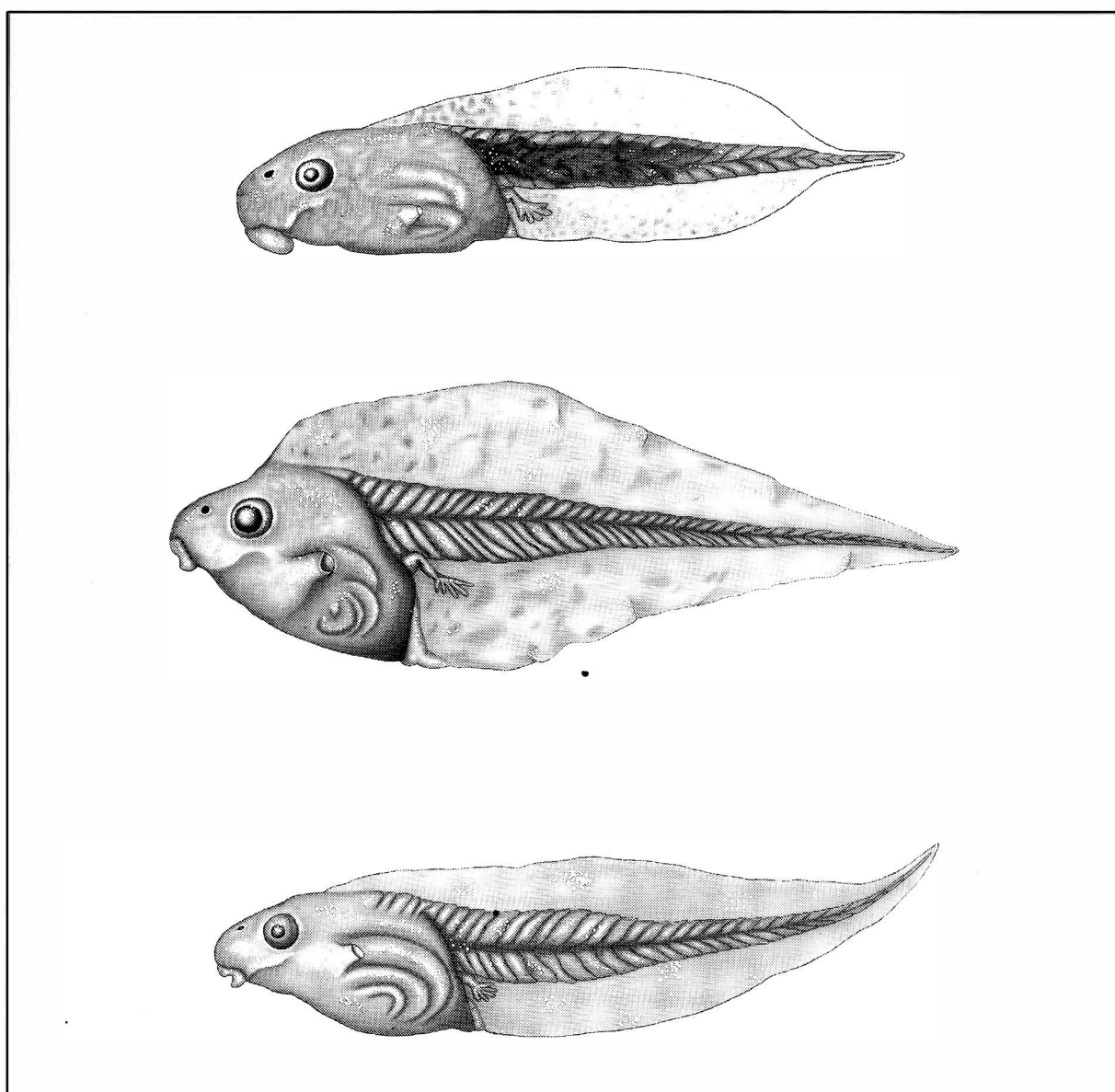


Volume 7, Number 1

January 1997

ISSN 0268-0130

THE HERPETOLOGICAL JOURNAL



Published by the
BRITISH HERPETOLOGICAL SOCIETY
50th Anniversary Year 1947-1997

Indexed in
Current Contents

The Herpetological Journal is published quarterly by the British Herpetological Society and is issued free to members. Articles are listed in *Biological Abstracts*, *Current Awareness in Biological Sciences*, *Current Contents*, *Science Citation Index* and *Zoological Record*.

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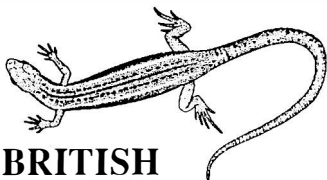
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FRONT COVER: Tadpoles of the genus *Scinax*. (R. de Sa, R. Wassersug & A. I. Kehr)

THE DIET OF THE FOUR-LINED SNAKE (*ELAPHE QUATUORLINEATA*) IN MEDITERRANEAN CENTRAL ITALY

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The feeding habits of the four-lined snake (*Elaphe quatuorlineata*) were studied in a hilly, Mediterranean locality in central Italy (Tolfa mountains, province of Rome). The adult prey consisted exclusively of rodents (about 77% of the diet) and birds (including nestlings and eggs, about 23% of the diet). Birds represented the main part of the diet during spring-time (April, May and June), whilst rodents accounted for 100% of the diet from July to November. The juveniles were found to prey exclusively on lacertid lizards. There was a significantly positive correlation between prey mass and predator mass, but the snakes tended to prey on organisms of small size in relation to themselves. Some general remarks on the snake assemblages of the Tolfa mountains are also presented.

INTRODUCTION

In recent years much field effort has been devoted to studying the feeding habits of snakes in the Mediterranean regions of central Italy, and accurate data are now available on ecologically diverse taxa, such as *Vipera aspis* (Luiselli & Agrimi, 1991; Capizzi, Luiselli, Capula & Rugiero, 1995), *Coluber viridiflavus* (Capizzi *et al.*, 1995; Rugiero & Luiselli, 1995), *Elaphe longissima* (Luiselli & Rugiero, 1993; Capizzi *et al.*, 1995), *Coronella austriaca* (Rugiero, Capula, Filippi & Luiselli, 1995), *Coronella girondica* (Agrimi & Luiselli, 1994), *Natrix natrix* and *Natrix tessellata* (Luiselli & Rugiero, 1991; Filippi, Capula, Luiselli & Agrimi, 1996). On the contrary, there is very little information available on the diet of the biggest Mediterranean species (in terms of both body length and body mass, e.g. see Böhme & Scerbak, 1993), the four-lined snake *Elaphe quatuorlineata* (Pozio, 1976; Cattaneo, 1979; Capizzi *et al.*, 1995; Rugiero & Luiselli, 1996). This is due to the fact that *E. quatuorlineata* usually (i) occurs in scattered populations, (ii) has low population density, and (iii) is extremely elusive for much of its annual activity cycle (Bruno & Maugeri, 1990; Filippi, 1995).

The aim of this paper is (i) to provide an accurate description of the dietary habits of *E. quatuorlineata*, (ii) to compare these data with the available information on this species' feeding habits, and (iii) to compare the diet of this species with that of other sympatric snakes (genera *Vipera*, *Elaphe*, *Coluber* and *Coronella*).

MATERIALS AND METHODS

This study was conducted in two areas of the Tolfa mountains (Rota, 150 m a.s.l., and Canale Monterano, 250 m a.s.l.). This is a hilly region situated approximately 60 km north of Rome, where the bioclimate is characterized by a cold winter (without snow-covering), a rainy spring and autumn, and a dry and hot summer (hypomesaxeric subregion of type B according to Tomaselli *et al.*, 1973). Rainfall and air temperatures of the study area during 1964-1994 are given in Fig. 1. The vegetation consists of riverine woodland (*Ulmus campestris*, but also *Salix* sp., *Populus* sp.), large areas covered by shrubby pasture (*Spartium junceum*, *Cytisus scoparius*, *Prunus spinosa*, *Rubus ulmifolius*, *Crataegus monogyna*) and mesophilous forests (*Quercus cerris*, *Ostrya carpinifolia* and *Quercus pubescens*) (Spada, 1977). Four-lined snakes are rather

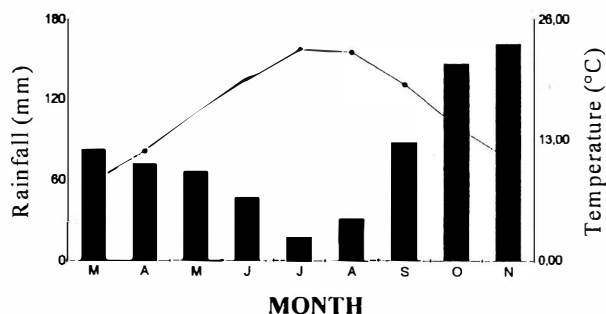


FIG. 1. Average air temperature and mean rainfall per month at the study area. Data from the Meteorological Centre at Civitavecchia (Rome).

rare and elusive, and are generally confined to stony and grassy areas (Filippi, 1995).

The data shown were mainly collected between spring and autumn 1995, with little information recorded in spring and autumn 1993-1994. Sampling was carried out primarily between 0700 and 1530 hr, and occasionally in the late afternoon. Snakes were captured by hand, sexed by examining the external tail morphology, weighed, and a measure of total length (TL, to the nearest 0.5 cm) was taken. For future identification each snake was marked by scale-clipping and paint-marking the dorsal parts. Stomach contents and faecal pellets were collected by gentle palpation of the snake abdomen until regurgitation or defecation occurred (Rugiero *et al.*, 1995). With this snake, in fact, it is quite easy to identify the food eaten by examining faecal pellets under an optical microscope: identification of hairs was done by analysis of medulla, cuticula and cross-section analyses. Unlike other colubrids (e.g. *Natrix natrix*), *E. quatuorlineata* usually does not defecate for defence upon capture, and so the faeces are not too liquid to be used for identification. No specimen was killed or injured during the study. The prey items were identified to the lowest taxon possible. The ingested biomass (calculated only from prey contained in stomachs) was calculated on the basis of the fresh weight if the prey was in optimal condition, or the mean weight of the species if it was not (e.g. see Luiselli & Agrimi, 1991). After examination and measurement, the snakes were forced to ingest the disgorged prey. This was usually found to be an easy procedure, particularly if the prey had recently been captured. When the snake did not re-ingest, the item was placed in 75% ethanol. After laboratory examination, all the remains of the faecal pellet were also preserved in 75% ethanol for further examination.

Data was analysed with SAS version 6.0 (1985), all tests being two-tailed with $\alpha = 0.05$. In the text the means are followed by \pm one standard deviation (SD).

RESULTS

During this study we handled 31 different snakes (17 males and 14 females) on 58 occasions. Apparent sex ratio was close to equality (binomial test: $P > 0.5$). The females averaged significantly greater TL than males (mean = 132.14 ± 32.11 cm [range: 86.1 - 177.4 cm] against 112.82 ± 21.55 cm [range: 56.2 - 145.3 cm]; $t = 2.01$, $df = 29$, $P = 0.027$), this being in agreement with morphometric data from other regions in central Italy (Rugiero & Luiselli, 1996b). For the above comparisons, both juveniles and adults are included. The snakes weighed on average 376.23 ± 215 g.

A summary of the diet data obtained from *E. quatuorlineata* is presented in Table 1. We obtained 65 prey items from both stomach contents and faeces.

Identifiable prey items were obtained from faeces of 39 snakes (some captured repeatedly: 67.2% of the total number of processed animals), while only 13 individuals (22.4% of the total number of processed animals)

TABLE 1. Summary of the diet data obtained from *Elaphe quatuorlineata* of the Tolfa Mountains (Rome, Italy). Data come from analysis of both faecal pellets (39 individuals) and stomach contents (13 individuals).

Prey type	<i>n</i> in faeces	<i>n</i> in stomachs	<i>n</i> in total	%
REPTILES				
<i>Podarcis muralis</i>	3	-	3	4.6
MAMMALS				
<i>Apodemus sylvaticus</i>	8	3	11	16.9
<i>Mus domesticus</i>	1	1	2	3.1
<i>Clethrionomys glareolus</i>	7	4	11	16.9
<i>Muscardinus avellanarius</i>	4	-	4	6.2
<i>Rattus rattus</i>	3	-	3	4.6
<i>Rattus norvegicus</i>	1	2	3	4.6
Unidentified rodents	13	-	13	20.0
BIRDS				
<i>Turdus merula</i> nesting	-	3	3	4.6
<i>Turdus merula</i> adult	-	1	1	1.5
<i>Carduelis</i> sp.	1	-	1	1.5
<i>Serinus</i> sp.	2	-	2	3.1
Unidentified passerines	4	-	4	6.2
Unidentified eggs	3	1	4	6.2
Total	50	15	65	100.0

had prey in the stomachs. These frequencies differed significantly (χ^2 with 1 df, $P < 0.05$), thus suggesting that to obtain a large number of food items in ecological studies on *Elaphe quatuorlineata* it is much more convenient to examine faeces than stomach contents. Moreover, from the same faecal pellet it was frequently possible to obtain more than one prey item (mean number of prey / pellet = 1.35), thus demonstrating that a faecal pellet may provide data not only on the latest snake meal, but also on the previous one. However, it is obvious that, when more than one prey item is found in a single pellet, it is not possible to recognize which of them has been eaten first.

The diet consisted only of vertebrates, and almost all the items eaten (over 95% of the total) were endotherms. Rodents, accounting for about 72% of the total diet, were eaten significantly (χ^2 , $P < 0.05$) more frequently than birds (accounting for about 23% of the total diet), and were also the principal food resource in terms of biomass percentage (Table 2). Shrews and other insectivores were not preyed upon by four-lined snakes, although these minute mammals are widespread in the study areas (Contoli, 1977) and are frequently eaten by other snakes, e.g. *Vipera aspis* (Capula & Luiselli, 1990). Passerine birds were prey at all life stages, including eggs, nestlings and adults. Males and females were similar in their taxonomic diet composition ($\chi^2 = 0.87$, $df = 1$, $P > 0.1$), but the largest prey (i.e. the six *Rattus* eaten) were all ingested by females. Our sample of immature snakes (specimens shorter than 80 cm TL, always easily recognizable by

TABLE 2. Relative biomass (B, in g and as percentage of total biomass, %B) of the prey items found in the stomach contents of *Elaphe quatuorlineata* from the Tolfa mountains (Rome, Italy).

Prey	n	B	%B
<i>Apodemus sylvaticus</i>	3	45.4	7.9
<i>Mus domesticus</i>	1	12.5	2.2
<i>Clethrionomys glareolus</i>	4	137.5	23.9
<i>Rattus norvegicus</i>	2	321.5	55.8
<i>Turdus merula</i> nesting	3	21.7	3.8
<i>Turdus merula</i> adult	1	26	4.5
Unidentified egg	1	11	1.9
Total biomass		575.6	100.0

their spotted livery, see Bruno & Maugeri, 1990; Böhme & Scerbak, 1993) was too small ($n=6$) for drawing firm conclusions about eventual ontogenetic dietary shift. However, the fact that all the three lizard prey were ingested by juveniles (individuals shorter than 75 cm TL) suggests that there may be a preference for lizards in the juveniles compared with the adult diet based on endotherms. This ontogenetic dietary pattern is rather common among Mediterranean snakes (e.g. *Vipera aspis francisciredi*, see Luiselli & Agrimi, 1991), and has already been suggested for *Elaphe quatuorlineata* (Böhme & Scerbak, 1993; Rugiero & Luiselli, 1996).

A considerable seasonal change was observed in the composition of the snake diet (Fig. 2). Birds were eaten only between April and June, and accounted for 75% of the total diet during these spring months. Conversely, rodents represented 100% of the diet from the beginning of July to mid-November.

Mean ingested biomass per snake was $38.33 \pm 55.6g$ (10.2% of the average snake body mass). The prey mass / predator mass ratio averaged 0.125 ± 0.123 , and

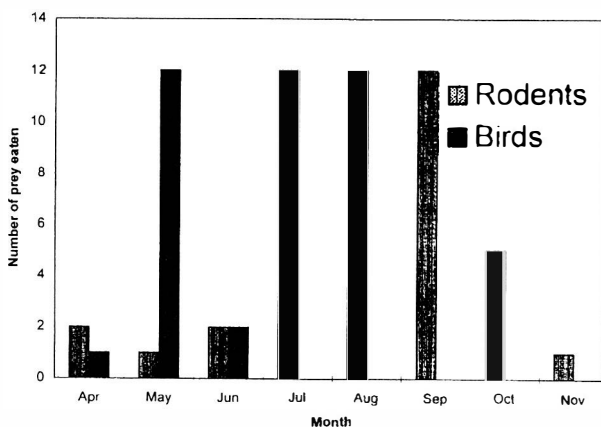


FIG. 2. Seasonal dietary changes in *Elaphe quatuorlineata* from the Tolfa mountains (Rome, Italy). Numbers represent the amount of the main prey types (birds and rodents) found in the guts of the snakes. Nestlings and eggs are included in the term "birds".

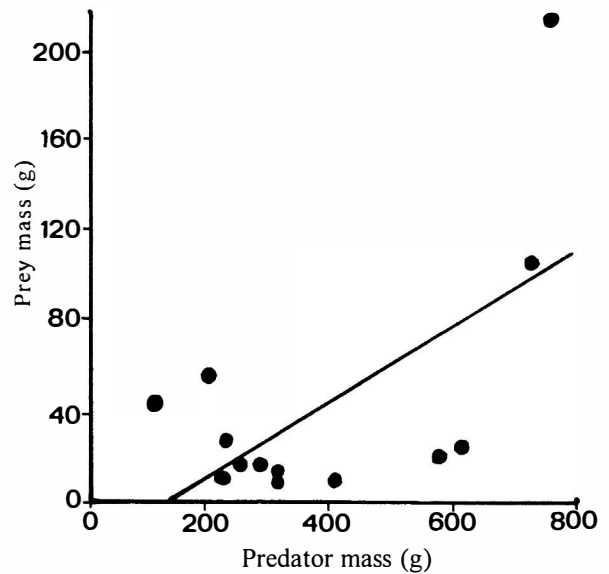


FIG. 3. Relationship between prey mass and predator mass in *Elaphe quatuorlineata* from the Tolfa mountains (Rome, Italy). Statistics: $r=0.63$, $n=13$, ANOVA: $F_{1,11}=7.24$, $P=0.02$.

ranged between 0.028 and 0.4. Prey mass and predator mass were significantly correlated ($r=0.63$, $n=13$, ANOVA: $F_{1,11}=7.24$, $P=0.02$, see Fig. 3).

DISCUSSION

On the whole, the taxonomic dietary composition of four-lined snakes in the Tolfa mountains resembles that previously described for this species (Cattaneo, 1979; Böhme & Scerbak, 1993; Capizzi *et al.*, 1995; Rugiero & Luiselli, 1996). Birds (including eggs) accounted for about 23% of the total diet, while they represented from about 15% to over 80% of the prey in other Mediterranean *Elaphe quatuorlineata* populations (Cattaneo, 1979; Capizzi *et al.*, 1995; Rugiero & Luiselli, 1996). The presence of bird remains in the diet suggests that four-lined snakes have semi-arboreal predatory habits. Although a direct relationship between arboreality and avian prey has not always been observed in snake studies (Shine, 1983; Luiselli & Rugiero, 1993), this suggestion seems to be reliable in the case studied, as (i) these snakes were occasionally seen in trees at heights of more than 4 m (Filippi, 1995; Capizzi & Luiselli, unpubl. data), and (ii) semi-arboreal or strictly arboreal rodents (i.e. *Rattus rattus* and *Muscardinus avellanarius*) were also eaten.

Interestingly, the diet composition of *E. quatuorlineata* changed seasonally, with a spring diet based on avian prey and a summer-autumn diet based on rodent prey. Considerable seasonal changes in snake diets have rarely been documented (but see Agrimi & Luiselli, 1992), but a nearly identical trend to ours has already been observed in another four-lined snake population from a coastal locality of the Roman county (Cattaneo, 1979). Thus, this comparative evidence suggests that a seasonal dietary change (from a spring diet based on birds to a later diet based on rodents) could be

TABLE 3. Summary of some major ecological traits of the snake species co-existing in the Tolfa mountains (Rome, central Italy). Data from several papers by Luiselli & associates (see references) and original, unpublished material.

Species	Mean body size (cm)	Primary prey	Secondary prey	Habitat feature
<i>Vipera aspis</i>	60-75	rodents + shrews	lacertids	mesophilous and damp woods
<i>Natrix natrix</i>	70 - 120	frogs + toads	fish	riverine and damp woods
<i>Natrix tessellata</i>	50 - 100	fish (over 90% of prey)	-	streams and their banks
<i>Coronella girondica</i>	40 - 60	lacertids	arthropods	grassy areas
<i>Coronella austriaca</i>	40 - 60	lacertids	rodents	damp woods
<i>Coluber viridiflavus</i>	90 - 120	rodents	lacertids	all areas, but mainly dry
<i>Elaphe longissima</i>	100 - 130	rodents	lacertids	woods
<i>Elaphe quatuorlineata</i>	100 - 170	rodents	birds	bushy pastures

a general pattern in the Mediterranean *E. quatuorlineata* populations. These seasonal dietary changes are probably due to remarkable fluctuations in the levels of prey availability, as many snakes tend to prey on the most common prey types available in the environment (Agrimi & Luiselli, 1992; Capizzi *et al.*, 1995; Rugiero *et al.*, 1995; Luiselli, 1996). In fact, most passerine birds nest in the spring months at the study area.

Another main point emerging from our study is that, although the four-lined snakes are large and vigorous colubrids, able to capture large and vigorous prey (such as brown rats or rabbits, see Pozio, 1976 and this study), they usually tend to capture relatively small prey. In this regard, it should be noted that the average prey mass / predator mass ratio observed in our *E. quatuorlineata* is even lower than that observed in a small and comparatively less vigorous predator such as *Coronella austriaca* (Rugiero *et al.*, 1995). Prey mass / predator mass ratio observed in *Elaphe quatuorlineata* was similar to that (0.18) reported as usual for colubrids by Pough and Groves (1983), while the mean value for viperids was 0.36. However, the four-lined snakes tended to select prey of appropriate size to their own, as demonstrated by the statistically significant positive correlation between prey mass and predator mass (Shine, 1991).

SNAKE ASSEMBLAGES IN THE TOLFA MOUNTAINS

Summarized ecological aspects of snakes in the Tolfa mountains are presented in Table 3. The annual activity cycle (length of the active period, reproductive timing, etc) of all Tolfa snakes is almost identical (Filippi, 1995). However, in this territory there are two ecologically diverging snake groups: (i) the "semi-aquatic" species (including the two *Natrix* species), and (ii) the "terrestrial" species. Group (i) typically partitions the available food resource (Luiselli & Rugiero, 1991; Filippi *et al.*, 1996), while the same pattern is not so clear among the members of group (ii). This latter group consists of two "subgroups": subgroup (1) includes the lacertophagous species (*Coronella austriaca* and *Coronella girondica*), that are very similar in diet composition (Agrimi & Luiselli, 1994; Rugiero *et al.*,

1995) and other ecological traits (Capula, Luiselli & Rugiero, 1995). As a consequence, they partition very clearly the habitat resource: their distributions are perfectly complementary (coexistence in the same place has never been observed), with *Coronella austriaca* restricted to wet woodlands and *Coronella girondica* restricted to sunny open grassy zones with walls and stones. The subgroup (2) includes morphologically diverging taxa (such as vipers and colubrids) characterized by terrestrial habits and a diet shifting from ectotherms to endotherms with age. It is suspected (and this will be studied in the immediate future) that the juveniles of subgroup (2) are potential competitors for food with the two *Coronella* species, and in fact these latter are especially concentrated in places where the density of the other snakes, primarily *Coluber viridiflavus*, is very low (Rugiero *et al.*, 1995). Among the snakes of subgroup (2) there are no marked differences in diet composition or in habitat features, and there are several places where all four taxa (*Vipera aspis*, *Coluber viridiflavus* and two *Elaphe*) are sympatric (Filippi, 1995). Thus, further studies are necessary to better define the ecological niches of these taxa. On the whole, the tendency is that (i) *Vipera aspis* and *Elaphe longissima* inhabit wetter areas than *Coluber viridiflavus* and *Elaphe quatuorlineata* (Filippi, 1995), and (ii) the dietary habits of *Elaphe quatuorlineata* and adult *Vipera aspis* are more strictly limited to endothermic prey than those of *Coluber viridiflavus* and *Elaphe longissima*.

ACKNOWLEDGEMENTS

The authors are gratefully indebted to Dr Umberto Agrimi (Istituto Superiore di Sanità, Rome), Dr Massimo Capula (Università "La Sapienza", Rome) and two anonymous reviewers for helpful comments on the manuscript, and to Dr Ernesto Filippi and Dr Lorenzo Rugiero for useful discussion on four-lined snake ecology. Miss Veronica Trujillo Jesus and Miss Fatima Evangelisti kindly co-worked in the field and collected some important data. Avv. Dr Claudio Petrucci is thanked for having permitted investigations on his private properties, normally closed to the public.

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Accepted: 21.5.96

UTILIZATION OF ENERGY AND NUTRIENTS IN INCUBATING EGGS AND POST-HATCHING YOLK IN A COLUBRID SNAKE, *ELAPHE CARINATA*

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This paper reports data on the mobilization of some yolk and eggshell nutrients and their incorporation into hatchlings and post-hatching yolk in an oviparous colubrid snake, *Elaphe carinata*. The incubation time at $30 \pm 0.3^\circ\text{C}$ averaged 50.5 days. During incubation, pliable-shelled *E. carinata* eggs increased in wet mass. Dried shells from freshly laid eggs averaged 8.1% of the entire egg dry mass. Freshly laid eggs had significantly heavier shells than did hatched eggs with the same wet mass at oviposition. Dry mass conversion from egg contents of the freshly laid egg to hatchling averaged 81.1%. During incubation, approximately 63.7% of non-polar lipids and 72.1% of energy in egg contents of the freshly laid egg were transferred to the hatchling, with 36.3% of non-polar lipids and 27.9% of energy used for embryogenesis. Shells from freshly laid eggs had a higher level of calcium but a lower level of magnesium than did shells from hatched eggs. Fully developed embryos could obtain all magnesium from yolk but withdrew approximately 30.5% of their total calcium requirements from sources other than yolk. A few days after hatching, a decrease in post-hatching yolk dry mass was accompanied by an increase in carcass dry mass. This confirms that post-hatching yolk could be used to support early growth of hatchlings.

INTRODUCTION

Unlike viviparous reptiles that rely upon vitellogenesis and, in various degrees, placentation for embryonic nutrition (Thompson, 1977, 1981, 1982; Stewart & Castillo, 1984; Stewart, 1989; Stewart, Blackburn, Baxter & Hoffman, 1990; Stewart & Thompson, 1993; Thompson & Stewart, 1994), oviparous reptiles lay eggs in which the stored energy and material generally exceed the needs for producing a complete hatchling (Kraemer & Bennett, 1981; Troyer, 1983, 1987; Wilhoft, 1986; Congdon & Gibbons, 1989; Fischer, Mozzotti, Congdon & Gatten, 1991). It is a common pattern in oviparous reptiles that embryos use yolk as the source of all organic and most inorganic nutrients and eggshell as the additional source of specific minerals (e.g. calcium). A portion of yolk (i.e. post-hatching yolk) may remain unutilized until the time of hatching. However, egg and hatchling components and conversions of energy and/or material from egg to hatchling vary considerably among species (Ewert, 1979; Congdon, Gibbons & Greene, 1983; Congdon, Tinkle & Rosen, 1983; Wilhoft, 1986; Fischer, Mozzotti, Congdon & Gatten, 1991). The proportional amount of calcium withdrawn by the embryo from the eggshell is likewise variable, although the embryonic mobilization pattern of calcium in most oviparous reptiles seems to

be consistent (Packard & Packard, 1984, 1986, 1988, 1989; Packard, Packard & Gutzke, 1984; Packard, Short, Packard & Gorell, 1984; Packard, Packard, Miller, Jones & Gutzke, 1985; Shadrix, Crotzer, McKinney & Stewart, 1994). Such variabilities should be related to several factors, e.g. nest micro-environment, costs of embryonic development, a trade-off between clutch number or clutch size and hatchling quality, etc.; thus more detailed and extensive studies of egg and hatchling components would be very helpful in our understanding of reproductive investments and reproductive strategies in oviparous reptiles.

Additionally, the function of post-hatching yolk still remains to be well addressed, although it has been known that post-hatching yolk can be used to support the hatchling's early activities (Kraemer & Bennett, 1981; Troyer, 1983; Wilhoft, 1986; Congdon & Gibbons, 1989). It can be expected that post-hatching yolk may strongly influence the values of energy and material transferred from egg to hatchling. The possible contribution of post-hatching yolk to subsequent growth of newly emerged young is, however, not clear.

Elaphe carinata is a large sized colubrid snake that is widely distributed in the southern provinces of China (including Taiwan), northward to Henan, Shaanxi and Gansu (Zhao & Adler, 1993). Several aspects of biology and ecology of this species have been previously

examined, but little information on incubation is available other than incidental notes (see Huang & Jin, 1990). In 1994 and 1995, we incubated *E. carinata* eggs under constant temperature and humidity regimes to determine (1) conversions of energy and some nutrients from egg to hatchling during incubation, (2) sources of calcium and magnesium for embryogenesis, and (3) post-hatching yolk and its significance to the hatchling's early growth.

MATERIALS AND METHODS

Three gravid *E. carinata* were collected from the field in Baiquan, Dinghai, Zhoushan Islands (29°32'–31°04'N, 121°30'–123°25'E), Zhejiang province, eastern China, in mid-June 1994; one gravid *E. carinata* was collected from the same site in mid-June 1995. Snout-vent length (SVL) ranged from 1220 to 1275 mm, and body mass (excluding the clutch) from 548 to 569 g. The snakes were maintained individually in 800 x 800 x 800 mm wire cages until oviposition (mean=18.5 days). We obtained three clutches in 1994 and one clutch in 1995. We removed eggs from the cages, numbered, measured and weighed them within 6 hr of oviposition, and then randomly selected two eggs from each clutch and opened them. Egg contents (embryo and yolk) of the freshly laid egg were removed, placed in pre-weighed small glass dishes and weighed to the nearest 0.1 mg. Shells from freshly laid eggs were rinsed briefly, weighed to the nearest 0.1 mg, and then frozen for later analysis. All the dissected freshly-laid eggs contained a small embryo, which was too small and fragile to be sampled separately, and therefore was included with the yolk.

The remaining eggs were one-third buried on a moistened sand substrate, and incubated in four glass containers (200 x 200 x 200 mm) with ventilated covers, in a constant temperature chamber at 30±0.3°C. The incubation medium consisted of dry sand and water in a mass ratio of 4:1; water was added periodically to maintain the initial water content. We measured and weighed each incubating egg to the nearest 1 mg at weekly intervals before day 42, and at daily intervals thereafter, up to one day prior to hatching. Hatchlings were measured and weighed immediately after they left the eggs. Shells from hatched eggs were rinsed briefly, weighed to the nearest 0.1 mg, and then frozen. Ten hatchlings (1–3 from each clutch; hereafter 0-day hatchlings) were frozen immediately after hatching. The remaining 11 hatchlings (2–3 from each clutch; hereafter 7-day hatchlings) were fasted at room temperatures (26–38 °C) for seven days, and then frozen. The preserved hatchlings were later thawed, dissected and separated into carcass, yolk sac and fat bodies.

All samples for determination of non-polar lipids, ash, calories, calcium and magnesium were dried to a constant mass in an oven at 65°C, weighed, and then ground with a mortar and pestle. Non-polar lipids were extracted from all samples of egg contents, carcass,

post-hatching yolk and fat bodies for a minimum of 5.5 hr using absolute ether in a Soxhlet apparatus. The mass of non-polar lipids in each sample was calculated as the difference in sample dry mass before and after extraction.

Ash and caloric values of samples of egg contents, carcass, post-hatching yolk and fat bodies were determined using a GR-3500 adiabatic bomb calorimeter (Changsha Instruments). Titrations were performed on the residue after calorimetry to correct for nitrogenous wastes. Samples of eggshells were burned in a muffle furnace at 550°C for 24 hr to determine ash mass.

Samples for calcium and magnesium determinations were weighed out into glass tubes and digested completely in hot concentrated nitric acid. Digestates were brought to volume in volumetric glassware and stored in a refrigerator until analysis for calcium and magnesium. Concentrations of the two elements in digestates were determined with a WFX-1B model atomic absorption spectrophotometer (The 2nd Beijing Optical Instruments). To check if there were any differences in the levels of calcium and magnesium between shells from freshly laid eggs and shells from hatched eggs, we took equal samples from each shell, pooled separately the samples from freshly laid eggs and hatched eggs and treated them as two different samples.

Because all components of egg contents of freshly laid eggs and 0-day hatchlings were highly correlated with total egg wet mass at oviposition and because there were intra-clutch variations in egg size (we will report data elsewhere), we compared all means using analysis of covariance (ANCOVA) with total egg wet mass at oviposition as the covariate which was a significant source of variation in all analyses. The

TABLE 1. Components and *F* values of ANCOVA for eight freshly laid *Elaphe carinata* eggs and ten 0-day hatchlings (including post-hatching yolk and fat bodies). Data were expressed as adjusted mean±1 SE, with total egg wet mass at oviposition as the covariate. Symbols immediately after *F* values represent significance levels: NS *P*>0.05, * *P*<0.05, ** *P*<0.01, and *** *P*<0.001.

	Freshly laid egg	Hatched egg	<i>F</i>
	Egg contents	Total hatchlings	
Wet mass (g)	34.8±0.2	25.7±0.2	956.40***
Dry mass(g)	8.41±0.1	6.82±0.07	169.20***
Water (g)	26.4±0.2	18.9±0.2	949.82***
Organic mass (g)	7.72±0.1	6.04±0.07	217.28***
Ash mass (mg)	687.0±23.1	780.1±25.0	6.48*
Non-polar lipids(g)	2.59±0.06	1.65±0.04	160.64***
Calcium (mg)	93.8±3.6	135.0±4.5	37.84***
Magnesium (mg)	32.9±1.3	31.6±1.0	0.61 ^{NS}
Energy (Kcal)	50.9±0.5	36.7±0.6	288.18***
	Eggshell	Eggshell	
Dry mass (mg)	739.4±16.8	642.2±11.1	22.49***
Organic mass (mg)	534.8±11.8	489.0±7.9	10.07**
Ash mass (mg)	204.6±5.3	153.2±3.4	64.23***

homogeneity of slopes was checked prior to testing for differences in the adjusted means. The levels of calcium and magnesium in the egg contents of freshly laid eggs and posthatching yolks, and the level of non-polar lipids of 0-day hatchlings and 7-day hatchlings, were compared by analysis of variance (ANOVA); percentage data were arc-sine transformed before the ANOVA. We used a partial correlation analysis to test the relationships between carcass dry mass, posthatching yolk dry mass and fat-body dry mass. Descriptive statistics are presented as mean \pm 1SE.

RESULTS

Female *E. carinata* laid pliable-shelled eggs. Clutch size in our sample averaged 7.5 \pm 1.2 (range 5-10, $n=4$). Freshly laid eggs averaged 36.2 \pm 1.3 g (range 26.3-45.1, $n=30$) wet mass, 58.8 \pm 1.5 mm (range 49.4-77.2, $n=30$) length and 30.8 \pm 0.7 mm (range 24.4-36.0, $n=30$) width. During incubation, eggs increased in wet mass and, one day prior to hatching, weighed 128.3 \pm 1.4% (range 117.5-136.5, $n=21$) of total egg wet mass at oviposition. The incubation time averaged 50.5 \pm 0.1 days (range 50.0-51.0, $n=21$). Hatchlings at hatching averaged 26.2 \pm 1.2 g (range 18.4-33.1, $n=21$) wet mass, 361.1 \pm 8.3 mm (range 308.3-418.5, $n=21$) SVL and 83.2 \pm 3.3 mm (range 62.1-103.3, $n=21$) tail length.

Egg contents of freshly laid eggs averaged 75.9% water by mass (Table 1). Egg contents of freshly laid eggs averaged 91.8% organic material, 8.2% ash, 30.8% non-polar lipids, 1.12% calcium and 0.39% magnesium by dry mass (Table 1). Shell from freshly laid eggs averaged 8.1% of total egg dry mass, and 72.3% organic material and 27.7% ash by dry mass (Table 1). Shells from freshly laid eggs had a higher level of calcium (12.07%) but a lower level of magnesium (0.83%) than did shells from hatched eggs (calcium: 7.88%; magnesium: 0.98%).

The 0-day hatchlings averaged 73.5% water by mass (Table 1). These hatchlings averaged 88.6% organic material, 11.4% ash, 24.4% non-polar lipids, 1.98% calcium and 0.46% magnesium by dry mass (Table 1). Shells from hatched eggs averaged 76.1% organic material and 25.9% ash by dry mass (Table 1).

The 0-day hatchlings contained lower quantities of total dry mass, organic mass, non-polar lipids and energy, but higher quantities of calcium and ash than did egg contents of freshly laid eggs (Table 1). There was no significant difference in the quantity of magnesium between egg contents of freshly laid eggs and 0-day hatchlings (Table 1). Shells from freshly laid eggs had higher quantities of total dry mass, organic mass and ash than did shells from hatched eggs (Table 1). There were no significant differences in the levels of calcium and magnesium between egg contents (calcium: 1.12 \pm 0.04%, range 0.89-1.30%, $n=8$; magnesium: 0.39 \pm 0.02%, range 0.32-0.47%, $n=8$) of the freshly laid egg and post-hatching yolks at hatching (calcium:

1.01 \pm 0.04%, range 0.83-1.27, $n=10$; magnesium: 0.44 \pm 0.02%, range 0.36-0.55, $n=10$) (calcium: $F_{1,16}=1.92$, $P>0.05$; magnesium: $F_{1,16}=2.63$, $P>0.05$).

During incubation, 81.1% of dry mass, 63.7% of non-polar lipids and 72.1% of energy in egg contents of the freshly laid egg were transferred to the hatchling, with 18.9% of dry mass, 36.3% of non-polar lipids and 27.9% of energy used for embryogenesis (Table 1). Fully developed embryos could obtain all magnesium from the yolk but withdrew 30.5% of their total calcium requirements from sources other than yolk (Table 1).

The 7-day hatchlings had significantly heavier carcasses than did 0-day hatchlings with the same total hatchling wet mass at hatching ($F_{1,18}=104.01$, $P<0.001$) (Table 2). In 0-day hatchlings, we found that there was a strong negative correlation between post-hatching yolk dry mass and carcass dry mass when holding total hatchling dry mass and fat-body dry mass constant ($r=-0.99$, $t=17.19$, $df=6$, $P<0.001$), there was no significant correlation between fat-body dry mass and carcass dry mass when holding total hatchling dry mass and post-hatching yolk dry mass constant ($r=0.37$, $t=0.98$, $df=6$, $P>0.05$) and there was no significant correlation between fat-body dry mass and post-hatching yolk dry mass when holding total hatchling dry mass and carcass dry mass constant ($r=-0.56$, $t=1.66$, $df=6$, $P>0.05$) (Table 2). When data from 0- and 7-day hatchlings were pooled, we again found that there was a strong negative correlation between posthatching yolk dry mass and carcass dry mass when holding total hatchling dry mass and fat-body dry mass constant ($r=-0.98$, $t=20.30$, $df=17$, $P<0.001$), there was no significant correlation between fat-body dry mass and carcass dry mass when holding total hatchling dry mass and post-hatching yolk dry mass constant ($r=0.24$, $t=1.02$, $df=17$, $P>0.05$) and there was no significant correlation between fat-body dry mass and post-hatching yolk dry mass when holding total hatchling dry mass and carcass dry mass constant ($r=-0.35$, $t=1.54$, $df=17$, $P>0.05$) (Table 2). 7-day hatchlings (21.6 \pm 0.6%, range 18.6-25.1%, $n=11$) had a lower level of non-polar lipids than did 0-day hatchlings (24.4 \pm 0.3%, range 22.1-25.7%, $n=10$) ($F_{1,19}=16.82$, $P<0.001$).

TABLE 2. Data, expressed as mean \pm 1SE, based on ten 0-day hatchlings and eleven 7-day hatchlings of *Elaphe carinata*. All mass units are in g.

	0-day hatchling	7-day hatchling
hatchling wet mass at hatching	26.7 \pm 1.9	25.7 \pm 1.70
hatchling wet mass 7 days after hatching	-	25.0 \pm 1.70
decrease in wet mass	-	0.70 \pm 0.12
hatchling dry mass	7.08 \pm 0.46	6.30 \pm 0.43
carcass	4.12 \pm 0.27	4.74 \pm 0.25
yolk	1.75 \pm 0.14	0.51 \pm 0.05
fat bodies	1.21 \pm 0.10	1.05 \pm 0.11
% water of hatchling	73.5 \pm 0.30	74.8 \pm 0.20

DISCUSSION

The majority of oviparous squamates lay pliable-shelled eggs (Packard & Hirsch, 1989), but the proportional amount of shell in total egg dry mass and the level of calcification of shell are quite different among squamates (Ji, unpubl. obs.). Additionally, a few squamates (e.g. some geckos) lay rigid-shelled eggs, although the structure of their egg shells is actually quite different from that of crocodilians and some turtles that also lay rigid-shelled eggs (Packard & Hirsch, 1989; Packard & DeMarco, 1991). We are presently not very certain if a pliable-rigid shelled egg continuum, in turtles (Lamb & Congdon, 1985; Congdon & Gibbons, 1985), also exists in squamates. Thus more detailed studies of eggshells of squamates would be of great value in substantiating this claim. Because data on ash content of eggshell (Lamb & Congdon, 1985) and the proportional amount of shell in total egg dry mass (Congdon & Gibbons, 1985) have been used to classify turtle eggs, we have paid attention to these data in squamates. Similar to that reported for pliable-shelled eggs of other squamates (Packard & Packard, 1988), *E. carinata* eggs increased in wet mass and swelled during incubation because of a net gain of water absorbed from the incubation environment. However, we are unable to demonstrate the relative contributions of water vapour exchange (Kam & Ackerman, 1990) and liquid water transportation (Packard & Packard, 1988) to egg water uptake.

Because *E. carinata* embryos at the start of incubation have only a negligible body size, we can reasonably consider the transference of energy and material from egg to hatchling during incubation as an approximation to the transference overall. This makes it possible to compare our data with those for other oviparous reptiles with freshly laid eggs containing very small embryos, or near the oviparous end in the oviparity-viviparity continuum (Shine, 1983). *E. carinata* exhibited relatively high conversions of energy and material from egg to hatchling. Dry mass conversion from egg contents of the freshly laid egg to hatchling in *E. carinata* (81.1%) was greater than the values reported for the American alligator (79%; Fischer, Mazzotti, Congdon & Gatten, 1991) the chicken turtle (72%; Congdon, Gibbons & Greene, 1983) and the painted turtle (72%; Ewert, 1979). The proportion of non-polar lipids transferred from egg to hatchling in *E. carinata* (63.7%) was less than the value reported for the American alligator (74.3%; Fischer, Mazzotti, Congdon & Gatten, 1991), but greater than the values reported for some turtles and lizards (50-60%; Congdon, Tinkle & Rosen, 1983; Wilhoft, 1986; Ji, 1992).

The above comparisons indicate that conversions of materials from egg to hatchling vary considerably among species; however, any general explanations of these variabilities are unknown at this time because of the lack of data. We feel that data from studies of paren-

tal reproductive investment, embryonic metabolism and ecology of neonates would be very valuable. For example, it is well known that the costs of embryonic development vary considerably among reptiles (Dmi'el, 1970; Black, Birchard, Schuett & Black, 1984; Vleck & Hoyt, 1991), parental investment in each offspring should be related to its survivorship (Congdon & Gibbons, 1989; Fischer, Mazzotti, Congdon & Gatten, 1991) and incubation conditions have an impact on resultant hatchlings (Gutzke & Packard, 1987; Packard, 1991). Additionally, we recommend the use of data from caloric determinations, because neither dry mass conversion efficiency nor lipid conversion efficiency provides enough information on the costs of embryogenesis and/or the exact level of parental investment in each egg. Samples of eggs and hatchlings with different lipid and ash contents might differ considerably in energy density (Ji, 1992, 1995).

The pattern of use of the shell as a secondary source of calcium for development by *E. carinata* embryos is the same as that in other oviparous squamates (Packard, Packard & Gutzke, 1984; Packard, Packard, Miller, Jones & Gutzke, 1985; Packard & Packard, 1988; Shadrix, Crotzer, McKinney & Stewart, 1994), turtles (Packard, Short, Packard, & Gorell, 1984; Packard & Packard, 1986) and the American alligator (Packard & Packard, 1989). The level of calcium withdrawn by *E. carinata* embryos (30.5%) from sources other than yolk was much less than the values reported for crocodilians and turtles (50-80%; Bustard, Jenkins & Simkiss, 1969; Jenkins, 1975; Packard & Packard, 1984, 1989). Among squamates, it was also less than the value reported for the skink *Eumeces fasciatus* (39%; Shadrix Crotzer, McKinney & Stewart, 1994), but greater than the value reported for the colubrid snake *Coluber constrictor* (20%; Packard, Packard & Gutzke, 1984). The differences presumably reflect the interspecific differences in eggshell structure and/or allocation of minerals between eggshell and yolk.

Studies of magnesium metabolism in embryonic oviparous reptiles have been extremely limited. As in the American alligator (Packard & Packard, 1989), *E. carinata* embryos obtain all magnesium for their development from the yolk. The result that shells from hatched eggs were lower in calcium level but higher in magnesium level than shells from freshly laid eggs implied that developing embryos selectively withdrew calcium from the shell, providing additional evidence which demonstrated that it was not necessary for *E. carinata* embryos to withdraw magnesium from the eggshell.

Although we did not sample at different stages of incubation, the fact that there were no significant differences in calcium and magnesium levels between egg contents of the freshly laid egg and posthatching yolk at hatching might suggest that the two minerals were not accumulated by the developing *E. carinata* embryos in the yolk. The fact also implied that the embryonic calcium mobilization pattern in *E. carinata*

was similar to that seen in most other oviparous reptiles (Packard, Packard & Gutzke, 1984; Packard, Short, Packard, & Gorell, 1984; Packard, Packard, Miller, Jones & Gutzke, 1985; Packard & Packard, 1986; Packard & Packard 1988; Shadrix, Crotzer, McKinney & Stewart, 1994).

One of the most interesting findings in this study was that a decrease in post-hatching yolk dry mass was accompanied by an increase in carcass dry mass a few days after hatching. This finding indicates that at least a portion of nutrients in the post-hatching yolk can be transferred to the carcass. This finding also indicates that posthatching yolk is not only one of the energy sources for newly emerged young, as suggested by some investigators (e.g. Congdon, 1989; Congdon & Gibbons, 1989; Fischer, Mozzotti, Congdon & Gatten, 1991), but also plays an important role in the hatchling's early growth. Post-hatching yolk, together with fat-bodies, in the hatchling was thought to be one (parental investment in care) of the two components of pre-ovulatory parental investment (parental investment in embryogenesis and parental investment in care; Congdon, 1989), but whether the two components are constant characteristics for a specific species remains unclear. Some investigators (Packard, 1991; Vleck, 1991) pointed out that the two components in oviparous reptiles vary reciprocally in response to the incubation conditions. Thus, for future studies, it could be very interesting to test the differences in carcass dry mass, post-hatching yolk dry mass and fat-body dry mass of hatchlings from different incubation conditions. Compared to post-hatching yolk, fat-bodies in *E. carinata* hatchlings seem to be used mainly for hatchling maintenance. An obvious decrease in the level of non-polar lipids in 7-day hatchlings primarily reflects a decrease of storage lipids.

ACKNOWLEDGEMENTS

We thank X. Z. Zheng for assistance both in the field and in the laboratory and F. Braña, M^a de los Angeles Marcos Garcia and V. Perez-Mellado for hosting and helping XJ during his research stay in Spain. We also thank two anonymous reviewers for useful comments. This work was supported by a grant from the National Natural Science Foundation of China to XJ (NNSFC-39270124). A grant from Paos' Foundation supported XJ while writing this paper in Spain.

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DESCRIPTION OF TADPOLES OF THREE SPECIES OF *SCINAX* (ANURA: HYLIDAE)

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Larval morphological characteristics have been used to cluster species of *Scinax* in seven species groups and to support the monophyly of some of these groups. However, our present knowledge of *Scinax* tadpoles is incomplete; currently, tadpoles of only 21 of the approximately 80 recognized species have been described. Herein, we describe and illustrate the external morphology and oral disc characteristics of larval *Scinax berthae*, *S. nebulosa*, and *S. boesemani*. The presence of a "labial arm" supporting the P3 tooth row in *S. boesemani*, and its absence from *S. nebulosa*, is discussed in the light of our limited knowledge of tadpoles of species of other *Scinax*.

INTRODUCTION

The genus *Scinax* consists of approximately 80 species grouped in seven species groups (Duellman & Wiens, 1992; Peixoto & Weygoldt, 1987). The species in this genus exhibit a rich diversity of tadpole external morphology. An analysis (in progress) by one of us (AIK) of tadpole morphology and character evolution in *Scinax* brought to our attention the lack of information on larval characteristics for several species in this genus. An examination of tadpoles available in collections successfully located tadpoles of three species whose larval characteristics have not been reported. Herein we describe the tadpoles of *Scinax nebulosa* and *S. boesemani*, redescribe the tadpole of *S. berthae*, and provide comments on larval habitat and biology.

MATERIALS AND METHODS

The following descriptions are based on material preserved in 10% buffered formalin. Descriptive terminology follows that of Altig (1970) and Kehr & Williams (1990). The morphometric variables considered are those suggested by Lavilla & Scrocchi (1986). Museum abbreviations are: KU: University of Kansas, Natural History Museum; USNM: National Museum of Natural History, Smithsonian Institution; CECOAL: Centro de Ecología Aplicada del Litoral, Corrientes, Argentina. Measurements were taken with dial calipers and recorded to the nearest 0.1 mm; for detailed information on how measurements are taken refer to Lavilla & Scrocchi (1986, Figure 1). These variables are abbreviated as follows: TL (total length), BL (body length), TaL (tail length), BW (body maximum width), BWE (body width at eyes), BWN (body width at nostrils), BH (body maximum height), FH (fin height), TMH (tail muscle height), RSD (rostrospiracular dis-

tance), SPD (spiracular-posterior distance), FN (fronto-nasal distance), NO (narial-ocular distance), N (nostril diameter), E (eye diameter), EN (extranarial distance), IN (internarial distance), EO (extraorbital distance), IO (interorbital distance), ODW (oral disc width), RG (rostral gap), MG (mental gap). One tadpole was measured for each species. Tadpoles were staged using Gosner's table of normal development (Gosner, 1960). Drawings were made with the aid of a camera lucida attached to a Wild M3C stereomicroscope.

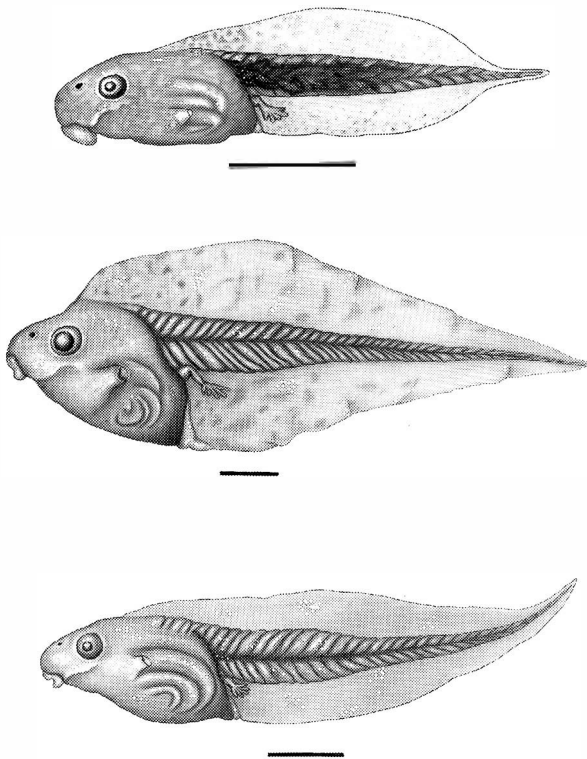
We consider illustrations to be a most important component of tadpole descriptions, consequently in the discussion we identify with an asterisk (*) those descriptions that included tadpole illustrations.

DESCRIPTIONS

SCINAX BERTHAE (BARRIO, 1962)

See Fig. 1 and 2 (top). The tadpole of *Scinax berthae* was mentioned briefly by Gallardo (1987). This description lacks morphometrics and illustrations, and did not identify voucher specimens. Here we describe the tadpole of *S. berthae* based on specimens collected at Punta Lara (34°47'S; 58°01'W), Province of Buenos Aires, Argentina, by A. Kehr on February 10, 1988. A subset of these individuals was raised through metamorphosis to confirm the species identification. An additional specimen has been deposited in the U.S (USNM 346876). The specimen illustrated (CECOAL 001) is at Gosner Stage 37 and has the following measurements: TL = 21.8, BL = 8.4, TaL = 13.4, BW = 5.3, BWE = 4.8, BWN = 4.0, BH = 4.5, FH = 4.7, TMH = 2.2, RSD = 6.0, SPD = 2.4, FN = 1.1, NO = 0.8, N = 0.3, E = 1.3, EN = 2.6, IN = 2.1, EO = 4.6, IO = 2.8, ODW = 2.3, RG = 1.0. Tadpoles of *S. berthae* are characterized by an overall ovoid body that is wider than high (BW/BH

FIG. 1. Tadpoles of: *Scinax berthae*, Gosner stage 37, CECOAL 001 (top); *Scinax nebulosa* Gosner stage 37, KU130154 (middle); and *Scinax boesemani* Gosner stage 37, USNM291285 (bottom). Bars = 5 mm.



= 1.17). The snout is rounded both in lateral and dorsal views. The nostrils are dorsolateral, located nearer to the eyes than to the snout. The eyes are lateral. The spiracle is single, sinistral, and lateral; although it opens below the mid-level of the body, it is visible in dorsal view. The vent tube is 2.0 mm long, lies along the ventral mid-line, and opens slightly dextrally. The tail represents about 62% of the total length. The tail fin height is slightly greater than that of the body. The dorsal fin extends onto the body and is slightly higher than the ventral fin. The height of the ventral fin is subequal to the height of the tail musculature. The shape of the tail tip is flagelliform, with a rounded tip.

The oral disc is anteroventral. A single row of medium-sized marginal papillae borders the oral disc. The labial tooth row formula is: 2(2)/3. The length of row A1 is 2.2 mm and that of A2 is 2.0 mm. On the posterior labium, the length of row P1 is 2.0 mm, P2 is 1.9 mm, and P3 is 1.8 mm. The length of the beak is approximately 1.0 mm. The upper and lower beaks are serrated and approximately 20% keratinized (as suggested by pigmentation). The upper beak is broadly W-shaped and the lower beak is V-shaped.

In life, the body is brown dorsally and has a wide, brownish inter-orbital band. The body is pale brown laterally. The caudal musculature is brown, and has a wide, irregular, darker brown longitudinal band for about half of its length. This band is flanked above and below by pale yellow bands. The dorsal band extends posteriorly for about 80% of the total tail length,

whereas the ventral one extends for only about 20% of the tail length. The colouration of preserved specimens is similar to that of living individuals. In lateral view the body colouration is light brown with small brownish and reticulate spots. The yellow tail bands disappear in preserved specimens. The area of the throat is semi-transparent and the intestinal coils are visible through the skin. The tail fins are transparent with small, brown, patches of melanin. These melanin patches are more abundant on the ventral fin, and they tend to accumulate on the first quarter in the dorsal fin.

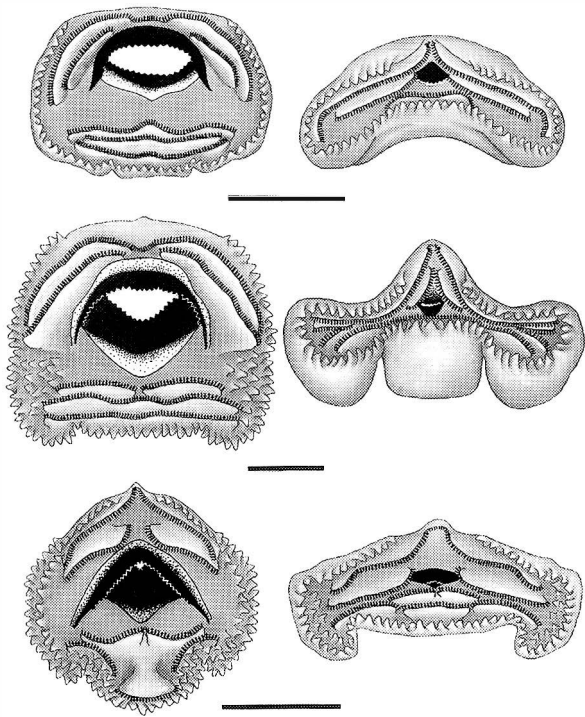
Biology. The breeding season of *Scinax berthae* extends from late September through December; eggs are unpigmented, about 0.9 mm in diameter, and deposited underwater, attached to the submerged stems of aquatic vegetation (Barrio, 1962). The tadpoles were collected in a small temporary pond on flooded lowlands within a gallery forest. This pond was approximately 5 m long and 3 m wide, with a maximum depth of 0.4 m; however, water depth varied with occasional rains and flooding from the Rio de la Plata. The pond had a muddy bottom with large accumulation of organic matter, and little sun exposure. Gallardo (1987) reported larvae to exhibit "abrupt and quick movements."

SCINAX NEBULOSA (SPIX, 1824)

See Fig. 1 and 2 (middle). The description is based on specimens identified by M. L. Crump and W. E. Duellman and deposited in the herpetological collection of the Natural History Museum, The University of Kansas. Duellman & Wiens (1992, p. 20) subsequently treated tadpoles from this lot as *S. nebulosa*. Illustrations and measurements are for a representative Stage-37 tadpole from lot KU 130154. These specimens were collected at IPEAN, 3 km E. Belém, Pará, Brazil, on 11 April, 1970, by M. L. Crump and W. E. Duellman. The measurements are as follows: TL = 52.3, BI = 14.8, TaL = 37.6, BW = 9.0, BWE = 8.9, BWN = 7.3, BH = 16.0, FH = 17.9, TMH = 5.0, RSD = 9.3, SPD = 4.1, FN = 1.8, NO = 1.4, N = 0.5, E = 2.0, EN = 5.3, IN = 4.5, EO = 8.6, IO = 8.5, ODW = 3.6, RG = 1.0. In tadpoles of *Scinax nebulosa* the body is higher than wide (BH/BW = 1.78). Neuromasts are clearly visible dorsally. The nostrils are dorsolateral, nearer the eyes than to the tip of the snout. Eyes are lateral. Eye diameter is 2.0 mm, and pupil diameter is 0.8 mm. The spiracle is single, sinistral, and located laterally in an approximately 45° angle with the horizontal axis of the body. The spiracle opening is located immediately below the mid-level of the body and is slightly visible dorsally. The vent is dextral. The length of the tail represents approximately 72% of the total length. The FH is approximately 12% higher than the body height. The dorsal fin largely extends onto the body. The tail fins are of about equal height, and about 1.5 x the height of the caudal musculature. From the middle of the tail caudally, the tail fins taper uniformly to a narrow tip.

The oral disc is almost terminal. The oral disc possesses well-developed ventrolateral folds. A row of

FIG. 2. Closed (right column) and opened (left column) oral discs of: *Scinax berthae* CECOAL 001 (top); *Scinax nebulosa* KU130154 (middle); and *Scinax boesemani* USNM291285 (bottom). Bars = 1 mm.



large marginal papillae borders the oral disc. Submarginal papillae form patches within the ventrolateral folds. The labial tooth row formula is: 2(2)/3 (1). In the anterior labium, tooth rows A1 and A2 are about equal in length (3.2 mm). At the middle of A1 there are about 40 teeth/mm. In the posterior labium, tooth rows P2 and P3 have an equal length of 2.9 mm, whereas P1 is slightly shorter (2.7 mm). The maximum length of the beak is 1.8 mm. The upper and lower beaks are pigmented and serrated. The upper beak is broadly W-shaped and is 80% keratinized (=pigmented), whereas the lower beak is V-shaped and 60% keratinized (=pigmented).

Colouration in life was registered in M. Crump's field notes (MLC 1766) as follows: "Dark olive green-grey above. Venter silvery-white. Tail grey; tail fin tannish-grey, some faint orange with dark pigment spots. Iris bronze with dark pigment accumulation anteriorly and posteriorly. In deep swamp pond." In preservative, these tadpoles are light brown, almost whitish. The caudal fins are transparent with brown melanin spots that accumulate more heavily on the anterior half of the dorsal and ventral fins.

Biology. No reports are available on the biology and natural history of tadpoles of this species.

SCINAX BOESEMANI (GOIN, 1966)

See Fig. 1 and 2 (bottom). The following description is based on specimens deposited in the herpetological collection of the National Museum of

Natural History, Smithsonian Institution. The tadpoles were collected at Kaieteur National Park (elevation approximately 480 m), Potaro-Siparuni State, Guyana, on March 30, 1989, by R. P. Reynolds and subsequently identified and assigned to this species by R. Altig. Illustrations and measurements are for a typical Stage-37 tadpole (USNM 291285). The measurements are as follows: TL = 34.3, BI = 11.5, TaL = 22.8, BW = 6.5, BWE = 6.5, BWN = 4.8, BH = 7.7, FH = 7.5, TMH = 3.0, RSD = 6.8, SPD = 3.5, FN = 1.3, NO = 1.1, N = 0.2, E = 1.8, EN = 3.1, IN = 2.7, EO = 5.9, IO = 5.0, ODW = 2.0, RG = 0.5. Tadpoles of *Scinax boesemani* have a high body shape (BH/BW = 1.18). The snout is rounded in dorsal and lateral views. The nostrils are dorsolateral, nearer the eyes than to the tip of the snout. Eyes are lateral. The spiracle is single, sinistral, and lateral. The spiracle opening is located immediately below the mid-level of the body. The vent is short (0.7 mm) and dextral. The tail represents about 66% of the total length. The FH is less than the body height. The dorsal fin extends onto the body. The tail fins are of equal height, and are about 25% shorter than the height of the tail musculature. The tail uniformly tapers to a slender flagelliform tip.

The oral disc is anteroventral and has ventrolateral folds. The oral disc is bordered by a row of medium-sized marginal papillae; a row of submarginal papillae is found laterally. Additional patches of submarginal papillae are found within the ventrolateral folds. The labial tooth row formula is: 2(2)/3 (1-2). On the anterior labium, tooth row A1 is 1.67 mm while A2 is slightly shorter, 1.57 mm. At the middle of A1 there are about 36 teeth/mm. In the posterior labium, tooth row P1 is 1.6 mm long and P2 is 1.7 mm. P3 is short (0.5 mm) and positioned at the end of an extended arm. The maximum length of the beak is 1.1 mm. The upper and lower beaks are V-shaped, strongly serrated, and about 70% keratinized (= pigmented).

Colouration in life is not available. Preserved specimens are very light yellow in colour, almost whitish, without spots or reticulation. Caudal fins are completely transparent. The body skin is transparent and the intestinal coils and other internal organs are visible through the skin laterally and ventrally.

Biology. There is no information available on the natural history of this species. The tadpoles collected at Kaieteur National Park were found along the sandy bottom of a stream with approximately 30-35 cm of water.

DISCUSSION

The genus *Scinax* was recently resurrected by Duellman & Wiens (1992) to include many medium to small Central and South American hyliid treefrogs previously placed in the genus *Ololygon*. The tadpoles of less than one third of the recognized species of *Scinax* are known; these tadpoles show an exceptionally high amount of ecological and morphological diversity. Larval characteristics and reproductive biology (e.g.,

oviposition site) are important features that have been used to support the monophyly of some species groups (Duellman & Wiens, 1992).

Ecologically, *Scinax* tadpoles range from being ground bromeliad inhabitants (i.e. *S. perpusilla* species group) to stream-associated forms (i.e. *S. catharinae* species group). However, most are found among vegetation in small temporary ponds (e.g. *S. rostrata* species group). The tadpoles described to date range from some with extremely high tail fins and filamentous tail tips (i.e. pond forms) to species with elongated tails and much reduced tail fins (i.e. semi-arboreal species). This amount of larval diversity raises the question of whether differences among the tadpoles could be used to identify monophyletic units within *Scinax*.

Scinax berthae is placed currently in the *Scinax staufferi* species group. Of the 13 species recognized in this group (Duellman & Wiens, 1992), the tadpoles were previously known for only three: *S. staufferi* (Duellman, 1970*; León, 1969); *S. squalirostris* (Cei, 1980*); and *S. parkeri* (Vizotto, 1967). The description of the tadpole of *S. berthae* provides additional information. However, the features that these tadpoles share seem to be widespread within *Scinax* and not sufficient to define this group or to suggest relationships to other species groups in the genus.

Scinax nebulosa is one of nine species currently included in the *Scinax rostrata* group (*S. boulengeri*, *epacrorhina*, *garbei*, *kennedyi*, *pedromedinae*, *proboscidea*, *rostrata*, *sugillata*, and *nebulosa*, Duellman, 1972; Duellman & Wiens, 1992; Frost, 1985). The tadpoles of only four of these species are known: *S. boulengeri* (Duellman, 1970*); *S. rostrata* (Duellman, 1970*; Hero & Mijares Urrutia, 1995*); *S. garbei* (Duellman, 1978); and *S. sugillata*, (McDiarmid & Altig, 1989-1990*). The tadpole of *S. pedromedinae* has never been fully described although Duellman & Wiens, 1993, briefly mentioned this tadpole. Known tadpoles of the *S. rostrata* group (including *pedromedinae*) share the presence of an "arm" on the posterior labium that supports the P3 tooth row (McDiarmid & Altig, 1989-1990), except for the *S. rostrata* tadpoles described by Duellman (1970). However, McDiarmid & Altig (1989-1990) questioned the identity of the tadpole described by Duellman (1970). Furthermore, Duellman & Wiens (1992) included *S. rostrata* among the species having fang-like teeth and a labial arm supporting the lowermost tooth row. Recently, Hero & Mijares-Urrutia (1995) redescribed the tadpole of *S. rostrata* based on tadpoles collected in Venezuela and reared through metamorphosis to confirm identification, and these tadpoles possess a labial arm supporting the P3 tooth row. This labial arm is absent in the *S. nebulosa* tadpole described here. If the presence of a labial arm is a synapomorphy for the *S. rostrata* group (and furthermore relates the genus *Scarthyla* to the *S. rostrata* group, as suggested by McDiarmid & Altig, 1989-1990), then either we need

to remove this species from the *S. rostrata* group or explain the lack of labial arm in specimens here described as *S. nebulosa*. A taxonomic rearrangement based on this single larval character is premature given the lack of information on larvae for the other four species in the group. A possible explanation could be that the sample we have described as *S. nebulosa*, considered as such by Duellman & Wiens (1992), are in fact another species of *Scinax* and not *S. nebulosa*.

The last tadpole described is that of *Scinax boesemani*, which is a member of the *S. x-signata* species group. According to Duellman & Wiens (1992) and Frost (1985), there are six species in this group, but only the tadpoles of two species have been described, *S. cruentomma* (Duellman, 1978) and *S. acuminata* (Mecolli, Dixon & Yanosky, 1994*). Once again, there are not enough tadpoles described to help define this group on larval characters. However, one characteristic is worth noting. The presence of a P3 tooth row supported by an extended arm that is similar to that described for species of the *S. rostrata* group may indicate a closer relationship of *S. boesemani* to that group than previously thought. Alternatively, additional data on tadpole biology, feeding behaviour, and diet are needed to explain this apparent convergence in oral structure. A modified P3 tooth row is not present in *S. cruentomma* or *S. acuminata*.

ACKNOWLEDGEMENTS

We thank the following colleagues for the loan of specimens: W. E. Duellman, Natural History Museum, The University of Kansas; and Roy W. McDiarmid, National Museum of Natural History, Smithsonian Institution. We are also grateful to Linda Trueb, Ron Altig, William E. Duellman, and Ron Heyer for comments on this manuscript. Arturo I. Kehr was financially supported by Consejo Nacional de Investigaciones Científicas y Técnicas, CONICET, from Argentina, through a Postdoctoral External Fellowship. Rafael de Sá's participation in this study was generously supported by the Faculty Research Committee, University of Richmond. Richard Wassersug was supported by the Natural Science and Engineering Research Council of Canada.

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Accepted: 11.6.96

STUDIES ON MORBIDITY AND MORTALITY IN SMOOTH SNAKES (*CORONELLA* SPP.)

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Data on morbidity and mortality in European smooth snakes, *Coronella austriaca* and *C. girondica*, were collated and a limited amount of clinical and pathological material was examined. There proved to be a paucity of published information and much of that available related to captive reptiles. *Coronella* spp. appeared to be susceptible to diseases that are well recognised in other reptiles in captivity - for example, pneumonia, ophthalmitis, nephritis, salpingitis and hepatitis. Mites were commonly associated with anaemia. Data from captivity are of some relevance to free-living populations, particularly when *Coronella* spp. are translocated or captured and studied in confinement. Information on health and disease needs to be collated and made available to those who are working on these species. There is also an urgent need to collect field data, not only in order to ascertain the prevalence of diseases and infections in free-living populations but also to establish databases on "normal" snakes. Protocols are presented to assist in the compilation and standardization of findings in live and dead specimens.

INTRODUCTION

There are two European species of *Coronella* both of which can reach a length of 50-60 cm. *C. austriaca* (the smooth snake) occurs in Europe as far east as Russia and southern Scandinavia and south to Italy and Greece. In Britain it is at the northern limit of its range and is found in a few small areas of heathland: eastern Dorset; the New Forest district of Hampshire, and adjacent south-eastern corner of Wiltshire; Hampshire-Surrey border between Farnham and Haslemere, and north-western Sussex. *C. girondica* (the southern smooth snake) is present in the south of France, Italy, the Iberian peninsula and NW Africa (Arnold & Burton, 1978; Street, 1979).

In Britain smooth snakes are sometimes rescued from doomed habitats and translocated to protected areas as a conservation measure. However, there is no information available on the diseases of free-living snakes or on the implications of disease transmission by such translocations. Here we present some preliminary data on health and disease in *Coronella*, and propose a protocol for health monitoring.

MATERIALS AND METHODS

Thirty-eight letters were sent to individuals and herpetological journals in Europe and North America. These requested information on disease in captive or free-living *Coronella* spp. There were nine responses to the letters, of which only four respondents were able to supply any data.

Two dead specimens of *C. girondica* were received from Spain. These were radiographed and examined *post mortem*: a selection of tissues was taken and processed for histopathological investigation. Three faecal samples from free-living specimens of *C. austriaca* were obtained from A. H. Gent's PhD study on this species in the New Forest area of Britain (Gent, 1988). These were examined microscopically as wet mounts in normal saline. Records from a subsequent study in the same locality were supplied by M. Gaywood (pers. comm.). Data from post mortem examinations of captive *C. austriaca* (18 specimens) and *C. girondica* (three specimens) over 40 years were provided by the Zoological Society of London (ZSL).

A literature search was carried out for references to disease in *Coronella* spp.

RESULTS

The findings in 18 *C. austriaca* examined *post mortem* at the ZSL are summarized in Table 1. Some conditions occurred in combination. Six specimens were known to be males, and one was a female. Findings included pneumonia, pulmonary congestion and oedema, inanition, and nephritis. In two out of the three specimens of *C. girondica* examined by ZSL the main finding was inanition. Anaemia was reported in both species and was associated with mites and, in one specimen of *C. girondica*, with haemogregarine blood parasites.

The two dead specimens of *C. girondica* received from Spain showed no abnormalities radiographically, grossly, or on histopathological examination.

TABLE 1. *Post mortem* findings in eighteen specimens of *C. austriaca* (ZSL data).

Finding	Number of snakes	%
Pneumonia	7	38.8
Inanition	3	16.6
Nephritis	1	5.5
Peritonitis	1	5.5
Salpingitis	1	5.5
Gastric dilatation	1	5.5
Anaemia/mites	1	5.5
Hepatitis	1	5.5
Respiratory ascariasis	1	5.5
Unknown	1	5.5

The faecal samples of *C. austriaca* contained vegetable matter, presumed to have been ingested accidentally or within the digestive tract of prey, but no evidence of endoparasites or abnormalities.

Gaywood observed 28 *C. austriaca* in the wild and recorded an ocular lesion in one snake. Gent observed 129 snakes and recorded abnormalities in 16 of them. Gaywood and Gent's findings are summarized in Table 2. The majority of the affected animals had lesions attributable to trauma.

The literature search yielded a few specific references to disease in *Coronella* spp. These were mycotic abscessation of the liver (Reichenbach-Klinke & Elkan, 1965), experimental infection of *C. austriaca* with the cestode *Ophiotaenia europaea* (Biserkov & Genov, 1963) and a report from what was then Czechoslovakia of a young *C. austriaca* with duplication of its head (Zidek & Zidek, 1985).

DISCUSSION

There appears to be a paucity of information on the diseases and pathology of *Coronella* spp. and very little relevant stored material. This may have led to bias in interpretation of findings in this paper as most of the data were from *post-mortem* specimens at the ZSL together with some observations of findings in free-living snakes. It is clear, however, that *Coronella* spp., in common with most other reptiles, are susceptible to

TABLE 2. Observations on free-living *C. austriaca* (Gaywood and Gent data)

Finding	Number of snakes
Truncated tail	5
Scarring	5
Trauma	4
Eye lesions	2
Predation	1
Abrasion/bruising	1
"Bulge" in body	1
Tick	1

physical injuries; this, as studies on other species of snake have shown (Greene & Hardy, 1989; Willis *et al.*, 1982), can reduce survival *per se*, and probably predispose to infection (Cooper & Jackson, 1981).

It is possible that infectious and/or non-infectious diseases can have an adverse effect on free-living snakes. When a species such as *C. austriaca* is at the edge of its range, and also occurs in fragmented habitats, it could be particularly sensitive to changes in climate and/or habitat (Frazer, 1983). There is increasing evidence that disease can be significant in threatened vertebrate populations, especially when it is coupled with other factors such as habitat destruction, inbreeding depression, malnutrition or toxic chemicals (Cooper, 1989). However, most of the current work on this subject has been on mammals and birds: there is a need for comparable research on reptiles. An important prerequisite is the establishment of a database on normal values and some preliminary work has been performed - for example, on the cloacal flora of British reptiles (Cooper *et al.*, 1985).

More data on morbidity and mortality of *Coronella* spp. would be valuable, especially relating to free-living populations. Information from captive animals may also be relevant.

A multi-disciplinary approach is desirable in studies on the biology of *C. austriaca* and *C. girondica*; a veterinary input can help in elucidating the significance of disease. Studies in the field should as a routine include clinical examination for health and disease; where feasible, simple laboratory tests should be performed. Examination of faeces for parasites can be combined with analysis of samples for food items (Rugiero *et al.*, 1995). A suggested protocol for examination of live snakes is shown in Appendix 1 and of dead snakes in Appendix 2. Standardisation of records could do much to improve our knowledge and understanding of the part played by disease in these species.

ACKNOWLEDGEMENTS

We are grateful to Dr. James Kirkwood and Ms. Kathy Thorpe for providing and permitting us to reproduce data from the records of the Zoological Society of London, Dr. A. H. Gent and Mr. M. Gaywood for making available to us their observations on free-living *Coronella austriaca* and for providing faecal samples, and to Messrs Nacho Marco-Sanchez and Miguel Rafa for submitting the two specimens of *C. girondica*. The Library of the Royal College of Veterinary Surgeons performed a literature search and staff of the Hunterian Institute, Royal College of Surgeons of England, assisted with laboratory investigations.

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Accepted: 8.7.96

APPENDIX 1. Protocol for health monitoring of live *Coronella* spp.

BASIC	
<i>Observation and examination</i>	
(1)	Presence or absence of: a. clinical signs of disease b. injuries or external lesions c. ectoparasites
(2)	Standard data on sex, age and reproductive status coupled with the following: a. bodyweight b. measurements c. condition score
(3)	Gross appearance of: a. faeces/urates b. sloughed skin
<i>Laboratory tests</i>	
(1)	Presence or absence of protozoan and metazoan parasites in faeces.
(2)	PCV (haematocrit) and total blood protein.
(3)	Differential blood counts plus presence or absence of parasites or cellular abnormalities in blood smears.
ADDITIONAL INVESTIGATIONS, IF PERSONNEL AND FACILITIES PERMIT	
(1)	Bacteriological examination of swabs from: a. trachea b. rectum/cloaca
(2)	Blood tests - complete haematology and biochemistry, DNA studies.
(3)	Examination of serum for antibodies (serology).

Whenever possible - and always if an animal appears to be in ill-health - a full clinical examination should be carried out and supporting laboratory tests performed. In this case a standard clinical sheet should be completed.

APPENDIX 2. Protocol for health monitoring of dead *Coronella* spp.

BASIC:

- (1) *Gross examination:*
The following data should be coupled with standard data on sex, age and reproductive status
 - a. bodyweight
 - b. measurements
 - c. condition score
 - d. appearance of internal organs
 - e. presence or absence of fat
 - f. presence or absence of ectoparasites
 - g. presence or absence of endoparasites in alimentary or respiratory tract
 - (2) *Toxicology:*
Submission or retention (frozen) of carcass or tissues for analysis (e.g. for chlorinated hydrocarbon pesticides, heavy metals).
-

ADDITIONAL INVESTIGATIONS, IF PERSONNEL AND FACILITIES PERMIT

- (1) *Bacteriology:*
 - a. heart blood
 - b. intestinal contents
 - c. any significant lesions
 - (2) *Histopathology:*
 - a. lung
 - b. liver
 - c. kidney
 - d. any significant lesions
 - (3) *Other tests:*
Submission or retention (frozen/fixed) of tissues for virology, mycoplasmaology, electronmicroscopy, DNA studies, etc.
-

Whenever possible a full *post-mortem* examination should be carried out and supporting laboratory tests performed. In this case a standard *post-mortem* sheet should be completed.

SHORT NOTES

HERPETOLOGICAL JOURNAL, Vol. 7, pp. 23-25 (1997)

ON TERMINOLOGY FOR THE
DESCRIPTION OF THE HEMIPENES
OF SQUAMATE REPTILES

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The use of morphological differences of the hemipenes as systematic characters in the Squamata dates from the seminal papers of Cope (1893, 1895, 1896). Subsequently, the hemipenial features of snakes have been widely used as a basis for higher classification and in species recognition (e.g. Dunn, 1928; Bogert, 1940; Myers, 1974; Branch, 1986).

While utilization of the characteristics of snake hemipenes in systematic studies is now *de rigueur*, until recently little attention has been given to these structures in lizards. This is partially because the streamlined habitus of snakes provides a reduced set of features for phylogenetic reconstruction that are plagued by extensive homoplasy. The search for additional informative structures has thus taken advantage of the substantial variation in the relatively large snake hemipenes. In contrast, lizards have a wider range of external and internal characters that are thought to be subject to less homoplasy, and hemipenes are generally smaller structures than in snakes.

Renewed attention to lizard hemipenes as a rich mine of data (Uzzell, 1965; Presch, 1978; Branch, 1982; Arnold, 1986; Böhme, 1988, 1991; Frost & Etheridge, 1989) confirms Cope's (1896) perspicacity in identifying their value in systematics. However, this revival of interest raises questions of homology and the need for a uniform terminology applicable to all squamate hemipenes. Dowling & Savage (1960) presented an overview of the variation in snake hemipenes and an updated standardized terminology for description that has been further refined by McDowell (1961), Myers & Campbell (1981), and Branch (1986), especially with regard to the position of the sulcus spermaticus. Generally, lizard hemipenes may be described utilizing the same set of terms as these authors. However, Klaver & Böhme (1986) and Böhme (1988), in the most comprehensive review of lizard hemipenes to date, proposed a number of new descriptors for specialized features not found in snakes. Böhme (1988) also provided a revised set of definitions for uniform description of lizard hemipenes.

The present paper is intended to clarify definitions, resolve inconsistencies and integrate the terminology applied to hemipenial variation for lizards and snakes into a broader scheme applicable to all squamates. Issues to be treated relate primarily to regional

characterization and differentiation, details of ornamentation and apical specialization. Terms that are concordant between Dowling & Savage (1960) and Böhme (1988) are not discussed but are accepted as standardized descriptors. The terminology for variation in the sulcus spermaticus of snakes provided by McDowell (1961), Myers & Campbell (1981) and Branch (1986) also should be applied to conditions in lizards, including amphisbaenians, when appropriate.

Most squamate hemipenes are differentiated into two or three regions by the degree and kinds of ornamentation (e.g. calyces, papillae, spines). The basal one-fifth to one-half is often naked but may have some distinctive features (e.g. hooks, naked pocket, small spines). A central zone consisting of about one-half to one-third of the penial length is usually differentiated from both the basal sector and the distal one-third to one-fourth of the organ. Klaver & Böhme (1986) introduced the terms pedicel, truncus and apex for the proximal (basal), central and distal areas, respectively. The very tip (apex) of the hemipenes often has a distinctive terminal structure (e.g. papilla, awn, disk) while the rest of the distal region is differentiated (e.g. spinous, calyculate, papillate). For this reason it seems best to refer to the distal sector as the apical region and describe the terminal specializations separately.

Other terminal specializations include structures called "horns" and "cups" by Branch (1982), and a series of bizarre features, which will be discussed below, found only in chamaeleons (Klaver & Böhme, 1986). The "horns" (Branch, 1982) of varanid lizards are extensions of the divided retractor muscle that do not evert and lie in the lumen of the retracted hemipenis. The terminal papillae and awns of the few snakes having them appear to be similar structures. Terminal papillae and awns also occur on the hemipenes of some macroteiid lizards (Böhme, 1988, Fig. 24). Nevertheless the varanid structures are so distinctive that it seems best to recognize them separately as hemipenial *cornua* (sing. *cornus*).

The "cups" described by Branch (1982) in varanids are substantially different from those that he subsequently recognized in some boid snakes (Branch, 1986). The latter are the same paired structures called apical disks by Cope (1895) and Dowling and Savage (1960) and may be terminal or lateral to the apex. The varanid lateral "cups" form slight depressions to strongly concave areas demarcated by a thick fleshy ridge surrounding a hemipenial cornus. They occur in relatively few species and are paired or only one is present. (Branch, 1982; Böhme, 1988). There appears no need to coin any special terms for these features which may be simply described.

Klaver & Böhme (1986) described and standardized terminology for the remarkable apical pedunculi, auriculae and rotulae unique to chamaeleons. These authors also described two kinds of unusual features in members of the chamaeleon genus *Brookesia* as terminal "horns" and "crests". Species in this genus have

either a pair of "horns" or a pair of "crests" terminally. There is considerable similarity between "horns" and pedunculi and "crests" and auriculae or rotulae. Because of the uncertainty of homology or lack thereof it seems inappropriate to coin any new terms for these structures following Klaver & Böhme (1986).

Cope's (1893) descriptions are based on uneverted hemipenes, which led him to adopt an ambiguous terminology for the longitudinal and transverse or pinnate folds that he observed in his preparations. He referred to these folds collectively as laminae. In addition he called both the longitudinal and transverse or pinnate folds plicae. Dowling & Savage (1960) standardized Cope's terms to "flounce" for non-calyculate transverse or pinnate folds because they could make no distinction between flounces and plicae in this context. In addition they pointed out that Cope's longitudinal plicae are folds of membranous tissue that disappear when the organ is everted. Peters (1974) obfuscated the situation by equating flounces with plicae and stating that flounces disappear when the hemipenes are everted. As shown by Dowling & Savage (1960) and Böhme (1988), flounces are definite structures but what Cope called longitudinal plicae are not. Although the latter disappear as the hemipenes are everted there are other structural differentiations of the pedicel (e.g. fleshy ridges, naked pockets) that may be present in both inverted and everted states.

Cope (1895) described the truncus and apical region of macro- and microteiids as covered by thin transverse, slightly overlapping folds which he called "transverse laminae". He contrasted this condition with the fleshy flounces observed in many other lizards. Böhme (1988) recognized the differences between "laminae" and flounces and coined the term *paryphasmata* as a descriptor for the latter. Unfortunately, he chose to use "plicae" for the laminate structures. Because of the dual and confusing usage of "plicae" for flounces and transitory longitudinal folds (Cope, 1893, 1895; Peters 1974) and "laminae" for flounces, longitudinal "plicae" and Böhme's (1988) plicae (Cope 1896), I recommend that these terms not be used in squamate hemipenial descriptions. I propose that the descriptive and unambiguous term *petalum* (pl. *petala*) be applied to the thin transverse overlapping folds found in lizards and called plicae by Böhme (1988).

Petala and flounces of lizards may exhibit differences in micro-ornamentation as described for snakes (Dowling and Savage, 1960). The surface of the petala in some species is covered with minute spines (Böhme, 1988). In several microteiids (Gymnophthalmidae) the petala have an internal skeleton of closely packed small calcified spines. Böhme (1988) proposed the term *spiculae* for these structures to distinguish them from other spinous features of the hemipenes. Although Branch (1982) coined the term "frill" to denote deeply scalloped flounces that are characteristic of many varanid lizards, these flounces do not differ sig-

nificantly from similar structures found in other squamates.

It should be noted that petala have not been reported for any snake. Also unknown in snakes are the hemibacula (Böhme, 1988), unique internal supportive mineralizations within the large apical cornua of the hemipenes of some varanid lizards (Branch, 1982; Card & Kluge, 1995).

Böhme (1988) concluded that the basic kinds of ornamentation found on the apical region and/or truncus of hemipenes was characteristic of major groups of lizards: Iguania and Gekkota having calyces but lacking petala and flounces; Scincomorpha having petala and lacking calyces and flounces; Anguimorpha having flounces but lacking calyces and petala.

Subsequently, Böhme (1989) reviewed the structure of the hemipenes in amphisbaenians. They resemble those of teiid lizards in ornamentation by having petala and lacking calyces and flounces, or are nude. Partially on the basis of the penial characteristics, Böhme regarded them as scincomorphs fitting into his overall generalizations on hemipenial features for major lizard groups.

While these generalizations have much merit it needs to be pointed out that flounces occur sporadically in Iguania and Scincomorpha as well. In the former the distal calyculate area may gradually grade into a series of transverse ridges (Böhme's *Randleisten*) toward the base as the number of longitudinal connecting ridges are reduced. In some representatives of the scincomorph families Xantusiidae (Böhme, 1988, Fig. 23), Gymnophthalmidae (Böhme, 1988, Figs. 24, 28) and Scincidae (Noble and Bradley, 1933, Fig. 12) a portion or most of the ornamentation consists of thick fleshy transverse folds (called *Ringfalten* and *Ringwülste* by Böhme) differing only slightly from the flounces found in the Anguimorpha.

The distinction between petala and flounces is one of degree. The former are thin, closely set and slightly imbricate, and the latter fleshy, more widely spaced and non-overlapping. Somewhat intermediate conditions seem to occur in some scincomorphs (e.g. Presch, 1978, Fig. 2) suggesting that a character transformation from flounces to petala or vice versa has occurred more than once among lizards.

Another area needing clarification is the use of the term *capitate* for the hemipenes of some lizards (Branch, 1982; Frost & Etheridge, 1989). In snakes *capitate* describes organs in which a distinct transverse naked groove, or a pair of grooves in some bilobed forms, completely encircles the organ (or each lobe), except where the sulcus spermaticus passes through the groove(s). The groove separates the differentiated apical region(s), called a *capitulum* (pl. *capitula*), from the truncus.

No known lizard has the *capitate* condition. Branch's (1982) usage is ambiguous. Frost & Etheridge (1989) used *capitate* to describe lizard hemipenes that have the apical region calyculate and

distinctly differentiated in ornamentation from the truncus or truncus plus pedicel. Since there is no bounding naked groove in these cases and consequently no capitulum, this term should not be applied in lizard hemipenial descriptions.

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Accepted: 26.4.96

HERPETOLOGICAL JOURNAL, Vol. 7, pp. 26-27 (1997)

TEMPERATURE RELATIONSHIPS OF THE TROPICAL TREE LIZARD (*UROSAURUS BICARINATUS*) FROM THE CAÑÓN DEL ZOPILOTE, GUERRERO, MÉXICO

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Tree lizards of the genus *Urosaurus* live in a diversity of habitats ranging from xeric to mesic conditions (Wiens, 1993). Each habitat presents the individuals living in them with unique thermal environments. For example, tree lizards living in desert habitats will be exposed to higher ambient temperatures than tree lizards living in mountain habitats (Smith & Ballinger, 1995). Such contrasts in environmental temperatures may not necessarily lead to differences in active body temperatures. For example, desert and mountain habitats supporting populations of *Urosaurus ornatus* in south-eastern Arizona and south-western New Mexico had different air temperatures, but lizards did not differ in body temperatures or thermal tolerance (Smith & Ballinger, 1994, 1995). However, *U. ornatus* and *U. graciosus* in a different habitat (desert riparian) have slightly higher body temperatures than *U. ornatus* from the desert and mountain populations (Vitt, Van Loben Sels, & Ohmart, 1981; Smith & Ballinger, 1995). Thus, there does appear to be intrageneric variation in active body temperature. To determine if there is a phylogenetic component and/or an environmental component to this variation, additional information on other species from different habitat types and localities is needed. In this note, we report on the temperature relationships of *U. bicarinatus* from an arid tropical scrub habitat in Guerrero, México. Little else is known about the biology of this species (see Ramírez-Bautista, Uribe-Peña, & Guillelte, 1995), and, except for *U. ornatus* and *U. graciosus*, the genus in general (Wiens, 1993).

Our study was conducted in the Cañón del Zopilote north of Chilpancingo, Guerrero (600 m elevation), 14 km south of Mexcala, a small town on the Rio Balsas. The area is situated in arid tropical scrub (the most xeric portion of the Bosque Tropical Caducifolio of Rzedowski, 1988). Dominant vegetation includes a va-

riety of cacti including large *Neobuxbaumia* spp., and trees such as *Bursera* spp., *Acacia* spp., *Lysiloma tergemina*, *Mimosa benthami*, *Ficus contifolia*, *Ficus petiolaris*, and *Pithecellobium dulce*, among other species. The area lies in the rain shadow of the Sierra Madre del Sur which makes the interior Balsas River basin extremely xeric. There is a pronounced rainy season from late May until September at which time the late afternoon and evening storms produce torrential rains. *Urosaurus bicarinatus* is active throughout the year.

A total of 81 lizards were captured by hand or by shooting with a rubber band. Body temperatures (T_b ; to the nearest 0.1°C) were obtained using quick-reading cloacal thermometers. Care was taken to prevent temperature from being influenced by handling, and all lizards requiring extensive effort to capture were excluded. Body temperatures were only collected from active lizards (i.e. foraging or basking). Due to logistic constraints, collections were concentrated in the morning throughout the study. Air temperature (T_a ; at 5 cm above substrate where lizard was first observed, using a shaded bulb to nearest 0.1°C) and substrate temperature (T_s ; on substrate where lizard was first observed, using a shaded bulb to nearest 0.1°C) were measured at the site of capture. We also measured snout-vent length (SVL; to nearest mm) using a ruler. Standard parametric analyses were performed. All measurements are reported as mean \pm one standard error. Least squares means (LSM) from analysis of covariance are often used to represent means corrected for differences in T_a .

All lizards collected were observed on *Acacia* trees. Mean SVL was 40.8 ± 0.7 mm. Males were larger than females [42.1 ± 0.9 mm ($n = 51$) vs. 38.6 ± 0.9 mm ($n = 30$); $df = 79$, $t = 2.61$, $P = 0.011$]. Body temperatures averaged 34.6 ± 0.6 °C. The T_a at the site of capture had a mean of 29.9 ± 0.4 °C, and the T_s at the site of capture had a mean of 31.6 ± 0.6 °C. Air and surface temperatures were closely related ($r^2 = 0.88$, $P < 0.0001$; $T_s = -4.84 + 1.22T_a$). Body size (SVL) did not have a significant influence on T_b ($r^2 = 0.004$, $P = 0.56$), T_a ($r^2 = 0.005$, $P = 0.52$), or T_s ($r^2 = 0.002$, $P = 0.72$).

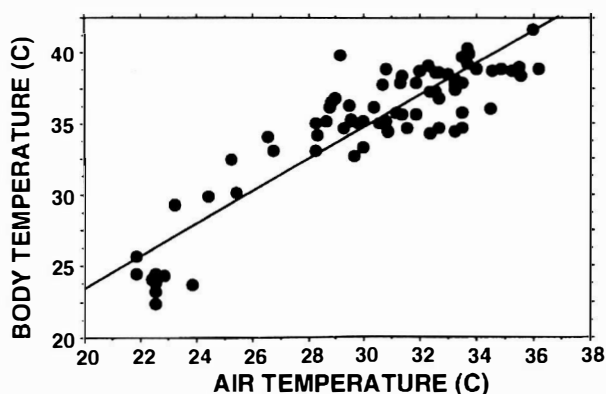


FIG. 1. Least squares regression of body temperature vs. air temperature for *Urosaurus bicarinatus*. The regression equation is provided in the text.

Body temperature was positively correlated with T_a (Fig. 1; $r^2 = 0.82$, $P < 0.0001$; $T_b = 0.85 + 1.13 T_a$), as well as T_s ($r^2 = 0.81$, $P < 0.0001$; $T_b = 7.26 + 0.86 T_s$). There was a positive relationship between the time of day and T_b ($r^2 = 0.61$, $P < 0.0001$; $T_b = 14.6 + 1.9 \text{ Hour}$). Air temperature ($r^2 = 0.61$, $P < 0.0001$; $T_a = 14.0 + 1.5 \text{ Hour}$) and T_s ($r^2 = 0.004$, $P = 0.56$; $T_s = 11.4 + 1.9 \text{ Hour}$) also increased as the day progressed (at least into early afternoon).

Males (LSM: 35.0 ± 0.3 °C) had a slightly higher mean T_b than females (LSM: 33.9 ± 0.4 °C) (ANCOVA with T_a as covariate; $F_{1,78} = 4.78$, $P = 0.03$). The interaction between sex and T_a was not significant, suggesting that the slopes of the T_b on T_a regression did not differ between males and females (this interaction term was therefore not included in the final analysis). Males and females did not have different T_a 's (29.8 ± 0.56 °C vs. 30.2 ± 0.7 °C; $df = 79$, $t = -0.47$, $P = 0.64$) or T_s 's (31.6 ± 0.76 °C vs. 31.5 ± 0.9 °C; $df = 79$, $t = 0.12$, $P = 0.91$).

The mean T_b of *U. bicarinatus* reported here is very similar to the mean T_b 's of the desert and montane populations of *U. ornatus* (34.8°C and 35.0°C , respectively) in Smith & Ballinger (1995), but $2\text{--}3^\circ\text{C}$ less than the means for *U. ornatus* and *U. graciosus* in desert riparian habitats in Vitt *et al.* (1981). Air temperatures in this study were on average higher than those found at either site in Smith & Ballinger (1995), but slightly lower than the T_a 's in Vitt *et al.* (1981). The fact that the populations of *U. ornatus* in the desert riparian, and the desert and montane habitats differ more than some of the species do, suggests that something in addition to phylogenetic relationships may be determining active body temperatures in the genus *Urosaurus*.

Local environmental conditions may be partially responsible for some of the observed differences. The fairly high T_b 's of the central Arizona *U. ornatus* and *U. graciosus* may be related to the high ambient temperatures of their habitats (see Vitt *et al.*, 1981), compared to the relatively lower ambient temperatures for the desert and low montane *U. ornatus* (Smith & Ballinger, 1995) and arid tropical scrub *U. bicarinatus*. Indeed, local mean T_a for 26 populations of lizards in the genus *Sceloporus* accounted for just over 50% of the variation in mean T_b (Lemos-Espinal, Smith, & Ballinger, in press).

Another important consideration may be the degree of arboreality of the species in question. *Urosaurus bicarinatus* appears to be strictly arboreal: no individuals were observed on the ground, and all individuals remained in trees during capture. These findings support the assertion that the clade including *U. bicarinatus* is strictly arboreal (Wiens, 1993). The importance of arboreality and terrestriality arises when the microclimate of a perching lizard is considered. Different perches can have different biophysical properties

(see Bakken, 1989) and thus for a given T_a , individuals on different perches can have different T_b 's. Such considerations may help explain the differences in T_b observed in the studies on *Urosaurus*, since each species tends to vary in the extent of their arboreality. Indeed, in *U. ornatus* in a low montane habitat, individuals using different substrates did in fact have different T_b 's (Smith & Ballinger, 1995). At this time we do not have enough information to make any conclusions about the sources of active body temperature variation in the genus *Urosaurus*, but hope that more data will be forthcoming to allow for additional analyses.

Acknowledgements. We thank three anonymous reviewers for their comments on this manuscript. Partial support for this research was provided by the School of Biological Sciences of the University of Nebraska-Lincoln. Some logistic support for GRS during manuscript preparation and data analysis was provided by the Kellogg Biological Station, Michigan State University.

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Accepted: 10.5.96

HERPETOLOGICAL JOURNAL, Vol. 7, pp. 28-30 (1997)

THE USE OF PHALANGES FOR AGE DETERMINATION IN THE SMOOTH NEWT, *TRITURUS VULGARIS* L.

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Since the early work of Senning (1940), skeletochronology has been used to gain an insight into the population biology of a wide range of amphibians (e.g. Smirina & Rocek, 1976; Gittins, Steed & Williams, 1982; Gibbons & McCarthy, 1983; Caetano, Castanet & Francillon, 1985; Verrell & Francillon, 1986). This technique has been shown to be the most reliable method of ageing amphibians when mark-recapture data are unavailable (Halliday & Verrell, 1988). A pattern apparent in the long bones, of rapid summer growth bands and winter lines of arrested growth (LAGs), analogous to tree rings, has been well documented and proven to be annual by comparison with data from marked animals caught over a number of years (Gibbons & McCarthy, 1983) and also by the injection of fluorescent dyes into captive animals (Caetano & Castanet, 1987).

For the larger amphibians, particularly the anurans, the phalanges are normally examined (e.g. Gittins *et al.* 1982; Gibbons & McCarthy, 1983; Reading, 1991; Flageole & Leclair, 1992; Guarino, Angelini & Cammarota, 1995), precluding the need to sacrifice any animals and thus making the technique compatible with mark-recapture or other ecological investigations. However, the understanding of the population biology of small-bodied amphibians, such as the smooth newt (*Triturus vulgaris*), has been hampered by the need to sacrifice large numbers of animals to extract the humerus or femur. Miaud (1991) investigated the age structure of three species of *Triturus* (*T. cristatus*, *T. alpestris* and *T. helveticus*) using skeletochronology. For the two larger species he was able to examine phalanges, but for *T. helveticus* he found it necessary to utilise the humerus. Guyetant *et al.* (1991), however, did manage to use the phalanges of *T. helveticus* for skeletochronology. Francillon-Vieillot, Arntzen & Geraudie (1990) have used the phalanges to determine age in *Triturus cristatus* and *T. marmoratus*. Halliday & Verrell (1988) suggested that the phalanges of the smooth newt are unsuitable for skeletochronology, being too cartilaginous and subject to remodelling. The immediate problem, however, is the tiny size of the toe bones (0.5 - 1 mm in length). This note outlines how both the difficulties of bone structure and bone size have been overcome, allowing the reliable use of the phalanges in the determination of age in the smooth newt.

As part of a three year field study, 167 smooth newts were caught at a small pond (elevation 60 m) and marked by removing the 4th toe of the hind right leg. Animals ranged in size from 71 - 95 mm total length. The removed digits were preserved in 70% alcohol and stored in labelled tubes. In the laboratory the proximal phalanx was dissected from the digit, decalcified for 1 hour in Rapid Decal© and thoroughly rinsed. Because of the size of the bones, it was not possible to rinse them under running water; instead, they were placed in sealed tubes of water and agitated vigorously. The bones were then subjected to a standard wax-embedding procedure (Gabe, 1976), but dehydration and wax-embedding of the bones was carried out by hand, again because of their small size, as automated manipulation by Histokinette© (American Optical, Type E7326) was found to be unreliable, with considerable bone losses occurring during the process. Before wax-impregnation it was found useful to stain the phalanges briefly in Eosin. This made the bones more visible for the final embedding when the tissue needed to be aligned perpendicularly in the wax mould, and also allowed the bones to be seen through the wax when trimming the wax blocks for sectioning.

Serial sectioning of the phalanges showed that the mid-diaphyseal region of the shaft contained the greatest breadth of periosteal bone (in which the growth bands are laid down), and the smallest marrow cavity diameter. Endosteal growth, which can sometimes obscure the earliest growth rings, was also found to be at a minimum in this region. The phalanges were sectioned transversely at a thickness of 10 - 12 µm, heat-mounted onto microscope slides and left to dry for 24 hours. The wax was then removed using xylene and the sections were gradually rehydrated over a period of 4 hours. Harris' Haematoxylin was used to stain the tissue and immersion for as little as five minutes proved sufficient to show up the LAGs. Differentiation with acid alcohol was found to be unnecessary.

While the LAGs in the humerus of *Triturus vulgaris* are known to be laid down annually (Hagström, 1977; Verrell & Francillon, 1986), it was necessary to show that the pattern of haematoxylinophilic lines visible in the phalanges corresponded to the LAGs in the humerus. To this end 10 animals, including two juveniles caught terrestrially, were sacrificed (under licence) and a comparison made between the number of LAGs visible in the humerus and in the phalanges. Table 1 shows that a close approximation was obtained between the two bones.

Endosteal resorption was found to be no more severe in the phalanx than the humerus. In animals older than 2 years of age the first LAG was found to be resorbed to some extent, but normally this remodelling was asymmetrical and some part of the first LAG was always visible, even in the oldest animals. In some phalanges false lines and partial double lines confused the reading, as also reported by Verrell & Francillon (1986) for

TABLE 1. A comparison of the numbers of LAGs recorded from humerus and phalanx bones in 10 newts.

Newt No.	Humerus	Phalanx
1	5	5
2	3/4	4
3	5/6	5/6
4	1	1
5	3	3
6	3	3
7	2	2
8	3	3
9	3	3
10	4	3/4

the humerus of this species. While it was usually possible to come to a conclusion as to the number of true LAGs in these bones by examining a series of sections, 25 (15%) were not sufficiently clear to allow an age estimate - a proportion comparable to the skeletochronological study of the phalanges of *T. cristatus* by Miaud, Joly & Castanet (1993). Of the remaining 142 phalanges, it was possible to give a precise age estimate in all but eight animals (5.6%). For these eight animals an error margin of 1 LAG was employed (e.g. 4/5 LAG; 5/6 LAG).

The youngest animal encountered in the study pond showed three LAGs, while the oldest animal had seven. (A fuller analysis of the demography of this study population is being prepared.) It is suggested that the method commonly used when referring to fish ages i.e. 3+, 4+ etc. should also be used in skeletochronological investigations of amphibians, as it is normally the number of winters an animal has survived that is counted rather than the true age of the animal.

In conclusion, by modifying standard skeletochronological techniques it has proved possible to determine the age of smooth newts by using the phalanges. In 80% of cases a precise age estimate was reached, in a further 5% an error margin of 1 LAG was necessary; and for 15% of the sample it was not possible to make an estimate. It is envisaged that this adapted technique could be applied to all small-bodied amphibians as it is compatible with mark-recapture and other ecological investigations and it removes the need for large scale sacrifices as required in humerus-based age determination.

Acknowledgements. I would like to thank Leslie Penny, Department of Physiology, Trinity College, Dublin, for technical advice which improved the histological technique described, and Julian Reynolds and Jacques Castanet for their useful comments on an earlier draft of the paper.

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Accepted: 16.10.96

BOOK REVIEWS

Biology of North American Tortoises. Fish and Wildlife Research Technical Report Series 13. R. B. Bury & D. J. Germano (eds.). (1994). United States Department of the Interior, National Biological Survey. Washington, D.C.

The contributed papers making up Bury and Germano (1994) present a thorough overview of the state of conservation biology of the gopher tortoises, the four extant species of the genus *Gopherus* native to North America. *Biology of North American Tortoises* is also of interest because of its attitude toward conservation as a scientific discipline.

The authors and editors of this volume hope to forward the conservation biology of tortoises in a co-operative, non-governmental fashion. The papers have been contributed by the "Guild of North American Tortoise Research Biologists", a loose association formed in 1989. According to the introductory chapter by the editors, the guild was formed to facilitate "rigorous and objective research to provide better knowledge and a solid basis for the effective conservation of tortoises" (p. 3). The guild, made up of university researchers, government biologists and others involved in tortoise research, apparently strives to accomplish research and present the biology of tortoises, without discussion or involvement in government regulations or attempts at conservation advocacy.

The "Guild's" model of conservation biology as a neutral objective factor in conservation decisions is in contrast to more personal, passionate approaches that are sometimes criticized as being less than "rigorous". However, one must wonder whether it is really possible to divorce the purpose of conservation biology from the empirical study. The biological questions of conservation biology are not isolated from the applied issues that are removing animals from habitats and habitats from animals.

Despite the apparent distancing of the "Guild" from government regulation, the authors of the papers in this volume do approach management issues and cast criticism on both published reports and current management practices.

An earlier volume, also edited by Bruce Bury (Bury, 1982), touches on some of the themes of the present work, but has a different orientation and purpose. The chapters in Bury (1982) present a species by species review of the conservation status of each of the four species of tortoises native to North America. The earlier work is also an important reference work, in many ways the predecessor to the I.U.C.N. conservation action plans.

The contributed chapters begin in systematics and move through biogeographic studies to ecology and autecology, culminating in a review of the state of research on North American tortoises by the editors.

While comprising only four living species, the systematics of the genus *Gopherus* reveals that the status of the taxa is surprisingly complex. In addition to the extant *Gopherus agassizii*, *G. berlandieri*, *G. flavomarginalis* and *G. polyphemus*, three recently extinct species (*G. praecedens*, *G. hexagonata* and *G. canyonensis*) and six older extinct species extend *Gopherus* into the Oligocene. Charles Crumly's review of the systematics of the group reveals that while there is evidence that *Gopherus* is monophyletic there is no strong evidence of the phylogenetic positions of the four species and that some taxonomic designations (such as the status of the genus *Xerobates*) are still problematic.

Crumly's review is more than a report on the systematics of a single, small group: it is also a primer on numerical taxonomy which includes appendices explaining the techniques used and presenting a data matrix of the raw character states. This feature is a very valuable introduction to the process of numerical taxonomy, indicating the potential of this volume as a teaching tool for herpetology classes.

The remaining chapters continue the high standards set by Crumly by reviewing the whole-organism biology of the North American tortoises in a logical and complete manner. This book should find space on the bookshelves of every whole-organism herpetologist, as a model of integration and review. As a teaching tool, this volume could form the basis for a complete course in vertebrate conservation biology or herpetology. While some fields are not covered by the present volume - notably missing is a direct treatment of population genetics - this is a well-rounded introduction to our contemporary understanding of a fascinating group of vertebrates.

Bury and Germano (1994) is available from the Publications Unit, U.S. Fish and Wildlife Service, 1849 C Street N. W., Mail Stop 130, Webb Building, Washington, D.C. 20240, U.S.A.

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Reptiles del noroeste, nordeste, y este de la Argentina. Herpetofauna de las selvas subtropicales Puna y Pampas. J. M. Ceí. (1993). 952 pp. Museo Regionale de Scienze Naturali Torino, Monografia XIV. (Cloth).

In 1986, Ceí authored an important monograph, *Reptiles del centro, centro-oeste y sur de la Argentina* that, true to its title, covered the reptilian fauna of southern Argentina (Gudynas, 1988). Citing difficulties such as the great geographical expanse of Argentina and the paucity of data for the subtropical and Puna regions, Ceí (1986) explained that a separate book about the reptiles of northern and eastern Argentina would have to wait. Only seven years later, he completed the current volume summarizing the taxonomy, distribution, and natural history of 211 species and subspecies of reptiles occurring in the northwest, northeast and east of Argentina.

The format, size (25.0 x 17.5 cm), and high-quality binding and paper used in the 1986 book are repeated for this monograph. The text is in Spanish with dichotomous keys in English as well, a thoughtful inclusion that gives the book broader appeal and makes it easier to use for non-Spanish readers. The monograph begins with a long (48 pages) introduction packed with information, but suffering from a lack of focus. Included here are disjointed sections on comparative morphology of hemipenes, chromosomal variation, and a review of biogeography of southern South America as it relates to the reptile fauna. The point is to emphasize the importance of these features in the study of reptiles in Argentina, but the material does not relate clearly to the rest of the book.

The list of taxa included is given after an historical essay about the influence of cladistics on systematics of reptiles, and the importance of classifications based on shared, derived characters. It is not surprising then, that the systematic arrangement presented is based primarily on recent revisions incorporating cladistic approaches (e.g. Cadle, 1988; Estes & Pregill, 1988; Estes *et al.*, 1988; Frost & Etheridge, 1989). Ceí returns repeatedly to these works throughout the text.

Though the book is clearly not intended for use in the field, the subset of keys I tried in the field with fresh specimens worked well enough, especially when coupled with the extensively illustrated descriptions and colour photographs. The bulk of the monograph (537 pages) is comprised of taxon accounts.

Genera and families are diagnosed briefly when introduced, then species and subspecies accounts are organized by synonymy, diagnosis, description, distribution, and a summary of natural history. Recent literature is cited throughout the book, resulting in 519 references that themselves are a gold mine of both peer-reviewed and grey literature on the herpetology of southern South America.

The extensive set of 378 colour photos on 126 colour plates, gang-bound at the rear of the book, aid in the species identifications and add enormously to its appeal. Though there is large variation in their quality, individual photographs show dorsal and ventral views of specimens, different sexes and ages of species, habitats, and close-ups of important diagnostic characters. More than 100 other figures in the text (many with colour photographs and line drawings) illustrate details of anatomy, colour pattern, phylogenies, and even natural history, such as a snake and its prey.

If the book falls short anywhere, it is with the range maps. Localities are plotted for taxa with relatively few known localities, while the ranges of better known species are denoted only by vague lines or unclear shading (e.g. *Chelonoidis*, *Tupinambis*, *Tropidurus*, *Bothrops*). The approximate distributions are just that, and leave the unfortunate impression that much material in museums may have been ignored.

Though an extensive *fe de errata* accompanies the book, many other errors ranging from typographical to omissions in the literature cited can be found without looking very hard. The unnecessarily high frequency of errors is an unfortunate distraction from this otherwise high-quality, well illustrated book.

The 10 appendices were added to keep the book up-to-date while in press. Appendices 2 and 3 include a review of recent *Liolaemus* taxonomy and an additional 4 accounts for *Liolaemus* species not listed at the front of the book. These species accounts are complete with figures in colour and a range map. Despite the attempt to make the book current, the database of Argentine herpetology is growing so fast that a few species descriptions (e.g. *Sibynomorphus lavillai*, *Lystrophis matogrossensis*) published in 1993 (Scrocchi & Cruz, 1993; Scrocchi, *et. al.*, 1993) did not make it into the book.

The poor maps and errors in editing hardly detract from the overall importance of this book. Its utility ranges far beyond the area it was designed to cover, and it is already a primary herpetological reference for countries bordering Argentina. Those whose studies focus on South American herpetofauna will find this book a necessity, and others should appreciate it for the wealth of information it contains.

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A Natural History of Amphibians. Robert C. Stebbins & Nathan W. Cohen. (1995). 316 pp. Princeton University Press, Princeton New Jersey. £19.95 (cloth).

Until fairly recently, most books on amphibian natural history fell into one of two categories. There were regional treatments, which provided detailed accounts of species occurring in just one part of the globe; and there were broader-based but less-authoritative texts whose main selling point was their glossy pictures. All this changed in 1986 with the publication of Duellman and Trueb's monolithic treatise which provided the first up-to-date and comprehensive account of amphibian biology to be published since Noble's *The Biology of the Amphibia* of 1931. Since then Duellman and Trueb has become the definitive starting point for researchers new to the field of amphibian biology. With the publication of *A Natural History of Amphibians* we see not a challenger to Duellman and Trueb, but instead a very different type of book which neatly occupies an unfilled niche. Whereas Duellman and Trueb is very much a scientific reference book, Stebbins and Cohen have produced exactly what the title states: a highly readable but authoritative natural history.

Within its 20 chapters, Stebbins and Cohen cover evolution, internal structure and function, ecology, behaviour and conservation. After introducing the major groups and their basic life histories in chapter 1, the authors go on to provide an overview of environmental physiology and structure and function in the subse-

quent nine chapters. These topics lead logically to a consideration of water and temperature relationships in chapters 11 and 12, while the latter part of the book is devoted more to behavioural and ecological aspects such as responses to predators, home ranges and territories, migrations and reproduction. The last two chapters are probably the most topical as they deal with *Contributions of Amphibians to Human Welfare* and *Declining Amphibians* respectively. Most of the chapters are relatively short which enhances the readability of the book, although some subjects are given more cursory attention than others. No doubt the balance of subjects covered reflects the authors' own interests. Vocalization, for example, is given rather lavish treatment in chapter 10, while competition among larvae (on which a voluminous literature exists) warrants just a single paragraph in the chapter on food habits.

The authors' obvious affection for their subjects comes across throughout the book, and although the text is well-referenced, it is also enlivened by anecdotal observations. Scientific names are provided for all species within the text, and at first mention the geographical occurrence of the species is also given. There are no colour plates, complex graphs or tables of statistics within this book. Instead the text is attractively illustrated by line drawings (most of them by the authors) and well-reproduced black-and-white photographs. This strategy has no doubt enabled the publishers to keep the price of the book well within the budget of the average impoverished student, which is to be welcomed.

In their preface, Stebbins and Cohen state that "Topics discussed in the book apply to amphibians worldwide". This is broadly true, but there is no doubt that the book has a strong North American emphasis. The list of literature cited runs to some 45 pages, but there are some significant European studies which are not mentioned. In the section on mate selection, for example, there is no mention of the extensive work on the European common toad *Bufo bufo*, which has shown that random or non-random mate selection depends on the length of the breeding season - if the season is short there is no time for mate assortment and pairing is random; if the breeding period is longer larger competition between males leads to the displacement of smaller males from females (e.g. Davies & Halliday, 1977; Reading & Clarke, 1983; Hoglund & Robertson, 1987).

The final chapter on declining amphibians is probably the most comprehensive account of this controversial topic published to date. The authors provide over twenty case-histories of species which have suffered declines in recent years, many of them from causes which are unknown. The authors acknowledge that these are "selected examples", but even so the fact that some 15 of the cases cited are species from western North American will do little to convince sceptics that declining amphibians represent a global problem. There are no cases listed from Europe, despite some

well-documented examples from this region (e.g. Semb-Johansson, 1992; Beebe *et al.*, 1990). The authors go on to provide an objective account of possible causes of amphibian declines. Intriguing, if rather speculative, is the section on the “endocrine connection”, which suggests that certain chemicals released into the environment may result in the production of enzymes that degrade hormones. This may have detrimental consequences for amphibian development, growth and reproduction. At the end of their discussion, the authors sensibly call for a more integrated research strategy combining the expertise of toxicologists, wildlife biologists and naturalists to address the problem of amphibian declines. They also list ten topics for future research on toxic chemicals and amphibian declines. I would add an eleventh to their list which is comparative work on other vertebrate taxa: the question of whether amphibians are declining faster than other groups remains unanswered, and only comparative research on other groups will determine whether they really do deserve special attention.

Packed with useful, up-to-date and attractively-presented information, *A Natural History of Amphibians* is a delightful and evocative read. It is authoritative enough to provide a concise and user-friendly introduction to the subject for new researchers, while its lively readable style makes it easily accessible to the amateur herpetologist. I can do no more than reiterate the authors’ stated aim that “This book has been written for a general audience, for the pleasure and edification of anyone, anywhere, interested in learning about the ways of amphibians that grace our planet”.

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A Monograph of the Colubrid Snakes of the Genus Elaphe Fitzinger. Klaus-Dieter Schulz. (1996). 439pp. Koeltz Scientific Books, Koenigstein, Germany. DM 200 (cloth).

Among colubrid snakes, many species of the genus *Elaphe* have been among those which have had the most contact with humans, either through their ability to survive in populated areas in the wild, or due to their amenability to captivity. At the same time, there are many species in this genus which are still only known from a mere handful of specimens. Until now, there has been no thorough review of the biology of the species of this genus. Schulz’s treatise is therefore likely to fill a real gap.

For his monograph, Schulz deliberately chose a wide concept of *Elaphe*, including species allocated by other workers to the genera *Gonyosoma*, *Senticolis* and *Bogertophis*. As he points out, the genus *Elaphe* is almost certainly para- or polyphyletic with or without these taxa, and a thorough review of the phylogeny of all related colubrine snakes would be required to remedy this situation. Recent publications which appeared after Schulz’s book confirm this position (Keogh, 1996; Dowling *et al.*, 1996).

The book is divided into two main parts: a general introduction to the genus *Elaphe* occupies the first 75 pages, and the main part consists of individual accounts of the 40 species of *Elaphe* recognized by the author.

The first part consists of sections on the synonymy of the genus, morphology (including tables of scale counts and excellent drawings of the hemipenes of representative species), fossil record, systematics, distribution (including distribution tables of species by country, zoogeographical region and altitude), natural history (primarily a compilation of natural history observations), colour variation and mutation (including a useful table of the occurrence of ontogenetic pattern and colour mutation), and ratsnakes and man (myths, conservation, and a six page section on captive husbandry).

Given the rather heterogeneous nature of the genus, these sections often come across as rather piecemeal compilations of natural history observations, although this does not stop them from being interesting. The two-page section on systematics consists of a grouping of the species of the genus into informal species groups on the basis of the author’s subjective perceptions of differences in “behaviour, reproductive biology and morphological aspects (pholidosis, body and hemipenis structure)”. Due to this essentially evidence-free approach, this section appears largely redundant.

The individual species accounts present available information on each species under the headings of type, locality, holotype, subspecies, description, scutellation, distribution, natural history, husbandry and literature. Where subspecies are recognized, the information on types and type locality, distribution and description is presented separately for each subspecies. A full syn-

onymy of each species and subspecies is also provided. Each species or subspecies section is accompanied by excellent line drawings of the side and top of the head. Further fine line drawings illustrate the body patterns of many species, including geographic variants and subspecies. The distribution of each species is very generously illustrated on one or several full-page maps. In the case of all but the most common species, individual locality records are marked as dots on the maps. Unfortunately, Schulz does not provide the sources for all locality records - this would have been a tremendous asset for other workers, as well as allowing these locality records to be checked in the future. Specific taxonomic problems affecting some species are discussed in some detail, often with further maps or other relevant illustrations. The length of each species account varies from two (*E. perlacea*) to 14 pages (*E. obsoleta*), depending on the amount of information available and the number of recognized subspecies.

Two appendices list the vernacular names of the various *Elaphe* species in 39 languages (only species found locally for most languages) and the museum material examined by the author (unfortunately without locality information). The bibliography constitutes a major asset of this book: 2810 references are numbered in alphabetical order. For each species, the numbers of the relevant references are listed after the rest of the account.

The book is copiously illustrated with 58 high-quality colour plates, generally with eight photographs per plate. Forty-nine plates show live specimens of the various species, six illustrate aspects of the natural history of the genus and its interactions with man, and three show preserved specimens. The rationale for the inclusion of some of the photographs of preserved specimens is unclear, as the same taxa were already illustrated with perfectly good shots of live specimens. The author has done an admirable job in assembling colour photographs of live specimens of all but three of the species of the genus (*E. cantoris*, *E. leonardi* and *E. perlacea*, which are illustrated as paintings and preserved specimens). For most species, the photographs illustrate a wide selection of patterns, including geo-

graphic variants and juvenile patterns. Many of the taxa or pattern morphs have never been illustrated before, at least to the knowledge of this reviewer. Practically all the photographs are generally excellent portraits of coiled snakes, which are exactly what are needed for simply illustrating the appearance of the animals. From an artistic point of view, a greater variety of poses, with perhaps more larger photographs of particularly striking animals, might have been desirable.

The text is generally very readable. However, the translation from German has left a considerable number of scars in the shape of poor punctuation, grammar or syntax. The quality of manufacture appears excellent, and the very generous amount of space devoted to illustrations, photographs and maps make this tome a pleasure to consult.

Despite a number of smaller problems, this is a book that should be of considerable use for a variety of readers. Although this is not primarily a book about husbandry, it contains plenty of useful information for herpetoculturists, and should be warmly recommended to those interested in increasing their knowledge about their animals. Professional herpetologists will benefit from much of the other information contained in the species descriptions, and the enormous bibliography will be an asset for anyone seeking to further broaden their knowledge of the genus. The achievement of the author is thus considerable, and appears even greater in the light of the fact that he is an amateur and not a professional herpetologist.

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