

The Natural History of *Necturus*: II

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Respiration

Necturus has permanent external gills, simple internal lungs, and a skin well supplied with blood vessels; all of which have been reported functional in respiration.

Gill respiration seems to be the usual mode. Periodically but somewhat irregularly, the gills are fanned forward, becoming bright red (crimson); as they are brought back against the body they become dull ruby red (slaty grey). Fanning seems to aid the flow of blood through the gills. The gills of the two sides may be waved independently (Willey 1918).^{*} These movements seem to be controlled by the temperature of the water, for in cool or cold water the gills are held close to the body for long periods of time, while the branchiae shrink both in length and diameter, and become very dark (Kneeland 1858). As the water warms, gill-movement increases. Stewart (1923) noted the following average movement-rate of gills at the temperature indicated: 8.5°C., 22.6/minute; 8.8°C., 26/minute; 11.3°C., 29/minute. I have counted fanning movements of as many as 140 times per minute in water at 30°C. A decrease in dissolved oxygen does not alter gill-movement rate (Babak 1913).

Under normal circumstances, the *Necturus* stay on the stream or lake bottom. Trips to the surface, made by captive animals, are unusual, and are possibly escape movements, or a reaction to a lack of food (Willey 1918). In water poorly aerated, or in warm water (approaching 30°C.) the *Necturus* become restless (almost panicked!) rise to the surface, and appear to gulp air. The mouth opens, and yawning, gasping, or gulping motions are made, though Whipple (1906) and Willey (1918) say there is no evidence air is swallowed. *Necturus* may temporarily float with the nostrils above water (Kneeland 1858), but usually they soon settle, or swim back to the bottom. Willey (1918) says a floating *Necturus* is a moribund *Necturus*. After a time, part of the gulped air is expelled through the gill clefts, but whether any of it actually enters the lungs I cannot say. Eycleshymer (1906), Hurter (1911), Sayle (1916) and Newbigin (1908) believed that the lungs play a considerable role in respiration;

^{*} The complete bibliography will be printed following the last paper of this series.

Wiley (1908), on the other hand, held that the lungs do not function in respiration. Luckhardt and Carlson (1920) denied that *Necturus* swallows air; but Bishop (1926) believed that part of the air in some instances is taken into the lungs. On repeated trips to the surface, the *Necturus* may expel bubbles of air as they break surface, causing small popping sounds.

Bruner (1914) reported regular oscillations of the floor of the mouth, useful in breathing under water as well as during air breathing; the elevation of the pharyngeal floor being brief and conspicuous, and the depression so slow as to be easily overlooked. During depression, mouth and gill slits are closed, so water enters only through the nares. During elevation, water is forced out usually through the gill slits, and sometimes through the mouth, but not through the nares.

Internal choanal valves (flap-like structures without musculature, and therefore acting mechanically) are described by Bruner. They prevent the return of water through the nares, and also function in pulmonary respiration. According to Bruner, *Necturus* periodically interrupt their under-water bucco-pharyngeal respiration and practice pulmonary respiration. In preparation, they raise the floor of the pharynx, thus expelling most of the respiratory water. In aspiration, the jaws are pushed up above water, the mouth is opened, and gill slits are closed by constrictor muscles. In expiration, the abdominal walls quickly contract, and air is forced from the lungs; this is usually completed while the mouth is open. Inspiration of air is accompanied by a wave (of expansion? Bruner does not specify) which passes along the trunk from anterior to posterior. No air escapes from the nares; they remain water-filled during the entire process, blocked internally by the choanal valves. Constrictor muscles close the gill clefts, and thus prevent escape of air through these openings. When inspiration is complete, the glottis closes, retaining the air in the lungs. Now, as *Necturus* returns to aquatic bucco-pharyngeal respiration, excess air in the mouth and pharynx is expelled, because its presence would more or less hinder aquatic respiration (Bruner)..

Bruner observed no pulmonary respiration during 90 minutes of observation of specimens in water at 56°F. In fresh water at 69°F., the rate observed was 5.7 per hour; while in impure water (a small amount, in which specimens had been kept overnight) at 69°F. the rate was 9 pulmonary respirations per hour.

Wilder (1901) reported in *Desmognathus* a condition in

which capillaries in the pharynx and esophagus constitute an effective area for respiratory exchange, serving as a functional "lung"; pharynx and esophagus can be dilated and constricted in respiration. Willey (1918, 1920) could see in *Necturus* only gill movements in respiration; he observed no pulsations in the pharyngeal floor, movement of choanal valves, or dilation of the intestinal area. (My observations, while limited, corroborate Willey's.)

The lungs of *Necturus* are simple, poorly vascularized, and lack alveoli. Their function is probably largely hydrostatic. *Necturus* lacks the Y-shaped prepubic cartilage and associated muscles which Whipple (1906) showed help to control the shape of the lungs in many aquatic urodeles in which a hydrostatic function of lungs is known. Because he could not see any increase in girth or buoyancy in *Necturus* after repeated trips to the surface, Willey (1918) suggested that the lungs may be filled with air by gaseous diffusion from the blood as in the air bladder of fishes. Excess gas may be voided through the glottis.

There is one recorded observation of a *Necturus* partly out of the water, which Bennett (1937) said was apparently breathing atmospheric air. Yet mudpuppies removed from the water are in difficulty. On removal from the water they secrete quantities of mucous material. After a time they convulsively open and close the mouth, as if gulping air, but no "swallowing" motions are observed. They are unable to survive out of water for more than a few hours (Kneeland 1857—one hour; Garnier 1888—two to three hours; Eycleshymer 1906—three to four hours). The lungs are inadequate for survival in air.

Under somewhat special conditions the animals may be able to get along without gills. Gills often lack fibrillae (Hurter 1911). Kneeland (1858) reported the circumstances in which the gills were nibbled almost entirely from one specimen by fish, without hampering the *Necturus* in its activities. Others (Hay 1891; Bennett 1937) have noted the occasional absence of gills in certain specimens. Willey (1918) extirpated the gills without apparent harm to the *Necturus*. Lungs could probably be removed without putting the animals in respiratory difficulty.

In well-aerated water the skin alone will supply the needed oxygen (Dawson 1920). The skin is well supplied with blood; large vessels under the skin assist in cutaneous respiration (Noble 1931). Cutaneous blood-supply is especially rich in the region of the tail (Dawson 1920). Blood vessels in *Necturus* extend

only into the dermis (Dawson 1920); in *Cryptobranchus* the capillaries extend into the epidermis (Noble 1931).

It appears then that in well-aerated water, or cool water, the skin alone may suffice for respiration; gills are used in addition

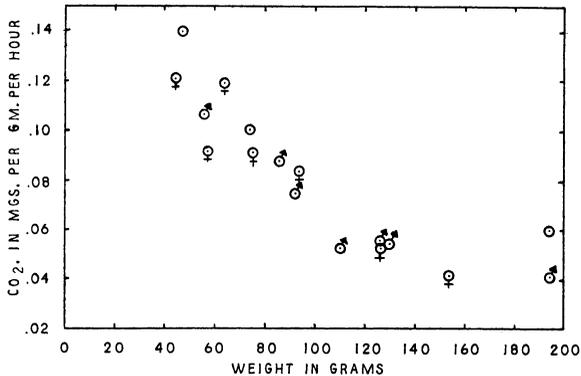


FIG 1. Influence of weight on CO₂-production in *Necturus*. (Data from H. M. Smith, *Biological Bulletin*, 48, 1925).

in ordinary stream and lake conditions, and lungs are pressed into service (possibly?) only as means of surviving in poorly-aerated water, or in water which raises the metabolic requirements to a level which skin and lungs cannot supply.

Finally, too much oxygen may be as harmful as too little. Incidental to the study of the toxicity of oxygen on various parasites, Cleveland (1925) noted that oxygen at 3.5 atmospheres kills young *Necturus* in fifty to sixty hours.

The carbon dioxide production per unit of weight in *Necturus* decreases as the weight of the animal increases (Figure 1). Small *Necturus* release more CO₂ per unit of weight than do larger *Necturus*; females usually release less than do males. Also, there are daily fluctuations in the "quality" of CO₂ production.

Starvation seems to increase the production of CO₂ per unit of weight (Figure 2). The smaller volume of tissue in a starved animal actually produces more carbon dioxide than the greater volume of tissue in the non-starved animal. Starvation of other Amphibia seems to produce a decrease in carbon dioxide output (Harvey M. Smith, 1925).

Sound-Production

Gibbes (1853) was the first to make any mention of sound production in *Necturus*: . . . Occasionally rising to the surface, they would open their mouths and take in a bubble of air, which

was immediately after passed out beneath the surface of the water with a sound as of a faint squeak, the only approach to voice that was perceived. . . . In an article on the breathing apparatus, Kneeland (1858) noted that "these animals, even when their branchiae are in full play, occasionally come to the surface and swallow air, which they emit in the water with a faint squeak, by means of the voluntary muscle with which the lungs are supplied."

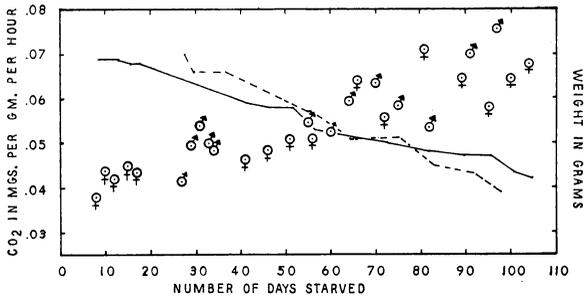


FIG. 2. Influence of starvation on CO₂-production in *Necturus*. The female (solid line) weighed 139 gms. on Day 8, and 112 gms. on Day 104. The male (broken line) weighed 140 gms. on Day 27, and 109 gms. on Day 97. (Data from H. M. Smith, *Biological Bulletin*, 48, 1925).

Bennett (1937) reported a distinct "bark" emitted every few minutes, or only once or twice a day, depending on the impurity of water. The "bark" was heard only when the animals were in shallow water. In deep water, Bennett's pets never barked, but "made a peculiar bubbling sound".

Maslin (1950) studied the general problem of the production of sound in caudate Amphibia, but unfortunately did not include *Necturus*. He reported four ways in which the Caudata produce sounds: (1) As the mouth is opened, air breaks the moist seal of the lips; the method is based on inspiration of air, not expiration. "Clicking", "clucking", or "kissing" sounds are produced. (2) Air is forced through the branchial fissures. "Whistling" sounds are produced. (3) An air-reservoir or resonating chamber is emptied, forcing air through a vibrating valve. "Squeaking" sounds are produced. Interestingly, this is the method of sound production used by the lungless salamanders; Maslin was uncertain whether the "vibrating valve" was in the esophagus, the nares, or at the lips. (4) The air store is pulmonary, and the valves are located in the larynx. "True voice" is produced.

Sounds are produced by *Necturus* either by inspiration of air when the mouth is opened above water, or by forcing air through the gill slits. If the air is forced through the gill slits before the head is submerged, definite "squeaks" might be produced; otherwise, only bubbling sounds would issue.

Necturus has a tiny glottis located well back in the pharyngeal floor; there is a diminutive larynx; and simple paired lungs are present. The glottis is patent; when the gas-filled lungs are squeezed, bubbles issue from the glottis. However, it is not certain that *Necturus* ever breathes atmospheric air, so there may be no opportunity to produce true voice.

Though probably mute, *Necturus* is not deaf. That is to say, it is responsive to vibrations which jar against it in the water. Vibrations may be transmitted to the otic region through either of two routes. A levator scapulae muscle connects the suprascapula and the floor of the otic region; vibrations received through the pectoral appendage might be transmitted through this muscle to the ear. Or, vibrations may be transmitted to the columella of the ear through the mandible. The mandible articulates with an ossified area of the quadrate; the quadrate touches the squamosal, and a process of the latter joins the columella. Also, the mandible joins the hyoid through a mandibulo-hyoid ligament; and the ceratohyal joins the quadrate by a hyosuspensorial ligament (Huxley 1874a, b; Cope 1889; Reed 1914, 1915, 1920; Kingsbury & Reed, 1909a, 1909b). Instead of an ear to the ground, *Necturus* needs to keep its chin to the ground to hear!

The scattered lateral line organs of *Necturus* are also reported to be receptors of sound. Dye (1921) suspended some *Necturus* in wire cages in aquaria, so vibrations reaching them had to travel through the water. A wire outside the aquarium was made to vibrate at 120 times or less per second. Normal mud-puppies showed three types of responses: (1) rate of gill movements increased and was maintained at a higher rate for a brief period; (2) gills, if moving, stopped; (3) the whole animal moved suddenly, as if startled. After the above responses were noted, the VII and IX cranial nerves (which innervate the lateral line system) were cut; and the responses practically stopped. Operated animals were tested at 2-day intervals. Doubtful responses to sound were noted on the 18th day; on the 21st day the animals responded as they did before the operation.

Kuroda (1926) found evidence that lizards, frogs and toads can hear, but found none for turtles or Urodeles (*Triton* and *Hynobius*).

The first noted Occurrence of *Dasyopus bellus* in Texas

Bob H. Slaughter

A small group of persons, "The Dallas Prehistorical Society", has for several years been collecting fossil bones from the second of a series of alluvial terraces of the Trinity River. We have assembled a rather extensive fauna. Our faunal list has not been published in full, although some specimens have been reported as new species. As some time will elapse before the faunal paper will be ready for publication, it seems well to report here the first Texas record of *Dasyopus bellus* (Simpson).

The "T-2 Terrace" (local usage) stands some 70 feet above the stream level at Dallas, and is divided into 4 easily recognizable units: in ascending order, (1) basal gravel (Hill), (2) clean laminated sand (lower Shuler), (3) sandy clay, becoming less sandy toward the top (upper Shuler), and (4) dark gumbo, separable from the upland soils only by the presence of small caliche nodules (Richards).

Although there are a few erosional exposures, most of the fossils have come to us from excavations to secure sand and gravel for construction. Crook & Harris (1958) concluded that deposition of the terrace deposits were made during an interglacial or interstadial. Certain faunal elements and two carbon dates (Brannon *et al.*, 1957)—both indicating an age in excess of 37,000 B.C.—suggest the last interglacial (Sangamon?). Both carbon dates were from the lower portion of the upper Shuler, while the specimen here described was collected by R. K. Harris and myself from the upper Shuler near its contact with the overlying "Richards", in association with *Mammut*, *Mammuthus*, *Bison* (large), *Camelops*, *Castor*, *Testudo*, and at least 2 species of horses. The locality is on Hickory Creek, near its junction with the Trinity River in southern Denton County. Our *Dasyopus bellus* material was sent to Walter Auffenburg at the University of Florida for comparison with material from that State, and no important differences were noted.