THE BEHAVIOUR OF SOUTHERN AFRICAN ANURAN TADPOLES WITH PARTICULAR REFERENCE TO THEIR ECOLOGY AND RELATED EXTERNAL MORPHOLOGICAL FEATURES

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In the course of investigations involving southern African tadpoles, begun in 1953 with a comparative morphological bias and subsequently continued with a systematic bias, it was necessary to collect nearly all species for study purposes. Besides the systematic observations published (van Dijk 1966 and 1971a), a considerable body of observations on the behaviour and ecology of southern African tadpoles has accumulated, largely because a knowledge of the behaviour of the animals is essential for efficient collecting. As with the adults there is a discernible association between the microhabitats and aspects of the behaviour such as locomotory modes, feeding and predator avoidance (van Dijk 1971b). The morphology of the tadpoles, like that of the adults, is well correlated with the behaviour, particularly the locomotory modes. In this connexion it must be borne in mind that less obvious features of the morphology may permit two or more types of behaviour which ultimately lead to obvious differences in morphology. This is easily seen in the adults, where disc-toed arboreal *Leptopelis* dig under moss using a reciprocating movement of the hind-limbs similar to that used in climbing, and a more specialized fossorial species, *L. bocagei*, has lost the discs and acquired digging spurs (van Dijk 1971b, Fig. 1).

The bibliography in the 1966 paper, referred to above, should be consulted for articles illustrating the various tadpoles. When examining such articles it should be remembered that photographs taken in aquaria very often do not reflect the characteristic habit of the tadpoles.

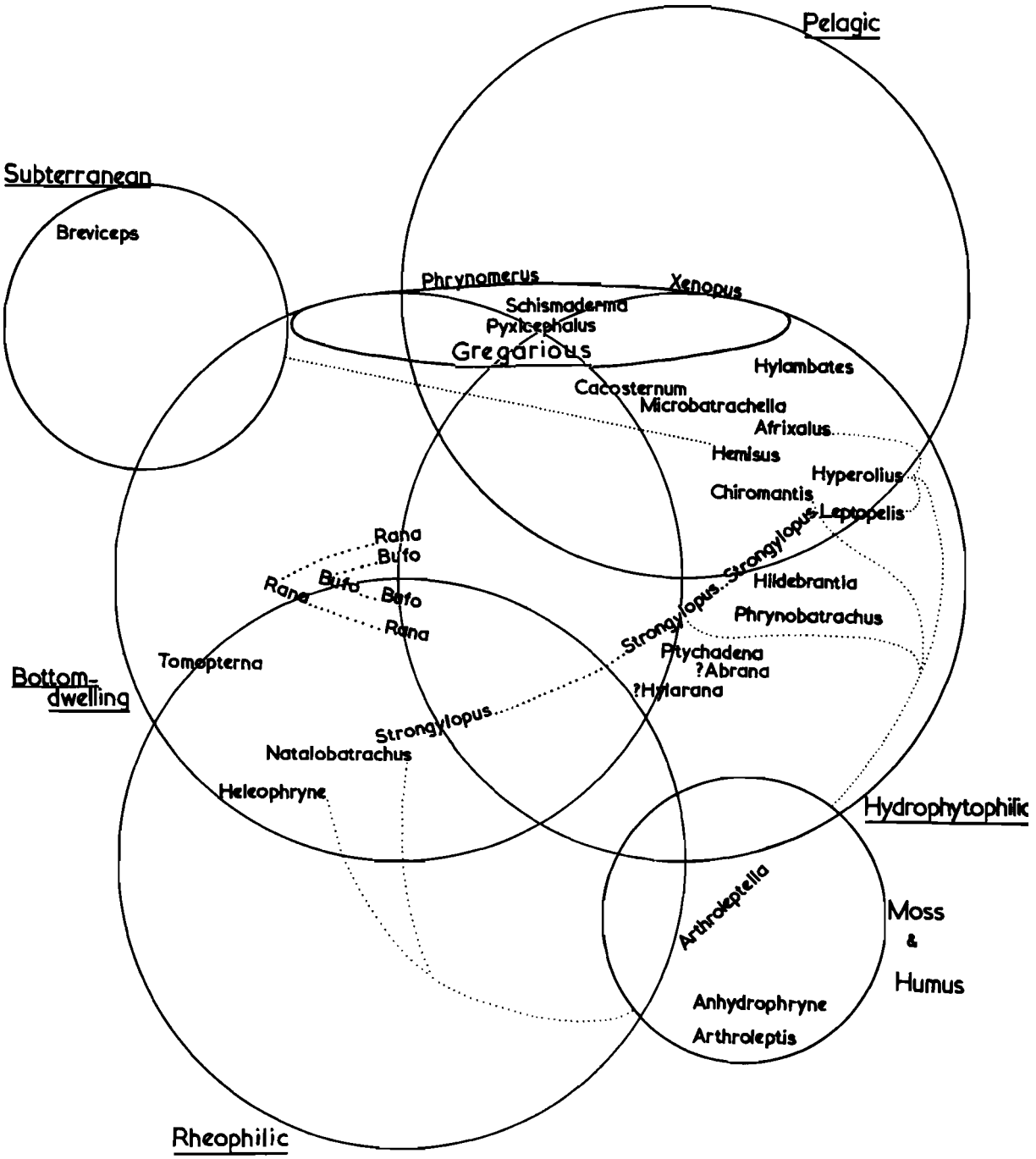
Terminology

It has been found possible to distinguish among southern African tadpoles modes of behaviour which are characteristic at about the generic level, and occasionally at species level. The major features of behaviour which must be considered are whether, if the tadpoles are able to choose, they prefer flowing water (i.e. are *rheophilic*, being torrent- or stream-dwellers) or still water, whether they are *pelagic** or bottom-dwelling, whether, if they are able to choose, they prefer regions free of macroscopic vegetation or are *hydrophytophilic*, and whether or not they are *gregarious*.

Pelagic

There are two genera of tadpoles which are pelagic in open water, namely *Phrynomerus* and *Xenopus*. Both are open-water filter-feeders, *Phrynomerus* maintaining a more or less horizontal position and *Xenopus* an oblique head-down position; in both cases the tip of the tail is

* Footnote: Pelagic refers to marine organisms. It is used here as it does not imply active swimming and includes the situation where animals are associated with submerged macroscopic vegetation away from the bottom as in the case of the *Sargassum* fauna.


Pelagic
Subterranean
Breviceps
Phrynomerus
Xenopus
Schismaderma
Pyxicephalus
Gregarious
Hylambates
Cacosternum
Microbatrachella
Afrixalus
Hemisus
Hyperolius
Chiromantis
Leptopelis
Strongylopus
Rana
Bufo
Rana
Bufo
Bufo
Rana
Strongylopus
Hildebrantia
Phrynobatrachus
Ptychadena
?Abrana
?Hylarana
Strongylopus
Tomopterna
Bottom-dwelling
Natalobatrachus
Heleophryne
Hydrophytophilic
Arthroleptella
Moss
&
Humus
Anhydrophryne
Arthroleptis
Rheophilic

narrow dorso-ventrally and pointed and vibrates to maintain the characteristic attitude. The tip of the tail of undisturbed *Xenopus* is bent upwards distally, so that the animals appear to be suspended by the tip of the tail. In both genera the individuals in a pool all tend to face in the same direction at about the same depth, suggesting gregariousness, but *Phrynomerus* tadpoles have been observed to orientate themselves against a very slow current (dust particles at the surface were observed to move at a few millimetres per second) and the presence of common orientation of a group may prove to be a rheotaxis and not gregariousness. Characteristic of these pelagic genera is, besides open-water filter-feeding and apparent gregariousness, the tendency of the groups of tadpoles, when disturbed, to disperse and remain poised without going to the bottom or continuing towards the cover of vegetation. Associated with avoidance of the bottom is a degree of transparency and reflectivity of the broad head region, so that a predator tends to see the shadow of the tadpole on the bottom more easily than the tadpole itself. Colouration is disruptive. Features of the morphology associated with the filter-feeding habit are the terminal mouth, the absence of horny mouthparts (rostrodonts or "jaws", and keratodonts or "teeth") and the large single median spiracle (*Phrynomerus*), characteristic of Microhylidae, or large paired ventral spiracles (*Xenopus*), characteristic of Pipidae. Associated with the pelagic habit are the broad head with lateral eyes, the long tail, anteriorly deep and posteriorly drawn out into a fine tip, and the transparency, reflectivity and disruptive colouration mentioned above.

Pelagic/Hydrophytophilic

The lateral position of the eyes and the anteriorly deep and posteriorly drawn out tail are also seen in the pelagic hydrophytophilic tadpoles of the genus *Hylambates (including Kassina)*, some *Cacosternum (C. boettgeri* and *C. nanum)*, *Microbatrachella* (to judge from Hewitt's 1926 description and from the related genus *Cacosternum)*, *Hemisus*, and *Chiromantis* (eyes not quite lateral). Lateral eyes and a long pointed tail which is anteriorly not very deep and posteriorly gradually tapered to a point are found in the pelagic hydrophytophilic tadpoles of *Hyperolius*, *Afrixalus*, and *Leptopelis*. The tadpoles of *Hyperolius*, *Leptopelis* and *Strongylopus fasciatus*, unlike those mentioned earlier (*Hylambates*, *Cacosternum* spp., *Hemisus* and *Chiromantis*), appear to spend much of the time resting on, or hanging from, leaves and branches of hydrophytes. *Afrixalus* tadpoles are often seen drifting in patches of open water between plants, and this is associated with the terminal mouth and reduced mouthparts and somewhat dorso-ventrally flattened head of this essentially filter-feeding genus. The significance of the pointed tail, particularly when the tip is drawn out and the tail is anteriorly deep, is that the tip can be vibrated to provide balance (and buoyancy control?) without moving the animal forwards, and to permit slow and accurate movements among the plants, while movements of the deeper anterior region of the tail serve for swift, vigorous movements.

Pelagic hydrophytophilic tadpoles tend to have disruptive colouration, with speckles on the body and particularly the tail (except some smaller species – *Cacosternum* spp., some *Hyperolius*

FIGURE 1

Modes of Behaviour and related Ecological Situations of southern African Anuran tadpoles.

Each mode is represented as an area enclosed by a boundary line. Areas of overlap indicate overlap of modes and bias towards one overlapping mode is indicated by the name of the genus involved being placed as far as possible into that mode, i.e. it approaches the boundary (or boundaries) of the mode (or modes) away from which there is bias. Where a name is placed close to a mode, but outside of it, a tendency towards that mode is indicated.

Dotted lines from extra-aquatic modes indicate early development out of water, in the case of *Hyperolius* and *Afrixalus* in some species only, in the case of *Heleophryne* on stream-side gravel (according to Visser, 1971) or rocks and of *Natalobatrachus* on stream-side rocks or trees.

Repetition of names linked by dotted lines represents a range of modes of behaviour in the genus; in the case of *Strongylopus* from left to right the name represents *S. wageri* and *S. hymenopus*, *S. grayi* and *S. fasciatus* respectively.

and *Afrixalus* – or young tadpoles, in which cases the tail fins are transparent). There is often a deeply pigmented region posteriorly on the tail with a fairly abrupt margin anteriorly so that the posterior region of the tail and the head-trunk appear as two unconnected, untadpole-like masses. Bearing in mind that insects – dragonfly nymphs, waterbugs and waterbeetles – and leeches are major predators, this camouflage may be quite effective, particularly for tadpoles which rest on, or hang from, parts of waterplants, and it is among these that this type of pigmentation is seen. In the genus *Hemisus* dense connective tissue over the proximal part of the tail muscles very effectively disrupts the outline of the muscles and may visually truncate the tail, aided by a pigmented region anteriorly or posteriorly.

For some obscure reason which may be related to maintenance of trim when swimming, the vent in all pelagic hydrophytophilic tadpoles except the recent recruit *Strongylopus fasciatus* is to the side (right) of the base of the tail, away from the margin of the ventral fin, while the vent in all other aquatic tadpoles is associated with the ventral tail fin margin, with the exception of non-pelagic *Cacosternum* spp., which may have been derived from pelagic species with basidextral vent, and the related monospecific genus *Microbatrachella*. The spiracle opens to the left in all southern African aquatic tadpoles other than *Phrynomerus* and *Xenopus*, but the smooth passage of water is less likely to disturb trim than irregular passage of faeces of variable specific gravity. It is perhaps significant that both the vent and the spiracle/s in *Phrynomerus* and *Xenopus* are symmetrically situated, facilitating maintenance of trim, while the large size of the spiracle/s not only reduces resistance to the large volume of water passing through the food-filtering system but also reduces the jet effect produced by the outflowing water. A thorough study of comparative functional morphology and locomotory behaviour in connexion with compensatory trim movements should be rewarding.

Hydrophytophilic

The tadpoles of *Phrynobatrachus, Ptychadena* and probably *Hildebrantia, Abrana* and *Hylarana* are hydrophytophilic (with pointed tails), but not pelagic, the eyes being dorsally directed, not lateral. *Phrynobatrachus* tadpoles have small mouthparts and anteriorly deep tails, and some degree of pelagic filter-feeding probably occurs. As *Hildebrantia* and *Abrana* have only one species and *Hylarana* only two species in southern Africa, the non-pelagic hydrophytophilic habit involves mainly the genus *Ptychadena*. Some *Ptychadena* and *Hylarana* are speckled in such a way as to provide good camouflage in vegetation. The rostrodonts ("horny jaws") of some *Ptychadena* species are strongly developed (and deeply pigmented) as in all species of *Strongylopus* and *Hylambates* (including *Kassina*). *Hylambates* tadpoles have been observed in the field biting repeatedly on thick stems of hydrophytes, and they destroy the macroflora in an aquarium, where they also may be seen to attack animals such as mosquito larvae and pupae and water-snails. A similar macrophagous habit may be expected in *Strongylopus* and some *Ptychadena* species.

Rheophilic

Stronglylopus tadpoles range from a hydrophytophilic form with a pointed tail-tip and pelagic habit *(S. fasciatus)* through a bottom-dwelling-hydrophytophilic form with somewhat rounded tail-tip (*S. grayi*) to torrent-dwelling forms with tails with rounded tips (*S. hymenopus* and *S. wageri*). An interesting feature of *S. wageri* is the black-tipped tail, which is to be expected in

hydrophytophilic tadpoles and not in a species known only from torrents in the Drakensberg, Qudeni, Sabie and Nkandhla. Kept in an aquarium, these tadpoles prove to spend much of the time hanging from vegetation by their mouths. The tadpoles of *Natalobatrachus,* although inhabitants of forest torrents, have tails with pointed tips. It would be interesting to learn whether these tadpoles inhabit vegetation in back-waters. Observations have been confined to the early stages and laboratory-reared later stages.

The tadpoles of the genus *Heleophryne* are classic examples of torrent tadpoles. The oral disc is expanded into a very broad sucker, the head is streamlined with dorsal eyes, the abdomen is flattened and the hind-limbs are covered by a protective ventral skin flap during development to the five-toed stage. The rostrodonts ("jaws") are reduced (*H. natalensis*) or absent, while the keratodonts (horny "teeth") are very numerous in many rows, and these keratodonts serve to scrape algae off rocks to which the tadpole adheres, the sucker being moved gradually over the surface of the rock. The colouration of *Heleophryne* tadpoles often matches that of the rocks very well, particularly the light Table Mountain Sandstone boulders, the tadpoles sometimes having similar speckles. The tadpoles are commonly found in situations where the water surface is constantly changing shape, which, together with resulting changing reflections from the water surface and changing patterns of light on the submerged boulders, makes these tadpoles extraordinarily difficult to see. The tadpoles swim strongly and have a tail which is deeper midway along its length than is usual in torrent tadpoles, while the tail-tip is rounded, but not as bluntly as in other torrent tadpoles.

Bottom-dwelling

The tadpoles of *Tomopterna, Rana* and *Bufo* are mainly found in streams or pools with relatively poor vegetation, and are bottom-dwelling. The tadpoles of *Rana vertebralis* and *R. umbraculata* (if distinct from the former) have expanded oral discs, and the long shallow tails with rounded tips common in torrent tadpoles, also seen in *Bufo rosei, B. amatolica* and *B. gariepensis nubicola.* The tadpoles of *Rana angolensis* and *R. fuscigula* have somewhat pointed tails; they tend to occur in stream back-waters. *Rana vertebralis* (and *R. umbraculata*) tadpoles and the tadpoles of *Strongylopus hymenopus* and *S. wageri* are exposed to high light intensities in the clear mountain streams which they inhabit and the lateral line organs are protected by pigment, while the pupil of the eye of the *Rana* species is protected by an *umbraculum,* a projection of the iris; the two *Strongylopus* species have a pigmented flap of skin (elygium) over the inner edge of the eye serving the same function as an umbraculum. Behaviour associated with these features remains to be described.

Gregarious

Of the aquatic tadpoles two gregarious species remain to be mentioned, *Schismaderma (Bufo) carens* and *Pyxicephalus adspersus.* Both species swarm, *S. carens* forming characteristic pelagic masses which rise and sink in the water. Tadpoles of both species are black and have stout bodies and tails, with the tips of the tails rounded and hence less prone to damage than tails with pointed tips. The black bodies of the masses of tadpoles may serve as a heat trap, while the protection against predators offered by gregariousness is probably considerable. The mechanism by which cohesion of the tadpole masses is maintained is not known. The swarms occur in muddy water

with low visibility, but it is not known whether the swarms break up at night. The possibility of pheromones being involved is suggested by the very accurate synchrony of development observed, at least in *S. carens,* and the known existence of alarm substances and growth inhibitors in tadpoles supports this view. It is quite possible that one substance may perform the function of controlling growth, and be an attractant in low concentrations, and a repellant in the higher concentrations which issue from an injured individual. *S. carens* tadpoles have, behind the eyes, a flap of skin which may have the auxiliary gaseous exchange function mooted for it (cf. references to *S. carens* in van Dijk 1966, particularly Charter and MacMurray 1939), but should also be considered as a possible proximity sense organ.

Subterranean and other Extra-aquatic

Some tadpoles (*Breviceps*) are subterranean, and some occur on or in humus (*Arthroleptis*) or under humus in shallow burrows (*Anhydrophryne*) or on moss, typically near waterfalls (*Arthroleptella*) others become aquatic after a period in burrows (*Hemisus*), on humus (*Leptopelis*), or on vegetation above water (*Chiromantis* in foam nests, *Afrixalus fornasinii* and *Hyperolius pusillus* and *concolor),* or on vegetation or rocks above torrents *(Natalobatrachus),* or on gravel (Visser 1971) or rocks at the edges of torrents (*Heleophryne*). (See dotted lines from the bottom right and top left of the diagram). In the extra-aquatic conditions the behaviour of the tadpoles, although characteristic, is largely determined by the conditions in which they are situated. There is some variability, for instance, in the behaviour of *Breviceps* tadpoles, depending on the amount of water in the albumen, the tadpoles swimming in a frothy mass if there is sufficient water.

Systematic field observations of the behaviour of southern African tadpoles has only recently become feasible with the near completion of work on the identification of tadpoles of this region. As there are about five times as many anuran species in southern Africa as found in Europe, it will be some time before it is possible in southern Africa to identify tadpoles by their behaviour as Eibl-Eibesfeldt (1953) has done in Europe. Numerous problems relating to tadpole behaviour, which are amenable to investigation under simulated natural-, and sometimes laboratory-, conditions, have become evident; investigations into some of these are in progress.

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