OBSERVATIONS ON THE POSTCRANIAL MORPHOLOHY, ONTOGENY AND PALAEOBIOLOGY OF *SCLEROCEPHALUS HAEUSERI* (AMPHIBIA: ACTINODONTIDAE) FROM THE LOWER PERMIAN OF SOUTHWEST GERMANY

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The temnospondyl amphibian *Sclerocephalus* is described in four ontogenetic stages: larval, juvenile, adult and late adult. In particular the postcranial anatomy was observed. Some specimens preserve stomach contents, consisting of paramblypterid fishes and small amphibians (*Micromelerpeton, Apateon*). In one specimen, the remains of a small *Sclerocephalus* were found. Larval and juvenile individuals probably lived in a different habitat than adult and late adult ones. In the juvenile, adult and late adult stages, *Sclerocephalus* was the top predator in its environment. **?** Amphibia, Limnarchia, Actinodontidae, *Sclerocephalus haeuseri*, postcranial morpholgy, ontogeny, palaeobiology, Lower Permian, Germany

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The limnarchian amphibian *Sclerocephalus* is one of the best-known representatives of this group in the Lower Permian of Central Europe. The type species, *S. haeuseri,* was described by GOLDFUSS (1847), but the holotype is lost now (BOY, 1988). Later *Sclerocephalus* specimens were described or referred to by several researchers (e.g. AMMON, 1889, BOY, 1976, 1988, BRANCO, 1887, BROILI, 1908, 1926, BURMEISTER, 1850, CREDNER, 1893, FRITSCH, 1901, HEYLER, 1975, MEYER, 1857, 1858 ROMER, 1947 & WERNEBURG, 1983, 1989, 1992). At present, three species are known: the type species, *Sclerocephalus haeuseri* GOLDFUSS, 1847, *Sclerocephalus bavaricus* BRANCO, 1887 and *Sclerocephalus jogischneideri* WERNEBURG, 1992. Other species referred to *Sclerocephalus* do not belong to that taxon, e.g. "*Sclerocephalus*" *latirostris* JORDAN, 1849 (= *Cheliderpeton latirostre* sensu BOY, 1993), "*Sclerocephalus" labyrinthicus* GEINITZ, 1861 (= *Onchiodon labyrinthicus* sensu e.g. WATSON, 1919) and "*Sclerocephalus*" *credneri* FRITSCH, 1901 (= *Onchiodon labyrinthicus* sensu WERNEBURG, 1993 and *Capetus palustris* sensu SEQUEIRA & MILNER, 1993). On the other hand some larval individuals of *Sclerocephalus* where first misinterpreted and therefore described as or referred to other taxa. ROMER (1939) first pointed out that *Branchiosaurus amblystomus* described by CREDNER (1882, 1885, 1886 and 1893) and AMMON (1889) has to be referred to *Sclerocephalus.* CREDNER'S specimens are today assigned to *Onchiodon* (sensu e.g. BOY, 1990). Later BOY (1972) recognised that *Leptorophus levis* BULMAN, 1928 (= *Branchiosaurus levis* in WATSON, 1963) and *Pelosaurus longiscutatus* THEOBALD, 1958 may represent larval individuals of *Sclerocephalus*.

Sclerocephalus had a wide palaeogeographical distribution (see WERNEBURG, 1988) and is recorded throughout the Autunian. The oldest known species is *Sclerocephalus bavaricus* BRANCO, 1887 from the Altenglan-Formation (Lower Autunian) of Ohmbach (Rheinland Pflalz, SW Germany). It is represented by only one incomplete skeleton (MB Am.442) with a well-preserved skull.

The type species *Sclerocephalus haeuseri* is the most well known and is represented by a large number of articulated skeletons, found in the Saar-Nahe area in Southwest Germany (Rheinland Pfalz and the Saarland). Two subspecies were recognised by BOY (1988); *S. h. haeuseri* GOLDFUSS, 1847 and *S. h. jeckenbachensis* BOY, 1988. It is also the only species of which all ontogenetic stages are present.

Many new specimens, which clearly show different ontogenetic stages, have been found during the last decade. They also provide new data concerning the diet of these amphibians. This paper characterises the stages of ontogeny of *Sclerocephalus haeuseri* and discusses its autecology. Results include those of an unpublished report by the senior author (LOHMANN, 1996).

MATERIAL AND METHODS

MATERIAL EXAMINED. PMNB uncataloged. larval individual, complete skeleton with soft tissue preservation, length 8.5 cm; PMNB 393, larval individual, complete skeleton with soft tissue preservation, length 9.5 cm; GMS 307, larval individual, skull and pectoral girdle, skull-length 16 mm; PMNB 85, juvenile individual, complete skeleton with soft tissue preservation, length 13 cm; PMNB 308, juvenile individual, complete skeleton with soft tissue preservation, length 11 cm; PMNB 177, juvenile individual, complete skeleton with soft tissue preservation, length 12,5 cm; PMNB 179, juvenile individual, skull and parts of the pectoral girdle, skull length 18 mm; GMS 24, juvenile individual, skull and parts of the pectoral girdle, skull length 25 mm; GMS 228, juvenile individual, complete skeleton with soft tissue preservation, length 14 cm; GMS 395, juvenile individual, complete skeleton with soft tissue preservation, length 24 cm; GMS 394, juvenile individual, skull and anterior half of the body with soft tissue preservation, skull length 35 mm; GMS 52, juvenile individual, complete skeleton with soft tissue preservation, length 30 cm; PMNB 174, juvenile individual, almost complete skeleton with soft tissue preservation, length 22 cm; GMS 396, juvenile individual, complete skeleton with soft tissue preservation, length 26 cm; PMNB 93, juvenile individual, complete skeleton with soft tissue preservation, length 26 cm; PMNB 103, juvenile individual, complete skeleton with soft tissue preservation, length 25 cm; GMS 348, juvenile individual, complete skeleton with soft tissue preservation, length 28 cm; PMNB 415, juvenile individual, complete skeleton with soft tissue preservation, length 29 cm; GMS 226, juvenile individual, complete skeleton with soft tissue preservation, length 30 cm; PMNB no. No., juvenile individual, complete skeleton with soft tissue preservation, length 26 cm; PMNB GRE-1, juvenile individual, complete skeleton with soft tissue preservation, length 48 cm; PMNB PDC 327, adult individual, complete skeleton, length 74 cm; PMNB BGC 69, adult individual, complete skeleton, length 72 cm; PMNB BGC 112, adult individual, complete skeleton, length 79 cm; BSPHG-1981 I99, adult individual, skull and partial skeleton, skull length 16 cm, PMNB BGC 112, late adult individual, complete skeleton, length 182 cm. GMS P/70, adult individual, isolated sacrum, length ca. 10 cm. Private collection SKO, adult individual, complete skeleton, length 82 cm

REFERRED MATERIAL; About 800 coprolites from the collections PMNB, GMS, GPIM and SKO.

LOCALITIES AND AGE. All larval and most of the juvenile specimens are from the locality Rümmelbach/Gresaubach (Top L-O 10). One juvenile specimen has been found in Gresaubach (PMNB GRE-1, Top L-O 10) and in Wörsbach (PMNB uncataloged, Top L-O 10). The adult individuals are from the localities Niederhausen an der Appel (PMNB PDC 327, L-O 8), Jeckenbach (PMNB BGC 69, L-O 6), Odernheim (SKO uncataloged, L-O 6) and Raumbach (SKO no Nr., L-O 6). The late adult individual was found in Jeckenbach (PMNB BGC 112, L-O 6). The isolated sacrum was found in St. Wendel (GMS P/70, L-O 5). The observed coprolites are from different horizons, reaching from Q 1 to L-O 10. In general the layers containing the specimens belong to the so-called Lower Rotliegendes (Autunian in the European stratigraphy sensu BOY & FICHTER = Gzehlian / Asselian in the global stratigraphy sensu DEITZE, 2000).

METHODS. All specimens were photographed in detail and have then drawn proportionally with a radiograph. For smaller individuals a WILD M-3 binocular with drawing mirror was used.

ABBREVIATIONS OF INSTITUTIONS AND PRIVATE COLLECTIONS - **BSPHG**. Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich; **PMNB**. Pfalzmuseum für Naturkunde, Bad Dürkheim; **GMS**. Geologisches Museum der Saarberge AG, Saarbrücken; **GPIM**. Geologisch-Paläontologisches Institut, University of Mainz; **MB**. Museum für Naturkunde, Berlin; **SKO**. private collection KRÄTSCHMER, Odernheim.

GEOLOGICAL ABBREVIATIONS – **L-O**. Lauterecken-Odernheim-Formation (current stratigraphy Lauterecken-Formation L-O 1 + L-O 2, Jeckenbach-Odernheim-Formation L-O 3 – L-O 10 (3 = lowermost / 10 = uppermost). **Q** Quirnbach-Formation (Q1 = lower / Q2 = upper) (see DIETZE, 2000, Fig. 1)

ANATOMICAL ABBREVIATIONS – **Cl**, clavicle; **Cr**, caudal rib; **Ct**, cleithrum; **F**, femur; **Fi**, fibula; **H**, humerus; **I**, interclavicle; **Il**, ilium; **Is**, ischium; **Mc**, metacarpus; **P**, pelvis; **Ph**, phalanges; **Pu**, processus uncinatus; **R**, radius; **Sc**, scapula; **St**, stomach contents; **Ti**, tibia; **U**, ulna; **Va**, ventral armour.

SYSTEMATIC PALAEONTOLOGY*

AMPHIBIA Linnaeus, 1758

TEMNOSPONDYLI Zittel, 1890

LIMNARCHIA Yates & Warren, 2000

STEREOSPONDYLOMORPHA Yates & Warren, 2000

ARCHEGOSAUROIDEA Meyer, 1857

ACTINODONTIDAE Lydekker, 1885

Sclerocephalus Goldfuss, 1847

Sclerocephalus haeuseri Goldfuss, 1847

MORPHOLOGY OF THE ADULT POSTCRANIAL SKELETON OF *SCLEROCEPHALUS HAEUSERI* - The vertebral column consists of 37-39 rhachitomous vertebrae (25 presacrals and 12-14 caudals). The neural arches are high and robust, with those of the atlas-axis-complex only visible in late adult individuals. The neural spine of the fourth cervical vertebra is somewhat shorter; a feature that is also known in other temnospondyls such as *Eryops* (MOULTON, 1974) and *Balanerpeton* (MILNER & SEQUEIRA, 1994).

The transversal processes are short but prominent. They are posterolaterally directed and bear large, vertical diapophyses, which are laterally oblique. Pre- and postzygapophyses are well-developed and about equal in size. The main bodies of the prezygapophyses are situated at a somewhat higher level than those of the postzygapophyses.

The proximal articulation surface of the ribs is relatively broad, because of the coossification of the capitulum and tuberculum. The second to fourteenth ribs bear a prominent processus uncinatus distalis close to their posterior margin. These processus are hook-like and contact the anterior margin of the following rib. The second, third and fourth ribs are the longest. The following ribs taper slightly in length back to the fourteenth or fifteenth vertebra and then rapidly to the sacrum. The shoulder girdle consists of the interclavicle (which is the central ventral element) and the paired clavicles, scapulocoracoid and cleithrum. The interclavicle is a relatively flat bone of rhombic shape. Its ventral surface bears numerous cristae and furrows, which run from the edges to the centre. The clavicles are flat, triangular bones. They are medially curved in their ventral section and broadly contact the interclavicle. Their dorsal process has a posteriorly directed tip that contacts the ventral process of the cleithra. Their ventrolateral margin also bears some furrows. The scapulocoracoids are the most prominent bones of the shoulder girdle. The shoulder blade is formed as a broad, posteromedially directed, dorsal process. It articulates with the clavicle anteroventrally and with the cleithrum anterodorsally. The coracoid part of the scapulocoracoid is situated ventrally on the posteroventral margin. In the posterior margin is a prominent glenoid surface. Above the latter, a large supraglenoid foramen is developed. The cleithra are flat, arch-shaped bones with a triangular outline. They contact the scapula blade with their posteromedial margin. Ventrally they run out in a sharp process that meets the dorsal process of the clavicle in about the anterior mid-section of the scapula blade.

The humerus is robust and moderately elongated. It is of tetrahedal shape (MECKERT, 1993 sensu ROMER, 1939) and is therefore similar to the humerus of *Eryops* (MINER, 1925). Proximally, a prominently convex head is developed underneath of which the processus latissiumus dorsi and the crista pectoralis are situated posteriorly and the crista dorsalis is situated anteriorly. The distal surface is clearly anteroposteriorly expanded. It bears a relatively small processus supinator and a somewhat larger ectepicondylus anteriorly, as well as a very prominent entepicondylus posteriorly.

The radius and ulna are relatively short elements, with the radius clearly more robust. Its ends are slightly widened, while the shaft is somewhat concave. The ulna is of a more slender shape. Only the proximal part that bears the olecranom is clearly widened and somewhat medially directed. The olecranom is very prominent and only ossified in late adult individuals fully.

The manus is well ossified in late adult individuals and has been described in detail by MECKERT, 1993. The phalangeal formula is 2/2/3/3. On the ventral part of the body, between the interclavicle and the sacrum, there is a compact ventral armour, consisting of epidermal scales. BOY (1988) and BROILI (1926) have described this armour in detail. Generally there are long, sharp scales in the midsection and oval or circular scales laterally. At the level of the forelimbs, there is a prominent recess on each side of the armour. The ossification of these scales had already started in the late larval stage, in individuals with a skull length of approximately 20 mm (BOY & SUES, 2000).

The pelvis is very robust; its most prominent element is the ilium. It consists of two parts; a ventral part that is fan-shaped anteroposteriorly and bears most of the acetabulum, and a dorsal part that is elongate-rectangular shaped and curved posteriorly. The ventral section of the pelvis consists of the pubis and ischium, which together represent a somewhat triangular shaped plate.

The hind-limbs are well developed in adult specimens. The femur is a massive rectangular bone that is clearly the largest element of the limbs. Its proximal end is broadened and somewhat more prominent than the distal one. The fourth trochanter is weakly developed and is situated proximally. In the distal half, the shaft is still robust and terminates in a relatively straight articulation surface. The tibia and fibula are much shorter than the femur, and the fibula is again somewhat shorter than the tibia. The tibia is less robust and has a slender distal portion. It contacts the tibiale ventrally and the intermedium medially. The fibula is a massive bone that has a clearly expanded distal end with a medially directed tip. This tip touches the intermedium, while the medial margin contacts the fibulare. The metacarpals are only visible in late adult individuals. Very well developed are the tibiale, intermedium and fibulare. The tibiale is situated laterally. It is the smallest of the proximal metacarpals and has a triangular shape. The intermedium sits between the tibiale and fibulare and has an oval shape, while the medially situated fibulare is very prominent and roughly triangular. The phalanges are rod-like and terminate in a claw-shaped phalanx. The phalangeal formula varies between 2/2/3/3/3 and 2/2/2/3/3.

MORPHOLOGICAL VARIATION DURING THE ONTOGENY **-** Four ontogenetic stages (larval, juvenile, adult and late adult) will be characterised by features of the postcranial skeleton. The pectoral girdle is not considered as it has already been described by MECKERT (1993). For a detailed description of ontogenetic changes in the cranium see BOY (1988).

I. LARVAL STAGE (skull length from ca. 0,8 cm to ca. 2,5 cm) – The basis for observations of the anatomy in the larval stage is an 8 cm long specimen (PMNB uncataloged) (Fig. 1) with well-preserved body outlines and carbonaceous imprints of the external gill. The basibranchiale was probably cartilaginous in this stage. It ossifies in the juvenile stage and is prominently developed in adult individuals (BOY, 1972, 1988; BOY & SUES, 2000). The ceratobranchials were arranged in up to four rows and situated laterally at the level of the shoulder girdle. They probably also consisted of cartilage, but had attached to them small bony plates, so-called gill-teeth ("Kiemenzähne" after BOY, 1972) (Fig. 2). Each gill-tooth bears approximately 5 spine-like denticles, which vary by one or two spines. Similar structures are known in *Micromelerpeton* (BOY, 1995) and *Gerrothorax* (NILSSON, 1946). The hypobranchials, hypohyals and ceratohyals were not preserved.

The limbs are developed and conspicuous in the Bad Dürkheim specimen (uncataloged). They are only slightly ossified. The humerus is very short and nearly quadratic in shape; the radius and ulna are weakly developed, but the radius is clearly the longer of the two. Elements of the manus are not recorded and were probably cartilaginous in this stage. The femur has a rectangular outline in lateral view. It is relatively short, very robust and longer than the less developed tibia and fibula. Elements of the pes are present but badly preserved. The centra are rhachitomous and bear paired neural arches with low neural spines (Boy, 1972). The ribs of the 1st-14th vertebra are ossified. They have a rod-like shape and are slightly broadened proximally. A clear development of a capitulum and tuberculum appears not to be present. The sacral rib is slender. Caudal ribs have not been recorded. The sacrum is relatively weak and not as robust as the well-developed shoulder-girdle (see Meckert, 1993). The tail occupies approximately 50 % of the body length. In all observed larval individuals, no traces of stomach contents could be found.

II. JUVENILE STAGE* (skull length from ca. 3,5 cm to ca. 7,5 cm) – The rrepresentative for the description of the juvenile stage was a 26 cm long specimen with clearly visible body-outlines (PMNB uncataloged) (Fig. 3). In this stage, the external gill has been lost. The limbs are clearly more ossified than in the larval stage. The humerus shows no major differences to that in the larval stage. Radius and ulna are about as long as the humerus. Both the radius and ulna are approximately equal in length, but the radius is somewhat more robust. The femur is elongate-rectangular in shape with slightly expanded proximal and distal ends. It is clearly more robust and about twice as large as the tibia and fibula. The tibia is rod-shaped and slightly expanded distally. The metapodials are not ossified, while the phalanges are clearly visible. Claw-like terminal phalanges are developed. The specimen GMS 394 shows that the vertebrae are well-ossified and bear lower neural arches and spines as in the adult stage. The ribs are more robust than in the larval individual. The 2nd to 14th presacral ribs are club-like and broadened laterally. The sacrum is more robust than in the larval individuals. Between 12 and 14 caudal ribs are presented. The second and the third ribs, distal to the sacral rib, are the longest.

The tail occupies about 45 % of the body length, but is shorter than in the larval individuals.

III. ADULT STAGE (skull length from ca. 9,5 cm to ca. 16 cm) – The representative specimen of the adult stage is a well-preserved skeleton 74 cm in length (PMNB-PDC 327) (Fig. 4). In general, the body is somewhat more compact than in the larval or juvenile stages. The humerus is robust, but not as stout as in the juvenile individuals. Its proximal and distal ends are still cartilaginous (see also BROILI, 1926; BOY, 1988). Ulna and radius are about equal in length, but the radius is somewhat more robust. In both, the shaft is inwardly curved, with the ulna showing a more prominent inflexion. The phalanges are somewhat broader than in the juvenile stage and still not completely ossified. Also the metacarpus is not completely ossified. The hind-limb elements are similar in shape to those in the juvenile specimens, but are more robust. Metatarsals are present.

The vertebrae are well developed. The pleurocentra are slender and of rhachitomous shape (SCHOCH, 1999: 107). BOY (1988) describes the intercentra as unpaired with a low semicircular shape and the neural arches as robust and relatively high. This could also be observed on PMNB-PDC 327.

All ribs are strongly developed and have a coossified capitulum and tuberculum. This is especially visible in the second to fourteenth ribs where the proximal ends are club-like broadened. These ribs bear a hook-like processus uncinatus distalis posteriorly. In large individuals, there are lateral depressions visible on the second to sixth ribs. Sacrum and shoulder-girdle are robust and the sacrum is now completely ossified. The tail is somewhat shorter than in the juvenile stage. It occupies about 40 % of the body-length.

IV. LATE ADULT STAGE (skull length 18 cm +) - The late adult stage was based on PMNB-BGC 112 (Fig. 5). In general the body is clearly shorter than in the previous stages and all bones are well ossified. The humeri are robust and slightly elongated. The metapodials are completely ossified. Of the atlas-axis-complex only the neural arches are visible. The club-shaped tuberosities on the proximal end of the ribs are now more bow-shaped and can clearly be observed to the seventh rib (but possibly extended to the ninth). Also the lateral depressions, mentioned for the adult specimens, can be recorded to the seventh or nineth rib, and are now deeper. The sacrum is extremely robust. The tail is again shorter then in the former stages, but does not differ much from that of the adult stage (it also occupies approximately 40 % of the body-length).

HABITAT RECONSTRUCTION

During the Lower Permian, the Saar-Nahe Basin in Southwest Germany was traversed by several river systems. In some areas water was trapped in low relief, forming lakes (DIETZE, 1999). These lakes (Tab. 1) normally existed only for a relatively short geological period, but contained a well-balanced ecosystem (palaeocommunities after BOY, 1998 sensu JÄRVINNEN et. al. 1986), composed of large amphibians (e.g. the limnachian *Archegosaurus*), small amphibians (e.g. the branchiosaurs *Micromelerpeton* and *Apateon*), large fishes (e.g. the xenacanthodian freshwater sharks *Xenacanthus* and *Orthacanthus*), small fishes (e.g. the amblypterid *Paramblypterus* or the acanthodian *Acanthodes*), as well as a variety of different invertebrates (e.g. ostracods, bivalves, shrimps) (BOY, 1998). One of the larger lakes was Lake Humberg (L-O 10) that extended over an area of 3400 km^2 and deposited nearly the whole Saar-Nahe Basin (STAPF, 1990). BOY (1994) mentioned, that lake deposits from Lake Humberg can be divided into four phases. *Sclerocephalus* is found (together with *Paramblypterus uvernoyi* and *Apateon pedestris*) only in the first phase, when the Lake was deepest. In other lakes, such as in Lake Odernheim (L-O 8), *Sclerocephalus* was found together with the large branchiosaur *Micromelerpeton* (BOY, 1994) or with the small freshwater shark *Triodus* (Lake Klauswald, L-O 9, after DIETZE, 1999).

BOY (1988) concluded that juvenile *Sclerocephalus* individuals might have lived in shallow lakes. Following our investigations, we suggest that juvenile *Sclerocephalus* lived in large, relatively deep lakes of the Rümmelbach-Humberg type. Recent extensive excavations by the Pfalzmuseum für Naturkunde in Bad Dürkheim in the corresponding localities Gresaubach/Lebach and Humberg/Odernheim (Top L-O 10) support this suggestion as only larval and juvenile individuals have been found. It therefore is suggested that these lakes were being used as spawning grounds whilst adult individuals lived in another environment. Also, this could explain why, in lakes where adult and late adult individuals are common, as in Lake Jeckenbach (L-O 6) (STAPF, 1990), larval and juvenile individuals are rare or absent.

DIET DURING THE ONTOGENETIC STAGES

As mentioned above, no stomach contents could be associated with the larval specimens. Most probably their diet consisted of plankton and malacostracans (as the common *Uronectes*) or maybe small insects. BOY (1993) suggested that larval *Sclerocephalus*, similar to some recent amphibians could have caught its prey with a suck-snap method (see BRAMBLE & WAKE, 1986). Juvenile individuals caught large prey. As mentioned above, a complete, large *Paramblypterus* with its head folded backwards was found in the stomach of PMNB (uncataloged = described juvenile individual). Altogether six fish-bearing specimens were observed (only one in a public collection, PMNB, uncataloged, fig. 3); another one (GPIM-N 1166) was mentioned by BOY (1988). We therefore conclude that *Sclerocephalus* swallowed these fishes whole. In numerous specimens scales of paramblypterids, and also traces of small amphibians such as *Apateon* and *Micromelerpeton,* have been found. As a rarity, one of the observed specimens (GMS, uncataloged) clearly contained remains of a smaller *Sclerocephalus* in its stomach. This is the first record of cannibalism in this taxon.

Adult and late adult individuals were primary piscivores, in which *Paramblypterus* represents the common prey. Observations of stomach-contents and a large number of coprolites showed that smaller amphibians and probably smaller *Sclerocephalus* individuals also belonged to the prey. Acanthodians were never present as stomach contents or in the coprolites. These fishes were very common in the environment of *Sclerocephalus* and of moderate size, but had large spines anteriorly to their fins. It is possible that the more heavily built adult and late adult *Sclerocephalus* individuals mostly did not hunt actively, but watched for prey next to the shore and caught them with the suck-snap method. If we take this as a basis, *Paramblypterus* and small amphibians were an easier prey than the spine-bearing acanthodians.

CONCLUSIONS

In the first ontogenetic phases, *Sclerocephalus haeuseri* was well adapted to its aquatic habit, which is especially perceptible in the slender shape of the body, the weakly ossified limbs and the long rudder-tail. Larval individuals are up to 10 cm in length. Their jaws were not very strong and bore only slightly developed teeth (BOY, 1988); therefore their diet must have consisted of plankton and probably insects or malacostracans.

In the juvenile stage, individuals could reach a length up to 50 cm. They still had a slender body-shape and a long tail and probably were active hunters. Stomach-contents and coprolites contain remains of paramblypterids and small amphibians, including smaller individuals of *Sclerocephalus*. The prey was swallowed entirely.

It is conspicuous that some Lakes, especially those of the "Rümmelbach-Humberg-Lake" type, nearly exclusively yielded larval and juvenile individuals (up to the late juvenile stage (= late “metamorphic” stage after BOY & SUES, 2000) or subadult stage (tab. 1). We therefore conclude that adult *Sclerocephalus haeuseri* might have changed their habit from fully aquatic to amphibious. Adults probably visited the habit at of the younger ones to spawn; therefore they are rarely recorded in these layers.

According to BOY (1998) both juvenile and adult / late adult individuals were the so-called top-predators in their environment (Fig. 6). In Lake Niederkirchen *Sclerocephalus* shared this position with the freshwater shark *Orthacanthus senckenbergensis*. In Lake Humberg, as mentioned above, *Sclerocephalus* was only recorded in the first of four phases. In the second phase the position as top-predator was held by the freshwater shark *Xenacanthus meisenheimensis* (BOY, 1994), while in the fourth phase the top-predator position was shared by the archegosaurids *Archegosaurus* and *Cheliderpeton*. The latter is the closest relative to *Sclerocephalus* (YATES & WARREN, 2000) and is also known in different ontogenetic stages (BOY, 1993, STEYER, 2000)

In the adult / late adult stage, *Sclerocephalus* was specialised on paramblypterids, but also cached smaller amphibians such as *Apateon* or *Micromelerpeton*. Although *Acanthodes* was very common in the lakes, it was not recorded in the stomach-contents or coprolites and therefore probably did not belonged to the prey. The limbs were well ossified in the adult stage, so that these individuals also could have been terrestrial from time to time.

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Footnotes

* of p. 6: Here we follow the most recent analysis by YATES & WARREN (2000).

* of p. 11: BOY & SUES (2000) present two grow stages between larval and adult stage: Early "metamorphic" and Late "metamorphic". These stages are primary laid down on cranial features. As we could not observe significant differences within the postcranium, we will here still use the term juvenile.

Figures

Fig. 1: Larval individual (PMNB uncataloged) in dorsal view. Scale-bar = 1 cm.

Fig. 2: Gill-teeth (“Kiemenzähne”), which were attached at the ceratobranchial filaments. Scale-bar = 1 mm

Fig. 3: Juvenile individual (PMNB uncataloged) in dorsal view. In this specimen, scales of paramblypterids are visible as stomach contents (St). Scale-bar=1cm.

Fig. 4: Adult individual (PMNB PDC-327) in dorsal view. Scale-bar = 5 cm.

Fig. 5: Late adult individual (PMNB BGC-112) in lateral view. In this stage the ventral armour (Va) is clearly visible. Scale-bar = 20 cm.

Fig. 6. Proposed food chain of *Sclerocephalus* in the larval, juvenile and adult / late adult stage.

Fig. 7. Idealised reconstruction of the four ontogenetic stages: **a**. larval, **b**. juvenile, **c**. adult and **d**. late adult. The right side of the body shows the dorsal bones, the left side shows the ventral elements.

Tab. 1: Distribution of the ontogenetic stages of *Sclerocephalus haeuseri* in different lake localities (primary based on unpublished excavation reports of the Pfalzmuseum für Naturkunde, Bad Dürkheim).

Tab. 1

LAYER	LAKE	LAKE-SIZE	LARVAL	JUVENILE	ADULT	LATE ADULT
L-O 10	Rümmelbach-Humberg	ca. 3400 km^2	14	ca. 100	0	0
L-O 9	Ruthweiler	ca. 10 km^2	?1	0	0	0
L-O 8	Odernheim	ca. 760 km^2	31	ca. 100	2	0
L-O 7	Jeckenbach-Heimkirchen	ca. 230 km^2	0	4	ca. 50	8
L-O 6	Niederkirchen	ca. 40 km^2	0	2	2	2
Q 2	Quirnbach	ca. 500 km^2	0	0	0	1
Q1	St. Wendel	ca. 40 km^2	0	2	20	3

Figures

Fig. 1: Larval individual (PMNB uncataloged) in dorsal view. Scale-bar = 1 cm.

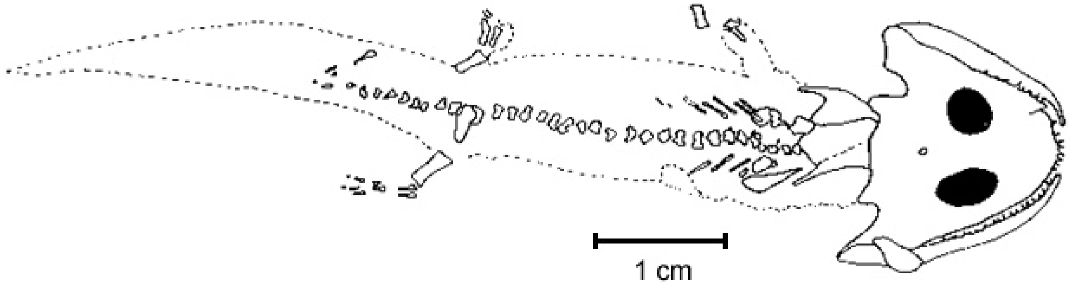


Fig. 2: Gill-teeth (“Kiemenzähne”), which were attached at the ceratobranchial filaments. Scale-bar = 1 mm

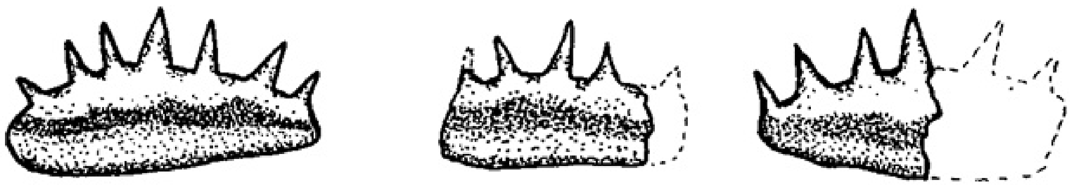


Fig. 3: Juvenile individual (PMNB uncataloged) in dorsal view. In this specimen, scales of paramblypterids are visible as stomach contents (St). Scale-bar=1cm.

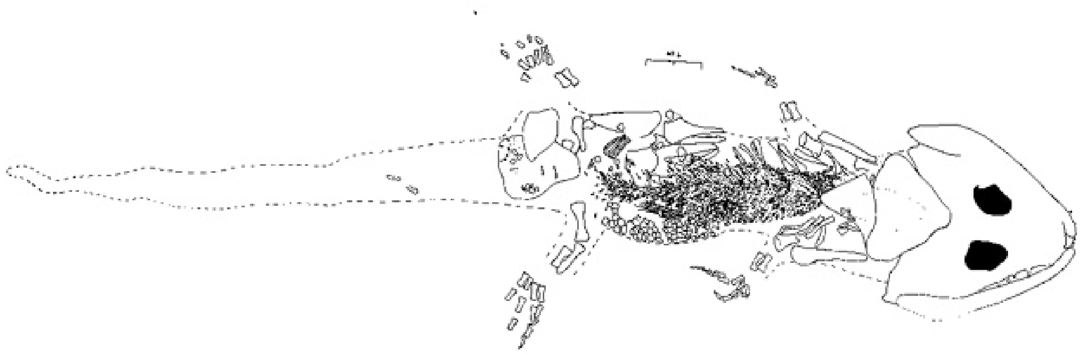


Fig. 4: Adult individual (PMNB PDC-327) in dorsal view. Scale-bar = 5 cm.

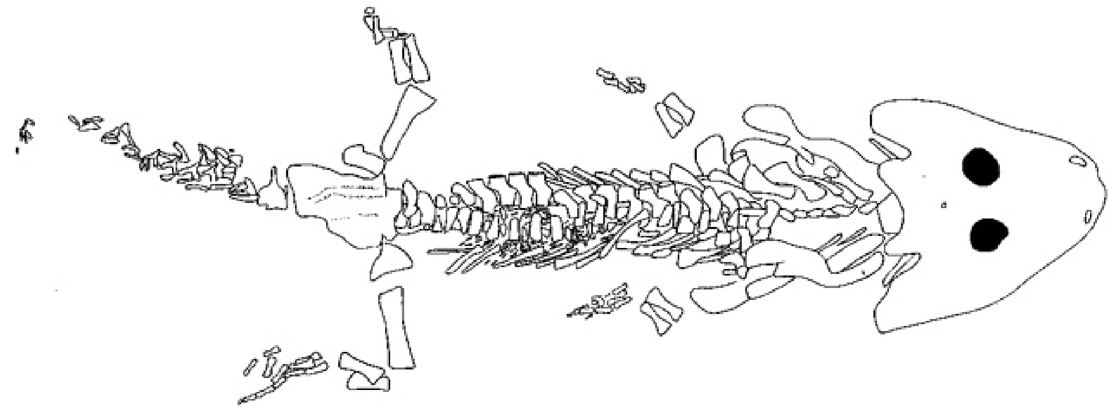
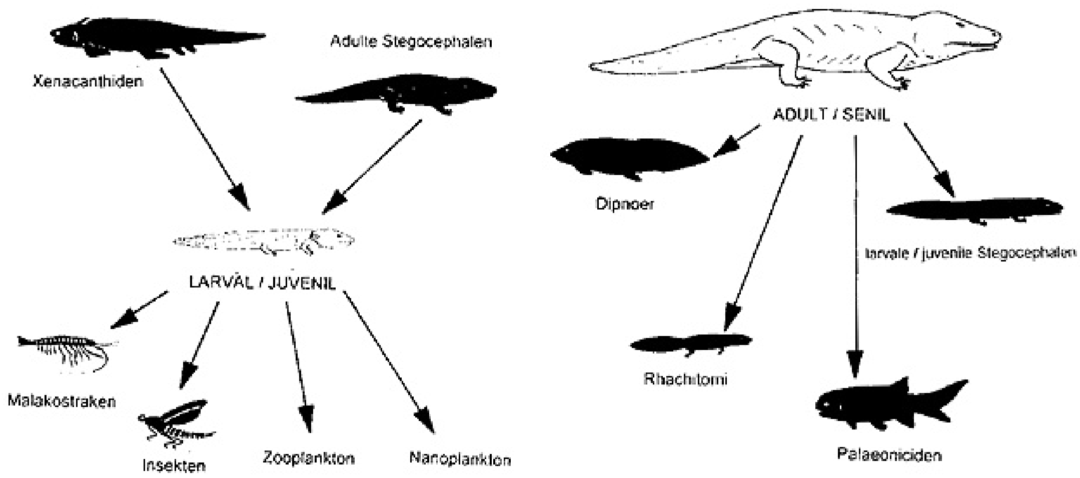


Fig. 5: Late adult individual (PMNB BGC-112) in lateral view. In this stage the ventral armour (Va) is clearly visible. Scale-bar = 20 cm.

Fig. 6. Proposed food chain of *Sclerocephalus* in the larval, juvenile and adult / late adult stage.



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