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# ANURAN DENTITION: DEVELOPMENT AND EVOLUTION

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Dentitional development was studied in 3 anuran species differing in their adult teeth morphology: in *Pipa carvalhoi* (Pipidae) and *Pyxicephalus adspersus* (Ranidae) which have non-pedicellate teeth and in *Pelobates fuscus* (Pelobatidae) displaying the occurrence of pedicellate teeth typical for anurans and all recent amphibians. It was revealed that generalized pattern of anuran dentitional ontogeny includes 2 main stages. Stage I is represented by the teeth of the first generation, which are non-pedicellate and calcify from the center of calcification appearing in the ventral portion of teeth and gradually spreading along the full dental length. Stage II is represented by the pedicellate teeth of the second and later generations which calcify separately in their ventral and dorsal portions. Usually a more or less pronounced noncalcified zone remains in these teeth to divide them into calcified crown and pedicel. However, this pedicellate structure of typical anuran teeth may be lost due two phenomena: 1) paedomorphosis may result in the loss of Stage II of dentitional development (pipids) and 2) acceleration of skull development accompanied by the hypercalcification may result in the complete calcification of teeth and in the elimination of a zone of division (*P. adspersus*). In both cases the non-pedicellate teeth appear although these non-pedicellate conditions are ontogenetically distinct.

**Key words:** Anurans, Teeth, Pedicely, Development.

## INTRODUCTION

A similar tooth morphology displayed by recent amphibians is considered to be the main evidence supporting the validity of the subclass Lissamphibia which includes anurans, salamanders, and apodans (Parsons and Williams, 1962; Bolt, 1977; Milner, 1988). Because of its importance in the discussions of phylogenetic affinities of modern amphibians and their relationships to fossil forms, dental morphology of recent amphibians has received considerable attention of numerous scientists (Beneski and Larsen, 1989; Clemen and Greven, 1977, 1980; Greven, 1984, 1989; Greven and Laumeier, 1987; Lawson, 1965; Oltmanns, 1952; Parsons and Williams, 1962; Shaw, 1985, 1989; Taylor, 1977; Wake, 1976; Wake and Wurst, 1979; etc.).

The typical amphibian tooth is composed principally of dentine, but the tip is overlain by a thin layer of enamel (Gillette, 1955; Kerr, 1960; Shaw, 1986).

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Each tooth consists of two very distinct parts, a crown and a pedicel (Fig. 1), which are separated by a ring of noncalcified dentine and/or connective tissue (i.e., dividing zone).

Such divided (pedicellate) dental morphology is characteristic for all adult apodans and salamanders with the exception of some caudate amphibians that do not complete metamorphosis (Greven, 1989). However, in contrast with apodans and caudates, anurans display the occurrence of great diversity in their adult dental morphology. First, a lot of anuran species lack any signs of dentition (e.g., bufonids, rhinophrynids, brachycephalids, rhinodermatids, most microhylids, some pipids, etc.). Second, a lot of anuran species belonging to different families display the occurrence of non-pedicellate teeth, i.e. teeth which are not divided into the crown and pedicel and lack any signs of the noncalcified dividing zone.

Teeth without such a division have been described in *Xenopus laevis* (Shaw, 1985; Greven and Laumeier, 1987), *X. tropicalis* (Parsons and Williams, 1962), *Pipa carvalhoi* (Trueb and Cannatella, 1986) among pipids, in *Pyxicephalus adspersus* among ranids (Parsons and Williams, 1962), in *Phyllobates bocagii*, *P. granuliventralis* (Parsons and Williams, 1962), *Dendrobates tricolor*, and *D. antho-*

*nyi* (Greven and Laumeier, 1987) among dendrobatids, in *Ceratophrys* species (Noble, 1931; Lehman, 1968; Schultze, 1970; Greven and Laumeier, 1987) among leptodactylids, and in *Hemiphractus proboscideus* (Shaw, 1989; Shaw and Ellis, 1989) and *Gastrotheca riobambae* (Greven and Laumeier, 1987) among hylids.

The diversity of the anuran dental morphology is so great that even within one anuran family one can find: a) completely edentate species, b) species having non-pedicellate teeth, and c) species with amphibian typical divided teeth. For example, among leptodactylids *Batrachophrynus*, *Lynchophrys*, *Sminthillus*, and some *Physalaemus* and *Telmatobius* species lack dentition (Duellman and Trueb, 1986), whereas *Ceratophrys* species have non-pedicellate teeth, and most representatives of this same family possess pedicellate teeth.

Apparently, the occurrence of great diversity of anuran dentition is difficult to explain on the functional grounds as many anuran closely-related species with similar mode of life and similar diet show quietly different dental morphology. Thus, upper-jaw dentition is present in *Pipa carvalhoi* but is absent in *P. parva* (Trueb and Cannatella, 1986). Similarly, among myobatrachids *Uperoleia marmorata* has teeth, whereas *U. rugusa* is edentate (Davies, 1989). Among ranids *Cacosternum capensi* displays the occurrence of dentition, whereas *C. namaquense* is deprived of it (de Villiers, 1931).

However, there is some evidence indicating the dentitional ontogeny to account for the great diversification of the anuran teeth morphology. In contrast with apodans and caudates, teeth appear lately in the anuran ontogeny and, consequently, they may be greatly affected by paedomorphosis which is a common event among anurans (Smirnov, 1994a). Moreover, teeth of the first generation were shown to be non-pedicellate in some anuran species (Tesche and Greven, 1989). The latter circumstances permitted Greven (1989) to propose that non-pedicellate dental structure in *Xenopus* results from the paedomorphic underdevelopment. Though the hypothesis about the leading role of dentitional ontogeny in the providing dentitional diversity seems to be rather prospective, it needs data on the teeth development. However, anuran teeth ontogeny appears to be surprisingly poorly studied. Especially little is known about the process of tooth calcification, i.e., the process which is directly connected with the development of the pedicellate tooth structure.

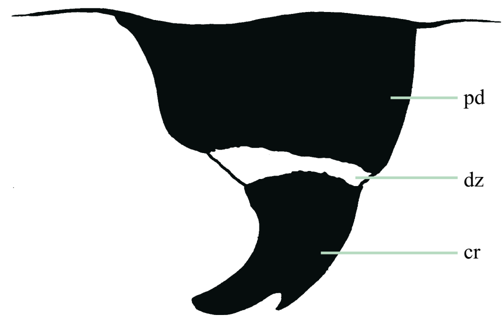


**Fig. 1.** Pedicellate anuran tooth. cr) Crown, dz) dividing zone, pd) pedicel. Calcified regions are solid black.

This predicts the aims of the present paper which are twofold: firstly, to study the anuran dentitional ontogeny (with special emphasis on the process of tooth calcification); and, secondly, to analyze the possible role of ontogeny in the providing diversity in the anuran dental morphology.

## MATERIAL AND METHODS

Development of dentition was studied in tadpoles of different Gosner stages (Gosner, 1960) and in postmetamorphic animals ranging from newly metamorphosed to adult sexually matured frogs. Specimens of 3 anuran species differing in their adult teeth morphology were used in this study: *Pyxicephalus adspersus* (Ranidae) and *Pipa carvalhoi* (Pipidae) which have non-pedicellate teeth and *Pelobates fuscus* (Pelobatidae) displaying the occurrence of divided (pedicellate) teeth. Additional information was obtained from examination of size(age)-differing specimens of *Xenopus laevis* (Pipidae). All individuals of these species were laboratory-reared either in our laboratory (*Pipa carvalhoi*, *Pelobates fuscus*, and *Xenopus laevis*) or in the Moscow Zoo (*Pyxicephalus adspersus*). Specimens used in the present study are listed in Tables 1 and 2.

These specimens were cleaned in KOH solution and stained with Alizarin-red S as whole mounts. Alizarin staining of whole mounts was found to suit the purpose of the present study as in such preparations viewed under a binocular dissecting microscope, all stages of development of individual teeth can be easily determined. Moreover, large numbers of teeth can be examined without sectioning and the calcification pattern of a whole tooth can be seen in one field.

Additional observations were made on two postmetamorphic specimens of *P. adspersus* prepared for

SEM study. Right maxillae were chemically cleaned of soft tissue in 5% KOH, rinsed in water, dehydrated in a graded ethanolic series, air dried, mounted on metal stubs, coated with gold and viewed with scanning electron microscope of the TGbingen University (Germany).

In addition, tooth morphology and dental development were examined in adult specimens of *Alytes obstetricans*, *Discoglossus pictus*, *D. galganoi*, *Bombina orientalis*, *B. bombina*, *B. variegata* (Discoglossidae), *Pelobates syriacus*, *Scaphiopus bombifrons*, *S. hurteri*, and *Leptobrachium hasselti* (Pelobatidae), *Pelodytes caucasicus* (Pelodytidae), *Hyla arborea* (Hylidae), *Colostethus trinitatus* (Dendrobatidae), *Crinia signifera* (Myobatrachidae), *Pseudopaludicola pusilla* (Leptodactylidae), *Rhacophorus leucomystax* (Rhacophoridae), and *Rana ricketti* and *Conraua crassipes* (Ranidae).

## RESULTS

The most detailed information on the teeth development was provided by the series of *Pyxicephalus adspersus* specimens. That is why this species was selected as a basis for description of the dentitional ontogeny.

In *P. adspersus*, the first indications of dentition were found in tadpoles of Stage 42. The dental lamina of the upper jaw shows several cone-shaped tooth-anlage: seven tooth germs related with the maxillae and three related with the premaxillae. All of them are not ankylosed to the respective bones and are calcified only slightly — only the distal portion of one third of the full length of the tooth anlagen. The maxillary tooth germs vary in their length, the three middle ones being larger if compared with the first anterior germ and the three posterior tooth anlagen (Fig. 2*a*). These larger dental units display the more advanced calcification then their smaller neighbors: half of their full length is calcified whereas in other maxillary tooth germs the calcification is spread along only 1/3 of their length (the caudalmost dental unit lacks any signs of calcification).

Tadpoles of Stage 43 display the occurrence of eight maxillary dental units. In some larvae, all of them are partly calcified, whereas in other specimens of this same stage of development the two caudalmost tooth germs do not show any indications of calcification. As a whole, if compared with tadpoles of Stage 42, dental units of larvae of Stage 43 are more calcified and in the largest tooth germs the calcification spreads along the 2/3 of their full length. How-

**TABLE 1.** Developmental Larval Series Examined

| Species | Stage | TL | SVL |
|---|---|---|---|
| *Pyxicephalus adspersus* | 40 | 49 | 21 |
| | 42 | 57 | 22 |
| | 42 | 55 | 21.5 |
| | 43 | 46.5 | 20.5 |
| | 43 | 42 | 20 |
| | 43 | 43 | 20.5 |
| | 44 | 33 | 20 |
| | 44 | 28 | 22 |
| | 44 | 27 | 22 |
| | 44 | 24 | 20 |
| | 45 | 18 | 17 |
| | 45 | 18 | 19 |
| | 45 | 21.5 | 20 |
| | 45 | 24 | 23.5 |
| *Pelobates fuscus* | 44 | 35 | 24 |
| | 44 | 30 | 24 |
| | 44 | 29 | 26 |
| | 45 | 25 | 24 |
| | 45 | 26 | 25 |
| *Pipa carvalhoi* | 44 | 20 | 11 |
| | 45 | 12 | 10.5 |

**Note.** Stage) Gosner (1960) stage; TL) total length (including tail); SVL) snout-vent length, mm.

**TABLE 2.** Developmental Postmetamorphic Series Examined

| Species | SVL | Species | SVL | Age |
|---|---|---|---|---|
| *Pyxicephalus adspersus* | 17 | *Pelobates fuscus* | 21 | 2 days |
| | 24 | | 22 | 2 days |
| | 25 | | 24 | 2 days |
| | 27 | | 20 | 4 days |
| | 29 | | 21.5 | 4 days |
| | 70 | | 21.5 | 4 days |
| | 90 | | 24 | 4 days |
| | 100 | | 30 | 1 month |
| | | | 32 | 2 months |
| | | | 43 | |
| | | | 56 | |
| *Xenopus laevis* | 16 | *Pipa carvalhoi* | 12 | 1 day |
| | 20 | | 14 | 7 days |
| | 28 | | 16 | 10 days |
| | 34 | | 20 | |
| | 54 | | 50 | |
| | 70 | | | |

ever, all dental units are still not ankylosed to the bone. Some tadpoles of Stage 43 display the appearance of very small tooth germs situated in the dental lamina between the largest maxillary dental units (Fig. 2*b*): these newly appeared germs lack any signs of calcification and lie somewhat medially respectively to the older dental units.

All tadpoles of Stage 44 examined in the current study possess two groups of teeth consisting of: a) large dental units with pronounced calcification of their ventral portion and b) small dental germs without calcification situated between these larger partly calcified teeth. The degree of calcification in the large teeth of the first group varies in different tadpoles: calcification is spread along 2/3 of the dental length in specimens with only slightly shortened tails and spreads along almost the full dental length in specimens retaining small rudimentary tails. However, even in these most advanced (within the Stage 44) tadpoles teeth are not ankylosed to the maxillary bone and their most dorsal portion remains noncalcified. Nevertheless, in one specimen, among the group of large teeth displaying different degrees of calcification one tooth was found to be calcified completely and to be ankylosed to the maxillae. In this same specimen, teeth of Group II display more advanced state of their ontogeny: their ventral halves are calcified and some of them show the appearance of a new center of calcification on the labial surface of their dorsal portion.

Specimens of Stage 45 show the more advanced stages of dentitional development. In one specimen (SVL = 18 mm), all large teeth but for the most caudal one are completely calcified and ankylosed, whereas small dental units (Group II) situated between them display the occurrence of calcified tips (Fig. 2*c*). In an other specimen (SVL = 21.5 mm), all teeth of Group I are completely calcified and ankylosed, whereas teeth of Group II are greatly enlarged in their size (if compared with previous specimen) and the three anterior ones are now larger than the neighboring teeth of Group I. All teeth of Group II display the occurrence of the calcified ventral portion, whereas two dental units among the highest teeth show the appearance of an additional separate center of calcification on the labial surface of the dorsal dental portion (Fig. 2*d* ). In the third specimen (SVL = 24 mm), dentition includes completely calcified and ankylosed teeth of Group I and situated between them are teeth of Group II. Five anterior teeth of Group II are higher than the neighboring teeth of Group I and display different degrees of calcification: in one tooth only ventral half is calcified, in two other teeth besides the calcified ventral portion a separate center of calcification is present on the labial surface of their dorsal portion, and in the remaining two other teeth both ventral and dorsal portions are calcified and only a narrow noncalcified ring-zone separates them (Fig. 2*e*). These two teeth are ankylosed to the maxilla. The caudalmost teeth of Group II are small and have only the ventral portion calcified. In the fourth specimen of Stage 45 examined in the present study (SVL = 18 mm), all teeth of Group I are completely calcified and some of them display the beginning of the process of resorption: at the base of the lingual side of these teeth there appears a cavity (lacuna) partially filled by a small dental germ of a new generation. Among teeth of Group II, only two large and two small teeth retain the divided (into calcified ventral and partly calcified dorsal portions) state, whereas other teeth of this Group are com-

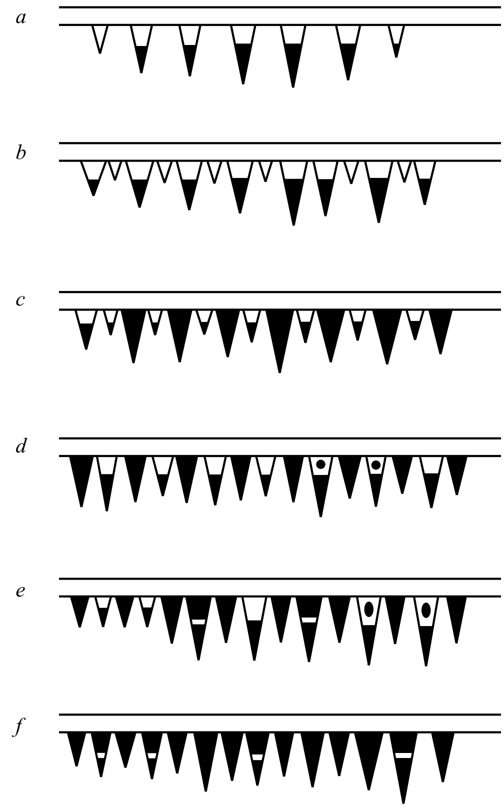


**Fig. 2.** Dentitional morphology in *Pyxicephalus adspersus* tadpoles (labial aspect). *a*) Gosner Stage 42; *b*) Stage 43 – 44; *c* – *f*) Stage 45.

pletely calcified and any indications of their previously divided state are not retained (Fig. 2*f*).

Newly metamorphosed froglets also display a similar state of dentition which may be briefly described as follows: teeth of Group I are completely calcified and ankylosed and teeth of Group II vary from being represented by dental units calcified only in their ventral half to ankylosed teeth fully calcified with intermediate state when both ventral and dorsal dental portions are calcified but are divided by a noncalcified ring-zone.

The next stage of dentitional development is displayed by recently metamorphosed specimens in which the resorption of the teeth of Group I (its beginning was observed in tadpoles of Stage 45) results in the loss of these teeth. This process is accompanied by the appearance of empty sockets in the dental surface of the maxillary in the places where lost teeth were previously ankylosed. Sometimes remnants of the labial wall of the lost teeth are visible near such sockets. At these same sites new dental germs (Group III), represented by unankylosed cones with ventral calcified portion appear. The loss of the teeth belonging to Group I is a gradual process and the number of lost teeth depends upon the age (size) of the postmetamorphiic animals: in a specimen with SVL = 17 mm, only one tooth of Group I was lost, four teeth were lost by a froglet with SVL = 24 mm, and all teeth of Group I but one were lost in an animal with SVL = 29 mm. Consequently, as a loss of the teeth of Group I and their replacement with the teeth of Group III proceed gradually, these new teeth are represented by dental units displaying different stages of their ontogeny: some of them are merely small cones a with calcified ventral portion, others are high (longer than neighboring functional teeth of Group II) teeth calcified only ventrally, and the third type are high teeth with calcified ventral and dorsal portions separated by more or less narrow non-calcified ring-zone. A combination of several processes (a resorption and loss of the teeth of Group I, a continuation of development of the teeth belonging to Group II, and the appearance of the teeth of Group III) results in the complicated pattern of dentition which includes teeth of different generations differing in the degree of their ontogeny.

Examination of tooth morphology in adult individuals of *P. adspersus* of different size (age) revealed that their dentition includes: a) ankylosed teeth which are completely calcified and in which no zone of division separating dorsal and ventral portions is visible, b) ankylosed and completely calcified teeth with a slightly distinguishable zone of division, c) ankylosed teeth, evidently divided into dorsal and ventral portions by a noncalcified zone, d) unankylosed teeth with a completely calcified ventral portion and with a more or less calcified labial wall of the dorsal portion, e) unankylosed teeth in which only the ventral portion is calcified, and f) dental germs (with a calcified or noncalcified ventral portion) situated in the resorption lacuna in the lingual wall of completely calcified functional teeth.

All these states were observed in metamorphosing tadpoles and young postmetamorphic individuals as stages of development of teeth belonging to Group II. These circumstances suggest that in *P. adspersus*, teeth of the second and later generations have a similar ontogenetic trajectory which includes the following stages: I) small dental completely noncalcified germs, II) small dental germs with calcified ventral portion, III) high dental units with calcified ventral portion, IV) teeth with calcified ventral portion and additional calcification on the labial wall of the dorsal portion, V) ankylosed teeth with calcified ventral and dorsal portions separated by a more or less pronounced noncalcified ring-zone, VI) ankylosed completely calcified teeth without a zone of division into ventral and dorsal portions.

## DISCUSSION

By examining the dentition of differently aged individuals ontogenetic trajectories can be constructed (Fig. 3). Comparison of dental development in *P. adspersus* reveals that the process of calcification differs in teeth belonging to different generations. In dental units of the first generation (our Group I) calcification which firstly appeared in the ventral portion of the teeth, spreads upper-word along the full dental length. In teeth of the second and later generations, calcification results from the fusing of independently calcified ventral and dorsal portions. In both cases fully developed teeth are non-pedicellate though these non-pedicellate conditions are ontogenetically distinct. Morphologically, completely developed teeth of the first and of the second generations are absolutely indistinguishable as may be seen from Fig. 4. Also, teeth of the first and of the second (and later) generations differ in the timing of their ankylosis: teeth of the first generation become ankylosed only after their calcification is completed, whereas in later dental generations ankylosis precedes the complete calcification which continues in already ankylosed teeth.

For comparison, we studied dentitional development in *Pelobates fuscus* (Pelobatidae) which displays the typical anuran pedicellate state of teeth and in *Pipa carvalhoi* (Pipidae) which shows the occurrence of non-pedicellate teeth morphology.

In these species, dentitional development is retarded if compared with *P. adspersus*: for example, tadpoles of Stages 44 – 45 display the occurrence of teeth which are calcified only ventrally; the complete teeth calcification is firstly recorded only in the postmetamorphic animals (in 2 – 4 days after metamorphosis is completed in *P. fuscus* and 10 days in *P. carvalhoi*). Nevertheless, the first stages of dentitional development are similar to those described for *P. adspersus*. Teeth of the first generation are non-pedicellate and their calcification firstly appears in the ventral portion of the teeth and gradually spreads along the full dental length.

However, teeth of the second (and later) generation differ: they are pedicellate in *P. fuscus* but non-pedicellate in *P. carvalhoi*. Moreover, the process of their calcification greatly differs in these two species. In *P. carvalhoi* teeth of the second (and later generations) always calcify as a result of continuation of calcification which firstly appears in their ventral portion (similar pattern of dental calcification was also observed in age-differing postmetamorphic specimens of *Xenopus laevis*, an other pipid species examined in the present study). In *P. fuscus* the second generation of teeth calcify in a different manner: firstly calcification appears in the ventral portion of teeth and a lately independent center of calcification appears on the labial surface of their dorsal portion. This second calcification gradually spreads along the dorsal portion of teeth resulting in the formation of a calcified dental pedestal, separated from the calcified dental crown by a more or less pronounced zone of division. A similar mode of dental development was previously described in the adult ranid *Rana pipiens* (Gillette, 1955), the hylid *Hyla cinerea* (Goin and Hester, 1961) and was observed also in adult specimens of *Discoglossus pictus*, *Alytes obstetricans*, *Bombina bombina*, *B. variegata*, *B. orientalis* (Discoglossidae), *Pelobates syriacus*, *Leptobrachium hasselti*, *Scaphiopus bombifrons*, *S. hurteri* (Pelobatidae), *Pelodytes caucasicus* (Pelodytidae), *Rhacophorus leucomystax* (Rhacophoridae), and *Rana ricketti* and *Conraua crassipes* (Ranidae) examined in the present study.

On the other hand, Tesche and Greven (1989) have found that in *Discoglossus pictus* and *Bombina orientalis* (Discoglossidae) as well as in *Rana temporaria* and *R. cyanophlyctis* (Ranidae) teeth of the first generation are non-pedicellate, whereas juveniles and adults of these species have pedicellate teeth. The process of their calcification was not studied. However, given the results obtained in the present study, it seems reasonable to suggest that in these anuran species teeth of the first generation also calcify from a single center of calcification appearing in the ventral portion of dental units.

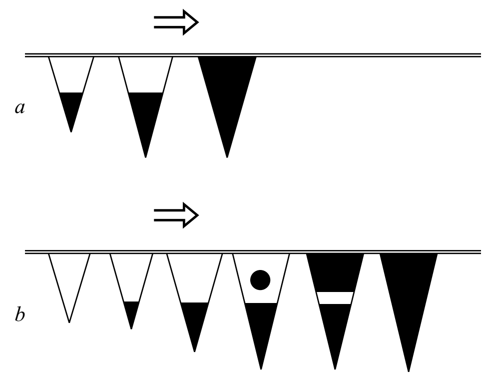


**Fig. 3.** Dentitional ontogeny in *Pyxicephalus adspersus* (labial aspect). *a*) Tooth of the first generation (Stage I), *b*) tooth of the second and later generations (Stage II).

Moreover, in a newly metamorphosed specimen of *Conraua crassipes* examined in the present study, among teeth of the first generation calcified only ventrally we observed several teeth which were almost completely calcified and only a narrow dorsal dental rim separating them from the maxilla remained noncalcified. Such dental state indicates the teeth of the first generation of *C. crassipes* to calcify from the single center of calcification.

The sum of these data when combined with data on dentitional development in *Pyxicephalus adspersus* and *Pelobates fuscus* indicates typical anuran dentitional development to include two main stages. Stage I is represented by the teeth of the first generation, which are non-pedicellate and calcify from the center of calcification appearing in the ventral portion of teeth and gradually spreading along the full dental length. Consequently, Stage II is represented by the teeth of the second and later generations which calcify separately in their ventral and dorsal portions. Usually a more or less pronounced noncalcified zone remains in these teeth to divide them into calcified crown and pedestal.

Arising from these observations, there appear to be two questions: 1) why do *Xenopus laevis* and *Pipa carvalhoi* lack Stage II of anuran dentitional develop-

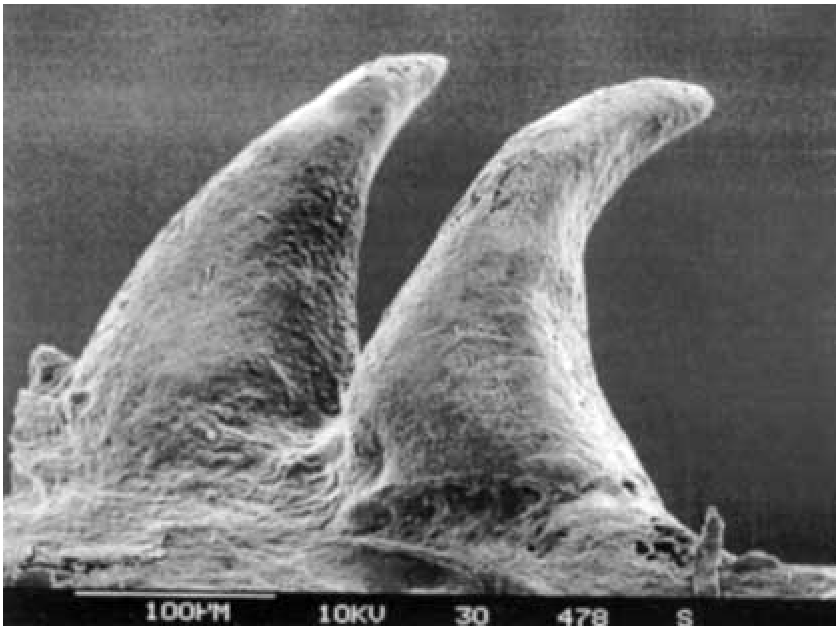


**Fig. 4.** SEM photograph of the maxillae teeth of the newly metamorphosed *Pyxicephalus adspersus* (labial aspect). Left) Tooth of the first teeth generation, right) tooth of the second teeth generation.

ment and 2) why does *Pyxicephalus adspersus* lack the zone of division in the teeth of the second and later generations characteristic of anuran typical dental morphology?

To answer the first question, one must take into consideration that pipids are paedomorphic frogs in which a lot of typical anuran features appearing late in anuran ontogeny are lost or severely underdeveloped (Smirnov, 1994b). Given the overall paedomorphic trend in pipids, it seems reasonable to propose that later stages of dentitional development (Stage II) during which the pedicellate teeth appear, were omitted in pipid ontogeny. Similar phenomenon seems to occur in the neotenic caudate *Siren lacertina* in which the severe paedomorphic underdevelopment caused the loss of adult pedicellate teeth and the retention as definitive ones larval non-pedicellate teeth (Greven, 1989). If this is the case in pipids, then one might expect that more pronounced overall paedomorphic underdevelopment is accompanied by more pronounced dental underdevelopment. It seems to be the case. If compared with *Xenopus* species, most of recent pipids display a greater degree of paedomorphic underdevelopment (for example, they lack the quadrato-jugals, palatines, and vomers which being the late-appearing bones are usually lost in paedomorphic anurans, whereas *Xenopus* retains the vomers and sometimes — the palatines (Smirnov, 1994b). Simultaneously, most of them lack any signs of dentition.

Concerning the second question (why does *Pyxicephalus adspersus* lack the zone of division which is characteristic of typical anuran (and recent amphibian) teeth), it seems reasonable to propose that the loss of this zone of division is caused by the accelerated rate of calcification displayed by frogs of this species. If compared with the most of other anuran species for which the rate of dermal skull development is known, *P. adspersus* displays a very rapid rate of dermocraniogenesis: all cranial dermal bones appear prior to the end of metamorphosis and such features of adult anuran skull as the absence of the frontoparietal fontanelle and the appearance of a contact between the anterior process of the squamosal and the maxillae are recorded in tadpoles of Stages 44 – 45. Consequently, whereas usually early postmetamorphic anurans possess skulls which are greatly underdeveloped if compared with their adult cranial state, newly metamorphosed individuals of *P. adspersus* show the occurrence of a dermal skull similar to that of adult frogs (the only obvious difference is the absence of dermal sculpturing which appears later). Surely, the accelerated rate of dermal skull development is accompanied by an accelerated rate of calcification. Consequently, the latter permits the teeth of *P. adspersus* to calcify in a greater degree than usual for most anurans and the zone of division between the ventral (crown) and dorsal (pedicel) dental portions becomes eliminated before the progressing process of tooth resorption stops the process of calcification.

Based on these results, it seems reasonable to propose that two phenomena account for the providing dental diversity in anurans. Namely, paedomorphosis results in the dentitional underdevelopment whereas secondary acceleration of skull development results in the dentitional hypermorphosis. To testify this assumption, one must analyze the anuran dental morphology in terms of paedomorphosis and acceleration of skull ontogeny.

If the supposition that acceleration of skull ontogeny may lead to the loss of pedicel is correct, then one might expect the presence of non-pedicellate teeth in those anuran species which display an accelerated rate of dermal skull development. Earlier it was shown that anuran species with pronounced dermal cranial sculpturing usually show the accelerated rate of cranial development if compared with anuran species lacking this dermal ornament (Smirnov, 1995). Consequently, it is among anuran species with developed dermal cranial sculpturing that one may expect the occurrence of secondarily non-pedicellate adult teeth. Indeed, most of the species in which the presence of non-pedicellate teeth was recorded display the occurrence of greatly developed dermal cranial ornament, e.g., *Ceratophrys* species (Noble, 1931; Lehman, 1968; Schultze, 1970; Greven and Laumeier, 1987) among leptodactylids and *Hemiphractus proboscideus* (Shaw, 1989) and *Gastrotheca riobambae* (Greven and Laumeier, 1987) among hylids [these two species belong to the group of the casque-headed hylids which are characterized by the presence of strong cranial ornament (Trueb, 1970)]. Consequently, based on these data, it may be concluded that the acceleration of dermal cranial development leads to the elimination of the dental zone of division and to the appearance of the non-pedicellate tooth state.

Similarly, if paedomorphosis affects the anuran dental morphology, then one might expect the common occurrence of underdeveloped dentition in those species which were shown to be paedomorphic. It seems to be the case. The complete absence of any dentition is a characteristic feature for many paedomorphic species [for example, *Cacosternum namaquense* among ranids (de Villiers, 1931); *Notaden*, *Myobatrachus*, *Pseudophryne*, and some *Uperoleia* species among myobatrachids (Davies, 1989)]. The paedomorphic loss of dentition explains the wide distribution of edentate state in small-sized anuran species. Usually small body size indicates the paedomorphic (progenetic) origin of anuran species (Trueb and Alberch, 1985). And it is among these small frogs that a large number of edentate species is recorded [for example, *Brachycephalus* and *Psyllophryne* among brachycephalids, *Sminthillus* and some *Physalaemus* species among leptodactylids, *Rhinoderma* among rhinodermatids, etc. (Duellmann and Trueb, 1986)]. Given these facts, it is not surprising that among anurans with non-pedicellate teeth there is a lot of small-sized species: *Phyllobates bocagii* and *P. granuliventralis* (Parsons and Williams, 1962), *Dendrobates tricolor* and *D. anthonyi* (Greven and Laumeier, 1987) as well as *Colostethus trinitatus* (Dendrobatidae), *Crinia signifera* (Myobatrachidae), and *Pseudopaludicola pusilla* (Leptodactylidae) examined in the present study. Obviously, the non-pedicellate state of teeth in these small-sized anuran species was generated through underdevelopment. Only Stage I of the typical anuran dentitional ontogeny was realized whereas Stage II was omitted because of the paedomorphic nature of these anurans.

Based on the facts presented in the current study, it may be concluded that the great diversity of the anuran dentition is provided mainly by two phenomena: paedomorphosis and acceleration of dermal cranial development. Paedomorphosis may result in the complete loss of any dentition or in the dental hypomorphosis, whereas acceleration of dermal cranial development may lead to the dental hypermorphosis. Surprisingly, both hypomorphozed and hypermorphozed dental states have a similar — non-pedicellate — morphology, though this non-pedicellate morphology is ontogenetically distinct.

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