First direct evidence of a vertebrate three-level trophic chain in the fossil record

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We describe the first known occurrence of a Permian shark specimen preserving two temnospondyl amphibians in its digestive tract as well as the remains of an acanthodian fish, which was ingested by one of the temnospondyls. This exceptional find provides for the first time direct evidence of a vertebrate three-level food chain in the fossil record with the simultaneous preservation of three trophic levels. Our analysis shows that small-sized Lower Permian xenacanthid sharks of the genus *Triodus* preyed on larval piscivorous amphibians. The recorded trophic interaction can be explained by the adaptation of certain xenacanthids to fully freshwater environments and the fact that in these same environments, large temnospondyls occupied the niche of modern crocodiles. This unique faunal association has not been documented after the Permian and Triassic. Therefore, this Palaeozoic three-level food chain provides strong and independent support for changes in aquatic trophic chain structures through time.

Keywords: Acanthodii; food web; gut contents; Permian; Temnospondyli; Xenacanthidae

1. INTRODUCTION

Among fossil organisms, inferences of trophic interactions are generally based on indirect evidence such as tooth morphologies, tooth marks produced by predators or scavengers and coprolites, whereas gut contents and soft-bodied structures are rarely preserved (Martill *et al.* 1994; Cavin 1996; Richter & Baszio 2001; McAllister 2003). Moreover, empirical behavioural data of fossil predator–prey relationships are generally limited to isolated cases of single ingested prey items and most of these finds are generally considered to represent isolated occurrences without or with little potential for deeper insights into past trophic organizations or community structures (Maisey 1994).

So far, only a few fossil predator–prey relationships have been documented in the fossil record: e.g. from the Devonian of Canada, Ohio (USA) and Scotland based on direct evidence (Arsenault 1982; Williams 1990; Ahlberg 1992); Upper Carboniferous of Spain based on assumed direct evidence (Soler-Gijón 1995); Permo-Carboniferous of the Saar-Nahe Basin based on indirect and direct evidence (Boy 1993*b*; Heidtke 2007*a*); Lower Jurassic of Germany based on gut contents (Hauff 1953); Upper Jurassic of Solnhofen (south Germany) based on gut contents, direct and indirect evidence (Viohl 1990); Lower Cretaceous Santana Formation of Brazil based on direct evidence (Wilby & Martill 1992; Maisey 1994); Upper Cretaceous of Morocco based on direct evidence (Cavin 1996); Eocene of the Green River Formation (USA) based on direct evidence (Grande 1984); and the Eocene Messel Lake in Germany based on fish coprolites (Richter & Baszio 2001). The lack of information about gut/intestine contents is generally due to taphonomic processes, incomplete sampling of gut contents or inadequate observations.

Although the high number of exceptionally preserved vertebrate skeletons in the Permo-Carboniferous lakes of the Saar-Nahe Basin might provide detailed insights into predator–prey relationships and coevolutionary patterns of early vertebrate communities, only selected taxa have been used to reconstruct simplified food webs (Boy & Sues 2000). The Saar-Nahe Basin is located in southwest Germany and represents a molasse trough at the southern margin of the Variscan orogeny that was filled with fluvio-lacustrine sediments (Schäfer 1989). In this depression, short-living lakes of varying size were connected to the marine-paralic foreland throughout the uppermost Carboniferous, enabling faunal exchanges between lakes and with the sea. The connections were subsequently restricted and disconnected during the uppermost Carboniferous (Schneider *et al.* 2000).

The specimen that forms the focus of this study comes from the last stage of the Lower Permian Lake Humberg, which was one of the largest and longest-lasting lakes in the Saar-Nahe Basin (Boy & Sues 2000). Lower Permian xenacanth sharks are considered to have been fully adapted to freshwater conditions due to the interrupted connections between the Saar-Nahe Basin and the sea. This interpretation is also supported by the presence of xenacanthid egg capsules, indicating that sharks did not only sporadically enter the lakes in pursue of prey but also reproduced in these freshwater environments (Heidtke 2007*b*).

In this paper, we (i) describe the first direct evidence of a fossil vertebrate three-level trophic chain, and (ii) present a complex food web for a Permian lake ecosystem.

2. MATERIAL AND METHODS

The xenacanth specimen, *Triodus sessilis*, described here comes from Lebach near Saarbrücken (southwest Germany). It is preserved dorsoventrally in a siderite concretion containing skeletal remains such as the jaws with associated teeth, pectoral elements and placoid scales (figure 1*a*). The posterior half of the specimen is missing, as is the counterpart

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Figure 1. *Triodus sessilis* with ingested prey items. (*a*) Photograph of a specimen from the Lower Rotliegend of Lebach, southwest Germany (UHC-P 0682). (*b*) Line drawing of digested temnospondyl larvae. Left: an almost complete specimen of *Cheliderpeton latirostre* with the remains of ingested juvenile acanthodian. Right: skull of *Archegosaurus decheni*. as, acanthodian scales; br, branchial apparatus; cla, clavicle; ?clei, cleithrum; fem, femur; fs, acanthodian fin spines; gs, gastral scalation; hum, humerus; icl, interclavicle; il, ilium; man, mandible; mc, Meckel's cartilage; mca, metacarpalia; mta, metatarsalia; na, neural arch; or, orbit; pas, parasphenoid; pf, pectoral fin; pg, pectoral girdle; phal, phalanges; pq, palatoquadrate; ps, xenacanthid placoid scales; r, ribs; rad, radius; sk, skull; sta, stapes; ul, ulna.

of the slab. It is, nevertheless, of immense importance, because it is the only known example of a shark with two amphibian preys (*Archegosaurus decheni* and *Cheliderpeton latirostre*) preserved in its gut. In turn, one of the amphibians shows the remains of a digested acanthodian fish (*Acanthodes bronni*). The sediments yielding the specimen belong to the Upper Odernheim Unit of the Lower Rotliegend Meisenheim Formation, which is of the lowermost Permian age (Königer *et al.* 2002) and represents the final stage in the development of Lake Humberg. The specimen is deposited in the Pfalzmuseum für Naturkunde (Pollichia-Museum), Bad Dürkheim, Germany under catalogue no. UHC-P 0682.

3. RESULTS

The small xenacanth genus *Triodus* occurs with several species in the Carboniferous and Permian of the Saar-Nahe Basin (*T. sessilis* being the most common species), indicating that it represents a common inhabitant of these lakes

(Hampe 1989). The assignment of the specimen described here to *T. sessilis* is supported by its dental morphology, which is characterized by grasping teeth with ornamented cups of which the median one is very enlarged, a flat root with large coronal tubercle and a concave basal tubercle.

The preservation of the two temnospondyl amphibians located in the digestive tract of *T. sessilis* is remarkable, in that it indicates that these two amphibians were preyed upon only shortly before the death of the predator (figure 1). The skull of *A. decheni*, which is approximately 35 mm long, is preserved in dorsal aspect together with its right mandible. The elongate choana, the basal plate and the cultriform process of the parasphenoid are visible, because the dermal skull roof is partly eroded. The stapes is located on the right-hand-side of the basal plate and has undergone almost no displacement from its anatomical position. Its longitudinal axis is oriented laterally and its distal end points into the squamosal embayment ('otic notch'). Remnants of the paired atlantal neural arch are
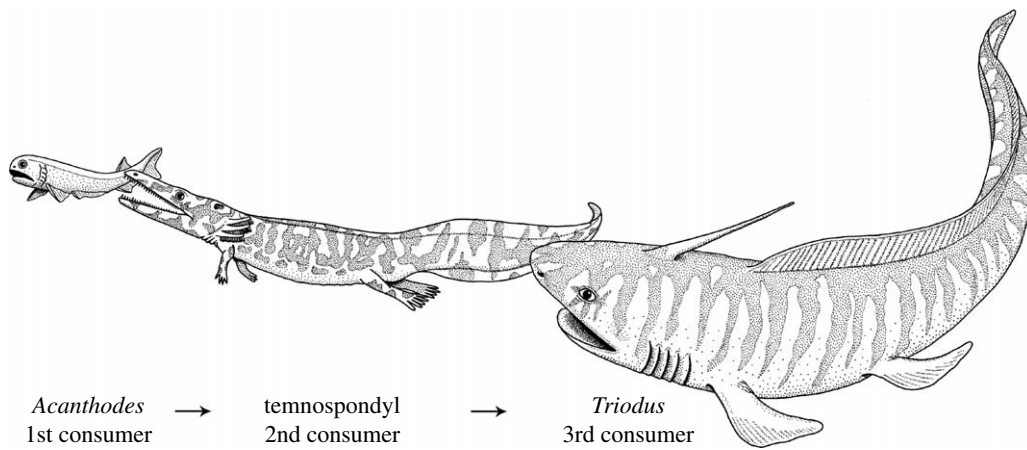
Figure 2. Three-level food chain of Lower Permian Lake Humberg, as exemplified by the specimens presented here. The short food chain involves three trophic levels (primary (*Acanthodes*), secondary (larval temnospondyls) and tertiary consumers (*Triodus*)) and is most efficient as it transfers as much energy as possible to the shark. From left to right: juvenile *A. bronni*; larval temnospondyl; *T. sessilis*.

situated at the posterior margin of the basal plate. The slender, triangular outline of the skull and the narrow jugal lateral to the orbit identifies it as a larval *A. decheni*. The larval phase in *A. decheni* ended with the resorption of external gills and the branchial dentition at a skull length of approximately 150 mm. Adult individuals reached skull lengths of more than 280 mm (Witzmann 2006).

The second temnospondyl ingested by *T. sessilis*, *C. latirostre*, consists of an almost complete skeleton including the ventral scalation (figure 1*b*). Its vertebral column is aligned parallel to the longitudinal axis of the shark with the skull being located anteriorly in the intestine. Almost no sutures are recognizable on the badly crushed dermal skull roof. In spite of this, its shape can be identified with some approximation on the basis of the lateral tooth rows and the nasal bones. Its length in the sagittal midline is approximately 50 mm long. The left and right mandibles are better preserved and are 58 mm long. Although the skull is slender in outline, it does not taper anteriorly to the extent observed in *A. decheni*. Furthermore, the jugal width lateral to the orbits is broader in this specimen allowing its assignment to *C. latirostre*. In the axial skeleton, only the undifferentiated, paired neural arches and the short, straight ribs are ossified. Fragments of the dermal pectoral girdle are preserved and only the stout ilium is ossified. The fore- and hindlimbs are poorly ossified. The size of the skull and the poor degree of ossification indicate that this specimen is either a larva or an early juvenile. *Cheliderpeton latirostre* reached an adult skull length of more than 140 mm (Boy 1993*a*). The location and orientation of the two temnospondyls correspond perfectly to the inferred position and direction of the gut/intestine of *Triodus* and do not represent an artefact.

The delimitation of the acanthodian fish by the vertebral column, the ventral scales and the pectoral and pelvic girdles of *C. latirostre* confirms it as a prey item of this temnospondyl. The acanthodian specimen is very incomplete with only the body and associated fin spines being preserved, indicating an advanced phase of digestion (figure 1*b*). The size and fin spine morphology identify the specimen as a juvenile of *A. bronni*. So far, only adult temnospondyls have been assumed to feed on acanthodians (Boy 1993*b*). The specimen described here and additional information show that juvenile acanthodians

actually constituted a major food resource also for larval *A. decheni* and *C. latirostre*, which most probably were very specialized and preyed predominantly on *Acanthodes* (F. Witzmann 2004, unpublished PhD thesis; this study).

4. DISCUSSION
In the Saar-Nahe Basin, the direct evidence (stomach contents) of predator–prey interactions were only reported from few large acanthodian fishes and tetrapods representing only two trophic levels (Boy & Sues 2000; Heidtke 2007*a*). Both larval and adult *Archegosaurus* and *Cheliderpeton* were piscivorous and preyed predominantly on *Acanthodes* (Boy 1993*b*; F. Witzmann 2004, unpublished PhD thesis). The recovery of an exceptionally preserved specimen of the Permian xenacanthid, *T. sessilis*, with two preserved temnospondyls in its digestive tract and an acanthodian ingested by one of these amphibians is consequently of major importance. It provides the first direct evidence of predator–prey relationships including vertebrates of three different trophic levels in an ancient lake system (figure 2). It has long been assumed that *Triodus* fed exclusively on acanthodians (e.g. Hampe 1989). *Triodus sessilis* (approx. 0.5 m long) was the smallest xenacanthid in the Permian Lake Humberg of the Saar-Nahe Basin. Two additional xenacanthids, *Lebacha-canthus* (approx. 3.5 m long) and *Xenacanthus* (approx. 1 m long), also thrived in this lake. Xenacanth sharks are generally considered to represent the earliest fully freshwater-adapted chondrichthyans (Compagno 1990).

Based on the exceptional specimen described here and data from the literature, it is possible to reconstruct not only the first fossil three-level trophic chain containing exclusively vertebrates but also the complex trophic interrelationships in the final stage of Lake Humberg development. The food-web reconstruction depicted here is far more complex with more direct links than previously assumed. However, it displays trophic complexities very distinct from those found today in fluvio-lacustrine settings, and we assume that modern-type trophic relationships in these environments evolved very late, probably after the Triassic when modern teleost lineages appeared. The Lake Humberg food web is predator-heavy and highly biased towards piscivores and batrachophagous taxa (those feeding on amphibians), indicating that predator–prey
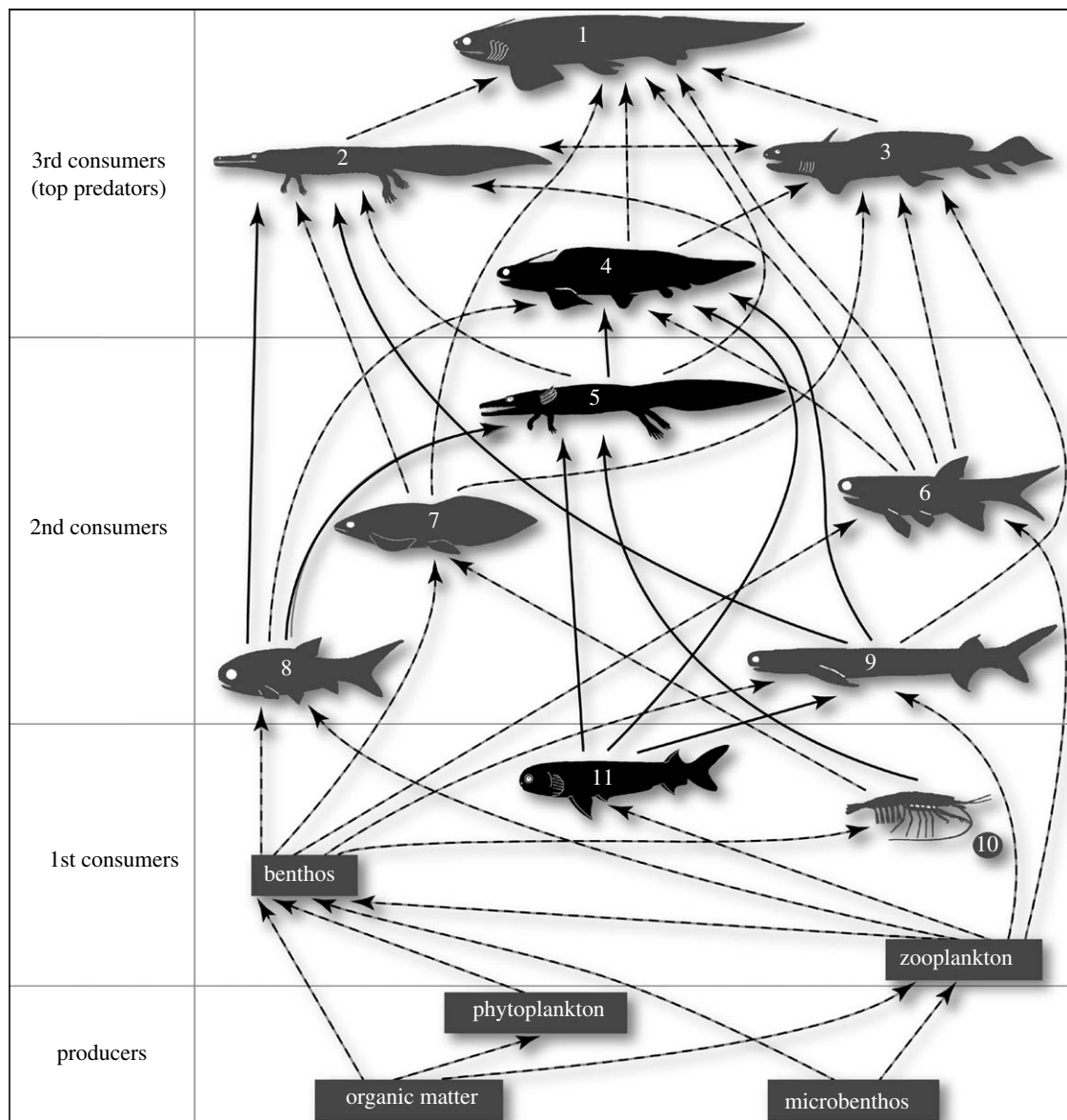
Figure 3. Generalized Early Permian food web of Lake Humberg based on indirect (dashed lines) and direct (solid lines) evidence. Direct evidence is based on gut contents or food items in the mouth/pharyngeal cavity. Indirect evidence is derived from functional–morphological interpretations and analogy with extant sharks and non-mammalian tetrapods. We identify four trophic levels with 8 direct and 31 indirect links. 1, *Lebachacanthus*; 2, adult *Archegosaurus/Cheliderpeton*; 3, *Orthacanthus*; 4, *Triodus*; 5, larval *Archegosaurus/Cheliderpeton*; 6, Palaeoniscidae; 7, *Conchopoma*; 8, Paramblypteridae; 9, adult *Acanthodes*; 10, *Uronectes*; 11, juvenile *Acanthodes*. Figures not to scale (data from Boy & Sues (2000), F. Witzmann (2004, unpublished PhD thesis), Heidtke (2007*a*,*b*) and this study).

interactions may be more important than planktivore-controlled structures (figure 3). Although fish-eating predators are the most common taxa in Lake Humberg, the high number of omnivores indicates the stability of this complex food web according to recent concepts (e.g. Rooney *et al.* 2006). This indicates that the establishment of trophic levels became well adapted during the final stage of lake development, suggesting that macroevolutionary patterns provided some sort of control protecting established ecosystems against perturbations caused, for instance, by invasion of new species. We hypothesize that the top-most position within the food web (4th trophic level) of Lake Humberg was occupied by large xenacanth sharks (*Xenacanthus* and *Orthacanthus*) preying on other sharks, paramblypterid and acanthodian fishes and amphibians. However, the direct evidence for this assump-

tion is not supplied by fossils even though several hundred xenacanth specimens have been recovered up to now. *Triodus sessilis* also was an apex predator but at a lower order. The two larval temnospondyls, which are secondary consumers (3rd trophic level), were obviously attacked and swallowed completely tail first by *Triodus* during their pursuit of juvenile acanthodians (1st consumer feeding on ostracods and plankton, 2nd trophic level; Boy 1993*b*) as specified by their orientation (figures 1 and 2). The acanthodian prey item had to be repositioned in a lengthwise position by *Cheliderpeton* as indicated by the orientation of its fin spines before swallowing after it had been overtaken, analogous to extant crocodiles, for example (Cleuren & De Vree 2000). *Triodus* is considered an ambush predator of near-shore environments (Schneider *et al.* 2000), where larval temnospondyls also

dwelled to avoid predators of the open lake such as large xenacanths and adult temnospondyls (4th trophic level).

5. CONCLUSION

This example of a Palaeozoic three-level food chain clarifies well that continental aquatic trophic chain structures changed through time and are not independent of macroevolutionary changes (Thompson 1999). During the Palaeozoic, top predators in piscivore-dominated fluvio-lacustrine ecosystems were represented by large xenacanth sharks and adult aquatic temnospondyls. In the Mesozoic, both modern and extinct lacustrine ecosystem types still existed (Sinichenkova & Zherikhin 1996), but xenacanth sharks and temnospondyls were ecologically replaced by aquatic amniotes (Warren 2000), hybodont and neoselachian sharks and bony fishes in post-Triassic ecosystems. Batrachophagous sharks are obviously absent from post-Triassic ecosystems and amphibians do not play an important role in post-Triassic lacustrine food webs at all. The diet of extant marine sharks and those invading fluvio-lacustrine environments (no modern shark lives exclusively in freshwater environments) contains a wide array of prey items but no amphibians have been reported from any stomach content analyses so far (e.g. Wetherbee & Cortés 2004). Interestingly, all extant euryhaline and obligate freshwater sharks occur in tropical and warm-temperate rivers and lakes, which are also frequented by some large newts and salamanders, e.g. sirenids, amphiumids and cryptobranchids (Duellman & Trueb 1986). However, modern sharks seemingly do not prey on these amphibians despite their sporadic co-occurrence. The reasons for this are still not comprehensible. Modern freshwater teleosts, conversely, are known to prey on larval amphibians (Smith *et al.* 1999), and we assume that amphibian larvae regularly were preyed upon by bony fishes in post-Palaeozoic lacustrine ecosystems. In the Palaeozoic, freshwater-adapted sharks were the main predators of temnospondyl amphibians, which occupied a niche that is filled by large teleosts and crocodiles in post-Triassic environments.

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