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# Metabolic Correlates of Activity in the Caecilian *Geotrypetes seraphini*

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Metabolic factors involved in energy production during activity were examined in the West African caecilian *Geotrypetes seraphini occidentalis*. This species exhibits violent escape behavior during stimulation but fatigues rapidly. Measurements of oxygen consumption and lactate production during activity indicate that nearly 90% of the energy produced during 2 min of activity is derived from anaerobic sources. The pattern of oxygen consumption during activity and the morphology of the integument and lungs of caecilians suggest that oxygen uptake is primarily pulmonary rather than cutaneous.

THE Amphibia, once a much larger and more diverse group, is now represented by only three extant orders: Anura (frogs and toads), Urodela (salamanders) and Gymnophiona (caecilians). Information concerning the interrelations and derivations of these groups is of considerable evolutionary importance, but at present their phylogeny is only a subject of speculation. One of the principal difficulties in elucidating these relationships is the almost total lack of information about the Gymnophiona, in contrast to the data available for anurans and salamanders. This paper presents some of the first comparative physiological observations among these three groups. Such comparative studies will eventually produce a broader picture of the biology of these animals and hopefully clarify their relationships.

Caecilians are blind and limbless burrowing animals, confined to tropical regions. Because of their propensity for life in burrows, stream banks or murky water, they are seldom seen or collected by biologists. Virtually no physiological measurements have been made on caecilians. Resting metabolic rate, a fundamental measurement of energetic expenditure, has been reported for only one species (Sawaya, 1947). The present study examines metabolism during rest and stimulated activity, the relative contributions of aerobic and anaerobic metabolism to this activity and the pattern of oxygen debt in the West African caecilian *Geotrypetes seraphini occidentalis*. This species lives in burrows in sandy mud banks of forest streams in the lowland humid tropics. Adult animals are rather small, attaining a maximal length of 400 mm and a diameter of 10–15 mm. They are a dull purplish-gray and are marked

with superficial annulae caused by the pull of muscle-connective tissue elements on the skin. *Geotrypetes* is a member of the Caeciliidae, a relatively generalized family.

## MATERIALS AND METHODS

Juvenile specimens of *Geotrypetes seraphini occidentalis* (mean weight, 1.93 g) were collected in Tafo, Ghana. They were transported to the United States and housed at 20–25 C in either aquaria with damp soil or plastic containers with moist paper towels for several months before experimentation. The animals remained healthy, constructed burrow systems in the soil or hid under the paper towels, and fed regularly on earthworms. Animals were fasted for at least two days before experimentation.

Oxygen consumption at 20 C was measured in a small manometric chamber connected to a Warburg manometer, as previously described by Bennett and Licht (1973). The chamber contained wet filter paper to provide an atmosphere saturated with water vapor; a small dish containing 15% KOH absorbed carbon dioxide. The animal sat within a small wire cage on an electrical grid through which electrical shocks could be delivered. The chamber was immersed in a constant temperature water bath set at  $20 \pm 0.2$  C. Appropriate thermobarometric controls were made with each determination.

Oxygen consumption during rest and during and after activity was measured individually in four animals. An animal was weighed, placed in the metabolism chamber, and permitted at least two hours to attain a resting condition and thermal equilibrium. Oxygen consumption was then measured for

one hour, during which metabolic rates were low and uniform. Animals were stimulated electrically (5–10 volts) for 2.0 min. Oxygen consumption was measured during and after activity over intervals of 5 to 15 min until postactive oxygen consumption was indistinguishable from previous resting levels. Measurements of oxygen consumption were converted to STP and expressed as  $\text{cm}^3$  of oxygen per g body weight per hour.

Anaerobic energy production was determined by measurement of total lactate content. Four animals were used to determine the pattern of anaerobic energy generation; their rarity precluded the use of more than one animal in each activity state. However, the variability within an activity group of such measurements on other amphibians and on reptiles is small (Bennett and Licht, 1972, 1974), and these single measurements probably indicate the true parameters fairly accurately. The animals were weighed and left undisturbed overnight in individual containers containing wet paper towels in a constant temperature cabinet at  $20 \pm 0.2$  C. Animals were removed the following day and stimulated manually for 30 sec, 2 min or 10 min. The animals moved rapidly around in their containers at activity levels comparable to those obtained by electrical stimulation. Immediately after activity the animals were decapitated and total lactate content was measured according to the method of Bennett and Licht (1972). One unstimulated animal was used as a resting control. Lactate content is reported as mg lactate per g body weight.

The morphology of the integument of *Geotrypetes* was examined histologically to assess its capacity for oxygen exchange. It was compared to that of a plethodontid salamander, *Batrachoseps attenuatus*, which relies almost entirely on cutaneous oxygen exchange.

## RESULTS

The diurnal resting metabolic rate of *Geotrypetes seraphini* is  $0.037 \pm 0.003 \text{ cm}^3 \text{ O}_2/(\text{g} \times \text{hr})$ . The rate of oxygen consumption during two min of activity is too low to determine accurately, so it was integrated with the first five min postactivity measurement. Oxygen consumption during this period increases more than 400% above resting levels to a mean value of  $0.159 \pm 0.012 \text{ cm}^3 \text{ O}_2/(\text{g} \times \text{hr})$  (Fig. 1). Aerobic scope, the difference between resting and

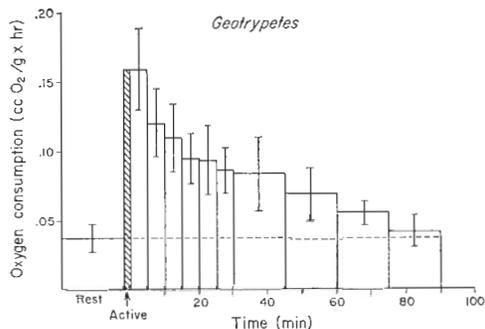


Fig. 1. Oxygen consumption in *Geotrypetes seraphini* during rest and during and after 2 min of stimulated activity at 20 C. Resting levels were maintained for one hr before stimulation. Measurements of oxygen consumption during and after activity were measured over 5 to 15 min intervals, indicated by the width of the vertical bar. Mean values of four animals are reported; vertical lines indicate 95% confidence limits of the means.

maximal oxygen consumption, in *G. seraphini* is  $0.122 \text{ cm}^3/(\text{g} \times \text{hr})$ . Maximal levels of oxygen consumption are attained during or immediately after activity; thereafter, it decreases exponentially until it returns to preactive resting levels in approximately 75 min after cessation of activity. The oxygen debt, the total amount of oxygen in excess of resting levels consumed during and after activity, is  $0.062 \text{ cm}^3/\text{g}$ .

During activity, *Geotrypetes* respond violently for the first minute of stimulation. They move rapidly, coil and uncoil, thrust with their heads as though seeking shelter. They fatigue rapidly, however, and activity level decreases with sustained stimulation. They become very lethargic after about five minutes, but are still capable of slow locomotion. The rate of lactate formation parallels this behavioral sequence. Lactate content of the resting animal was 0.20 mg/g; animals stimulated for 30 sec, 2 min and 10 min had contents of 0.53, 0.70 and 0.95 mg lactate/g, respectively. The maximum rate of lactate formation, the anaerobic scope (see Bennett and Licht, 1972), occurs during the first 30 sec of activity and equals 0.65 mg lactate/(g  $\times$  min). The anaerobic capacity, the amount of lactate formed during activity to near exhaustion, is 0.74 mg lactate/g in *Geotrypetes*.

The relative contribution of aerobic and anaerobic energetics to total energetic output can be estimated by calculation of the

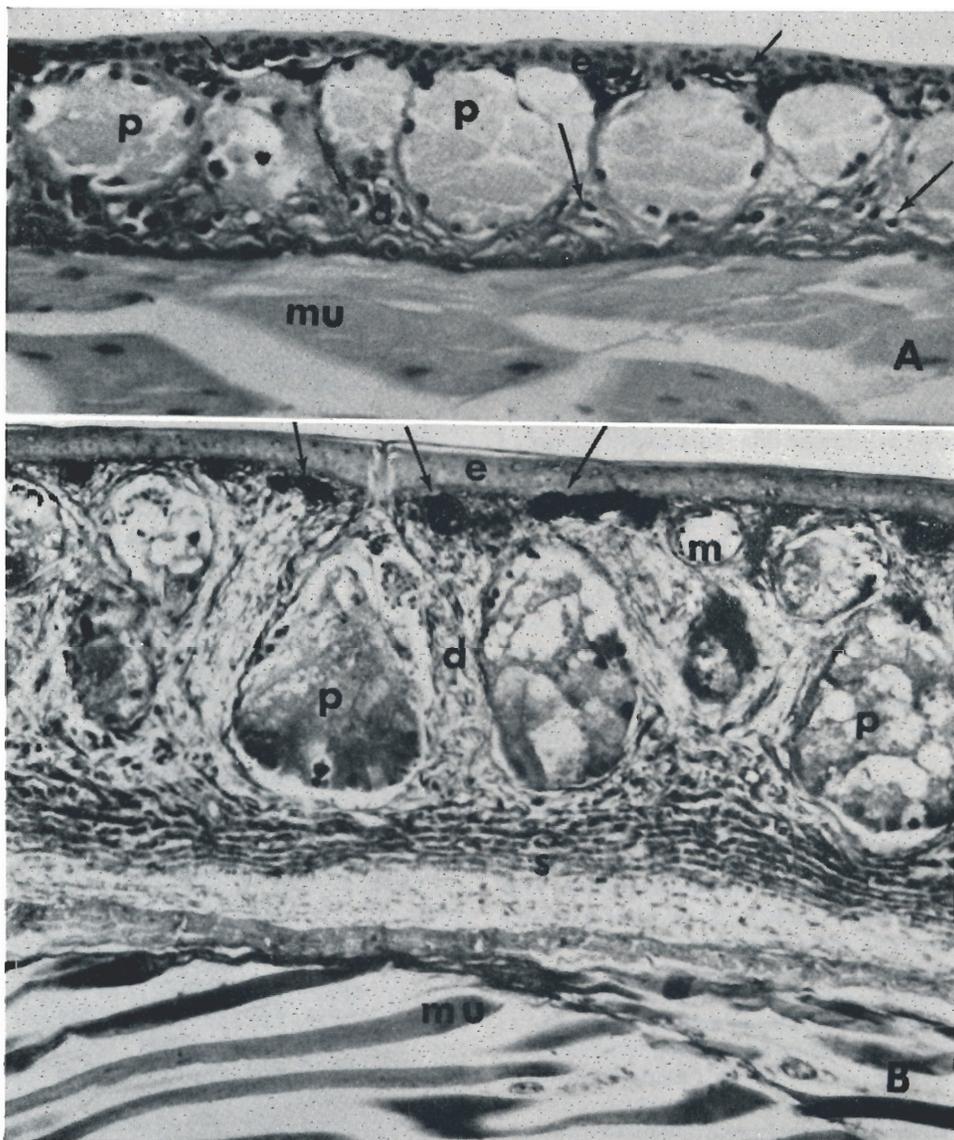


Fig. 2. A. Skin of *Batrachoseps attenuatus*; parasagittal section, 100 X. B. Skin of *Geotrypetes seraphinii*; parasagittal section, 100 X. Abbreviations: d = dermis; e = epidermis; m = mucous gland; mu = muscle; p = poison gland; s = stratified dense dermis. Capillaries are indicated by arrows; these are intended to show structure and not numerical distribution. Note particularly the differences in epidermal thickness, dermal structure, and capillary distribution between the two species. (Photomicrographs courtesy of P. Hermes.)

amount of ATP produced by each metabolic pathway. These are estimated from measurement of lactate content and oxygen consumption according to the equations of Bennett and Licht (1972):

$$1.0 \text{ mg lactate formed} = \\ 0.0167 \text{ millimoles ATP}$$

$$1.0 \text{ cm}^3 \text{ O}_2 \text{ (STP) consumed} = \\ 0.290 \text{ millimoles ATP}$$

During a 2-min burst of activity, *Geotrypetes* forms 8.9 millimoles ATP/g body weight anaerobically and 1.2 millimoles ATP/g aerobically; the total ATP formation during activity is 10.1 millimoles/g. Thus, 88% of

its energetic production is anaerobic, or 7.3 times as much ATP is produced anaerobically as aerobically. During the first 30 sec of activity, 5.4 millimoles ATP/g are produced anaerobically. If oxygen consumption is maximal during this time, 0.3 millimoles ATP/g would be produced aerobically, and 95% of the ATP production would come from anaerobiosis.

The integuments of both *Geotrypetes* and *Batrachoseps* are highly glandular structures (Fig. 2). Despite this obvious common feature, there are substantial morphological differences. The skin of the caecilian is over twice as thick as that of the salamander. The epidermis of *Geotrypetes* is three to six layers deep and is tightly organized; that of *Batrachoseps* is much looser and is only two cell layers deep. The dermis of *Geotrypetes* is thick and is organized as a loose dermis above, containing glands and scale pockets, and a dense stratified dermis below. The dermis of *Batrachoseps* is loose and contains several kinds of skin glands, some extending through the entire layer. Especially noteworthy is the distribution of capillaries in the skin. *Batrachoseps* has many large capillaries at the epidermal-dermal junction, and numerous smaller ones throughout the dermis. *Geotrypetes* has a few large capillaries at the epidermal-dermal border and essentially none throughout the deep dermis.

#### DISCUSSION

*Geotrypetes* is revealed by this study to be primarily dependent on lactate formation for energy during activity. This anaerobiosis permits a very rapid activity response, such as fast withdrawal into a burrow or grabbing and tearing a prey. Observations on feeding and predator avoidance in this species suggest that a rapid response is used in both situations. *Geotrypetes* (and other terrestrial caecilians) have two modes of prey manipulation. If an elongate prey item, such as an earthworm, is met head-on, *Geotrypetes* seizes it in its jaws and ingests it by successive bites. If the prey is met laterally, *Geotrypetes* grabs it with its jaws and retreats further into its burrow, rapidly spinning its body around and around so that the sides of the burrow are used to shear off parts of the prey protruding from the mouth. This second feeding mode requires rapid activity of short duration. Anaerobiosis affords the activity response, but limits the length of

time during which maximal activity can be sustained. Endurance is low; high levels of activity cannot be maintained for more than two or three minutes. Such a response is not particularly surprising in a vermiform animal which does not travel long distances and can rely on its burrow as a refuge from predation. It is known that the snake *Miodon acanthias* preys upon *G. seraphini*, and that it pursues the caecilian a short distance into its burrows in soft, sandy soil of streambanks (Cole, 1967). Cole reports great activity and fast re-burrowing in a few seconds when he unearthed *G. seraphini*, and he suggests that disturbance of the burrow by predators (human or snake) causes a rapid retreat deeper into the burrow.

Sawaya (1947) reported resting metabolic rate in two individuals of *Typhlonectes compressicauda*, members of the aquatic family Typhlonectidae. Rates for each were 0.049 cm<sup>3</sup> O<sub>2</sub>/(g × hr) (137 g; 21.7 C) and 0.149 cm<sup>3</sup> O<sub>2</sub>/(g × hr) (64 g; 24.8 C). We have also determined that resting oxygen consumption in a 12-g individual of *Caecilia occidentalis* at 15 C was 0.045 cm<sup>3</sup> O<sub>2</sub>/(g × hr). An extensive study (Mendes, 1945) on resting oxygen consumption in *Siphonops annulatus* cannot unfortunately be compared because of the inadequately reported metabolic data and the lack of control of body temperature. Our values for resting metabolic rate in *Geotrypetes*, considering differences in body size and temperature, are substantially below those measured for *Typhlonectes* and *Caecilia*. They are also considerably below most values reported for anurans and urodeles of comparable size (Hutchison, 1971), including *Hyla regilla* and *Batrachoseps attenuatus* measured with identical apparatus and techniques (Bennett and Licht, 1973b). However, due to lack of data and standardization of measurement techniques, it is impossible to determine at this time whether the maintenance requirement (resting metabolism) of caecilians is different from that of other amphibians.

The capacity of *Geotrypetes* for rapid or sustained anaerobiosis is not exceptional when compared with that of some anaerobic anurans and urodeles, even though its activity pattern appears limited by anaerobic factors. Anaerobic scope is within the range of those of eight species of amphibians (range: 0.12–1.31 mg lactate/(g × min) (Bennett and Licht, 1974). Anaerobic capacity is also intermediate to those of these same

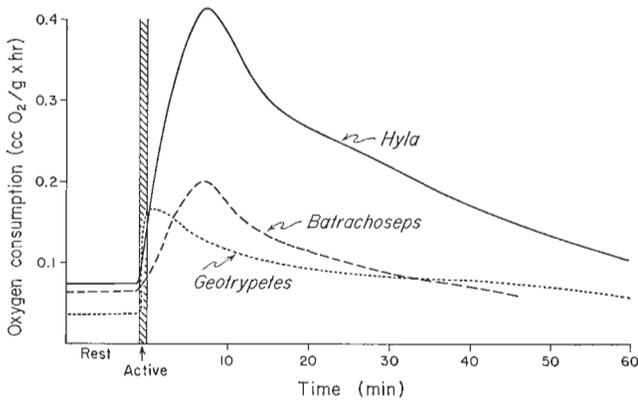


Fig. 3. Oxygen consumption before, during and after activity at 20 C by *Geotrypetes seraphini*, *Hyla regilla* and *Batrachoseps attenuatus*. Data for *Geotrypetes* are taken from Fig. 1; data on *Hyla* and *Batrachoseps* are from Bennett and Licht, 1973b.

eight species (range: 0.12–1.45 mg lactate/g) (Bennett and Licht, 1974). Within the context of amphibian metabolism, *Geotrypetes* appears to possess only moderate capabilities of both aerobiosis and anaerobiosis. Its activity energetics resemble those of *Hyla regilla* in many respects, particularly in the total amount of energy mobilized during activity and the proportion of that energy derived anaerobically (Bennett and Licht, 1973). *Geotrypetes* and *Hyla* are moderate anaerobes, in contrast to the strongly anaerobic *Batrachoseps* and the aerobic *Bufo* (Seymour, 1973; Bennett and Licht, 1973). Whether the activity physiology of *Geotrypetes* is representative of caecilians as a group is unknown: considerable interspecific differences occur among both the urodeles and anurans (Bennett and Licht, 1973, 1974). However, the intermediate position which this animal occupies in the observed range of amphibian activity responses suggests at least that there must be broad overlaps in the physiological capacities of these three groups.

Anurans and urodeles utilize their integument as a site of oxygen uptake and carbon dioxide release. The proportion of total oxygen consumption derived by cutaneous respiration in these groups can be substantial (Hutchison et al., 1968; Whitford and Hutchison, 1965), and plethodontid salamanders, such as *Batrachoseps*, rely almost exclusively on the skin as the site of oxygen uptake (Elkan, 1955; Czopek, 1962; Whitford and Hutchison, 1965). The extent of reliance on cutaneous respiration in caecilians has not

been determined. Elkan (1958) concluded that there is no extensive oxygen uptake in the bucco-pharyngeal region of *Schistometopum thomensis*. Several authors (Sarasin and Sarasin, 1887; Fuhrmann, 1912; Sawaya, 1941; Mendes, 1941; Lawson, 1966) have stated that the presence of integumentary capillaries suggests that the integument is important in gas exchange. Cutaneous carbon dioxide release has been reported in *Siphonops* and *Typhlonectes* (Mendes, 1941; Sawaya, 1947). However, experiments performed attempting to partition pulmonary and cutaneous oxygen uptake suggest that the magnitude of the latter is small. In the aquatic species *Typhlonectes compressicauda*, 94% of the oxygen uptake is pulmonary (Sawaya, 1947). Anaesthetized, and consequently non-ventilating, *Siphonops annulatus* showed a greatly reduced oxygen uptake (Mendes, 1945).

The pattern of oxygen consumption during and after activity in *Geotrypetes* supports the contention that oxygen uptake in caecilians is primarily pulmonary and not cutaneous. Oxygen consumption rises rapidly and reaches maximal values during or immediately after activity (Fig. 3). In contrast, the rise in oxygen uptake in *Batrachoseps*, an animal reliant entirely upon cutaneous oxygen exchange, is slow, and maximal values are not attained until 5 to 15 min after cessation of activity. *Hyla regilla* has a factorial increment of oxygen consumption during activity similar to that of *Geotrypetes*, but further increments in oxygen uptake occur after cessation of ac-

tivity. This pattern of delayed aerobic scope in *Hyla* and *Batrachoseps* was interpreted as a reflection of the time necessary to increase cutaneous oxygen uptake (Bennett and Licht, 1973). Presumably a pulmonary system with a variable respiration rate is capable of a more rapid adjustment to changes in oxygen demand than a non-ventilated cutaneous system.

These conclusions regarding the site of oxygen uptake are supported by the morphological structure of the integument and lungs of caecilians in contrast to those of urodeles and anurans. The more compact and less vascular integument of caecilians is less well suited for cutaneous oxygen uptake than is that of a lungless salamander (see Results section). The lungs of caecilians are complex, highly vascular structures in contrast to the absence of lungs in plethodontids and some other salamanders, and to the simple sac-like lungs of the majority of salamander and frog species. Terrestrial caecilians have a single, elongate lung that is highly compartmentalized. In many species, including *G. seraphini*, the lung compartments are supported by rings of cartilage to which smooth muscle tissue is attached, providing a passive recoil mechanism to ventilate the lung. The pulmonary epithelium is extensively elaborated, and is highly vascularized. The presence of a structurally complex lung and an integument with a morphology which does not suggest efficient cutaneous respiration indicates that oxygen consumption is primarily pulmonary in caecilians.

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