SOCIETAS
HERPETOLOGICA
ITALICA

HERPETOLOGIA SARDINIAE

Editor: *Claudia Corti*

EDIZIONI Belvedere

SOCIETAS HERPETOLOGICA ITALICA

7° CONGRESSO NAZIONALE

Oristano, Promozione Studi Universitari Consorzio1, Via Carmine (c/o Chiostro)
1-5 ottobre 2008

Esempio di citazione di un singolo contributo/*How to quote a single contribution*
Angelini C. & Utzeri C., 2008. Survival analysis of two populations of *Salamandrina perspicillata* (pp. 15-17). In: Corti C. (ed.), 2008. Herpetologia Sardiniae. *Societas Herpetologica Italica*/Edizioni Belvedere, Latina, "le scienze" (8), 504 pp.

Biogeographic implications of intriguing relationship patterns of endemic amphibians of the Gulf of Guinea Islands.

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Key words: Amphibians, Gulf Guinea Islands, West Africa.

Three of the four Gulf of Guinea islands are surrounded by seawater from a depth of 2,000 to 4,000 meters and have never been attached to mainland Africa; they are thus classic oceanic islands. The fourth and northern-most island, Bioko (Fernando Pó) is a continental island whose fauna and flora reflect close relationship with the African mainland.

The two central islands of the archipelago, São Tomé and Príncipe, are geologically quite old (at least 13 and 31 my respectively; Lee *et al.*, 1994). The islands have been largely neglected by biologists since the end of the 19th Century, but the first decade of the 21st Century has seen a renewed interest in the study of the endemic herpetofauna of these two islands with their seven amphibian species and at least eight, possibly ten reptiles (Measey *et al.*, 2007), as well as studies of many other poorly known *taxa*.

The presence of an amphibian fauna on these oceanic islands has prompted a number of recent studies to determine their taxonomic validity and affinities to members of their African mainland congeners. In 2007, Measey *et al.* (2007) examined the São Tomé endemic rocket frog (*Ptychadena newtoni*) and on the basis of sequence from 16S rRNA, cyt*b* and cox1 genes, confirmed its *status* as an endemic species. They hypothesized a dispersal model by rafting based in part on extant ocean currents and seasonal surface water salinity data to explain how earlier amphibian colonizers might reach the islands. However, their study also revealed a surprising relationship between *P. newtoni* and other continental members of the genus (n = 82); along with 16S rRNA sequence data from Vences *et al.* (2004) their dataset represented 14 putative species. They concluded that *P. newtoni* is more closely related to a clade composed of populations of putative *Ptychadena mascareniensis* from Egypt, Kenya and Tanzania than to any other species from West, Central and South Africa and Madagascar.

Perhaps the best-known Gulf of Guinea island example of this curious relationship with the East African fauna is the São Tomé endemic caecilian, *Schi-*

stometopum thomense, seemingly a most unlikely disperser; the only other member of the genus, *S. gregorii*, is found in coastal river drainages of Kenya and Tanzania. This relationship was previously suggested by morphological synapomorphies (Nussbaum, 1985; Nussbaum & Pfrender, 1998), and the recent rediscovery of the East African species allowed molecular confirmation of the relationship (Wilkinson *et al.*, 2003) who employed 12S and 16S rRNA gene sequences.

Drewes & Wilkinson (2004) studied the relationships and *status* of the two endemic oceanic island hyperoliid treefrogs, *Hyperolius thomensis* and *H. molleri*, analyzing sequences of the 12S and 16S ribosomal genes and the valine tRNA; included in the comparison were five additional species of *Hyperoliu*s, including a sample from Bioko, the northern-most island in the Gulf of Guinea. Results indicated that the two oceanic island species are sister species which together consistently form a clade with *Hyperolius cinnamomeoventris*, a species that is thought to occur across sub-Saharan Africa - the sample employed in the study was collected by the author in Uganda. At the time of publication sequences from only about 12% of the recognized species of *Hyperolius* were available for comparison, and so sampling was inadequate to draw strong inference other than that the two island endemics were, indeed, nested within *Hyperolius*.

A larger sample size was available in the study of Uyeda *et al.* (2007), who examined the relationships of the two island puddle frogs (*Phrynobatrachus*), finding mean inter-island sequence divergence of 21% (cyt*b*, 12S rRNA, 16SrRNA and valine-tRNA). The ingroup contained samples from 12 species from West, Central and East Africa, as well as *P. cornutus* from the island of Bioko. The clade formed by the two endemic island *Phrynobatrachus* is sister to a clade made up entirely of East African species from Ethiopia, Kenya, Tanzania and Malawi, a pattern reminiscent of that seen in Measey *et al.* (2007) in the *Ptychadena* study. This relationship is reiterated in two larger constructs by Zimkus (unpubl.) where a cladogram and a Bayesian phylogram included 47 and 37 congeneric species respectively.

The curious Gulf of Guinea-East African connection is not limited to amphibian *taxa*. Ongoing work by David Vieites, Adam Leache and the author indicates that the endemic diurnal geckos (*Lygodactylus*) of São Tomé, Príncipe and Annobón (southern-most in the archipelago, age 4.8 my) form a clade with Ghanaian samples, and these together form the sister group to a wide range of East African samples; also included in the study are Malagasy, South African, Brazilian and other West African populations. Endemic species of land snails (genus *Bocageia)* show a similar relationship pattern (Gascoigne, 1994), and a morphology-based phylogeny of flowering plants of the family Acanthaceae by Hedren (1989) indicates that the São Tomé endemic acanthus, *Justicia thomeensis*, is most closely related to a group of primitive species occurring in East Africa (Kenya, Tanzania, Mozambique and eastern South Africa).

None of the seven examples given above can be said to be compelling, due

to the absence of data from the large intervening Congo Basin which may harbor any number of unsampled *taxa* which could help explain the apparent disjunct nature of these relationships. Moreover, sequence comparison is relatively new, and many species in well understood groups are not yet represented in the GenBank collections. However, the results of these studies at least show a pattern that should not be ignored and which requires extensive further study.

The fact that the oldest island in the Gulf of Guinea archipelago, Príncipe, is *minimally* 31 my old suggests it has been "available" for colonization from continental Africa (and perhaps elsewhere) since the early Oligocene; similarly, São Tomé has been a potential target since the mid-Miocene. An assessment of geomorphological changes on the source continent during this time period is required in order to construct an hypothesis that explains the presence of floral and faunal elements with East African affinities.

The current topography of the central part of Africa presents many obvious geomorphological (and climatological) barriers to the East -West movement of terrestrial organisms like amphibians: these include (E to W) the Kenya and Ethiopia Domal uplifts, the Gregory Rift, the elevated Lake Victoria Basin, the Western (Albertine) Rift and the Ruwenzori Mountains and uplifted continental margins (Congo River cataracts). The current directionality of the Niger River would not suggest an avenue for East-West movement, although the present Congo originates in NW Zambia and is only narrowly separated from a broadly defined East Africa by the Zambian Muchinga Mountains.

Goudie (2004) provides an excellent review of geological evidence pertaining to the paleohistory of African drainages suggesting that not only were none of these modern morphological barriers present until well after the emergence of the island of Príncipe, but that "prior to the formation of the Gregory Rift (about 15 Mya) East Africa seems to have been dominated by a N-S trending arch of crystalline rocks which formed the continental watershed, with rivers draining east to the Indian Ocean and west towards the Atlantic across the line of the present Western Rift Valley". There is growing evidence that the present Congo Basin was occupied by a freshwater lake or series of lakes up to the present 500 m contour (including modern day Kisangani, DRC) as late as the Pliocene Epoch but may have been linked with the Atlantic as early as the Miocene; E-W flow would have been augmented by doming and rifting further to the east which began in the Oligocene but reached its peak in the Miocene, by which time the island of São Tomé had emerged. Moreover, early Pliocene sea-levels rose at least 125 m which would mediate the present Congo River cataracts as barriers to rafting (see Measey *et al.*, 2007). Similarly, geological data support a scenario in which substantial rivers flowed out of the Western Sahara towards the Atlantic Ocean in the Miocene, and large areas of northeastern Africa have certainly communicated with the Atlantic via Lake Megachad, the Benue and Niger Rivers during wetter, more recent peri-

ods. Despite the distances involved, geological evidence supports the probability of mesic corridors, *i.e.* potential dispersal routes, existing between modern East Africa and the Gulf of Guinea Islands since the early Oligocene which coincides with the emergence of the oldest member of the Gulf of Guinea archipelago.

The East African affinities of the older elements of the Gulf of Guinea biota, *i.e.*, the amphibians, can be explained by an early major colonization event or series of colonization events from a source fauna originally inhabiting then-contiguous East and Central Africa. The persistence of this early fauna on the islands to the present day might be explained by the early colonizers out-competing subsequent invasions from the nearby West African fauna. This hypothesis can be tested, supported or falsified by analysis of samples from intervening Congo Basin, Angola and upper Niger Delta, areas that remain intellectual *terra incognita* to the present day.

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