Papéis Avulsos de Zoologia

PAPÉIS AVULSOS ZOOL., S. PAULO, 32 (1): 1-13 20.IV.1978

COMMENTS ON THE ONTOGENY OF *TYPHLONECTES OBESUS*, PARTICULARLY ITS DENTITION AND FEEDING

MARVALEE H. WAKE

A number of species of caecilians (Amphibia: Gymnophiona) are known from few specimens. One such species is *Typhlonectes obesus*, a member of the aquatic South American family Typhlonectidae. The species was described from a single specimen (Taylor, 1968) and two other specimens were tentatively referred to the species. Three more specimens were recognized by Taylor (1973) in the collections of the California Academy of Science, and data on these and the type specimen were presented. Another group of specimens, a female with several oviducal fetuses, is located in the Museum of Comparative Zoology collection, and the female was identified as *T. obesus* by Taylor but has not yet been mentioned in the literature.

A sample of ten specimens of *Typhloenctes obesus* collected by W. Ronald Heyer of the United States National Museum and P. E. Vanzolini of the Museu de Zoologia, São Paulo, on 8-9 January, 1975, on the Rio Ipixuna, Tapauá, Amazonas, Brasil, is of particular interest. It not only extends our knowledge of the species, but it provides new information on caecilian ontogeny and especially on dentitional morphology and feeding habits. The specimens are juveniles, some at approximately birth size. I have been fortunate to be able to compare these specimens with the MCZ adult and fetuses and the California Academy of Science material, so that oviducal fetuses, recently born juveniles, and adults were available for study. Information on osteological and gonad development, meristic characters, and fetal and adult tooth development and morphology is presented here. Stomach contents were analyzed in order to provide more information for interpretation of certain of the unique dentitional features of *T. obesus*.

MATERIALS AND METHODS

Eleven juveniles, three adults, and five fetuses of the species were examined. Table 1 includes meristic data on external characters, including tooth counts, and the sex of the specimens. Data included in the table on the type specimen (AMNH 71434), two Taylor specimens (EHT-HMS 1729, 1731), and on three specimens located at

---

Department of Zoology and Museum of Vertebrate Zoology, University of California, Berkeley, CA 94720.

the California Academy of Science (CAS 12541-3) are from Taylor (1968, 1973). Tooth data for CAS 12543 were apparently not recorded by Taylor because the specimen is apparently a newborn and has the full complement of numerous *fetal* teeth (pers. obs.). Of the USNM series, five specimens (USNM 201692-6) are housed at the United States National Museum, and five with Dr. P. E. Vanzolini at the Museu de Zoologia da Universidade de São Paulo, São Paulo, Brasil (MZUSP numbers 49892-6). One juvenile (USNM 201696) and one fetus (MCZ 89471) were cleared and stained according to standard procedures so that information on ossification state and tooth development patterns could be obtained. Stomachs, intestines, and rectums were incised: contents were gathered in vials of 70% ethanol and examined microscopically. Glycerine mounts of tooth crowns of *T. obesus* and *T. compressicauda* were prepared and examined.

TYPHLONECTID TOOTH MORPHOLOGY

The family Typhlonectidae, including *T. obesus*, is aquatic, inhabiting pools and slow-moving streams and rivers throughout north and central South America east of the Andes. Several morphological adaptations to the aquatic habitat distinguish members of the family. These adaptations include the development of both lungs, rather than the left one only as in terrestrial caecilians, muscular valves that close nostrils and internal nares in these air-breathing forms, and a complex arrangement of the muscles of the vent so that males can 'clasp' females during copulation in mid-water. So far as is known, all species in the family are viviparous. The fetuses of various species in the family have the pre-birth dentition characteristic of viviparous caecilins. There is considerable variation in crown morphology among species.

The distinctive fetal and adult tooth shapes and functions in the gymnophione amphibians have received considerable recent attention (Parker, 1956; Parker and Dunn, 1964; Wake, 1976, 1977a, 1977b). It has been thought that there was species-specific variation in tooth morphology among fetuses, but that tooth crown structure was basically the same in adults of all species, including oviparous forms. The adult crown has been described as a bicuspid, conical, more or less recurved structure typical of most amphibians by several workers (Lawson, 1965a, 1965b; Parker, 1956; Parker and Dunn, 1964; Taylor, 1968; and Wake, 1976). Adult teeth are arrayed on one or two rows on upper and lower jaws, and the pattern of replacement is that typical of amphibians generally (Lawson, 1965a, 1965b; Wake, 1976). Fetal teeth, however, have very distinctive crown shapes, ranging from spoon-shaped with a single apical spike to pegs surmounted by an array of spicules. Fetal teeth occur in multiple rows on each jaw in various arrangements (Wake, 1976).

Interest in the teeth of *T. obesus* was aroused upon examination of the series of juveniles. Their teeth are relatively numerous, and their tooth crowns are broadly spatulate, rather than the conical structures of juvenile and adult specimens of other species in the genus that I have examined. The question arose as to whether that shape was a juvenile condition, or one analogous to the fetal state, or one characteristic of adults of the species.

Examination of the cleared and stained fetus (115 mm total length) revealed that the pattern of dentition was that characteristic of typhlonectid fetuses (fig. 1). The teeth were arranged in some nine rows on the lower jaws, with reduced numbers of rows posteriorly on each ramus. Tooth pedicels were fused, so that the teeth formed a patch with a broadly mineralized base arcing well above the mineralized bones of the lower jaw. Tooth crowns were expanded somewhat distally, and the distal margin was slightly crenulated. In contrast to the condition seen in advanced fetuses of other typhlonectid species (fig. 2), only the expanded portion of the crown was mineralized. The neck of the crown did not stain with alizarin, nor did the distal part of the pedicel. Only the fused base of the pedicel was mineralized. In further contrast to fetuses of other species, three to four rows of elongate, pedicellate teeth were borne on the maxillary-premaxillary margins. These teeth were twice as long as the teeth of the lower jaw, were not arranged as fused patches, and had crowns of different shape than those of the lower jaw. The crowns were only slightly if at all dilated distally, and the tip and part of the neck were mineralized. No distal crenulations were observed. Regions of the crown and the pedicel at the joint were not mineralized. Only in fetuses of *T. obesus* have I observed erupted teeth in the upper jaws, though well developed tooth buds are present in the maxillary-premaxilary dental lamina of a number of species (Wake, 1976). No teeth were present on vomers or palatines.

The teeth of the juveniles occur in a basically adult type of arrangement. The upper jaws have a single row of teeth on the maxilary--premaxillary margins and a single row in a vomero-palatine arc. The lower jaws have a single labial row of teeth and bear one to ten 'splenial' teeth in a lingual row medially on the jaws. Table 1 gives the number of teeth found in these rows; figure 3 shows the correlation of tooth numbers in these rows with size of the specimens as indicated by measurement of total length. Tooth number increases in splenial, maxilary-premaxillary, and vomero-palatine rows with increased size, and presumably age, in this species. That phenomenon is typical of most amphibians, with the rate of growth and of tooth addition diminishing with age. However, the phenomenon seems not to occur in the labial tooth row of the lower jaw of *T. obesus.* Figure 3 indicates that tooth number increases rapidly with growth up to approximately 200 mm; the number of teeth in the row is then constant above that size. Animals from 193 mm to 438 mm have 36-37 teeth in the labial dentary row. The sample size is very small, but the contrast is obvious.

In juvenile *obesus*, both crown and pedicel are well mineralized. The joint is not fused and is bound by the typical ligaments. Crowns are flattened, rather than conical, and spatulate with a slight lingual depression (figs. 4a and b, 5). The crowns are slightly recurved, and are bicuspid with both cusps dilated and the labial cusp forming the crest of the tooth. The distal margins or crest is a smooth to slightly ragged curve, but is not marked by regular denticulations as is a fetal tooth. The neck of the crown narrows, but expands slightly at the joint with the pedicel. Crowns of teeth of the lower jaw are slightly shorter and more dilated than are those of teeth of the upper jaw (figs. 4a vs. 4b). Necks of lower jaw teeth are not as constricted and their pedicels are much stouter. A medial dentary tooth is 0.4 mm long (crown plus pedicel), 0.25 mm wide at its base, and has a pedicel 0.24 mm in diameter. A medial maxillary tooth is 0.6 mm long, 0.2 mm at greatest width, and has a pedicel 0.14 mm in diameter. Measurements were made on the largest teeth observed in the cleared and stained specimen.

The pattern of tooth replacement is the modified alternate type found in most caecilians (Lawson, 1965b, Wake, 1976). Virtually every tooth family contains a functional tooth; evacuated loci and new ones occur posteriorly in the tooth rows. This provides a complete, uninterrupted tooth series as an armature through most of the arc of the tooth row.

The teeth of the marginal row of the upper jaw are oriented horizontally, so that they form a line parallel to the floor of the mouth. I do not consider this to be a preservation artifact. The teeth of the lower jaw are oriented vertically on the jaw in a manner capable of incising. The functional properties of these teeth are discussed below.

The jaw of the adult MCZ specimen had been damaged and many tooth crowns were lost, so counts and certain comparisons could not be made, but the CAS material was so utilized. Adult tooth crowns are of similar shape, but of larger size, than those of the juveniles. In contrast to the juvenile tooth described above, a crown from the MCZ female adult *obesus* is 0.58 mm long, and 0.35 mm wide at its base; the dilated distal part of the crown is 0.23 mm wide (fig. 5). The tooth of an adult female *T. compressicauda* which was excised for comparison is 0.82 mm long (crown plus pedicel), the pedicel is 0.37 mm wide at its base, and the crown is 0.45 mm long. The crown is 0.28 mm in diameter at its joint with the pedicel and tapers to a point that is less than 0.03 mm in width (fig. 6). Adults of *T. obesus* appear to have teeth that are arranged on the jaw in a 'typical' adult pattern, but to have teeth whose crown morphology is distinctive and unlike that of adults of other species of caecilians, including presumably closely related species.

STOMACH CONTENTS

The stomach of the adult female specimen was dilated but empty. It had been opened previously, so it is possible that contents were removed. Of the five juveniles, three had well digested material in the intestine. Unidentifiable organic material, as well as bits of rock and of wood, were found in the lower intestine. Two juveniles had identifiable material in the stomach. Each had ingested a single insect pupa which was only slightly digested. The pupae are likely coleopteran (fide Roy L. Caldwell). The significance of these contents in terms of feeding and dentitional morphology is considered in the discussion.

GONAD DEVELOPMENT

The gonads of the fetuses could not be distinguished as ovaries or testes. Of the juveniles, gonads were small and not yet functional except in the largest specimen of the sample, a recently matured male. Eight of the ten specimens were immature females, as evidenced by the presence of thin, strandlike saccular ovaries with few, unyolked ova. One male was immature with elongate, narrow testes of few, nearly equal-sized lobes. The matured male had small testes also of few lobes, but there was some anterior lobular fusion and lobes were in active spermatogenesis. These data and osteological evidence suggest that maturation occurs at approximately 190-200 mm total length. The amount of growth, amount of ossification. and gonad condition also suggest that maturation occurs during the second year after birth as in *Geotrypetes seraphini* (Wake, 1977b).

OSTEOLOGICAL DEVELOPMENT

In both the cleared and stained fetus and juvenile virtually all elements were mineralized. The fetus was less advanced in growth than the juvenile in that centra and componentes of the neural arches of the terminal vertebrae were mineralized but not fused, the elements of the suspensorium were weakly mineralized, and spaces between bones of the skull roof were greater. In both specimens rib heads were mineralized but ribs were weakly mineralized if at all, and those posterior to mid-body were progressively less mineralized, which is typical of the extreme cephalization shown in caecilian development. Neither specimen had developed the ossification of skull elements that provides overlap of skull components. Skull to body proportions were typical of fetal and very young caecilians, with relatively shorter, broader heads and wider gape than in well developed adults.

DISCUSSION

The juvenile specimens were collected in leafy debris accumulated between logs of a floating house on the Rio Ipixuna. Like other species of the genus, they are totally aquatic. They must, however surface periodically in order to gulp air. Rather little oxygen is obtained via cutaneous respiration by caecilians (Mendes, 1941, 1945; Sawaya, 1941, 1947; Bennett and Wake, 1974), especially when compared with amphibians of other orders. Sawaya (1947) demonstrated that the aquatic *Typhlonectes compressicauda* is highly dependent on inspired air with 94% of oxygen uptake being pulmonary. Typhlonectids have some modifications to facilitate their aquatic existence, such as muscles and valves to close the nares while under water and the development of bath lungs rather than just one, and these modifications are appropriate to air-breathing by aquatic animals living in water that is probably of low oxygen tension.

The presence of bits of rock and wood in the stomachs of *T. obesus* suggests that at least some feeding involves the substrate, and the presence of pupae in stomachs suggests that they were obtained from a surface to which the pupae had been attached. Since the pupae cannot yet be identified even to family, I do not know whether the emergent adults are aquatic. The structure of the pupae suggests that they are probably maintained in air, rather than water, because of the structure of their exoskeletons and other characteristics.

T. obesus probably forages at the water's surface at least occasionally in order to scrape prey items such as pupae from rocks and logs. The stomach contents and the place of collection indicate this possibility. These air-breathing forms swim in a sine-wave pattern not dissimilar from the terrestrial burrowing locomotor pattern, so it is possible that they could move about on rocks and vegetation at the sides and surface of the watercourse for some time. Their dependence on water is secondarily derived and restrictions to that habitat are not particularly evident.

The unusual dentition of *T. obesus* appears to be related to scraping. This suggests a possible restriction of prey items to 'fixed' rather than freely moving items. The teeth with dilated crowns are well adapted to scraping, and the orientation of upper and lower teeth so that they do not occlude could facilitate scraping from surfaces of different angles. Further, the dilated crowns of the adult teeth are very similar to the crown shapes found in fetuses of certain species. Dilated crowns without apical spikes or ridges are typical of fetuses of *Chthonerpeton viviparum* and *Nectocaecilia petersi,* both typhlonectids, and *Schistometopom thomense,* a caeciliid (Parker and Dunn, 1964). Comparisons of Parker ond Dunn's illustrations of letal teeth of these species with the *T. obesus* tooth in figure 5 show pronounced similarities of crown shape and proportions. The crown morphology of fetal teeth is thought to be an adaptation for scraping the wall of the oviduct in order to obtain epithelial cell secretions and to further stimulate that secretion (Salthe and Mecham, 1974; Wake, 1976, 1977a, 1977b). It therefore seems consistent to conclude that the crown morphology of adult *T. obesus* is adapted to scraping prey items from a substrate; this conclusion is supported by the composition of the stomach contents. It therefore follows that there is not a single adult tooth type that is characteristic of all caecilians, but that teeth may be modified according to habitat and to prey type. Further, caecilians may focus on certain classes of food items, rather than being totally opportunistic carnivores as had been supposed previously.

ACKNOWLEDGEMENTS

I am particularly grateful to W. Ronald Heyer, United States National Museum, for suggesting that I examine the caecilians, for permission to clear and stain a specimen and to dissect stomachs, and for criticizing the manuscript. I also thank Patricia Haneline and Ernest E. Williams, Museum of Comparative Zoology, Harvard University, for the loan of the female specimen with fetuses, and for their cooperation in allowing me to clear and stain a fetus, and Alan Leviton, California Academy of Science, San Francisco, for the loan of their *Typhlonectes* material. I thank Roy L. Caldwell, Department of Zoology, University of California, Berkeley, for examining the insect pupae, and David B. Wake, Museum of Vertebrate Zoology, University of California, Berkeley, for reading the manuscript. Gene Christman, Museum of Vertebrate Zoology, executed the graphs, and Teriann Asami typed the manuscript.

This work was partially supported by a grant from the Johnson Fund, American Philosophical Society, and by funds from the Committee on Research, University of California, Berkeley. Initial examination of the USNM material was done at the British Museum (Natural History) while there on sabbatical. I am grateful to A. G. C. Grandison and her staff for provision of space and facilities.

REFERENCES

Bennett, A. F. & M. H. Wake, 1974. Metabolic correlates of activity in the caecilian *Geotrypetes seraphini*. *Copeia 1974*: 764-769.

Lawson, Ronald, 1965a. The teeth of *Hypogeophis rostratus* (Amphibia, Apoda) and tooth structure in the Amphibia. *Proc. Zool. Soc. London 145*: 321-326.

Lawson, Ronald, 1965b. The development and replacement of teeth in *Hypogeophis rostratus*. *J. Zool. 147*: 352-362.

Mendes, E. G., 1941. Sobre a respiração (esofágica, traqueal e cutânea) do *Siphonops annulatus* (Amphibia-Gymnophiona). *Bol. Fac. Fil. Ciên. Let. Univ. São Paulo 1941*: 283-304.

Mendes, E. G., 1945. Contribuição para a fisiologia dos sistemas respiratório e circulatório de *Siphonops annulatus* (Amphibia-Gymnophiona). *Bol. Fac. Fil. Ciên. Let. Univ. São Paulo 1945*: 25-67.

Parker, H. W., 1956. Viviparous caecilians and amphibian phylogeny. *Nature 178*: 250-252.

Parker, H. W. & E. R. Dunn, 1964. Dentitional metamorphosis in the Amphibia. *Copeia 1964*: 75-86.

Sawaya, P., 1941. Contribuição para o estudo da fisiologia do sistema circulatório do anfíbio *Siphonops annulatus* (Mikan). *Bol. Fac. Fil. Ciên. Let. Univ. São Paulo 1941*: 207-270.

Sawaya, P., 1947. Metabolismo respiratório do anfíbio Gymnophiona *Typhlonectes compressicauda* (Dum. et Bibr.). *Bol. Fac. Fil. Ciên. Let. Univ. São Paulo 1947*: 51-56.

Taylor, E. H., 1968. The Caecilians of the World: A Taxonomic Review. University of Kansas Press. Lawrence, Ka. 848 pp.

Taylor, E. H., 1973. A caecilian miscellany. *Univ. Kansas Sci. Bull. 50*: 187-231.

Wake, M. H., 1976. The development and replacement of teeth in viviparous caecilians. *J. Morph. 148*: 33-64.

Wake, M. H., 1977a. Fetal maintenance and its evolutionary significance in the Amphibia: Gymnophiona. *In press, J. Herpet.*

Wake, M. H., 1977b. The reproductive biology of caecilians: an evolutionary perspective. *In* Reproductive Biology of Amphibia. S. Guttman and D. Taylor, eds. *In press*, Plenum Publ.

Table 1. Measurements and counts for adult and juvenile *Typhlonectes obesus*.

	Total length (mm)	Head width (mm)	Head length (mm)	Body width (mm)	Ratio body length/width	Nostril to eye (mm)	Tentacle tonostril (mm)	Primary annuli	Sex	Dentary teeth	Maxillary-premaxillary teeth	Vomero-palatine teeth
USNM 201695	114	6.0	7.0	7.9	14.4	3.5	.5	78	Imm ♀	19	28	2
USNM 201696	137	6.4	8.7	10.0	13.7	3.9	.6	75	Imm ♀	23	37	13
MZUSP 49892	139	6.2	8.4	11.0	12.6	4.2	.7	81	Imm ♀	14	23	11
MZUSP 49894	141	7.5	9.4	10.0	14.1	4.4	.7	78	Imm ♀	19	34	3
MZUSP 49893	145	7.0	9.0	10.4	13.9	4.4	.7	78	Imm ♀	17	25	2
(USNM 2406)	151	7.0	8.5	11.6	13.0	3.9	.5	73	Imm ♂	18	32	8
USNM 201692	158	7.1	9.8	11.2	14.1	4.5	.8	81	Imm ♀	20	28	11
USNM 201694	162	7.0	9.1	13.1	12.4	4.3	.8	80	Imm ♀	24	26	0
MZUSP 49896	171	6.3	8.9	12.5	13.6	4.3	.7	79	Imm ♀	24	31	15
MZUSP 49895	193	8.0	11	16.8	11.5	4.8	.8	83	♂	36	36	26
CAS 125421	290	10.2	15	15	19	4.2	.7	86	♀	36	42	39
EHT-HMS 1729	316	7	12	15	21	4.5	.7	82	NA	NA	NA	NA
AMNH 71434	373	12	16	32	12	5.9	.7	88	♀	36	40	38
MCZ A-79908	412	15	21	37	11.1	7.5	1.0	84?	♀	NA	NA	NA
EHT-HMS 1731	420	9.3	17	24	17.5	5.3	.8	85	NA	NA	NA	NA
CAS 125422	438	5.2	19	18	24	4.2	.7	83	♀	37	46	48

Legend: Imm = Reproductively immature; NA = not available

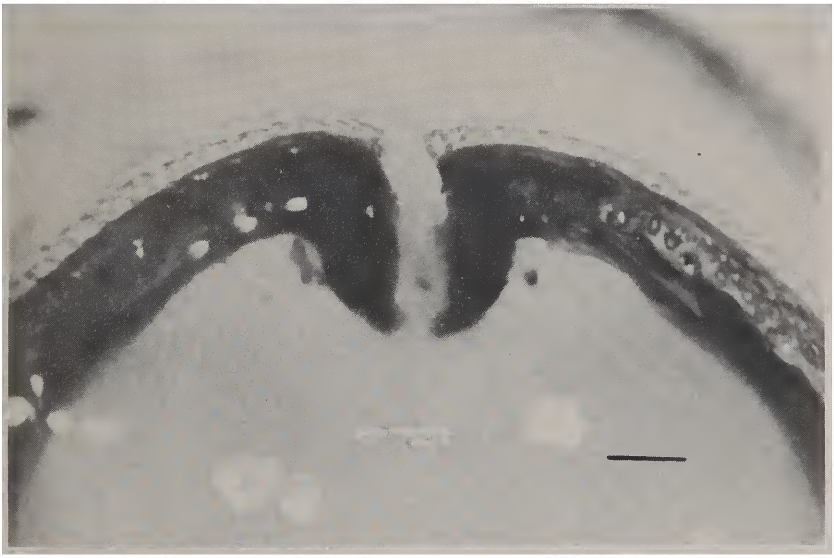

Figure 1. Dentition of 115 mm TL *Typhlonectes obesus* fetus. Dentaries of cleared and stained specimen. Note that tooth crowns but not pedicels are mineralized and darkly stained. Bar equals 0.5 mm.

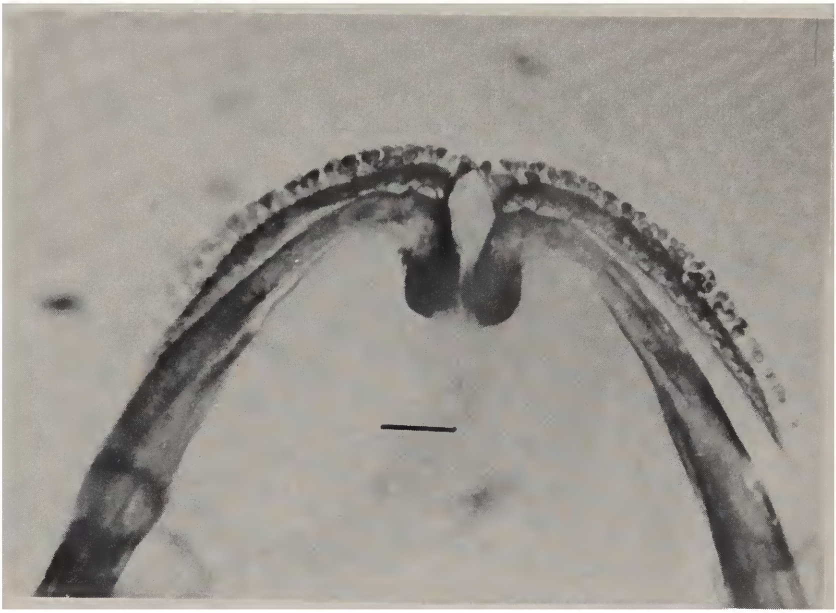

Figure 2. Dentition of 75 mm TL *Typhlonectes compressicauda* fetus. Compare dentaries and tooth structure with those of *T. obesus*. Bar equals 0.5 mm.

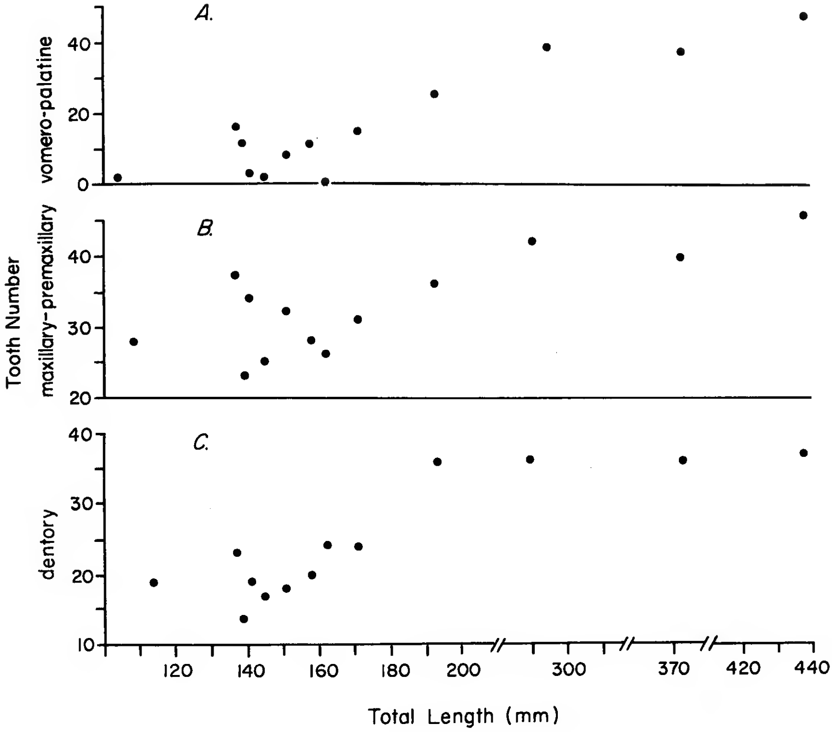

Figure 3. A. Vomeropalatine tooth number plotted vs. total length in *T. obesus*. B. Maxillary-premaxillary tooth number plotted vs. total length in *T. obesus*. C. Dentary tooth number plotted vs. total length in *T. obesus* C. Dentary tooth number plotted vs. total length in *T. obesus*. Note in all three graphs there is considerable scatter and addition of tooth loci in juveniles < 200 mm TL, but that tooth numbers increase only slightly after that size.

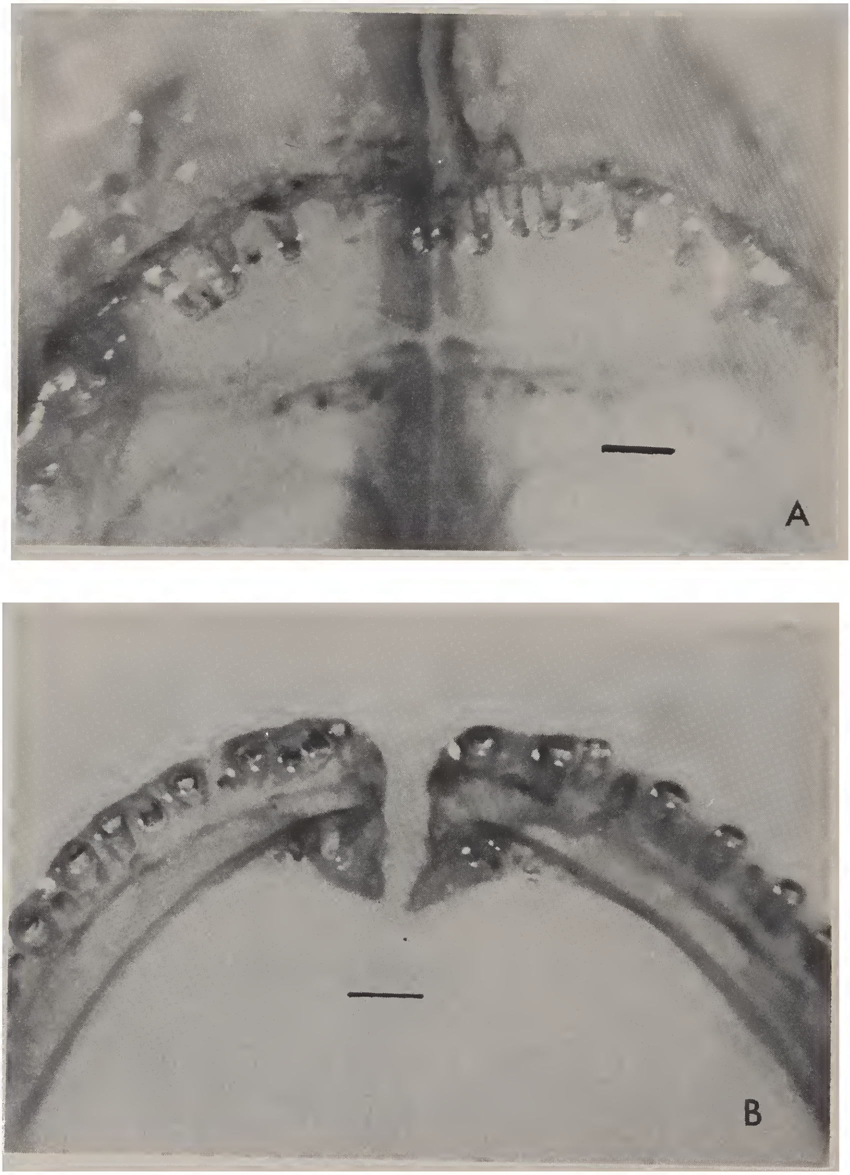

Figure 4. Juvenile dentition of 137 mm TL *T. obesus*. A. Dentary teeth. B. Maxillary-premaxillary teeth. Note differences in shape. Bar equals 0.5 mm.

Figure 5. Tooth crown of adult *T. obesus*. Note the dilated apex. Bar equals 0.1 mm.

Figure 6. Tooth crown and pedicel of *T. compressicauda*. Cleared and stained specimen. Compare shape of crown with that of *T. obesus*.

T. compressicauda has the adult tooth morphology seen in most caecilian species. Bar equals 0.1 mm.