

BEAUFORTIA

SERIES OF MISCELLANEOUS PUBLICATIONS

INSTITUTE OF TAXONOMIC ZOOLOGY (ZOOLOGICAL MUSEUM)
UNIVERSITY OF AMSTERDAM

No. 322

Volume 25

October 15, 1976

On the origin of the anuran body-form (Amphibia: Anura)

D. HILLENIUS

ABSTRACT

To explain the typical form of the anuran body, the following hypothesis is proposed: The ancestors of Anura, Urodela and Gymnophiona, having probably much in common, were potential competitors, so they each had to develop in a different ecological direction: Gymnophiona in the soil, Urodela on the surface of the soil specializing in the capture of slow moving prey and the Anura on the surface of the soil in the hunting of swift moving prey. Presumably the ancestors of the anurans were slow animals themselves and had to wait hiding until prey passed by. Also, to protect the body against dehydration it was necessary to dig into the soil and — because of the need to catch swift moving prey — to dig backwards, so that the head remained free. In the following discussion several characteristics of recent anurans and of probable ancestral anurans are examined in the light of this hypothesis.

INTRODUCTION

The form of the anuran body so clearly differs from the general tetrapod type, that it probably originated as an adaptation to some very special circumstances.

Some of the most obvious characteristics are:

- the absence of the external part of the tail;
- the very short vertebral column; between the skull and the pelvic girdle there are 5—9 (usually 8) vertebrae;
- the pelvic girdle tilts sharply towards the posterior;
- the urostyl, formed by the fusion of the tail vertebrae into one bone;
- the extreme reduction of the ribs.

As Griffiths (1962) remarks, the Anura possess “an extreme morphological uniformity” and therefore I think it is possible that the conditions still exist that induced this form to evolve. On the other hand considerable variation in behaviour can be found in all the families, under similar conditions. As may be expected these different conditions induced special adaptations,

Received: June 28, 1976

[63]

and strongly influenced form and behaviour, but the basic anuran type is clearly discernable in all specialized forms. Roughly we may distinguish four ecological-ethological ways of living: jumping, swimming, climbing and burrowing, or, in terms of the environment, those types which live on the soil, in the water, in trees and shrubbery, and in the upper layers of the soil. In many families and even in the same species one finds often combinations of these types; almost all frogs and toads are able to jump a little and to swim. Our question is: is it possible to find in one of these main types the original one that perhaps gave rise to the anuran form?

When we take into consideration that *Triadobatrachus massinoti* (Piveteau) from the Lower Triassic, belongs perhaps to the anuran line, though the body only partly shows the typical anuran characteristics, and when we go as far as Schmalhausen (1968) and Watson (1940) to consider *Amphibamus* and other Dissorophids from the Upper Carboniferous as the first steps in the anuran direction, we have to search for evolutionary trends that in the early stages of development already possess selective value. This last point is of importance because some of the earlier hypotheses are valid only if it is assumed that the anuran body arose from a more salamander-like one without gradual modifications.

ARBOREAL CLIMBING AND JUMPING

In many families tree-frog-like forms occur, with many similar adaptations. In quite different systematic groups too, we find comparable adaptations in form and behaviour. For instance, the hind legs of squirrels, some climbing and jumping lemurs, marsupials, monkeys (especially the smaller South American species), or the adhesive pads on fingers and toes of *Tarsius*, and its large frog-like eyes.

But it seems improbable that life in trees or shrubs was the original ecological background of the anuran evolution. It does not account for the loss of the tail, the origin of the urostyl, the shortening of the body, the reduction of the ribs (see table I).

TERRESTRIAL JUMPING

Most toads and frogs are able to jump and their hind legs seem to be designed especially for just that, so it is not unreasonable to regard this way of locomotion as the main formative influence on the anuran body. Indeed, many authors accept this hypothesis and suggest that the main reason for jumping was to escape from predators. Schmalhausen (1968) and Hecht (1962) suggest that the immediate ancestors of the frogs lived on riverbanks and that they escaped danger by jumping into the water, their original habitat. Inger (1962) agrees with this suggestion, but sees no necessity for assuming a riparian habitat; jumping for escape may be just as functional on dry land, as can be observed with many contemporary frogs.

I have some reservations. For instance it is not clear why the tail should disappear as an adaptation to the saltatorial function; many jumping vertebrates do have a tail, which even assumes an important function in jumping, namely to maintain equilibrium, and to steer (jerboas, squirrels, kangaroos, etc.). The shortening of the body is understandable, but not the extreme reduction of the ribs. *Triadobatrachus* and still more so *Amphibamus* do not fit this hypothesis of anuran evolution; their hindlegs were not strong enough to effect an efficient escape by jumping, so this hypothesis seems improbable.

Apart from that it remains incomprehensible why salamanders could survive without any mechanism for swift escape, and yet developed about the same time.

Griffiths (1963) mentions several objections to the hypothesis that anurans obtained their characteristic form on land. In regard to *Triadobatrachus* he states: "It is difficult to believe that such a relatively long and, because of its loosely bound ectochordal centra, flexible span could have transmitted the controlled thrust necessary for jumping."

Though Estes & Reig (in Vial, 1973) do not attach as much importance to this argument, they presume that in general "an aquatic origin and habitat for pro-anurans and perhaps for true anurans as well" is correct.

I agree that part of the formative influence on the anuran body was caused by jumping, but to catch prey rather than jumping to escape. It is a striking fact that — apart from the *Pipidae* and other purely aquatic species — all anurans catch their prey by the perfect interaction of binocular vision, the exact estimate of distance and a well directed forward thrust, caused by a symmetrical action of the hind legs. It seems to me that jumping can be regarded as a later development of this movement. Even a slight modification in this direction would be of advantage, and thus could have selective value. Gans & Parsons (1966) emphasize saltation as a means of escape (from land into water), but they too find it difficult to explain the origin of this behaviour, when the escape effect could hardly have had any discernible advantage.

For this reason perhaps, the fossil *Triadobatrachus*, for which this objection is most clear, is repeatedly called by them "problematical" or "highly debatable".

But I agree completely with another one of their ideas (p. 95), namely that: "One way in which the necessary motorunit "training" for symmetrical activation may have been developed would be as the outgrowth of a feeding movement. The animal might ordinarily feed from a position in which the front of the trunk was supported on anteriorly inclined forelimbs. The head was brought within snapping distance of the prey by moving the trunk forward, rotating it over the supports formed by the forelimbs, with their feet remaining in stationary contact with the ground. This scheme permits a gradual development of synchronization. The anterior push could initially be produced by either hindlimb, though its velocity and presum-

ably its effectiveness would increase as the hindlimbs became synchronized."

In their summary (p. 97) they return to this possibility: "Such a symmetrical form of locomotion, as opposed to the lateral undulatory and asymmetrical mode typical of primitive tetrapods and their fish ancestors, may also have been used in catching prey, but such an assumption is not necessary for our theories." So (according to Gans & Parsons) a symmetrical form of locomotion might have started as a feeding movement, from which proper jumping developed as an escape technique.

Later on it is possible that jumping was used also in catching prey, but according to Gans & Parsons this assumption is not necessary.

Assumption or not, it is a plain fact that catching prey by means of a symmetrical movement of the hind legs (often jumping) is the normal behaviour in all anurans which are not purely aquatic. In this regard the jumping behaviour of *Ascaphus* is significant. *Ascaphus* is generally regarded as one of the most primitive anurans and can easily be caught (if found). "The species impresses me as being rather sluggish" (Stebbins, 1951). "When placed on land they were awkward and stupid in action and appearance and made little effort to escape" (Wright & Wright, 1949). Yet it possesses strikingly long hindlegs.

In September 1975 I myself saw some specimens along Wilson Creek, North California, on land under stones. They remained sitting as I found them. After a while one specimen made a jump of approximately 60 cm high and just as far, a big jump considering the length of the animal (2.5 cm). After that it remained where it was, so I could easily catch it. Another specimen got on its back and remained like that, with quiet breathing movements of the throat (compare the panicky behaviour of *Rana* e.g. in the same circumstances). But the first time I offered them live crickets for food, *Ascaphus* proved to be able to make perfectly well directed jumps. A cricket walking against one of the walls was caught at the first try by means of a jump over a distance of 30 cm. Nevertheless, as stated above, jumping cannot be the explanation for a number of typical anuran characteristics as for instance the loss of tail.

SWIMMING

The main champion of the hypothesis that anurans originated in water is Griffiths (1962). Most interesting is his thesis that *Triadobatrachus* was a larva, at least a form almost at the end of metamorphosis. His discovery of the still unconnected tail vertebrae in larvae of *Megophrys major* instead of an urostyle gives handsome support to this thesis. Another important argument is the fact that Pipidae, normally living their whole life in water, belong to the oldest and most primitive families.

But strong objections can be made. As Inger (1962) puts it: "To hypothesize that a tailed, long-bodied amphibian living in water lost an efficient form of aquatic locomotion and gradually acquired the new, less efficient system of the frogs is to suggest a long-term trend that was always at a

serious disadvantage. Furthermore, in the early stages of evolution of long hind-legs, the limbs would have been relatively weak sources of power and tail, if still present, could hardly have made up the difference because of problems in coordination. "Saltatorial" swimming requires rigidity of the torso in the horizontal plane; caudally powered swimming requires flexibility."

Big morphological changes are in general the answer to radical changes in the environment. When the environment (water) remains the same more or less, we can only expect improvement of existing adaptations; it is highly improbable that they would be replaced by totally different characters.

Besides, representatives of several families, which secondarily adapted themselves to a completely aquatic life, may show characteristics comparable with those in the Pipidae, thus these characteristics need not indicate the original form. In other words the aquatic life of the Pipidae may also be a secondary adaptation.

Perhaps one more argument may be made against water as the original environment in which the symmetrical movements of the hind legs developed. From both *Ascaphus* and *Leiopelma* it is stated that in swimming they use their hind legs alternately. Stebbins (1951) noted that "When placed in an aquarium both animals (*Ascaphus*) swam rather slowly, frequently using their hind legs alternately". Turbott, cited in Stephenson & Stephenson (1957) stated that "In water, *Leiopelma hochstetteri* swims with a characteristic alternate action of the hind-limbs".

A NEW HYPOTHESIS: DIGGING BACKWARDS

There exists one more way of behaviour common to toads and frogs belonging to the most divergent families: digging backwards into the soil by means of the hind feet. In these species the feet are usually equipped with hard horny processes ("spades"), outgrowths of the inner metatarsal tubercle or prehallux. I propose the hypothesis that digging backwards was one of the main formative influences on the early anurans, that which literally caused their anuran condition.

In my opinion Parsons & Williams (1963) presented a convincing theory on the close relationship of modern Amphibia, so closely related indeed that they probably were derived from the same ancestral group. But even if one prefers an alternative theory one must assume that the recent three groups of amphibians, in physiological respects closely similar, were in the beginning potential competitors for the same food (small animals: worms, snails, insects, other arthropods).

It is self-evident that they had to repulse each other ecologically, forcing themselves into divergent specializations. I think that the original boundaries of their niches are still evident: Gymnophiona in the soil, Urodela and Anura at the surface, the Urodela specializing in catching slow moving animals — worms, snails —, and the Anura specializing in catching swifter

prey — “small terrestrial arthropods” (Romer, 1958). No doubt the first amphibians were slow moving animals. For specialists in capturing slow prey this would be no handicap; they could find their food either by smell or by vision, or by both. Moreover, worms and snails generally live in a humid environment hidden in the soil, under stones, moss, etc., only to emerge at night. To prey on them, salamanders adapted themselves to the same environment, hiding in the day-time, and emerging at night (apart from the fact that several species live at least part of their lives in water).

For a slow animal that needs to catch swiftly moving prey there exists only one possibility: to place itself under cover and to develop a quick catching technique. Classical examples of this kind of predation can be found in the larvae of the ant-lion (*Myrmeleonidae*) and of tiger beetles (*Cicindela*). But Dr. R. H. Cobben, Wageningen, told me that in order to catch insects it would not be necessary to place oneself under cover, it would be enough simply to keep quiet. So there must be another reason why the larvae of ant-lions and tiger beetles hide themselves as they do. Perhaps the anuran ancestors would lose too much water by simply lying still on the surface of the soil. To protect the bulk of the body against dehydration, hiding in the soil would be an advantage and so it is imaginable that digging itself into the soil had survival value.

In most animals the common way to dig is to use the front legs and to enter the burrow head first. But in the case of animals that only need to keep quiet in order to capture swift prey, the head should be the last part of the body to be hidden in the soil, in other words the ancestors of frogs and toads originally pressed themselves into the soil, then later dug themselves in. When observing a small moving object it would be necessary to emerge quickly, and to snap. In brief, here the idea of Gans & Parsons is fitting: “necessary motorunit “training” for symmetrical activation” was “the outgrowth of a feeding movement”.

In this connection it is interesting to note Schmalhausen’s remark (p. 109): “We know that even *Eugryinus* fed on insects. Perhaps this is partly correlated with the elaboration of the jumping ability.”

DISCUSSION

Below is a list of characteristics common to all anurans or occurring in many divergent families. Some characteristics may be explained in more than one way, but I hope to demonstrate that the only explanation valid for all of them collectively is the one suggested in my hypothesis. All arguments are summarized in table I.

1. — The absence of an external tail. In digging backwards a tail obviously would be an obstacle. Compare the degeneration of the posterior part of the body in crabs, also characterized by hiding first their rear in the sand or under stones, and holding their head and claws ready for catching prey and for defense.

2. — The behaviour of digging backwards into the soil is found in many anuran families (Bufonidae, Ceratophryninae, Ranidae, Microhylidae, Pelobatidae, Rhinophrynidae). Associated with this behaviour the inner metatarsal tubercle has increased in size and is hardened into a "spade". In all these cases the spade is formed on a prehallux. as described by Linda Trueb (in Vial, 1973): "In addition to five digits, the hind foot of anurans bears a prehallux on its medial margin, adjacent to digit I. The prehallux consists of one or more bones articulating proximally with a central tarsal element. (. . .) The prehallux, although present in all frogs, is best developed or hypertrophied in burrowing forms. (. . .) Early in anuran evolution, these organs (prepollex and prehallux), may have been an innovation, which has come to be functionally discrete among modern frogs."

In this connection it is worth noting Noble's remark: "Since the prehallux forms the core of the "spade" in burrowing Salientia, it is sometimes considered a neomorph. It is, to be sure, hypertrophied in burrowing types, but as it also occurs in non-burrowing species it would seem to be a primitive inheritance."

In other tetrapod groups digging backwards rarely occurs. It might be assumed that it independently evolved several times in anuran families. However, in all these cases digging is performed by the same organ, which is shaped in the same way and formed from the same structures, thence the probability of convergence becomes slight. In this event the common ancestors of recent burrowers probably were endowed already with this organ.

Because we do not know of any use for this organ other than digging, its function was probably the same in the ancestral group.

Additional support for this point I find in Poynton's (1964) remarks on the phylogenetic relationships of some ranid genera. For several reasons Poynton concludes that the burrowing genus *Tomoptera* comes closest to a possible ancestral stock of *Rana s.l.* and also that the related genera *Pyxi-cephalus* and *Hildebrandtia* (both burrowing) are more primitive than *Rana*, *Hylarana* and *Ptychadena*. He even thinks it probable that the retention of the primitive condition (metatarsals bound) is the result of a tendency in these three groups to burrow. On the other hand he states: "But it is impossible to derive *Rana*, *Hylarana* and *Ptychadena* directly from either *Pyxi-cephalus*, *Tomoptera* or *Hildebrandtia* on account of the burrowing habit of the latter three." Without argument it seems that Poynton regards the riparian/swimming condition the more primitive, although this is contrary to his own conclusions about the relative primitive position of the burrowing genera. If we accept my hypothesis the contradiction ceases to exist.

3. — The shortening of the trunk. Within the tetrapods the anurans are exceptional in possessing only 5—9 presacral vertebrae, usually 8. This is often explained as being an advantage to a jumping animal (see for instance Schmalhausen p. 106: "The shortening of the trunk and the elongation of the appendages were the consequence of adaptation to a new form of locomo-

tion by saltation"). But then it is inexplicable why none of the other known vertebrate jumpers show comparable adaptations, at least as far as the shortening of the vertebral column is concerned. If one thinks of a primitive tetrapod, trying to hide itself by burrowing backwards into the soil, then the tendency to shorten the rump becomes understandable. In this respect too the short, broad bodies of crabs offer a comparable adaptation.

4. — The wedge-shaped or tapering form of the rear of the body is very practical for thrusting backwards into the soil.

5. — Closely associated with this conic rear mentioned above is the fusion of the internal caudal vertebrae into a single, non-articulating bone, sharply pointed backward. The absence of any function of the tail could have led to the disappearance of the tail vertebrae, but instead they fused into the urostyl. In my opinion this means that another function existed with a different formative selection.

Considering the fact that the pointed rear end of the urostyl did not fuse with the pelvic girdle, it is difficult to conceive of this situation as strengthening the pelvic girdle, as a saltatorial adaptation.

6. — In relation to the vertebral column the pelvic girdle tilts sharply towards the posterior. In general the position of the girdles and various joints associated with them is such that the connecting muscles use as little force as possible. In some cases the position of the girdle is caused by the direction of a pulling force, sometimes of a pushing force. A good example of the first principle is the pelvic girdle in bats, which is almost level with the vertebral column. In contrast the girdles and legs of elephants, which are practically at right angles to the vertebral column, form an example of the second principle.

The orientation of the pelvic girdle in anurans may be explained by assuming either a pushing force forward as in jumping, or by a reverse pulling force caused by digging backwards with the hind legs.

Considering the many other jumping tetrapods in which this striking orientation of the pelvic girdle does not occur, I feel justified in assuming that the pulling action of digging backwards was the formative influence.

7. — In many anuran families there is a tendency to inflate when in danger. This character may be found in many digging animals, and is a supplementary means of clinging to the sides of the burrows in cases of emergencies.

8. — One of the important functions of ribs is the protection of important organs against injury. The reduction of the ribs in anurans indicates that this need has decreased. Especially when considering the fact that in many species the skull is well armoured, it is suggested that the rest of the body is protected already by other means, e.g. by being hidden in the soil.

In salamanders too the ribs are reduced, but as the body is much more elongated than in frogs, the short ribs still offer protection against injury from above, furthermore salamanders also spend a great part of their lives hidden in soil, under moss, under stones, behind bark, etc.

It is true that the *Gymnophiona*, still more adapted to subterranean life, possess well developed ribs, but since these animals lack limbs and girdles, the ribs are indispensable for muscle attachment.

9. — The large subcutaneous sacs seem to have no function in an aquatic animal, but in more terrestrial animals they might serve as water reservoirs.

10. — All anurans which are not purely aquatic like the Pipidae respond to the stimulus of small moving objects by a well directed jump forward or at least a swift move of the head within snapping distance. Many families possess additionally a tongue especially adapted for seizing swift moving prey.

11. — All anurans, including the aquatic Pipidae, possess the peculiar habit of using the hands of the fore limbs in handling prey. This is all the more remarkable because no other amphibians or lizards exhibit this behaviour. In my opinion the behaviour is connected with the habit of snapping at all small moving objects, which makes it necessary to remove a lot of undesirable detritus, uneatable things, leaves or too large a prey. Salamanders and lizards use their sense of smell in addition to their eyesight, in order to distinguish between edible and inedible items.

Indirectly this might be an argument for the terrestrial origin of the Pipidae. It is true that they use their hands in their search for food, but when handling prey their behaviour does not differ from the comparable behaviour of other anurans, whether *Ascaphus* or *Rana*.

12. — In my opinion the naked skin of all amphibians (the small internal scales in the skin of *Gymnophiona* are not significant) is an adaptation to life on land, hidden in the soil or under stones, etc. Probably amphibians have descended from scaled ancestors, with the original fish scales. The fact that amphibians lost these scales, whereas reptiles developed a secondary growth of scales suggests that an important modification occurred in the amphibian way of life.

The scaled skin in reptiles clearly has the function of protecting the body against dehydration and to a lesser degree against injury. So we must conclude that this double function was lacking in amphibians. The naked amphibian skin, however, is particularly well suited for absorbing water, which would be an absurd adaptation in aquatic animals, but quite appropriate in a terrestrial animal. When surrounded by soil dehydration is curbed and water can even be absorbed.

The function of scales as armour against injury is of little importance for an animal hiding in the soil (see also point 8).

13. — Inger (1962), Gans & Parsons (1966), Schmalhausen (1968) and others emphasize that the first anurans were threatened by rapacious reptiles. Schmalhausen is explicit: "In Permian times there were already many predatory reptiles (*Limnoscelis*, *Captorhinus*, and many Therapsida) which could feed on small reptiles, but in particular there were terrestrial forms of Stegocephalia which through their inferior mobility became easy prey for these predators. Only small forms leading secretive lives hidden under rocks

or burrowed into forest litter or soil (Microsauria), and also riparian forms with well-developed sense organs which, at the approach of predators, leaped quickly into the water and hid in waterweed or muddy soil, could escape this destruction.”

This is not entirely logical, because in water rapacious fish and Stegocephalia also occurred. “The position of the small riparian Stegocephalia became critical.” Schmalhausen suggests that the first anurans withdrew to small rivulets in mountain areas. This would have caused the scarcity of anuran fossils from the Mesozoic. Only after the great saurians became extinct could the great expansion of the anurans have started.

A handsome argument for his case is the occurrence of a sucking mouth in the larvae of most anurans, which might be a relict from the period when larvae had to maintain themselves in rapid currents. In elaborating this argument Schmalhausen mentions another peculiarity of all tadpoles: “In anuran larvae external gills of the same type present in urodele Amphibia (which were also present in larvae of labyrinthodonts) are developed first. Thereafter, however, with development of opercular folds covering the base of the external gills, the latter were reduced, and farther ventrally under the folds new “internal” gills were developed which were homologous neither to the gills of urodele Amphibia nor to fish gills.” He explains this as a result of living in cold rapid flowing water, rich in oxygen, so that the original gills could be reduced. Indeed when comparing larvae of modern salamanders living in stagnant versus flowing water it is clear that the latter possess the smaller gills. So the larvae of the early anurans would have lost their original external gills, but later, when they invaded lower and warmer areas they had to develop gills again.

But this hypothesis will not stand because all recent anuran larvae especially adapted to life in cold rapid currents possess secondary, internal gills too. However, quite a different explanation is possible, less definite perhaps than my other points, but finding justification in relation to these points.

Possibly early anurans, spending the greater part of their lives hidden in the soil reproduced themselves by means of large eggs in which complete metamorphosis took place. This could account for the vanishment of the original larval stage, together with the primary external gills.

After the extinction of the large saurians in the Mesozoic the need to live hidden became less stringent, and other environments could be invaded. From this point of view recent tadpoles are secondarily derived, with secondary gills. Thence the habit of laying large eggs on land, in which complete metamorphosis takes place, occurring in widely different families, would not be a convergent adaptation but a relict of an original anuran characteristic.

In Lynch (in Vial, 1973) the various developmental patterns are grouped in 5 stages. “Stage 1. Frogs in this stage lay numerous, small (about 1 mm in diameter), pigmented eggs in water. The entire developmental sequence occurs in water.” Via 3 interstages we arrive at stage 5. “This stage is com-

plete direct development (. . .) the eggs are large, few in number, and non-pigmented and they develop in the skin or pouch on the back of the parent” or “— the more common case — the few, large, and non-pigmented eggs are laid in a terrestrial situation, the larvae complete their development within the eggmembranes, and upon hatching, metamorphosed frogs leave the eggs.”

These five stages of developmental patterns together form one of 38 characteristics of Anura, in which Lynch tries to determine the sequence of evolution. In general he can discern three categories among these 38 characteristics. “First-Degree Characteristics” are those of which the “inference of evolutionary sequence (primitive to derived) has the highest degree of confidence. Primitive character states are those which are represented in most or all amphibian groups (Urodela, Gymnophiona, and extinct orders) and in anurans. Other states of these characteristics found in frogs are considered to be derived. The primitive state in the subset (Anura) is more likely to be widespread among representatives of closely related groups of the set (Amphibia) than is a derived state in the subset (Anura).”

According to Lynch the developmental pattern belongs to the “First Degree Characteristics” and he has no doubts that “Free living aquatic larvae represent the primitive amphibian and anuran condition. Departures from this pattern are derived.” This is a contradiction to the criteria, on which he based his own system. As we argued before the common tadpole is not a primitive larva, and can therefore not be compared with the larvae of the Urodela or Gymnophiona. This implies that the developmental pattern does not belong to Lynch’s “First Degree Characteristics” of which the evolutionary sequence is so certain.

If we take into consideration only the various stages of developmental pattern, the repeated convergent evolution of stage 5 via 4, 3 and 2 from 1 is just as probable as the reverse. But in combination with the other considerations put forward in this paper the greater probability seems to be the sequence from 5 to 1, from a few, large eggs with direct development via various interstages to numerous, small eggs with complete larval development in water. When we consider several stages of a character and want to know which of them is the most primitive, and which is derived, it is important to know which stage belongs to a successful group, especially when this character stage may be of influence to the success. Stage 1 of Lynch’s list is to be found among the most successful Anura, a.o. the genera *Rana* and *Bufo*. In this case the success can be measured in the width of range and the tendency towards expansion. Relatively less successful are the frogs of stage 5, with direct, terrestrial development.

Anyone looking around on Madagascar has more chance to meet with the imported ranid *Ptychadena mascareniensis* than with one of the more than 120 endemic frogs, most of which show stages 3—5. Mrs. R. M. A. Blommers-Schlösser, who collected and studied for years Malagasy frogs confirms this impression: one finds *Ptychadena* almost everywhere on the island, whereas

the many endemic species with specialized breeding methods are rare. It may be true — as Lynch puts it — that frogs with direct development “account for a relatively impressive percentage of frog species” and that they are “widely distributed among frog families”, however, seeking for frogs and toads anywhere in the world one will find many more species that represent stage 1 than any other kind.

Lynch’s remark “the apparent rarity of direct development is best explained as *naiveté* of holarctic-oriented herpetologists, rather than an assessment of frogs on a world-wide, particularly tropical, basis” is illustrative for the fact that in the holarctic regions, in which most of the naive herpetologists live, the commonest stage of developmental pattern is 1. No doubt these regions are reached by Anura relatively late and in this conquest stage 1 proved clearly to be the most successful way of development. Good reason to assume that stage 1 is derived, not ancestral.

A sound argument in support of this thesis can be found in Bogart’s (1974) karyosystematic study of frogs in the genus *Leptodactylus*: “A fairly plausible, parsimonious history can be derived based on chromosomes and life history. (. . .) I contend that a 26-chromosome karyotype and terrestrial breeding could be primitive conditions in the genus *Leptodactylus* and that the *marmoratus* group” (which is terrestrial breeding i.e. stage 5) “can provide important insight concerning the evolution of several genera of leptodactylid frogs”.

14. — The development of hind legs in the older forms, regarded by many authors as ancestors of recent anurans such as *Triadobatrachus* and some Dissorophids (see Schmalhausen, 1968, Griffiths 1963, several authors in Vial, 1973) is so slight that it seems unlikely that they were of much use for jumping and this is the more so when we think of intermediates between salamander-like forms and *Triadobatrachus* e.g.

Probably these early hind legs were not of much use either for supplementing the tail-fin for swimming. So it is difficult to imagine that a selective influence on the hind legs was caused by a tendency to escape by jumping or swimming.

However, it is possible to ascertain some typically anuran tendencies such as the shortening of the rump, degeneration of the tail, degeneration of the ribs, reduction in the number of vertebrae, etc. In this connection it is not too important to consider specific earlier groups as ancestors of the anurans such as *Eugyrinus* and *Amphibamus* (see Schmalhausen, Watson). The main point is that these small changes in form already provide an advantage in the tendency to press themselves backwards into the soil, and later on aided further by digging movements of the hind legs, so that selective influence in the direction of the anuran form is inherent from the beginning. As a summary I have listed in tabular form my arguments and several possible assessed theories.

TABLE 1. The four main behavioral patterns of living anurans and their relationship to the evolution of 13 typical anuran characteristics. *Triadobatrachus* and other possible ancestors are listed in the last column (+ means that the indicated way of behaviour might have had a positive selective influence on the indicated characteristic).

behavioral patterns					characteristics
arboreal jumping (terrestrial) swimming digging backwards combined with jumping forward to catch prey					tailless
					spade, "sixth toe"
		+	+	+	shortening of the rump 5—9 presacral vertebrae
					tapering abdomen
					urostyl
		+	+	+	backward tilt pelvic girdle
					inflating the body
					reduction ribs
			+	+	subcutaneous lymphatic sacs
			+	+	snapping at moving objects
					use of hands in handling food
					naked skin
			+	+	complete metamorphosis in large eggs
				<i>Triadobatrachus</i> <i>Eugyrinus</i> <i>Amphibamus</i> , etc.	

ACKNOWLEDGEMENTS

I am grateful to Mrs. R. M. A. Blommers-Schlösser (Amsterdam) and to Dr. M. Hoogmoed (Leyden) who read and discussed my manuscript and inspired me to new arguments. I am much indebted to Dr. T. Paul Maslin, Boulder, Colorado, for not only critically reading my manuscript but also for the great help he gave in improving the english.

REFERENCES

- BOGART, JAMES P.
1974 A Karyosystematic study of Frogs in the genus *Leptodactylus* (Anura: Leptodactylidae). — *Copeia*, 1974 (3): 728—737.
- GANS, C., & T. S. PARSONS
1966 On the Origin of the Jumping Mechanism in Frogs. — *Evolution* 20 1: 92—99.
- GRIFFITHS, J.
1963 The Phylogeny of the Salientia. — *Biol. Rev.*, 38: 241—291.
- HECHT, M. K.
1962 A reevaluation of the Early History of the Frogs. Part I. — *Syst. Zool.*, 11 (1—4): 39—44.
1963 A reevaluation of the Early History of the Frogs. Part II. — *Syst. Zool.*, 12 (1—4): 20—35.
- INGER, R. F.
1962 On the terrestrial Origin of Frogs. — *Copeia*, 1962 (4): 835—836.
- NOBLE, G. K.
1931 *The Biology of the Amphibia*: 1—577 (Dover Publications Inc.).
- PARSONS, T. S. & E. E. WILLIAMS
1962 The Teeth of Amphibia and Their Relation to Amphibian Phylogeny. — *J. of Morphol.*, 110 (3): 375—383.
1963 The Relationship of the modern Amphibia: a Reexamination. — *Quart. Rev. Biol.*, 38: 26—53.
- POYNTON, J. C.
1964 The Amphibia of Southern Africa. — *Ann. Natal Mus.*, 17: 1—334.
- ROMER, A. S.
1958 Tetrapod limbs and early tetrapod life. — *Evolution*, 12: 365—369.
- SCHMALHAUSEN, I. I.
1964 *The Origin of Terrestrial Vertebrates* (transl. 1968): i—xxi, 1—314. (Univ. of Missouri Press, Columbia).
- STEBBINS, R. C.
1951 *Amphibians of North America*: i—xvii, 1—539 (Univ. of California Press).
- STEPHENSON, E. M. & N. G. STEPHENSON
1957 Field Observations on the New Zealand Frogs, *Leiopelma* Fitzinger. — *Trans. roy. Soc. New Zealand*, 84 (4): 867—882.
- VIAL, J. I., Ed.
1973 *Evolutionary Biology of the Anurans*: i—xii, 1—470 (Univ. of Missouri Press, Columbia).

WATSON, D. M. S.

1940 The Origin of Frogs. — Trans. roy. Soc. Edinburgh, **60** (1): 195—231.

WRIGHT, A. H. & A. E. WRIGHT

1949 Handbook of Frogs and Toads of the United States and Canada: i—xii, 1—640.
(Comstock Publishing Company. Inc., Ithaca, New York).

Dr. D. HILLENUS

Institute of Taxonomic Zoology (Zoological Museum)

of the University of Amsterdam

Plantage Middenlaan 53

Amsterdam 1004 — The Netherlands