Sex dimorphic dentition and notes on the skull and hyobranchium in the hynobiid salamander *Pachyhynobius shangchengensis* Fei, Qu & Wu, 1983 (Urodela: Amphibia)

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> Abstract

A noticeable sex-dimorphic dentition is described in the hynobiid salamander *Pachyhynobius shangchengensis*. In the upper and lower jaw, the male possesses pedicellate teeth with a chisel- or spearhead-like crown, i.e. secondary (labial) cusps of teeth are largely reduced, whereas the primary (lingual) cusps are flattened antero-posteriorly and exhibit sharp edges. In contrast, females have pedicellate, somewhat flattened teeth more variable in shape, but with small bladed labial and large bladed lingual cusps. Vomeres of both sexes bear typical bicuspid, pedicellate teeth. Skulls including the hyobranchium are largely ossified with some minor differences between males and females. However, females appear to lack the *pars hypohyalis* in the hyobranchial apparatus.

> Kurzfassung

Wir beschreiben eine auffällige geschlechtsspezifische Bezahnung bei *Pachyhynobius shangchengensis*. Das Männchen besitzt im Oberkiefer und Unterkiefer zweigeteilte Zähne mit einer meißel- oder speerförmigen Krone, d.h. deren sekundäre (labiale) Spitze ist weitgehend reduziert, während die primäre (linguale) jedoch abgeflacht ist und scharfe Kanten besitzt. Im Gegensatz dazu sind die ebenfalls zweigeteilten, z. T. abgeplatteten Zähne des Weibchens viel variabler in der Gestalt, jedoch deutlicher bicuspid mit scharfkantigen großen primären und kleinen sekundären Spitzen. Die Vomeres besitzen in beider Geschlechtern typische bicuspide, zweigeteilte Zähne. Schädel und Hyobranchium sind weitgehend ossifiziert und zeigen einige eher geringfügige Unterschiede zwischen Männchen und Weibchen. Allerdings scheint dem Weibchen eine ausgeprägte *pars hypohyalis* im Hyobranchialapparat zu fehlen.

Introduction

Typically, teeth of metamorphosed Amphibia consist of a bicuspid crown and a pedicel separated from the crown by an annular zone of weakness, which is lingually broader than labially ("pedicellate teeth": Parsons & Williams, 1962; Greven, 1989; Clemen & Greven, 1994; for a more recent review see Davit-Beal *et al.*, 2007). This zone of division is considered as an apomorphic character of extant Amphibia (= Lissamphibia of several authors), supporting their monophyletic origin (see Parsons & Williams, 1962;

Duellman & Trueb, 1985; Davit Béal *et al.*, 2007). From the two cusps, generally the lingual one is larger than the labial one and both may have blades, but deviations occur regarding their size and appearance.

In Urodela modifications of the bicuspid tooth apex are known only in two families. Some ambystomatids have disc- or club-shaped crowns, which are, however, principally bicuspid; a sexual dimorphism of these teeth was not mentioned (Beneski & Larsen, 1989). Male plethodontids exhibit sex-specific elongated conical monocuspids in the premaxillae controlled by androgens, i.e. monocuspidity depends on the reproductive cycle and teeth on the same locus can switch

between being monocuspid and bicuspid (e.g. Noble & Pope, 1929; McBride Stewart, 1958; Wake, 1966; Wake et al., 1983; Ehmcke & Clemen, 2000; Greven et al., 2004).

In the present article we report on a remarkably modified and very probably sex-dimorphic dentition in the poorly known aquatic urodele *Pachyhynobius shangchengensis* Fei, Qu & Wu, 1983, a member of the Hynobiidae. In addition, we present some drawings of the skull, the lower jaw and the hyobranchial apparatus suggesting further sex-dimorphic traits.

Material and methods

Two adult males (total length 19.0 and 15.0 cm; snout vent length 11.5 and 9.0 cm) and two females (total length 17.5 and 16.7 cm; 15.2 cm; snout-vent length 10.5 cm both) of *Pachyhynobius shangchengensis* were obtained from a commercial dealer.

The skull and the lower jaw including the hyobranchium of the 19 cm-male and the 17.5 cm-female were fixed in buffered formalin after Lillie (Romeis, 1968) and then stained and cleared (Park & Kim, 1984). After analysis the same preparations were used for scanning electron microscopy (SEM). The dentigerous bones were carefully excised and the adhering tissue was removed by 1% pancreatin in tetraborate buffer. From the 15 cm-male and the 16.7-female the same parts of the head were fixed in 2.5% glutaraldehyde in 0.1 mol/l cacodylate buffer, pH 7.2, for several days. Preparations were dehydrated immediately after fixation or after examination (stained and cleared specimens), critical-point-dried, sputtered with gold and viewed in a Hitashi-Scanning electron microscopy.

Results

Skull and lower jaw: The description refers to stained and cleared specimens of a single male and a single female. However, a rough examination of the two other specimens available did not reveal noticeable differences. Drawings in figure 1 are largely self-explanatory. Therefore we give only a brief outline here focussing mainly on the dentigerous bones.

The skull of the male is slightly longer and wider than that of the female. Except some parts of the occipto-otic region and of the hyobranchial apparatus, skull elements are completely ossified in both sexes. Bilateral pairs of septomaxillary (sm) and lacrimal (l)

bones are present. The large nasals (n) contact prefrontals (pf), frontals (f), underlie the *processus dorsales praemaxillares* (pdp) of the premaxillae (pm), and tightly approach the anterior end of the maxilla. The frontals overlap anterior parts of the parietals (p). The prefrontal (pf) overlaps slightly the anterior tip of the frontal and touches the lacrimal. Parietals (p) are separated by a moderately wide fontanelle.

The paired premaxillae (pm) and maxillae (m) form the upper jaw arcade; they bear a continuous row of teeth. The posterior ends of maxillae bulge out laterally, especially in the male, and are in close contact with the pterygoids (pt), bones that contact the quadrate. The cartilaginous *processus pterygoidalis* (ppt) arises from the quadrate and extends to (female) or beyond (male) the maxillary bulge. The vomeres (v) are large and almost triangular. The edentate anterior parts broadly touch the *partes palatinae* of premaxillae and in part of maxillae and surround the medio-anterior edges of the choanae. Behind the space for the intermaxillary gland the two vomers tightly juxtapose each other medially. Posteriorly they separate from each other forming the acute angles of the triangle. This part bears a single row of teeth. In females this row runs less acute-angled. Posterior vomerine parts overlap the anterior parasphenoid (ps). The parasphenoid (ps) extends from closely behind the intermaxillary gland to the occipito-otic region covering the ossified orbitosphenoid (os) and the prootic (po). Laterally the occipito-otic region is connected with the squamosal. The latter is attached to the fully ossified quadrate.

The left and right dentaries, somewhat stronger in the male (Fig. 1 e, f), are syndesmotically connected in the middle; they bear a single tooth row each. Each dentary encloses Meckel´s cartilage (Mc), which is partly covered by the prearticular (pa). The posterior

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Fig. 1 a –f: Skull, lower jaw, and hyobranchial apparatus of an adult male (a, c, e) and an adult female (b, d, f). **a,c** Skull, dorsal view; **b,d** skull, ventral view; **e, f** lower jaw and hyobranchial apparatus. Abbreviations: **ar** articular; **ac** antorbital cartilage; **ag** angular: **bbI, bbII** basibranchials I andII; **cbI, cbII** ceratobranchials I and II; **cy** ceratohyal, **cq** cartilaginous part of the quadrate; **d** dentary; **f** frontal; **fp** *foramen palatinum*; **hbI, hb II** hyobranchials I and II; **l** lacrimal; **m** maxilla; **Mc** Meckel´s cartilage; **n** nasal; **ooc** occipito-otic region; **os** orbitosphenoid; **p** parietal; **pa** prearticular; **pdp** *processus dorsalis praemaxillaris*; **pf** prefrontal; **pm** premaxilla; **po** prootic; **ps** parasphenoid; **pt** pterygoid (pterygoidal portion of the palatopterygoid); **ppt** *processus pterygoidalis*; **q** quadrate; **s** squamosal; **sm** septomaxilla; **sy** syndesmose; **v** vomer; **vt** vomerine teeth. Dermal bones: black; replacement bones: stippled; cartilage: grey; hidden edge of bony or cartilaginous elements: dotted lines; pits and elevations: dashed lines; white points: established teeth; white circle: locus without tooth. In **b** and **d** the cartilaginous ethmoidal region is omitted.
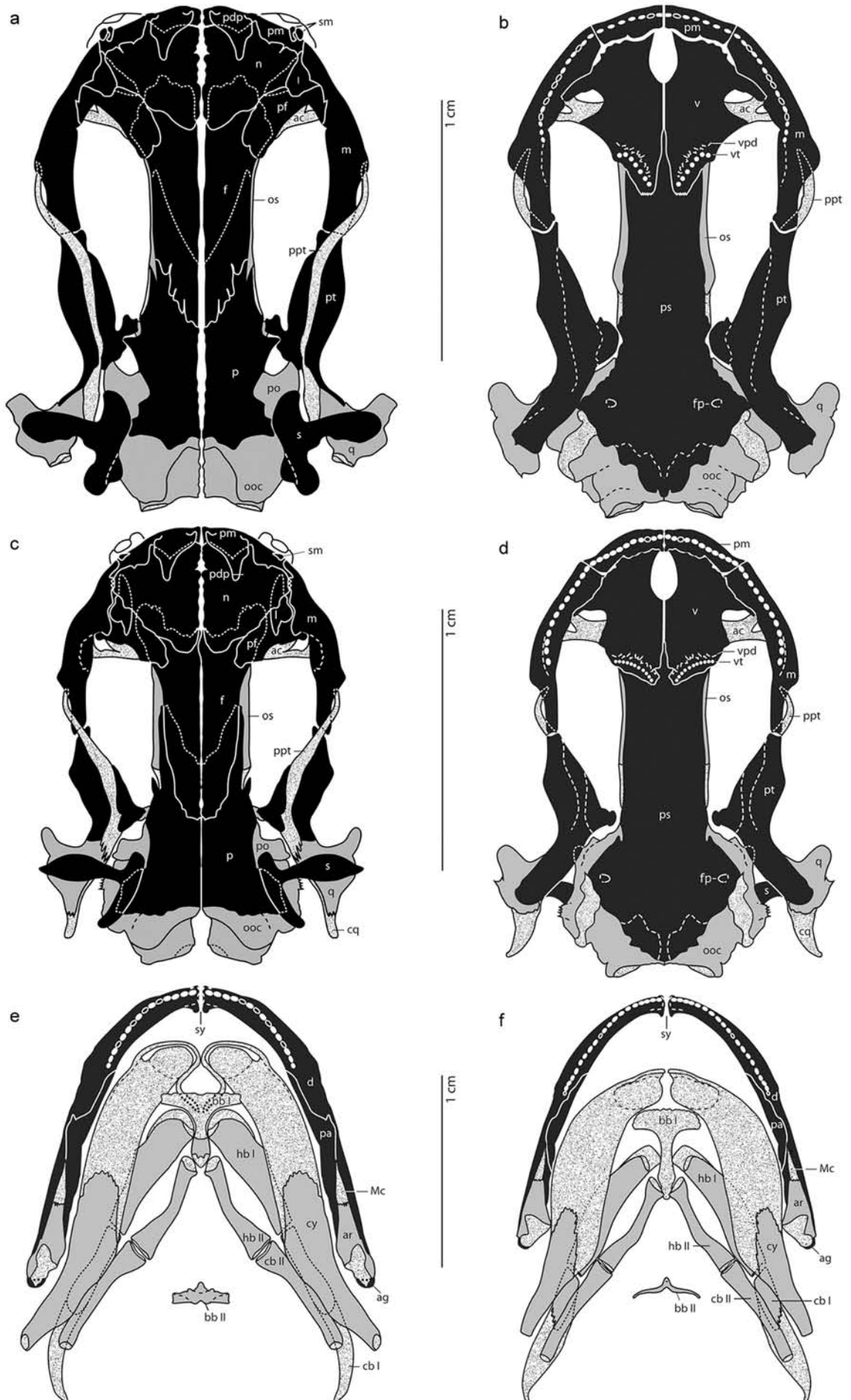
end of Meckel's cartilage is the articular bone (ar) and the socket. Ventrally, the angular (ag) is present.

Hyobranchial apparatus: Elements of the hyobranchial apparatus are named herein according to STADTMÜLLER (1936) and TRUEB (1993). From anterior to posterior the hyobranchial apparatus in both sexes consists of one pair of strong, but largely cartilaginous ceratohyals (cy), two pairs of ossified hypobranchials (hbI, hbII), two pairs of predominantly ossified ceratobranchials (cbI, cbII) - the epibranchials of other authors - and the midventral elements, i.e. the anterior basibranchial I (bbI) (partly ossified in the male) and the fully ossified posterior basibranchial II (bb2II). Hypobranchial I and ceratobranchial II are very probably not fused. In the male each ceratohyal exhibits a small anterior extension (= *pars hypohyalis* according to STADTMÜLLER, 1936), which describes a curve backwards and contacts the basibranchial I (Fig. 1 e). In the female ceratohyals show only very short extensions, which do not reach the basibranchial I. (Fig. 2 f).

Dentition: All dentigerous bones, i.e. premaxillae, maxillae, vomers and dentaries, of the female and the male bear a single row of pedicellate teeth. In the symphyseal zones between the premaxillae, and between each premaxilla and maxilla, the row is continuous (Fig. 2a, 3 a); between the dentaries, however, a distinct gap is present (Fig. 2 h, 3 h). Typically, teeth are ankylosed in a pleurodont condition (Fig. 2 h).

Male

Upper jaw: Between the adjacent premaxillae (Fig. 2 a, b) and between premaxilla and maxilla (not pictured) only a small incomplete fissure, if any, is seen indicating fusion of the respective bones to a large extent. Teeth are markedly flattened postero-anteriorly (labially-lingually) and possess only a weak secondary (labial) cusps. The crown is asymmetrical, nearly straight with sharp blades reaching the dividing zone and roughly resembling a chisel (Fig. 2d-g). The dividing zone is lingually broader than labially (Fig. 2 e - g) and largely closed. This does no always hold for the labial zone, which shows often a distinct fissure (Fig. 2 g).

Lower jaw: Inclination and flattening of lower jaw teeth resembles those of upper jaw teeth. However, the crown is spear-like (Fig. 2 i). The blades do not reach the dividing zone and again the zone of division appears largely closed (Fig. 2 k).

Vomer: The *partes dentales* are elevated and bear aborally recurved teeth. The pedicel exceeds the *pars dentalis* labially (Fig. 2 l, m). Teeth are typically bicuspid showing a rather conical primary (lingual) cusp and a small bladed secondary (labial) cusp. A dividing zone is present, but appears sealed (Fig. 2 m). However, most of the crowns have been lost during preparation (Fig. 2 l).
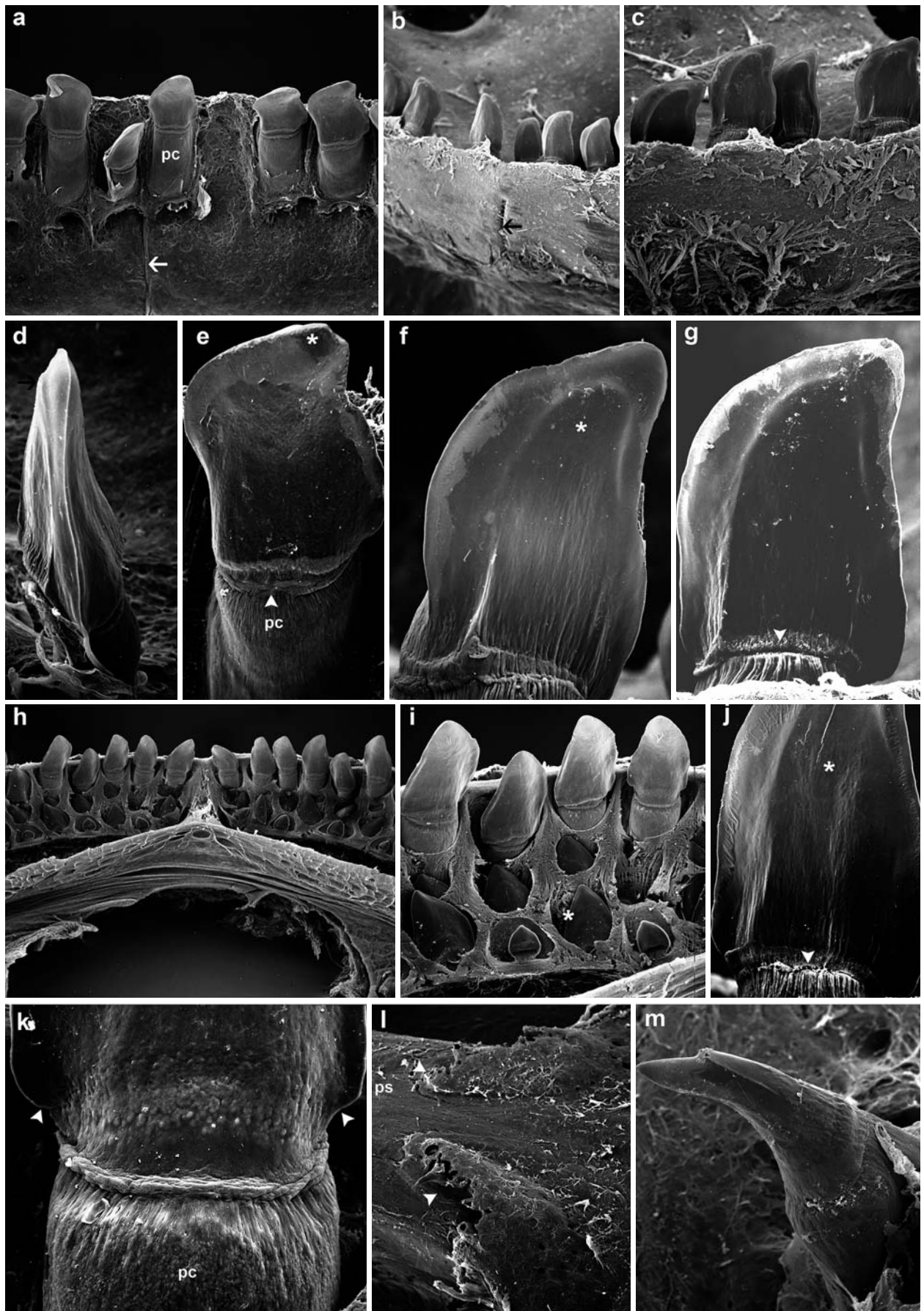
Female

Upper jaw: The crowns of premaxillary teeth are highly variable ranging from being conical to flattened, but most have two distinct cusps (Fig. 3 b-e). Primary and secondary cusp may exhibit sharp edges (Fig. 3 e). The same holds for the maxillary teeth (Fig. 3 f,g).

Lower jaw: Also on the dentaries shape and size of teeth is variable (Fig. 3 h). Teeth decrease in height antero-posteriorly (Fig. 3 h). All are clearly bicuspid with a distinct dividing zone. When viewed from lingual, crowns resemble spear-heads, but a secondary labial cusp is always present (Fig, 3 i, k, l, m).

Vomer: The vomer bears typical bicuspid teeth. Most have lost their crowns (Fig. 3 j). Both cusps are bladed (Fig. 3 n).

Fig. 2 a-m: Dentition of the male. **a** Ajacent premaxillae, lingual view, showing a small fissure (arrow), pedicel (pc), 40 ×; **b** adjacent premaxillae, labial view; fissure (arrow), 30 ×. **c** premaxilla (left side) and maxilla (right side), labial view, 40 ×; **d** nearly straight premaxillary tooth, lateral view; very small secondary cusp (left side), 150 ×; **e** zone of division (arrowhead) of a premaxillary tooth, lingual view, and lateral extension of the primary cusp (asterisk), pedicel (pc), 150 ×; **f** premaxillary tooth, labial view, with a small largely closed dividing zone and weak secondary cusp (asterisk), 200 ×; **g** labial dividing zone (arrowhead), premaxillary tooth, 200 ×; **h** adjacent dentals separated by a distinct gap; teeth show a slight inclination medially; **i** spear-headed dentary teeth; replacement teeth (asterisk), 50 ×. **j** dentary tooth; the labial zone of division is a small fissure (arrowhead); nearly indistinct secondary cusp (asterisk), 150 ×; **k** dentary tooth, lingual view, with a closed dividing zone and bladed edges (arrowheads), pedicel (pc), 300 ×; **l** vomeres (arrowheads) with elevated *partes dentales*; most teeth have lost their crowns (arrowheads); ps parasphenoid, 20 ×; **m** bicuspuid and aborally recurved vomerine tooth, lateral view, 200 ×.

Discussion

We report herein for the first time on teeth of a hynobiid salamander, which differ between males and females and deviate mainly in males from the typical more or less conical bicuspid and pedicellate teeth known from the majority of Urodela. In addition, examination of the skull and namely of the hyobranchial apparatus give evidence of further probably sex-specific traits. Drawings of the skull, the lower jaw and the hyobranchial apparatus of hynobiids including *Pachyhynobius shangchengensis* either consider single elements important for taxonomic purposes (see Fei *et al.*, 1983; Zhang & Hu, 1985; Ye *et al.* 1993) or stress the organisation typical for the species or the genus rather than emphasize possible sex-dimorphism (see Stadtmüller, 1936; Lebedkina, 1979, 2005; Duellman & Trueb, 1986; Cox & Tanner, 1989; Trueb, 1993; Smirnov & Vassilieva, 2002).

Generally, Urodela show differential age-independent sex-specific morphometric traits and males are often larger than females. Regarding *P. shangchengensis* the sparse literature allows for these differences. The measurements given for the male and female holotype of *Xenobius melanonychus* (see Zhang & Hu, 1985) very probably synonymous with *P. shangchengensis* (Fei *et al.*, 1983; Zhang & Hu, 1985; Zhao, 1988) are in line with ours (e.g. snout-vent length: ♂ 11.4 cm; ♀ 10.6 cm; head width: ♂ 2,3 cm; ♀ 2,1 cm; see Zhang & Hu, 1985; see also Raffaeli, 2007).

Organisation of the skull and lower jaw correspond to the descriptions given for a hynobiid skull in general (see Stadtmüller, 1936; Lebedkina, 1979, 2005; Duellman & Trueb 1986; Trueb 1993). In *P. shangchengensis* there are marginal differences between females and males such as the arrangement of vomerine teeth (see below), the long *processus pterygoidalis* of the male etc. probably due to the different size of the sexes. More noticeable, however, is the lack of the *partes hypohyales* of the ceratohyals in the female. Such extensions are pictured for several *Hynobius*-species and *Onychodactylus fischeri* (e.g. Stadtmüller, 1936; Cox & Tanner, 1985; Smirnov & Vassilieva, 2002) and are present already in metamorphosed juveniles (see figures in Stadtmüller, 1936), i.e. their absence in the female of *P. shangchengensis* cannot be assigned to an immature specimen. If this feature should be confirmed using a wider material, it might represent a permanent sexually dimorphic character, i.e. hyperplastic in nature resulting from hormone-mediated proliferation events that occurred relatively early during development (Emerson, 2000).

Arrangement of teeth corresponds to that of other metamorphosed hynobiids, i.e. a single row of teeth on all dentigerous bones, a semicircle upper jaw arcade (premaxillae and maxillae) and a lower jaw arcade (dentaries) with the tooth row interrupted at the symphyseal zone and with replacements typically from the posterior of the bones (e.g. Lebedkina 1979, 2005; Zhao *et al.*, 1988; Adler & Zhao, 1990; Vassilieva & Smirnov, 2001; Smirnov & Vassilieva, 2002; Jömann *et al.*, 2006; Zhang *et al.*, 2006; Greven *et al.*, 2007). In the female of *P. shangchengensis* teeth rows of the two vomeres approach one another medially in a nearly transverse row with only a slight inclination resulting in the posterior replacement of teeth typical for stream-type hynobiids (see Zhao *et al.*, 1988; Zhang *et al.*, 2006; Greven *et al.*, 2007). In the male, the row begins laterally with a very short anterior, transverse part including only two teeth and extends in an oblique row directed posteriorly. Thus, replacements occur rather in lateral direction.

Also teeth of *P. shangchengensis* are remarkable. In the upper and lower jaw teeth have a distinct, but very compact annular suture between crown and pedicel. This suture is lingually broader than labially as known from teeth of the majority of Urodela. If present, this suture, called also dividing zone or zone of weakness, is less mineralized or in part unmineralized compared to the pedicel and crown (see Clemen *et al.*, 1980; Moury *et al.*, 1988; Greven *et al.*, 1989; Bolte *et al.*, 1996). When treated with enzymes or lye to remove soft tissue from dentigerous bones, the dividing zone of such teeth often show collagen fibres or especially in larvae breakthroughs to the pulp (e.g. Clemen & Greven, 1979). This was not the case in *P. shangchengensis* in most teeth of the upper and lower jaw indicating heavy secondary mineralization after establishing the weak zone in ontogeny (see Wistuba *et al.*, 2002).

Fig. 3 a–n: Dentition of the female. **a** Ajacent premaxillae, lingual view; vomer (v); choana (ch), vomerine teeth (vt), fissure between premaxilla and maxilla, 20 ×; **b** conical bicuspid, worn premaxillary tooth, labial view, 150 ×; **c** premaxillary teeth with asymmetrical crown and weak secondary cusps (asterisk), labial view, 150 ×; **d** ditto; note the labial small dividing zone (arrowhead), 200 ×; **e** bicuspid premaxillary tooth, 500 ×; **f** variously shaped maxillary teeth, labial view, 80 ×; **g** bicuspid maxillary teeth, 150 ×; **h** adjacent dentals are separated by a distinct gap, 20 ×; **i** posterior end of a dentary with small teeth; replacement tooth (asterisk), 60 × x; **j** vomerine *pars dentalis*, lingual view, 50 ×; **k** bicuspid dentary tooth, labial view, 150 ×; **l** the most posterior dentary tooth (see i), 400 ×; **m** dentary teeth, lingual view; the primary cusp is hidden by the secondary cusp, 130 ×; **n** bicuspid vomerine tooth, 200 ×.
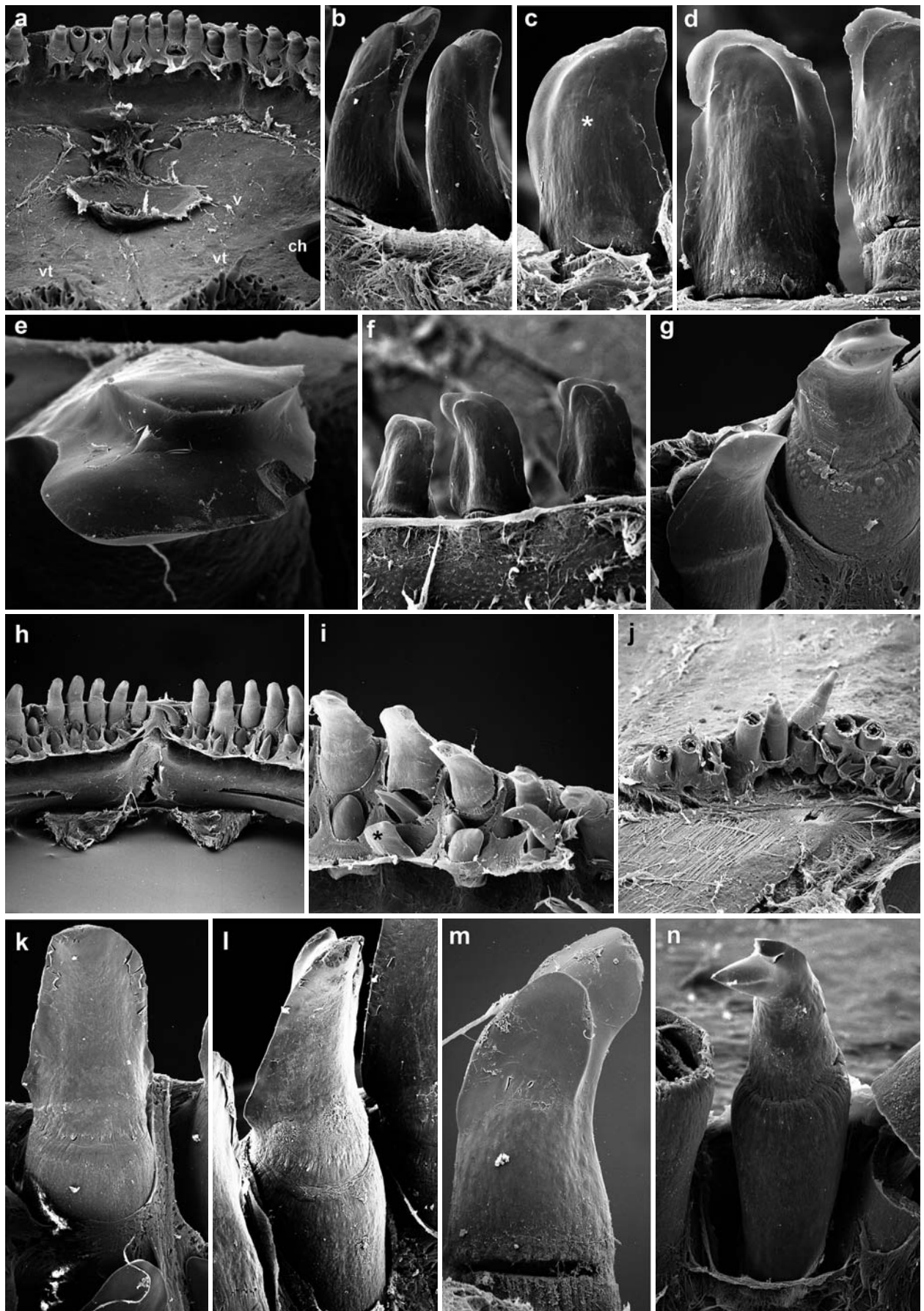
Unlike other hynobiid teeth (e.g. GREVEN & CLEMEN, 1985; VASSILIEVA & SMIRNOV, 2001; SMIRNOV & VASSILIEVA, 2002; GREVEN et al., 2007), the crown of teeth in the premaxillary-maxillary row of the male of *P. shangchengensis* resembles chisels and/or a spearheads. In the female there is the tendency of the teeth of the upper and lower jaw to become flattened, but in each case a minor and a major cusp is visible. Assuming largely compliant prey, chisel- or spearhead crowns that form a smooth not serrated blade may facilitate slicing of large victims rather than piercing it as slender and smooth-edged teeth do.

Development of secondary sexual characters in vertebrates including teeth is mediated by hormones and is either permanent or seasonal (e.g. EMERSON, 2000). The small number of animals examined and the missing information on the date of capture and how long the animals were kept in captivity do not allow a deep discussion about this matter. *P. shangchengensis* is an endemic salamander restricted to the Dabieshan area in Central China, which inhabits slow-flowing hill streams in subtropical and tropical moist lowland forests (ZHANG et al., 2006; see IUCN 2007). Size and length of the animals available for this study correspond to data given for adults (see ZHANG & HU, 1985; YE et al., 1993). However, the testes of the male did not contain mature spermatozoa (not pictured) and the female oviduct was in a quiescent state (see Figure 7 in GREVEN, 2002). This would argue for a permanent sexual dimorphism of teeth. Worth to be mentioned is the fact that teeth of the vomeres of both, females and males, are not modified, i.e. they resemble the most widespread bicuspid and conical "urodele tooth", indicating that this system is not affected by the mediating hormones.

To our knowledge currently sexual dental dimorphism is only known from a single urodele taxon. In male plethodontids the upper jaw protrudes beyond the lower jaw and enlarged modified, i. e. monocuspid teeth are visible, even when the mouth is closed (WAKE, 1966; WAKE et al., 1983; EHMCKE & CLEMEN, 2000; GREVEN et al., 2004). These teeth gash open the female's skin during courtship to transfer pheromones secreted by the chin gland into her blood stream (summarized in HOUCK & ARNOLD, 2003). Shape, number and size of these teeth obviously are correlated with changes in the testes and the breeding season being typically bicuspid outside the breeding season (*Desmognathus fuscus*: NOBLE & POPE, 1929; *Eurycea bislineata*: MCBRIDE-STEWART, 1958). Some, perhaps non-seasonal breeders may, however, constantly bear these monocuspids. Their androgen-dependent morphogenesis has been already demonstrated by NOBLE & POPE (1929) and expression of androgen receptors was demonstrated immunohistochemically in the mesenchymal cells adjacent to the dental lamina of the

premaxillae in male *Bolitoglossa schizodactyla*. Also in this species the vomerine tooth systems do not answer to the hormonal stimulus, i.e. teeth remain bicuspid and pedicellate throughout life (EHMCKE et al., 2003).

Acknowledgements

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