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HOW MANY TIMES HAS TERRESTRIAL BREEDING EVOLVED IN ANURAN AMPHIBIANS? *

(PUBBLICAZIONI DEL CENTRO DI STUDIO PER LA FAUNISTICA ED ECOLOGIA TROPICALI DEL C.N.R.: CCVI)

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In anuran amphibians, the typical aquatic reproductive pattern is well known. Frogs or toads deposit large numbers of eggs in the water which later hatch into free-swimming tadpoles. The tadpoles feed, grow, metamorphose, and leave the water as juveniles. Aspects of terrestrial development or parental care of eggs would seemingly be rare exceptions in the Anura. Recent reviews (Salthe & Duellman, 1973; Salthe & Mecham, 1974; Lamotte & Lescur, 1977; McDiarmid, 1978) document the fact that anuran reproductive patterns are extremely diverse and complex. There are many instances of terrestrial development in a number of lineages (see Figs 1 and 2 for some examples) and parental care is present in at least some species representing 14 of the 20 families listed by McDiarmid (1978). Recent theoretical hypotheses have been derived from the study of life history strategies of animal groupings which demonstrate much less reproductive ecological and ethological variability than do frogs (Trivers, 1972; Wilson, 1975; Dawkins & Carlisle, 1976; Stearns, 1976;)

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It is surprising that the evident diversity in anurans has not been exploited to test such hypotheses. Even though documentation of various methods of reproduction is available for many anurans, few studies have dealt with ecological or genetical correlations, energetics, parental investment or sociobiology in the Anura. McDiarmid (1978) summarized the available information, provided additional information from his work with Centrolenella, and emphasized the theoretical importance of such studies. McDiarmid (1978) and Maynard Smith (1977) pointed out the need for more detailed information concerning comparative reproductive behaviour in anuran amphibians.

**IS TERRESTRIAL BREEDING PRIMITIVE OR ADVANCED?**

An important aspect of comparative reproductive studies is to ascertain the events which have led to terrestrial breeding in so many divergent lines of frogs. The shift from an aquatic to a terrestrial mode of reproduction must involve a host of coordinated biological alterations. The physical and embryological characteristics of the eggs are altered in terrestrially breeding species. All terrestrially breeding species produce fewer, but larger, eggs than do aquatic breeders (Salthe & Mecham, 1974). The mechanisms for obtaining oxygen and releasing nitrogenous material would be altered. Terrestrial eggs would require additional protection from dessication. Mechanisms must evolve for prolonging development and utilizing additional yolk stores. Altered mating behaviour and parental care of the eggs or tadpoles is characteristic of many terrestrial breeders (McDiarmid, 1978). It may be assumed that all these changes would involve considerable genetic restructuring. Therefore, it is difficult to believe that terrestrial breeding has evolved independently many times, even within subfamilies. Surely, the host of genetically determined alterations which would be necessary to convert an anuran from an aquatic to a terrestrial breeder would be more comprehensive than many other characters which are considered evolutionarily significant, such as the fusion or dissociation of pectoral elements, the shift from a vertical to a horizontal pupil, or even the position used by the male when he grasps the female during amplexus.

*Leiopelma*, from New Zealand, is considered by most authorities to be the most primitive living genus. All three species of *Leiopelma* have direct, terrestrial development including parental care (Stephenson & Stephenson, 1957). Many other species of anurans, like *Leiopelma*, are associated with regions which are known to be zoogeographically old and maintain many endemic forms. *Rhinoderma* of Chile (Fig. 2), the sooglossids of the Seychelles Archipelago, and the egg-brooding hylid frogs of South East
Brasil (see references in Lamotte & Lescure, 1977) are but a few examples of frogs which live in such areas and have terrestrial development. In certain advanced families of anurans where the majority of the species are aquatic breeders, the small percentage of the species which do have terrestrial breeding behaviour are not considered to be the most advanced members in these families even though they are considered to have a derived behaviour. The Australian Cycloraniinae are considered to be an ancient group which may have invaded South America to provide the nucleus for a neotropical leptodactylid radiation (Lynch, 1971). Two genera of cycloranine frogs (Kyarranus and Philoria) have terrestrial development (Moore, 1961; Littlejohn, 1963). Terrestrial development is apparently present in some myobatrachine genera such as Myobatrachus and Metacrinia (Lynch, 1971) which are not considered advanced members of the subfamily. In South America, the Alsodini may be the basal group for the majority of the leptodactylid neotropical radiation (Lynch, 1971). Two of the four alsodine genera (Batrachyla and Thoropa) are terrestrial breeders. The terrestrially breeding sooglossids have been implicated in the early evolution of ranids (Griffiths, 1960), pelobatids (Noble, 1931) or leptodactylids (Lynch, 1971). In the family Ranidae, the terrestrially breeding genera are included in subfamilies which were probably derived from an early radiation such as Platymantis from the Philippines (Alcala, 1962) and the African genera Arthroleptis, Anhydrophryne, Artholeptella and Leptopelis (Lamotte & Lescure, 1977). The terrestrially breeding bufonids appear to have arisen very early in the evolution of toads (Grandison, 1978) and the terrestrially breeding microhylids are not considered among the most advanced members in the family Microhylidae (Parker, 1934; Bogart & Nelson, 1976).

Yet, terrestrial breeding is usually considered to be derived in all these groups. McDiarmid (1978) states that there is little doubt that the primitive reproductive mode of frogs is aquatic and involves external fertilization of eggs, free-swimming tadpoles, metamorphosis, and the terrestrial existence of juveniles and adults. He bases his classification of parental care on this presumption. In numeric studies of leptodactyloid frogs (Lynch, 1971, 1973; Heyer, 1975; Heyer & Liem, 1976) the primitive character state (0) was used for aquatic development while the derived state (1) was used for species which completed their development in a terrestrial environment. Lynch (1973) extended his cladistic analysis to include all the family groupings. In the absence of confirmation from fossil material, the definition of primitive character states is a subjective exercise and the criteria used to define primitive states is surprisingly variable (Inger, 1967; Kluge & Farris, 1969; Lynch 1971, 1973; Heyer, 1975).

This paradoxical situation may be more apparent than real. Lynch (1973) defined five developmental stages which were applied to his cladistic
Fig. 1. — Aspects of terrestrially breeding species. A: an Eleutherodactylus johnstonei Barbour male from Haiti watches over a clutch of direct-developing eggs; B: the same eggs 19 days later; C: a Phyllobates trivittatus (Spix) male from Peru transports tadpoles on his back; D: a Plectonotus fissilus (Miranda-Ribeiro) female from South East Brasil assists her young to emerge; E: developing tadpoles of Centrolenella fleishmanni (Boettger) from South East Brasil; F: developing tadpoles of Hyla sarayacuensis Shreve from Peru.

analysis of anuran family groupings. LYNCH's stage 3 consisted of frogs which laid eggs in a terrestrial environment but whose tadpoles completed their development in an aquatic environment. Stage 3 frogs were grouped with frogs which demonstrated completely aquatic development (stages 1 and 2) and coded as primitive (0) as opposed to completely terrestrial development (stages 4 and 5) which were considered to be derived frogs (1). In a similar manner, HEYER (1975) recognized eight life history states to be present in leptodactylid frogs (A to H) but, for coding purposes, he grouped all the states where tadpoles were present (A to G) as being prim-
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ative (0) and only frogs which demonstrated direct development (state H) as derived (1). Ardila-Robayo (1979), using a different coding scheme, distinguished between Lynch's (1973) states 4 and 5 but also grouped state 3 with the aquatic developing species as being primitive (0).

Fig. 2. — Aspects of terrestrially breeding species. A: tadpoles develop in the vocal sacs of male Rhinoderma darwini Duméril & Bibron from Chile; B: territorial behaviour is demonstrated in Dendrobates pumilio Schmidt from Costa Rica; C: Nectophrynoides tornieri (Roux) from Tanzania is ovoviviparous; D: Nectophryne africana Buchholz & Peters from the Cameroun has aquatic eggs but they are large and few in number. The eggs can be seen through the female's abdomen.

DEFINITION OF TERRESTRIAL BREEDING

I believe terrestrial breeders should include those taxa which have demonstrated the ability to overcome the physiological, embryological, behavioural, and genetic problems of producing viable zygotes in a terrestrial environment. Once terrestrial development has been achieved, selection could be invoked which would result in a variety of divergent strategies. Early terrestrial breeders could be similar to that defined by stage 3 of Lynch (1973) which he classified as primitive. I see little justification for the, perhaps anthropomorphic, assumption that the evolutionary trend in
frogs is unidirectional and culminates in direct development or viviparity. In order to exploit altered environmental conditions, an evolutionary advantage may be realized if terrestrial breeders revert to more aquatic dependence. This opinion was expressed earlier (Bogart, 1974). A putative, early, terrestrially breeding species would be one which produced relatively few, large, yolk-laden eggs in a moist terrestrial environment. The tadpoles probably had a relatively abbreviated free-swimming life. I also see little justification for the assumption that laying large numbers of small, pigmented eggs in an aquatic environment is a primary mode of reproduction in the Anura. Furthermore, «... it should be emphasized that there is no reason assuming that the small eggs of Rana are primitive. The branchiosaur ancestor of frogs and urodeles arose from labyrinthodonts and these ancient Amphibia were almost indistinguishable from some cotylosaur reptiles. Possibly these labyrinthodonts had not developed the amnion, allantois, or calcareous egg membranes of modern reptiles, but it is not improbable that the eggs were well provided with yolk.» (Noble, 1931).

THE CHROMOSOMES OF TERRESTRIAL BREEDERS

In most aquatic breeding frogs, the karyotype is conservative and even slight differences in chromosome morphology or numbers of chromosomes are deemed to be significant discoveries with systematic and evolutionary importance. Finding a group of 20-chromosome African Bufo among the cosmopolitan 22-chromosome species was an exciting discovery (Bogart, 1968, 1972; Morescalchi & Gargiulo, 1968; Doyle & Beckert, 1970). Conservative karyotypes are found in other aquatic breeding frogs such as the North American 24-chromosome species of Hyla (Bogart, 1973) and the majority of the species in the genus Rana (Moreescalchi, 1973). According to Moreescalchi (1973), most of the higher Amphibia have reached an end point in karyological differentiation, although a few groups have bridged some genetic impasse through polyploidy or centric fission.

Terrestrially breeding species exhibit extreme variability in chromosome morphology and number. As well, many terrestrial breeders have telocentric chromosomes which are only rarely encountered among aquatic breeding species. Chromosome numbers in the neotropical leptodactylid genus Eleutherodactylus range from 18 to 36 and many of the species have telocentric chromosomes (Bogart, 1970, 1973). Adenomera, another terrestrially breeding leptodactylid genus, contains species with as many as nine pairs of telocentric chromosomes and has chromosome number differences between the species (Bogart, 1974). The 30-chromosome species of Hyla of the neotropics which deposit eggs on leaves have telocentric
chromosomes, as do phyllomedusids and egg brooding hylid genera in South America (BOGART, 1973 and unpublished). Chromosome number variation and the presence of telocentric chromosomes are evident in the dendrobatid frogs of South America (BOGART, 1973 and unpublished), *Leiopelma* of New Zealand (STEPHENSON et al., 1972), and ranid frogs of the genera *Cardioglossa* and *Leptopelis* (BOGART & TANDY 1981). Many other terrestrial breeding species such as the sooglossids (BLOMMERS-SCHŁÖSSER, 1978; NUSBAUM, 1979) from the Seychelles and certain species of *Mantidactylus* (BLOMMERS-SCHŁÖSSER, 1978) from Madagascar have telocentric chromosomes. Exceptions do exist in that some aquatic breeding species have telocentric chromosomes and that some terrestrial breeders have no telocentric chromosomes but, in general, the correlation is robust.

The available data suggest that related species of anurans which live in isolated areas and produce relatively few eggs demonstrate the greatest amount of chromosomal variation. The chances for fixation of chromosomal mutations would be enhanced through reduced numbers of offspring, territoriality, and subsequential inbreeding within small isolated groups. The eventual chromosomal distinctiveness if isolated populations would be expected to be a major factor in speciation. Fixation of chromosomal mutations would be much less likely to occur in large, randomly interbreeding populations of species which produce large numbers of eggs.

WHITE (1973), WILSON et al., (1974), and BUSH (1975) compared chromosome evolution in various animal groups but they were apparently unaware of the karyotypic variability and ethological diversity among anuran amphibians. They all considered frogs to have a conservative karyotype which varied little over long time periods. The anuran chromosomal and behavioural data may be applied profitably to the modes and mechanisms of speciation which were outlined by BUSH (1975). Anuran reproductive strategies form a continuum from terrestrial to aquatic development. The aquatic breeding species often produce thousands of eggs (r-strategists) but the terrestrially breeding females lay few eggs (K-strategists?). *Sminthillus limbatus* (Cope) females of Cuba are reported to lay single, direct-developing eggs (NOBLE, 1931). The DNA content which has been reported in anuran amphibians (MORESCALCHI, 1973) shows remarkable, even intrageneric, variability which does not seem to be correlated to reproductive strategies or chromosome variability.

**CONCLUSION**

Karyotypic stability appears to have evolved among species which produce large numbers of eggs in an aquatic environment. These species would relate to the end point in karyotypic differentiation which was
discussed by Morescalchi (1973). Major karyological changes may still be accomplished among such species through polyploidization (Morescalchi, 1973; Bogart, 1980). Rapid chromosomal evolution involving centric fusion or fission events is characteristic of terrestrially breeding taxa. Certain terrestrially breeding taxa may form a basic nucleus in major lineages of advanced frogs. Direct development and viviparity may be derived from basic, terrestrially breeding species and these derived species would be expected to produce even fewer eggs. They would continue to demonstrate karyotypic variability which would be an important factor in speciation. Eleutherodactylus would fit this hypothesis. Under certain circumstances, aquatic development may also be derived from a terrestrially breeding mode to maximize some evolutionary advantage of increased egg production in favourable aquatic environments. The intermediate stages would involve relatively large, aquatic eggs. Such eggs present problems in obtaining adequate oxygen supply. Some present species are able to circumvent such problems through behavioural adaptations such as circulating water around the eggs (e.g. Nectohpryne, see Scheel, 1970) or through the production of a floating foam nest.

At present, I do not believe it is possible to answer the basic question concerning the number of times terrestrial breeding has evolved in anuran amphibians. My intent has been to provoke additional study and thought. The problem is, I feel, basic to an improved understanding of anuran systematics. Terrestrial development could predate the evolution of all present day anurans and be maintained in major lineages, providing genetic plasticity to found additional lineages. If terrestrial development, and the consequent chromosomal variability, can be easily derived in advanced taxa of all present lineages, then karyotypic oscillations would be expected and studies which attempt to find any chromosomal relationships among higher taxa would be exercises in futility.

SUMMARY

Aspects of the breeding biology of anurans have been used as generic criteria in a number of families and, in some instances, species may not be adequately classified without knowledge of their breeding biology. Terrestrial breeding has been used as justification for recognizing advanced genera or species, however, there is little available evidence that this mode of reproduction is either derived or advanced. It is becoming increasingly apparent that some species may have phylogenetic affinities which are independent of their present continental distribution. The possibility exists
that terrestrial breeding may have been well established in early anurans and that it is maintained in varying diverse genera of most anuran families. Common ancestry would be a reasonable explanation for the evolution of terrestrial development in so many genera. Genetic selection involving physiological, embryological, and behavioural parameters of terrestrial breeders must surely be more involved than could be adequately explained by remarkable convergence. Perhaps some of the taxonomically valid characters, such as the architecture of the pectoral girdle, are more pliable and could conceivably be the result of minor genetic alteration. Terrestrially breeding anurans have variable karyotypes including variable numbers of chromosomes and the presence of telocentric pairs. Most aquatic breeders have conservative karyotypes which consist mostly of metacentric and sub-metacentric chromosomes. Speciation is assumed to be rapid among terrestrial breeders which may provide the basis for the evolution of major lineages of advanced frogs.

RIASSUNTO

I vari aspetti della biologia riproduttiva degli Anuri sono stati usati come criteri per la suddivisione in generi di varie famiglie; e in certi casi si è constatato che anche le specie non potevano ricevere un’adeguata sistemazione senza tener conto della loro biologia riproduttiva. La riproduzione di tipo terrestre è servita di base per il riconoscimento di generi e specie progrediti, ma in realtà non esistono prove sicure per decidere se tale tipo di riproduzione sia progredito o secondario, derivato. Comunque sta diventando sempre più chiaro che alcune specie possono avere affinità filogenetiche indipendenti dalla loro attuale distribuzione continentale, ed è possibile che la riproduzione terrestre fosse ben affermata negli Anuri primitivi e che si sia mantenuta, con varie modalità, in generi diversi della maggior parte delle famiglie. L’esistenza di un’origine comune spiegherebbe ragionevolmente l’evoluzione dello sviluppo terrestre in generi così numerosi. La selezione genetica delle forme a riproduzione terrestre, interessante parametri fisiologici, embriologici e comportamentali, dovrebbe essere più coinvolta e più adeguatamente spiegabile che non l’esistenza di una straordinaria convergenza. Forse alcuni dei caratteri tassonomicamente validi, come ad esempio l’architettura della cintura toracica, sono più flessibili di quanto non si ritenga e non si può escludere che possano essere il risultato di alterazioni genetiche di minore importanza. Gli Anuri a riproduzione terrestre hanno cariotipi varì, con numero di cromosomi variabile e presenza di paia telocentriche; la maggior parte di quelli a riproduzione acquatica, invece,
hanno cromosomi metacentrici e submetacentrici. Si suppone che la speciazione sia rapida nelle forme a riproduzione terrestre, le quali potrebbero essere alla base della evoluzione delle principali linee filetiche degli Anuri più progrediti.

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