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Dentigerous bones, dentition and dental laminae in the hynobiid salamander *Ranodon sibiricus* Kessler, 1866 (Amphibia, Urodela)

Zahntragende Knochen, Bezahnung und Zahnleisten bei dem Hynobiiden *Ranodon sibiricus* Kessler, 1866 (Amphibia, Urodela)

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Summary: Among Urodela the hynobiids appear to be an ancient lineage, which seem to have conserved several plesiomorphic characters. Such ancestral characters might also include dental pattern and dentition. Using scanning electron microscopy and histological sections, the tooth systems of larvae, juveniles and adults of the hynobiid salamander *Ranodon sibiricus* were documented and briefly compared with the tooth systems of other Urodela. Adults had three (upper jaw arcade, lower jaw arcade, and the paired vomers), larvae had five tooth systems, those retained in the adults and the paired palatines and coronoids (splenials of some authors) including their dental laminae. The palatine of our youngest larva bore two rows of teeth, all other dentigerous bones bore a single row of teeth. Post-metamorphosed specimens largely retained the larval pattern, i.e. single rows of teeth and replacements posterior to the tooth rows in labial direction. Attachment of teeth was horizontal and more or less pleurodont depending on the particular bone and numbers of previous dentitions. Succession of differently shaped tooth generations followed the typical urodele pattern from larval "non-pedicellate" monocuspids via several, larval "subpedicellate" monocuspids to metamorphosed pedicellate bicuspids in a particular order. Even in the adult, bicuspidity of teeth and shaping of the zone of division separating the crown from the pedicle varied considerably. In larvae with a delayed metamorphosis the palatines were edentulous. In the upper jaw arcade no gap was seen in the tooth row between the two premaxillae and the premaxillae and maxillae indicating a single continuous dental lamina; in the lower jaw the edentulous gap between the dentaries argues for two dental laminae. Histological sections reveal clearly separated vomerine and palatinal dental laminae in larvae. Already before regression of the palatine and the coronoid, dental laminae of the two bones became regressive, the coronoid lamina later than the palatinal one. Dental systems as realized in larval and metamorphosed *R. sibiricus* are widespread among Urodela and appear to represent a highly conserved character.

Urodela, dentition, tooth systems, larval and transformed teeth, delayed metamorphosis, dental laminae, conserved character

Zusammenfassung: Innerhalb der Urodelen gelten Hynobiiden als altertümliche Gruppe, die eine Reihe plesiomorpher Merkmale konserviert zu haben scheinen; dazu gehören wahrscheinlich auch das Bezahnungsmuster und die Bezahnung selbst. Anhand von rasterelektronenmikroskopischen Aufnahmen und histologischen Schnitten beschreiben wir noch einmal die Zahnsysteme von einige Larven, Juvenilen und Adulti des Hynobiiden *Ranodon sibiricus* und vergleichen diese kurz mit den Zahnsystemen anderer Urodelen. Die Erwachsenen haben drei (Oberkieferbogen, Unterkieferbogen, paarige Vomeres), Larven jedoch fünf Zahnsysteme, und zwar die, welche vom Adulten nach der Metamorphose zurückbehalten werden sowie die paarigen Palatina und Coronoide (die Splenialia mancher Autoren) jeweils mit ihren Zahnleisten. Die Palatina der jüngsten uns zur Verfügung stehenden Larven trugen zwei Zahnzeilen, alle übrigen zahntragenden Knochen jedoch nur eine Zahnzeile. Metamorphosierte Exemplare behalten weitgehend das larvale Muster bei, d.h. eine Zahnzeile sowie Zahnersatz in labialer Richtung hinter der Zahnzeile Die Verankerung der Zähne ist in Abhängigkeit von Knochen und der Anzahl vorangegangener Dentitionen horizontal sowie mehr oder weniger pleurodont. Die Abfolge unterschiedlich gestalteter Zahngenerationen folgt dem typischen bei Urodelen verwirklichtem Muster von larvalen einspitzigen Zähnen ohne abgesetzten Sockel über larvale einspitzige Zähne, bei denen die Grenze zwischen Sockel und Krone nur angedeutet ist, bis zu metamorphosierten zweispitzigen Zähnen mit einem durch eine Ringnaht deutlich abgesetzten Sockel. Bei den Adulti sind Ausprägung der Zweispitzigkeit und Erscheinungsbild der Ringnaht sehr variabel. Bei zwei Larven, deren Metamorphose offenbar verzögert war, waren die Palatina bereits zahnlos. Der Oberkieferbogen hat eine durchgehende Zahnzeile und daher wahrscheinlich auch eine Zahnleiste, welche die beiden Prämaxillaria sowie die Grenze zwischen Prämaxillare und Maxillare lückenlos begleitet, während zwischen den beiden Dentalia im Unterkiefer eine solche Lücke in der Zahnzeile vorhanden ist. Die Zahnleiste entlang des larvalen Vomer und Palatinum ist deutlich getrennt. Bereits vor dem metamorphosebedingten Abbau des Palatinum und des Coronoid werden deren Zahnleisten regressiv, und zwar die des Coronoids später als die des Palatinum. Die für larvale und metamorphosierte *R. sibiricus* hier beschriebenen Zahnsysteme sind weitgehend identisch bei einer großen Zahl von Urodelen verwirklicht. Es scheint sich um hoch konservierte Merkmale zu handeln.

Urodela, Bezahnung, Zahnsysteme, larvale und metamorphosierte Zähne, verzögerte Metamorphose, Zahnleisten, konservierte Merkmale

1. Introduction

Previous studies have examined the pattern of dentition of representative members of extant paedomorphic and post-metamorphosed Urodela to show the variation of this pattern, the diversity of tooth shapes during ontogeny (summarized in Clemen & Greven 1994) and most thoroughly studied by Davit-Beal et al. (2006) focusing on ontogenetical changes of a single tooth family (for review see also Davit-Beal et al. 2007), the course of dental laminae (not considered systematically as yet; see also Davit-Beal et al. 2007) and the site of tooth replacement. Some of these features are considered to be valuable tools for phylogenetical considerations for a long time (for review see Clemen & Greven 1994). According to these studies three "tooth systems" can be distinguished in post-metamorphosed salamanders: (1) the upper jaw arcade consisting of the paired premaxilla and maxillae and the accompanying continuous dental lamina; (2) the lower jaw arcade formed by the paired dentaries accompanied by a dental lamina that is interrupted in the symphyseal zone; and (3) the vomerine system consisting of the two vomers, each accompanied by a dental lamina. In larvae and some paedomorphic forms, two further systems are present: the palatinal portions of the paired palatopterygoids and the paired coronoids each with their dental laminae. Teeth were typically monocuspid and "non pedicellate" in early larvae and bicuspid and pedicellate in transformed specimens. In this case the tooth consists of a crown that articulates with a basal pedicle; crown and pedicle develop in the enamel organ. These patterns appear rather constant among Urodela; deviations primarily concern the vomerine system and the number of tooth rows established on the bones.

Among Urodela, the Hynobiidae are characterized by several plesiomorphic traits, e.g., external fertilization and a separate angular bone in the lower jaw (e.g. Schmalhausen

1968; HECHT & EDWARDS 1977; LARSON & DIMMICK 1993; GAO & SHUBIN 2001; LARSON et al. 2003) and are considered as an ancient lineage of extant urodeles. Within Hynobiidae morphological analyses (ZHAO et al. 1988) and molecular data (LARSON et al. 2003) are inconsistent, but more recently complete sequences of mitochondrial genomes indicate convergent development of several morphological characters in different hynobiid lineage. Further, *Onychodactylus* appears to be the sister-group of all other living hynobiids (ZHANG et al. 2006).

Skull ontogeny including the dentigerous bones and dentitional pattern of the endangered (see IUCN 2006) hynobiid species, *Ranodon sibiricus*, is amazingly well studied (see particularly the summarizing work by LEBEDKINA 1979, now available in an English translation, LEBEDKINA 2005). VASSILIEVA & SMIRNOV (2001) re-examined LEBEDKINA's (l.c.) stained and cleared specimens that cover a nearly complete ontogenetic series with regard to the succession of teeth from hatchlings to adults. Authors revealed the sequence of structurally different tooth generations, i.e. "non-pedicellate", monocuspid teeth precede "subpedicellate" monocuspids in larvae that start active feeding, pedicellate teeth in and after metamorphosis, and pedicellate bicuspid teeth after metamorphosis, a pattern known from a variety of transforming Urodela (see also GREVEN 1989; CLEMEN & GREVEN 1994; DAVIT-BEAL et al. 2007). More recently JÖMANN et al. (2005) published some supplementing data on the skull, in particular of larvae with a delayed metamorphosis, and included a few notes on dentition.

In the present study a survey is given on some aspects of dentitional ontogeny in *R. sibiricus*, which is based on the literature and examination of the material used in our previous study on cranial ontogeny (JÖMANN et al. 2005). We show dentition of all developmental stages available to us by means of scanning electron micrographs despite the risk of reiteration. Unlike VASSILIEVA & SMIRNOV (2001), we focus on the apex and the zone of division that separates the crown from the pedicle and on the attachment of teeth to the dentigerous bones. In addition, we include some histological sections to follow the course of dental laminae in the mouth roof and briefly touch on possible plesiomorphic traits in the tooth systems.

2. Material and methods

The material examined corresponds largely to that used in a previous article (JÖMANN et al. 2005, herein also a more detailed characterisation and staging of the specimens according to the tables of LEBEDKINA 1979, 2005; KUZMIN & THIESMEIER 2001). We studied (nr. 1) larva (38 mm TL, stage 16); (nr. 2) larva at the beginning of metamorphosis (41 mm TL, stage 16-17); (nr. 3) larva in metamorphosis (60 mm TL, stage 19); (nr. 4) larva in advanced metamorphosis (only the head was available); (nr. 5, 6) larvae with delayed metamorphosis (67 and 73 mm TL, stage 19); (nr. 7) juvenile (75 mm, stage 20); (nr. 8) subadult (95 mm TL, stage 22); and (nr. 9) adult (approx. 112 mm TL).

Scanning electron microscopy (SEM): Dentigerous bones were excised from the stained and cleared specimens used in the previous article (JÖMANN et al. 2005) and the tissue was removed by 1% pancreatin in tetraborate buffer. The cleaning process was regularly controlled and the time needed for cleaning varied considerably. We did not use any other macerating agent to save the delicate bones and teeth especially in the younger stages. Nevertheless, cleaning did not satisfyingly succeed in all preparations. During this procedure replacement teeth and largely resorbed teeth were lost. Further, specimens may have suffered of some demineralisation.

A single head of a larva in an advanced stage of development (palatine teeth were already missing) (larva nr. 4 a; nearly stage 18; no further data available and not listed above), fixed in 2.5% glutaraldehyde in 0.1 M cacodylate buffer and embedded in paraplast was freed from paraplast. All preparations were dehydrated in an ascending ethanol series, critical-point dried, sputtered with gold and examined in a Hitachi-Scanning Electron Microscope.

Heads of a larva in metamorphosis (larva 3 a; nearly stage 19; no further data available and not listed above) and a larva with delayed (90 mm TL; larva 6 a; nearly stage 19) fixed in glutaraldehyde or neutral formaldehyde, respectively, were embedded in paraplast, sectioned transversally at 7 µm and stained with Azan or Trichrom-Goldner (ROMEIS 1989).

3. Results

3.1. Larva (nr. 1) (Figs 1a-f)

Toothed bones were premaxillae, vomers, palatines (=anterior palatinal portion of the palatopterygoid; homology with the palatine of other vertebrates is doubtful, e.g. SCHOCH, 1998), dentals and coronoids.

Premaxillae (Fig. 1 a), vomers (Fig. 1 b), dentaries (Fig. 1 d), and coronoids (Fig. 1f) bore a single row of teeth (monostichous dentition), whereas the palatine has two rows (bistichous dentition) (Fig. 1 c).

Teeth of all bones were ankylosed with a broad base. The basis of dentary teeth was thickened lingually (Fig. 1 d). Attachment varied from nearly acrodont, i.e teeth are attached more or less horizontal on the surface of the bone (vomer, coronoid, palatine) to slightly pleurodont, i.e. teeth are attached by one side to the inner surface of the bone (dentary, premaxilla). Openings to the pulp varied in size and shape ranging from a large opening (premaxilla: Fig. 1a), and several small accesses (vomer: Fig. 1 b, palatine: Fig. 1 c; dentary: Fig. 1 d; coronoid: Fig. 1 f).

Teeth were monocuspid, undivided and were curved more or less lingually with the exception of coronoid teeth, which were straight (Fig. 1 f).

3.2. Larva at the beginning of metamorphosis (nr. 2) (Figs 2a-i)

Dentigerous bones as in the previous stage. The disintegrating anterior and median portion of the palatine was toothless (Fig. 2 f).

All bones including the palatine bore a single row of teeth. Size and shape of teeth vary considerably even on the same bone (Fig. 2). On the premaxilla and dentary the most posterior teeth were smaller and sturdy, more anteriorly, teeth were slender and curved more or less inwards (Figs 2 a, c, g).

Ankylosis has changed to a pleurodont condition (premaxilla: Fig. 2 a; dentary: Fig. 1 g). In the latter the bases of teeth was wider than the shaft (Fig. 2 c). On the other bones ankylosis was horizontal and teeth were broad-based. Premaxillary teeth had a larger pulpal access (Fig. 2 b) than vomerine, dentary and coronoid teeth, which showed several smaller openings.

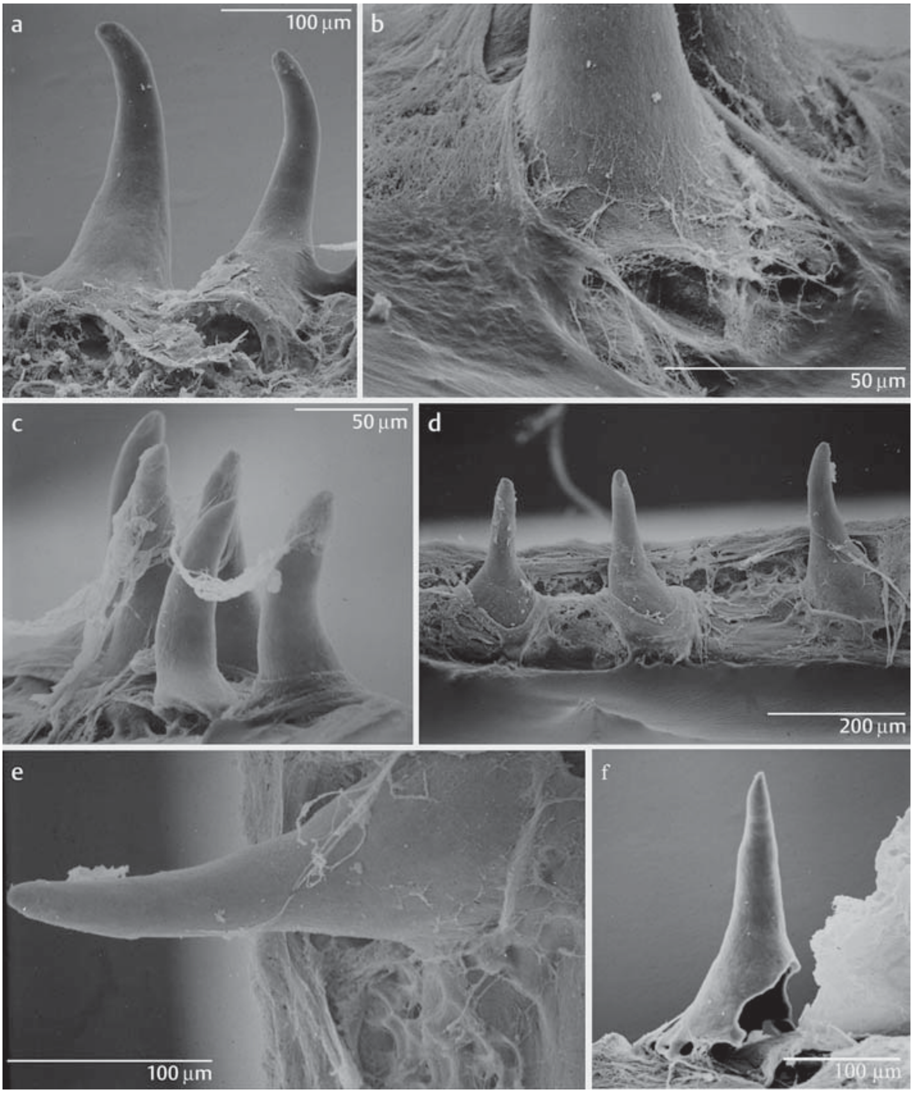
Teeth were monocuspid and undivided. Teeth showed at best a globular ring between the basis and the crown (e.g. dentary: Fig. 2 g).

3.3. Larvae in metamorphosis (nr. 3) (Figs 3a-h)

Premaxillae, maxillae, vomers, and dentaries bore a single row of teeth. Palatines and coronoids were largely disintegrated. The palatines were entirely toothless. The coronoid showed resorption pits (Fig. 3 g). Ankylosis of teeth largely as in the previous stage. Dentition of maxillaries was pleurodont (Fig. 3 a), that of the vomers slightly pleurodont due to remnants of previous dentitions (Fig. 3 e).

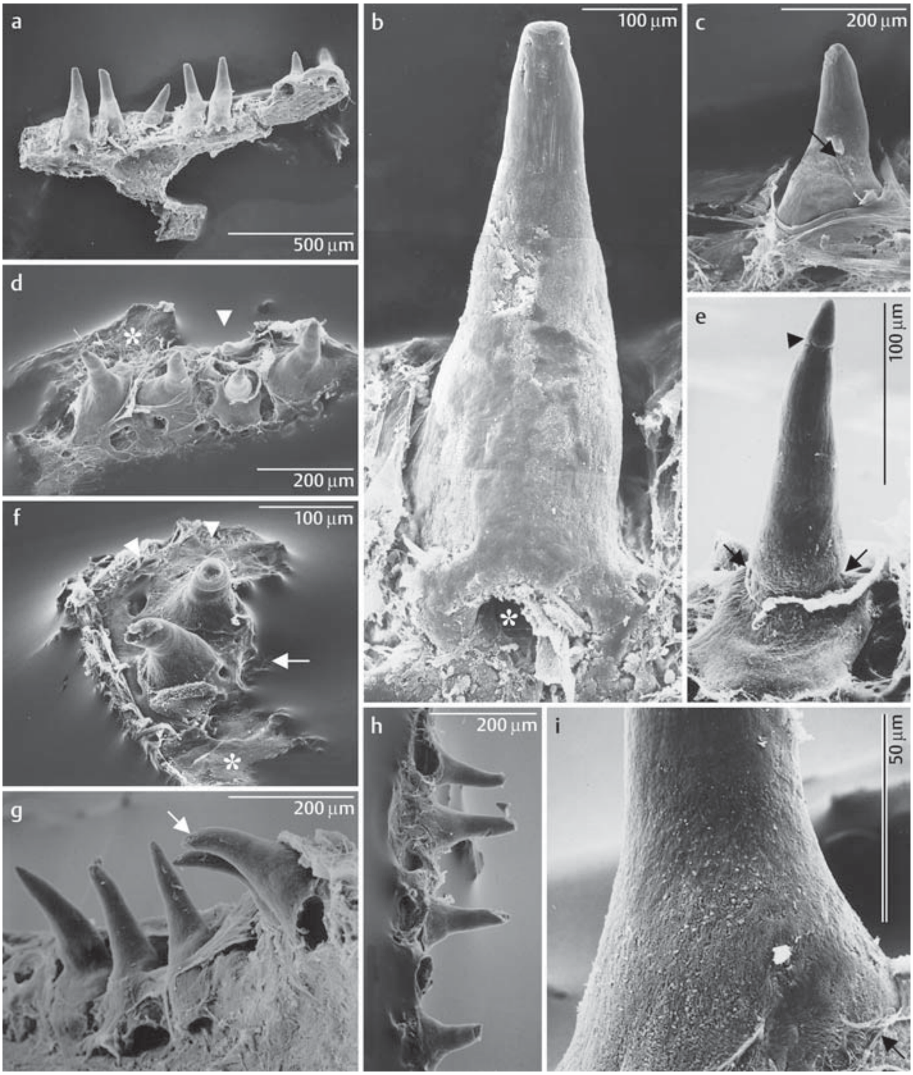
Pulpal accesses were large and few (premaxilla, maxilla, dentary: Figs 3 a, d, f) or smaller and more numerous (vomer: Fig. 3 e).

Teeth of the premaxilla, maxilla and dentary were monocuspid and incipiently divided (Fig. 3 a, f), teeth of the vomer, however, monocuspid and undivided (Fig. 3 e). The zone of division was more distinct lingually



Figs 1 a-f: Larva nr. 1. **a** Premaxillary teeth, lingual view, with broad basis and slight pleurodont attachment. **b** Vomerine tooth, lingual view. **c** Palatine with two rows of teeth, bases touch one another, caudal view. **d** Dentary, lingual view; attachment of teeth is more or less pleurodont and teeth are widely separated. **e** Dentary, medio-lingual view; broad-based tooth. **f** Straight coronoid tooth with signs of basal resorption.

Abb. 1 a-f: Larve nr. 1. **a** Prämaxillarzähne, lingual, mit breiter Basis und leicht pleurodonter Verankerung. **b** Vomerzahn, lingual. **c** Palatinum mit zwei Zahnzeilen. Die basalen Abschnitte der Zähne berühren sich fast, caudal. **d** Dentale, lingual; mehr oder weniger pleurodonte Verankerung der weit voneinander getrennen Zähne. **e** Dentale, medio-lingual, mit breitbasigen Zähnen. **f** Gerader Zahn auf dem Coronoid mit Resorptionsnarben an der Basis.



Figs 2 a-i: Larva at the onset of metamorphosis (nr. 2). **a** Premaxillary, lingual view; with pleurodont dentition. The more posterior teeth (left side) differ in size and shape from the median ones (right side). **b** Tooth of the median premaxilla, lingual view, with pulp opening (asterisk). **c** Posterior sturdy premaxillary tooth; the basis is thickened (arrow). **d** Anterior outgrowth of the vomerine plate (asterisk); the missing portion of the vomerine plate (arrowhead) is an artefact. **e** Vomerine tooth, medio-lateral view, with enamel cap; prospective dividing zone (arrow). **f** Monostichous dentition of the palatine, top view, caudal; toothless anterior (arrowheads) and median disintegrating portion (arrow); bony bridge between the palatine and the pterygoid (asterisk). **g** Dentary, lingual view; posterior teeth (arrow) are smaller as the anterior and more curved. **h** Coronoid, lingual view, with horizontally ankylosed teeth. **i** Coronoid tooth, lingual view, with boundary between the basis and the bone (arrow).

Abb. 2 a-i: Larve am Beginn der Metamorphose (nr. 2). **a** Prämaxillare, lingual, mit pleurodont verankerten Zähnen. Die hintersten Zähne (links) unterscheiden sich von den mittleren (rechts). **b** Zahn aus der Mitte des Prämaxillare, lingual; Öffnung zur Pulpa (Stern). **c** Hinterer untersetzter than labially (Figs 3 a, b). The surface of the teeth became rougher in the direction of the dividing zone (dentary, Fig. 3 f). The single tooth established on the coronoid was monocuspid and undivided; the shaft above the broad basis appeared waisted, perhaps a result of a partial demineralisation (Figs 3 g, h).

Pedicles were bulged at the lingual side, but were not broadened significantly (premaxilla, maxilla, dentary). They were distinctly separated from the zone of ankylosis and did not touch each other. Teeth were bent inwards, i.e. lingually (Figs 3 c and d), or were nearly straight (dentary: Fig. 3 f).

3.4. Larva in an advanced stage of metamorphosis (nr. 4 and 4 a) (Figs 4 a-i)

Number of rows, ankylosis of teeth and pulpal accesses as in the previous stage; coronoids regressive and without teeth.

In the upper jaw dentition was continuous without a gap in the symphyseal zones between the premaxillae and between premaxilla/maxilla; vomers did not have contact each other; their *partes dentales* were situated in the midst of the bone and their laterocaudal edges lied at the level of the choana (that mark the lateral boundary of each vomer) (Figs 4 a, e-g).

Teeth were either bicuspid and divided (premaxilla: Figs 4 b, c), monocuspid and divided (maxilla: Fig. 4 d), monocuspid and incipiently divided posteriorly or bicuspid and divided anteriorly (dentary: Figs 4 h, i) or monocuspid and undivided (vomer: Figs 4 e -g). On the dentary, the anterior teeth near the symphysis were larger and bicuspid. Posteriorly teeth became smaller and were monocuspid and broad-based (Fig. 4 h, right side).

Each tooth had a large dominant lingual opening to the pulp (Fig. 4 d, h) or a larger and several small (vomer, Figs 4 e-f). Teeth were curved inwards; in the bicuspids, two cusps were of nearly equal size (Figs 4 c, i).

3.5. Larva with delayed metamorphosis (nr. 5 and 6) (Figs 5 a-l)

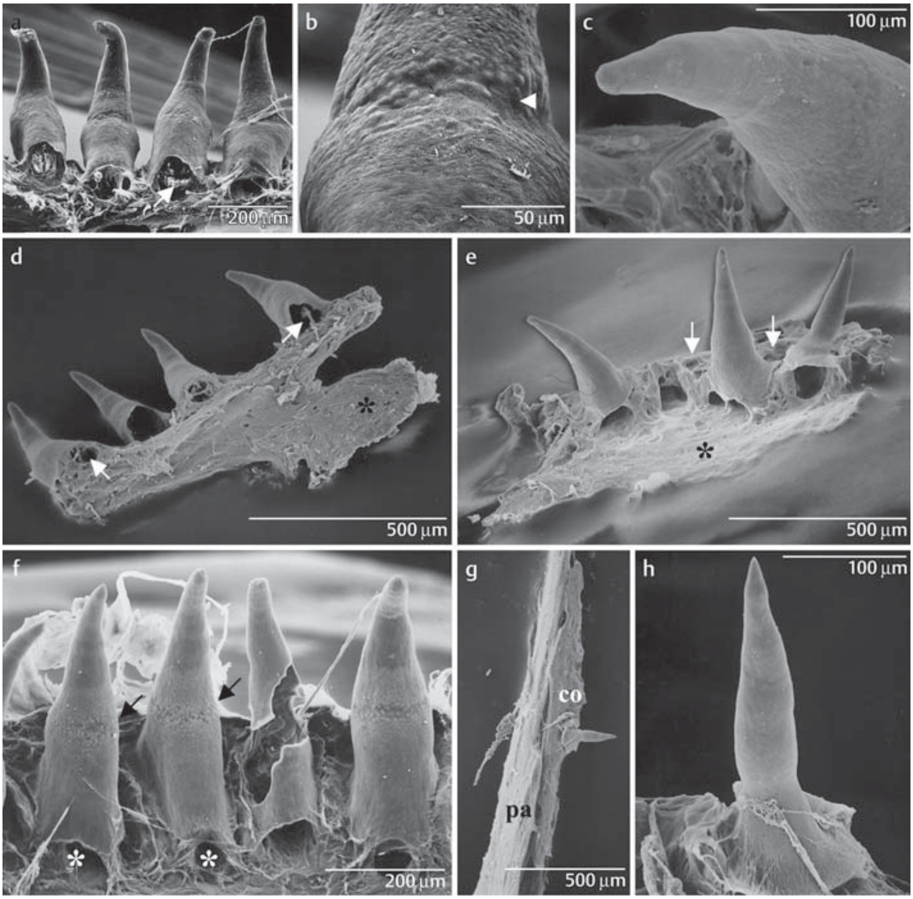
Premaxillae, maxillae, vomers, dentaries and coronoids with a single row of teeth; palatine regressive without teeth. Dentition was pleurodont (premaxillae, maxillae, dentaries), slightly pleurodont (on the vomer; the *pars dentalis* was now situated in the posterior third of the vomer: Figs 5 e,d f) or broad-based and nearly horizontal (coronoid: Fig. 5 k, l). Large pulpal accesses were seen in the teeth attached in a pleurodont condition and smaller and more numerous accesses in teeth attached horizontally (Fig. 5 g). Teeth were all monocuspid with an dividing zone indicated by a globular surface (maxilla: figs 5 d). Transversal ridges (premaxilla: Fig. 5 a), incisions (dentary: Fig. 5 j) or a waist (Fig. 5 k, l) might be a result of partial demineralisation..

3.6. Juvenile specimen (nr. 7) (Figs 6 a-i)

Number of tooth rows, ankylosis of teeth and pulpal accesses as in larva nr. 4 (see above); coronoids no longer present. Vomerine teeth shifted near the posterior edge of the bone (Fig. 6 f).

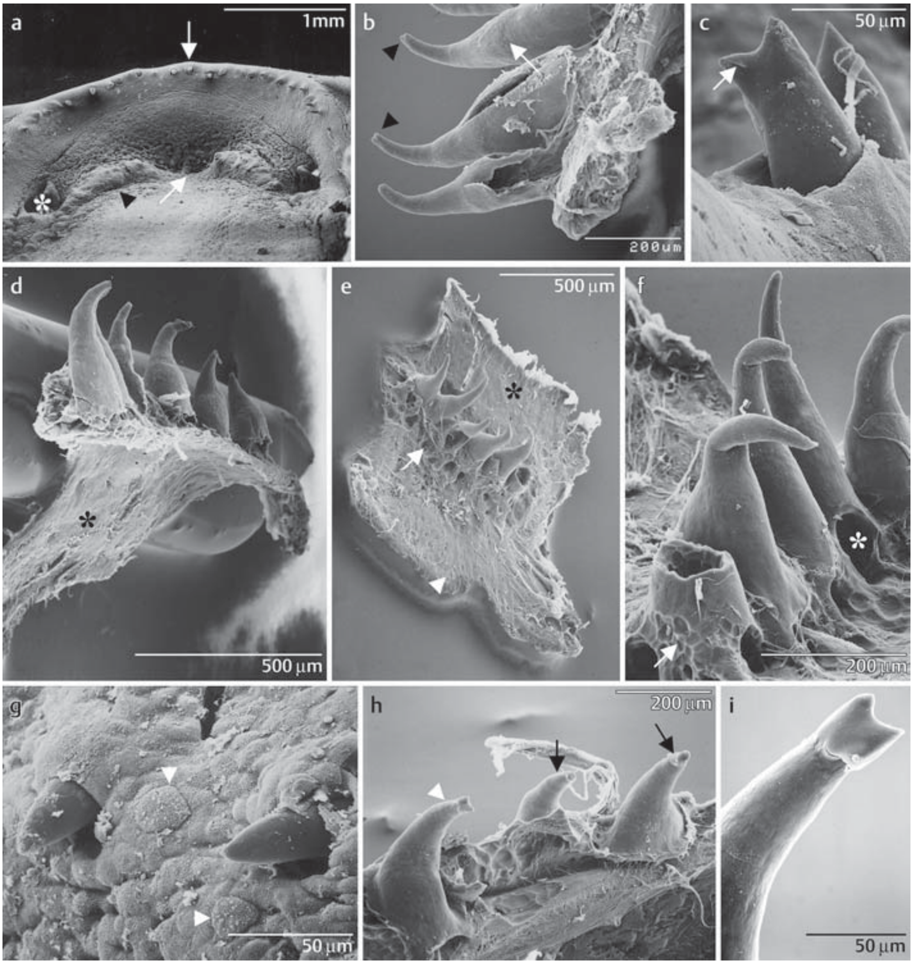
Teeth of all dentigerous bones were bicuspid and divided (premaxilla, maxilla: Figs

Prämaxillarzahn mit verdickter Basis (Pfeil). **d** Vorderer Bereich der Vomerplatte (Stern); ein Teil der Vomerplatte (Pfeilkopf) ist präparationsbedingt nicht mehr vorhanden. **e** Vomerzahn, mediolateral, mit Schmelzkappe und prospektiver Ringnaht (Pfeil). **f** Einzeilige Bezahnung des Palatinum, Aufsicht; zahnloser vorderer (Pfeilköpfe) und mittlerer im Abbau begriffener Teil (Pfeil); Knochenbrücke zwischen Palatinum und Pterygoid (Stern). **g** Dentale, lingual; die hinteren Zähne (Pfeil) werden kleiner und sind gekrümmter. **h** Coronoid, lingual, mit horizontal verankerten Zähnen. **i** Zahn auf dem Coronoid, lingual, mit deutlicher Grenze zwischen Basis und Knochen (Pfeil).

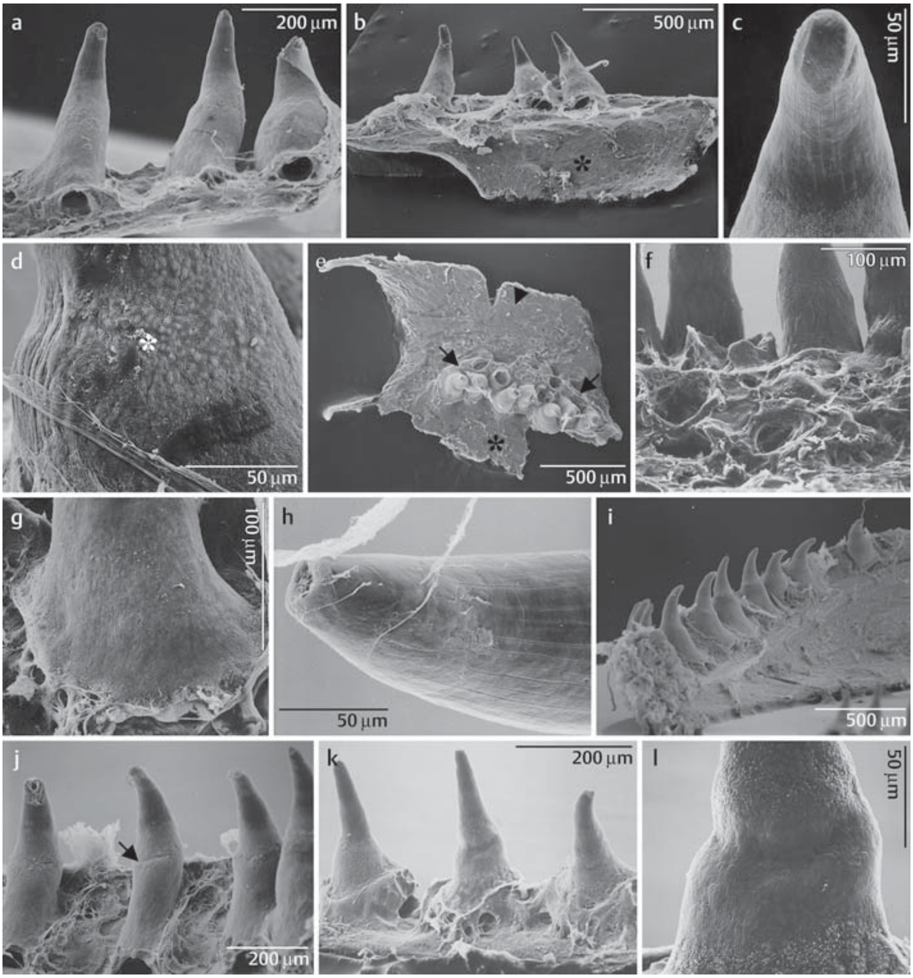


Figs 3 a- h: Larva in metamorphosis (nr. 3). **a** Premaxillary, lingual view; attachment of the lingually curved teeth is slightly pleurodont; teeth have a large pulpal access each (arrow). **b** Incipient dividing zone (arrowhead) of a premaxillary tooth, lingual view. **c** Apex of a maxillary tooth. **d** Maxillary teeth with large pulpal accesses (arrows); *processus facialis maxillaris* (asterisk). **e** Vomer, lingual view; labial remnants of previous dentitions (arrows); *pars palatina* (asterisk). **f** Dentary, lingual view; putative divided (arrows) teeth are attached in a pleurodont condition; large pulpal openings (asterisks). **g** Single coronoid tooth, lingual view; resorption of the coronoid (sp) from posterior (below) to anterior (on the top); prearticular (pa). **h** Detail of figure g. Straight "non-pedicellate" coronoid tooth.
Abb. 3 a-h: Larve in der Metamorphose (nr. 3). **a** Prämaxillare, lingual; die Zähne sind lingual gekrümmt, pleurodont verankert und haben einen großen Zugang zur Pulpa (Pfeil). **b** Sich bildende Ringnaht (Pfeilkopf) eines Prämaxillarzahnes, lingual. **c** Spitze eines Maxillarzahns. **d** Maxillarzahn mit großen Pulpazugängen (Pfeile); *processus facialis maxillaris* (Stern). **e** Vomer, lingual: labiale Reste früherer Dentitionen (Pfeile); *pars palatina* (Stern). **f** Dentale, lingual; die geteilten Zähne sind pleurodont verankert und haben große Pulpaöffnungen (Sterne). **g** Einzelner Zahn auf dem Coronoid, lingual; Resorption des Coronoids (co) von hinten (unten) nach vorn (oben); Präarticulare (pa). **h** Ausschnitt aus Abbildung g. Gerader nicht zweigeteilter Zahn auf dem Coronoid.

Figs 4 a-i: Larvae in an advanced stage of metamorphosis (nr. 4, 4a); preparations with (a, c, g) and without (b, d-f, h, i) soft tissue. **a** Premaxillae and vomers, symphyseal region (arrow on the top) with continuous dentition, lingual view; vomers (arrowhead); gap between vomers (arrow); choana (aste-

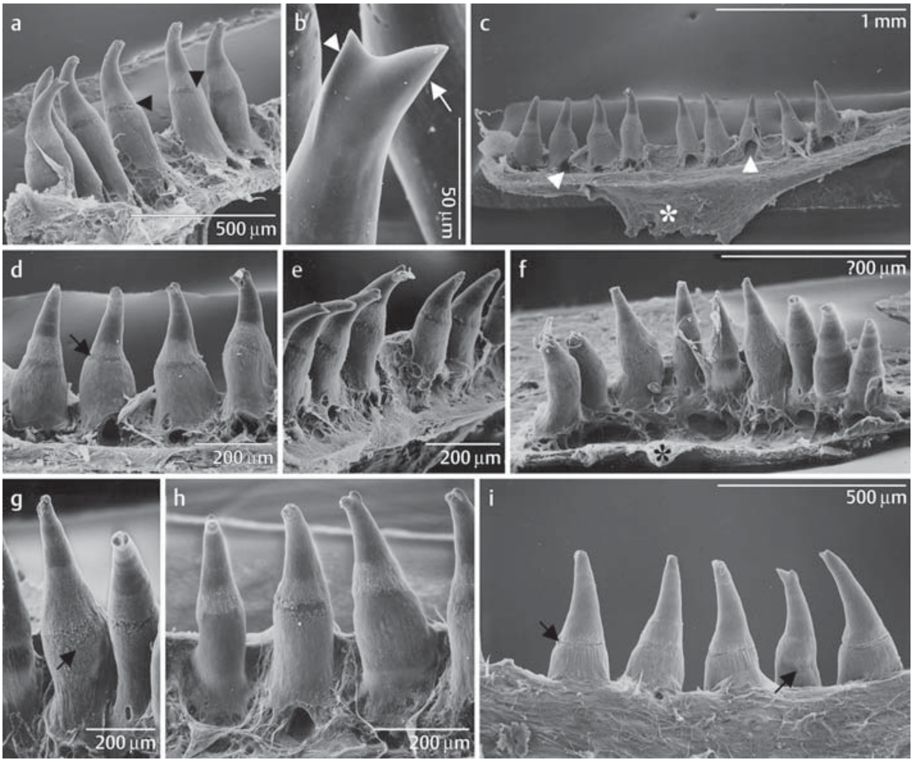


risk). **b** Premaxillary teeth with incipient bicuspidity (arrowheads) and zone of division (arrow). **c** A bicuspid (arrow) and monocuspid tooth side by side in the upper jaw, frontal view. **d** Maxilla with lingually curved teeth attached in pleurodontous condition; *processus facialis maxillaris* (asterisk). **e** Vomer; *pars dentalis* with remnants of previous dentitions (arrow) in the middle; vomerine plate (arrowhead) and *pars palatina* (asterisk). **f** Monocuspid vomerine teeth; pulpal access (asterisk); Howship lacunae in the pedicle (arrow). **g** Monocuspid vomerine teeth penetrating the oral epithelium; taste buds (arrowheads), lingual. **h** Dentary, lingual view; the posterior teeth (arrows) are monocuspid, the anterior tooth (arrowhead) is bicuspid. **i** Apex of an anterior bicuspid dentary tooth with distinct enamel cap.
Abb. 4 a-i: Larve in fortgeschrittenem Stadium der Metamorphose (nr. 4, 4a). Präparate mit (a, c, g) und ohne (b, d-f, h, i) Weichgewebe. **a** Prämaxillaria und Vomeres; Symphysenregion (Pfeil oben) mit einer lückenlosen Bezahnung, lingual; Vomeres (Pfeilkopf); Lücke zwischen den Vomeres (Pfeil); Choane (Stern). **b** Prämaxillarzaähne mit Anzeichen von Zweispitzigkeit (Pfeilköpfe) und Ringnaht (Pfeil). **c** Benachbarter bicuspider (Pfeil) und monocuspider Zahn im Oberkiefer, von vorn. **d** Maxillare mit lingual gekrümmten, pleurodont verankerten Zähnen; *processus facialis maxillaris* (Stern). e Vomer; *pars dentalis* mit Resten früherer Dentitionen (Pfeil) inmitten der Vomerplatte (Pfeilkopf); *pars palatina* (Stern). **f** Monocuspide Vomerzähne; Pulpazugang (Stern); Howshipsche Lakunen im Sockel (Pfeil). **g** Monocuspider Vomerzahn durchdringt das Mundepithel; Geschmacksknospen (Pfeilköpfe). **h** Dentale, lingual; monocuspide, hintere Zähne (Pfeile), bicuspider vorderer Zahn (Pfeilkopf). **i** Dentale; Apex eines vorderen bicuspiden Zahnes mit deutlicher Schmelzkappe.



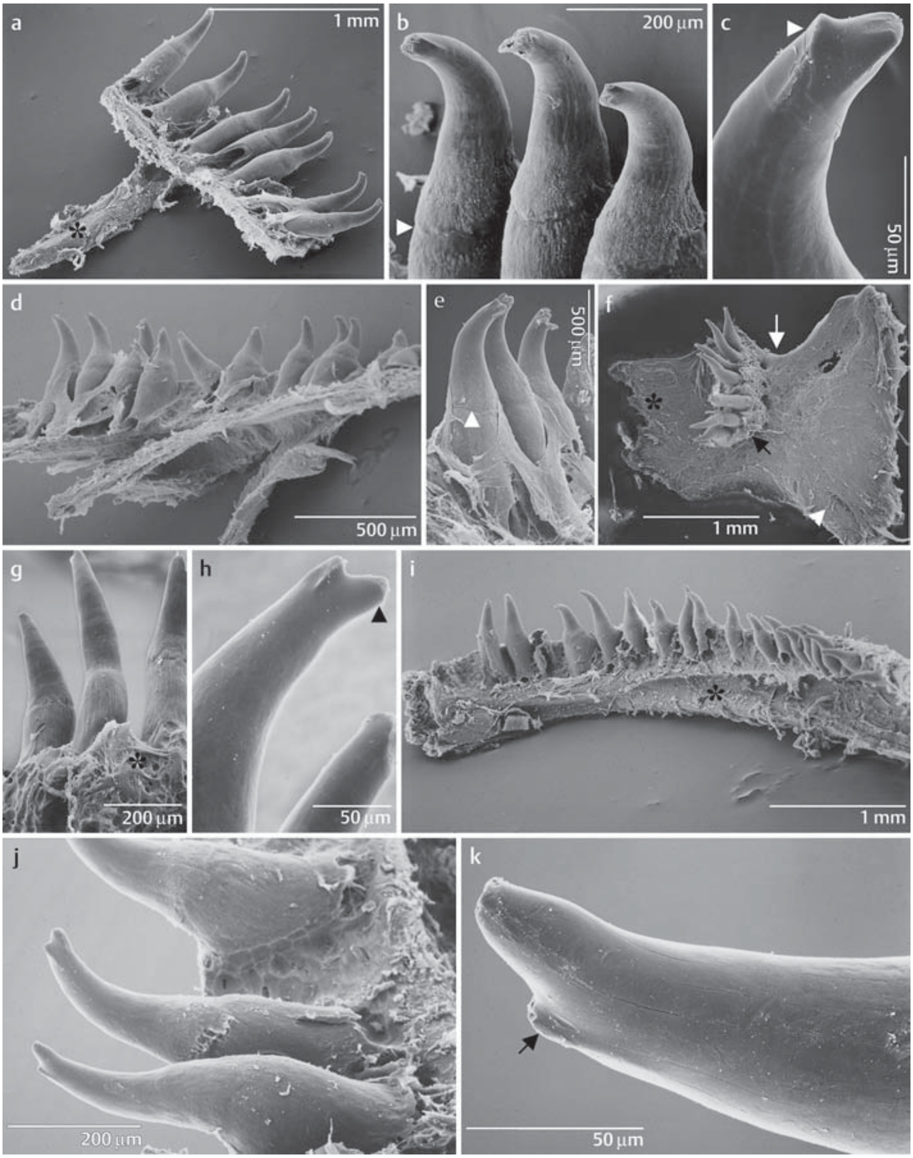
Figs 5 a-l: Larvae with delayed metamorphosis (nr. 5 and 6). **a** Premaxillary teeth, lingual view. **b** Maxillary teeth, lingual view; a dividing zone can hardly be recognized; *processus facialis maxillaris* (asterisk). **c** Apex of a maxillary tooth. **d** Maxillary tooth with a lingual bulge (left side) and globular surface (asterisk). **e** Vomer with *pars dentalis* (arrows) shifted more caudally; vomerine plate (arrowhead); *pars palatina* (asterisk) broken off (right side). **f** The anterior edge of the vomerine *pars dentalis* with remnants of previous dentitions, labial view. **g** Vomerine tooth with a broad basis and numerous small pulpal accesses. **h** Vomerine tooth with a worn-out apex. **i** Dentary with *pars dentalis*; teeth attached in a pleurodont condition increase in height posteriorly. **j** Attachment of dentary teeth is pleurodontous, lingual view; zone of division (arrow). **k** Coronoid teeth, lingual view, are horizontally attached. **l** Waisted coronoid tooth, lingual view.

Abb. 5 a-l: Larven mit verzögerter Metamorphose (nr. 5 und 6). **a** Prämaxillarzähne, lingual. **b** Maxilarzähne, lingual; eine Ringnaht ist kaum zu erkennen; *processus facialis maxillaris* (Stern). **c** Apex eines Maxillarzahnes. **d** Maxillarzahn mit lingualer Ausbuchtung (links) und globulärer Oberfläche (Stern). **e** Vomer mit *pars dentalis* (Pfeile) nach caudal versetzt; Vomerplatte (Pfeilkopf); *pars palatina* (Stern) gebrochen (rechts). **f** Vordere Kante der *pars dentalis* des Vomer mit Resten früherer Dentitionen, labial. **g** Vomerzahn mit breiter Basis und zahlreichen Pulpazugängen. **h** Vomerzahn mit abgenutztem Apex. **i** Dentale mit *pars dentalis*; die pleurodont verankerten Zähne werden nach hinten hin größer. **j** Pleurodont verankerte Zähne, lingual. Ringnaht (Pfeil). **k** Die Zähne auf dem Coronoid sind horizontal veankert. **l** Zahn auf dem Coronoid mit Taille, lingual.



Figs 6 a-i: Juvenile (nr. 7). **a** Premaxilla, lateral view; teeth have high, slender pedicles; dividing zone (arrowheads). **b** Premaxillary tooth with a small, labial (arrowhead) and a slightly larger lingual (arrow) sharp edged cusp. **c** Maxillary teeth with large pulpal accesses (arrowheads); *processus facialis maxillaris* (asterisk). **d** Pediclelate (arrow) maxillary teeth, lingual view. **e** Lingually recurved maxillary teeth. **f** Vomer, lingual view; *pars palatina* (asterisk). **g** Slender vomerine teeth with a globular dividing zone (arrow**)**, lingual view. **h** Dentary, lingual view; teeth have slender and long pedicles. **i** Dentary teeth, labial view; note the varying aspect of the dividing zone (arrows).
Abb. 6 a-i: Juvenis (nr. 7). **a** Prämaxillare, lateral; die Zähne besitzen hohe, schlanke Sockel; Ringnaht (Pfeilkpfe). **b** Prämaxillarzahn with kleiner, labialer (Pfeilkopf) und geringfügig größerer lingualer (Pfeil) scharfkantigen Spitze. **c** Maxillarzahn mit großen Pulpazugängen (Pfeilköpfe); *processus facialis maxillaris* (Stern). **d** Maxillarzahn mit Sockel (Pfeil), lingual. **e** Lingual gekrümmter Maxiallarzahn. **f** Vomer, lingual; *pars palatina* (Stern). **g** Schlanker Vomerzahn mit globulärer Ringnaht (Pfeil), lingual. **h** Dentale, lingual; die Zähne sind schlank und haben lange Sockel. **i** Zähne auf dem Dentale, labial, mit unterschiedlich ausgeprägter Ringnaht (Pfeile).

6 a, b, c; dentary: Figs 6 h, i; vomer: Figs 6 f, g). The dividing zone in the upper jaw was lingually more distinct than labially (Figs 6 c-e). In dentary teeth the dividing zone showed a deep cleft at the labial side, whereas lingually the cleft showed some material perhaps not or weakly mineralized (Figs 6 h, i). The dividing zone of vomerine teeth was characterized by a globular ring (Figs 6 f, g). Apices of teeth were curved lingually and had two distinct cusps, the labial one was smaller and sharper than the lingual one (Figs 6 b, i). In a labial view, slender pedicles towered above the anterior edge of the bone (Figs 6 i). Blades of cusps in vomerine teeth were not clearly conspicuous (Fig. 6 g).



Figs 7 a-k: Subadult specimen (nr. 8). **a** Premaxilla, lingual view; *processus dorsalis praemaxillaris* (asterisk). **b** Lingually curved premaxillary teeth with a small lingual dividing zone (arrowhead). **c** Premaxillary tooth, lateral view, with differently shaped cusps; labial blade (arrowhead). **d** Maxilla. **e** Maxillary teeth with a thin zone of division (arrowhead), lateral view. **f** Vomer; *pars dentalis* (black arrow) between the *pars palatina* (asterisk) and vomerine plate (arrowhead); gap for the choana (white arrow). **g** Anterior portion of the vomerine *pars dentalis* with remnants of previous dentitions (asterisk), lateral view. **h** Vomerine tooth with a blunt lingual cusp (arrowhead). **i** Dentary, lingual view, with ascending *pars palatina* (asterisk). **j** Dentary teeth are pleurodontously attached. **k** Dentary tooth with greatly reduced labial blade (arrow).

Abb. 7 a-k: Subadultus (nr. 8). **a** Prämaxillare, lingual; processus dorsalis praemaxillaris (Stern). **b** Lingual gekrümmte Prämaxillarzähne mit kleiner lingualen Ringnaht (Pfeilkopf). **c** Prämaxillarzahn,

3.7. Subadult (nr. 8) (Figs 7 a-k)

Number of tooth rows, ankylosis and curvature of teeth and pulpal accesses as in the previous stage.

Teeth of all dentigerous bones were bicuspid and divided (Figs 7 a-k). The apex of the teeth had two cusps, the labial one smaller than the lingual. However, proportion between the two cusps varied considerably (see Figs 7 c, h, j, k).

3.8. Adult (nr. 9) (Figs 8 a-k)

Number of tooth rows, anchorage and curvature of teeth and pulpal accesses as in the previous stage. In the upper jaw only maxillary teeth were available.

All teeth were bicuspid and divided (Figs 8 a-k). The dividing zone was deeper labially than lingually (Figs 8 d, e, h) showing a small ring like depression lingually (Fig. 8 k).

From the cusps, the labial one was significantly reduced (maxilla: Fig. 8 c; vomer: Fig. 8 f); both cusps may have blades (maxilla: Fig. 8 c). Teeth of the dentary showed a slight reduction of the labial blade; the lingual cusp was rounded off (Fig. 8 i). Here teeth were strongly recurved, so that the larger blade was nearly horizontal (Fig. 8 j); the most posterior tooth differed from the other teeth by its broad pedicle, its sturdy shape and several pulpal accesses (Fig. 8 l).

3.9. Dental laminae (Figs 9 a-h)

Dental laminae are two layered derivates of the *stratum basale* of the oropharyngeal epithelium. The face of the dental laminae turned towards the oropharyngeal epithelium was covered with dense connective tissue that amalgamated with the *tunica propria*.

In the larvae in metamorphosis and with delayed metamorphosis (both approximately stage 19), the upper jaw arcade (premaxillae and maxillae) had a single continuous dental lamina at the lingual side. Due to the lack of an adequate histological series, this is concluded by the fact that the symphyseal zones between the two premaxillae and the premaxilla/maxilla were small and the tooth row did not show any gap.

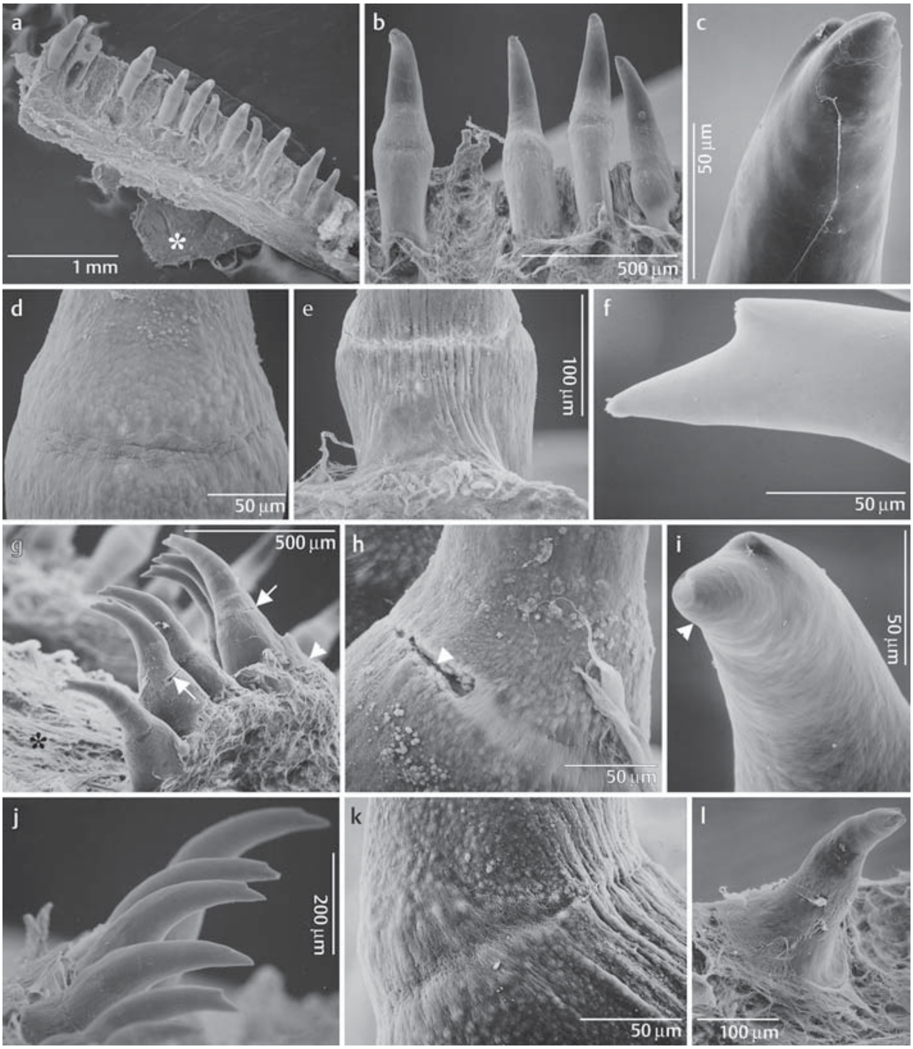
Vomers possessed their own dental lamina each. At the level of the choana (Fig. 9 a) and posterior to the choana the dental lamina still produced tooth buds (Fig. 9b); before disappearing it became one-layered and tooth buds could not be seen (Fig. 9c). The posterior end of the vomerine dental lamina was clearly separated from the palatinal dental lamina by connective tissue (Fig. 9 d). The palatinal dental lamina began with a process entirely surrounded by connective tissue (Fig. 9 e); more posteriorly its terminus fused with the oral epithelium and was productive (Fig. 9 f). Beyond the last tooth bud, the unproductive dental lamina was shortened (Fig. 9 g). Posteriorly, the dental lamina disappeared, although parts of the degenerating palatine were still present (Fig. 9 h).

4. Discussion

4.1. Attachment and succession of differently shaped tooth generations

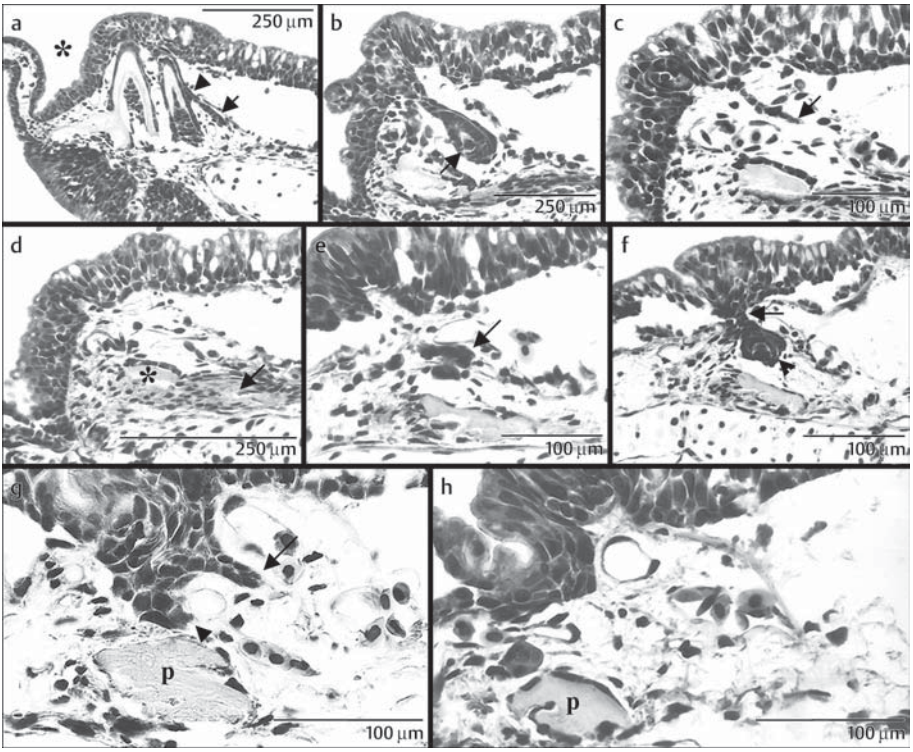
Succession of differently shaped and divided teeth described by Vassilieva & Smirnov (2001) for *Ranodon sibiricus* and pictured herein for some stages more thoroughly closely

lateral, mit unterschiedlichen Spitzen; labiale Schneide (Pfeilkopf). **d** Maxillare. **e** Maxillarzähne mit dünner Ringnahr (Pfeilkopf), lateral. **f** Vomer; pars dentalis (schwarzer Pfeil) zwischen *pars palatina* (Stern) und Vomerplatte (Pfeilkopf); Lücke für die Choane (weißer Pfeil). **g** Vorderer Teil der *pars dentalis* des Vomer mit Resten früherer Dentitionen (Stern), lateral. **h** Vomerzahn mit stumpfer lingualer Spitze (Pfeilkopf). **i** Dentale, lingual mit aufsteigender *pars palatina* (Stern) .**j** Pleurodont verankerte Zähne des Dentale. **k** Zahn des Dentale mit stark reduzierter labialer Schneide (Pfeil).



Figs 8 a-l: Adult specimen (nr. 9). **a** Maxillary, lingual view, and *processus facialis maxillaris* (asterisk). **b** Slender pedicles of maxillary teeth, lingual view. **c** Maxillary tooth, lingual view, with two different cusps. **d** Zone of division of a maxillary tooth, lingual view. **e** Zone of division of a maxillary tooth, labial view. **f** Apex of a vomerine tooth, lateral view. **g** Vomerine teeth with distinct labial dividing zones (arrows); *pars palatina* (asterisk) and *pars dentalis* (arrowhead). **h** Dividing zone of a vomerine tooth, lateral view. Note the incision labially (arrowhead). **i** Dentary tooth with a blunt lingual cusp (arrowhead). **j** Lingually curved dentary teeth; note the varying bicuspidity. **k** Zone of division in a dentary tooth, lateral view. **l** The most posterior tooth of the dentary is sturdy, bicuspid and broad-based.

Abb. 8 a-l: Adultus (nr. 9). **a** Maxillare, lingual, und *processus facilais maxillaris* (Stern). **b** Schlanke Sockel der Maxillarzähne, lingual. **c** Maxillarzahn, lingual, mit zwei unterschiedlichen Spitzen. **d** Ringnaht eines Maxillarzahns, lingual. **e** Ringnaht eines Maxillarzahns, labial. **f** Apex eines Vomerzahns, lateral. **g** Vomerzähne mit deutlicher labialer Ringnaht (Pfeile); *pars palatina* (Stern) und *pars dentalis* (Pfeilkopf). **h** Ringnaht eines Vomerzahns, lateral. Man beachte den labialen Einschnitt (Pfeilkopf). **i** Zahn des Dentale mit stumpfer lingualer Spitze (Pfeilkopf). **j** Lingual gekrümmte



Figs 9 a-h: Dental laminae of the vomer (a-c), between vomer and palatine (d), and the palatine (e-h); cross sections. **a** Dental lamina (arrow) with associated replacement tooth (arrowhead); choana (asterisk). **b** Dental lamina at the level of the choana with tooth bud (arrow). **c** Before disappearing posteriorly the dental lamina becomes one-layered (arrow). **d** Between vomer (asterisk) and palatine (arrow) a dental lamina is absent. **e** Free rostral end of the palatine dental lamina in the subepithelial connective tissue (arrow). **f** Connection of the dental lamina with the oral epithelium (arrow); most anterior tooth bud (arrowhead). **g** Short dental lamina (arrow) near the palatine (p) approx. 7 µm behind the last tooth bud. **h** In the section following g the dental lamina is absent; palatine (p).

Abb. 9 a-h: Zahnleisten des Vomer (a-c), zwischen Vomer und Palatinum (d) und Palatinim (e-h); Querschnitte. **a** Zahnleiste (Pfeil) mit Ersatzzahn (Pfeilkopf); Choane (Stern). **b** Zahnleiste in Höhe der Choane mit Zahnkeim (Pfeil). **c** Vor ihrem Verschwinden wird die Zahnleiste einschichtig (Pfeil). **d** Zwischen Vomer (Stern) und Palatinum (Pfeile) fehlt die Zahnleiste. **e** Freies rostrales Ende der palatinalen Zahnleiste im subepithelialen Bindegewebe (Pfeil). **f** Verbindung der Zahnleite mit dem Mundepithel (Pfeil); hinterster Zahnkeim (Pfeilkopf). **g** Kurze Zahnleiste (Pfeil) nahe des Palatinum (p) etwa 7 µm hinter dem letzten Zahnkeim. **h** Im Folgeschnitt ist die Zahnleiste nicht mehr vorhanden; Palatinum (p.).

Zähne des Dentale mit unterschiedlicher Zweispitzigkeit. **k** Ringnaht eines Zahns auf dem Dentale, lateral. **l** Der hinterste Zahn auf dem Dentale ist untersetzt, zweispitzig und breitbasig.

corresponds to that seen in the majority of transforming Urodela (CLEMEN & GREVEN 1994; see DAVIT-BEAL et al. 2006, 2007): Tooth germs appear at sites where the dentigerous bones will develop in most cases already during the embryonic period. Anchorage of the (functional) small, conical and undivided teeth takes place during the mineralization process of these bones (see also LEBEDKINA 2005) and teeth are attached to the bones horizontally (palatine, vomer, coronoid) or slightly pleurally (premaxilla, dentary). The mode of ankylosis appears to be dictated by the shape of the dentigerous bone and by the number of previous dentitions. In our material a pleurodont ankylosis was seen on the premaxillae, maxillae and dentaries, obviously right from the start but with increasing pleurodont attachment in later stages. On the palatine and coronoid teeth were always horizontally attached, on the flattened vomer, however, initially horizontally and later slightly pleurodont due to remnants of previous dentitions (see also CLEMEN & GREVEN 1979). Obviously, there is the tendency to reduce and enlarge accesses to the pulp with an increasing pleurodont attachment. Broad-based teeth seen on bones (e.g. dentaries, maxillae) bearing anteriorly a pleurodont dentition, always were horizontally attached and showed several pulpal accesses. Generally, the conical teeth of very young urodele larvae have a small non-vascularized pulp and a tubular dentine (BOLTE et al. 1996). Such teeth were suggested to be conserved organs representing an ancestral character for gnathostomes (SIRE et al. 2002). In the majority of Urodela these "early" larval teeth (undivided, conical, broad-based, monocuspid) are replaced by conical monocuspids that may gradually change from a "non-pedicellate" (a pedicle cannot be distinguished) to a pedicellate condition (the pedicle is separated from the crown by a more or less complete distinct zone of division) *via* various intermediate stages named "subpedicellate" by some authors. Not until metamorphosis teeth become replaced by fully divided (=pedicellate), bicuspid teeth, and bicuspidity seems to develop also *via* intermediate stages. This was mentioned for instance in the articles of BENESKI & LARSEN (1989 a, b) and (BOLTE & CLEMEN 1991) and demonstrated unequivocally by DAVIT-BEAL et al. (2006).

Terminology of these three major ontogenetic stages is inconsistent in literature. BENESKI & LARSEN (1989 b) distinguished in their SEM-pictures "for clarity and consistency" (p. 166) 1) non-pedicellate teeth (stage I) with a distal monocuspid apex (covered entirely by enameloid) and a proximal shaft (not covered by enameloid), 2) subpedicellate teeth (stage II) with a distal monocuspid crown (only its apex is covered by enameloid) and a proximal base separated from the crown by an abrupt increase in width and/or a lingual fibrous zone of division, and 3) pedicellate teeth (stage III), with a distal crown consisting of the modified, i.e. bicuspid, apex, and shaft (the apex is entirely covered by enamel, the shaft only in its distal part), and a proximal pedicle separated completely by an annular zone of weakness (see Fig. 1 in BENESKI & LARSEN 1989 b; see also VASSILIEVA & SMIRONOV 2001). Apart from the fact that the apex of larval teeth probably possesses true enamel and enameloid instead of enameloid alone (see BOLTE & CLEMEN 1992; BOLTE et al. 1996; KOGAYA 1994, 1999; WISTUBA et al. 2002), this terminology, although adopted by various researchers, does not meet the real conditions and appears highly arbitrarily. By definition non-pedicellate teeth do not show a dividing zone between the distal and proximal part by LM and SEM. However, their "proximal shaft" or base definitely lacks dentine tubules such as the pedicles of transformed teeth (BOLTE et al. 1996). That means that early larval teeth possess a true pedicle. Further, VASSILIEVA & SMIRNOV (2001) describe on the basis of their stained and cleared specimens that mineralization of small non-pedicellate teeth begins from a single apical mineralization centre and proceeds in apico-basal direction, whereas mineralization of "subpedicellate" and pedicellate teeth starts from an apical and a basal centre moving in apico-basal and basal apical direction, respectively. There is evidence by TEM-micrographs that also in early larvae two mineralization fronts exist (*Ambystoma mexicanum:* WISTUBA et al. 2002).

Typically, in bicuspid teeth the lingual cusp is elongated, but sharper than the labial one. Compared to the relative time the dividing zone develops, the change of the tooth crown from monocuspids to bicuspids seems to take place in a relatively shorter period around metamorphosis.

Only in a few metamorphosed urodeles teeth deviate from the bicuspid type; e.g., in some *Ambystoma* species basic cusp shapes of pedicellate premaxillary teeth are disc or club (see BENESKI & LARSEN, 1989a), which, however, all can be attributed to the bicuspid type; male plethodontids have premaxillary teeth that secondarily changed to cone-shaped monocuspids under the influence of testosterone during the breeding season (e.g., NOBLE & POPE 1929; EHMCKE et al. 2003; GREVEN et al. 2004).

In adult *R. sibiricus* the shape of the two cusps of teeth is rather variable, mainly regarding the lingual cusp, which probably cannot solely be attributed to the fact that bicuspidity develops gradually on the different dentigerous bones (see below). Also the zone of division that creates the pedicellate condition in metamorphosed urodele teeth and is considered an apomorphic character of extant Amphibia (e.g., PARSONS & WILLIAMS 1962; DUELLMAN & TRUEB 1986; GREVEN 1989; AX 2001; the latter author also gives reasons why to cancel the term "Lissamphibia" used for the extant Amphibia) shows a considerable variation. A transverse annular zone of division was lacking in our youngest larva (and is lacking also in earlier stages; see VASSILIEVA & SMIRNOV 2001); in later stages this zone appears to be indicated only by a more or less globular area around the tooth and curvature of teeth might indicate the future region of the dividing zone (e.g., DAVIT-BEAT et al. 2006). Even in adults this zone was often remarkably less distinct when compared to other metamorphosed urodeles. We don't know, whether this variability is a question of the age of the animals, i.e. fully metamorphosed and older adults may be expected to show a more conspicuous zone division as seen in a variety of Urodela, or caused by a heavier or even secondary calcification of the collagenous fibres bridging the gap between crown and pedicle (MOURY et al. 1985; GREVEN et al. 1989; WISTUBA et al. 2002). Regarding the ontogenetic sequence studied by VASSILIEVA & SMIRNOV (2001), a secondary mineralization of this zone is improbable. Generally, in *R. sibiricus* development of both characters (bicuspidity and zone of division) seems more variable and partly less conspicuous as in other Urodela.

4.2. The fate of dentigerous bones during ontogeny and direction of dental replacements

As in other Urodela, also in *R. sibiricus* development and replacement of the differently organized teeth takes place at different times depending on the particular dentigerous bone and its fate during further development. Tooth replacement in all dentigerous bones, typically is posterior to the tooth row in labial direction. Development of dentigerous bones of *R. sibiricus* and their degradation or remodelling during metamorphosis was thoroughly described by LEBEDKINA (summarized 1979, 2005, see also JÖMANN et al. 2005); the various tooth generations and their temporally shifted development were illustrated by VASSILIEVA & SMIRNOV (2001). The latter observations are deepened herein and broadened with regard to the palatine and the coronoid.

The typical sequence of differently shaped tooth generations has been used to classify "early" (see above), "late" larval teeth (monocuspid, "subpedicellate") and "transformed" or "metamorphosed" teeth (see above) in several Urodela including paedomorphic species (e.g., CLEMEN & GREVEN 1977, 1980, 1994; GREVEN & CLEMEN 1980). Initially, larval dentigerous bones of *R. sibiricus* bear "non-pedicellate", i.e., "early" larval teeth (see also VASSILIEVA & SMIRNOV 2001). The later the bone develops in ontogeny, the more developed teeth (in the direction of the "late" larval tooth) are established, i.e., very early tooth stages are left out on bones developing late in ontogenesis, e.g., on the maxilla. "Late" larval teeth are first established on the premaxilla, then on the dentary and later on the developing maxilla. At this time vomerine and coronoid teeth (a single established tooth in larva 3) were from the "early" larval type. Palatinal teeth in larva 3 were, however, lacking. It was shown by VASSILIEVA & SMIRNOV (2001) that the coronoid as well as the palatinal dental laminae appear to be able to produce short-lived "late" larval teeth (named by the authors "subpedicellate"). Actually, we found "late" larval teeth on the coronoid of the specimens with delayed metamorphosis. The discrepancies regarding the palatine may be attributed to our limited material and the large variations suggested for the development of dentition in *R. sibiricus* (see the discussion in VASSILIEVA & SMIRNOW 2001).

Metamorphosed bicuspid teeth are first produced in the upper and lower jaw. All premaxillary and the most maxillary teeth of larva 4 in advanced metamorphosis had (incipient) bicuspids, whereas dentaries bore transformed teeth anteriorly and teeth of the "late" larval type posteriorly, i.e., transformation of teeth takes place from the anterior to posterior. The vomers still had "early" larval teeth. After metamorphosis all systems still present show bicuspid divided teeth. In larvae with delayed metamorphosis all systems present at this time had "late" larval teeth.

Regression of the palatinal tooth system begins relatively early. This is stressed by the fact that in the larvae with delayed metamorphosis palatinal teeth were totally absent (see above). After multiple hibernation as assumed for *R. sibiricus* larvae (KUZMIN & THIESMEIER 2001; see the discussion in JÖMANN et al., 2005), the palatine is separated from the pterygoid, still fully developed, but free of teeth. At this time the dental lamina of the coronoid appeared still active.

Because of the relatively early degradation of these dental laminae a subsequent delivery of new teeth ceases. This leads to a toothless palatine, either permanent when larvae were hypopyhsectomized in time (*Salamandra salamandra*: CLEMEN 1978) or before complete resorption in course of metamorphosis when metamorphosis is delayed, e.g. by deep temperatures (*S. salamandra*: CLEMEN 1978; *R. sibiricus*: JÖMANN et al. 2005; the present article). Degradation of the palatinal portion of the palatopterygoid is considered as one of the key factors indicating the onset of metamorphosis (REILLY 1986, 1987; REILLY & ALTIG 1996). Onset, however, may be indicated earlier, e.g., by the less conspicuous degradation of dental laminae.

In brief, regarding chronology of tooth replacements as well a disintegration of certain dentigerous bones, *R. sibiricus* follows the pattern realized in all urodeles hitherto examined that undergo metamorphosis. The typical spatial and temporal differences regarding development of fully transformed bicuspid teeth and their transitory stages (see CLEMEN & GREVEN 1994 and the literature cited above) in the various tooth systems is very probably ascribed to different competences of the tooth producing tissue and its different sensitivities to the metamorphosing hormone (CLEMEN 1988 a, b; GREVEN & CLEMEN 1990).

Although briefly discussed in our previous study (JÖMANN et al. 2005), we again discuss herein the changes during remodelling of the vomerine system around metamorphosis. In most Urodela, these changes are remarkable and have been long used for phylogenetic considerations (e.g., LAURENT 1947; REGAL 1966; HECHT & EDWARDS 1977; ZHAO et al. 1988; CLEMEN & GREVEN 1994).

Apart from the fact that the larval vomer of *R. sibiricus* bears several rows of teeth rather than a single row (LEBEDKINA 1979, 2005; VASSILIEVA & SMIRNOV 2001; see above) and that the vomerine tooth rows are less parallel to the premaxillary arcade (see figures in LEBEDKINA 2005 and JÖMANN et al. 2005), the changes of the vomerine system during transformation of *R. sibiricus* are less conspicuous as in many other Urodela (for review see CLEMEN & GREVEN 1994). Metamorphosed *R. sibiricus* have a nearly transverse vomerine dentition more or less parallel to the upper jaw arcade with a tooth replacement posterior to the tooth row in labial direction, i.e. the labial replacement pattern is retained in transformed specimens. In other hynobiids more conspicuous changes occur (e.g., ZHAO et al., 1988; ADLER & ZHAO 1990; ZHANG et al. 2006). Here the *partes dentales* form a short anterior, transverse row and a longitudinal row directed posteriorly resulting in replacements posterior (in labial direction) to the transverse tooth row and lateral (in lingual direction) to the longitudinal tooth rows (GREVEN & CLEMEN 1985). The latter mode obviously has evolved more than once in Urodela (see the discussion in HECHT & EDWARDS 1977). *R. sibiricus* shares the transversely orientation of the vomerine dentition (and thus the posterior replacement of teeth) with the hynobiid genera *Liua*, *Batrachuperus*, *Pachyhynobius*, *Paradactylodon*, and *Onychodactylus* (ZHAO et al. 1988; ZHANG et al. 2006), which belong to stream-type hynobiids and obviously do not form a natural group (LARSON et al. 2003; ZHANG et al. 2006). Transversely oriented vomerine teeth were said to hinder escape of prey in those species feeding by suction in water (ZHANG et al. 2006). These functional suggestions do not contradict the assumption that a transverse tooth row with replacements in labial direction is a plesiomorphic character of hynobiids and perhaps of all Urodela (see the short discussion in JÖMANN et al, 2005). Fossils from the Early Cretaceous related to hynobiids, such as *Liaoxitriton* have also a transverse arrangement of the vomerine teeth (WANG 2004).

4.3. Multiple rows versus a single row of teeth

In the youngest larva available larvae (stage 16 according to LEBEDKINA's table, l.c.; see JÖMANN et al. 2005; late feeding larva according to VASSILIEVA & SMIRNOV 2001) we found only on the palatine clear signs of two rows of teeth without resorption pits. Dentaries, premaxillae, and, when established, maxillae bear a single row of teeth throughout ontogeny (VASSILIEVA & SMIRNOV 2001; LEBEDKINA 1979, 2005; JÖMANN et al. 2005) and postmetamorphosed specimens have a single row of teeth on all dentigerous bones. LEBEDKINA (1979, 2005) draws a single row of teeth on all dentigerous bones up to stage 7 with the exception of the coronoid (early feeding larva; see VASSILIEVA & SMIRNOV 2001). In her stage 8 the palatine shows two rows of teeth and two rows occur also on the vomer from her stage 9 up to resorption in the premetamorphic period (stage 17). Our youngest specimen did not clearly show two rows of teeth on the vomers. These findings show that already in "late feeding larvae" resorption of lateral margins of the vomer, but also of the palatine and the coronoid has led to the loss of teeth. In contrast to the findings of VASSILIEVA & SMIRNOW (2001) all teeth of our specimen (stage 16) were from the early larval type, i.e. monocuspid and entirely undivided (see above). These discrepancies may be attributed to individual variation.

According to our results and the findings of VASSILIEVA & SMIRNOV (2001), the sequence of tooth row numbers in the tooth systems of *R. sibiricus* is as follows (the first functional dentition of a dentigerous bones necessarily comprises a single row): the upper jaw and the dentary bear a single row throughout ontogeny, the vomers bear up to three rows in larvae and a single row in metamorphosed specimens. The coronoids bear up to three rows, and the palatines up to two rows that will be resorbed before metamorphosis. In other Urodela deviations from this pattern occur mainly with respect to the premaxillae and palate (e.g. in Ambystomatidae, where the palate is partly retained after metamorphosis) and vomer (e.g. in Plethodontidae) (see literature cited above).

Interestingly, the hynobiid, *Onychodactylus fischeri*, which is now considered as sister taxon of all other extant hynobiids (Larson et al. 2003; Zhang et al. 2006) and which largely resembles *R. sibiricus* in the traits discussed herein, has a single row on all dentigerous bones already in early developmental stages (Smirnow & Vassilieva 2002).

4.4. Dental laminae

Knowledge of number and course of dental laminae in larval and adult *R. sibiricus* is still incomplete, but the available data and indirect evidence from the position and continuity of tooth rows allow for some conclusion. The upper jaw is accompanied by a continuous dental lamina indicated by a continuous tooth row (and tooth buds) in the symphyseal region between the premaxillae and at the transition of the premaxilla/maxilla. Between the dentaries here and in other Urodela (e.g., Greven et al., 2002/2003) a gap in the tooth row may be indicative for a gap in the dental lamina. The paired coronoids, palatines and vomers are widely separated and have their own continuous dental lamina each. This pattern exactly corresponds to that found in the majority of extant Urodela. Exceptions have been documented and discussed elsewhere (e.g., Clemen & Greven 1994).

The larvae with delayed metamorphosis showed a fully developed palatinal portion of the palatopterygoid without teeth (see also Jömann et al. 2005). Thus, the dental lamina must have lost its capability to produce teeth at the onset of the lengthened late larval period. The dental laminae of the coronoid between vomer and palatine was, however, still active at this time (see the picture in Jömann et al. 2005).

4.5. Conclusions

As shown herein and in previous articles of various authors, the pattern of dentition, the succession of differently shaped tooth generations, the direction of replacements and the course and number of dental laminae (still unknown in detail, but indirectly inferred from gross morphology in part) of *Ranodon. sibiricus*, a representative of an ancient urodele lineage, fits very well in the pattern present in many other Urodela. The remodelling mainly of the vomerine system during metamorphosis appears comparatively inconspicuous. We suggest that many of the characters of the tooth systems summarized herein are highly conserved plesiomorphic traits in Urodela.

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