A TAXONOMIC REVIEW OF THE VARANUS (POLYDAEDALUS) NILOTICUS (LINNAEUS, 1766) SPECIES COMPLEX

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The status of the two nominal subspecies of *Varanus niloticus* (Linnaeus, 1766), viz. *V. n. niloticus* and *V. n. ornatus* (Daudin, 1803) is re-evaluated based on morphological (colour pattern, scalation, dimensions, outer genitals), ecological, and distributional data. Evidence is presented that both forms have markedly surpassed the subspecific level and have to be treated as two distinct, though closely related, species.

INTRODUCTION

In his subgeneric classification of the genus Varanus, Mertens (1942) placed the two tropical African monitor lizard species V. exanthematicus and V. niloticus in two different subgenera. Whereas he assigned the former together with the Indian V. flavescens to a joint subgenus *Empagusia* Gray, 1838 (type: V. flavescens), he accommodated the latter in a monotypic subgenus Polydaedalus Wagler, 1830. This largely phenetic classification has not been supported by subsequent studies. V. flavescens turned out to be unrelated to the African steppe monitors (see Ziegler & Böhme, 1997 and references therein), which, in turn, actually consist of three species: V. exanthematicus s. str., V. albigularis and the SW-Arabian V. yemenensis. Moreover, they turned out to be rather closely related to their largely sympatric congener V. niloticus and are therefore now jointly accomodated in the subgenus Polydaedalus (for a summary of these changes and an updated review of varanoid lizard classification in general see Böhme, 1988, and Ziegler & Böhme, 1997).

Varanus niloticus has a vast distribution area covering most of the African continent, with the exception of the Mediterranean zone in the north-west and the extreme south, as well as the huge desert areas of the northern and south-western part of the continent (cf. the sketch maps in Buffrénil, 1993, and Lenz, 1995). Due to a different colour pattern, Mertens (1938, 1942) distinguished two subspecies:

- *V. n. niloticus* (Linnaeus, 1766), characterized by 6-9 light crossbands or rows of light ocelli between foreand hindlimbs, and inhabiting the open areas outside the West and Central African rain forest;

- *V. n. ornatus* (Daudin, 1803), characterized by normally only 5 light cross-bands or oblique rows of light ocelli between the extremities, and inhabiting the western and equatorial forest block.

Mertens (1942) mentioned an additional distinguishing character, viz. the colour pattern of the tail which has broader – and therefore fewer– light crossbands in V. n. ornatus (12) than in V. n. niloticus (16-18). He further assumed craniological differences between both forms, but due to scarce skull material with partly insufficient locality data he was unable to demonstrate them. His scale counts proved to be a little more conclusive, but he finally considered both subspecies to be distinguished only by their colour pattern.

If one considers the numerous papers dealing with $V_{\rm m}$ niloticus from different viewpoints, it seems that Mertens' (1938, 1942) concept of these two subspecies has been largely accepted until present (e.g. Dunger, 1967; Branch, 1988; Buffrénil, 1993; Bennett, 1995; Lenz, 1995). The differences in colour pattern as described by Mertens (1942) are, however, not the only distinguishing features between the two forms of the Nile monitor. As well as biological differences, we are aware of additional morphological distinguishing characters (see our personal communications in Lenz, 1995: p. 10) that have been reiterated already in popular articles (see Faust & Bayless, 1996). In view of our very new genital-morphological results (Ziegler, 1996; Ziegler & Böhme, 1997), it seems appropriate to reconsider the taxonomic status of the two V. niloticus forms on the basis of new morphological and distributional analyses.

MATERIAL AND METHODS

Our study is based on material kept in the Zoologisches Forschungsinstitut and Museum A. Koenig, Bonn (ZFMK), the Zoologische Staatssammlung, Munich (ZSM), the Natural History Museum, London (BM), and the Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt/Main (SMF). From literature data we refer also to voucher specimens kept in the Zoologisches Museum, Hamburg (ZMH).

In the course of preliminary investigations, we evaluated only locality and tongue colour data following a first assignment based on colour pattern. Here we were greatly supported by B. Hughes, London, who provided data from more than 80 *V. niloticus* specimens deposited in the BM and some additional specimens from his own collection. The metric and meristic values are derived from 69 ZFMK and ZSM specimens; we incorporated only a few SMF specimens in our investigations, as the numerous data of Mertens (1942) that

	V. n. niloticus			V. n. ornatus		
	N	Range	Mean±SD	Ν	Range	Mean±SD
Light dorsal cross-bands between the extremities	36	611	7±1.2	33	4–6 (1x4, 31x5, 1x	5±0.3
Light cross-bands of the tail	32	10-18	13±2.3	33	9-12	10±0.9
Colour of tongue	97	pigmented (blueish-black)		57	light (whiteish-p	ink)

TABLE I. Morphological characteristics of V. n. niloticus and V. n. ornatus.

are incorporated in our study are already based on SMF material.

The genital-morphological findings and terminology are based on the works of Ziegler (1996) and Ziegler & Böhme (1997).

The distribution maps were plotted on the basis of the specimens investigated by the authors and B. Hughes and supplemented by unambiguous data from the literature.

RESULTS

MORPHOLOGICAL CHARACTERS

Colour pattern. Sorting the studied Nile monitor material by the number of light dorsal cross-bands or oblique rows of light ocelli resulted in a separability of nearly 100%, in juveniles as well as in adults: 5 rows in ornatus, and markedly more in the nominate form; a similar situation is found concerning the light crossbands of the tail (Table 1).

Tongue colouration. We found a highly consistent correlation between these colour pattern characters and the colouration of the tongues (we excluded artefacts such as a later depigmentation due to alcohol storage for several decades). Whereas specimens of the nominotypic form constantly have fully pigmented,

dark tongues, all *ornatus* specimens studied had unpigmented, light, whitish to pink tongues. Only in very rare cases were some small dark flecks observed on these tongues, and if so, only in their hindparts (e.g. ZSM 140/1975 from Yaoundé, Cameroon: 5 light dorsal bands, 9 light tail bands, 158 midbody scales). In view of this constant, additional distinguishing character we are able to assign the 2 specimens of *ornatus* with a slightly deviating colour pattern (ZSM uncatalogued: Mundame, 4 light dorsal bands, 11 light tail bands; ZSM 619/0: Gabon, 6 light dorsal bands, 10 light tail bands, 161 midbody scales: see also Table 1) clearly to *ornatus*.

Differing from this character combination is only a Nile monitor photographed near Mombasa, Kenya. This specimen (available only as a photograph) has a colour pattern similar to typical *V. n. niloticus*; it shows, however, a light, whitish tongue which is otherwise typical of *ornatus*. Another specimen, likewise from eastern Africa (BM 1969. 404: Condocuanza, Mozambique) has also a light (faded?) tongue, as does a specimen from NE Africa (BM 1906.7.25.3: Egypt, Luxor) (Hughes, pers. comm.). For a discussion of these and other exceptional specimens see further below.

TABLE 2. Scalation characteristics of V. n. niloticus and V. n. ornatu	<i>s</i> .
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	V. n. niloticus			V. n. ornatus		
	Ν	Range	Mean±SD	Ν	Range	Mean±SD
Scales across the head from rictus to rictus (after Mertens, 1942)	/	43-56	Ĩ	/	5060	1
Oblique ventral scale rows from gular fold to insertion of hindlegs (after Mertens, 1942)	11	77–94	88±5.6	16	80-95	90±4.5
Scales around midbody (after Mertens, 1942)	12	137–165	154±8.1	15	146-175	90±4.5
Scales around midbody (own data)	32	136–183	153±10.3	31	149–174	161±5.4
Scales around midbody (own data + Mertens, 1942)	44	128-183	153±9.8	46	146175	162±6.7



FIG. 1. Histogram of scales around midbody, based on Mertens' (1942) and own data. * = V. n. *niloticus* (ZFMK 2784) from Egypt, surroundings of Cairo (black tongue, 8 light dorsal crossbands between the extremities, 14 light crossbands of the tail).

Scalation. The results of the scale counts done by us are summarized in Table 2, where we incorporated also the scalation data published by Mertens (1942). However, he did not give the sample sizes on which his values relied (oblique ventral scale rows from gular fold to insertion of hindlegs for *V. n. niloticus* 75-94, mean = 88, for *V. n. ornatus* 80-97, mean= 89; scales around midbody for *V. n. niloticus* 128-165, mean= 153, for *V. n. ornatus* 146-175, mean= 164). Therefore, we compiled the raw data from Mertens' (1942) paper – as far as possible – in our Table 2 and calculated their mean values and standard deviations. The most useful scale character to separate both forms is the midbody scale count which we illustrated by a histogram (Fig. 1).

Head proportions and dimensions. Like Mertens (1942), we did not have sufficient skull material with reliable data available to carry out a comparative craniological study. Nevertheless, it became evident from our material that adult *V. n. ornatus* have a much more massive skull architecture than equal-sized adults of the nominotypic form (see also Mertens, 1942: pl. 27; Dunger, 1967: pl. 1). Fig. 2 documents this situation by illustrating the heads of two roughly equal-sized males, the *ornatus* male having a markedly more compact, higher and blunter head (and consequently also skull) than the *V. n. niloticus* male.

Here we can report also on an extremely large (though partly damaged) *V. n. ornatus* skull of unknown sex from Ureca, Bioko Island, Equatorial Guinea (ZFMK 14889). It measures from tip of snout to occiput 14.2 cm, from tip of snout to the hindmargin of the squamosum 15.0 cm; the lower jaw (from tip of snout to the posterior end) measures no less than 15.2 cm (cf. the data published by Haacke & Groves, 1995).

Genital morphology. Available were the everted organs of several representatives of both sexes of the nominotypic form (ZFMK 17521, 32389, 35565-6, 61141-2, 2 specimens ZFMK uncatalogued) as well as of *V. n. ornatus* (ZFMK 9399, 58217, 61132, 61137, 61140). Detailed descriptions of these organs can be found in Ziegler (1996) and in Ziegler & Böhme (1997). We restrict ourselves here only to highlight the differences between the two taxa in question.

The outer genital organs (of both males and females) of *V. n. niloticus* tend to have fewer (5-10) paryphasmata (versus 8-12 in *V. n. ornatus*). These are completely divided in the longitudinal axis in the former, and not completely divided in the latter, the most proximal 1-2 paryphasmata being uninterrupted.

DISTRIBUTION

The locality data of the museum specimens used in this study have been plotted on a map of Africa - separately for each of the two taxa - and have been supplemented by locality records for both V. n. niloticus and V. n. ornatus according to literature data (see legend of Fig. 3). For a better documentation of para- resp. sympatry, we provided an additional map for west and western central Africa, where we numbered each locality and gave the voucher references in the legend (Fig. 4).

From these maps it is evident that V. n. niloticus inhabits the extended savanna areas of Africa except the



FIG. 2. Head proportions of two roughly equal-sized adult males of *V. n. niloticus* and *V. n. ornatus*. Left: *V. n. niloticus* (ZFMK 17521) Senegal, Diattacounda, leg. W. Böhme, 10.-26. 12. 1975 (1.65 m); right: *V. n. ornatus* (SMF 49832) "French Congo, Province Orientale", Epulu, leg. B. Grzimek, 4.3.1954 (1.60 m).



FIG. 3. Rough distribution of *Varanus n. niloticus* (black circles) and *Varanus n. ornatus* (white circles) in Africa; marked area: tropical rain forest, swamp forest and mangrove, modified after Martin (1989). Locality data from examined specimens of BMNH, SMF, ZFMK and ZSM and according to Mertens (1942, 1971), Laurent (1964), Dunger (1967), Papenfuss (1969), Pienaar (1978), Auerbach (1987), Branch (1988), Lanza (1990) and Böhme et al. (1996); for more detailed information see overview in Buffrénil (1993).



FIG. 4. Rough distribution of *Varanus n. niloticus* (black circles) and *Varanus n. ornatus* (white circles) in West Africa (for origin of localities see caption of Fig. 1). 1 Abidjan / 2 Abuko National Park / 3 Accra / 4 Akwu / 5 Ashantee / 6 Bandia / 7 Batouri / 8 Bibundi / 9 Bipindi / 10 Bissau / 11 Bogou / 12 Bolama / 13 Boughari / 14 Bubaque / 15 Calabar / 16 Cape Mount / 17 Carnot / 18 Casamance / 19 Cotonou / 20 Dagana / 21 Dahomey / 22 Dibongo / 23 Duala / 24 Ebolowa / 25 Evinayong / 26 Bioko / 27 Freetown / 28 Gabon / 29 "Gabon City" = Libreville / 30 Great Popo / 31 Idenau / 32 Ikom / 33 Yaoundé / 34 Jebba / 35 Johann Albrechts Hill / 36 Cameroon Mountain / 37 Kayes / 38 Keta / 39 Kete / 40 Mt. Kupe / 41 Lagos / 42 Little Popo / 43 Longji / 44 Makurdi / 45 Malimba / 46 Mamfe / 47 Mbour / 48 Medina / 49 Monrovia / 50 National Park W / 51 Niger Delta / 52 Nyaake / 53 Numan / 54 Obubra / 55 Ogooue / 56 Rembo / 57 Robert Port / 58 Sangmélima / 59 Sérédou / 60 Sette Kama / 61 Sumbuya / 62 Teshie / 63 Thiès / 64 Tinto / 65 Trarza / 66 Umuahia / 67 Victoria / 68 Wanie Rukula. Addendum: 69 Bahr Aouk / 70 Bobo Dioulasso / 71 Chari / 72 Fitri / 73 Niger / 74 Chad.

true deserts, whereas *V. n. ornatus* has a distributional pattern restricted to the Upper Guinean and western Lower Guinean forest block, with some records also at the eastern margin of the latter. Numerous localities document sympatric overlap of the two forms not only at the joint margins of their respective distribution areas, but also within them (e.g. Liberia, Ghana, Nigeria, Gabon and SW Zaire).

There are some doubtful or problematic localities of voucher material studied by us which have not been included in our maps. These are:

- ZSM 7/1953: Lake Chad. This specimen has a white tongue (being darkened only in its hindpart), 5 light dorsal crossbands, 11 light tail bands and 166 scales around midbody, being thus a typical *ornatus*. We therefore consider its locality to be incorrect. - ZSM 618/0: "Kilwa, E Africa", having a white tongue, 5 light dorsal crossbands, 12 light tail bands and 168 scales around midbody, and thus being a typical *ornatus*, too. "Kilwa" may refer to a locality of the same name south

of Dar es Salam in Tanzania. We suspect the first locality to be the correct one but this is not certain.

- SMF 49832: "Epulu, Province Orientale, French Cong". This specimen has been illustrated by us above (Fig. 2) and is a typical *ornatus*. We did not map it because we are not aware of a locality Epulu in the ex-French Congo (today People's Democratic Rep. Congo), although there is an Epulu in the Province Orientale of Upper Zaire (= ex-Belgian Congo). Both possibilities would fit the distribution area of *V. n. ornatus*, but we cannot yet decide upon the correct one.

DISCUSSION

MORPHOLOGICAL DIFFERENCES

Our results clearly show that the two forms of Nile monitors are not only separable by their colour pattern, as supposed by Mertens (1942), but also by (1) the colouration of their tongues; (2) by different (though overlapping) scale counts; (3) by head and skull proportions; and (4) by marked differences in the morphology of their outer genital organs. (1) The tongue colouration is strongly related to the body colour pattern, being always dark in the savanicolous *niloticus* and pinkish-whitish in the forest form *ornatus*. This drastic difference in tongue colouration in two closely related monitors is reminiscent of the situation in *Varanus indicus* and its sibling species *V. doreanus* in New Guinea (Böhme, Horn & Ziegler, 1994), where a functional significance in specific recognition has even been hypothesized, as an aggressive "threatening tongue-flicking" does play a role in ritual combats (Horn, Gaulke & Böhme, 1994). Böhme *et al.* (1994) consider the light tongues as the plesiomorphic condition, in which case *ornatus* would be the most primitive form within the Nile monitor complex.

(2) Although the scale counts show a broad overlap (Table 2, Fig. 1), there is a clear tendency in *ornatus* for increased values in all 3 parameters checked (i.e. across the head from rictus to rictus, ventral rows from gular fold to insertion of hind legs, and scales around midbody). As higher scale counts are generally considered to be more primitive than lower counts (see e.g. Hellmich, 1951, Peters, 1962: 456), also in this respect *ornatus* is the less advanced form.

(3) Already Mertens (1942) had observed that despite similar body proportions in both Nile monitor forms, the heads of *ornatus* were relatively larger and more robust, particularly in very old males. Although he assumed subsequently that also very old *niloticus* (s. str.) males should be able to achieve similar head proportions, our material suggests that indeed *ornatus* has a relatively much more robust head (see Fig. 2). The huge *ornatus* skull from Bioko Island reported on here seems to belong to the largest Nile monitor ever recorded (cf. Haacke & Groves, 1995).

(4) The differences in the structure of the outer genitals, in fact of the hemipenes as well as of the hemiclitores, have to be given particular weight as to the taxonomic distinctness of their semaphoronts, as they most likely play a role in sexual selection (Ziegler, 1996; Ziegler & Böhme, 1997). The constant existence of a largely closed lower paryphasman row strongly argues for a plesiomorphic condition of this character in *ornatus*.

ECOLOGICAL DIFFERENCES

In addition to the morphological differences discussed above, there are important differences in the ecology of both forms in respect of (1) habitat selection, and (2) phenology.

(1) As stated above, *V. n. niloticus* typically inhabits savanna biotopes in rather close association with water bodies (rivers), and is able to penetrate even desert areas along large river systems (e.g. Senegal river, Nile and others). However, it avoids deserts without sufficient permanent water (see Figs. 3 and 4). *V. n. ornatus*, in contrast, is a rain-forest form restricted to the African forest biota as far as they still exist (see Figs. 3 and 4).

(2) Obviously connected with this adaptation to two different biota, there is an important phenological difference between the two forms, pointed out for the Cameroon populations by Buffrénil (1993): "In the north of the country, north of Ngaoundéré, where the dryness of the soil is very marked from December to (inclusively) April, the Nile monitors aestivate in burrows, hollow trees or termite mounds for several months ('diapause estivale'). On the contrary, in the southern half of the country, where there is a very humid equatorial climate, the Nile monitors (probably the subspecies V. n. ornatus) do not undergo a 'diapause'" (our translation). An aestivation during the dry season has also been reported for Senegalese populations by Cissé (1976). We consider it unlikely that this ecological difference, which requires a very different physiological basis, should be simply due to an adaptational modification. Rather, we consider it to be selectively, i.e. genetically, induced. This view is corroborated by the map provided by Buffrénil (1993: p. 126), showing the distribution of estivating vs. nonestivating populations in Cameroon.

DISTRIBUTIONAL PATTERN

The answer to how to estimate and possibly reassess the taxonomic status of the two forms of Varanus niloticus relies largely on their distributional pattern: i.e. whether they occur in sympatry or not. Already the morphological differences, in particular those of the genital organs and the tongues, lead to the suspicion that both forms are exceeding the subspecies level. This is corroborated by the phenological differences which argue for a selectively induced divergent evolution into different biota. But the question of whether they should be regarded as semispecies within a superspecies *Varanus niloticus*, or as incipient (= in statu nascendi) species, can – apart from conceptual problems – be judged only from the biological criterion of unmixed sympatry (resp. syntopy) in nature. The distributional situation as documented here demonstrates a general broad parapatry, but gives several examples of true sympatry at various places of their ranges, and this not only at the periphery of the ornatus range. This rather complicated distributional pattern, particularly in West Africa and in Gabon/southern Zaire, reflects the dramatic climatic history of the African tropics. The shrinking of the rain forest belt as seen today is a rather recent phenomenon, i.e. only 6000-7000 years old (Martin, 1989; Kingdon, 1990; Maley, 1996). This enabled the savanna-inhabiting populations to penetrate the forest block at various places where they met with the forest-inhabiting *ornatus* populations, obviously without any indication of intergradation or hybridization, as would be expected from conspecifics. On the other hand, the forest block which reached its maximum extension only 7000 years ago (see above) had its minimum extension during the Pleistocene only 18 000 years ago, when the forest was reduced to very small relict patches in West Africa, southern Cameroon, eastern Zaire and possibly a narrow coastal strip in southern Kenya. So the recolonization of the entire Zaire basin by the rain forest is also a rather recent event (between 18 000 and 7000 ybp.). Interestingly, we failed to find literature records for the central Zaire basin. This could indicate that the forest fauna, including the Nile monitor, is slow in recolonizing the forest. Indeed, there are numerous faunal examples of a similar distributional pattern (Martin, 1989; Kingdon, 1990, and others).

It is, however, interesting to note that V. n. niloticus has also not been recorded from the Zaire basin, this "evolutionary whirlpool" (Kingdon, 1990), where savannas and forests replaced one another several times. The extant V. n. niloticus is therefore not an old pre-Pleistocene savanna relict, but rather a modern, and in most of its characters, derived form, as compared with *ornatus*. This latter form seems to represent the survivor of an older, morphologically plesiomorphic stock. Its disjunct distribution pattern within the lower Guinean forest block discussed above (see also Figs. 3 and 4) fits this assumption. It may be noted that Mertens (1942) considered also the possibility of a "polytopic" origin of the forest-dwelling *ornatus* populations.

CONCLUSION AND FUTURE PROSPECTS

The morphological, ecological and distributional evidence presented here leads us to the conclusion that the two traditional subspecies of the Nile monitor have to be regarded as full species:

- Varanus (Polydaedalus) niloticus (Linnaeus, 1766)

- Varanus (Polydaedalus) ornatus (Daudin, 1803).

As no new forms are currently involved, we refrain from discussing synonyms of both species in this paper. This could, however, well become necessary, when additional material from critical areas becomes available. Problems for future taxonomic research on Nile monitors in Africa are indicated by some single specimens which are currently regarded as aberrant or, in some instances, possibly mislabelled (see above). An additional example is ZMB 18823, labelled as originating from Arafalis Rock, Sinai peninsula, but most likely coming from Arafale, Eritrea (Mertens, 1942). Also a clear *ornatus* (ZSM 7/1953) from Lake Chad, discussed already above, certainly has wrong locality data.

Another problem is the variability of the colour pattern of *V. ornatus*. As can be seen from our Table 1, the number of light dorsal crossbands can be reduced or augmented. Previously Mertens (1942) reported that there were very rarely juvenile *ornatus* with only 3 dorsal bands. Moreover, he mentioned an adult specimen figured by Daudin (1803), also with 3 dorsal light cross-bands. He also reports on a sample from between ldenau and Bibundi (Mt. Cameroon), where next to one specimen with 3 crossbands (SMF 11608) others had four (SMF 11604, ZMH 2936, 3607, 3990 and 4406). An increase over the number typical of *ornatus*, viz. 5, was observed by Mertens (1942) only once, in a specimen from Molundu (SMF 11600): Due to an asymmetrical pattern it showed 6 light, dorsal crossbands.

Mertens (1942) considered the low numbers of dorsal cross-bands as being "reduced". If we compare, however, this situation with that of the steppe monitors, which share the subgenus *Polydaedalus* with the Nile monitors, again the forms with higher scale counts and less derived hemipenes (*V. albigularis*) have lower numbers of dorsal oblique rows of ocelli. These are increased in the northern *V. a. microstictus* and *V. exanthematicus* (see Laurent, 1964; Böhme *et al.* 1989). It seems therefore reasonable to consider low numbers of light dorsal cross-bands in *Polydaedalus* as primitive, and increased numbers as derived. For the *V. niloticus* complex this means that *V. niloticus* (s. str.) can also be regarded as the derived form with respect to its colour pattern.

A last point of future taxonomic research in Nile monitors concerns the light-tongued specimens which have been found outside the currently known distribution range of V. ornatus, but which have a dorsal pattern like V. niloticus (see above). It is therefore questionable whether this is due to individual or to geographical (i.e. taxonomically relevant) variation. The monitor from Luxor, Egypt, with its light (probably faded) tongue is most unlikely to represent a specimen of ornatus, as Egypt was not covered by rain forest even during the maximal forest extensions in Africa. The situation of the - also in life - whitish-tongued Nile monitors inhabiting the East African coast between Kenya and Mozambique may, however, well be different, because this East African coastal strip has been a forest refuge during Africa's unstable Plio-/ Pleistocene history.

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ERRATUM

In *Herpetological Journal* 7(4), p. 156, line 3 of Table 2 should be amended as follows: the Mean \pm SD for 'Scales around midbody' for *V. v. ornatus* should read 162 \pm 8.7 instead of 90 \pm 4.5.