specimen. An alternative identification for the two humeri proves difficult, as they do not agree with any other known tetrapod from the Lower Keuper. They bear close resemblance, however, to the humerus of the Permian temnospondyl *Eryops*, suggesting the presence of an as yet unknown temnospondyl.

K e y w o r d s : Lower Keuper, Middle Triassic, *Dinodontosaurus*, Synapsida, Temnospondyli.

Zusammenfassung

Ein isolierter Humerus aus dem Unteren Keuper (mittleres Ladinium, Mitteltrias) von Süddeutschland, der dem dicynodonten Therapsiden aff. *Dinodontosaurus* zugeordnet wurde, wird neu beschrieben. Ein weiterer, kleinerer Humerus mit vergleichbarer Morphologie könnte von demselben Taxon stammen. Mehrere morphologische Merkmale schließen eine Identifikation des Materials als aff. *Dinodontosaurus*, als Dicynodonten, ja sogar als Synapsiden überhaupt aus. Die Crista deltopectoralis zeigt eine Reihe von Tuberkeln, die vermutlich Muskelansatzstellen repräsentieren. Der Processus supinatorius ist sehr stark entwickelt und klar vom Rest des Knochens abgesetzt. Die distale Gelenkfacette ist in Querrichtung sehr schmal. Ein Foramen entepicondyloideum fehlt. Der Ectepicondylus besitzt eine tief konkave distale Oberfläche, zumindest beim großen und vermutlich adulten Exemplar. Eine Zuordnung der beiden Humeri ist problematisch, da sie mit keinem anderen aus dem Unteren Keuper bekannten Tetrapoden übereinstimmen. Eine große Ähnlichkeit besteht allerdings zum Humerus des permischen Temnospondylen *Eryops*, was als ein Hinweis auf einen weiteren Temnospondylen im Unteren Keuper gewertet wird.

Contents

1. Introduction

Dicynodonts are among the most common fossil tetrapods in the Late Permian and Lower and Middle Triassic of many parts of the world. Particularly rich findings have been made e. g., in Southern and Eastern Africa, China, parts of South America (particularly northern Argentina and southeastern Brazil), India and Western Russia (King 1988). Some regions, however, have a notoriously poor dicynodont fossil record. These include e. g., Australia and also Western and Central Europe (but see Dzik et al. 2008).

The Germanic Basin, although world-famous for its exceptional record of Triassic fossil vertebrates, has yielded only very few specimens of synapsids, and even fewer of dicynodonts, the only substantial findings, representing a very large kannemeyeriiform, being from the Upper Triassic of Silesia so far (Dzik et al. 2008). The only Middle Triassic specimen that can be referred to a dicynodont with some confidence is an isolated humerus from the Upper Muschelkalk of Avricourt in Lotharingia (eastern France) that was described by Broili (1921) and attributed to cf. *Placerias*. Lucas & Wild (1995) reconsidered this identification and suggested that the specimen was probably more closely comparable to the Chinese Middle Triassic dicynodont *Parakannemeyeria*. They identified it as aff. *Parakannemeyeria* sp., although they admitted (Lucas & Wild 1995: 8) that "assignment of Broili's specimen to

either *Kannemeyeria*, *Parakannemeyeria* or *Sinokannemeyeria* is impossible simply because of the lack of additional information". We think that the little information available on this specimen, that unfortunately was destroyed in World War II, is insufficient for any identification beyond ?Dicynodontia indet.

Judging from Broili's (1921) original account, it is conceivable that the specimen really represented a dicynodont, but it is impossible to verify this beyond doubt. At any rate it is the most likely record of a dicynodont from the Middle Triassic of the Germanic Basin that has been found to the present day.

Lucas & Wild (1995) described an additional isolated humerus from the lower part of the Lower Keuper (Middle Ladinian, Middle Triassic) which they identified as aff. *Dinodontosaurus*. The purpose of this paper is to reinvestigate the systematic position of this fossil and to describe an additional specimen that was found recently and can be attributed to the same taxon.

Institutional abbreviations

SMNS Staatliches Museum für Naturkunde Stuttgart, Germany
GPIT Paläontologisches Museum der Universität Tübingen, Germany
MCZ Museum of Comparative Zoology, Cambridge, Mass., USA

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2. Materials

SMNS 56891, an isolated, complete left humerus, original of Lucas & Wild (1995, figs. 3–5), from the Lower Vitriolschiefer, Lower Lower Keuper, Middle Ladinian, Middle Triassic, of Neidenfels near Crailsheim, Baden-Württemberg, Germany.

SMNS 90571, an isolated, almost complete right humerus from the Green Layer of the Untere Graue Mergel, Lower Lower Keuper, of the Schumann Quarry, Vellberg-Eschenau near Schwäbisch Hall, Baden-Württemberg, Germany.

MCZ 9230, an isolated left humerus of a small (probably juvenile) kannemeyeriiform dicynodont from the Santa Maria Formation, Middle Triassic of Brazil, probably *Dinodontosaurus* sp.

GPIT 1055, an isolated, very well preserved complete right humerus, attributed to *Dicynodon turpior* (von Huene 1935, pl. 10, fig. 8), and later identified as *Dinodontosaurus turpior* and chosen as a lectotype of that species by Cox (1965). Identified as *Dinodontosaurus* sp. by Lucas & Harris (1996).

3. Systematic palaeontology and description

Amphibia von Linné, 1758
?Temnospondyli von Zittel, 1887–90

Gen. et sp. indet.

The larger specimen, SMNS 56891 (Fig. 1A–D, Fig. 2A–D), is a left humerus, that measures around 80 mm in length. It was described in considerable detail by Lucas & Wild (1995), so lengthy redescription is unwarranted and only some of the features relevant to the discussion are pointed out below. The most noteworthy unusual features recorded in the original description are: the presence of four tuberosities on the deltopectoral crest, the absence of a foramen entepicondyloideum, and the presence of a large, plate-like supinator process.

The other humerus, SMNS 90571 (Fig. 1E–F), is very similar to SMNS 56891, but of much smaller proportions. It is a right humerus only about 40 mm in length. The bone is almost complete, lacking only a small part of the proximal end and part of the ectepicondyle. It is dorso-ventrally flattened, with strongly expanded proximal and distal ends. It shows torsion of only about 60 degrees, but the bone is certainly considerably flattened dorsoventrally. In dorsal view, the proximal and distal portions are of similar width. The shaft is robust, without an accentuated constriction. In ventral view, the similarities between this exemplar and SMNS 56891 are striking. In the most distal portion of the deltopectoral crest, there is a very large ventral protuberance, probably for insertion of the pectoralis muscle. The distal extremity of the bone has a rounded outline, and the differences between ect- and entepicondyle are not as clear as in the large specimen. Along the anterior margin of the ectepicondyle, there is a small salient that represents the supinator process, which is, however, fractured. In anterior view, even though the proximal part is not complete, it is possible to see the caput humeri which begins dorsally and extends up to the origin of the deltopectoral crest. The huge protuberance observed in ventral view projects interiorly. The deltopectoral crest occupies almost half of the length of the bone, but seems to be smaller than in SMNS 56891. The foramen entepicondyloideum is absent.

The relatively minor differentiation of the tubercles on the deltopectoral crest, the supinator process and the epicondyles, as compared to the double-sized specimen SMNS 56891 can be readily explained by assuming that SMNS 90571 represents a juvenile or immature individual of the same taxon. In all other respects the two specimens

are strikingly similar and there remains little doubt that they are from the same taxon, or at least very closely related forms.

4. Discussion

Dinodontosaurus is a Middle Triassic dicynodont genus that is known from numerous well preserved specimens, including complete skulls and articulated skeletons, from the Santa Maria Formation of Brazil and the Chañares Formation of Northern Argentina (VON HUENE 1935; ROMER 1943; COX 1965, 1968; LUCAS & HARRIS 1996). It has so far never been recorded outside of South America. The reason for LUCAS & WILD's identification remains obscure, as they admit (LUCAS & WILD 1995: 7): "SMNS 56891 does not correspond to any known Triassic dicynodont", a statement with which we fully agree. They compared the specimen in detail only with a humerus of a small kannemeyeriiform dicynodont (MCZ 9230) attributed to *Dinodontosaurus tener* (VON HUENE) (a species considered to be a nomen dubium by LUCAS & HARRIS 1996) from the Santa Maria Formation of Brazil. They stated (LUCAS & WILD 1995: 7) that "SMNS 56891 does not belong to *Dinodontosaurus* nor can it be readily assigned to any known Triassic dicynodont taxon", but suggested that greatest resemblance was found to *Dinodontosaurus* and determined it as aff. *Dinodontosaurus* in open nomenclature.

It is noteworthy that LUCAS & WILD (1995) list several important differences between the Lower Keuper humerus and the presumed *Dinodontosaurus* humerus MCZ 9230 which they used for comparison. In fact they did not provide any support for the identification of MCZ 9230 as *Dinodontosaurus*. To our knowledge, there are as yet no diagnostic features of a juvenile humerus by which *Dinodontosaurus* can be identified without doubt. Although the identification is probable, as *Dinodontosaurus* is the most common dicynodont in the Santa Maria Formation, it is at the present state of knowledge not recommendable to identify this isolated humerus to the species or even genus level. Furthermore, one is left to wonder why the authors did not use any of the better preserved and numerous *Dinodontosaurus* humeri available in Brazilian, American and German collections for comparison, but based their identification only on a single specimen of uncertain affinities.

The differences between SMNS 56891 and MCZ 9230 listed by LUCAS & WILD (1995) include: firstly, MCZN 9230 is more robust, with a broader deltopectoral crest, shorter and wider shaft and relatively broader distal end. Some of this proportional difference might be overexaggerated due to differential deformation of the two specimens. Nevertheless it is to a certain extent a valid difference. It does not preclude identification of SMNS 56891 as a dicynodont, though, and does not exclude a close affinity to *Dinodontosaurus*. The second feature concerns the presence of a well developed supinator process in SMNS 56891. Such a well-developed process is not just absent in MCZN 9230, but in all *Dinodontosaurus*-humeri known, and, in fact, in all other dicynodonts. This feature alone would be suggestive of the specimen representing a totally new dicynodont genus, or probably not a dicynodont at all. The third difference that LUCAS & WILD (1995) considered noteworthy concerns a pronounced dorsal concavity and ventral convexity of the anterior surface of the distal end of SMNS 56891. In fact this is an unusual morphology that is not present in any other dicynodont and, again, could serve to identify the specimen as belonging to a new genus, but does certainly not indicate a close relationship to *Dinodontosaurus*.

As the status of MCZ 9230 as *Dinodontosaurus* is slightly uncertain, we chose to do some further comparison of the Lower Keuper specimen to GPIT 1055, a complete, large, well preserved right humerus, attributed to *Dicynodon turpior* by VON HUENE (1935) (Fig. 1G). COX (1965), who referred this species to *Dinodontosaurus*, chose the specimen as the lectotype of *Dinodontosaurus turpior.* LUCAS & HARRIS (1996), although considering *D. turpior* as a nomen dubium, nevertheless admit that this material should be attributed to *Dinodontosaurus* sp., a decision with which we agree. Comparison of GPIT 1055 to the Lower Keuper specimens shows enormous differences.

To the three features considered by LUCAS & WILD (1995) in their original comparison, the following can be added, which they did not consider for identification, but mention in their description. The first is the unusual row of four tubercles on the distal part of the deltopectoral crest and a small salient near the proximal part of the articulation area. The two distalmost tubercles probably represent the areas of attachment of the pectoralis (ventral) and deltoideus (dorsal) muscles respectively (Figs. 1D, 2D). Nothing similar is known in other dicynodonts, either Permian or Triassic. The second feature concerns the total lack of an entepicondylar foramen. Such a foramen is a general feature of basal synapsids and it is present in all known dicynodont taxa in which the humerus is known. The lack of this foramen therefore makes identification as a dicynodont, or even a basal synapsid, highly unlikely. The morphology of the ectepicondyle, with its almost cylindrical cross-section, its pitted distal end and the high, plate-like supinator process along its anterior margin (Figs. 1B–D, 2B–D) resembles nothing found in any other dicynodont. The trochlea on the distal surface of the humerus is very narrow (Figs. 1D, 2D), occupying only less than a third of the distal surface, whereas the ectepicondyle is a very big and strongly flattened plate of bone. This

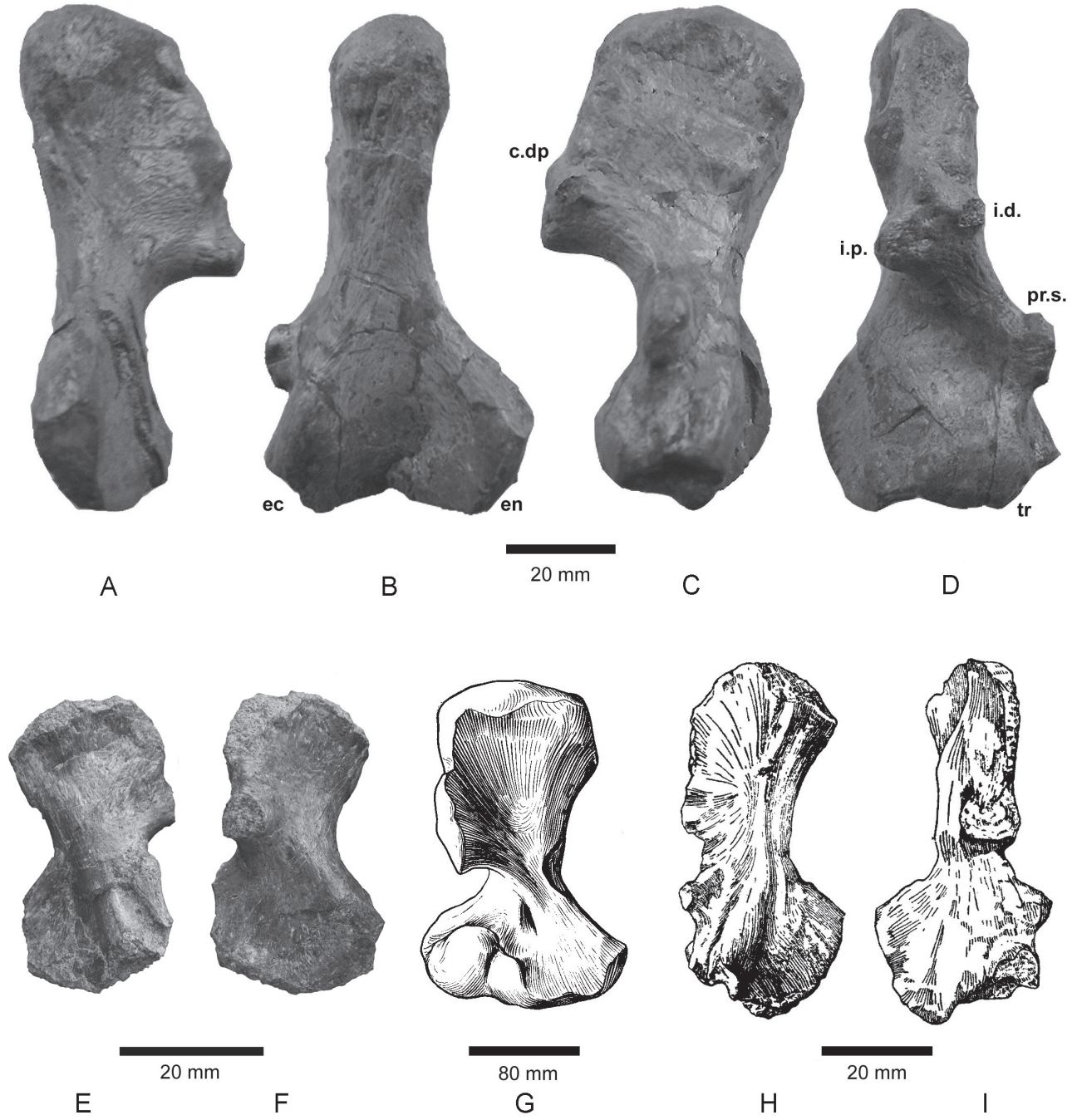

Fig. 1. A–D. ? Temnospondyli gen. et sp. indet., complete left humerus (SMNS 56891); lower Vitriolschiefer (Lower Lower Keuper, Middle Ladinian); Neidenfels near Crailsheim, Baden-Württemberg, southwestern Germany. – **A**. Posterior view. **B**. Dorsal view. **C**. Anterior view. **D**. Ventral view. – Abbreviations: c.dp = crista deltopectoralis, ec = ectepicondylus, en = entepicondylus, i.d. = insertion of musculus deltoideus, i.p. = insertion of musculus pectoralis, pr.s. = processus supinatorius.
E–F. ? Temnospondyli gen. et sp. indet., almost complete right humerus of a smaller individual (SMNS 90571); Untere Graue Mergel (Lower Lower Keuper, Middle Ladinian); Vellberg-Eschenau, Baden-Württemberg, southwestern Germany. – **E**. Dorsal and slightly posterior view. **F**. Ventral view.
G. *Dinodontosaurus turpior* (von Huene, 1935), lectotype, complete right humerus in ventral view; Santa Maria Formation (Middle Triassic); Chiniquá, Rio Grande do Sul, Brazil (modified from von Huene 1935).
H–I. *Dvinosaurus primus* Amalitzki, 1921, left humerus of an aquatic temnospondyl; Upper Permian; Northern Dvina, western Russia (modified from Sushkin 1936). – **H**. Dorsal view. **I**. Anterior view.

Fig. 2. A–D. ? Temnospondyli gen. et sp. indet., complete left humerus (SMNS 56891); Lower Vitriolschiefer (Lower Keuper, Middle Ladinian); Neidenfels near Crailsheim, Baden-Württemberg, southwestern Germany. – **A**. Posterior view. **B**. Dorsal view. **C**. Anterior view. **D**. Ventral view.
E–H. *Eryops megacephalus* Cope, 1877, left humerus; Lower Permian, Texas (after Pawley & Warren 2006). – **A**. Posterior view. **B**. Dorsal view. **C**. Anterior view. **D**. Ventral view.

morphology of the distal end of the humerus is also unknown in any other dicynodont.

Thus, considering the features that Lucas & Wild (1995) noted as relevant distinctions between SMNS 56891 and MCZ 9230, as well as the information gained from our additional comparison of SMNS 56891 to undoubted *Dinodontosaurus* material (GPIT 1055), we can support the conclusions of Lucas & Wild (1995) that SMNS 56891 is

not *Dinodontosaurus*, that it can not be readily referred to any other Triassic dicynodont taxon, and that it does not correspond in morphology to any other known Triassic dicynodont (Lucas & Wild 1995: 7).

Regarding all the features enumerated above, one is left to ask, why SMNS 56891 should be identified as a dicynodont at all. The only resemblances between the Lower Keuper humerus and true dicynodonts include that the bone is short, expanded widely both proximally and distally, has a long, well-developed deltopectoral crest and a short shaft, and that the distal and proximal ends are twisted. These are, however, mostly rather common features found in a variety of basal tetrapods and basal amniotes and they in no way indicate a close relationship to the Dicynodontia. To the contrary, many morphological features of the specimens, particularly the lack of an entepicondylar foramen, the large, plate-like supinator process, the shape of the ect- and entepicondyles, the narrow trochlea and the tubercles on the deltopectoral crest are so dissimilar to all other known dicynodonts, that referral to this group seems one of the least likely possibilities of identification. In our opinion, there is no sound evidence to identify either SMNS 56891 or the smaller, and probably juvenile, specimen SMNS 90571 as a dicynodont, and we also see no particular resemblance but instead even less similarity to any other basal synapsid.

Of course the question remains: if it is not a dicynodont, what else could it be? The Lower Keuper of the Germanic Basin includes a large variety of fossil amphibians and reptiles. The only synapsids that have been recorded hitherto are small cynodonts which remain largely undescribed (Schoch & Wild 1999; but see Hopson & Sues 2006). The humeri of known small cynodonts bear no particular resemblance to SMNS 56891 or SMNS 90571, and any identification can be positively excluded. All of the marine reptiles, placodonts, nothosaurs, pachypleurosaurs, thalattosaurs and tanystropheid protorosaurs that have been recorded from the Lower Keuper can equally be excluded from any closer comparison. Even though humeri are not known for all Lower Keuper taxa, they are known for a large variety of genera and species within all these groups, and they are all so different in morphology (in particular always much more elongated with much less development or even lack of a deltopectoral crest) that identification is impossible. There is also no resemblance to the humeri of rauisuchians and other archosauriforms that have been recently recorded from the Lower Keuper (Gower & Schoch 2009).

At any rate, fossil reptiles only form the minority of the fossil tetrapod finds in most Lower Keuper localities, except for the Hohenecker Kalk of the Upper Lower Keuper, which contains a typically marine fauna dominated by sauropterygians and placodonts. In all other Lower Keuper Fossillagerstätten, temnospondyl amphibians are dominant (Wild 1980; Schoch & Wild 1999) and have been recorded by numerous taxa (von Jaeger 1828; von Meyer & Plieninger 1844; von Huene 1922; Schoch 1997, 1999, 2006, 2008; Schoch & Werneburg 1999; Schoch & Milner 2000; Hellrung 2003; Damiani et al. 2009), a single chroniosuchid is also known (Witzmann et al. 2008).

In several of these, the humeri are quite well known. These include *Mastodonsaurus* (von Huene 1922; Schoch 1999), *Gerrothorax* (Hellrung 2003), *Plagiosuchus* (pers. obs.), *Trematolestes* (Schoch 2006) and *Callistomordax* (Schoch 2008). They are still unknown in the plagiosaurid *Plagiosternum* and the cyclotosaurid *Kupferzellia*. However, these taxa are likely to have been aquatic, as judging from what is known about the osteology of their closest relatives (Warren & Snell 1991; Schoch 2009).

All these aquatic Lower Keuper temnospondyls have humeri that are rather flattened and strongly to moderately expanded at both extremities, with little ossification of either the articulatory surfaces or zones of muscle attachment. These features are typical of most Triassic temnospondyls which are usually regarded as adapted to a highly aquatic mode of life (Warren & Snell 1991; Meckert 1993). It is therefore unlikely that SMNS 56891 and SMNS 90571 represent such aquatic temnospondyls.

At closer inspection, the two Lower Keuper humeri match those of Permian *Eryops* (Miner 1925; Pawley & Warren 2006; Fig. 2E–H) and Triassic *Lydekkerina* (Pawley & Warren 2005) quite well. In addition, the humerus of the enigmatic Permian genus *Peltobatrachus* is also generally similar, although shorter and only incompletely known (Panchen 1959). A more superficial resemblance is also found to the Permian aquatic *Dvinosaurus* (Sushkin 1936).

The Lower Keuper humeri agree with those of the four aforementioned genera in the possession of (1) a robust supinator process, (2) a clear separation of a pectoralis and deltoideus crest, (3) the very wide distal end, and (4) the tetrahedral morphology, with the broadened faces of proximal and distal ends aligned at a right angle. Among the Triassic stereospondyl temnospondyls, tetrahedral humeri are only known from *Lydekkerina* and plagiosaurids (Pawley & Warren 2005; Hellrung 2003).

In addition to the mentioned features, the humerus of *Eryops* shares with the Lower Keuper specimens clearly separated ect- and entepicondyles and a well ossified radial condyle, both characters absent in *Lydekkerina*. Therefore, we rate the resemblance with *Eryops* highly, and conclude that the Lower Keuper humeri probably stem from a 1.5–2 m long, amphibious or terrestrial temnospondyl.

Of course, the possibility that the Lower Keuper humeri stem from a taxon pertaining to another major group cannot be completely ruled out. Many humeral features of

terrestrial taxa – such as the clearly separated condyles, the supinator process, the morphology of the shaft, and the separation of pectoralis and deltoideus attachments – are found in a wide range of unrelated basal amniotes, temnospondyls, and seymouriids. Yet a comparison to the humerus of *Seymouria* for instance reveals fundamental differences (SULLIVAN & REISZ 1999), as is the case with amniotes. Therefore, the Lower Keuper humeri most probably stem from an eryopoid (sensu SCHOCH & WITZMANN 2009).

It is further to be emphasized that those features that clearly distinguish the Lower Keuper taxon from dicynodonts and synapsids in general are, in turn, in good agreement with an interpretation as a temnospondyl amphibian. These include the tubercles on the distal part of the deltopectoral crest, the supinator process, and the absence of an entepicondylar foramen.

So far, no fossil amphibian is known from cranial or other skeletal remains from Lower Keuper deposits which can be considered as a potential candidate for definite identification. The fact that so far only two isolated humeri have been found of the – presumably terrestrial – temnospondyl speaks in favour of the interpretation that it was an animal that did not live in the depositional area of the Lower Keuper sediments. As the Lower Keuper was deposited under more or less limnic to shallow marine or brackish conditions and as the animal must, from the morphology of its humerus, be assumed to have spent at least its adult life preferably on dry land, this is not surprising. The two humeri were probably washed in from a more terrestrial environment and were the only remains of the already decomposed skeletons that became fossilized. Although we cannot support their identification, we nevertheless agree with LUCAS & WILD (1995) that we are dealing with a terrestrial animal whose biotope was probably the Vindelician land emerging to the southwest of the depositional area of the Lower Keuper.

5. Conclusion

The re-identification of the alleged aff. *Dinodontosaurus* specimen described by LUCAS & WILD (1995) from the German Lower Keuper to the Temnospondyli underlines the importance of the correct evaluation of fragmentary and otherwise unique fossil tetrapod specimens. It also points to the difficulties and uncertainties related to vertebrate-based biochronological correlations which are based on such specimens. RAYFIELD et al. (2009), who also considered the material as undiagnostic (although not questioning its identity as a dicynodont) clearly identified "subjective opinions regarding the taxonomic assignments of key specimens" as one of the most critical aspects regarding the validity of the Triassic land-vertebrate biochronology advocated by LUCAS and co-workers in many papers. The case of the misidentified Keuper dicynodont discussed above provides further support to the conclusions of RAYFIELD et al. (2009), and it once again demonstrates the importance of careful and correct taxonomic work in vertebrate paleontology as the basis for any more general concepts and higher-order hypotheses.

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