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THE PRODUCTION OF SOUND IN CAUDATE AMPHIBIA

By T. PAUL MASLIN*

In 1765 Dr. Alexander Garden, of Charlestown, South Carolina, sent John Ellis, of London, several specimens of a two-legged salamander. Garden thought they might represent a new group of animals and suggested that Ellis send on to Linné some notes he had made concerning their anatomy and natural history. This Ellis did, and also sent on a small specimen. Linné in his letter of acknowledgement commented on the species and suggested that the name *Siren* would be appropriate. Apparently these notes and the specimen accompanying them reached Linné just before publication of his 12th edition of the *Systema Naturae*, for a description of this new amphibian under the name of *Siren lacertina* appears in a non-paginated addendum of this edition.

On June 5, 1766, Ellis read an account of this new salamander, along with Linné's letter of acknowledgement, to the Royal Society of London. This communication, however, was not published until 1767. In this letter Linné suggested that the animal might be a larval lizard (terrestrial salamander); but he expressed doubt of his own opinion by drawing attention to Garden's observation that the animal could produce sounds. In this letter he states, "Further, the croaking noise or sound it makes does not agree with the larvas of these animals", that is, larval lizards. Ellis does not quote Garden's notes in his communication to the Royal Society, but they do appear elsewhere.

After publishing the name of this new amphibian, Linné apparently turned over Garden's notes and the specimen he received to one of his students, Abraham Oesterdam, who then wrote a short dissertation on the animal. This paper was apparently published shortly thereafter in 1766. In 1769, however, Linné republished the dissertation in his *Amoenitates Academicæ*, Vol. 7, and in an addendum called attention to Ellis' paper and figures which appeared, as stated above, in 1767. In this paper Oesterdam states that "this animal lives in the watery marshes of South Carolina; as much in the water as out, for it climbs up out of the water onto the trunks of trees and onto branches which slip into the water; when the marshes dry where it lives, especially at that time of year in which it doesn't rain for several months, it sings in a querrulous voice almost like that of young ducks but more sharply and clearly as Dr. Garden says in his letter."

A number of years later Barton (1821, p. 29), in his paper on this species, denies that the animal can produce such sounds, and adds, "But the siren is not wholly

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mute. At times, he is heard to give out a hissing noise, but no ways entitled to the appellation of cantus, or song. This noise has often been noticed, and mentioned to me by my pupils, and others." Barton then comments on the fallibility of naturalists and cites a statement by Bomare to the effect that the cry of the Water Newt very nearly resembles that of the frog. This statement, Barton writes, is denied by Spallanzani, who observes that "it is only when they arise to the surface of the water, to expel the old air from the lungs and to inhale fresh, that the observer hears a sort of very low whistle, scarce perceptible at the distance of four paces." This statement Barton took from an English translation of Spallanzani which appeared in 1789. I have seen neither this nor later translations, but the original Italian appeared in 1776, the same year in which Oesterdam published his dissertation on *Siren lacertina*. It is probable then that Bomare's paper, which I have not seen, appeared before this and would constitute the first record of a salamander producing sound.

Barton (1821, p. 29) further states that the sounds produced by *Siren lacertina* probably resemble those made by *Proteus anguinus* Laurenti. In 1801 Shreiber describes in his scholarly paper on this species the sounds produced by this animal. He was unable to procure live specimens in his studies, but his friend Baron Zois, who lived in the vicinity of Lake Czerknitz and collected for him, gave him a considerable amount of data on the natural history of this blind salamander. Shreiber (p. 245) reports that Baron Zois told him in correspondence that "it often produces a hissing kind of noise, pretty loud, more so than one should expect from so small an animal, and resembling that produced by drawing the piston of a syringe."

Another salamander whose sound-producing ability has been known for some time is *Megalobatrachus japonicus* (Temminck). Ishikawa (1904) quotes from a Chinese text in which it is stated that "it makes a sound which resembles a child's cry and on that account is called the childfish." Ishikawa, who had had extensive field experience with the animals, agrees with this and states, ". . . that the animal can emit a curious sound is true, but it is very different from a child's cry with which it could scarcely be confused."

Sowerby (1925, p. 79) also reports on the sound production of *Megalobatrachus* in China. He was unfamiliar himself with the animals in the field but states that "when handled it makes a peculiar cry like that of a newborn infant, for which reason the Chinese popular name is *Wa Wa Yu*, or 'child fish'." It is also known as the *Na Yu*.

Hay (1888, p. 317) reported that *Amphiuma means* Garden could produce sounds. During his studies of this salamander he had occasion to place one in a shoe box from which it made repeated attempts to escape. On one occasion, during an unsuccessful attempt to climb out, the salamander fell and then "uttered a shrill sound somewhat like a whistle or the peeping of a young chicken." Cope (1889, p. 456) made a similar report. He did not cite Hay, but it seems likely that he was

familiar with Hay's report. He writes that "Prof. J. A. Ryder, of the University of Pennsylvania, has kept this species in captivity. He states that its voice is so loud that it can be heard from one room to another of the building of the school of biology." Baker (1937, p. 209), in his study of the life history and breeding habits of *Amphiuma*, has made more critical and detailed observations of the sound which it produces. He states that "a sound of out-rushing air from the branchial fissures was noted several times during this investigation; it usually accompanied some change in the environment or some feeling of discomfort. This may be the 'whistle' to which Hay referred. Once when an *Amphiuma* escaped during the night and crawled behind a bookcase, it was located by this noise; again as one was tossed from its basin of water onto the muck in its cage it made this noise while still in the air. Still again when *Amphiuma* were first moved from aquaria to a new cage containing the muck this noise was noted as they pushed their way through the mud and seemed to seek for water." Then later in his conclusions he adds (p. 216), "Specimens in captivity were observed to give a sort of whistle when in distress or introduced into a new environment. This is apparently caused by an outrush of air from the branchial fissure since they have no voice."

The first mention of a plethodont salamander producing sound is a brief allusion to *Desmognathus* by Cope in 1889 (p. 221). At that time Cope believed that the *Amphiumidae* could be derived from the *Plethodontidae* and in support of this hypothesis cited a number of miscellaneous characters common to members of the two families. In this discussion he states, "*Amphiuma means* also resembles the species of *Desmognathus* in the possession of a chirrup or whistle. I do not know of another American salamander which possesses a voice."

About ten years later Ritter and Miller (1899, p. 697), in their discussion of the life history of *Aneides lugubris lugubris* (Hallowell), a Californian plethodont, quote a student of theirs who found a clutch of eggs guarded by an adult female. When the salamander was "uncovered and disturbed she 'squeaked like a mouse.' This sound was one of the first things that attracted his attention. This squeak is frequently produced by adults when first taken, but rarely while they are in confinement." Storer (1925, p. 133) has observed the same phenomenon. He states that "on rare occasions *Aneides* has been heard to utter a mouse-like squeaking note. Miller (M. S.) records two instances of this sort, once in the wild and once when a captive individual was being stimulated with an electric current in the laboratory. I have heard it on at least one occasion. How this salamander, without lungs or a vocal pouch, produces its note is unknown."

Geyer (1927, p. 27), after briefly reviewing the subject of sound production in salamanders, records three further instances of species producing sounds. Among these is a third plethodont, namely *Eurycea bislineata* (Green). His observations were made on captive specimens under circumstances in which the salamanders were in particularly good health and in a well-kept terrarium. On several occasions

during July, 1926, Geyer heard soft squeaking sounds emitted at about one second intervals for periods of approximately an hour at a time. Geyer interpreted these sounds as being a part of the breeding behaviour of the species.

In the same paper Geyer (*loc. cit.*) reported on species of two additional families, namely the Salamandridae and Ambystomidae. On two occasions in 1927 he heard a captive specimen of *Salamandra salamandra taeniata* utter a soft peeping sound. And on a June evening in 1926 he heard a captive *Ambystoma maculatum* housed in a large terrarium make a soft grunting sound, which he describes as sounding like "unk" in which the "u" is scarcely voiced. Later a friend to whom he had sent the salamander heard the same sound.

Wolt (1927) in a short editorial comment following Geyer's paper quotes a letter from a Dr. E. Jacob in which Jacob states that the "fire salamander" (*Salamandra salamandra taeniata*?) and possibly *Triturus alpestris* make noises similar to those described by Geyer.

Myers (1930, p. 57) reports on the production of sound by another ambystomid. In his discussion of *Dicamptodon ensatus* (Eschscholtz) in California he states that "Mr. Hoover (Theodore J. Hoover, owner of Rancho del Oso, Waddell Creek, Santa Cruz Co., Calif.) tells me that *Dicamptodon* is rare, but that individuals are occasionally uncovered when cleaning up rubbish in the woods. One such that he obtained is in the collection. He further states that the animal utters a noise or 'bark' and says that he has had his attention called to specimens in this way."

Werner (1912) in Brehm's *Tierleben* briefly discusses under the various species-accounts the sound production attributed to *Amphiuma means*, *Megalobatrachus japonicus*, and *Siren lacertina* without contributing any data not previously recorded. But in his discussion of European *Triturus* he mentions that the animals squeak when abruptly moved from water or when roughly handled. They also produce a clucking sound in their natural habitat at the surface of the water. Werner may have been referring to Bomare's and Spallanzani's descriptions of such sounds.

Nobel (1931, pp. 409-410) briefly discusses sound production in salamanders. He rather summarily dismisses Geyer's hypothesis that the "voice" of salamanders plays a part in the breeding process and states that "in all these cases the sound is probably accidental and associated with the sudden emptying of the lungs or buccal cavity. At least it is not known to have any significant effect on the behavior of the creature's associates." This dismissal also includes Ritter and Miller's reports of sounds produced by *Aneides*.

FURTHER RECORDS AND OBSERVATIONS

In addition to these earlier records, I have heard two additional species producing sounds. On a collecting trip to Mt. St. Helena in northern Napa County,

California, in 1941, during the month of March, I found a number of adult *Triturus t. torosus* (Rathke) in a small, heavily shaded stream. When these animals were fished from the stream by hand, they uttered low-pitched kissing sounds. After repeating the noise four or five times the salamanders then resorted to simple attempts to escape by writhing through my fingers. Furthermore they could not be induced to produce sounds subsequent to their initial capture, even though some specimens were returned to the stream for a few minutes and then recaptured.

The second observation pertains to *Ambystoma tigrinum nebulosum* Hallowell. During the winter and spring of 1947 I had occasion to keep a collection of about twenty specimens of this salamander in a dark box. The floor of the box, covered with peaty soil, was moistened periodically. On those occasions when the lid of the box was opened and the salamanders were disturbed, either to introduce food or to wet the soil, the animals moved about excitedly and uttered clicking or kissing noises. As in the previous account of *Triturus* these sounds were produced only during the initial stages of excitement. After a few moments of teasing, the salamanders could be induced to run for short distances but would no longer produce the clicking noises.

I can also corroborate the reports of Ritter and Miller (1899) and Storer (1925) concerning the squeaking noises of *Aneides lugubris lugubris* (Hallowell). On a number of occasions, possibly fifteen or twenty, between the years 1936 and 1945 I have heard these animals produce sounds. As the behavior of the animals at these times follows much the same pattern I shall record only two observations. In one instance in the city of Berkeley, California, during a sunny morning while cleaning up a north-facing cement porch laid at ground level, I uncovered an *Aneides* from beneath a cardboard carton. I did not notice the animal until I had begun sweeping the leaves and litter off the cement porch. My attention was first attracted to it by the squeaking noises it emitted as I roughly swept it along with the leaves. These sounds were produced in single, short bleats of about half a second's duration. When I realized what was producing these clearly audible sounds, I prodded the animal more gently as it attempted to scramble away. Each touch of the broom aroused a squeak and momentarily halted the animal's efforts to escape. This sound was repeated five or six times, after which the salamander would no longer squeak no matter how violently it was touched.

On another occasion, while seeking *Aneides* in a damp garden in Berkeley, I uncovered a subadult specimen beneath a small board lying against a wooden fence. Immediately upon being exposed the animal reared itself on its legs so that the body was raised high above the ground. The tail was bent upwards proximally and then arched downwards so that the tip hung just free of the ground. The head also was bent sharply upwards and the mouth held gapingly open. This

ferocious-looking position it held for possibly twenty seconds as I stooped to observe it. Then upon being touched with a twig it closed its mouth and, bending its head down, arching its back slightly, and raising the floor of its mouth, it emitted a squeak, then returned immediately to its former position. This performance was repeated each time the animal was touched. It did not orientate itself to face my aggression nor change its position in any way, regardless of where it was touched. Possibly a minute later the animal slowly began to relax and thereafter could not be induced to utter a sound.

Most of the *Aneides* I have heard producing squeaks were not adult animals but about three-quarters full grown. Occasionally a large adult will squeak, but then only briefly.

I have also heard *Dicamptodon ensatus* (Eschscholtz) emit sounds on several occasions. One specimen, collected on March 11, 1940, at Sempervirens Creek, 1100 feet, Big Basin, Santa Cruz County, California, was particularly loquacious. It was found beneath a stone on a small sandy flood flat in a deeply shaded redwood canyon. As soon as the stone was lifted the animal raised its head, bracing its forefeet firmly against the ground. Shortly after, it began walking off, but just as I touched it to pick it up it gave a violent lateral jerk of its body and simultaneously barked. Startled, I withdrew my hand, and the salamander again resumed its attempts to escape. It barked again when I finally caught it. The specimen was taken back to my laboratory alive and placed in a terrarium where it was kept for several weeks. Here also it could be induced to bark by being picked up or teased with a probe. Usually these barking noises were accompanied by the violent lateral lurching I first noticed, but on several occasions the only visible body movements were a sudden contraction of the lateral abdominal musculature and a parting of the lips during the bark. The bark itself is loud, relatively low pitched, but surprisingly resonant and clear toned. It roughly sounds like an explosive "ah".

METHODS OF SOUND PRODUCTION

The methods whereby sound is produced in salamanders are quite variable. The simplest type appears to be the clicking, clucking, or kissing sounds observed in *Salamandra salamandra*, *Triturus alpestris*, *Triturus similans*, and *Ambystoma tigrinum nebulosum*. These salamanders seem to produce such sounds simply by opening the mouth, thereby allowing air to break the moist seal of the adpressed lips as it enters the buccal cavity, and they can augment these sounds in intensity by the simple expedient of closing the nares during the process, thereby lowering the buccal pressure as the mouth is opened and permitting the air to enter the cavity more explosively. This is apparently the case in the two species I have observed. This method is based on buccal inspiration rather than expiration.

Amphiuma means, according to Baker (1937), produces its whistling sounds by forcing air through the branchial fissures. As these fissures are relatively small, it is understandable that air under pressure escaping from the slits could produce a sound of considerable intensity. Baker cannot corroborate Hay's (1888) observation of a shrill sound; to Baker the sound was whistle-like, not a clear whistle or peep. Regardless of the exact nature of the sound it seems apparent that this method of sound production is based on the principle of expiration of air and on the mechanical effects of a resonating mass of air in the buccal cavity. With a proper adjustment of the size of the air mass in the buccal cavity and of the outlet from this air reservoir, it is possible that a clear whistle could be produced.

The squeaking noise produced by plethodont salamanders introduces a third method of sound production—namely, a vibrating valve associated with a resonating chamber. While it is of interest that this sound is produced by salamanders without lungs, the actual production of such sound is dependent simply on an air reservoir, within which the pressure may be raised, and a vibrating valve, through which the air under pressure may be forced. The air reservoir in plethodonts is the buccal cavity, which is emptied by forceful contraction of the floor of the mouth, as I have observed in *Aneides*. The position of the valve, however, is a problem I have not been able to solve from my own observations. Air may escape from the buccal cavity in three ways: down the oesophagus, out the nares, or through the lips. Because of the shrillness and distinctness of the sound I doubt if it is oesophageal. If it were, one would expect the sound to be more muted. As far as the nares and lips are concerned, both structures are closed during sound production. This in itself is essential in order to build up sufficient buccal pressure; but whether the air escapes between the lips or out of the nares could not be determined. Attempts were made to photograph *Aneides* during the act of producing sound, but with no success.

A fourth type of sound production is also valvular, but in this type the air reservoir is pulmonary and the valves are located in the larynx. Sounds produced by such a mechanism can be described as being true voice. Apparently *Megalobatrachus japonicus* is possessed of true voice, judging from the meager descriptions of the sounds it produces, and, I suspect, this is true also of *Ambystoma maculatum*.

In order to determine the mechanics involved in the voice of *Dicamptodon ensatus*, a specimen of this species was dissected and compared with an example of *Ambystoma tigrinum nebulosum*. The tracheal region is surprisingly simple in both species. The anterior end of the trachea is encircled by a mass of muscle fibers, which constitute the *musculus constrictor laryngis* (see Fig. 1). At the anterior end of the median ventral raphe of this muscle two slender muscles extend laterally, one on each side. These are the *musculi cephalo-dorso-subpharyngii*. These

muscle bands are interrupted laterally by an inscription and then continue dorsally around the *musculus opercularis* to their origins on the cranium. In both species the *pars dorsalis*, lateral and dorsal to the inscription, consists of three distinct heads rather than two as Edgeworth (1920) found in several other families of salamanders. Posterior to the heads of the *pars dorsalis* a long slender band, the *musculus dilator laryngis*, also arches around the *m. opercularis* from its origin on the dorsal fascia and passes medially towards the larynx. Just before reaching the larynx the muscle bends anteriorly, passing dorsal to the belly of the *pars pharyngis* of the *m. cephalo-dorso-subpharyngis*, and is inserted by a round tendon,

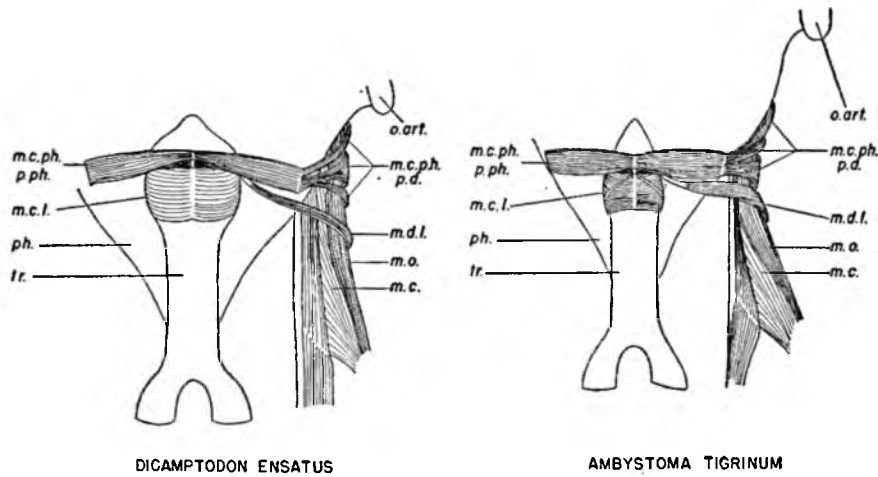


FIGURE 1. Ventral view of the larynx and associated structures of *Dicamptodon ensatus* and *Ambystoma tigrinum nebulosum*. m.c., musculus cucullaris; m.c.l., musculus constrictor laryngis; m.c.ph., musculus cephalo-dorso-subpharyngis; m.d.l., musculus dilator laryngis; m.o., musculus opercularis; o.art., os articular; ph., pharynx; tr., trachea.

the *ligamentum dilator laryngis*, near the anterior end of the larynx in front of the *m. constrictor laryngis*. These three muscles, the only ones associated with the larynx, are similarly disposed in the two species (see Fig. 1); neither a *m. laryngis ventralis* nor a *dorsalis* is present. The only conspicuous difference between the two species lies in the greater size and relative width of the *m. constrictor laryngis* in *Dicamptodon*.

Serial sections of the larynx of both species reveal that the smaller larynx and the associated trachea of *Ambystoma* are considerably simpler than those of *Dicamptodon*. The laryngeal skeleton of both species consists of a mixture of chondroid tissue and hyaline cartilage. In *Ambystoma* the *pars laryngis* of the

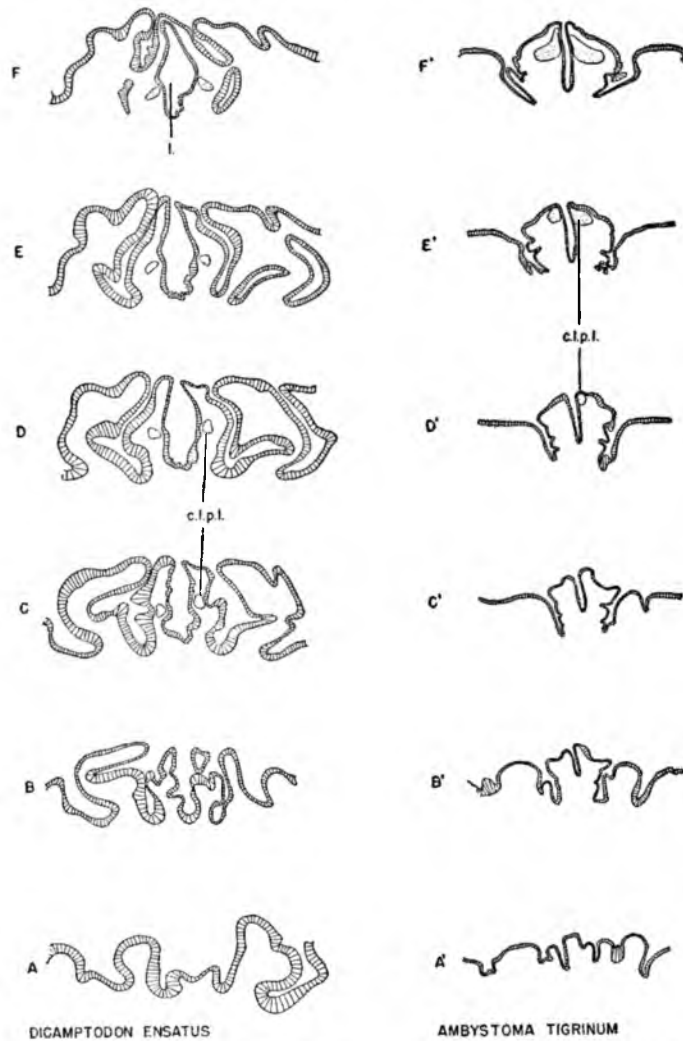


FIGURE 2. Transverse serial sections of the larynx and trachea of *Dicamptodon ensatus* and *Ambystoma tigrinum nebulosum* selected at intervals of 200 microns. Epithelium crosshatched, chondroid tissue (pseudocartilage) openly stippled, cartilage closely stippled. c.l.p.l., cartilago lateralis, pars laryngis; l., larynx.

cartilago lateralis first appears as a process of chondroid tissue in the dorsal medial edge of the longitudinal fold of the glottis (see Fig. 2D', c.l.p.l.). This process

rapidly increases in size posteriorly, assuming a triangular aspect in cross section (Fig. 2F', 3G'-I'), the smallest point of the triangle being dorsal, and the lateral point forming the *processus muscularis* to which the *ligamentum dilator laryngis* is inserted. Just at the level of the anterior edge of the *m. constrictor laryngis*, the ventro-medial corner of the chondroid-tissue triangle gives way to hyaline cartilage (Fig. 3J'). At this same level the *ligamentum dilator laryngis* is inserted on the *processus muscularis*, which here is not cartilaginous. The two triangular skeletal masses now alter in their cross-sectional form. The vertical median leg of each triangle becomes bent laterally into the body of the triangle and the skeletal masses then assume a crescentic form, one on either side of the larynx (Fig. 3K'-L'), the hyaline cartilage being confined to the medial ventral edge of these masses. This relationship persists through the length of the larynx (Figs. 4, 5). Just posterior to the posterior edge of the *m. constrictor laryngis* the cartilaginous portion of the laryngeal skeletal mass becomes separated from the chondroid-tissue portion (Fig. 4R') and continues for a short distance posteriorly as an increasingly slender cartilaginous splint closely paralleled by its mate of the opposite side. These splints soon come to an end, so that the *pars trachealis* of the *cartilago lateralis* consists then of two continuous masses of chondroid tissue, obtusely crescentic in cross section, passing down the entire length of the trachea.

In *Dicamptodon* the *pars laryngis cartilaginis lateralis*, or arytenoid, first appears as a laterally located process of cartilage in the lateral walls of the glottis some distance below its dorsal edges (Fig. 2C). This process descends still further as it proceeds posteriorly and assumes a flattened form with the lateral edge more ventrally disposed (Fig. 2F). At the level of the anterior edge of the *m. constrictor laryngis*, a mass of chondroid tissue appears adpressed to the dorso-lateral face of this flattened plate of cartilage, and at this same point the *ligamentum dilator laryngis* is inserted on the ventro-lateral edge of this combined cartilage-pseudo-cartilage plate (Fig. 3G). This edge then is the *processus muscularis* of the *cartilago lateralis*. Posterior to this the chondroid tissue on each side rapidly increases in size, forming two huge masses roughly rhombic in cross section (Fig. 3L), with their medial faces concave to enclose the lateral folds of the larynx, which is cruciform in cross section at this level. The cartilaginous portion of these masses remains medio-ventral in position and consists of two flattened plates intimately joined to the chondroid tissue above.

At the level of the center of the larynx, spaces appear in the chondroid tissue of the arytenoids (Fig. 4N). These spaces consist of anteriorly directed blind pockets about 400 microns deep, one on each side. Posteriorly they open on either side into the larynx (Fig. 4P). A short distance posterior to these openings, at the level of the posterior margin of the *m. constrictor laryngis*, the cartilaginous por-

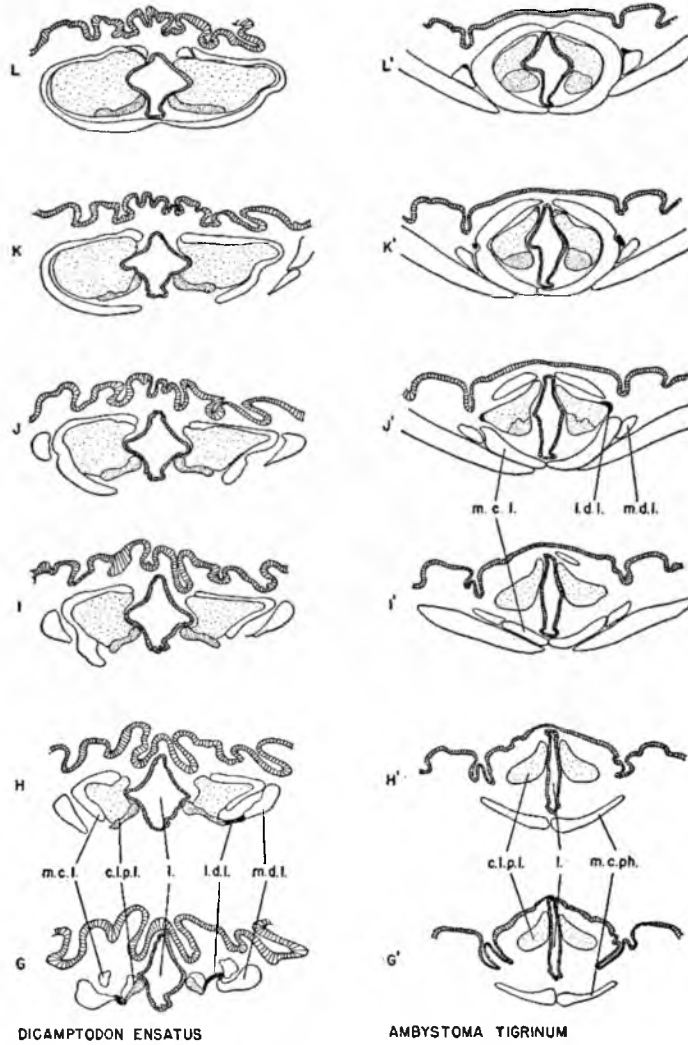


FIGURE 3. Transverse serial sections of the larynx and trachea of *Dicamptodon ensatus* and *Ambystoma tigrinum nebulosum* selected at intervals of 200 microns (continued). Epithelium cross-hatched, chondroid tissue (pseudocartilag) openly stippled, cartilage closely stippled, ligaments black, muscles simply outlined. c.l.p.l., cartilago lateralis, pars laryngis; l, larynx; l.d.l., ligamentum dilator laryngis; m.c.l., musculus constrictor laryngis; m.c.ph., musculus constrictor pharyngis (not shown in *Dicamptodon ensatus*); m.d.l., musculus dilator laryngis.

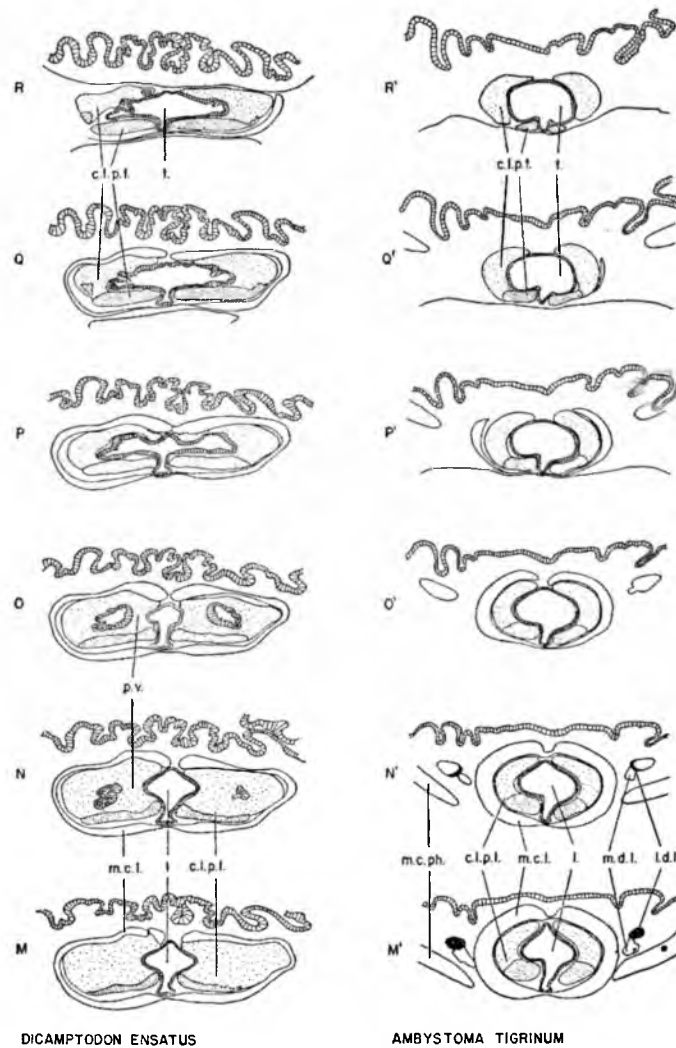


FIGURE 4. Transverse serial section of *Dicamptodon ensatus* and *Ambystoma tigrinum nebulosum* selected at intervals of 200 microns (continued). Epithelium cross-hatched, chondroid tissue (pseudocartilage) openly stippled; cartilage closely stippled, ligaments black, muscle simply outlined. c.l.p.l., cartilago lateralis, pars laryngis; c.l.p.t., cartilago lateralis, pars trachealis; l., larynx; l.d.l., ligamentum dilator laryngis; m.c.l., musculus constrictor laryngis; m.c.ph., musculus constrictor pharyngis (not shown in *Dicamptodon ensatus*); m.d.l., musculus dilator laryngis; p.v., plica vocalis; t., trachea.

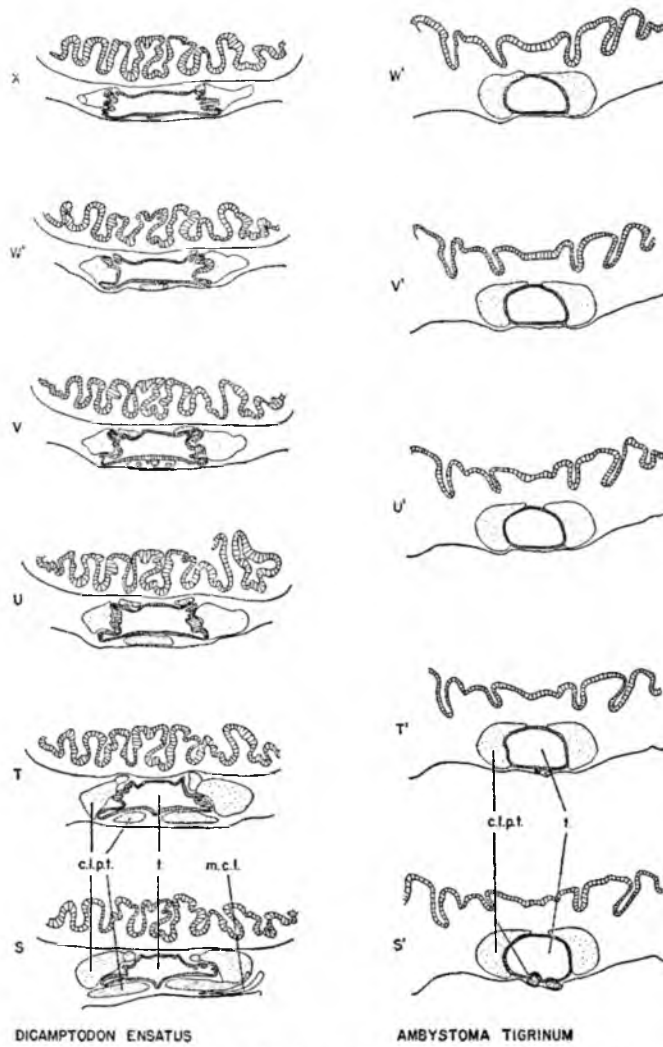


FIGURE 5. Transverse serial sections of *Dicamptodon ensatus* and *Ambystoma tigrinum nebulosum* selected at intervals of 200 microns (continued). Epithelium cross-hatched, chondroid tissue (pseudocartilage) openly stippled, cartilage closely stippled, muscle simply outlined. c.l.p.t., cartilago lateralis, pars trachealis; m.c.l., musculus constrictor laryngis; t., trachea.

tions of the arytenoids become separated from the chondroid tissue (Fig. 4R) and then continue posteriorly as two flattened plates (Fig. 5 S-T). At the same level two new cartilaginous elements appear in the dorsal medial edges of the chondroidal tissue. The ventral cartilages meanwhile join to form a single median tongue (Fig. 5U). This tongue then gives way to chondroidal tissue, within which are located islands of cartilage (Fig. 5V), and shortly posterior this median mass comes to an end in a slender point (Fig. 5X).

In the tracheal walls the persistent columns of cartilage in the dorso-lateral regions give rise to cartilaginous processes directed transversely and ventrally. Two pairs of such processes arise successively, and then the longitudinal cartilages bend laterally and ventrally, finally occupying a ventro-lateral position. There then arise in succession two additional pairs of dorsally directed processes like the tines of a rake. The cartilage and the chondroid tissue associated with it then end just anterior to the bronchi.

From the above description of *Dicamptodon* it is evident that an apparatus exists of considerable complexity which serves for the production of sound. The tracheal walls are reinforced with pectinate cartilages suggestive of rudimentary tracheal rings. The larynx is massive and is equipped with rudimentary *plicae vocales* (Fig. 4 N-O) which are reminiscent of the cords in the Anura, except that in *Dicamptodon* no recesses occur anterior to the *plicae*. The vestibule of the larynx possesses hyaline cartilages in its lateral walls rather than simple chondroid tissue, and on these cartilages are inserted the *m. dilatores laryngis* thereby affording a more precise control of the laryngeal apparatus.

PURPOSE OF SOUND PRODUCTION IN SALAMANDERS

Certain sounds produced by salamanders are obviously adventitious to normal respiration. In a partially closed system in which air movements occur, sound production of some sort can hardly be avoided, although frequently such sounds are nearly inaudible. The kissing or clicking sounds of newts (Spallanzani, 1776; Werner, 1912) respiring at the surface of water are an example of this.

From the production of such sounds by air-breathers it seems but a step for animals to capitalize on the phenomenon and to make deliberate use of such noises. It further seems logical that such sounds would, at first, be purely defensive. Before an ability of this sort could be selectively tolerated the character would have to be variable. But those animals most successful in producing sound would depart the most from the norm of that species. Such an abnormality would have a high survival value, in that normal predators of the species might possibly shun an individual distinctly abnormal in its behavior pattern. This avoidance might be deliberate on the part of the predator or simply an inability to follow through a sequence of reflexive actions dependent on a normal sequence of re-

sponses of its prey which reciprocally serve as the stimulating factors in the behavior of the predator. If the normal or expected sequence of responses of the prey are disrupted by an abnormal act, such as the production of an unexpected sound, the chain of reflexive acts on the part of the predator might be broken. This concept is suggested by the behavior of *Aneides lugubris* during the production of its squeaking noises. I have described above how the animal performs a series of acts culminating in a squeak, but this behavior is not accompanied by an effort to escape. The animal produces its sound, then appears to wait for the potent magic of its unusual behavior to ward off evil. It seems likely that other types of sounds serve a similar purpose, such as the kissing sounds produced by *Triturus torosus* larvae and the terrestrial stages of *Ambystoma tigrinum*. Such sounds as those reported by Hay (1888) of *Amphiuma means* may serve a similar purpose.

If such behavior patterns are sufficiently eccentric to have survival value as defense mechanisms, they also might act as a barrier to normal mating. A new behavior might be sufficiently abnormal to disrupt a sequence of acts essential as precursors to successful breeding. It seems to me, then, that only after an abnormal act, through positive selection pressure, becomes normal for a species can such an act secondarily be adapted to sexual behavior. That certain salamanders have reached this level in the evolution of voice seems indicated by Geyer's (1927) observations of the sounds produced by *Eurycea bislineata*, *Ambystoma maculatum*, and *Salamandra salamandra taeniata*. As Geyer indicated, these salamanders produced sounds under circumstances which could hardly be interpreted as defensive, and his suggestion that they have some sexual significance seems likely.

The more complicated behavior of *Aneides lugubris* and *Dicamptodon ensatus* seems to be an advance over the simple defense mechanisms described above. In these animals the production of sound is accompanied by acts of behavior apparently adapted to accentuate the startling phenomenon of sound production. *Dicamptodon* is still further advanced in that the noises it produces are intimately associated with efforts to escape. A higher level of behavior would be one in which the sound production and its associated acts of behavior were actually aggressive. It is possible that this level of a behavior has been reached by some salamanders, but so far no observations of such a pattern have been made.

CONCLUSIONS

1. Salamanders can produce sounds of various sorts.
2. They produce sound by sucking air through suddenly parted lips; by blowing air through a narrowed orifice, such as a gill; and by forcing air through a vibrating valve.

3. In *Dicamptodon ensatus*, vocal cords are present and the animal is possessed of true voice.
4. The production of simple aspirant and clicking sounds in some salamanders is accidental.
5. In some salamanders the production of sound is deliberate.
6. Sound production in most salamanders is a part of a defense mechanism.

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