DEVELOPMENT OF *LEPTOPELIS VIRIDIS CINNAMOMEUS* (BOCAGE) WITH NOTES ON ITS SYSTEMATIC POSITION

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The taxonomic studies of J. Poynton (1964a, 1964b and 1966) and A. Schiotz (1967) indicate a remarkable parallel between the speciation of the genus *Leptopelis* in West, South and East Africa. The tree, ground and fossorial forms in each locality show convergent characteristics with minor variations. The fossorial habit is occupied in West Africa by *L. bufonides* and in South and East Africa by *L. bocagei* (Loveridge 1953; Stewart 1967), the latter being larger and lacking the warty dorsum of the former.

However another semi-fossorial species *L. viridis cinnamomeus* which extends south-east from Katanga to northern Mozambique, complicates the taxonomy of *Leptopelis* in Malawi. Parker (1931, 1938) treats *L. bocagei* as a vicariating form of *L. viridis*. Poynton (1966) suggests that both *L. bocagei lebeaui* of Schmidt and Inger (1959) and *L. concolor* of Poynton (1964a) are representatives of a single species which forms a cline from Central Africa to Zululand. Following Laurent (1964), Poynton calls these *L. viridis cinnamomeus*, distinguishable from *L. bocagei* by fingers that do not taper towards their ends, and from *L. concolor* by the presence of pectoral glands. There would thus be a gradation in the degree of adaptation to ground life and the fossorial habit ranging from *L. viridis* and *L. concolor* through *L. viridis cinnamomeus* with its considerable variation, to *L. bocagei*. The following data on the development of *L. viridis cinnamomeus* are presented to support this "transitional" interpretation of the subspecies.

L. viridis cinnamomeus were collected in the Blantyre area on November 17th, 1968, after the first heavy rains of the year, and kept in an aquarium on moist earth at 24°–27° C, room temperature. By November 18th the pair were in amplexus about two inches below the surface of the soil. The male had shovelled away earth from behind and below him, while keeping a hold on the female, to form a shallow pit, backed by the glass of the aquarium. Eggs were laid during the night and were found in groups in the soil after the burrow had been vacated by the parents. Eggs placed in water died while normal development was achieved in eggs kept in slightly moist soil. After thirty days the egg membranes were ruptured by the strong thrashing of the tadpole's tail. Eggs were transferred to shallow petri dishes containing pond water, into which subsequent tadpoles were allowed to hatch.

Apart from the absence of any definite tapering of the fingers the female fitted Stewart's description of *L. bocagei*. A full description of the male will be given below.

Total Body Length, 52 mm. Colour, a brown-black dorsal saddle mottled at centre and periphery, venter cream-white; interorbital bar, 11 mm; limbs with a thin white line along the periphery; internarial distance, 7 mm; tympanum, 4 mm in diameter bearing supratympanic fold; canthal ridge present; nostril closer to eye than to the tip of the snout; vertical pupils; pectoral glands present. Limbs: front fingers free not tapered; back limbs with thin web reaching to the sub-articular process of the third toe; toe disc hardly expanded; tibia 12 mm; femur 20 mm; length of inner metatarsal tubercle x 1½ length of inner toe.

TABLE OF DEVELOPMENT AT 24–27°C

Time after laying	*Stage*	*Observations*
20 hrs	Early blastula	Embryo size 4,5–5 mm in diameter, cream-yellow.
26 hrs	Mid-blastula	Distinct animal pole area of paler looking cells –3 mm in diameter. This area represents a thin covering of cells above the blastocoel and is an indication of blastocoel size.
30 hrs	Late blastula	Animal pole area – 3,5 mm in diameter.
34 hrs	Onset of gastrulation	Lip of blastopore apparent.
38 hrs	Early gastrula	Animal pole area 3,75 mm. Lip of blastopore crescent 2–4 mm long.
43 hrs	Mid gastrula	Animal pole area 4 mm. Yolk plug 2,6 mm.
56 hrs	Late gastrula	Animal pole area reduced to 3,5 mm. Yolk plug 0,4 mm diameter. Size of embryo 5,5 mm.
64 hrs		Animal pole area 0,9 mm in diameter. Yolk plug reduced to a point.
69 hrs		Animal pole area disappears as blastocoel obliterated completely.
3½ days	Early neurula	Embryo 6,5 mm. Neural folds appearing. Remains of blastopore still visible.
4½ days	Mid neurula	Appearance of discrete neural axis. Embryo elongating.
5½ days	Late neurula	Neural folds closing. Elongate neurula lying on yolk mass.
6½ days	Early tadpole	Prominent head bulge.
7 days		Head bulging out away from yolk sac. Neural tube fully closed.
8 days		Eye cups appearing.
8½ days		Eye and mouth visible. Head movements. Heart pale. Gill primordia visible.
9 days	External gill	Melanocytes on dorsum forming pigment. Three sets of primordia of external gills on each side.
10–14 days		Prominent beating heart and vascularised gills on each side.
		Blood vessels vascularising yolk round which tadpole is curved, head to tail. Pineal body marked by absence of pigment over mid-dorsal region of the head.

15 days	Internal gills	Right gill resorbed leaving left external gill, pointing away from yolk mass. Yolk served by extensive network of blood vessels. Complex anastomoses in tail serving respiratory needs. Fig. 1 and Fig. 2. Left gill resorbed.
17 days		Yolk showing coiling imposed by formation of gut.
23 days		Heavy pigmentation on tail and dorsum. Teeth appearing on mouth armature. Yolk almost absorbed and signs of faeces in rectum. Spiracle on left side. Tail, strong movement.
25 days		Mouth armature more complex. Post. limb buds evident. Pineal patch still unpigmented, sensitive to light. Fig. 3.
26–30 days	Hatching	Hatching. Tadpoles average head to tail 25 mm, tail x 2 body length.
4 months	Metamorphosis	Acceleration of limb growth. Appearance of vivid green colour on dorsum and on dorsal surface of legs. Tadpoles crawl on rocks. Average 60 mm. Head to tail. Fingers and toes with marked suckers. Fig. 4 and 5.
4 months + 4 days	Froglet	Tails absorbed within 48 hours 15 mm of tail absorbed in 24 hours. Froglets out of water. Vivid green dorsum. Eyes enormous. Fig. 6.
4 months + 14 days		Digital suckers of froglet reduced to typical adult size.

Development therefore takes full advantage of the rainy season, extending in Malawi from November to March. During the period from November to December when rains can be erratic, or heavy rain is followed by prolonged drought, or late rains, development takes place within the egg membranes with a plentiful supply of yolk and metabolic water. Although yolk supplies are extensive and gastrulation prolonged, the tadpole, unlike burrowers such as *Breviceps mossambicus* and *Arthroleptis* species, does not reach metamorphosis within the egg.

The tadpoles of *L. viridis cinnamomeus* have one complete and three divided rows of teeth above the jaws, and three complete rows below. There are a double row of papillae below and single papillae at the sides of the jaw. The papillae at the sides of the jaw are expanded – see Fig. 7 – at the level of the upper jaw. A dorsal view of the mouth shows further expansions – see Fig. 8. Jaw shape resembles Wager's (1965) drawing of *L. natalensis* although both lower and upper jaws appear stronger and more substantial.

The most interesting feature of the young froglet is its remarkable similarity to *L. viridis*

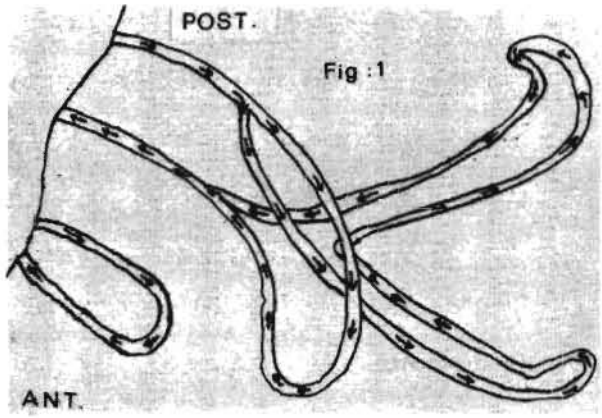

Fig 3

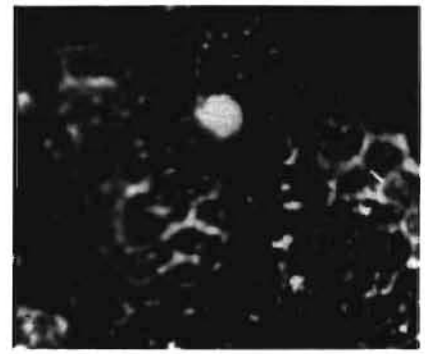

FIGURE 1: Blood flow in external gills. FIGURE 2: External gills left side, 10–14 days. FIGURE 3: Head, mid-dorsal region, showing clear area above pineal, 25 days.

in colour and in its possession of small digital suckers. The froglet has a vivid green dorsum and is able to stick to the glass of the aquarium with ease. The expansion of the tips of the digits is most noticeable on fingers IV and III. Within two weeks of resorption of the tail this expansion is no longer visible and the young froglet spends most of its time on the ground away from water. This feature coupled with the colour change from sedge green to mottled brown represents the loss of characters associated with the tree habit and adaptation to the ground habit.

The progressive adaptation to the fossorial habit, with development of metatarsal tubercles, loss of suckers, colour change from sedge green to brown is shown in West Africa in the contrast between *L. viridis* and *L. bufonides*. In Central Africa this tendency to take up a ground – shallow fossorial habit is clearly shown in *L. viridis cinnamomeus*.

It is therefore instructive to notice how features associated with the tree habit are expressed transiently in the young froglet before adult adaptations to shallow burrowing appear.

FIGURE 4: Dorsal view. Resorption of pigmented tail half complete, 4 months, ×2. FIGURE 5: Ventral view ×2, showing digital pads, 4 months. FIGURE 6: Froglet ×2 showing increased development of eyes.

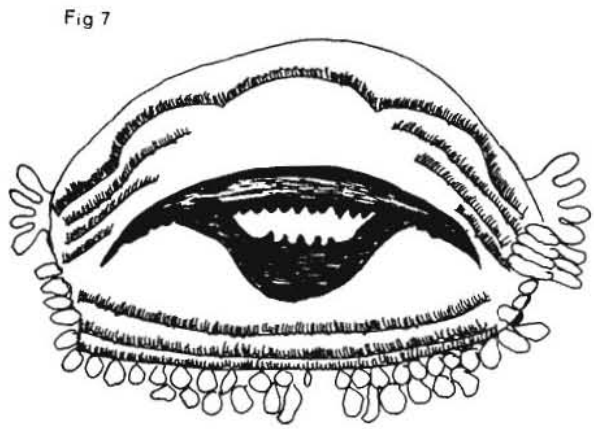

FIGURE 7
Diagram of tadpole mouth at 2 months.

FIGURE 8
Dorsal view of tadpole mouth × 50.

The development of *L. viridis cinnamomeus* showing adaptations to tree and ground habits at different phases of ontogeny, supports an interpretation of this subspecies as a population of *L. viridis* in the process of adopting the fossorial habit.

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