ASPECTS OF THE ECOLOGY OF VARANUS NILOTICUS (REPTILIA, VARANIDAE) IN SOUTHEASTERN NIGERIA, AND THEIR CONTRIBUTION TO THE KNOWLEDGE OF THE EVOLUTIONARY HISTORY OF V. NILOTICUS SPECIES COMPLEX

Francesco M. ANGELICI* & Luca LUISelli**

RéSUMÉ


SUMMARY

The Afrotropical Varanus niloticus is subdivided in two distinct subspecies which are morphologically easily recognizable from each other. Boehme & Ziegler (1997) concluded that these two forms have markedly surpassed the subspecific level and have to be treated as distinct species, the one typical of savannas (V. niloticus) and the other of rainforest biota (V. ornatus). These authors also reported on the sympatric occurrence (without hybridization and intergradation) of both the forms in the Niger Delta (southeastern Nigeria), which is a further demonstration of the specific status of these taxa.

* FIZV, via Cleonia 30, I-00152 Rome, Italy.
** Institute of Environmental Studies DEMETRA. Via dei Cochi 48/B, I-00133 Rome, Italy; and via Olona 7, 00198 Rome, Italy.

We studied the ecology of monitor lizards in southeastern Nigeria between September 1996 and July 1998. Including both free-living and dead specimens offered in local bush-meat markets, we determined the taxonomic status of several dozens of monitor lizards, all were typical ornatus. Omatus specimens were observed not only in forest biota, but also in derived savannas and cultivated lands of southeastern Nigeria and of the Lagos state, where the two forms were said to coexist. Thus, as far as southern Nigeria is concerned, the coexistence of these two Varanus "species" is still in doubt. In general, Nigerian ornatus proved to be habitat generalists, but they were found mainly in secondary swamp forests and along riverine forests. Nigerian ornatus did not show any aestivation phase, contrary to niloticus from other African countries. There was evidence of a strong reproductive seasonality in these lizards. Main food of Nigerian ornatus were crabs, a very abundant food resource in the environment. About 10% of the total number of prey items were vertebrates. Food niche breadth of adults was wider than that of juveniles. Some general implications of the presented ecological data for the evolutionary history of Varanus niloticus species complex are discussed. In addition, some data on the relationships between monitor lizards and local human populations are presented and discussed.

INTRODUCTION

The Nile Monitor, Varanus (Polydaedalus) niloticus, with a wide distribution covering most of the African continent (de Buffrénil, 1993; Lenz, 1995; Boehme & Ziegler, 1997), is the largest African varanid lizard. Based on morphological, phenological, and habitat differences, Boehme & Ziegler (1997) concluded that two forms (Varanus niloticus niloticus (Linnaeus, 1766) and Varanus niloticus ornatus (Daudin, 1803)) have markedly surpassed the subspecific level and have to be treated as distinct species: V. niloticus and V. ornatus. These two species can be easily discriminated on the basis of several morphological characteristics, including scalation, colour pattern, body proportions, tongue colour, and outer genitals (for a detailed list of these characteristics, see Boehme & Ziegler, 1997).

Apart for the above-exposed morphological differences, Boehme & Ziegler (1997) highlighted that the two species also differ from each other in terms of phenology (V. niloticus is characterized by a prolonged aestivation phase during the dry season, contrary to V. ornatus which is active the year round) and habitat selection (V. niloticus typically inhabits savanna biotopes in rather close association with water bodies, whereas V. ornatus is a rainforest form restricted to the African forest biota). Thus, Boehme & Ziegler (1997) concluded that these differences argue for a selectively induced divergent evolution into different biota. Moreover, whether the two monitor forms should be regarded as semispecies within the Varanus niloticus superspecies or as incipient species, is partially solved by the fact that the distribution pattern demonstrates a general broad parapatry, but with some examples of true sympathy at various places of their ranges, without any indication of intergradation or hybridization (Boehme & Ziegler, 1997). Sympatric occurrence of the two forms was observed, according to Boehme & Ziegler's map, in Liberia, Ghana, Nigeria, Gabon, and Zaire. With regard to Nigeria, sympatric occurrence of niloticus and ornatus was observed in the surroundings of Lagos and in the Niger Delta.

Since 1996, we are conducting detailed field researches on reptile distribution and ecology in the Niger Delta and in other areas of southeastern Nigeria (e.g. see Akani et al., 1998a, 1998b; Luiselli & Angelici, 1998; Luiselli et al., 1998). Thus, we have frequently observed free-ranging monitors, and we have collected biological information on this species complex which is extremely relevant because it is relative to one of the few regions in which both the forms are said to be sympatric.
By means of the data collected in the field, we try to answer to the following questions:

(1) Are the two monitor forms really found in sympatry, and, if so, in which kind of habitats are they in fact sympatric?
(2) What are the habitat preferences of monitors in southeastern Nigeria?
(3) Do Nigerian monitors exhibit phenology characteristics (i.e. aestivation phase during the dry season) which, according to Boehme & Ziegler (1997), can be attributed to genetically induced ecophysiological modifications?
(4) What do Nigerian monitors feed on?
(5) Based on answers to all these questions, is there any additional support for the view that *ornatus* and *niloticus* are two distinct species?

Moreover, we address some notes on the relationships between monitors and local people, in order (i) to provide some new information of anthropozoological interest, and (ii) to give some considerations of interest for monitor conservationists.

**MATERIALS AND METHODS**

**STUDY AREAS**

All observations presented here were done during several field research expeditions, carried out between September 1996 and July 1998, in three different groups of localities, all situated in southeastern Nigeria (Fig. 1). A group of localities is situated in the eastern axis of the Niger Delta (region of Port Harcourt, Rivers State, $04^\circ 45'\ N$, $07^\circ 01'\ E$); a second group of localities is situated in the surroundings of Eket (Akwa-Ibom State, $04^\circ 50'\ N$, $07^\circ 59'\ E$), a third group of localities is situated in the Cross River State: in the Oban Hills ($05^\circ 20'\ N$, $08^\circ 21'\ E$), in the swamp forests of Itu ($05^\circ 14'\ N$, $07^\circ 59'\ E$), and in the surroundings of Calabar ($04^\circ 48'\ N$, $08^\circ 21'\ E$).

The climate is typical for a tropical sub-Saharan country, with well-marked dry and wet seasons with relatively modest monthly fluctuations in maximum and minimum temperatures. The dry season extends from November to April, and the wet season from May to October (with some year-to-year variations). Mean monthly maximum temperatures range between 27 and 34 °C, while minima vary between 22 and 24 °C. Study areas were situated within the Guinea-Congolian rainforest (White, 1983) in the Equatorial climatic zone (Von Chi Bonnardel, 1973).

The study region is heavily populated, with hundreds of small villages and towns interspersed within a patchy mosaic of cultivated lands, oil palm fields, plantations (banana, plantain, pineapple, yam, cassava, etc), open lands used for oil extraction platforms, forests, bush, and water bodies (Singh *et al.*, 1995). The widest portions of rainforest are found along the banks of the river tracts (riverine forests). Rainforest patches may have dry soil (lowland dryland forest) or may be seasonally flooded and inundated swamp forests. These swamp forests are dominated by *Raphia vinifera* and *Raphia hookeri*, and other common plant species are *Uapaca staudtii*, *Sterculia oblonga*, *Ceiba pentandra*, *Pandanus* sp., and *Pterocarpus santalinoides*; typical tree species include *Terminalia superba*,

---
Figure 1. — Map of Nigeria, showing the three main study areas.

*Piptadeniastrum africanum*, and *Lophira alata*. Mangroves (dominant species are *Avicennia* spp. and *Rhizophora racemosa*) are found along the brackish water river tracts, and form enormous extensions along the coast (“coastal mangroves”). It should be noted that mangrove forests of Nigeria are the widest in all of Africa and the third-largest in the world, and that approximately 60% of the Nigerian mangrove forest is situated in the Niger Delta (Singh et al., 1995). In general, the eastern Niger Delta localities are less covered by forests than those situated in the surroundings of Eket and, especially, of those situated in the surroundings of Calabar.

**METHODS**

This study is based on observations of free-living specimens and on examination of specimens which were killed by local people, and traded in local bush-meat markets.

Whether a monitor belong to the form *niloticus* or to the form *ornatus* was assessed only by examination of dead and captured specimens, since it was nearly
impossible to correctly discriminate the two forms by observing living animals in the wild (these monitors are very elusive, and typically exhibit far escape-distances, Angelici et al., unpubl. observations). We identified the examined specimens by their colour pattern, which is clearly different in the two forms (Mertens, 1942; de Buffrénil, 1993; Boehme & Ziegler, 1997). Moreover, we noticed in some specimens the colouration of the tongue, which is another crucial discriminant characteristic (Boehme & Ziegler, 1997). We did not check for scale counts and morphology of their outer genital organs.

Food data were collected by dissection of dead specimens, and analysis of their stomach contents. These specimens, which were offered as food in local markets (see also Akani et al., 1998), were sexed and measured for snout-vent length (SVL, to the nearest 5 mm) and tail length (TL, to the nearest 5 mm) before being dissected. The contents of the stomach were removed, placed in 75% alcohol, and later identified to the lowest taxon possible.

Observations of phenology and habitat of monitors were carried out by conducting field trips both in sunny and in rainy days. The everyday field work was done approximately from 0800 a.m. to 0600 p.m., but occasionally later in the evening. Random routes to locate animals were conducted throughout every habitat type available in the study areas. Time of observation (Lagos time) and habitat of sighting of each monitor specimen were recorded.

All statistical analyses were done with a SPSS (version for Windows) package. All tests were two tailed, and alpha was set at 5%. In the text, means are always followed by Standard Deviations. Niche breadths for numerical data were calculated with modified Simpson’s (1949) measure of niche breadth.

RESULTS AND DISCUSSION

TAXONOMY AND DISTRIBUTION

Because of the strong logistic problems which take place in surveying forests and river basins, at the present time it is impossible to give more than a rough description of the distribution of Nile monitors in southeastern Nigeria. However, as a general trend, these lizards are widespread and relatively common. The species is present in the whole Niger Delta, from the northwestern part (surroundings of Sapele, 05° 53' N, 05° 42' E) to the southeastern part (surroundings of Port Harcourt, 04° 45' N, 07° 01' E), and is locally very abundant (e.g. in Riverside and Bonny island, 04° 29' N, 07° 11' E, south of Port Harcourt; and along the riverine forests of the Orashi and Sambreiro rivers). We captured monitors also in the territories of Aba (Abia State), Ikot Ekpene, Uyo, Eket (all in Akwa-Ibom State), and Itu, Oban Hills, Ugep, and Calabar (Cross River State).

All the specimens examined for coloration pattern (total n = 73), which came from Niger Delta, Abia State, Akwa-Ibom State, and Cross River State, showed a typical ornatus pattern (sensu Mertens, 1938, 1942), and all those examined for tongue coloration (n = 29) had whitish tongue, as typical for ornatus individuals (cf. Boehme & Ziegler, 1997). The lack of niloticus specimens from our examined sample impeded comparative analysis of the head structure, which should be larger and more robust in ornatus than in niloticus specimens (Boehme & Ziegler, 1997).
The fact that all specimens from the Niger Delta were *ornatus* is noteworthy, since this is an area of supposed sympatry between the two forms (Boehme & Ziegler, 1997). Interestingly, even six adults (five males and one female) captured in a bushy derived savanna near Lagos (Lagos State) had a typical *ornatus* pattern, despite (i) in this area both subspecies are supposed to coexist (Boehme & Ziegler, 1997), and (ii) bushy savanna is generally considered to be a typical habitat for *niloticus* (Bayless, 1997; Boehme & Ziegler, 1997).

In general, our data cannot confirm the existence of sympatric populations of *ornatus* and *niloticus* in southeastern Nigeria, as indicated by Boehme & Ziegler (1997). However, the subspecies *niloticus* was observed in the northern and northeastern regions of Nigeria, including the Yankari Game Reserve (Luiselli & Angelici, unpublished data), the surroundings of Maiduguri and the Lake Tchad region (de Buffrénil, 1992, 1993; Luiselli & Angelici, unpublished observations), and the zone between Kano and the Lake Tchad (de Buffrénil, 1993).

**HABITAT CHARACTERISTICS**

It is difficult to define the habitat frequented by monitors in southeastern Nigeria, as *ornatus* specimens can be found in very different habitats in relation to the different environmental characteristics of the various localities inhabited by them. Thus, it was necessary to analyse monitor habitats both at a regional and at a local level.

At a regional level, we determined the habitats of capture of *ornatus* specimens in seven study areas of the eastern axis of the Niger Delta which were intensively surveyed during both the dry and the wet season (Table I). In these areas, however, we were unable to examine a number of monitors (> 20 specimens in each locality) enough for determining the habitat preferences of these lizards on a quantitative basis. This was done at an additional locality (surroundings of Eket), where we were able to examine for habitat characteristics more than twenty different specimens.

**TABLE I**

*Selected study areas within the Niger Delta territory (Port Harcourt region, Rivers State) where the main habitats frequented by Varanus niloticus ornatus were assessed. Data come from direct observations of free-living specimens or from examination of specimens captured in traps of local people.*

<table>
<thead>
<tr>
<th>Study area</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Habitats of Monitors</th>
</tr>
</thead>
<tbody>
<tr>
<td>Otari</td>
<td>N 04°53'22.3</td>
<td>E 006°41'19.7</td>
<td>Dryland forest - Rivers banks</td>
</tr>
<tr>
<td>Rumuji</td>
<td>N 04°57'19.3</td>
<td>E 006°46'28.1</td>
<td>Shrublands - Farmlands</td>
</tr>
<tr>
<td>Soku - Elem Sangama</td>
<td>N 04°40'39.8</td>
<td>E 006°40'54.2</td>
<td>Swamp forest - River banks</td>
</tr>
<tr>
<td>Tombia Forest</td>
<td>N 04°46'34.9</td>
<td>E 006°53'56.9</td>
<td>Dryland forest - Cultivations</td>
</tr>
<tr>
<td>Tombia Mangrove</td>
<td>N 04°46'50.9</td>
<td>E 006°51'53.9</td>
<td>Mangroves</td>
</tr>
<tr>
<td>Orashi River</td>
<td>N 04°44'43.1</td>
<td>E 006°38'10.1</td>
<td>Swamp forest - River banks</td>
</tr>
<tr>
<td>Peterside (Bonny)</td>
<td>N 04°29'14.9</td>
<td>E 007°10'04.8</td>
<td>Mangroves</td>
</tr>
</tbody>
</table>
Examination of the main habitats of capture of *ornatus* specimens in the seven study areas of the Niger Delta region shows that these monitors inhabit a very wide range of habitat types, from cultivations and farmlands to dryland forest, and from deltaic swamp forest to mangroves (Table I). This is also obvious if we compare the distribution of the localities where this taxon was observed (Fig. 2) with the schematic division of the study region (eastern Niger Delta, region of Port Harcourt) on the basis of the main environmental characteristics (Fig. 3). Moreover, interviews with selected hunters of local tribes suggested that monitors (in this case whether *ornatus* or *niloticus* is unknown) can be quite common in such different habitats as high mangrove (e.g. in Peterside, 04° 29' N, 07° 10' E), deltaic swamp forest (e.g. in Soku, 04° 40' N, 06° 41' E), and cultivations (e.g. in Tombia, 04° 46' N, 06° 54' E).

![Figure 2. — Map of the Port Harcourt region (eastern axis of the Niger Delta) showing the twenty-six localities of capture of Varanus niloticus ornatus. P.H. = Port Harcourt.](image)

Habitat types available to Monitor Lizards in Eket were divided in the following categories: primary lowland wet forest (habitat A), secondary lowland wet forest (habitat B), banks of the river Kwa-Ibo and of its tributaries (habitat C),
bushy boundary strip surrounding the forest (habitat D), former cultivations actually recolonized by vegetation (habitat E). Assessment of habitat characteristics of Monitor Lizards was based on 30 sightings (all relative to *ornatus* specimens). These animals were found in every habitat type available in the study territory, but mainly in the habitat types B and C (26.7% of the total number of records). However, there was no significant difference in the frequency of observation of Monitor Lizards in the various habitat types (Mann-Whitney U test, $U = 12.0, Z = -0.104, P = 0.92$).

Generally speaking, both qualitative information coming from the Niger Delta (Table I and Fig. 2 and 3) and quantitative information coming from Eket territory are consistent in showing that *V. n. ornatus* is habitat generalist in southeastern Nigeria. This evidence is in partial disagreement with Bayless' (1997) and Boehme & Ziegler’s (1997) suggestions that *ornatus* is exclusively a rainforest form restricted to the African forest biota as far as they still exist. According to Bayless (1997), both taxa are present in the “equatorial and tropical forest ecological region”, but *ornatus* is found only in the “tropical rainforest microhabitat”, whereas *niloticus* inhabits a wide range of microhabitats, from the “forest-savanna mosaic” to “scrub” and to “evergreen thickets”. Our data
definitely demonstrate that *ornatus* is also found in nearly the same wide variety of microhabitat types as *niloticus*, at least in southeastern Nigeria. Moreover, Bayless (1997) reported that *ornatus* is found only in regions with more than 1,600 mm rainfall per year, whereas *niloticus* is found in regions with 201 to 1,600 mm rainfall per year. Our study regions are characterized by a rainfall much exceeding 1,600 mm per year, thus suggesting that they can be inhabited only by *ornatus*, as our own data also indicated.

PHENOLOGY

During our investigations in southeastern Nigeria, we observed a total of 73 Monitor Lizards which were certainly attributed to one precise form (*ornatus* in all cases). The numbers of Monitor sightings in relation to season is presented in Table II. Specimens of *V. n. ornatus* were found all over the year, including both the dry and the wet seasons. However, higher numbers of specimens were found during the wet months than during the dry months (see Table II).

<table>
<thead>
<tr>
<th></th>
<th>J</th>
<th>F</th>
<th>M</th>
<th>A</th>
<th>M</th>
<th>J</th>
<th>J</th>
<th>A</th>
<th>S</th>
<th>O</th>
<th>N</th>
<th>D</th>
</tr>
</thead>
<tbody>
<tr>
<td>Numbers of Monitors</td>
<td>3</td>
<td>2</td>
<td>5</td>
<td>6</td>
<td>9</td>
<td>14</td>
<td>8</td>
<td>6</td>
<td>2</td>
<td>4</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td>Percent on the total</td>
<td>4.11</td>
<td>2.74</td>
<td>6.85</td>
<td>8.22</td>
<td>12.33</td>
<td>13.70</td>
<td>19.18</td>
<td>10.96</td>
<td>8.22</td>
<td>2.74</td>
<td>5.48</td>
<td>5.48</td>
</tr>
</tbody>
</table>

Our data showed that *ornatus* specimens from southeastern Nigeria do not exhibit any “diapause” during the dry season, whereas Monitor Lizards aestivate in burrows, hollow trees, and termite mounds in drier Afrotropical regions including Senegal and northern Cameroon (Cissé, 1976; de Buffrénil, 1993). De Buffrénil (1993) suggests that only populations of *niloticus* do aestivate, whereas those of *ornatus*, more linked to the very humid equatorial climate, may not aestivate at all. According to Boehme & Ziegler (1997), the aestivation phase is not a simple adaptational modification, but a selectively, genetically induced modification which is typical of *V. n. niloticus*. Our data can neither confirm nor reject the hypothesis given at above, but can at least confirm that aestivation is not likely to take place in free-ranging populations of Nigerian *ornatus*, as expectable from de Buffrénil’s (1993) suggestions on this taxon from other African countries.

Six *ornatus* females examined between late March and mid-April contained eggs in the abdomen, and hatching eggs were found in early May. Thus, despite the little amount of available data, it is likely that there is a pronounced seasonality in the reproduction of this species. It is interesting to note that the reproductive
seasonality of our ornatus specimens is very consistent with the findings of hatching eggs on early May in niloticus specimens from the Yankari Game Reserve in northeastern Nigeria (Butler, 1986).

FOOD HABITS

We collected detailed dietary data for the ornatus populations inhabiting the wet forests of Elem-Sangama (04° 40' N, 06° 40' E, Rivers State) and Eket (04° 50' N, 07° 59' E, Akwa-Ibom State).

Adults preyed on a wide variety of organisms, but crabs were the most important prey types in terms of frequency of occurrence (56.1% of the whole dietary spectrum). Vertebrates were rarely preyed on, but these Monitor Lizards proved to feed on both smaller conspecifics (1.7% of the total number of prey items) and newborn dwarf crocodiles Osteolaemus tetraspis (1.7%). On the whole, vertebrates constituted just over 10% of the total number of prey items. The juveniles fed only upon invertebrates, essentially crabs (77.8% of the diet).

The diet composition of males and females was significantly different ($\chi^2 = 78.85$, df = 9, $P < 0.00001$), whereas there were no statistically significant differences between juveniles and adult males ($\chi^2 = 4.71$, df = 9, $P > 0.8$) or between juveniles and adult females ($\chi^2 = 12.55$, df = 9, $P > 0.15$). The food niche breadth of juveniles was less wide than that of the adults ($B = 1.58$ versus 2.83), and this difference attained statistical significance ($P < 0.001$, Mantel test). The food niche breadth was very similar in the adults of both sexes (males: $B = 2.49$; females: 2.85; differences insignificant at Mantel test).

With regards to crabs, it should be noticed that these crustaceans are extremely abundant along the banks of creeks, rivers, ponds, and swamps of the rainforests and mangrove forests of southeastern Nigeria, where they probably represent an unlimited food resource which is crucial for the life of a variety of predators. In fact, crabs are used as food not only by Monitor Lizards, but also by other reptiles, birds, and carnivorous mammals. For instance, with regard to the study areas, crabs were found in the stomachs of young Nile crocodiles (Crocodylus niloticus), young and adult dwarf crocodiles (Osteolaemus tetraspis), in the faeces of genets (Genetta maculata), mongooses (Atilax paludinosus), and otters (Lutra maculicollis), and were also used as food by several bird species (Angelici, Akani & Luiselli, unpublished data).

The fact that juveniles showed a significantly narrower food niche breadth than the adults was quite expectable, as smaller body size could place a constraint over the variety of prey types they can capture and swallow. Compared with other varanids of similar size (e.g. see Cissé, 1980; Cowles, 1980; Shine, 1986a; Yeboah, 1993; Lenz, 1995; De Lisle, 1996), Nigerian V. n. ornatus preyed on vertebrates less frequently. We suggest that the great abundance of crabs in their environment is the main reason for the relative rarity of predation by monitors upon vertebrates: these large lizards, being opportunistic predators, feed mainly upon crabs simply because these crustaceans are extremely abundant and easy to capture. The significant intersexual difference in dietary composition observed in Nigerian ornatus is probably linked to the obvious sexual size dimorphism of the Varanus niloticus species complex (de Buffrénil et al., 1994; Boehme & Ziegler, 1997). In fact, it is well known that remarkable intersexual dietary differences are usually found in species with the one sex much larger than the other, and/or with remarkable differences in habitat characteristics (Shine, 1986b; Houston & Shine, 1993; Luiselli & Angelici, 1998).
Monitor Lizards are well known to people inhabiting small villages and towns. They represent one of the main meat types for villages situated along the rivers, including the Bonny, New Calabar, Orashi, and Sambreiro rivers, and their tributaries (Akani et al., 1998a). This is not surprising, as Nile Monitor meat is considered as a deliciousness in several African regions (e.g. see Irvine, 1960; de Buffrénil, 1991, 1992). Apart for the native African names, Monitor Lizards are usually called “iguanas” by English-speaking persons of southeastern Nigeria. It is interesting to note that they are sometimes considered as a kind of small crocodile, despite in most cases the hunters of bush-villages are perfectly able to discriminate between monitors (“iguanas”, that they correctly think to be giant lizards), Nile crocodiles (“crocodiles”), and dwarf crocodiles (“alligators”).

We observed trading of Monitor Lizards in bush-meat markets of Igbo, Idjaw, Ikwerre, Ogoni, Akwa-Ibom, and Calabari people. These varanids represented, together with fish, one of the most important meat sources for people from Peterside village (04° 29′ N, 07° 10′ E) and from Soku village (04° 40′ N, 06° 40′ E), other than probably from many other riverine villages. In these sites they were captured by means of self-made traps of indigenous design or by the use of canoe (see also de Buffrénil, 1992). Moreover, skins of these varanids were observed in the markets of several urban centres (Akani et al., 1998). Use of skins for tannery industry represents a main threat for Nile Monitors (Vernet, 1984; de Buffrénil, 1992, 1993), and it was calculated that approximately 1.5 to 2 millions of specimens are killed every year because of these reasons in the whole African continent (de Buffrénil, 1991). Despite this intense exploitation, Monitor Lizards are not apparently suffering for a very serious decline due to human hunting in the study regions of southeastern Nigeria, contrary to what happens in other African countries (de Buffrénil, 1992). It is likely that the habitat generalism of nigerian V. n. ornatus, as well as the existence of wide patches of high mangrove forest and of swamp forest, could permit these varanids to still survive even in these heavily populated and intensively exploited regions of southeastern Nigeria. Moreover, it should be noted that “iguanas” are considered “holy animals” (linked to local animistic religious practices, and locally named “Dgyou-dgyou” animals) in some territories of the eastern Niger Delta where, therefore, their hunting is in fact forbidden.

CONCLUSIONS

What are the main implications of the given data for the understanding of the evolutionary history of V. niloticus species complex?

A first obvious evidence is that the claimed occurrence of sympatric populations of niloticus and ornatus in southeastern Nigeria is not confirmed by our two-year long field surveys. Thus, more research should be done before accepting Boehme & Ziegler’s (1997) view about this remarkable coexistence of monitor forms in Nigeria. It is possible that the records of niloticus specimens from the Niger Delta are relative to aberrant ornatus or to mislabelled museum specimens (a common event in museum collections of African reptiles). Another possibility is that some niloticus specimens, imported from Kano for skin industry,
were traded in Port Harcourt, and thus thought to be captured in the Niger Delta by the observer. Thus, at least with regard to southeastern Nigeria, we are led to think that there is no evidence of unmixed sympathy (resp. syntopy) between the two monitor forms in nature. Of course, the situation could be different in other African countries where the two forms are said to be sympatric (Boehme & Ziegler, 1997).

The fact that Nigerian *ornatus* showed a remarkable generalism in terms of habitat selection is also interesting, because it demonstrates that this taxon is not linked exclusively to rainforest biota, as previously supposed to be. Thus, this habitat generalism of *ornatus* could place some problems to the theory of an incipient speciation process due to habitat isolation between the two forms. With regard to Nigeria, it is obvious that crucial regions to be explored are the ones characterized by derived savanna and Guinea savanna as major natural vegetation zones (e.g. the territories of Lokoja, Makurdi, Bida, and Ogbomosho), where the two Nile monitor forms could eventually occur in sympathy.

The clear evidence of a lack of aestivation in Nigerian *ornatus* mirrors data presented by de Buffrénil (1993) on this taxon, contrary to *niloticus* which is able to aestivate during the dry season. This eco-physiological difference is, according to Boehme & Ziegler (1997), a firm evidence of the status of different species of *niloticus* and *ornatus*: following these authors, in fact, this ecophysiological and behavioural difference should be necessarily selectively, i.e. genetically, induced. Contrary to these authors, we are led to think that the data actually available are too preliminary for stating any firm conclusion, and that this eco-physiological and behavioural difference could be easily explained by ecological (external) constraints rather than genetical differences. In fact: (i) there are some *niloticus* populations which are active all the year round exactly as is the rule for *ornatus* populations (Cissé, 1980); (ii) no experimental study has shown that *ornatus* cannot aestivate when the external conditions are so dry to constrain it to do so. It is well possible that *ornatus* usually do not enter into aestivation simply because the external conditions usually do not constrain them to do so. In fact, there are many reptile species which show similar kinds of intraspecific variation in some ecophysiological traits. For instance, *Vipera aspis* populations from Swiss Alps enter into hibernation during the cold winter months (Monney, 1996), whereas conspecific populations from Mediterranean central Italy are above-ground active also during the winter months, without showing any true hibernation phase (Saviozzi, 1994). Is this an indication that they are different or incipient species? Thus, we suggest to be more cautious with regard to Nile Monitors ecophysiology.

In conclusion, data presented in this paper suggest that, despite there are good morphological reasons for suggesting a subdivision of *V. niloticus* into two reproductively isolated species (Boehme & Ziegler, 1997), this view cannot be confirmed by both distribution and ecological data relative to Nigerian Nile Monitor populations. Detailed eco-physiological comparative work on both *ornatus* and *niloticus* is thus urgently required to definitely solve crucial problems about the *V. niloticus* species complex.

**ACKNOWLEDGEMENTS**

We are gratefully indebted to the companies "T.S.K.J. Nigeria Ltd." (Port Harcourt and Lagos), "Aquater S.p.A." (San Lorenzo in Campo), "Ecosystem s.r.l." (Bari), "DEMETRA", "F.I.Z.V."
(Rome), and "Amertex Oil & Gas Ltd." (Lagos) for supporting our research in Nigeria. Zena Tooze ("Cercopan", Calabar) and Dr Edoardo Politano ("Aquatex") are thanked for their friend collaboration. Prof. Godfrey C. Akani and Dr Ikomah F. Barieenee (both from Port Harcourt) helped us in the field, and collected several records. Dr Henry Manyo Ndoma and Dr Emmanuel Arikpo (both from Akampka) permitted examination of specimens stored in their collections. Dr Massimo Capula (Rome), Prof. Godfrey C. Akani, Dr Roland Vernet (Paris), and two anonymous referees critically reviewed earlier drafts of this paper.

REFERENCES


