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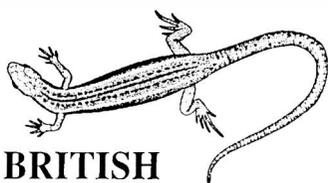
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## THE GENUS *ATRACTUS* (SERPENTES: COLUBRIDAE) IN NORTH-EASTERN ARGENTINA

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We present a revision of *Atractus* in north-eastern Argentina based on the examination of newly collected specimens and most of the material available in Argentinean museums. Four species are reported: *A. snethlageae*, *A. paraguayensis*, *A. reticulatus* and *A. taeniatus*. *Atractus badius* was erroneously cited as occurring in Argentina based on a specimen from Las Palmas, Chaco province which is reassigned to *A. snethlageae*. This record represents a considerable southern extension of the known range of the species. *Atractus paraguayensis* is redescribed based on three new specimens. This species was previously known only from the holotype reported from "Paraguay" without definite locality data. Adult and juvenile colour patterns in life are described. The validity of some diagnostic characters is discussed, and new diagnostic characters are given for *A. reticulatus* and *A. paraguayensis*. All species examined showed noteworthy variation in colour pattern. Sexual dimorphism is reported in all species. The distributional patterns and phytogeographic areas occupied by each species in Argentina are discussed. We also characterize morphological variation for each and provide a key for the Argentinean species.

*Key words:* *Atractus*, snake, classification, distribution, taxonomy

### INTRODUCTION

*Atractus* is a genus of fossorial snakes widely distributed in South America from Panama to northern Argentina. The genus contains approximately 80 species, most having restricted distributions (Savage, 1960; Peters & Orejas Miranda, 1970; Hoogmoed, 1980; Vanzolini, 1986; Scrocchi & Cei, 1991; Fernandes & Puerto, 1993; Fernandes, 1995a,b). The taxonomic status of most species is confused (Fernandes & Puerto, 1993), and museum specimens are rare (Fernandes, 1995a).

Serié (1915) cited one specimen of *Atractus badius* from Las Palmas, Chaco province, the first record of the genus in Argentina. Although a revision of all South American material referred to *A. badius* was suggested by Hoogmoed (1980), this record was repeated in all subsequent checklists of Argentinean snakes (Serié, 1921, 1936; Abalos & Mischis, 1975; Williams & Francini, 1991; Cei, 1993). Recently, *A. taeniatus* (Griffin, 1916) was revalidated by Williams & Gudynas (1991) based on six specimens from Entre Ríos and Misiones provinces in north-eastern Argentina. Alvarez, Rey & Cei (1992) described *Atractus reticulatus scrocchii* from Corrientes province, Argentina and Rio Grande do Sul state, Brazil. Thereafter the taxon was synonymized with *A. reticulatus* by Fernandes (1995b). Also, this author elevated *A. reticulatus paraguayensis* to specific status and distin-

guished it from *A. reticulatus* using coloration pattern and high ventral scale counts. *Atractus paraguayensis* is known only from the holotype, a specimen from "Paraguay" without definite locality data (Fernandes, 1995b).

A recent survey of Argentinean museums and the identification of newly collected material from north-eastern Argentina and southern Paraguay uncovered three new specimens of *Atractus paraguayensis*. Herein, these specimens are described, the identity of Serié's *A. badius* is reconsidered, and new distributional and morphological data for other Argentinean *Atractus* are discussed

### MATERIALS AND METHODS

Most specimens of *Atractus* in Argentinean Museums were examined, and new specimens were collected in north-eastern Argentina and border areas of southern Paraguay (Appendix 1). Standard methods for the study of ophidian taxonomy were used. Terminology for *Atractus* cephalic shields is that of Savage (1960). Ventrals were counted using Dowling's (1951) technique. Terminal spines were not included in subcaudal counts. Morphometric measurements were recorded with a dial caliper to the nearest 0.1 mm for the cephalic distances and with a ruler to the nearest millimeter for body lengths. Total length was measured from the tip of the snout to the tip of the tail, snout-vent length from the tip of the snout to the posterior edge of the anal plate, and head length from the posterior extremity of the jaw to the tip of the snout. The following abbreviations were used: TL/TOL: tail length/total length; HL/TOL: head length/total length; TL/SVL: tail length/snout-vent length (all given as percentages).

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## RESULTS

Four species of *Atractus* inhabit north-eastern Argentina: *A. snethlageae*, *A. paraguayensis*, *A. reticulatus* and *A. taeniatus*. All are small snakes with the following characteristics: head small (3.04-7.17% of total length, Table 1), not distinct from body; body subcylindrical; tail short (8-14% of total length, Table 1); eyes small with round pupils; dorsals smooth, in 15 or 17 rows without reduction; loreal present, entering orbit, loreal at least twice as long as postnasal; preocular absent; nostril bordered by two nasals; temporals generally 1+2; frontal shorter than parietals; rostral much less than half as large as prefrontal; inter-nasal much less than half as large as prefrontal; prefrontal at least one-and-a-half times as broad (measured along the margin of contact with the internasal) as long (measured along the median suture); prefrontals entering orbit; supraoculars small; single pair of chin shields separated from mental; anal plate entire; subcaudals divided; maxillary teeth 6-9, posterior maxillary teeth distinctly reduced.

## SPECIES ACCOUNTS

*ATRACTUS SNETHLAGEAE* CUNHA & NASCIMENTO

1983. *Atractus flammigerus snethlageae* Cunha & Nascimento, Bol. Mus. Par. E. Goeldi (Zool) (123): 19. *Type locality*: Colônia Nova, Gurupi river, road BR-316, 10 km before Gurupi, Pará, Brazil.

1986. *Atractus snethlageae* Vanzolini, Relatório Pesquisa N° 1, CNPq, Assesoria Edit., Brasília, : 23-25.

1990. *Atractus snethlageae* Zimmerman & Rodrigues, Yale Univ. Press, Mew Haven, : 4.

1993. *Atractus snethlageae* da Silva, Herpetol. Nat. Hist., 1: 53.

The specimen cited by Serié (1915) is reassigned to *A. snethlageae* (Cunha & Nascimento, 1983). *Atractus badius* is excluded from Argentina.

*Description*. Known in Argentina only from Serié's specimen (MACN 8764), a female collected in Las Palmas, Chaco province. *Atractus snethlageae* is a small snake (Table 1); temporals 2+1+2; seven supralabials, third and fourth entering eye; eight infralabials, first to fourth in contact with single pair of chinshields; dorsal scales smooth lacking apical pits, in 17-17-17 rows; ventrals 163; subcaudals divided, 23; anal plate entire.

Seven maxillary teeth are curved backward, the posterior four are distinctly smaller.

*Coloration*. Parietals scale whitish brown and irregularly speckled with minute brown dots; remaining dorsal and lateral surfaces of head brown; whitish band across occiput from posterior parietal edge to first nuchal scale rows and extending laterally to cover posterior temporals and two last supralabials; single black nuchal band followed by two lateral cream spots with

black margins; dorsum brown with transverse cream colored bands, each edged in black; cream colored bands two to three scales long and beginning on second row of dorsals, continuous or alternating across dorsal midline; 27/28 bands on body, four on tail; first two rows of dorsals, speckled with brown, whitish and black irregular alternating marks (Fig. 1); lower parts of infralabials and antero-lateral part of chinshields with black spots; belly yellowish anteriorly; central black or brown spots forming interrupted mid-ventral stripe extending to ventral 18; posterior to ventral 18, black spots irregularly distributed on belly, not arranged linearly; anal plate and subcaudals brownish with minute brown dots.

*Remarks*. Except for numbers of ventrals and maxillary teeth, the characteristics of the Argentinean specimen fit the diagnosis of *Atractus flammigerus snethlageae* provided by Cunha & Nascimento (1983). However, these differences are slight. Serié's specimen has 7 versus 6 maxillary teeth and 163 versus maximum of 160 ventrals observed in Amazonian specimens (Cunha & Nascimento, 1983, 1993). Other species we examined have 6 to 9 maxillary teeth and we suspect that *A. snethlageae* exhibits a similar range of teeth counts.

*A. flammigerus* is distinguished from *A. snethlageae* by fewer ventrals (145-150 in females of *A. flammigerus* versus 151-163 in females of *A. snethlageae*; 138-149 in males of *A. flammigerus* versus 137-155 in males of *A. snethlageae*), by keeled dorsal scales in the posterior part of the body in *A. flammigerus* versus smooth dorsal scales in *A. snethlageae*, and by the ventral color patterns: two rows of spots forming interrupted ventrolateral stripes in *A. flammigerus*, versus central spots forming a mid-ventral stripe in *A. snethlageae*. Both ventral patterns may be variable (Hoogmoed, 1980; Cunha & Nascimento, 1983), and may be of little diagnostic value. It is easily distinguishable from the other examined species by the coloration patterns and by the 17 dorsal rows (Table 2).

*Distribution*. The species *A. snethlageae* is known from central Amazonia in eastern Pará, Maranhão, Amapá, Manaus and Rondônia (Vanzolini, 1986; Zimmerman & Rodrigues, 1990; Cunha & Nascimento, 1983, 1993; da Silva, 1993). Hoogmoed (1982) considered *A. flammigerus sensu lato* to be a wide-ranging Amazonian species. The Argentinean specimen from Las Palmas, Chaco province, in the alluvial valley of the Paraguay River (Fig. 2), extends the known range of the species by more than 1000 km. Nevertheless, other Amazonian and wide-ranging tropical species have been found in the Paraguay and Paraná rivers valleys, such as *Imantodes cenchoa* (from the same locality, Serié, 1915), *Pseudoeryx plicatilis* (Giraudo, 1999), *Hydrops triangularis* (from a more southerly locality on the bank of the Paraná river, Williams & Couturier,

1984). Some authors have reported Amazonian floral elements from the gallery forests of these rivers valleys (Prado, 1993; Lewis *et al.*, 1994).

*ATRACTUS PARAGUAYENSIS* WERNER

1924. *Atractus paraguayensis* Werner. Sitz. Akad. Wiss. Wien., 133 (1): 40. *Type locality*: Paraguay.

1930. *Atractus reticulatus paraguayensis* Amaral. Mem. Inst. Butantan 4 (1929):27.

1995. *Atractus paraguayensis* Fernandes. Comun. Mus. Cienc. PUCRS, sér. zool., 8:38.

Recently, three new specimens of *A. paraguayensis* were collected and deposited in Argentinean museums (Appendix 1). The species was only known until now from the holotype specimen from "Paraguay", without definite locality.

*Description.* Based on three new specimens and data for the holotype provided by Fernandes (1995b). *Atractus paraguayensis* is a small snake. The percentage TL/TOL and TL/SVL of males are bigger than females (Table 1). Ventrals 157-166 ( $n=3$ ,

mean=162.8, SD=4.03) in females, and 163 in the male; subcaudals divided, 22-24 ( $n=3$ , mean=23, SD=1) in females, 30 in the male, with a tendency to sexual dimorphism in this character. All specimens have 1+2 temporals; seven supralabials, the third and fourth entering the eye; seven infralabials (six on the left side of FML 6238), the first to the fourth in contact with a single pair of chin-shields; dorsal scales smooth, lacking apical pits, and in 15-15-15 rows; one preocular; two postoculars; anal plate entire; and 7 maxillary teeth.

*Coloration.* The general coloration pattern of the three new specimens (one adult and two juveniles) coincides, with Fernandes's (1995b) description, except in some minor details (Fig. 1). The two juveniles have a distinctive white cephalic collar across the parietals and occipital that is faded in adult specimens. Similar collars have been observed in juveniles of other *Atractus* such as *A. reticulatus* and *A. taeniatus* (Fernandes, 1995b; and pers. obs.). The dark nuchal band is unbroken in all new specimens, therefore, the diagnostic character "dark nuchal collar interrupted" proposed by

TABLE 1. Morphometric characteristics of the *Atractus* species examined. The data is presented as mean±SD over range in parentheses and sample size ( $n$ ). New diagnostic characters between *A. paraguayensis* and *A. reticulatus* are emboldened. All measurements in mm. TL/TOL: tail length/total length; HL/TOL: head length/total length; TL/SVL: tail length/snout-vent length.

	<i>A. snethlageae</i>	<i>A. paraguayensis</i>		<i>A. reticulatus</i>		<i>A. taeniatus</i>	
	Female	Female	Male	Female	Male	Female	Male
TOL (mm)	325 $n=1$	281±103.6 (163-356) $n=3$	149 $n=1$	308.1±106 (111-410) $n=8$	265.7±52 (211-353) $n=1$	309.6±113.3 (149-450) $n=8$	288±65.37 (227-357) $n=3$
TL (mm)	27 $n=1$	24.3±9.29 (14-32) $n=3$	17 $n=1$	30.04±5.87 (12-39) $n=7$	33.16±5.87 (25.6-44) $n=7$	28±9.3 (14-45) $n=10$	34.3±8.02 (26-42) $n=3$
SVL (mm)	298 $n=1$	257±94.43 (149-324) $n=3$	132 $n=1$	282.6±89.9 (99-372) $n=8$	232.6±46.6 (181.5-309) $n=7$	281.6±104.6 (135-415) $n=10$	253.7±57.5 (201-315) $n=3$
HL (mm)	11.8 $n=1$	5.9±1.9 (6.3-8.0) $n=2$	8 $n=1$	10.62±1.68 (7.1-13) $n=8$	10.84±0.69 (10.12-12) $n=6$	13.5±3.8 (8.4-18) $n=7$	11.5 $n=7$
TL/TOL (%)	8.3 $n=1$	<b>8.63±0.34</b> <b>(8.3-9)</b> $n=3$	11.4 $n=1$	<b>9.87±0.62</b> <b>(9.2-10.8)</b> $n=7$	12.55±0.96 (11.4-14) $n=7$	9.2±1.1 (7.8-10.9) $n=10$	11.9±0.5 (11.5-12.5) $n=3$
TL/SVL (%)	9.06 $n=1$	<b>9.4±0.41</b> <b>(9.1-9.9)</b> $n=3$	<b>12.88</b> $n=1$	<b>10.96±0.76</b> <b>(10-12)</b> $n=7$	<b>14.36±1.26</b> <b>(13-16)</b> $n=7$	10.2±1.3 (8.4-2.2) $n=10$	13.5±0.7 (12.9-14.3) $n=3$
HL/TOL (%)	3.9 $n=1$	4.45±1.54 (3.4-5.5) $n=2$	6.06 $n=1$	4.11±1.33 (3.04-7.17) $n=8$	4.9±0.8 (3.88-6.11) $n=6$	4.7±0.7 (3.9-5.7) $n=7$	4.7 $n=1$

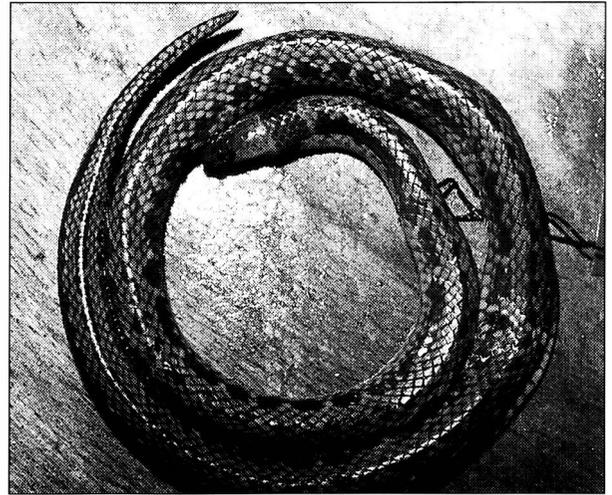


FIG. 1. *Atractus snethlageae* (MACN 8764) (left) and *A. paraguayensis* (FML 6221) (right).

Fernandes (1995b) cannot be used for this species' diagnosis. The dorsum is reddish-brown in live specimens (reddish-pink in *A. reticulatus*, Fernandes, 1995b and pers. obs.). The head is blackish, the parietal-occipital collar whitish-brown and irregularly speckled with brown dots. The collar extends to the three last supralabials, that are whitish. The nasals, preoculars and the first four supralabials are reddish-orange with minute brown dots. The parietal-occipital collar is followed by a dark nuchal band three to five vertebral scales long and extending laterally to the second dorsal row. Dorso-lateral series of dark spots, forming a distinguishable longitudinal stripe, and in the vertebral region, forming a narrow and interrupted stripe that extends to two contiguous paravertebral rows. The lateral and vertebral stripes are more regular and continuous on the tail. The lateral stripes extend from three to five scale rows; below the first two scale rows the background colour is reddish-orange. Dorsal scales are darkly-bordered. The belly is whitish-orange.

*Remarks.* Ventral numbers of female *A. paraguayensis* (157-166, mean=162.8 SD=4.03 n=3) overlapped those of female of *A. reticulatus* (147-164, mean=158.8 SD=6.31 n=6). The only male specimen of *A. paraguayensis* (163) had thirteen more ventrals than the highest number recorded for Argentinean *A. reticulatus* (150). Although useful in distinguishing between males, ventral number may not be a useful diagnostic characteristic of females. On the other hand, ratios of tail length to total length and snout-vent length for *A. paraguayensis* and *A. reticulatus* did not overlap in either sex (Table 1).

New material of both species supports Fernandes' (1995b) assertion that *A. paraguayensis* and *A. reticulatus* are distinct and valid species. Although similar, the two species differ from one another in colour patterns, meristic and morphometric characteristics (Tables 1 and 2). Their known distributions are parapatric; *A. reticulatus* occurs primarily in forested habitats of the "Paranaense" phytogeographic area, *A.*

TABLE 2. Differential characters among examined *Atractus* species.

Characters	<i>A. snethlageae</i>	<i>A. paraguayensis</i>	<i>A. reticulatus</i>	<i>A. taeniatus</i>
No. dorsal scale rows	17	15	15	15
Ventrals range				
Female	151-163	157-166	147-164	150-161
Male	137-155	163	141-150	141-146
Subcaudals range				
Female	22-25	22-24	23-27	23-26
Male	31-35	30	27-29	27-33
Dorsal coloration pattern	Brown with transverse cream bands	Two lateral and a narrow vertebral longitudinal stripe	Reticulate, without longitudinal stripe	Only a broad vertebral longitudinal stripe
Ventral coloration pattern	With dark spots	Immaculate	Immaculate	Immaculate

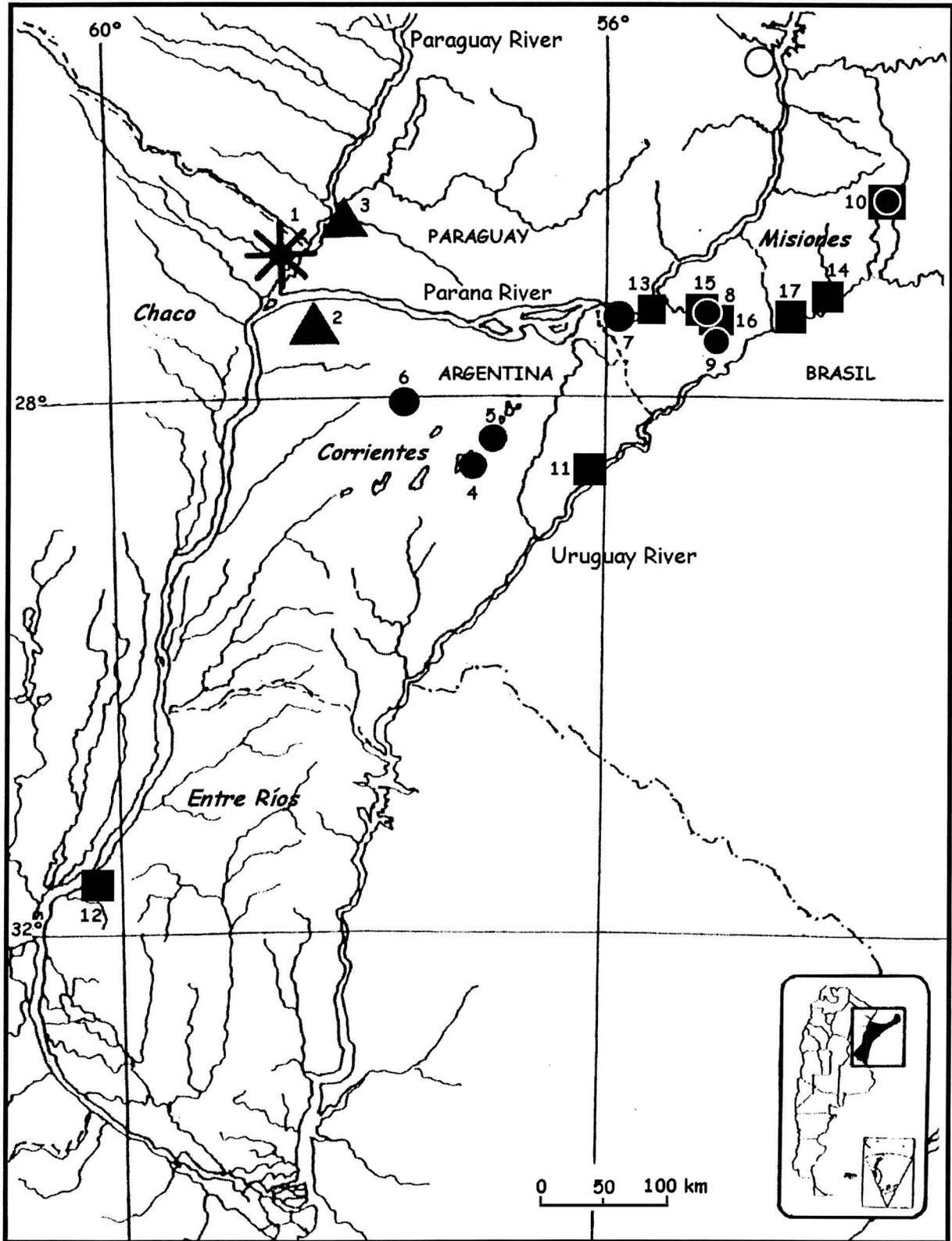


FIG. 2. Distribution of *Atractus* species in north-eastern Argentina and southern Paraguay: *A. snethlageae* (asterisks), *A. reticulatus* (circles), *A. paraguayensis* (triangles) and *A. taeniatus* (squares). Numbers reference localities listed in Appendix 1. Open circles are literature records (Alvarez *et al.*, 1992) for specimens not examined by us.

*paraguayensis* in open formations of the "Chaco" phytogeographic area.

The new specimens have two postoculars, and confirm Fernandes' (1995b) suggestion concerning the invalidity of the diagnosis character "One postocular" used for Amaral (1929) and Peters & Orejas Miranda (1970).

*Distribution.* The first two precise localities for *A. paraguayensis* are Pilar, Ñeembucú department, southern Paraguay, and Palmar Grande, Corrientes Province, north-eastern Argentina (Fig. 2). The two localities are in the transitional communities between Chacoan and Paranaense regions characterized by a complex mosaic of wetlands, grassland, palms, gallery rainforest and *Schinopsis balansae* forest (Prado, 1993; Carnevali, 1994).

#### *TRACTUS RETICULATUS* (BOULENGER)

1885. *Geophis reticulatus* Boulenger, Ann. Mag. Nat. Hist., 5 (16): 87. *Type locality:* San Lorenzo, Rio Grande do Sul, Brasil.

1992. *Atractus reticulatus scrocchii* Alvarez, Rey & Cei. Boll. Mus. reg. Sci. nat. Torino, 10 (2): 251. *Type locality:* San Miguel, Corrientes, Argentina.

*Description.* Based on 11 Argentinean and 4 Brazilian specimens (Appendix 1). *Atractus reticulatus* is a small snake. The females reach a greater total length. The males' TL/TOL and TL/SVL range and mean are larger than those of the females (Table 1). Argentinean populations have 147-164 ( $n=6$ , mean=158.8, SD=6.31) ventrals in females, and 141-150 ( $n=5$ , mean=144.4, SD=3.78) in males. The females' range and mean are larger than those of Brazilian populations (149-163, mean=156.98, Fernandes, 1995b); 23-27 paired subcaudals in females ( $n=4$ , mean=24.5, SD=1.91) and 27-29 in males ( $n=5$ , mean=27.6, SD=0.89). All specimens have 1+2 temporals; seven supralabials (six on

the right side for FML 6240), third and fourth entering the eye ( $n=15$ ); seven infralabials (eight on the left side for FML 1814-3), first to fourth in contact with a single pair of chin-shields ( $n=15$ ); dorsal scales smooth lacking apical pits, in 15-15-15 rows, one preocular and two postocular scales; anal plate entire; and 6-9 maxillary teeth.

*Coloration.* Based on 11 Argentinean specimens. The typical coloration pattern of Argentinean populations (Fig. 3) is head dark brown on rostral, internasals, prefrontals and frontals. Generally with parietal-occipital collar whitish-brown irregularly speckled with brown dots, extending to the last three supralabials, that are whitish. Nasals, preoculars and the first four supralabials more narrow with minute brown dots. The parietal-occipital collar is followed by the dark nuchal band, and together they extend to three vertebral scales (generally narrower than in *A. paraguayensis*). Dorsum reddish-pink in live specimens and greyish in preserved specimens, with a regular reticulate dark brown pattern formed by the dark edges of dorsal scales. This pattern is less evident on the first two rows and is darker close to the vertebral scales, occasionally forming a very fine vertebral stripe (FML 2690). The belly and the first dorsal scale row are creamish. A distinctive white nuchal collar is found in juveniles. The extent of the parietal occipital collar is variable, from the anterior parietal to the first two or three dorsal scales, and is not present in FML 2666. Some Brazilian populations showed differences in coloration patterns that were commented on by Fernandes (1995b). Colour pattern in *A. reticulatus* apparently lacks taxonomic significance because of its clinal variation (Fernandes, 1995b).

One specimen, CUNAM 121, was leucistic. Dorsally and ventrally, this specimen was uniformly whitish pink (creamish white in preservative, Fig. 3), and it

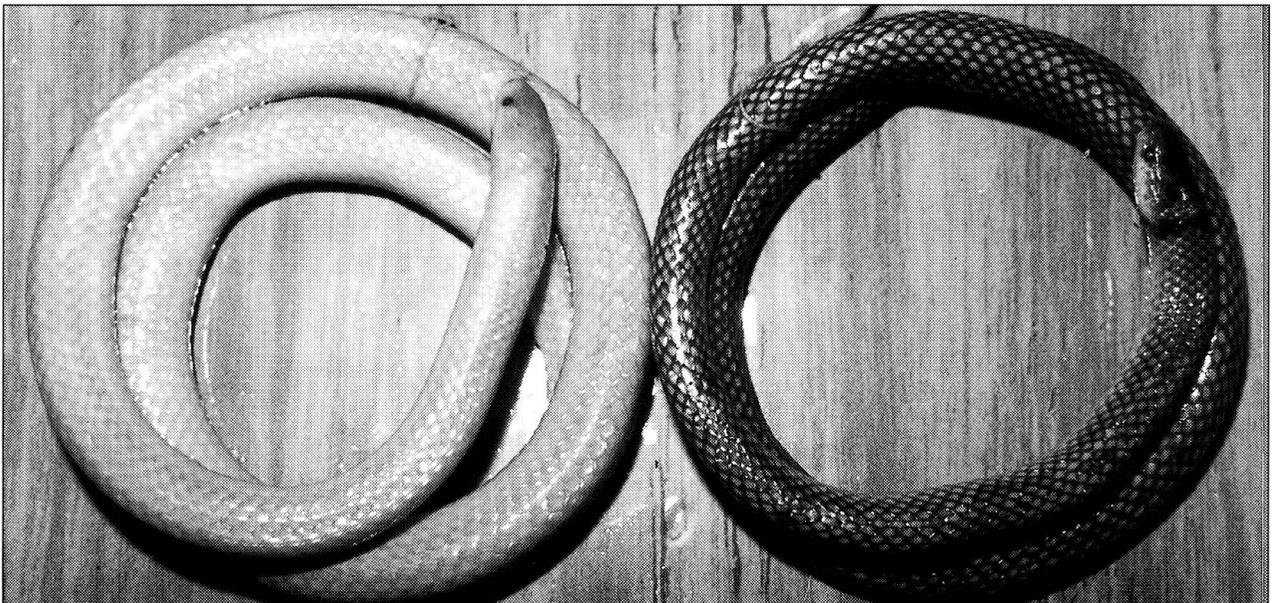


FIG. 3. A leucistic specimen of *Atractus reticulatus* (CUNAM 121) (left) compared to a specimen with the typical Argentinean pattern (CUNAM 140) (right).

lacked the dark cephalic, nuchal, and reticulate patterns of normal individuals.

*Distribution:* the distribution of *Atractus reticulatus* extends from the city of São Paulo, São Paulo south to São Lourenço, Rio Grande do Sul, Brazil and west to San Miguel, Corrientes, Argentina (Fernandes, 1995 b). This species has also been reported from Puerto Bertoni, Alto Paraná, Paraguay (Bertoni, 1939; Alvarez *et al.*, 1992). In Argentina, *A. reticulatus* was reported from north-eastern Corrientes and Misiones (Fig. 2, Appendix 1) in the Paranaense phytogeographic area. The species occurs in subtropical rainforest, Araucaria forest and savannas, as well as in transitional and semi-urban habitats.

*Remarks:* According to Fernandes (1995b) and in contrast to Alvarez *et al.* (1992), the Argentinean populations do not show substantive differences in coloration with respect to the holotype as described and illustrated by Boulenger (1885, 1894). *A. reticulatus* showed sexual dimorphism in number of ventrals and subcaudals, and in the ratio of tail length to total length (Figs. 4 and 5, Tables 1 and 2). Alvarez *et al.* (1992) concluded that Argentinean and Brazilian specimens they examined were not sexually dimorphic; however, the paratype UNNEC 257 was wrongly sexed as female.

*ATRACTUS TAENIATUS* GRIFFIN

1916. Griffin. Mem. Carnegie Mus., 7 (3): 173-174. *Type locality:* Santa Cruz, Bolivia.

*Description.* Based on 11 Argentinean specimens, and data for the holotype and other Bolivian specimens provided by Griffin (1916), McCoy (1971) and Williams & Gudynas (1991). The longest species of *Atractus* in Argentina. Females reach a greater total

length than males (Table 1). The males have a relatively longer tail than females with respect to the total length. Sexual dimorphism is evident in ventral and subcaudal counts: 150-161 ( $n=10$ , mean=153.5, SD=3.37) ventrals in females, 141-146 in males ( $n=3$ , mean=144.3, SD=2.89); 23-26 paired subcaudals ( $n=10$ , mean=24.2, SD=0.9) in females, 27-33 in males ( $n=3$ , mean=30, SD=3). All specimens have 1+2 temporals; seven supralabials, the third and the fourth entering the eye ( $n=10$ ); seven infralabials, the first to the fourth in contact with a single pair of chin-shields ( $n=10$ ); dorsal scales smooth, lacking apical pits, and in 15-15-15 rows; one preocular; two postoculars ( $n=10$ ); anal plate entire; 8 maxillary teeth.

*Coloration.* Based on 11 Argentinean specimens. The head is blackish with parietal occipital collar whitish-brown irregularly speckled with brown dots. There is a distinctive white collar (parietal occipital) in juveniles that is faded in adults. A dark nuchal band extends over two vertebral scales dorsally, and laterally extends to the corner of the mouth. A dark vertebral stripe extends to two contiguous paravertebral rows. This is regular or irregular, and has dark lateral projections in some specimens (Fig. 4). Laterally, there are very variable irregular dark spots on the dorsal scales. The first scale rows have the same colour as the belly, i.e. whitish-cream. In life the general coloration is reddish-pink and similar to *A. reticulatus*. The tail has the same pattern as the body.

*Distribution.* From south-eastern Bolivia in Santa Cruz (Griffin, 1916) and Buena Vista (McCoy, 1971), Santa Cruz department, eastward to several localities in Paraná state, Brazil (Moura Leite, Morato & Bérnils, 1996) and north-eastern Argentina - Misiones, Corrientes and Entre Ríos provinces (Williams & Gudynas, 1991; Cei, 1993; Rey & Lions, 1997; pers.

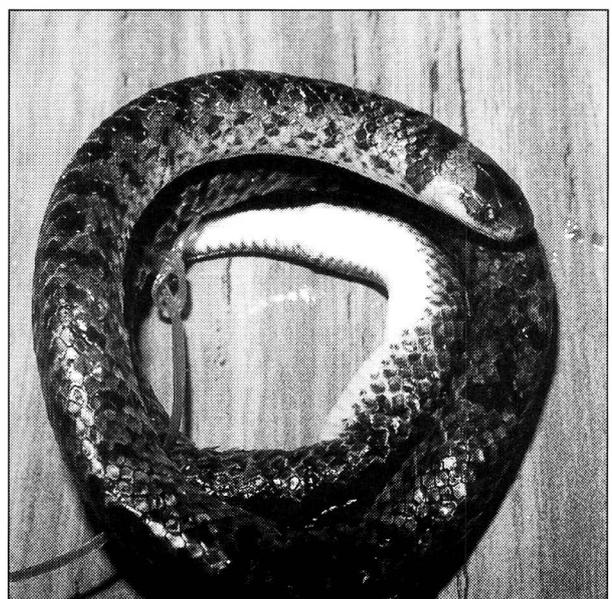
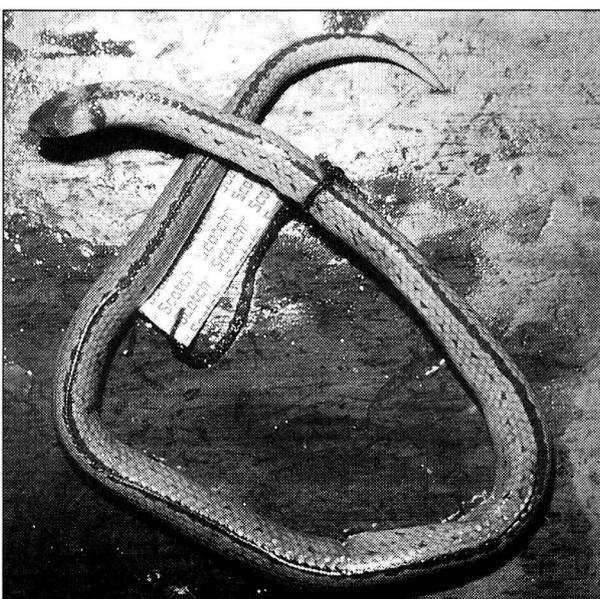


FIG. 4. A specimen of *A. taeniatus* with a regular vertebral stripe (FML 6220) (left) and a specimen with an irregular vertebral stripe (CUNAM 420) (right).

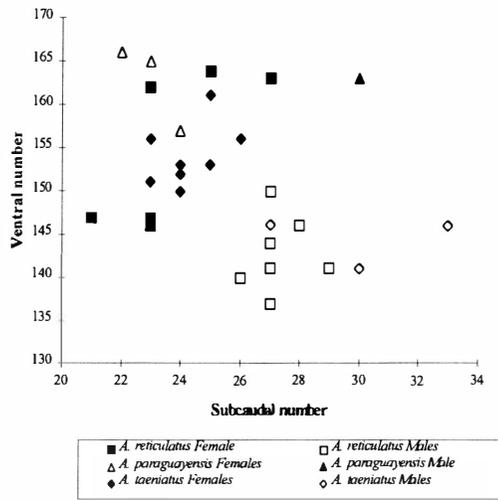


FIG. 5. Scatter plot of ventral and subcaudal number for males and females of *Atractus paraguayensis*, *A. reticulatus* and *A. taeniatus*.

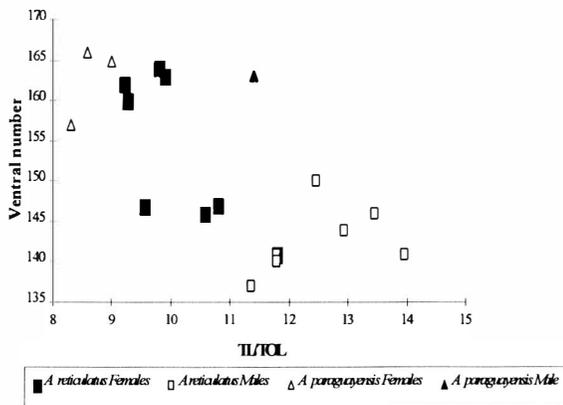


FIG. 6. Scatter plot of ventral number and tail length/total length (TL/TOL) for males and females of *A. paraguayensis* and *A. reticulatus*.

obs; Fig. 2). In Argentina the species was recorded from the Paranaense subtropical rainforest and Araucaria forest in Corrientes and Misiones provinces, and in gallery rainforest in Entre Ríos province. The geographic distribution of *A. taeniatus* coincides with the “Misiones” nucleus proposed by Prado & Gibbs (1993).

*A. taeniatus* is sympatric with *A. reticulatus* in Argentina, and the two species have been collected in the same locality.

Da Silva (1993) mentioned two specimens from Rondonia, Brazil as *Atractus* cf. *taeniatus*, but we could not examine them to compare with Argentinean populations.

**Remarks.** Lema (1994) pointed out that the juvenile mentioned by Williams & Gudynas (1991) is a new species, and that *A. taeniatus* therefore contains at least two new species, although no supporting data are presented in this regard. The Argentinean populations showed a remarkable polymorphism in the dorsal col-

oration, this should be considered in future revisions of these complex taxa.

The new data for ventral scale counts obtained by us (Table 2), are not consistent with the statement of Williams & Gudynas (1991) on the lack of sexual dimorphism in this character.

DISCUSSION

All species showed noteworthy intraspecific variation in coloration pattern, although each could also be diagnosed by characteristics of coloration and lepidosis (Figs. 1, 3 and 4, Tables 1 and 2).

*Atractus paraguayensis*, *A. reticulatus* and *A. taeniatus* showed sexual dimorphism in the number of ventrals and subcaudals, and in the ratio of tail length to both total length and snout-vent length (Fig. 5-6), too reported in the two first characters for *A. snethlageae* (Cunha and Nascimento, 1993).

*Atractus paraguayensis* has a parapatric distribution with respect to *A. reticulatus* and *A. taeniatus*, inhabiting more xeric western regions (transitional formations between Chacoan and Paranaense phytogeographic regions (Prado, 1994; Carnevali, 1994) (Fig. 2). *A. snethlageae* is known from only one record in gallery rainforest in the alluvial valley of the Paraguay river (Fig. 2), where other Amazonian and wide-ranging tropical species such as *Imantodes cenchoa*, *Pseudoeryx plicatilis* and *Hydrops triangularis* have been found. The distributional pattern of *A. reticulatus* coincides with the “Misiones” nucleus proposed by Prado & Gibbs (1993) for dry, seasonal South American forest.

The new specimens of *A. paraguayensis* confirm the specific status proposed by Fernandes (1995b).

KEY FOR THE SPECIES OF *ATRACTUS* FROM ARGENTINA

- 1. 15 dorsal scales rows; venter immaculate ..... 2
- 17 dorsal scales rows; venter with dark spots..... 4
- 2. Dorsal pattern with dark longitudinal stripes, regular or irregular, and sometimes with lateral projections.....3
- Reticulate dorsal pattern, without dark longitudinal stripes .....*A. reticulatus*
- 3. Dorsal pattern with two longitudinal lateral stripes, and a narrow, interrupted vertebral stripe ..... *A. paraguayensis*
- Dorsal pattern with a single, continuous broad vertebral longitudinal stripe, sometimes with lateral projections.....*A. taeniatus*
- 4. Dorsal pattern brown with transverse cream colored bands, each edged in black; venter yellowish, anteriorly with central black spots forming an interrupted mid-ventral stripe, and posteriorly with black spots irregularly distributed.....*A. snethlageae*
- Dorsal pattern creamish or reddish with symmetrical black blotches, alternating or fused into bands on the vertebral line; venter with regular transverse bars of black and cream.....*A. canedii*

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#### APPENDIX 1

*Specimens examined* (Numbers before localities are references for Fig. 2): Museum abbreviations are: CENAI: Centro Nacional de Investigaciones Iológicas collection, now in the MACN, Buenos Aires; CUNAM: Universidad Nacional de Misiones, Posadas, Misiones. FML: Fundación Miguel Lillo, Tucumán; MACN: Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires; MLP: Museo de La Plata, La Plata, Buenos Aires; and UNNEC: Universidad Nacional del Nordeste, Corrientes.

*Atractus snethlageae*. ARGENTINA: Chaco province: Bermejo Department: 1. Las Palmas MACN 8764.

*Atractus paraguayensis*. ARGENTINA: Corrientes province: San Luis del Palmar department: 2. Campo Grande UNNEC 82; PARAGUAY: Ñeembucú Department: 3. Pilar FML 6221 and 6238.

*Atractus reticulatus*. ARGENTINA: Corrientes province: General San Martín Department: 4. Colonia Carlos Pellegrini MACN 24452; 5. Ea. San Solano near from Carlos Pellegrini UNNEC 517; San Miguel Department: 6. San Miguel UNNEC 256 and 257 (the holotype and paratype from *A. reticulatus* respectively); Misiones Province: Capital department: 7. San Isidro quarter Posadas city FML 6240; 7. Posadas city CUNAM 121, 140 and 284; Candelaria department: 8. Ea. Santa Cecilia, 3 km eastern of Bompland city FML 6222; Leandro N. Alem Department: 9. Leandro N. Alem city CENAI 1556; San Pedro department: 10. 30 km to eastern of Cruce Caballero FML 2690; BRAZIL: Paraná state: Curitiba FML 6239, 1814-1, 1814-2 and 1814-3.

*Atractus taeniatus*. ARGENTINA: Corrientes province: Santo Tomé department: 11. Santo Tomé city, UNNEC 4979; Entre Rios province: Paraná department: 12. Urquiza MLP 637; Misiones province: Candelaria department: 13. San Juan stream, near from national route 12, specimen maintained in live; San Pedro department: 10. km to eastern of Cruce Caballero FML 6220; Guaraní department: 14. El Soberbio CUNAM 420; Oberá department: 15. General Alvear CUNAM 419; 16. Oberá city CENAI 2921, CENAI 3110 and 3111; San Javier department: 17. Puerto Londera MACN 9489 and 9490.

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## EGG RETENTION AND MORTALITY OF GRAVID AND NESTING FEMALE CHAMELEONS (*CHAMAELEO CHAMAELEON*) IN SOUTHERN SPAIN

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In a year of drought conditions, gravid chameleons showed difficulties at the time of oviposition and made unsuccessful attempts at nesting. Two females died while constructing nests and 10 females retained eggs in the oviduct after oviposition; death was subsequently confirmed for three of the latter. Female chameleons that died whilst laying eggs, or those that retained eggs, were smaller in body length and body mass and were in poorer physical condition than females that survived long after nesting. After depleting their reserves by allocating them to egg production, it is unlikely that some females were able to complete the gravid period in sufficiently good condition to survive the effort of nesting and oviposition,

*Key words:* *Chamaeleo chamaeleon*, reproduction, egg-retention, nesting, cost, mortality

### INTRODUCTION

Investment in reproduction requires the allocation of energy in the development of eggs or offspring to the detriment of other biological processes, such as growth. The cost of reproduction in reptiles has been reviewed by Shine (1980) and Shine & Schwarzkopf (1992), and can involve (1) survival (or mortality) costs that reduce the probability of survival of reproducing organisms (see also Schwarzkopf, 1993); and (2) energy costs, which imply the reduction of future fecundity as a consequence of higher allocation of energy to reproduction rather than growth. Both types of cost may be closely related, as a high energetic expenditure in reproduction may be the cause of mortality in some species, as has been reported for some snakes after giving birth (Madsen & Shine, 1993; Luiselli, Capula & Shine, 1996).

The common chameleon, *Chamaeleo chamaeleon*, is a medium-sized arboreal lizard that is widely distributed in North Africa, the near Orient and several areas of southern Europe (Schleich, Kästle & Kabisch, 1996). Its reproduction is annual, with summer courtship, autumn oviposition, and an incubation period of about 10 months (Bons & Bons, 1960; Blasco, Romero Sánchez & Crespillo, 1985; Cuadrado & Loman, 1999).

In this paper we report on mortality in reproductive female chameleons that we assumed to be related to the investment in reproduction during a period of drought. The reproductive characteristics of female chameleons of the population studied have been described elsewhere (Díaz-Paniagua, Cuadrado, Blázquez & Mateo, submitted), but are summarized here. Female chameleons annually lay a single clutch of 2-40 eggs in an underground nest which they dig at the end of a long

tunnel. Clutch size is correlated with maternal size. The comparison of a wet year with a dry year revealed that females made a higher investment in reproduction and suffered a lower mortality rate in the wet year, which was explained as a consequence of the lower availability of food during the dry year. The aim of the present study was to explain the cause of mortality of females by comparing characteristics of surviving and non-surviving individuals.

### METHODS

Data were collected in a coastal area of southern Spain (in Cádiz province), characterized by semi-abandoned agricultural fields of sandy soil, where dispersed thickets of broom shrub (*Retama monosperma*) or garden trees (*Prunus* spp. and *Myoporum tenuifolius*) are the main arboreal habitat for chameleons. The study was carried out during the autumn of 1995, the fourth year of a prolonged drought in the area. Rainfall during the year from September 1994 to October 1995 was 215 mm, whereas the mean annual rainfall over a 150-year period in this area was 573 mm  $\pm$  189 mm. During October and November 1995, an intensive search for female chameleons in this area was carried out by three persons walking slowly while inspecting the surrounding habitat. Once chameleons were located, they were measured (snout to vent length, SVL), weighed to the nearest 0.5 g and marked with nail polish spots on their limbs. We recorded information on nesting attempts by females and marked the locations of the nests. Egg retention after nesting attempts was assessed by abdominal palpation.

When possible, we weighed females before oviposition (gravid body mass, GBM) and after nesting (post-nesting body mass, PNM). The relative clutch mass (RCM) was estimated as the ratio of the difference between gravid and post-nesting body mass to post-nesting body mass ( $RCM = [GBM - PNM] / PNM$ ). For gravid females found recently dead, we considered the

mass of all eggs extracted as clutch mass, and their RCM was calculated as clutch mass divided by the body mass of the female without eggs. Of eleven females that we found dead, we only could record biometric data from nine individuals.

We estimated the physical condition of females using the residuals from a linear regression of log body mass (without eggs) on log SVL. For this purpose we included data from females that survived long after their nesting in 1996, a rainy year in which availability of resources appeared to be considerably higher than in 1995. For estimates of RCM and physical condition in live females retaining eggs after oviposition, we made a transformation of PNM by subtracting 1g (the approximate mean egg mass in 1995, Diaz-Paniagua *et al.*, submitted) per egg detected.

For comparisons, 1995 gravid females were categorized as (a) survivors: females whose survival was confirmed at least 30 days after successful egg-laying ( $n = 11$ ); (b) dead females: this group included females that were found dead before or after nesting and for which a cause of death was not evident, i.e. we excluded females killed by predators or vehicles ( $n = 11$ ); and (c) dead and egg-retaining females ( $n = 18$ ): females that were observed to retain eggs in the oviduct after a first oviposition, plus those of the former (b) group.

Comparisons of characteristics of dead and surviving females were made by ANOVA, and Pearson correlation coefficients were used to relate RCM and SVL. Linear regression was calculated for body mass and SVL after logarithmic transformation of the variables.

## RESULTS

During the nesting period of chameleons in 1995 we observed 87 females, of which 78 (90%) were confirmed to become gravid.

Nest construction requires a considerable effort by chameleons, as deduced from the time invested in it. On six occasions, we observed females starting and completing nest construction. Females usually started digging in the afternoon (about 1400 GMT) and continued during the next morning, averaging  $23.2 \pm 2.1$  hr (mean  $\pm$  SD) in a successful nesting event. While excavating the tunnel, the female chameleon frequently re-emerged to remove sand. When the tunnel was complete, the female came outside again and entered the tunnel backwards to lay its eggs. The tunnel was then closed by pushing sand into it. The process of nesting was concluded by completely camouflaging the tunnel entrance.

In the study year, we found gravid females making several unsuccessful attempts at nesting before construction of a successful nest. In total, we observed thirty unfinished nesting tunnels (referred to as attempts) and 47 successful nests. Unsuccessful nesting attempts may carry a high energetic cost for females, as females were observed digging for up to six hours, with tunnels as long as 48 cm, without laying. We also ob-

TABLE 1. Number of gravid females which were assumed to show difficulties at the time of oviposition.

	Death confirmed	Death not confirmed
Females which were not able to oviposit	7	2
Females retaining eggs after oviposition	3	7
Females dead after ovipositing	1	-

served two females that completed and closed tunnels in which they had not laid eggs, and also recorded two additional empty nests. Some females had severe physical difficulties laying, and made nesting attempts during successive days. One was observed making three successive attempts within a period of 18 days. The same female was found dead 31 days after the first observed attempt, still bearing her clutch. Another two females were found dying during nest construction, one before completing the tunnel, and the other after having laid three eggs and with six eggs still in her oviduct. Of those females for which a successful nesting was confirmed after unsuccessful attempts, one laid her eggs 16 days after the first nesting attempt; another was observed to make an attempt six days before nesting; three females made attempts two days before nesting and one was observed to make an attempt the day before nesting.

In 10 females, we observed egg retention after a first oviposition (Table 1); three of these females were later found dead, one dying 25 days after the first oviposition. We found no evidence of any female ovipositing twice in the same breeding season.

On one occasion, we observed a female that, instead of starting to dig a new tunnel, continued the construction of a tunnel that had been previously dug and abandoned by another female. Another case of opportunism is illustrated by a gravid female that was observed to lay its eggs in the nest that was being excavated by another female, both females being inside the nest tunnel at the same time.

Comparison of the characteristics of females from the three groups considered (Table 2) revealed that dead females did not differ significantly in SVL or GBM from survivors, but that they had significantly lower PNM (Table 2). Egg-retaining females were significantly smaller in SVL, GBM, and PNM than those surviving: all dead and egg-retaining females did not surpass 20 g body mass (without egg mass), whereas all those surviving ones had a PNM greater than 20 g. A wider range of RCM was observed in dead and egg-retaining females than in surviving females, although the mean values did not differ significantly (Table 2).

TABLE 2. Snout-vent length (mm); gravid body mass (g); Post-nesting body mass (g); and relative clutch mass of female chameleons, grouped into those surviving after nesting, those which died during the nesting season, and those for which egg retention was confirmed (this third group also included the females of the second group). All ANOVA values indicated compared the values of the group indicated with the group of surviving females.

	mean±SD	range	n	F	P
<i>Snout-vent length</i>					
Survivors	102.0±8.1	85-116	11		
Dead	97.7±9.6	87.5-118	9	1.2	NS
Egg-retaining	94.07±8.5	85-118	18	5.79	0.024
<i>Gravid body mass</i>					
Survivors	37.5±9.1	28-56	8		
Dead	29.2±7.2	18.4-42	9	4.39	0.054
Egg-retaining	28.7±6.4	18.4-42	16	6.9	0.016
<i>Post-nesting body mass</i>					
Survivors	24.1±3.7	20-30	8		
Dead	17.2±3.2	11.2-20	8	15.34	0.0016
Egg-retaining	17.9±2.9	11.2-21	14	17.62	0.0005
<i>Relative clutch mass</i>					
Survivors	68.9±12.2%	57.1-86.7	5		
Dead	67.1±26.2%	22.2-110%	8	0.02	NS
Egg-retaining	61.0±28.2%	20-110%	11	0.35	NS

However, we observed that in surviving females RCM was significantly correlated with SVL ( $r=0.947$ ,  $P=0.014$ ); this relationship was not significant in the case of dead and egg-retaining females ( $r_{\text{dead}}=0.449$ ,  $P=0.264$ ;  $r_{\text{egg-retaining}}=0.551$ ,  $P=0.07$ ). Only in the case of surviving females was GBM significantly correlated with SVL ( $\log \text{GBM} = -2.78 + 2.17 \log \text{SVL}$ ;  $R^2=0.778$ ).

In the analysis of physical condition, we compared the data of surviving 1996 females, of survivors in 1995 and of dead females in 1995. We found significant differences between the three groups ( $F_{2,27}=6.84$ ,  $P=0.0039$ ), and an *a posteriori* Duncan Test revealed that the group of dead 1995 females showed poorer condition than the other two groups. The regression of  $\log \text{PNM}$  on  $\log \text{SVL}$  showed a good fit to the data ( $R^2=0.525$ ). The condition index of dead females and of those surviving from 1995 is shown in Fig. 1.

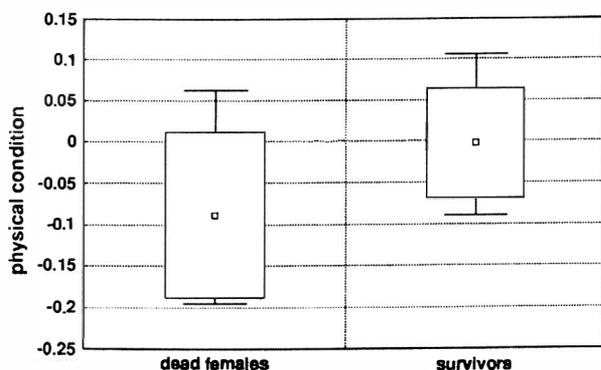


FIG. 1. Mean, standard deviation and range of the physical condition of dead and surviving females in 1995.

## DISCUSSION

The unsuccessful nesting attempts observed, and the cases of egg retention after a first oviposition, indicate that some females had difficulties in laying, or even became egg-bound. In birds, excessively large eggs may be a cause of egg-binding and intensive breeding may cause exhaustion in females (Arnall & Keymer, 1975). The high relative clutch mass of chameleons *per se* indicates that females allocate a high energetic investment to reproduction (Díaz-Paniagua *et al.*, submitted), which, because of the enormous clutch, may have a negative effect on maintenance activities, and be detrimental to the female's physical condition. For example, the large volume of eggs may constrain food intake (Bons & Bons, 1960). It is likely that, clutches being too large to be borne, some females concluded their gravid period in such poor condition that they were not able to manage the final effort required in the arduous processes of nesting and oviposition. Furthermore, this effort becomes even greater when they have to perform successive attempts, and may finally conclude in their exhaustion, and difficulty in laying eggs. With such costly nesting processes, it is probable that a portion of females have adopted opportunistic tactics of nesting in excavated tunnels, which in this study is illustrated by two females which were observed taking advantage of the efforts of other females, nesting in their tunnels but without interfering with their oviposition.

Some females were observed to die whilst nesting, others were not able to oviposit after tunnel construction and were then forced to make successive attempts,

and yet others only laid partial clutches, retaining some eggs in the oviduct. The inability to lay some eggs, or even the whole clutch, seems to be a cause of death in female chameleons, as only one of the 11 dead females recorded had laid a complete clutch. There is no evidence of resorption of shelled eggs in female reptiles (Blackburn, 1998), and in this study, neither a second oviposition nor expulsion of retained eggs was observed.

Mortality of female reptiles immediately after reproducing has been reported for viviparous snakes. Females in poor condition and with a high RCM commonly died, emaciated, after parturition (Madsen & Shine, 1993; Luiselli *et al.*, 1996). Similarly, we observed poor condition in chameleons, in which all but one dead female were small individuals with low body mass (excluding eggs). It is likely that, in a period of poor resource availability, these females would not be able to accumulate sufficient reserves to survive egg development, nesting and oviposition. This is also suggested by the lack of correlation between RCM and body size in dead females, whereas the correlation was significant in surviving females.

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## EARLY PLEISTOCENE HERPETOFAUNA FROM CAVA DELL'ERBA AND CAVA PIRRO (APULIA, SOUTHERN ITALY)

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The Early Pleistocene fissure fillings of Cava Dell'Erba and Cava Pirro (Apricena, Apulia, Southern Italy) have yielded abundant fossil vertebrate remains. The study of more than 14 000 amphibian and reptile remains revealed the presence of the following 18 taxa (6 amphibians and 12 Reptiles): *Triturus* cf. *T. alpestris*, *T. vulgaris* group, *Bufo bufo*, *Bufo viridis*, *Hyla arborea* group, *Rana* cf. *R. ridibunda* vel *Rana* kl. *R. esculenta*, *Testudo hermanni* group, *Emys orbicularis*, *Mauremys* sp., *Pseudopus* sp., *Podarcis* sp., *Lacerta* sp., *Blanus* sp., *Hierophis viridiflavus*, *Elaphe longissima*, *Coronella* cf. *C. austriaca*, *Natrix natrix*, *Vipera aspis* group. Some of the materials referred to "Colubrinae" indet. could represent taxa different from those listed above. The high taxonomic diversity, good preservation and abundance of the material place this herpetofauna amongst the most informative ever recovered in the European Quaternary. Some of the identified taxa are reported for the first time in Italy. Others are of particular interest as they help to fill present or past gaps in E-W disjunct ranges. The ecological requirements of the amphibians and reptiles suggest the presence of a typical Mediterranean landscape: a relatively dry environment with water bodies of temporary nature (at least those closer to the sites) surrounded by scattered trees or/and bushes.

*Key words:* amphibians, reptiles, palaeontology, early Pleistocene, late Villafranchian, Italy

### INTRODUCTION

The fossiliferous localities known as Cava Dell'Erba and Cava Pirro are situated near Apricena (Foggia province, Apulia, southern Italy) on the north-western slopes of the Gargano promontory. The presence of fossil remains in the area had been signalled at the beginning of the 1970s by Freudenthal (1971). During the following decades, systematic field research led by Florence University in collaboration with Camerino University and the Museo Civico of San Severo, established a wide collection of Neogene and Quaternary vertebrate remains. The Pleistocene fossil assemblage to which the materials here described belong consists of several mammals, birds, reptiles, amphibians and rare fishes coming from the sand-clay fillings of a karst network developed along the contact between a Mesozoic and a Pliocene succession. The fossil remains have been sampled from different karst fissures of two adjacent quarries. As there is evidence that the fissures were filled over a short time period, all the material has been considered as contemporary in geological terms (Abbazzi *et al.*, 1996).

Mammals have been the most extensively studied group from both a taxonomic and chronological point

of view: about 40 different taxa of small and large mammals have been described up to now (De Giuli & Torre, 1984; De Giuli, Masini & Torre, 1987; Santini, 1989; Masini & Santini, 1991; Colucci, 1993; Rook, 1994; Fanfani, 1995, 1999; Rook & Torre, 1996; Abbazzi & Masini, 1997; Lippi, 1997). An interesting feature of the mammal fauna is the contemporaneous presence of taxa typical of the Faunal Unit Farneta (Masini, Ficarelli & Torre, 1994; Gliozzi *et al.*, 1997), as well as new forms. Remarkable is, among others, the presence of the ancient bison *Eobison degiulii* - an ovibovine related to the musk ox group - the horse *Equus altidens*, an advanced form of the fallow deer *Pseudodama*, a deer close to *Megaceroides solilhacus*, the wolf *Canis* aff. *C. arnensis* (advanced form) and the arvicolid *Microtus* cf. *M. (Allophaiomys) ruffoi*.

The late Villafranchian elements of the mammal fauna suggest a late early Pleistocene age probably preceding the Jaramillo sub-magnetochrone as is also evidenced by the sediments geomagnetic polarity (Masini, Ficarelli & Torre, 1994). Therefore the fossil assemblage is considered to be one of the last Italian faunas of the late Villafranchian and Cava Pirro has been designated as the type locality of the Pirro Faunal Unit (Gliozzi *et al.*, 1997).

Works devoted to the remaining groups of vertebrates chronologically follow those of the mammals. An analysis of the herpetofauna has been undertaken only recently in a degree thesis (Delfino, 1996), and

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reports of a "large size" *Lacerta* (Delfino, 1995) and of amphisbaenians (Delfino, 1997). The present paper represents a summary and a revision of previous works.

#### MATERIALS AND METHODS

The materials analysed here are currently stored at the Department of Earth Science, University of Florence, and were excavated from Cava Pirro (PN) between 1983 and 1986, and from Cava Dell'Erba (DE) between 1991 and 1993. During the initial field research, each fissure was sampled without recording any stratigraphic detail, but in the more recent work each level of a single fissure was sampled independently.

These fissure fillings have been described by Abbazzi *et al.* (1996) and referred to the local lithostratigraphic unit number 8. Each sampled karst fissure bears a code (quarry-fissure-level; DE = Cava Dell'Erba, PN = Cava Pirro); the materials considered in this work come from 25 different fissures whose codes are listed in Table 1. At present the remains do not bear collection numbers.

#### SYSTEMATIC STUDY

##### AMPHIBIA LINNAEUS, 1758

Amphibians are well represented: 5048 remains (35.3% of all the material) have been referred to six taxa belonging to caudates and anurans.

##### CAUDATA SCOPOLI, 1777

The presence of caudates is demonstrated by a relatively small number of vertebrae and few other skeletal elements (174 altogether). All the remains, coming exclusively from the Cava Dell'Erba fissures, are from the family Salamandridae.

##### SALAMANDRIDAE GOLDFUSS, 1820

*Triturus vulgaris* Linnaeus, 1758

*Triturus vulgaris* group (Fig. 1).

Referred material: trunk vertebra: 4.

*Triturus cf. T. alpestris* (Laurenti, 1768) (Fig. 1).

Referred material: trunk vertebra: 7.

Trunk vertebrae are assigned to the genus *Triturus* on the basis of the following characters: opisthocelous; round condyle well distinct from the centrum; ventral vertical crests absent; rib-bearers well developed and connected to each other with a bony plate; neural arch unflattened and with neural spine (Gonzales & Sanchiz, 1986).

Four trunk vertebrae are characterized by a very small size (total length 1.8 mm); high neural spine flattened at the back and without dermal ossifications; well developed plates between centrum and dorsal rib-bearers; ventral foramina wide; and centrum connections having ventral rib-bearers with a developed arched anterior edge. These features clearly identify the

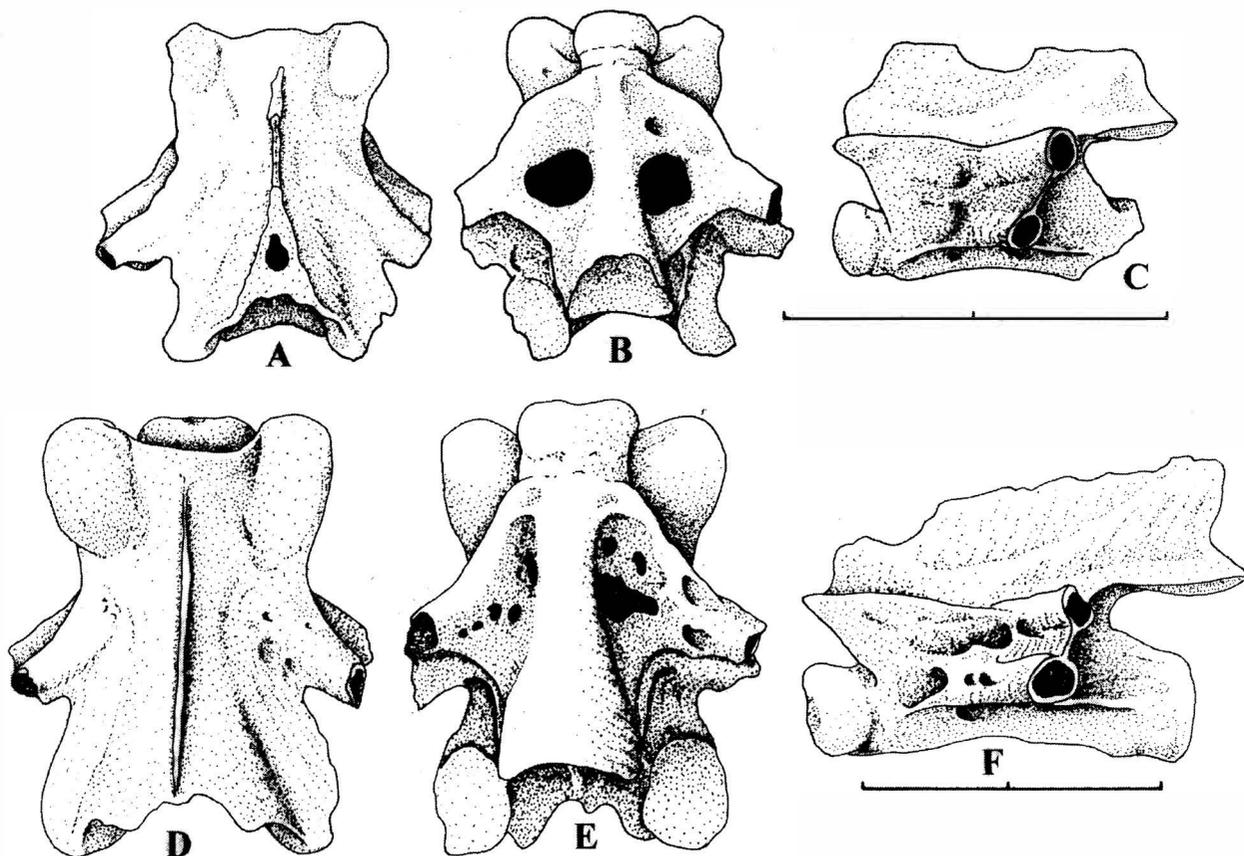


FIG. 1. *Triturus vulgaris* group, A, B, C: trunk vertebra, dorsal, ventral and left lateral views. *Triturus cf. T. alpestris*, D, E, F: trunk vertebra, dorsal, ventral and left lateral views. Scale = 2 mm.

Site:	<i>T. vulgaris</i> group	<i>T. cf. T. alpestris</i>	<i>Triturus</i> sp.	<i>B. viridis</i>	<i>B. bufo</i>	<i>Bufo</i> sp.	<i>R. esculenta/ridib.</i>	<i>Rana</i> sp.	<i>H. gr. H. arborea</i>	Anura indet.	<i>T. gr. T. hermanni</i>	<i>E. orbicularis</i>	<i>Mauromys</i> sp.	Emyidae indet.	Testudines indet.	<i>Podarcis</i> sp.	<i>Lacerta</i> sp.	<i>Pseudopus</i> sp.	Lacertilia indet.	<i>Blanus</i> sp.	<i>H. viridiflavus</i>	<i>E. longissima</i>	<i>C. cf. C. austriaca</i>	Colubrinae indet.	<i>N.atrix</i>	<i>V. aspis</i> group	Serpentes indet.	
DE 2D	0	0	X	X	X	X	0	X	X	X	/	/	/	/	/	X	X	0	X	X	X	X	X	X	0	X		
DE 6.2-2A	0	0	0	X	0	X	X	X	X	X	0	0	0	0	X	X	0	0	X	X	0	X	X	X	X	0	X	
DE 6.2-2B	0	0	X	X	0	X	0	X	X	X	0	0	0	0	X	X	0	0	X	X	0	0	X	X	X	X	X	
DE 6.2-3	0	0	X	X	X	X	0	X	0	X	0	0	0	0	0	X	0	0	X	0	0	0	X	X	0	X		
DE 6.2-4	0	0	X	X	X	X	0	X	0	X	X	0	0	0	X	X	0	0	X	X	0	X	X	0	X	0	X	
DE 6.2-4+5	0	0	0	0	0	X	0	X	0	X	X	0	0	0	X	X	0	0	X	0	X	X	0	X	0	0	X	
DE 6.2B-1	0	0	0	X	0	0	X	X	0	X	0	0	0	0	0	X	0	0	0	0	0	0	0	0	0	0	X	
DE 6.2B-3+4	0	0	0	X	0	X	0	X	X	X	X	X	X	0	X	X	X	0	X	X	X	0	0	X	0	0	X	
DE 6.2B-5	X	X	X	X	X	X	X	X	X	X	X	X	0	0	X	X	X	0	X	X	X	X	0	X	X	0	X	
DE 6.6 r	0	0	0	X	0	X	X	X	0	X	X	0	0	0	X	X	0	0	X	X	0	X	0	X	X	0	X	
DE 6.6-1A	0	0	0	X	0	X	X	X	0	X	0	0	0	0	0	X	0	0	X	0	0	0	0	0	0	0	X	
DE 6.6-1A cp	0	0	0	X	0	X	0	0	0	X	0	0	0	0	0	X	0	0	X	0	0	0	0	X	X	0	X	
DE 6.6-1B	0	0	0	X	0	X	0	X	0	X	0	0	0	0	0	X	0	0	X	0	0	0	0	X	X	0	X	
DE 6.6-2	0	X	0	X	0	X	0	X	0	X	0	0	0	0	X	X	X	0	X	0	0	0	X	X	X	0	X	
DE 6.6-3	0	0	0	0	0	0	0	X	0	X	0	0	0	0	0	X	0	0	0	0	0	0	0	0	0	0	X	
DE 6.6-4	X	X	X	X	0	X	X	X	X	X	0	X	0	0	X	X	X	0	X	X	X	0	X	X	X	0	X	
DE 6.6-5	0	0	X	X	0	X	X	X	X	X	0	0	0	X	X	X	X	0	X	X	X	0	0	X	X	0	X	
DE 11.1-2	0	0	0	0	0	X	0	0	0	0	/	/	/	/	/	0	0	0	0	0	0	0	0	0	0	0	0	
DE 11.1-3	0	0	0	0	0	X	X	X	X	X	/	/	/	/	/	X	0	X	0	X	X	0	0	0	0	0	X	
DE 11.1-4A	0	0	X	0	X	X	X	X	X	X	/	/	/	/	/	X	0	0	X	0	0	0	0	X	X	0	X	
DE 11.1-6A	0	0	0	X	0	X	X	X	0	X	/	/	/	/	/	X	0	0	X	0	0	0	0	X	0	0	X	
DE 11.1-7	0	0	X	0	0	0	0	X	0	X	/	/	/	/	/	0	0	0	0	0	0	0	0	0	0	0	X	
DE 11.1-9	0	0	0	0	0	0	0	0	0	0	/	/	/	/	/	0	0	0	0	0	0	0	0	X	0	0	X	
DE 11.1-9A	0	0	0	X	0	X	0	X	0	X	/	/	/	/	/	0	0	0	0	0	0	0	0	X	0	0	X	
DE 12.1-1A	0	0	X	X	0	X	0	X	0	X	/	/	/	/	/	X	0	0	0	0	0	0	0	X	0	0	X	
DE 12.1-2A b	X	0	X	X	X	X	X	X	X	X	/	/	/	/	/	X	0	0	0	0	0	0	0	X	X	0	X	
DE 12.1-2A c	0	0	0	X	0	X	0	X	X	X	/	/	/	/	/	X	0	0	X	0	X	0	X	X	X	X	X	
DE 12.1-2A t	0	0	X	X	0	X	0	X	X	X	/	/	/	/	/	X	0	0	X	0	0	0	0	X	X	X	0	X
DE 12.1-3A	0	0	X	X	0	X	0	X	X	X	/	/	/	/	/	X	0	0	X	0	0	0	0	X	X	X	0	X
DE 12.1-4A	0	0	X	X	0	X	0	X	X	X	/	/	/	/	/	X	X	0	X	0	0	0	X	X	0	0	X	
PN 1	0	0	0	X	X	X	X	X	X	X	X	X	0	0	X	X	X	0	X	0	X	0	0	X	X	0	X	
PN 2	0	0	0	0	0	X	0	X	0	X	X	X	X	X	X	X	0	X	0	0	0	0	0	0	0	0	X	
PN 5	0	0	0	0	0	0	0	0	0	0	X	X	0	0	X	X	0	0	X	0	X	X	0	X	X	0	X	
PN 5 b	0	0	0	0	X	0	0	X	0	0	X	0	0	X	X	X	0	X	0	0	0	X	0	0	0	0	0	
PN 6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X	0	0	X	0	0	0	0	0	0	0	0	
PN 9	0	0	0	0	X	X	X	X	0	X	X	0	0	X	X	X	X	0	X	0	X	X	0	X	X	0	X	
PN 11	0	0	0	0	X	X	0	0	X	0	X	0	X	X	X	X	0	X	0	0	X	0	X	0	0	0	X	
PN 11 spb	0	0	0	0	0	X	0	0	0	0	0	0	X	X	0	0	0	0	0	0	0	0	0	X	0	0	X	
PN 12	0	0	0	X	0	0	0	0	0	0	X	0	0	0	0	X	X	0	X	0	0	0	0	0	0	0	0	
PN 15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X	X	0	0	0	0	0	0	0	0	0	0	
PN 16	0	0	0	0	X	X	0	X	0	0	X	X	0	X	X	X	X	0	0	0	X	X	0	X	X	0	X	
PN 17	0	0	0	0	X	0	0	X	0	0	X	0	0	X	X	X	0	X	0	X	0	X	0	X	X	0	X	
PN 18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X	0	0	0	0	0	0	0	X	0	0	0	
PN 22 err.	0	0	0	0	0	0	0	X	0	0	X	X	0	0	0	0	0	0	0	0	0	0	0	X	0	0	X	
PN 22 sacca	0	0	0	0	0	0	0	0	0	0	X	0	0	0	X	0	0	0	0	0	0	0	0	0	0	0	0	
PN 22 in posto	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X	0	X	
PN 22 b	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X	0	0	0	
PN 24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X	X	0	0	
PN 24 b	0	0	0	0	0	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X	0	0	0	
PN 25	0	0	0	0	0	0	0	X	0	0	X	0	0	0	0	X	X	0	0	0	0	0	0	X	0	0	X	
PN 26	0	0	0	0	0	0	0	0	0	0	X	X	0	X	X	X	X	0	X	0	0	0	0	0	0	0	X	
PN 30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X	0	0	X	0	0	0	0	0	0	0	0	
PN 32	0	0	0	0	0	0	0	0	0	0	X	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
PN 34 err.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X	X	0	X	0	0	0	0	0	0	0	0	
PN 34 a	0	0	0	0	0	0	0	X	0	0	X	0	0	0	X	X	0	0	X	0	0	0	0	0	0	0	X	
PN 34 c	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X	X	0	X	0	0	0	0	0	0	0	X	
PN 34 d	0	0	0	0	0	X	0	0	0	0	0	0	0	0	0	X	X	0	0	0	0	0	0	0	0	0	0	
PN 35	0	0	0	0	0	0	0	0	0	0	X	0	0	X	X	X	0	0	0	0	0	0	0	0	0	0	0	

TABLE 1. Presence (X) or absence (0) of the taxa identified in the level and fissures analysed in this work. The chelonian remains of some fissures (/) have not been studied.

subgenus *Paleotriton* or “*vulgaris* group” that is represented in southern Italy by *T. vulgaris* and *T. italicus* only. A distinction between these species, considered possible by some authors (Holman, Stuart & Clayden, 1990; Holman & Stuart, 1991), but in some cases difficult by others (Sanchiz & Szyndlar, 1984), has not been attempted and the material is referred to the species group.

Seven vertebrae are slightly larger in size (total length up to 4 mm). They are characterized by a high neural spine that is narrow over the entire length of the vertebra; neural arch high in posterior view; well developed plates between centrum and dorsal rib-bearers. In ventral view, the anterior centrum connections with the ventral rib-bearers are slightly sigmoidal in shape and distinctly less developed than in the material referred to the *Triturus vulgaris* group. The ventral foramina are generally numerous and variable in size. These features fit well with those of *T. alpestris*. In the absence of more representative material, the fossil remains are referred to as *T. cf. T. alpestris*.

#### *Triturus* sp.

Referred material: maxilla: 2; parasphenoid: 1; humerus: 5; femur: 18; fibula: 1; rib: 1; scapulocoracoid: 3; ilium: 2; cervical vertebra: 8; trunk vertebra: 86; sacral vertebra: 7; caudal vertebra: 17; undetermined vertebra: 12.

Several vertebrae have been attributed only to the genus as they are partially damaged. Although according to Holman & Stuart (1991) it is possible to discriminate between the femora and humeri of *T. cristatus* and those of the group *T. vulgaris/T. helveticus*, in this work they have been referred to as *Triturus* sp. along with other skeletal elements of low diagnostic value. There is no reason to suppose the presence of a species (or a species group) different from those described above.

The larger cervical vertebrae, femora and humeri are characterized by strong crests for muscular insertion.

#### ANURA RAFINESQUE, 1815

Anuran remains are very common in the fissures of the two sites (4874 remains). In total 1633 fossil remains (carpals, metacarpal and metatarsal elements, phalanxes and other fragmentary elements) have been referred only to the order.

Three families are present: Bufonidae, Hylidae and Ranidae.

#### BUFONIDAE GRAY, 1825

##### *Bufo bufo* Linnaeus, 1758 (Fig. 2).

Referred material: sphenethmoid: 1; parasphenoid: 1; humerus: 3; radio-ulna: 3; scapula: 4; tibio-fibula: 1; ilium: 7; “atlas”: 2; vert. 2-8: 8; sacrum: 2; urostyle: 2.

##### *Bufo viridis* Laurenti, 1768 (Fig. 2).

Referred material: sphenethmoid: 23; exoccipital + prootic: 9; prootic: 3; squamosal: 6; frontoparietal: 17;

parasphenoid: 21; humerus: 132; radio-ulna: 170; scapula: 131; femur: 78; tibiofibula: 68; ilium: 241; “atlas”: 12; vert. 2-8: 9; sacrum: 108; urostyle: 96.

The osteology of *Bufo* has been discussed in detail by several authors (Sanchiz, 1977; Böhme, 1977; Bailon, 1999; Bailon & Hossini, 1990). The following discussion is limited to the most representative elements.

*Sphenethmoid*. Following Böhme (1977) the distinction between *B. bufo* and *B. viridis* based on this element is quite simple. It is wider than long in the former and approximately as long as wide in the latter. Only in *B. viridis* is the *sella amplificans* highly developed.

*Vertebrae*. All vertebrae of the genus *Bufo* are procoelous. *B. bufo* has dorsal vertebrae with condyles more robust and less broad than *B. viridis*. The sacral vertebra of *B. viridis* is characterized by the presence of anteroposteriorly wide sacral apophyses; a W-shaped neurapophysis and a deep notch, laterally opened, at the base of each sacral apophyses. In *B. bufo* the sacral apophyses are less wide and the neurapophysis has the shape of an inverted Y. The notch lateral to the neurapophysis is less developed (Sanchiz, 1977) or absent (Bailon, 1991).

*Scapula*. That of *B. viridis* is shorter and stockier than that of *B. bufo*; in the former it frequently displays a supraglenoidal *fossa*.

*Humerus*. The genus is characterized by a shaft that is rectilinear in males and more or less curved in females; the condyle is laterally (radially) shifted. In male *B. viridis*, the *crista medialis* is dorsally curved and long whereas it is approximately flat and restricted to the distal part of the epiphysis in *B. bufo*.

*Ilium*. *Bufo* is characterized by the presence of a dorsal prominence (= *tuber superior*) and the absence of an ilial crest (= *crista dorsalis*). In *B. bufo* the dorsal prominence is low and rounded, whereas in *B. viridis* it is slightly higher and frequently provided with a secondary anterior tubercle. In the latter species a deep notch (= *fossa preacetabularis*) is present.

*Femur*. It usually has a low ridge (deltoid crest) proximally flattened and forming a triangle in *B. bufo*; the ridge is higher, sharper and characteristically bifurcated in *B. viridis* (Sanchiz, 1977; Bailon, 1999).

All the skeletal elements referred to *B. bufo* are particularly large, robust and with well-marked crests.

##### *Bufo* sp.

Referred material: premaxilla: 2; maxilla: 3; angulosplenic: 68; sphenethmoid: 7; exoccipital: 1; exoccipital + prootic: 1; squamosal: 14; frontoparietal: 9; humerus: 60; radio-ulna: 71; carpal 2-4: 15; scapula: 91; coracoid: 56; clavicle: 7; femur: 117; tibiofibula: 90; ilium: 9; ischium: 13; “atlas”: 16; vert. 2-8: 502; sacrum: 8; undet. vert.: 33; urostyle: 2.

Due to its poor conservation or low diagnostic value, it has not been possible to assign the reported material to the species of *Bufo* found at the site.

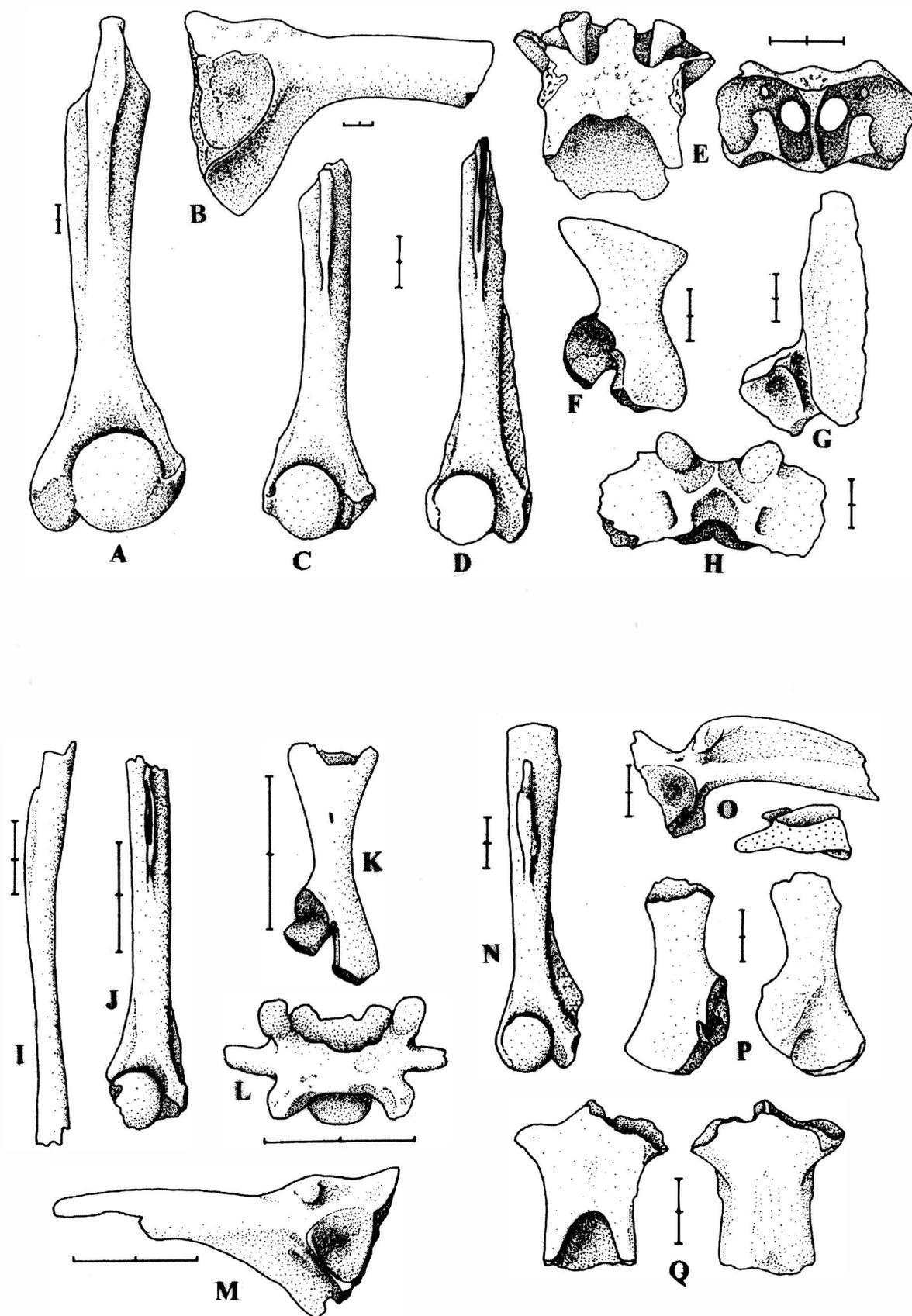


FIG. 2. *Bufo bufo*, A: left female humerus, ventral view; B: right ilium, lateral view. *Bufo viridis*, C: right female humerus, ventral view; D: right male humerus, ventral view; E: sphenethmoid, dorsal and anterior views; F: right scapula, external view; G: left frontoparietal-protitque-exoccipital, dorsal view; H: sacral vertebra, dorsal view. *Hyla arborea* group, I: femur, lateral view; J: right male humerus, ventral view; K: right scapula, external view; L: trunk vertebra, dorsal view; M: left ilium, lateral view. *Rana* cf. *R. ridibunda* vel *R. esculenta*, N: right male humerus, ventral view, O: right ilium, lateral and posterior views; P: left scapula, external and internal views; Q: sphenethmoid, dorsal and ventral views. Scale = 2 mm.

## HYLIDAE GRAY, 1825

*Hyla arborea* Linnaeus, 1758 (Fig. 2).

*Hyla arborea* group

Referred material: angulosplenic: 2; squamosal: 14; humerus: 13; radio-ulna: 4; scapula: 8; coracoid: 13; femur: 7; tibiofibula: 4; ilium: 54; "atlas": 1; vert. 2-8: 25; sacrum: 10; urostyle: 3.

*Vertebra*. Dorsal vertebrae are characterized by a short neural arch, a reduced neural spine, and condyle and cotyle small in relation to the vertebral body; the sacral vertebra displays moderately anteroposteriorly wide apophyses.

*Humerus*. The diaphysis is straight and the condyle is laterally shifted in a characteristic manner.

*Ilium*. *Hyla* may be distinguished from the other European anurans by the round, laterally oriented and one-lobed *tuber superior*, the *pars descendens ilii* ventrally expanded and the absence of an ilial crest (Sanchiz & Mlynarski, 1979).

*Femur*. Few elements, slender and with a small but evident and sharp proximal crest, have been attributed to *Hyla*.

Sanchiz & Mlynarski (1979), Sanchiz & Sanz (1980) and Sanchiz (1981) considered the specific allocation of fossil ilia belonging to the European *Hyla* as being impossible. More recently Holman (1992) stated that *H. arborea* and *H. meridionalis* can be identified by the morphology of the ilium. Since the taxonomic landscape of the European tree frogs is more complex than that considered by Holman for Britain (in the Mediterranean Basin: *H. arborea*, *H. intermedia*, *H. meridionalis*, *H. sarda*, *H. savignyi* and probably others- Lanza & Vanni, 1987; Dubois, 1995) the fossil material has been simply attributed to *Hyla arborea* group.

## RANIDAE GRAY, 1825

*Rana* cf. *R. ridibunda* Pallas, 1771

vel *R.* kl. *R. esculenta* Linnaeus, 1758 (Fig. 2).

Referred material: sphenethmoid: 1; humerus: 5; ilium: 58.

*Ilium*. The presence of a high ilial crest, the *corpus ossis ilii* relatively thick and stout (if observed on the *junctura*) and a well-developed *tuber superior* clearly indicate the presence of green frogs. The material has been referred to the group *R. ridibunda* vel *R.* kl. *R. esculenta* because the *tuber superior* is laterally flattened and anterior to the anterior margin of the *acetabulum*. In the other green frog, *R. lessonae*, the *tuber* is laterally prominent, steeper and lies over the anterior margin of the *acetabulum* (Böhme & Günther, 1979).

Sphenethmoid: in green frogs, the lateral processes are more individualized and the posterior chamber is, in ventral view, narrower than in brown frogs

Humerus: the genus *Rana* has straight diaphyses with the condyle located on the main axis at its base. The *crista medialis* is dorsally oriented only in male brown frogs.

Scapula: in dorsal view, the glenoid apophysis is partially hidden by the acromial apophysis. The internal crest is generally more developed in green frogs.

*Rana* sp.

Referred material: premaxilla: 9; maxilla fragments: 106; angulosplenic: 40; exoccipital: 2; squamosal: 2; frontoparietal: 4; humerus: 51; radio-ulna: 34; scapula: 64; coracoid: 18; metasternum: 2; omosternum: 10; femur: 11; tibiofibula: 39; fibulare: 3; ilium: 122; ischium: 13; "atlas": 9; vert. 2-8: 79; sacrum: 37; undet. vert.: 7; urostyle: 4.

The reported material has been referred only to genus level. All the remains of this genus are relatively small sized suggesting the presence of specimens smaller than the modern adult green frog.

## REPTILIA LAURENTI, 1768

Reptilia are represented by turtles, saurians, amphisbaenians and ophidians. Altogether 9264 remains (64.7% of all the material) have been referred to 13 taxa.

## CHELONII BRONGNIART, 1800

Overall, 1143 turtle remains have been identified. The determinations have been based on the general bone morphology of the shell elements and on the pattern resulting from the impression of the epidermal shields. The nomenclature of the shell epidermal shields and dermal bones follows Loveridge & Williams (1957).

In the present work, the genus *Mauremys* has been considered as a member of the family Emydidae and not Bataguridae as reported by David (1994). The *Testudo hermanni* group is a working taxon here considered as composed of *T. hermanni* and its supposed ancestor *T. globosa*, that is to say the Pleistocene members of this genus with two supracaudal horny shields (= two 12th marginals).

Both terrestrial (Testudinidae) and aquatic forms (Emydidae) are present.

Several skeletal elements (665), devoid of diagnostic value or too fragmentary to allow an accurate identification, have been attributed at order level.

## EMYDIDAE GRAY, 1825

*Emys orbicularis* Linnaeus, 1758 (Fig. 3).

Referred material: nuchal: 3; neural: 6; pleural: 22; peripheral: 35; epiplastron: 6; entoplastron: 2; hyoplastron: 4; hypoplastron: 7; xiphoplastron: 7.

*Mauremys* sp. Gray, 1869. (Fig. 3).

Referred material: peripheral: 5; suprapygal: 3; pygal: 1; epiplastron: 1; hyoplastron: 2; xiphoplastron: 4.

## TESTUDINIDAE GRAY, 1825

*Testudo hermanni* Gmelin, 1789

*Testudo hermanni* group (Fig. 3).

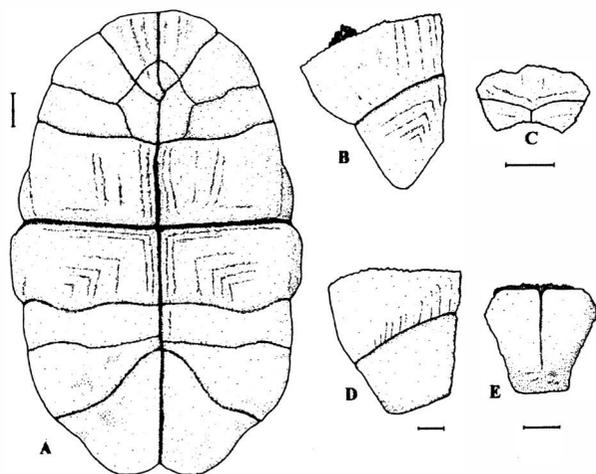


FIG. 3. *Emys orbicularis*, A: plastron, ventral view. *Mauremys* sp., B: right xiphiplastron, ventral view, C: suprapygal, dorsal view. *Testudo hermanni* group, D: right female xiphiplastron, ventral view, E: pygal, dorsal view. Scale = 10 mm.

Referred material: nuchal: 12; neural: 8; pleural: 48; peripheral: 120; suprapygal: 4; pygal: 10; epiplastron: 14; entoplastron: 5; hyoplastron: 29; hypoplastron: 15; xiphiplastron: 27; humerus: 25; radius: 5; ulna: 5; scapulocoracoid/acromion: 6; coracoid: 7; femur: 3; ilium: 4; ischium: 1; cervical vert.: 1.

**Nuchal.** In the three European genera *Testudo*, *Emys* and *Mauremys*, the nuchal bone is highly characteristic. The genus *Testudo* is characterized by thick nuchals in which the furrow between the first vertebral shield and the first marginal generally crosses the point at which the nuchal, the first peripheral and the first costal bone join.

Holman (1995) pointing out the diagnostic value of the shell bones in *E. orbicularis* and *M. leprosa* (there considered as a subspecies of *M. caspica*) emphasizes that in *E. orbicularis* the nuchal bone is "wider than long, anteriorly truncated, and has a cervical scute impression that is less than one-third the length of the bone", whereas it is "about as wide as long, not anteriorly truncated, and has a cervical scute impression that is more than one-third the length of the bone" in *Mauremys leprosa*. These characters have been taken into account but they seem to be somewhat variable in the modern and fossil material observed.

**Pygal and suprapygal.** The furrow between the 5th vertebral and the supracaudal horny shield/s approximately coincides with the suture between the suprapygal (= metaneural) and the pygal in *Testudo*, while it crosses the pygal in *Emys* and the suprapygal in *Mauremys*. This character easily allows identification of the pygal and the suprapygal in the three genera.

The pygal is sexually dimorphic in *Testudo*, being typically curved in males. This element is particularly meaningful in discriminating between living *T. hermanni* and other living European species: only the former (with few exceptions, Cheylan, 1981) shows a furrow corresponding to the boundary between the two

supracaudal horny shields (the caudal shield is divided in two parts). All the fossil pygals of *Testudo* from Cava Dell'Erba and Cava Pirro display a median furrow.

**Hypoplastron.** The border between the abdominal and the femoral shields forms an inverted 'U' in *Testudo*, whereas it is more rectilinear in *Emys* and *Mauremys*. The inguinal shield and consequently the furrow produced by its margins, is present only in the latter genus.

**Xiphiplastron.** The xiphiplastral notch is deeper in *Mauremys* than in *Emys* (Holman, 1995). Moreover the general morphology and the shape of the furrow between the femoral and anal shields are typical. This furrow is vaguely sigmoidal in *Emys*, but more rectilinear in *Mauremys* and in *Testudo*. The *Mauremys* fossil xiphiplastra are characterized by a lobed outer margin with a deep notch where the furrow between the femoral and the anal shields meets the border.

The xiphiplastron is highly characteristic and sexually dimorphic in *Testudo*: it is cranio-caudally compressed in *T. hermanni* (Cheylan, 1981) and particularly in males. The fossil xiphiplastra show the furrow between the femoral and anal shield with the shape typical of *T. hermanni* (see Cheylan, 1981).

All the *Emys* remains (some of them belong to one single specimen that has been partly reconstructed) are assigned to the only living species: *E. orbicularis*. The *Mauremys* fossil material is not allocated to specific level as we are not acquainted with any osteological differences between *M. caspica*, *M. leprosa* and *M. rivulata*.

More complex is the specific allocation of the *Testudo* remains. The presence of a median furrow on the pygal bone (as well as several other "hermanni-like" features) restricts the choice to the living species *T. hermanni* and its close fossil relative *T. globosa* Portis, 1890. The latter has been defined by Kotsakis (1980) as member of the genus *Testudo* with a pygal bone showing a median furrow and characterized by a carapax larger in its rear region, a long suprapygal, a short "saillie gulaire", xiphiplastra very wide at the back and shell bones thicker than those of *T. hermanni*. In the comparative material all these features - except the thickness - seem to vary considerably. It is noteworthy that the short "saillie gulaire" (= *bourrelet epiplastral* not much cranio-caudally developed) is characteristic of *T. hermanni* (and not of *T. graeca*; Cheylan, 1981) whereas a wide posterior carapax and xiphiplastra are typical of males (surprisingly, in the original description by Portis in 1890 of *T. globosa* there is a detailed list of male characteristics without referring them to sexual dimorphism). Moreover, Guyot & Devaux (1997) have recently reported that male *T. hermanni boettgeri* from Greece are characterized by a posterior shell broadening. Unfortunately, it has not been possible to establish the affinity of the analysed fossils to either of the two modern subspecies by the pectoral/femoral ratio as no plastron is complete.

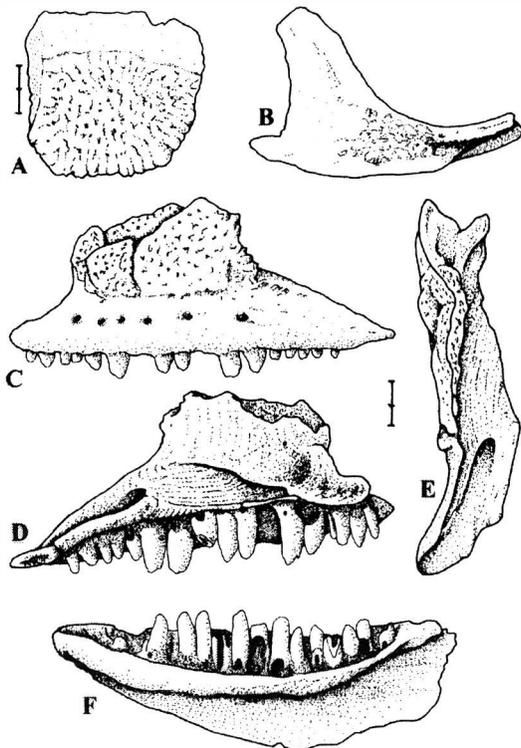


FIG. 4. *Pseudopus* sp., A: osteoderm. *Lacerta* sp., B: right jugal, lateral view; C, D, E: left maxilla, lateral, medial and dorsal views; F: right dentary, medial view. Scale = 2 mm.

A simple comparison between the remains from Cava Dell'Erba and Cava Pirro with those of *Testudo globosa* (the holotype and all the material preserved in the Geology and Palaeontology Museum, University of Florence) reveals that the remains here described are at least as thick as those of the fossil species.

It is worth mentioning that the meaning of the shell thickness is still an open problem: has it a taxonomic value or does it simply characterize an ecotype? On this subject, Cheylan (1981) has previously underlined that the greater thickness of the Villafranchian *Testudo hermanni* could be related to the optimal environmental conditions.

Since, according to Das (1997), "a larger size (and, to us, a greater thickness) may not by itself conclusively demonstrate a specific status", all the fossil material is referred to the group constituted by *T. globosa* and *T. hermanni*, here named after the living species as *T. hermanni* group.

#### EMYDIDAE INDET.

Referred material: neural: 1; pleural: 5; peripheral: 3; humerus: 3; coracoid: 5; femur: 1; cervical vert.: 3.

The listed materials (except the shell bones when well preserved) do not allow a distinction between *Emys* and *Mauremys*.

#### LACERTILIA OWEN, 1842

The bulk of the fossil material belongs to the order Lacertilia (6556 remains). Highly damaged elements

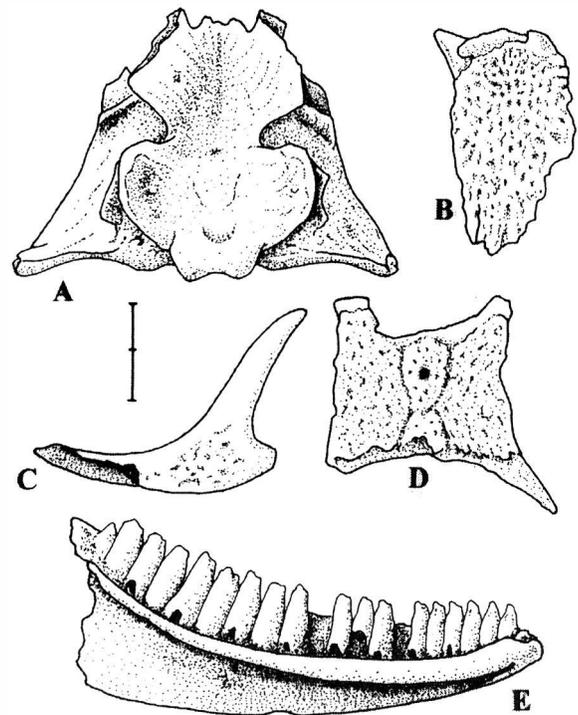


FIG. 5. *Podarcis* sp., A: basicranium, ventral view; B: postfrontal and postorbital, dorsal view; C: left jugal, lateral view; D: parietal, dorsal view; E: left dentary, medial view. Scale = 2 mm.

have been assigned only to order level (459 remains). Two families, Anguidae and Lacertidae, have been identified. Surprisingly, the former is represented by one item of remains only.

#### ANGUIDAE GRAY, 1825

*Pseudopus* sp. (Fig. 4).

Referred material: latero-dorsal osteoderm: 1.

One single osteoderm is referred to an unknown species belonging to the genus *Pseudopus*.

It is a left latero-dorsal osteoderm, roughly rectangular in shape, slightly wider than long (6.8 mm long and 7.9 mm wide). On the external side, a smooth surface is restricted to the cranial gliding area and to a small stripe on the left border whereas the remaining surface shows a vermicular pattern. There is no medial keel.

The general morphology and size of the osteoderm clearly indicates the presence of a member of *Pseudopus* and not of *Anguis*, the only other Pleistocene European member of the family Anguidae.

In the early Pleistocene Europe was inhabited by two species of *Pseudopus* (*sensu* Klembara, 1979): *P. apodus* and *P. pannonicus* (see references in Bailon, 1991). Following Estes (1983) and Holman (1998) *P. pannonicus* could be a larger form of *P. apodus* differing only for some minor traits.

The material described here, although larger in size than the modern comparative material of *P. apodus*, is assigned to *Pseudopus* sp., as it is too scarce to allow more detailed consideration.

## LACERTIDAE BONAPARTE, 1831

The taxonomic allocations of lacertid remains are almost entirely based on the morphology of teeth and teeth bearing bones. The dentition is characterized by the presence of pleurodont teeth - usually bicuspid, but sometimes tricuspid or canine-like (the few anterior maxillary teeth and those on the premaxilla) and approximately cylindrical. The number of teeth and the number of foramina in the lateral wall of dentaries and maxillae have not been taken into account for taxonomic allocation because they are related to the age and size of the animal (Rocek, 1980; Mateo, 1988; Mateo & Lopez-Jurado, 1997). The B or C caudal pattern *sensu* Arnold (1973) has not been evaluated as all the autotomic vertebrae are disarticulated or badly preserved.

Two forms of different size have been identified.

*Lacerta* sp. (Fig. 4).

Referred material: premaxilla: 16; maxilla: 41; dentary: 23; pterygoid: 9; splenial: 2; jugal: 3; supraocular osteoderm: 2; frontal: 2; postfrontal: 2; postorbital: 2; quadrate: 5; basicranium: 2; humerus: 7; scapulocoracoid: 2; femur: 6; tibia: 3; pelvis: 8; ilium: 5; dorsal vertebra: 46; sacral vert.: 6; anterior autotomic caudal vert.: 13; posterior aut. caudal vert.: 14; caudal vert.: 21.

*Podarcis* sp. (Fig. 5).

Referred material: premaxilla: 62; maxilla: 402; dentary: 609; pterygoid: 116; undet. teeth bearing bones: 390; splenial: 64; coronoid: 99; angular: 30; articular: 8; jugal: 124; supraocular osteoderm: 28; prefrontal: 60; frontal: 221; postfrontal: 22; postorbital: 12; parietal: 165; quadrate: 134; basicranium: 17; humerus: 298; ulna: 15; scapulocoracoid: 56; clavicle: 1; femur: 292; tibia: 120; pelvis: 340; ilium: 78; axis: 32; dorsal vertebrae: 1246; sacral vert.: 142; anterior autotomic caudal vert.: 63; posterior aut. caudal vert.: 53; caudal vert.: 557.

A small number of remains (238) is represented by large specimens. Maxillae have a relatively reduced number of teeth: between 16 and 17. At least 6 of the 7 best preserved maxillae display tooth-morphologic differentiation corresponding to that described by Mateo (1988) for the south-eastern population of *L. lepida*. The rear region of the fossils is characterized by some markedly reduced teeth whose number varies between 3 and 5. A careful examination with optical or scanning electron microscope (SEM) shows the presence of 2 or 3 tiny cusps on the crown of the posterior undamaged teeth. In dorsal view, the posterior process is laterally curved and the foramen for the *nerves alveolar superior* is placed in the posterior third of the dental lamina. The free region between the insertion of the ectopterygoid and that of the palatine is prominent and with a straight medial edge. The prefrontal process shows a massive *crusta calcarea* and the furrows be-

tween the postnasal, the two loreals, the frontonasal and the prefrontal scales are clearly visible. Six labial foramina are present. The 7th maxilla is characterized by its smaller size, a regular dentition and a posterior process less curved.

The large sized dentaries show the typical lacertid morphology. The tooth morphology is less heterogeneous than in the maxillae: in 3 of the 4 best preserved dentaries, 3 to 5 of the posterior teeth are slightly smaller.

The presence of a "heterodont" dentition recalls the fossil taxon *L. siculimelitensis* from the Middle and Upper Pleistocene of Sicily and Malta. Böhme & Zammit-Maempel (1982) attributed to this species a *Lacerta* dentary (Late Pleistocene, Malta) characterised by 5 little posterior teeth of conical shape. The same authors recognized as conspecific, some remains recovered from the Early Middle Pleistocene of Spinagallo (Sicily; then thought to be Late Pleistocene) and previously considered by Kotsakis (1977) as *Lacerta* sp.

Subsequently, Kotsakis has also reported this species from the Middle Pleistocene site of Poggio Schinaldo (only postcranials, Sicily; Esu *et al.*, 1986) and the Middle/Late Pleistocene site of Contrada Fusco (dentaries, not figured; Sicily; Kotsakis, 1996).

Estes (1983) synthesized the diagnosis of *L. siculimelitensis* in this way: "A large *Lacerta* (total length ca. 700-750 mm) with expanded molariform teeth and last few dentary teeth much reduced in size." Moreover, Holman (1998) quoted *L. siculimelitensis* as the "only *Lacerta* in which tooth expansion occurs" and considered it as an "unquestionably valid extinct Pleistocene species".

On the other hand, Mateo (1988) underlined the wide range of dental morphology variability between the living populations of *L. lepida*. He suggested that the diagnostic characters of *L. siculimelitensis* might fall within the range of variability of the living species and therefore cannot be used to support a specific allocation. Of the same opinion are Barahona & Barbadillo (1997).

The dental morphology of the large sized lacertids from Cava Pirro and Cava Dell'Erba seems to share some characters with the fossil species *L. siculimelitensis* and with some living populations of *L. lepida*. The morphology of the other skeletal remains does not provide any further taxonomic information. The size of some elements fits well with that of adult *L. lepida* whereas others suggest the presence of adult *L. viridis* group or subadult *L. lepida*. From the size and morphology we cannot exclude the presence of two different species. Therefore, all the material is referred only to genus level.

Most of the remains (5856) display a size comparable to that of a "big" *Podarcis* (e.g. *P. sicula* with a snout-vent length up to approximately 90 mm) and have been referred to *Podarcis* sp. on the basis of the jugal bone: the lower border of the lateral face is markedly stepped (Arnold, 1989).

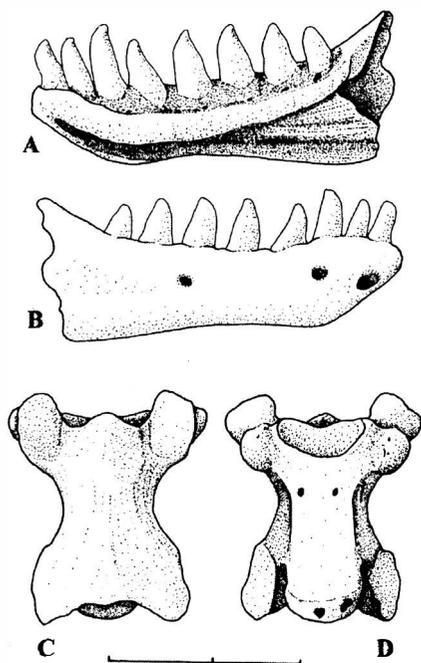


FIG. 6. *Blanus* sp., A, B: right dentary, medial and lateral views; C, D: trunk vertebrae, dorsal and ventral views. Scale = 2 mm.

Moreover, the postfrontal and postorbital bones do not show the furrow left by the parietal scale. The first character points to *Podarcis* - *L. agilis* group while the second allows discrimination of the two (Arnold, 1989: characters no. 17 and 39 respectively). Other characters perceivable on the fossil material are: maxilla with stepped posterior process; separate frontals (with few exceptions) with medial region constricted; occipital scale impression on the parietal; parietal with posterior edge straight, and with anterolateral crests and posterolateral crests just touching; osteoderm of the parietal reaches the posterior edge; jugal with evident quadratojugal process; anterior outline of the quadratum rounded; alar process of the prootic developed. Following Barahona & Barbadillo (1997), the abovementioned set of characters are present in *Podarcis*. The fossils differ from the skeletons of recent *P. muralis* and *P. sicula* (the only two species living in peninsular Italy at present) as follows: neurocranium lateral margins more anteroposteriorly divergent; basiptyergoid processes closer to basioccipital; more robust dentary; more convex dentary crest and presence of teeth on the pterygoids (not observed in the modern comparative material). The dentaries exhibit up to 22-23 (max. 25) robust teeth, sometimes regularly arranged and rather close to each other. Meckel's groove is generally wider than in any modern *Podarcis* or *Lacerta* observed. The maxillae show 18-19 teeth with the same characteristics. The lateral vertical wall is covered by the *crusta calcarea* but the furrows left by the horny scales are not visible.

The taxonomic allocation has been restricted to genus level as all these features are generally considered not diagnostic.

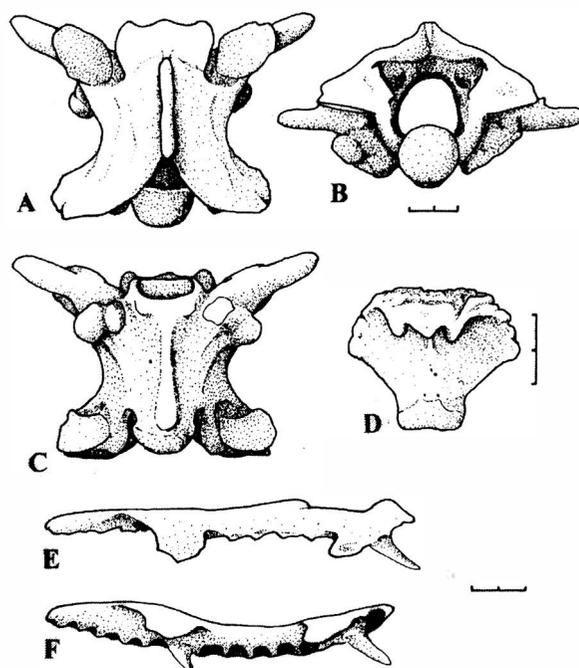


FIG. 7. *Hierophis viridiflavus*, A, B, C: trunk vertebra, dorsal, posterior and ventral views; D: basioccipital, ventral view; E, F: right maxilla, dorso-medial and medio-occlusal views. Scale = 2 mm.

#### AMPHISBAENIA GRAY, 1844

The 124 amphisbaenian remains are assigned to one genus only on the basis of the morphology of the dentaries and maxillae. It is possible to reasonably consider all the vertebrae as belonging to the same taxon, although they are not diagnostic at genus level (Estes, 1983).

#### AMPHISBAENIDAE GRAY, 1865

##### *Blanus* sp. (Fig. 6)

Referred material: dentary: 4; maxilla: 1; cervical vert.: 1; dorsal vert.: 106; caudal vert.: 12.

The taxonomic allocation of the remains referred to the order Amphisbaenia has been treated previously by Delfino (1997) and will be briefly summarized here (note that the remains from the fissure DE 16.2 have been considered in that paper also).

The dentaries display eight pleurodont, conical, pointed and non-striated teeth with a small cavity at the base. The fourth tooth is noticeably shorter. Meckel's groove is almost as long as the dentary and particularly wide under the sixth, seventh and eighth teeth. The only maxilla shows five teeth. The first is very small and supplementary (a small tooth is sometimes present in the first position - Bailon, 1991); the second is the largest. Due to the lack of reliable diagnostic features, all the material is attributed to *Blanus* sp. Holman (1998) erroneously quoted these remains as *Blanus* cf. *B. strauchi*.

#### SERPENTES LINNAEUS, 1758

The 1443 snake remains are mainly represented by vertebrae (1212; 84%). Although there are nearly twice

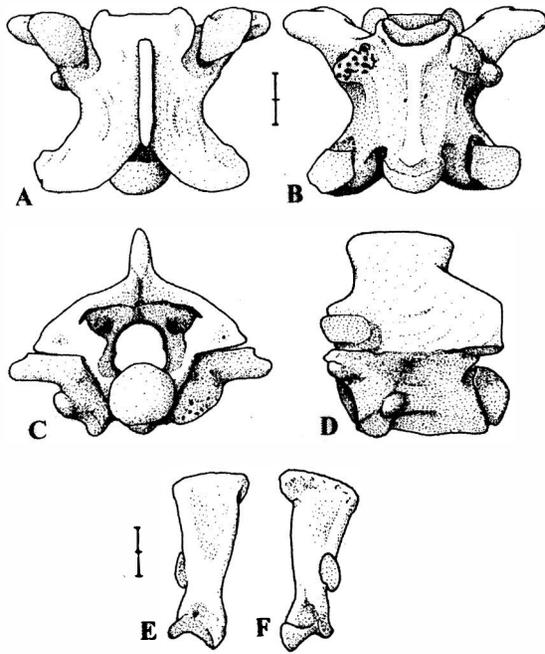


FIG. 8. *Elaphe* cf. *E. longissima*, A, B, C, D: trunk vertebra, dorsal, ventral, posterior and left lateral views; E, F: left quadrate, posterior and anterior views. Scale = 2 mm.

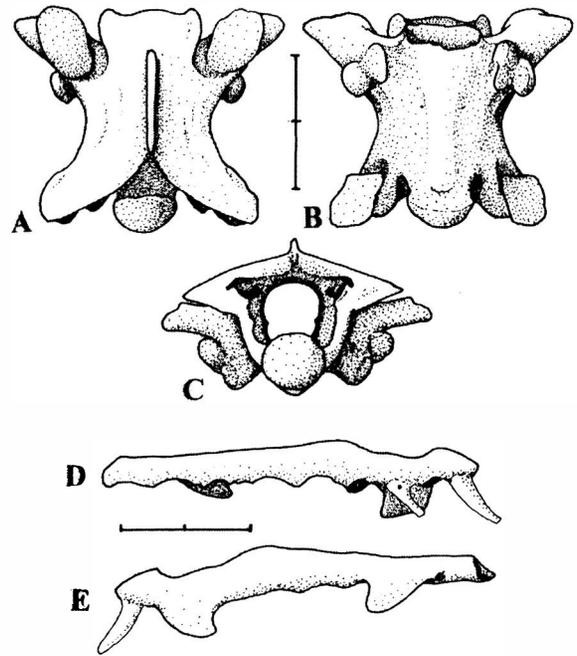


FIG. 9. *Coronella* cf. *C. austriaca*, A, B, C: trunk vertebra, dorsal, ventral and posterior views; D, E: left maxilla, lateral and dorso-medial views. Scale = 2 mm.

as many ribs as there are vertebrae in living snakes, they are underrepresented in the fossil material (181; 12.6%). Moreover, owing to their fragility, the cranial elements constitute only a small part of the sample (50; 3.4%). The taxonomic allocations are mainly based on the detailed descriptions by Szyndlar (1984, 1991a and 1991b) and Bailon (1991). Members of the families Colubridae and Viperidae have been identified.

COLUBRIDAE OPPEL, 1811

The European fossil members of this family are allocated to the generally accepted working taxa "Colubrines" and "Natricinae" based on the presence of a hypapophysis in the postcervical trunk vertebrae of the latter only (Szyndlar 1984). Although imprecise and sometimes misleading (Szyndlar, 1991b) this artificial subdivision has been used in this work.

*Hierophis viridiflavus* Lacépède, 1789 (formerly *Coluber viridiflavus*) (Fig. 7).

Referred material: maxilla: 1; quadrate: 1; basioccipital: 1; compound bone: 3; dorsal vertebra: 47.

*Elaphe* cf. *E. longissima* Laurenti, 1768 (Fig. 8).

Referred material: quadrate: 1; dorsal vertebra: 28.

*Coronella* cf. *C. austriaca* Laurenti, 1768 (Fig. 9)

Referred material: maxilla: 1; supraoccipital: 1; dorsal vertebra: 96.

*Natrix natrix* Linnaeus, 1758 (Fig. 10)

Referred material: maxilla: 1; parietal: 1; supraoccipital: 1; compound bone: 3; dorsal vertebra: 88.

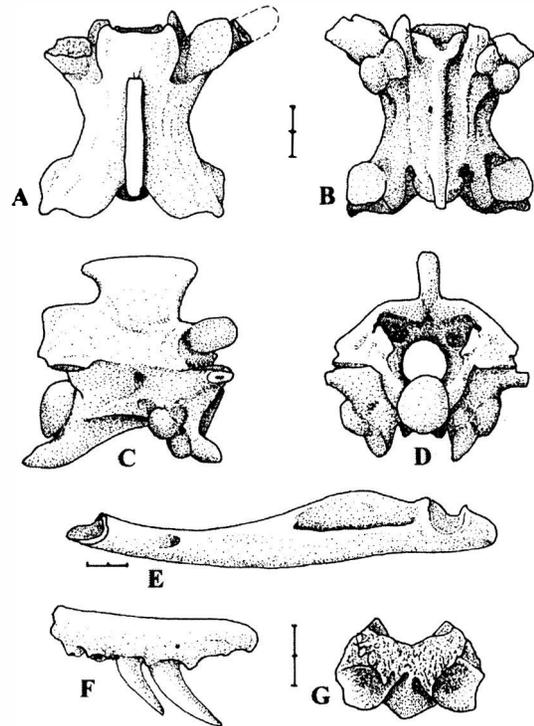


FIG. 10. *Natrix natrix*, A, B, C, D: trunk vertebra, dorsal, ventral, right lateral and posterior views; E: compound bone, lateral view; F: posterior fragment of left maxilla, lateral view; G: supraoccipital, dorsal view. Scale = 2 mm.

A distinction between the members of the genus formerly known as *Coluber* (now split into *Coluber*, *Hierophis* and *Hemorrhois*) and *Elaphe* is generally a difficult task if based on the vertebral morphology. Nevertheless, some fossil vertebrae have been allocated to *Hierophis viridiflavus* on the basis of a flat haemal keel widened at its rear end, and pointed prezygapophyseal processes only a little shorter than the prezygapophyseal facets.

*Elaphe longissima* vertebrae are characterized by a high and rounded haemal keel that is spatulate at the caudal end. The prezygapophyseal processes are relatively short and show a rounded tip (but slender and pointed in the smaller specimens of the comparison collection). As is usual in large specimens, the zygosphene is generally straight anteriorly (Szyndlar, 1991a).

Some small vertebrae have been referred to *Coronella* cf. *C. austriaca* because of the depressed neural arch (when observed in posterior view) and the short prezygapophyseal processes with a strongly constructed base. The haemal keel is generally broad and weakly demarcated; the parapophysis/diapophysis proportions are variable. The taxonomic term "cf." has been introduced in reference to the doubts on the reliability of the diagnostic traits expressed by Szyndlar (1991a).

Several hypapophysis-bearing trunk vertebrae belong to *Natrix natrix*. They show a neural arch vaulted when viewed from the back; a relatively high, markedly overhanging cranially and caudally neural spine; both hypapophyses and parapophyseal processes generally have obtuse tips though showing a degree of variability that could be related to the full size of the animal. The presence of these taxa is confirmed and strengthened by a few cranial elements.

**Maxilla.** One maxilla displays the typical morphology of *H. viridiflavus*: dorsal constriction, allowing the attachment of the maxillary ramus of the ectopterygoid, deep and well delimited anteriorly and posteriorly; prefrontal process blade-like and wider than the ectopterygoid process; tooth row (15 tooth positions) with a short posterior diastema corresponding to the ectopterygoid process.

The dorsal constriction is also present in *Coronella* but the two processes are similarly developed and there is no posterior diastema. *Natrix* does not display dorsal constriction and diastema; moreover the last few teeth are relatively more developed than those of the other species.

**Supraoccipital.** In *Coronella*, the supraoccipital and posterior areas display a similar degree of development whereas in *Natrix* the posterior area is reduced and the insertion area for the parietal is particularly broad.

**Basioccipital.** Only one basioccipital has been allocated to *H. viridiflavus* on the basis of its developed and three-lobed basioccipital crest.

**Quadrate.** *H. viridiflavus* has a triangular quadrate with a long dorsal crest overhanging anteriorly. A single quadrate is tentatively referred to *E. longissima*

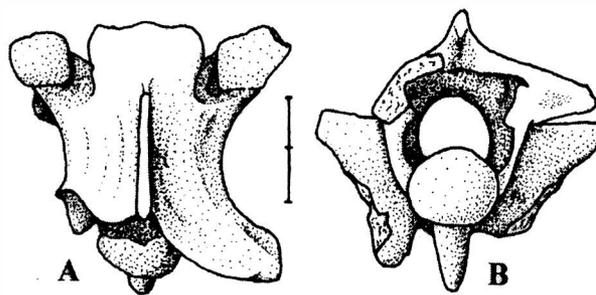


FIG. 11. *Vipera aspis* group. A, B: trunk vertebra, dorsal and posterior views. Scale = 2 mm.

because it displays a weakly developed quadrate crest, distinct stapedial process and dorsal crest (perpendicular to the main axis of the bone) anteriorly overhanging. The remains described and figured by Szyndlar (1984, fig. 34-11 and 36-10) and the specimens of the comparison collection also show a dorsal crest overhanging at the back.

**Compound bone (supra-angular + prearticular + articular).** *H. viridiflavus* is characterized mainly by the presence of a supra-angular crest (typical of "Coluber" and absent in *Elaphe*; Szyndlar 1991a). Other compound bones confirm the presence of *N. natrix* in having a medial flange slightly higher than the lateral flange, a supra-angular foramen typically far from the mandibular fossa and a massive and downwardly curved retroarticular process.

#### "COLUBRINES" INDET.

Referred material: dorsal vertebra: 318.

Several dorsal vertebrae without hypapophysis have been allocated to this working taxon without more precision as they belong to very young snakes or display features not reliably assigned to the identified taxa. It has not been possible to refer this material to other European snakes but it could well represent taxa different from those described above. In particular, some of them share some characters with *E. quatuorlineata* and *E. situla*. Their small number, the mixed set of characters and the absence of cranial elements do not allow a formal allocation of this material.

#### VIPERIDAE LAURENTI, 1768

*Vipera aspis* Linnaeus, 1758

*Vipera aspis* group (Fig. 11)

Referred material: dorsal vertebra: 2.

Only two dorsal vertebrae can be assigned to this taxon. Their morphology and size are slightly different, but common characters can be summarized as follows: vertebral body convex when observed in cross section; neural arch distinctly depressed with straight posterior border when observed in posterior view; short and pointed prezygapophyseal processes; oval-shaped and dorsally tilted prezygapophyseal facets; parapophyseal processes ventrally oriented; hypapophysis well developed; condyle and cotyle relatively large.

These features clearly identify the genus *Vipera* and the "European Vipers" in particular. The general shape of the vertebral body and hypapophysis indicate the presence of the *V. aspis* group (i.e. *V. aspis*, *V. ammodytes* and *V. latastei*; Szyndlar, 1991b). At least one other vertebra (from DE 12.1-2AC) resembles *V. ammodytes* in having a hypapophysis more robust, straight and ventrally directed. A specific allocation based on such poor material is not attempted.

#### SERPENTES INDET.

Referred material: Maxilla: 3; palatine: 1; pterygoid: 1; prefrontal: 1; frontal: 1; basioccipital: 1; supraoccipital: 1; dentary: 6; compound bone: 6; quadrate: 2; tooth bearing bone: 12; atlas: 2; dorsal vert.: 369; cloacal vert.: 6; caudal vert.: 174; fragmentary vert: 82; rib: 181.

All the remains without characters clearly referable to the above-identified taxa or with juvenile characters (e.g. lightly built skeletal elements, vertebrae with wide neural canal) have been referred to order level only.

#### DISCUSSION

On the whole, six taxa of amphibians and twelve of reptiles have been identified: their presence in each sampled level and fissure is summarized in Table 1.

Holman (1998) has recently suggested that Pleistocene European herpetofaunas should be considered rich when they contain 10 species. Thus, the high taxonomic diversity, good preservation and abundance of the remains described here place the herpetofauna amongst the most informative ever recovered in the European Quaternary.

The Cava Dell'Erba and Cava Pirro fossil assemblage provides a good opportunity to improve our understanding of the Italian herpetofauna living in the late early Pleistocene. Remains of *Triturus* cf. *T. alpestris*, *Blanus* sp., *Elaphe* cf. *E. longissima*, *Coronella* cf. *C. austriaca*, *Natrix natrix* and *Vipera aspis* group have been recovered for the first time in Italy.

The fauna consists of taxa which are considered to be Mediterranean (*Mauremys*, *Testudo*, *Pseudopus*, *Blanus*), as well as taxa that have a broad latitudinal range today (*Bufo bufo*, *Natrix natrix*, *Coronella austriaca*).

The main peculiarity of the assemblage is the coexistence of taxa still living in the area with a few others that are now restricted to either Iberia, or the Balkans and/or Asia Minor. The European distribution of *Pseudopus* is limited to the Balkans at present, but fossil evidence testifies to its presence in France (Bailon, 1991) and at least north-eastern Italy during the Middle Pleistocene (see references in Bon, Piccoli & Sala, 1991). *Mauremys* and *Blanus* display a disjunct North Mediterranean distribution at present, since they do not occur in the Italian peninsula but are widespread in Iberia and also in the Balkans and/or Asia Minor. Although

data from the Balkans are still lacking, the discovery of *Blanus* in Cava Dell'Erba suggests a possible east-west continuous distribution in the past along the northern Mediterranean coasts; the present disjunct range seems to be the result of the post early Pleistocene climatic changes. It is noteworthy that this genus, along with an endemic and peculiar fauna, was formerly present in the Gargano area during the late Miocene/early Pliocene (Cava Rodisano; Delfino, 1997) but the Pleistocene colonization is the result of a new immigration following the late Pliocene submersion of the area. At present *Mauremys* is widespread in all Northern Mediterranean peninsulas except the Italian, but its remains have previously been recovered from some Pleistocene sites in peninsular Italy (Kotsakis, 1980, 1981), and - surprisingly - from the late Pleistocene of Sardinia (Caloi, Kotsakis, Palombo & Petronio, 1981).

The presence of a newt closely related to *Triturus alpestris* fills the gap between the northern main range and the southern relict populations that are still present in southern Italy (Latium & Calabria; Societas Herpetologica Italica, 1996).

All the identified amphibians need water to lay eggs and for larval development, but only the green frogs spend almost all the year in water. Since only five fish vertebrae have been found amongst several tens of thousands of vertebrate remains, it is possible to suppose that there were physical barriers limiting the access of fish to the karst network (otherwise we can assume that fishes were not predated by the birds of prey that might have contributed to the accumulation of the vertebrate fossil assemblage). Moreover, fish can have negative influences on amphibians that leads to the decline and even extinction of the less tolerant amphibian species (e.g. *Triturus* and *Hyla*) due to competition and direct predation (for *Triturus* see Aronsson & Stenson, 1995). It could be that the water bodies (standing or gently flowing) close to the openings of the karst fissures were temporary and consequently unsuitable for fishes. This does not exclude the presence of water turtles as they are able to travel long distances from the permanent water in which they generally live.

The herpetofauna on the whole suggests the presence of a relatively dry environment with water bodies of a temporary nature (at least those closer to the sites) surrounded by scattered trees and bushes and/or very open woodlands. The substrate was probably partially rocky with areas of loose soil allowing amphibiaenians to burrow. This type of landscape corresponds to a typical karst area with scattered vegetation and seasonal shallow pools.

Assuming that their ecological requirements have not changed over time, thermophilous taxa as *Testudo*, *Mauremys*, *Pseudopus* and *Blanus* suggest a July average temperature of at least 23°C (for *Testudo hermanni* see Cheylan, 1981; Saint Girons, 1982). The present absence of *Mauremys*, *Pseudopus* and *Blanus* from the peninsula is probably explained by the lack of suitable

southern refugia there during the post early Pleistocene climatic fluctuations more than by the unsuitability of present-day conditions. Apparently, either the southernmost edge of Iberia and the Balkans were more hospitable than that of Italy during the Pleistocene, or perhaps the peninsulas were recolonized by populations coming from nearby regions (perhaps Turkey for the Balkans). In spite of the fact that a few taxa with wide Pleistocene ranges still survive in some of the southern peninsulas, Europe shows a living herpetofauna (at least at genus level) that is highly impoverished compared to those living in the past. Holman (1998) suggested that this poverty is probably the effect of the presence of some insuperable barriers, such as the Mediterranean Sea to the south and mountain ranges and seas to the east, preventing the recolonization of the area by the taxa that withdrew during the climatic changes since the end of the Miocene. In contrast, the absence of such barriers allowed North American herpetofauna to cyclically recolonize the northern regions and for this reason, it is now richer than the European fauna at the same latitude.

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## BREEDING MIGRATION AND OVIPOSITION OF THE CHINHAI SALAMANDER, *ECHINOTRITON CHINHAIENSIS*

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Breeding migration, oviposition, egg development and larval migration to water were studied in the Chinhai salamander, *Echinotriton chinhaiensis* during three consecutive breeding seasons. During 1997, 1998 and 1999, mainly females were found around the three ponds where breeding was recorded. Females migrate to breeding sites in late March and April and deposit egg clutches on the banks of the breeding ponds. Characteristic features of these egg-laying areas are high humidity, thick cover of plant debris and location on slopes bordering the water's edge. The eggs develop on land and hatch in early May, when the hatchlings are washed into the ponds during heavy rains. Experiments show that the eggs also develop normally when placed in water. In the natural habitat neither adults nor eggs were ever found in water. Reproduction in this species is dependent on a combination of very specific requirements, which make the species particularly sensitive to the environmental changes that threaten the scarce habitat in which it has been able to survive thus far.

*Key words:* *Echinotriton chinhaiensis*, *Echinotriton andersoni*, breeding, conservation

### INTRODUCTION

In this paper we present the first results of a three-year study of the ecology and life history of the Chinhai salamander, *Echinotriton chinhaiensis* (Chang, 1932). The genus *Echinotriton* consists of two species, *E. chinhaiensis*, occurring in Zhejiang in China, and *E. andersoni*, inhabiting the Ryukyu Islands, Japan (Nussbaum & Brodie Jr, 1982; Cai & Fei, 1984; Nussbaum, Brodie Jr & Yang, 1995). *Echinotriton* is unique among amphibian genera in having an anteriorly curved spine on the posterolateral surface of each quadrate. *Echinotriton* is most similar to *Tylotriton*, but differs in a number of significant morphological and life history features. The ribs of *Echinotriton* are free of muscular attachment distally, sharp-tipped, and often penetrate the skin through the primary warts (Nussbaum & Brodie Jr, 1982). The adults are completely terrestrial and deposit their eggs on land, whereas the larvae develop in lentic water bodies.

*E. chinhaiensis* is uniformly black on the dorsal and ventral surfaces, with only the underside of the tail, toes and fingers coloured orange (Fig. 1). It differs from *E. andersoni* in that it lacks the rows of secondary warts running on each side of the vertebral crest, between vertebral column and the row of primary warts sup-

ported by the ribs. Total length is approximately 12 cm in males and 14 cm in females. The body is broad and flattened; the head is broad and triangular in shape (Chang, 1932, 1936; Cai & Fei, 1984). In both sexes the cloacal opening consists of a longitudinal slit. When slightly opened, the cloaca of the female is smooth on the inside, whereas that of the male is more rugose. When carrying eggs, females have distended abdomens. *E. chinhaiensis* is known only from the type locality and two nearby valleys east of the city of Ningbo (respectively Chengwan, Ruiyansi and Qiushan, district of Beilun, province of Zhejiang, China), where it inhabits a forest area 100-200 m above sea level. Over the last 20 years, the species has been reported only incidentally from the type locality. Earlier exploratory work (Cai & Fei, 1984; Fei, 1992) signalled that the population of Ruiyansi still looked relatively healthy but was isolated and vulnerable, and had to be considered endangered. As a consequence, in 1988 *E. chinhaiensis* was listed in the grade 2 category of major state protected wildlife (Zhao, 1998), which implies that since that time the capture and handling of this salamander have been licensed by the state government.

Little is known about the reproductive biology of *Echinotriton*. Some information on occurrence and habits is available for the Japanese species, *E. andersoni* (Utsunomiya, Utsunomiya & Kawachi, 1978), and ecological work is in progress on a population in Okinawa (Satoshi Tanaka, pers. comm.). In the aforementioned preliminary work (Cai & Fei, 1984),

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FIG. 1. *Echinotriton chinhaiensis*, female (left) and male (right). Photo by M. Sparreboom.

the authors describe a neotype of the species and report on reproductive habits, defensive posture, habitat requirements and larval development. To a considerable extent reproductive success appears to be dependent on the site of egg deposition, from where the hatchlings must reach the pond (Cai & Fei, 1984; pers. obs.). Fei (1992) reports on the endangered status of this salamander. These papers form the starting point of the present study, in which we report our observations on female breeding migration and oviposition.

#### STUDY SITE

The study site is situated in the district of Beilun, east of the city of Ningbo in the south-eastern Chinese province of Zhejiang, at 29°8' N, 121°8' E. The region is characterized by an oceanic, subtropical climate, where four seasons can be distinguished and humidity is high all year round. Mean annual temperature is approximately 16°C. The temperature is higher than 10°C for about 234 days per year. Annual precipitation is about 2280 mm, with about 1880 mm of rain falling in May, the wettest month of the year. The valley in which the study site is located is surrounded by hills on three sides. Vegetation consists of secondary mixed forest of broad-leaved trees and pines. Streams and water holes—some of them natural, others man-made—are bordered by agricultural land. There is small-scale farming, with mainly orange orchards, tea plantations,

bamboo and flowering plants. Breeding was observed in three small ponds, two of which are situated 7 m apart, with the third located at approximately 200 m distance. During surveys of nine other water bodies in the valley—consisting of temporary and perennial streams, walled water tanks, water reservoirs for agricultural purposes and irrigation ditches—no salamanders, eggs or larvae were found.

The spawning habitats around the ponds to which the females migrate (Fig. 2) typically have dense plant cover; this vegetation is composed of an upper layer of evergreen broad-leaved trees, a middle layer of shrubs, and a lower layer of grasses, creating a dark and humid habitat. The egg-laying areas consist of slopes and flat ground directly bordering the ponds; the surface consists of loose soil and stones and is invariably covered by a thick leaf litter. The ponds in which the larvae develop are small (4.2–8.75 m<sup>2</sup>), shallow (25–36 cm at the deepest point) and semi-permanent. Their main source of water is rain and they have a pH of 6 to 7. Other amphibian species in these ponds include *Hylarana latouchii*, *Microhyla mixtura* and *Rhacophorus megacephalus* (Huang, Cai, Jin, Gu, Zhang, Guo & Wei, 1990; Fei, Ye, Xie & Cai, 1999), the tadpoles of at least the latter species forming part of the diet of the Chinhai salamander larvae.

#### METHODS

Our observations were made at three spawning sites between 7 April and 25 May 1997; from 25 March to 25 April 1998; and from 31 March to 24 April 1999. The surroundings of the ponds were searched by carefully raking the leaf litter and turning stones. In 1997 animals were measured, weighed and marked at the site of capture. Individual toe-clipping was applied by cutting a combination of two toes. Growth of toes in specimens marked during the first year and recaptured the second year was slow, allowing individual recognition. The toes were preserved in alcohol.

#### EFFECTS OF TOE-CLIPPING

In 1997 we began toe-clipping salamanders before they had spawned, but we noted that some females wandered off without spawning in the vicinity of the pond. Of the first 10 females marked in 1997, two were



FIG. 2. Breeding habitat (pond 1) of *Echinotriton chinhaiensis* in Ruiyansi Forest Park, Zhejiang, April 1999: dense vegetation cover on slopes of a small pond; the banks are covered with leaf litter. Photo by M. Sparreboom.

TABLE 1. Annual recaptures of adult female *Echinotriton chinhaiensis* at breeding sites in the Chinese province of Zhejiang. The 34 recaptures in 1999 represent 6 from 1997 and 28 from 1998. See text for details.

Year	No. of animals	marked	recaptures
1997	50	31	/
1998	88	53	17
1999	89	54	34

found near a large, recently-laid clutch, and both left the breeding area the day after being toe-clipped. The other eight individuals were about to start egg-laying at the time they were found and marked. Two of these animals were later found depositing their eggs under stones – too far from the water for the larvae to have a chance of reaching the pond. One animal deposited a large clutch at the place where we found it; five individuals left the breeding area before laying eggs or after having laid just a few eggs, and were not seen again. Noting this apparent disruption in the breeding routine, we decided to abandon toe-clipping before spawning. Consequently, in 1998 and 1999 we followed a different procedure: each day at 08.00 hr all animals we had found were taken to the field station, weighed and measured. They were kept individually in a box furnished with a moist strip of cotton until they had completed egg-laying. This usually took one or two days. After egg-laying the eggs were counted; the animals were weighed again and marked individually by toe-clipping (Donnelly, Guyer, Juterbock & Alford, 1994). Eggs and animals were returned to the capture site. We have no indication of inflammation or infections caused by clipping, as the animals moved out of the area and were not seen again that year. However, given the recapture percentage of >50% (Table 1), we trust that toe-clipping *per se*, if applied after oviposition, did not seriously affect individual survival and capacity to reproduce. Laboratory observations support this impression.

Due to the secretive habits of this species, we missed a number of migrating adults. Occasionally, we found new clutches after the female had already left. Table 1 does not include females whose presence we have inferred from these clutches.

Each clutch was marked with a stake to which a piece of white cloth or a sticker with a code was attached. Clutch size, location and type of substrate were described. Climatological data such as precipitation and temperature of water and nearby land surface were recorded daily.

Development of the embryos was studied in the laboratory. We kept the eggs under different conditions, both on land and in water (i.e. on soil, or at depths of 1 cm, 5 cm, 10 cm, 15 cm and 20 cm), and observed their development and hatching rate under controlled conditions. The correlation coefficient was used to test

for a relationship between hatching time and different water levels. Filtered spring water and running tap water were used; the water was changed every 48 hrs.

Observations of mating activity were conducted in the field station during two weeks in early April 1999. The sexes were kept separate until observation, which began at 23.00 hr and continued until 01.00 hr. Pairs of salamanders were placed together in a polyethylene container measuring 60 cm x 50 cm, furnished with soil and a hiding place. A Sony video camcorder with infrared capability was used to observe and record behaviour patterns in the dark. Room temperature varied from 10°C to 16°C and was similar to the temperature outside.

## RESULTS

### FEMALE MIGRATION

During the three consecutive egg-laying seasons of our study, the presence of 60 adult females was established in 1997 (50 individuals actually seen, plus 10 individuals whose presence was suggested by an egg-clutch), 88 in 1998 and 105 in 1999 (89 animals actually seen and 16 detected by their clutches). Two males were found in 1997, three in 1998, and three in 1999, which suggests a 'local' sex ratio of about 30:1. The number of males that was found at the breeding sites is too low to have a reliable estimate based upon it.

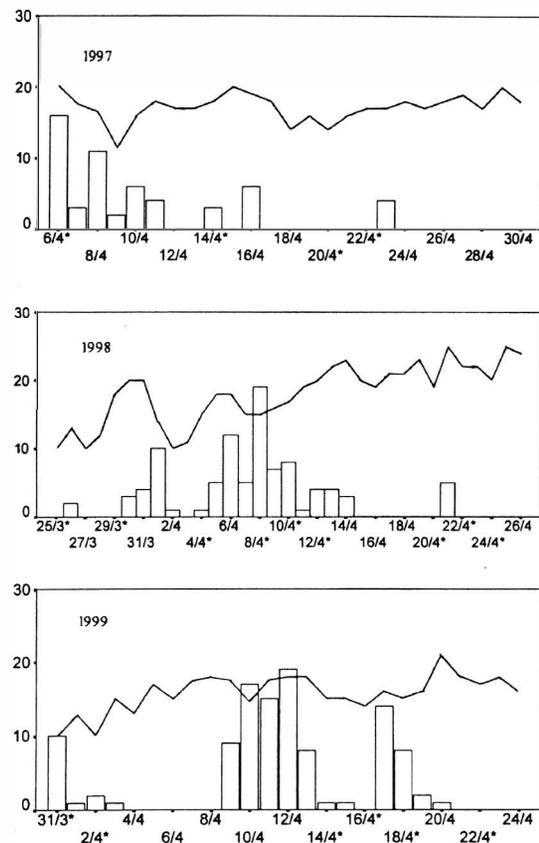


FIG. 3. Migration of female *Echinotriton chinhaiensis* to breeding site in three consecutive years (1997-99); vertical bars indicate no. migrating individuals; continuous line indicates temperature trend; \*, rainy days.

In 1998 we recaptured 55% of the females marked in 1997, and in 1999 we recaptured 53% of the animals first marked in 1998 and 19% of those marked in 1997 (Table 1).

The migration data for 1997, 1998 and 1999 are shown in Fig. 3. All eggs were deposited between 26 March and 22 April. The animals do not migrate simultaneously but in waves, showing a relation to the variations in temperature and rainfall. Migration was most frequent on days with an air temperature of  $17.7 \pm 3.8^\circ\text{C}$ , ( $n=4$ , data for 1997 and 1998). The surface temperature at the breeding sites was around  $8^\circ\text{C}$  at the end of March, gradually rising to  $15^\circ\text{C}$  at the end of April. Migration mostly took place on humid or rainy evenings between 19.00 hr and 24.00 hr, showing a peak around 21.00 hr. It often followed a thunderstorm after dusk. Migration was sometimes curtailed temporarily when it rained heavily. During the breeding season of 1999 very few migrating animals could be observed directly. There were no thunderstorms that year.

The females stayed in the egg-laying places for about three days and then wandered off. Females leaving the breeding site after laying were not found again the same year. Only on two occasions in 1997 was a female found who had wandered off before spawning and after being toe-clipped, but who migrated in again several days later to lay eggs.

#### EGG-LAYING BEHAVIOUR

Usually egg-deposition takes about two days. Having arrived at the spawning area, the female chooses a suitable spot and makes a simple and shallow 'nest'. By turning round and pressing her head and body against the muddy forest floor she creates a space on the mud floor under the leaf litter. Exactly how the female prepares the ground we have been unable to observe. The female's body and head are often covered with mud at this time, which suggests that she has engaged in some kind of digging activity. Approximately one day after arriving at the spawning site the female starts laying eggs. Her cloaca is slightly opened and fluids excreted



FIG. 4. *Echinotriton chinhaiensis*, female laying eggs, visible after removal of leaf litter. Photo by M. Sparreboom.

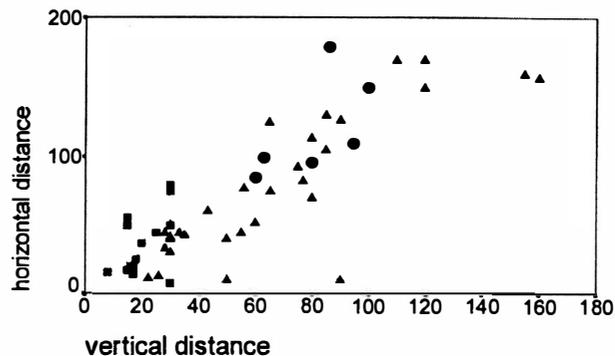


FIG. 5. Distribution of egg-masses of *Echinotriton chinhaiensis* on the banks of the three breeding sites studied, expressed in distance from the water (cm).

from her cloaca indicate the beginning of egg-deposition. The female lays her eggs one by one, taking about one hour for two eggs. We found no variation in egg-laying speed. Some eggs may be deposited singly, and some grouped in a cluster, more or less sticking together by the outer jelly capsule. On five occasions we found egg clutches deposited in six or seven superimposed layers in one 'nest'. Females at a nesting site were usually found crouching more or less beside the eggs, their bodies coiled in a typical "S" shape (Fig. 4). Occasionally we found that females laid empty jelly capsules. This appeared to mark the end of spawning. When disturbed, females would temporarily stop egg-laying. Animals captured during oviposition and taken to the laboratory, would resume egg-laying after one day, on all kinds of substrate, and also in small, temporary holding boxes. Occasionally, clutches were found under stones or on a side of the slope facing away from the pond. Although the eggs in such clutches developed normally, the hatchlings most likely would not be able to find their way to the water and would die.

#### LOCATION OF NESTS

Egg clutches were always deposited under a thick layer of humid and rotting foliage. The substrate of a nest site included loose soil, humus and grass roots.

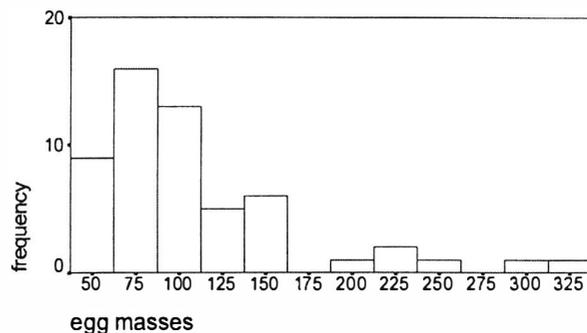


FIG. 6. Number of eggs (50 to 325) in egg masses ( $n=55$ ) found in the field, showing evidence of communal nesting. Mean  $\pm$  SE single clutch size measured in laboratory was  $69 \pm 21$ . Data gathered in 1997 and 1998.

TABLE 2. Hatching rate and duration of embryonic development in *Echinotriton chinhaiensis*, under experimental conditions. \* eggs placed on earthen substrate covered with leaf litter and sprayed every day; \*\* measurements refer to last-hatched embryos.

	simulated natural habitat*	water depth				
		1 cm	5 cm	10 cm	15 cm	20 cm
No. hatched	105 (94 %)	10 (100%)	10(80%)	10(80%)	10(90%)	10(80%)
Embryonic period	8-15.5	9-14.5	8-20.5	9.5-11.6	11.5-25.6	9.5-21.6
No. days to hatching	8	6	13	34	46	44
Hatchling SVL (mm)	17.4±0.7 n=50			20.5±2.1 n=3**		25 n=1**

This environment provides the necessary temperature, humidity and protection for embryonic development. The loose soil holds water while maintaining a degree of ventilation. Where such microhabitats were found, the clutches were scattered around the banks of the pond, close to the water's edge. The location of the egg-masses on the banks of the three egg-laying areas in 1997 is shown in Fig. 5. The vertical distance of the clutches to the water varied from 8 cm to 65 cm, with an average distance of 58 cm and a highest frequency at 30 cm. The horizontal distance of the clutches from the pond varied from 7 cm to 180 cm, with an average of 73 cm and a highest frequency at 45 cm. The gradients of the slope varied from mildly sloping away from the pond to flat to steep ( $-20^\circ$  to  $90^\circ$ ) and 95.7 % of the nest sites were on the slopes facing the water. Distance was positively correlated with gradient: the clutches found on flat land were usually located closer to the water than those deposited on slopes. In the field we found egg masses containing 50 to 325 eggs (Fig. 6). The average±SE single clutch size of clutches laid in the laboratory was  $69 \pm 21$  ( $n = 54$ ), and we assume that this was approximately the same in the natural habitat. Accordingly, a substantial number of the egg-masses found in the field (around 30%) were composed of multiple clutches, laid by two to five females, and accounting for about 50% of the total number of eggs. We actually observed that several females deposited their eggs at the same nesting site at about the same time, with some females laying their eggs on top of other eggs. We did not observe eggs being eaten by conspecifics, neither did we see any other forms of intraspecific competition at the breeding site.

#### DEVELOPMENT AND HATCHLING MIGRATION

The embryo of *E. chinhaiensis* develops on land, but can also develop normally and hatch in water, as our laboratory experiments show (Table 2). A high proportion of eggs hatched, both in a simulated terrestrial habitat (94%), and in water of different depths (80-100%). The proportions of eggs hatching at different water depths did not differ significantly ( $t=0.46$ ,  $P=0.14$ ) but there was a positive correlation between water depth and time to hatching ( $r=0.959$ ). Hatchling size also increased with increasing depth of water.

Chinhai salamander larvae have a limited capacity to move over land, namely by wriggling with rapid tail movements. By these tail movements, recently hatched larvae are even capable of leaping some 10 cm from the ground. Observations in the laboratory suggest that a number of hatchlings may reach the water, even if they are on level ground and are unaided by rains flushing them into the pond (Xie, unpubl.). In the natural habitat, plants and other obstacles, as well as predators, may form a fatal hindrance to the hatchlings' descent to the water.

## DISCUSSION

#### BREEDING MIGRATION

The vast majority of individuals we caught were gravid females on their way to – or just arrived at – the breeding sites. As all eggs are usually laid as one clutch within a short time, and male salamanders were not anywhere near at that time, we conclude that these females must have been inseminated prior to arrival at the spawning sites. The sex ratio at the breeding sites was heavily skewed towards females. The few males that were found were discovered under stones near the egg-laying sites at the beginning of the observation period. Intensive searching in the wider surroundings of the breeding sites did not produce more males. Cai & Fei (1984) collected more males in early April than in other seasons, but always fewer than they did females (25 males versus 42 females, captured over three years, 1978, 1979 and 1983). These males were mostly found during excavation works, some 50 m away from breeding ponds one and two, and not at the same sites as females. Our finding is similar to observations on *E. andersoni*, of which females constitute the vast majority of individuals caught near the breeding sites (Utsunomiya *et al.*, 1978; Satoshi Tanaka, pers. comm.). Apparently, only females migrate to the spawning sites. Males have a lower 'catchability' and are as hard to find as females outside the breeding season.

#### MATING

It remains unclear where, when and how mating takes place. We think that mating does not take place at the egg-laying sites immediately preceding oviposition.

Nor does it occur in water, as no adult has ever been found in water. Our observations in the experimental set-up at the study site in 1999 suggest that courtship and mating take place on land. Three males captured during the first days of April 1999 were used for these observations. These individuals were rather emaciated and had a slightly swollen cloacal region. They were seen pursuing females for several hours and showing various movements that could be interpreted as orientation and courtship behaviour. The females used for the experiments were captured during their migration to the spawning site and had probably already been inseminated. They were unresponsive to the males' approaches and hence no complete courtship sequence could be observed (Feng Xie & M. Sparreboom, pers. obs.). The three males showed activity during the first week of April only and from then on remained hidden, no longer showing any interest in the females. If the three males were latecomers, this observation might be considered evidence of a mating period earlier in the season, possibly in March. The earliest date we found sperm in the cloacas of females kept in captivity in Chengdu was 10 March (Feng Xie, pers. obs.). We have no evidence of insemination before the winter.

#### NESTING SITES

The 'nesting' sites are so specific that the presence of one or more females can almost be predicted. It appears that the female does not simply drop the eggs at the oviposition site, but makes a small clearing in the ground to receive the eggs. Females arriving later at the same place presumably do not need to make this effort, but profit from the 'pre-selected' oviposition site. Large eggs laid on land and eggs deposited in a single clutch are reproductive characteristics usually associated with parental care (Nussbaum, 1985), but in *E. chinhaiensis* we have not observed any form of parental care. The female leaves the oviposition site immediately after egg-laying. Utsunomiya *et al.* (1978) reported that female *E. andersoni* repeatedly push the eggs together with their snouts. We have not observed this phenomenon in *E. chinhaiensis*. Apart from this observation, our observations on oviposition and nesting site are largely in agreement with observations by Utsunomiya *et al.* (1978) on *E. andersoni* on Tokunoshima Island in Japan.

The habitat requirements of the animal lie within a narrow range and apparently few places are suitable for optimal egg development. Egg masses consisting of several clutches are the result. Such assemblages may have the advantage of keeping moisture inside the assemblage at a higher level. As was observed by Cai & Fei (1984) and Fei (1992), prolonged periods of drought are the greatest threat to survival and normal development of the eggs.

#### PREDATION

No direct evidence of predation on *Echinotriton* adults or eggs has been found. Occasionally animals

were found with a forelimb or foot missing, which may be the result of attempted predation. The finding of small clutches of about 50 eggs (Fig. 6) suggests that (1) a predator may have eaten some of the eggs; (2) some disturbance may have caused the female to wander off before completing oviposition; (3) the female may have chosen more than one suitable spawning site to distribute the eggs; or (4) is an indication of a lower fecundity of some individuals.

#### EVOLUTION OF TERRESTRIAL OVIPOSITION IN SALAMANDRIDS

If the development of the eggs can take place equally well in water and on land, as our laboratory experiments indicate, this raises the issue of what then may be the selective advantage of terrestrial oviposition for the species. Or is terrestrial oviposition a side effect of a specialization to a terrestrial life of the adult salamanders? At present it is only possible to speculate on the answers.

Terrestriality of reproductive modes has evolved many times in amphibians (Salthe & Mecham, 1974; Duellman & Trueb, 1986). For urodele amphibians examples can be found among plethodontids and ambystomatids (Petranka & Petranka, 1981; Jackson, Scott & Estes, 1989; Petranka, 1998), and also in the Salamandridae (Veith, Steinfartz, Zardoya, Seitz & Meyer, 1998). Within the family Salamandridae the genus *Salamandra* exhibits different stages of an evolution towards further independence from water. *Mertensiella luschani* is viviparous and not dependent on water bodies (Polymeni, 1994). In the genus *Tylostotriton* oviposition usually takes place in water, but in some species eggs may optionally also be laid on land (for *T. verrucosus*, see Kuzmin, Dasgupta & Smirina, 1994; for *T. kweichowensis*, see Tian, Shun & Li, 1997; Fleck, 1999; and for *T. shanjing*, see Yang, 1991, and Liu Zhijun, pers. comm.). In *T. wenzianensis* and *T. asperrimus* mating has not yet been observed, but both sexes enter water in summer whereas oviposition is on land (Deng & Yu, 1984; Fei, Ye & Yang, 1984; Ye, Fei & Hu, 1993). In the genus *Echinotriton* the tendency towards terrestrial oviposition has evolved further and the tendency to breed in water has been lost altogether.

Salthe & Mecham (1974) describe three basic reproductive patterns among salamanders: "In mode I, numerous relatively small, darkly pigmented ova are abandoned in the open in static water. In mode II, fewer but relatively larger unpigmented ova are fastened to the substratum in a limited area beneath objects in, or adjacent to, running water. The female usually remains in attendance. In mode III a very few, very large unpigmented ova are deposited in a nest hidden in, or under, objects on land and the female usually remains in attendance; development is direct (no larval stage), and this mode is restricted to plethodontids." The reproductive pattern of *Echinotriton* – large, unpigmented eggs deposited on land under leaf-litter;

adjacent to stagnant water; with the female not remaining in attendance – is exceptional among salamanders and does not fit into this classification. It shows some characteristics of Mode II of Salthe and Mecham (1974), and has probably evolved from the largely aquatic reproductive pattern as is found in *Tylototriton*, which is itself best understood as an example of the Mode I category.

#### CONSERVATION

As a consequence of its specialized reproductive mode, *E. chinhaiensis* has very specific requirements in its breeding environment. If one of the features that characterize its breeding habitat disappears, this salamander cannot survive (Fei, 1992). At the type locality, a pond which is surrounded by bamboo woods, we did not find a single salamander in April 1999, though we discovered a new locality in the valley of Qiushan, where we found two adult females. The suitable habitats are scarce. The known range of the species is limited to a very small area, which makes protection all the more a matter of great urgency. The immediate threats consist of, first, the use of pesticides, which are washed into the breeding ponds at the time the salamander larvae are developing. At the smallest of the three breeding ponds, eight egg-masses were found in March and April 1999, more than 100 young larvae were found in the pond at the end of June that year, but at the end of July, when the water was polluted by pesticides used in the neighbouring orange orchards, not a single larva was found. In the other two ponds, some distance from the orchards, many larvae could still be found (Chunmo Cai & Feng Xie, pers. obs.). Secondly, the terrestrial habitat is endangered by further encroachment on the forest, including activities such as felling trees, building roads and extending cultivation of the ground. During the last 15 years, more woodland in the immediate vicinity of the breeding sites has been cleared and the space used for orange and tea plantations, thus further reducing the species' habitat. At present, efforts are being made to raise public awareness about the importance of saving this species from extinction and to raise more funds for conservation. Sites have been designated where new ponds have now been dug as an insurance against catastrophes. To be effective in the long term, protective measures will have to be explained to the farmers in the valley. Such measures might include persuading farmers to limit their use of pesticides, to use other water sources for cleaning their equipment, and to limit further expansion of their cultivated land in the valley.

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## FORUM

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**MISCONCEPTIONS ABOUT COLOUR,  
INFRARED RADIATION, AND  
ENERGY EXCHANGE BETWEEN  
ANIMALS AND THEIR  
ENVIRONMENTS**

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coloration

“Long-wave IR radiation relationships are of crucial importance to the energy balance of ectothermic animals, but even so, they have either been ignored, or when they have been discussed with regard to reptilian thermal problems, largely misunderstood.” - Kenneth Stafford Norris, 1967

In a recent paper, Willemsen & Hailey (1999) described an intriguing geographic cline in plastron pigmentation in the tortoise *Testudo hermanni*, and suggested that differences in colour along this cline could be the result of a latitudinal cline of natural selective pressure related to thermoregulation in this species. Specifically, they suggested that the cline in plastron pigmentation could afford an adaptive benefit to lighter-pigmented animals in cooler environments by reducing radiant energy emittance from the animals. In other words, they propose that animals with lighter colour will radiate less energy, and thus, should be able to achieve higher body temperatures and/or remain active longer than would darkly-pigmented individuals. However, the physical mechanism of energy exchange proposed by Willemsen & Hailey (1999) is incorrect and leads to erroneous conclusions about natural selection. Their explanation is based upon a common misconception that colour and infrared radiation exchange by living organisms are related (Norris, 1967). This misconception stems from a misapplication of Kirchoff's Law, which states that emissivity equals absorptivity (Appendix 1) at the same temperature and wavelength (Çengel and Boles, 1998). However, animals emit energy at wavelengths different from those at which they absorb radiation in the ultraviolet, visible, and near-infrared wavebands.

The electromagnetic spectrum influencing an ectotherm's body temperature can be pragmatically divided into two wavebands (Tracy, 1982): (1) the waveband 290–2600 nm, which includes the ultraviolet, visible, and short-wave infrared, solar radiation that is transmitted through the Earth's atmosphere, and (2) the waveband 4000–50,000 nm, known as long-wave infrared or “thermal” radiation (Gates, 1980). Animals emit radiation in this latter waveband according to the Stefan-Boltzmann law, where the total energy emitted ( $E_b$ ) is given by  $E_b = A_s \epsilon \sigma T^4$  (Gates, 1980; Tracy, 1982; Mills, 1999). Thus, the radiant heat emitted is a function of the surface area of the object ( $A_s$ ), the emissivity of the object ( $\epsilon$ ) in the waveband 4000–50,000 nm, the Stefan-Boltzmann constant ( $\sigma$ ), and the fourth power of the object's temperature (in Kelvins). Most living organisms have a thermal emissivity ( $\epsilon$ ) of about 0.96–1.0 (Finch, 1972; Porter *et al.*, 1973; Tracy, 1978, 1982) averaged across the long-wave infrared waveband. Colour is a reflective property of organisms associated with the visible wavelengths for humans, in the waveband 400–750 nm, and thus, an animal's colour is not relevant with respect to infrared radiation (Norris, 1967; Tracy, 1982). To illustrate that this is a misunderstanding with a long history, consider the quote from Norris (1967), “It has sometimes been assumed that because a reptile is visibly black it reradiates at a greater rate than a white lizard... [however] visible color is not relevant to a lizard's capacities as a black body emitter, and both the light and dark lizards may emit long-wave radiation at the same rate per unit area.” While Kirchoff's Law specifies the relationship between an object's emissivity and absorptivity to radiation, energy is not emitted at all wavelengths. Instead, the amount and quality of radiation emitted is a function of the temperature of the emitting object according to the Stefan-Boltzmann Law, and the wavelengths in which this energy is emitted are given by Planck's Distribution Law (Gates, 1980). Throughout the range of temperatures achieved by living organisms, Planck's equation shows that no radiation is emitted at wavelengths shorter than about 4000 nm (Gates, 1980; Fig. 5.1, p 79).

Some of the confusion about radiant processes stems from the fact that solar radiation reaching the Earth's surface occurs in wavelengths between 290 nm and 2600 nm (Gates, 1962), including the ultraviolet, visible, and near infrared spectra. The absorption of energy in these wavelengths is not usually well correlated with the colour of the animal (Norris, 1967; Porter, 1967; Gates, 1980) because the energy in the visible spectrum represents less than half of the incident solar radiation (Gates, 1980; Campbell & Norman, 1998). Despite Norris's (1967) recognition that visible colour is a poor predictor of the total absorptivity of solar radiation in living organisms, this important point is not pervasive in the literature. For example, some investigators have attempted to control solar radiant absorptivity of operative temperature models (Tracy,

1982; Bakken *et al.*, 1985) with paints selected entirely on the basis of their colour (e.g. Vitt & Sartorius, 1999). In such cases, any correlation between absorptivity of solar radiation and the colour of the object is coincidental.

To estimate the total energy absorbed by animals in the solar waveband, one must know the absorptance of ultraviolet, visible, and short-wave infrared components of solar radiation. The percentage of the incident energy that objects absorb in these wavebands can be inferred from measurements with a spectrophotometer. Percentage absorptance must be integrated across the spectrum of the incident radiation (e.g. clear-day solar radiation or radiation filtered by a plant canopy; e.g. Gates, 1980, Fig. 8.17) to calculate an average solar absorptance for the incident radiant waveband (a specific example is given in Appendix 1).

The relationships between colour and absorption of solar radiation are not always predictable. For example, the lizards *Callisaurus draconoides* and *Holbrookia maculata*, as well as the house finch, *Carpodacus mexicanus*, have lower absorptances (Appendix 1) in the visible waveband than they do in the near infrared (e.g. Norris, 1967, Figs. 5 and 6; and Porter, 1967, Fig. 22). On the other hand, the carapace of the desert tortoise (*Gopherus agassizii*) has a higher absorptance in the visible wavelengths than in the near infrared (Fig. 1). Leaves of plants typically have a high absorptance across the ultraviolet and visible bands and extremely low absorptance throughout most of the near infrared (e.g. Gates, 1980; Figs. 8.20 and 8.21). Sometimes, absorptance in the visible waveband may be nearly the same as that in the near infrared. This is true for juvenile collared lizards, *Crotaphytus collaris*, (Norris, 1967; Fig. 16) and bullfrogs, *Rana catesbeiana*, (Porter, 1967; Fig. 21.). Black human skin obviously has higher absorptance than does white human skin in the visible waveband, and absorptivity in the near infrared wavelengths 750–1400 nm correlates with absorptance in the visible waveband; nevertheless, black and white skin have similar absorptance in the waveband 1400–2000 nm (Mount, 1979, Fig. 3.3).

An additional obstacle to predicting patterns among absorptivities for different wavebands for a given organism is the fact that some animals can change their colour and/or absorptance in the visible and near-infrared wavebands. For example, the snake *Crotalus cerastes* can be darkly coloured when it has a low body temperature and lightly coloured when it has a higher body temperature. However, the lighter colour phase absorbs more infrared energy (at wavelengths greater than 900 nm) than does the dark phase (Norris, 1967, Fig. 14). Conversely, dark and light phases of the lizard, *Uma scoparia*, have nearly identical absorptances in the near infrared waveband (e.g. Norris, 1967; Fig. 4).

Even surfaces with the seemingly highly-reflective colour white can have very varied levels of absorptance to solar radiation. For example, the white ventral sur-

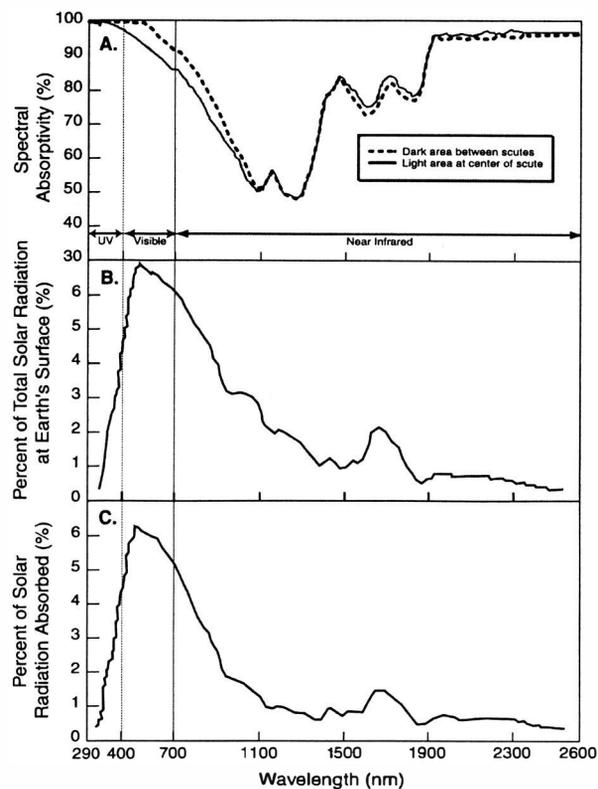


FIG. 1. (a) Absorptance (%) of dark and light portions of scutes on the carapace of an adult desert tortoise (*Gopherus agassizii*) from Clark County, Nevada, USA; (b) Percentage of incident solar radiation at the earth's surface on a clear day; and (c) the percentage of energy absorbed as quantified by the integration of the absorptance of tortoise scutes, with the clear day solar radiation curve.

face of a desert iguana has a mean absorptance in the solar spectrum of 41% (Norris, 1967), a white domestic cat had a measured absorptance of 44.5%, the absorptance of the white stripe of a skunk was 49.3%, the absorptance of a white swan was 36.7%, and the absorptance of white feathers of an Adelie penguin and a kingfisher were 32.4% and 33.9%, respectively (Gates, 1980).

In conclusion, visible colour is not a good predictor of long-wave infrared energy exchange between animals and their environments. Additionally, visible colour is not necessarily related to an animal's absorptivity in other portions of the solar spectrum. These facts indicate that the mechanism proposed by Willemsen & Hailey (1999) to explain the adaptive significance of the cline in plastron coloration in *Testudo hermanni* is not supported by the physical laws governing energy exchange, and therefore the evolutionary mechanisms underpinning the interesting geographic pattern remain to be explained.

#### APPENDIX 1:

##### DEFINITIONS AND CLARIFICATION OF TERMS

Definitions of terms from Hunt (1979):

*Absorptance*: "a ratio of the radiation absorbed by a body of material to the radiation incident upon it."

*Absorptivity*: "the ratio of the radiant energy number absorbed by a body to that falling upon it. It is equal

to the emissivity for radiation of the same wavelength.”

*Emittance*: “the ratio of the radiant energy...emitted from a surface at a given temperature to the energy emitted by a perfect black body at the same temperature.”

*Emissivity*: “the ratio of radiant energy emitted by a body to that emitted by a perfect black body. A perfect black body has an emissivity of 1; a perfect reflector, an emissivity of 0.”

*Reflectance*: “the ratio of radiation reflected from a surface to the total radiation incident on the surface.”

*Reflectivity*: “the ratio of radiant energy reflected by a body to that falling upon it.”

*Transmittance*: “The ratio of the radiation passing through a material to the radiation incident on the upper surface of that material.”

One additional definition comes from Campbell & Norman (1998):

*Transmissivity*: “the fraction of incident radiant flux at a given wavelength transmitted by a material.”

In general, the words absorptance and absorptivity are often used interchangeably and have no clear distinction in the literature (Holman, 1963; Hunt, 1979; Tabor, 1979; Campbell & Norman, 1998; Mills, 1999). This lack of distinction may cause confusion and thus merits a more careful treatment. More properly absorptivity is a property of the surface that can be expressed as a number that reflects a measured variable. Indeed, words ending in the suffix “-ivity” represent properties (e.g. conductivity, emissivity, diffusivity, etc.), and words ending in the suffix “-ance” represent values (Tabor, 1979). According to Kirchoff’s Law of Radiation, the sum of reflectivity, transmissivity and emissivity (at any particular wavelength) is one; emissivity and absorptivity are equal to one another at any particular wavelength.

Absorptivity (as well as reflectivity and transmissivity) of an organism’s surface is often expressed as a mean value integrated across a broad waveband (e.g. the integrated solar absorptance to clear-day solar radiation). When this integrated solar absorptance is calculated, it is defined by the spectrum of the incident radiation. Thus, an animal can have a mean solar absorptance for clear-day solar radiation, and an entirely different mean solar absorptance for radiation under a leaf canopy (e.g. Gates, 1980, Fig. 8.17) or under a cloudy sky, etc. In other words, integrated, or mean, solar absorptances are integrations of the properties of an organism’s surface with the spectrum of incident radiation. For example, the spectral absorptivity of a desert tortoise is given in Fig. 1a. When the curve (the dashed line in this example) is integrated with incident clear-day solar radiation (Fig. 1b), the result is the curve in Fig. 1c which is the predicted spectral absorption of clear-day solar radiation for that scute surface by a desert tortoise. When the area under

this curve (Fig. 1c) is integrated, the result is the integrated (or mean) absorptivity to clear-day solar radiation by the surface of a desert tortoise – in this case 83.6%.

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#### EDITOR’S NOTE

The authors of the article that stimulated this contribution, R. E. Willemsen and A. Hailey, provided the following response:

“We agree that although colour can affect absorption of the short-wave IR in sunlight, colour does not matter to emission of long-wave IR by a tortoise (or to absorption of long-wave IR emitted by the ground). Plastral colour can therefore have no effect on thermoregulation, and this explanation of the cline must join the other four already rejected. Of those considered, the only hypothesis remaining is random genetic differentiation; this would explain why pigmentation varied with latitude but not with altitude.”

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## BOOK REVIEWS

*Monitors. The Biology of Varanid Lizards (2nd edition)*. Dennis King and Brian Green (1999). 134 pp. Krieger Publishing Company, Malabar, Florida. US\$25.50 (paper).

"Monitors" is the second edition of a book originally published in 1993 as "Goanna - The Biology of Varanid Lizards". I suspect the new title is intended to give the book a wider appeal outside Australia. The book deals largely with the biology of Rosenberg's monitor lizard *Varanus rosenbergi*, and compares its biology to that of other *Varanus* species. It is extremely well written, at a level that biology students will have no problems with. Twenty one colour plates are included, six of them new additions.

The introductory chapter, like most of those following, is largely unchanged from the first edition. It includes a brief discussion of the evolutionary history of the monitor lizards, the largest and smallest monitors and the family's distribution. The taxonomy and phylogeny chapter discusses the fossil history of the group and changes in extant varanid classification since the work of Robert Mertens. It ends with a statement that the recognised subgenera are probably different enough to warrant generic status, which should keep the next generation of taxonomists busy for some time.

The chapter on feeding covers the diets of various monitor lizards, the use of olfaction for finding food and the morphology and function of the tongue, hyoid apparatus, jaws and teeth. A few inaccuracies and unjustified generalisations are apparent in this chapter. *V. olivaceus* occurs only in the north-east of the Philippines, not on the southern islands, and it is frugivorous rather than herbivorous. The teeth of varanids are not "always sharp and recurved". Several species undergo an ontogenetic change in tooth shape that results in broad, crushing teeth for dealing with hard shelled prey. According to the text both *V. salvator* and *V. griseus* regularly eat snails. Neither species possesses crushing dentition, and as far as I am aware, this claim is unsubstantiated in the literature. It seems particularly unlikely in the case of *V. griseus*, which inhabits desert regions where snails are very rare. Chapter 4 covers reproduction. The authors note that only one species of monitor (*V. salvator*) is known to produce more than one clutch of eggs per year. They concede that other species do so in captivity, but attribute this to "an unnaturally abundant supply of food". Multiple clutching in wild monitors is probably overlooked because virtually everything we know about their reproductive biology comes from dissections of dead animals. The frequency and speed at which monitor lizards can produce clutches of eggs in captivity, and their rather catholic diets, makes it almost inconceivable that multiple clutching is either a rare phenomena in the wild or that it only occurs in a few species. The most exciting

studies of breeding behaviour in recent years, by Tsellarius & Tsellarius (1996, 1997) on *V. griseus*, are mentioned in the text, but no references are given. Similarly, in Chapter 5 (General Behaviour) much is made of the ability of *V. albigularis* to count snails, but the work (Kaufman *et al.*, 1996) is not listed in the references.

Chapters 6-9 cover thermal biology, respiration, water use and energy and food. They are the most valuable parts of the book, providing concise details of aspects of *Varanus* physiology not available elsewhere. The authors emphasize the fact that monitor lizards can survive with very little energy input, but do not mention the lizards' extraordinary ability to assimilate large amounts of energy when it is available. The data presented for *V. rosenbergi* are interesting and convincing, but some of the more general tables are querulous. Table 6.2 lists activity temperatures taken by telemetry from various studies around the world, but the figures are scarcely comparable given the differences in methodologies used. Table 6.3 is devoted to one-off cloacal temperature readings for a variety of species in the wild and in captivity and is not at all enlightening.

The penultimate chapter covers parasites and is new to the second edition. The life cycles of hard ticks are discussed and a variety of endoparasites known to infest monitor lizards are listed. The final chapter, *Conservation and Management*, is the one that I had most problems with. I would have liked to have seen the authors take a less opinionated stance. The authors discuss conservation by region, and state that while all species in Australia are safe as a result of enlightened legislation, those in Asia and Africa are threatened by exploitation, primarily for the leather trade. In fact exploitation of monitor lizards in most places is exclusively for meat. They omit to mention that the countries that export lizard skins are unusually poor (e.g. Sudan, Chad and Mali) and while admitting that there is little evidence that exploitation has had a detrimental effect on populations, they consider it "likely" and state that reducing demand for skins would reduce the overall threat to the animals. In my opinion habitat destruction (primarily the removal of forests and mangroves) is by far the greatest threat facing monitor lizards in Africa and Asia. The authors relegate this factor to a small paragraph at the end of the chapter.

In summary, this book is a very useful guide for anyone with an interest in the biology of monitor lizards and a thorough treatment of the biology of *V. rosenbergi*. The authors are the best qualified guides to the subject you could hope for and the chapters on physiology are outstanding. But if you already own the first edition you should save your money. The amount of new material in the second edition is disappointing and many of the more interesting statements are not supported by references. The biggest weakness of this book is the lack of direct referencing and the very inadequate bibliography. Readers wishing to learn more

about a particular subject are directed to a condensed list at the end of the book arranged by chapters, which will limit the usefulness of the book to students and researchers to some extent.

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*Salamanders of the United States and Canada.* (1998). James W. Petranka. Smithsonian Institution Press, Washington and London. xvi + 587 pp. £46.95 (cloth)

Rather surprisingly, this handsome volume is the first detailed account of North American salamanders to be published since 1943, when Sherman C. Bishop's classic *A Handbook of Salamanders* first appeared. As Jim Petranka points out in his preface, since then over 1500 scientific papers on the natural history of North American salamanders have appeared and more than 30 new species described. North America has therefore been the pace-setter in salamander research, and as one of the leading lights in this arena, there are few people better qualified than Jim Petranka to synthesize the literature to date.

The author goes on to highlight the current problems involved in delimiting what is – and what is not – a species. Molecular biology has produced new insights into how species are defined, and controversy has often raged. North American salamanders have frequently been the subject of such controversies, and acknowledging the broad limitations of the biological species concept that he adopts, Petranka recognizes some 127 species within the pages of this book. The short introductory chapter goes on to cover salamander life history basics, including reproduction, ecological roles, and life history diversity. This is followed by a brief introduction to the main features to look for in salamander identification and morphology. These first two chapters are accompanied by some excellent line drawings that highlight features of interest. About three and a half pages are then devoted to a short review of the conservation biology of amphibians. Although threatened in many parts of the world, salamander declines are much less well documented or understood than those of frogs and toads. It is not known if this is simply a reflection of their distribution and diversity within the Class Amphibia (88% of amphibians are

anurans but fewer than 10% are salamanders), or whether they are generally doing better than their frog and toad relatives. This chapter offers no easy answers to this problem but provides a concise introduction to the issues. Comprehensive dichotomous keys to adult and larval salamanders follow. Given the high level of general similarity between species – and the level of geographical variation and plasticity frequently observed within species – the production of a key to salamander larvae is a bold step to take. The author wisely recommends raising larvae through metamorphosis to verify identification where appropriate.

The vast majority of the book consists of comprehensive species accounts. These are sensibly organized into families (and, where appropriate, subfamilies and tribes), with a short introduction to each main taxon preceding the individual species accounts. Each species account comprises sections on identification, systematics and geographical variation, distribution and habitats, breeding and courtship, reproductive strategy, aquatic ecology, terrestrial ecology, predators and defence, community ecology, and conservation biology. Inevitably, some species are much better studied than others and this is reflected by their coverage. The widespread tiger salamander (*Ambystoma tigrinum*), for example, receives a lavish 15 page treatment. In contrast, the rare flatwoods salamander (*A. cingulatum*) warrants just over three pages, and some of the poorly-known plethodontid salamanders yet rather less. However, every species account is accompanied by a clear distribution map, and black and white photographs of the adults (and sometimes eggs and larvae too). In addition, every species is featured in the colour plate section which fills some 48 pages in the middle of the volume. The book is worth buying for these stunning photographs alone. Just flicking through this section, the reader cannot fail to be impressed by the astonishing diversity of North American salamanders. European herpetologists may be particularly struck by plate 157 - the *Notophthalmus meridionalis* illustrated here bears uncanny parallels with our own *Triturus vulgaris*! Collating such a detailed photographic record of salamander diversity is no mean achievement in itself. Following the species accounts is a useful glossary of salamander terminology, and the book concludes with the literature cited, which runs to over 2000 published papers - surely the most comprehensive bibliography of its kind produced to date.

This book represents natural history at its very best. Although written by a scientist with a scientific audience in mind, the presentation is never dull and there is much here that will stimulate and enthrall the keen amateur herpetologist. The book will also be an essential reference tool for anyone involved with the conservation of salamanders, and the starting place for any student starting a project on these fascinating animals. Essential reading for all salamanderphiles.

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*Problem Snake Management. The Habu and the Brown Treesnake.* G. H. Rodda, Y. Sawai, D. Chiszar & H. Tanaka, eds. (1999). 534 pp. Cornell University Press, Ithaca and London. £35.50 (cloth).

Although introduced species belong to Jared Diamond's "evil quartet" of threats facing global biodiversity, there are relatively few documented cases of exotic reptiles posing ecological problems. Indeed, snakes and lizards are more often the victims rather than the offenders in this respect, as is clear from the devastation that has been wrought on the herpetofauna of many islands by introduced rats, mongooses, cats and other mammals. This herpetological contribution to the growing literature on problem species is therefore refreshing and novel.

Following a brief but thought provoking foreword by Harry Greene and a detailed introduction to the concept of – and the need for – snake management, this comprehensive volume is divided into seven parts. These are *Basic Biology*; *Venom and Human Health*; *Behavioural and Sensory Biology*, *Population Biology*, *Capture and Detection*, *Biological, Ecological and Chemical Control*; and *Conservation Biology*, which includes an epilogue. Each part comprises a brief introduction and four to ten essays (chapters) by over fifty different authors. Every essay and introduction concludes with its own extensive list of literature cited.

The first section on *Basic Biology* introduces us to the two snake species included in the title of the book, the Japanese pit-viper *Trimeresurus flavoviridis*, known as the habu, and the brown treesnake *Boiga irregularis*. These are the species chosen to discuss "snake management" as between them they have generated the majority of the world's research into and knowledge of the epidemiology of snake bite, affects of introduced snakes on native biodiversity, and techniques for the management of introduced snakes. Descriptions of the biology of both species are detailed and extensive, and serve to demonstrate how little we know about the majority of the rest of the world's snakes.

Other essays in the basic biology chapter include an investigation of seasonal fluctuations in spermatogenesis of the habu and an analysis of the frequency and pattern of power short-outs caused by brown treesnakes in Guam.

The second part, *Venom and Human Health*, considers in four essays, the history of bites by the habu and factors influencing their incidence, an assessment of the threat from brown treesnake bite to humans, and a description of the bite and venom delivery process of the two species.

*Behavioural and Sensory Biology* discusses in great depth the physiology and function of sensory organs in the habu and how repellents and toxins in bait prey might be used to control the spread, and absolute numbers, of this increasingly problematic species.

Laboratory studies of airborne odour detection in both species are explained and the chapter ends with an assessment of the possibilities, present and future, for pheromonal control of problem snakes through either repellency, attraction (trapping) or disruption of communication.

The section on *Population Biology* covers population trends, density, and individual snake movements both within and between habitats. Dispersal of the brown treesnakes between islands by incidental transportation on ships and aircraft is the subject of the first chapter in this section and emphasises the very real threat of further island colonization by this destructive species.

With over one hundred pages and ten essays devoted to the subject, *Capture and Detection* is the largest section of this volume. Trapping and exclusion barriers are discussed and much of the information from Japanese researchers on trap testing and efficiency has apparently never been published in the English language before. Rather than traps being used to secure an occasional passing snake, current methods have revealed that, for the brown treesnake at least, it is possible to capture significant portions of a population, on demand. Here used for control of problem snakes, these techniques of course have great potential for demographic study of other snakes and particularly, perhaps, endangered species.

One essay concerns the efforts to completely eradicate the habu from a small island in Japan over a period of ten years. Two further short contributions describe attempts to train dogs to detect habu in the wild and assesses the limitations, advantages and feasibility of using dogs for detecting brown treesnakes in Pacific cargo transport.

Papers in the section *Biological, Ecological and Chemical Control*, include the use of habitat modification to control habu populations and an analysis of dietary preference of the mongooses introduced in the early 20<sup>th</sup> century to control habu (needless to say mongooses failed in this regard, and not a single habu was found in over 1400 distinguishable prey items). Two, perhaps controversial, essays on the potential use of parasites, one blood and one gastrointestinal, to control both habu and brown treesnake populations are followed by a short but pertinent reminder of the potential risks involved in undertaking biological control programmes.

The last few essays in this section discuss the use of toxins, repellents, and fumigants to kill and control problem snakes, which provides rather unpleasant if interesting reading, and finally a comprehensive summary of past, present, and future strategies employed by the integrated management plan for the brown treesnake.

The final section of the book concerns *Conservation Biology*. The first two essays are overviews of the other introduced and established exotic herpetofauna of the Ryukyu and Mariana Islands. It was certainly news to

me – and disturbing news at that – that at least 19 species of reptile and amphibian have been either deliberately or accidentally introduced to Guam and surrounding islands. Ten of these species are reproducing and are established. A similar number are recorded from the Ryukyu's and of course their impact on native species of flora and fauna is essentially unknown.

Returning to the brown treesnake, two final essays discuss direct efforts to conserve native wildlife on Guam from the ravages of the ever-hungry treesnake population. Only three of Guam's twelve native forest birds species remain in the wild. One of these is the Mariana crow and the topic of one of these essays is the effort to prevent nest depredation of this endangered bird by treesnakes. The second paper discusses the development of exclusion zones from which snakes are excluded in order that endangered bird species might breed and rear young successfully.

Finally the epilogue consists of a brief summary, a commentary, of each of the earlier sections written by one of the contributing authors. The final few pages describe the "contribution of brown treesnakes and habu to science and society" in a broader context. Emphasising the correct perspective with which to view the problems presented by these two species, the author of these last few paragraphs reflects upon the great advances made in pest and wildlife management and the significant contribution made by the study of these two "problem snakes".

This book will prove a valuable reference to any herpetologist intent on studying snakes in the wild. Many of the trapping, fencing and detecting techniques discussed might prove useful in the study of many species and, I hope, endangered species especially. It is also an invaluable summary of research into the lives of two snakes which must rank among the most comprehensively studied snakes in the world, and makes interesting, startling, and some times disturbing reading. As someone involved with the breeding and conservation of snakes, this new perspective of thinking of snakes as pests posed something of a challenge to my powers of rational understanding!

I would unreservedly recommend this book to anyone with an interest in snake biology, but particularly to those involved in ophiological field research, pest/exotic species control, and conservation biology of small islands.

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*Patterns of Distribution of Amphibians: A Global Perspective.* William E. Duellman (Ed.) (1999) viii+633 pp., John Hopkins University Press, Baltimore. £45.00 (cloth).

This useful book is a synthesis of information on the global patterns of amphibian distribution from taxonomic and (especially) regional perspectives. It will be of greatest value to biogeographers and those requiring information on the amphibians of a particular geographic area, for example for conservation purposes. In this respect it falls somewhere between a textbook and a reference book, but is likely to be utilized equally well for both purposes. Indeed, the information presented has probably not been so comprehensively provided in any previous volume. Threats to amphibian diversity and appropriate conservation measures are covered and many chapters mention the amphibian decline phenomenon, on which there is also a section in Duellman's opening chapter. Many readers will find the figures relating to amphibian distribution by numbers of families/genera/species per region particularly fascinating.

The majority of chapters are devoted to consideration of distribution patterns in each of the world's regions (e.g. Nearctic North America, Temperate Eastern Asia, the Australo-Papuan Region), each region being equivalent to – or a subdivision of – one of the zoogeographic realms. Geographic, climatic and evolutionary amphibian distribution patterns are covered in the text of each chapter, often accompanied by maps, tables and graphs to elucidate a particular point (e.g. rainfall in Southern Asia). Each chapter also presents information on amphibian species distributions within a given region in tabular form for easy reference, and is appended with a comprehensive list of the literature cited in relation to that particular region. The tabular information presented for each region, however, is not standardized across all chapters (which would have been helpful, although perhaps extremely difficult), but some chapters present further tabular information covering, for example, elevational and topographic distribution patterns. The chapter on Middle America seems most comprehensive in this respect, and also contains a list linking each species found there to pertinent reference material.

Students from several areas of amphibian biology will find the book of interest, as will broader conservationists seeking specific information on amphibian distribution. Considering the vast amount of published material on amphibian distribution, this book does a good job of collating all the relevant work on this huge subject. Although this leads to rather dry reading at times, I am certain it will become a much-thumbed reference volume for those of us working in herpetological conservation or biogeography.

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*Status Assessment of Chameleons in Madagascar.* L. D. Brady & R. A. Griffiths. (1999). IUCN Species Survival Commission. IUCN, Gland, Switzerland & Cambridge, UK.

For nearly 20 years the size of the international, chameleon market has been rising and this rise was particularly dramatic since Madagascar entered the trade in the early 1980's. The rise in the number of chameleons being traded attracted concern from the international monitoring authority (CITES) in the early 1990's. It was decided that CITES member countries should suspend imports of chameleons until Madagascar's Management Authority had provided satisfactory information to CITES' Animal Committee that the collection of chameleons for the trade was sustainable. Commissioned by the IUCN, the authors were asked to provide a status assessment of chameleons on Madagascar, with this report being the result of their findings.

The 78-page report provides the reader with six chapters covering general background, sites and methods, results, trade, discussion and recommendations, references plus two Appendix sections, one providing a suggested management plan. It brings together scarce and widespread information, consolidating this with data from their past and current studies.

In the first chapter a general background and brief history of Madagascar accompanies a concise review of chameleon taxonomy. This is followed by a recent trade review highlighting the concerns of the IUCN and justifying the commissioning of the report. Considering the paucity of information at the start of this study the number of aims/objectives set by the IUCN appears ambitious, but despite this the following chapters address the aims in comprehensive style.

Chapter two covers methodological matters with details of fieldwork schedules and descriptions of sites used for surveys. Lee Brady was a member of the team that developed the current standard method of chameleon surveying, and the methodology is fully explained here. Satellite imagery together with previous ground surveys are used to define the ranges of ten rainforest species. The information on the sites provides an interesting insight to the many types of vegetation that exist on Madagascar and with the brief history of the regions/reserves, gives an informative read for any ecologist.

The main section of the report opens with results on chameleon ranges and a brief discussion of vegetation change. This is followed by informative reviews on the description, distribution, habitat and life history aspects of ten (five *Calumma* and five *Furcifer*) species of Malagasy chameleon.

Of great interest is the change in population structure over seasons, especially those based on snout-vent size and a comparison of the use of burnt and unburnt forest

by four of the *Calumma* species. Abundance is generally discussed before the authors go on to review the current abundance of ten (again, five *Calumma* and five *Furcifer*) of the 57 species on the island. An excellent Table grades habitat from 'Less' to 'More' disturbed and assigns chameleon densities to the relevant disturbance regime, enabling readers to view the impact of disturbance on species numbers. This Table relates to nine species, but the reader needs to be aware that there is no consistency in the treatment of species in the results section.

Description of the conservation strategy for Madagascar and how this relates to trading in chameleons comes next. Trade figures are provided for ten named species plus an unidentified species; these appear to indicate that CITES legislation is being observed. For those interested in welfare issues, there are sections on the procedure of transporting chameleons and mortality pre- and post-export. The history of trade levels is reviewed for each of the ten species, providing information on the peak trading years and captivity prospects. An interesting socioeconomic section discusses the wider human/conservation interface. The chapter ends with a wider look at issues of concern for chameleon populations, with the ever-problematic habitat loss featuring heavily and a brief discussion of the use of chameleons in traditional medicines and beliefs is also covered.

In the final chapter an attempt is made to bring all this information together. Starting with population and distribution trends, it goes on to cover the sustainability of trade, reduction of mortality, monitoring wild populations and finally a discussion. The sustainability of the trade highlights that no data exist on population estimates for the current legally traded species. Consequently there is an urgent need for monitoring of wild populations. To encourage this the authors provide a detailed ten-point guidance protocol for future monitoring programmes, accompanied by a further three point-backup for rapid or limited financial/manpower surveys. An 'Experimental management program' is also discussed. In addressing the possible lifting of the moratorium sometime in the future, the authors suggest many points regarding both trade controls and welfare that they would like to see implemented.

Due to the paucity of data, the authors inevitably express considerable caution both in relation to their findings and future recommendations. Nevertheless this report provides an essential piece of literature for anyone interested in wildlife conservation, wildlife resource use, sustainable development and welfare issues.

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# THE HERPETOLOGICAL JOURNAL

## INSTRUCTIONS TO AUTHORS

(revised July 2000)

1. The *Herpetological Journal* publishes a range of features concerned with reptile and amphibian biology. These include: *Full Papers* (no length limit); *Reviews* and *Mini-reviews* (generally solicited by a member of the editorial board); *Short Notes*; controversies, under *Forum* (details available from the Editor); and *Book Reviews*. Faunistic lists, letters and results of general surveys are not published unless they shed light on herpetological problems of wider significance. Authors should bear in mind that the *Herpetological Journal* is read by a wide range of herpetologists from different scientific disciplines. The work should therefore appeal to a general herpetological audience and have a solid grounding in natural history.
2. *Three* copies of all submissions, and illustrations, should be sent to the Scientific Editor. All papers will be subject to peer review by at least two referees. Authors are invited to suggest the names of up to three referees, although the editor may choose alternative referees to those suggested. Papers will be judged on the basis of the reports supplied by referees, scientific rigour, and the degree of general interest in the subject matter. The Editor's decision will be final.
3. Authors should consult a recent issue of the Journal regarding style. Papers should be concise with the minimum number of tables and illustrations. They should be written in English and spelling should be that of the *Oxford English Dictionary*. Papers should be typed or produced on a good-quality printer, and double-spaced with wide margins all round. The journal is typeset direct from the author's computer diskette, so all manuscripts should be prepared using a wordprocessor (preferably on a PC-compatible microcomputer). If figures are prepared using computer graphics, they should be supplied separately and NOT embedded in the text of the wordprocessor file. Preferred formats are MS Word for Windows (text) and MS Excel, Bitmap, TIFF, or JPEG files (graphics). It is not necessary to submit a computer diskette with the initial manuscript, but this will be required in the event of the manuscript being accepted for publication.
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5. The usual rules of zoological nomenclature apply.
6. Tables are numbered in arabic numerals, e.g. TABLE 1; they should be typed double spaced on separate sheets with a title/short explanatory paragraph above the table. Horizontal and vertical lines should be avoided.
7. Line drawings and photographs are numbered in sequence in arabic numerals, e.g. FIG. 1. Colour photographs can only be included at cost to the author. If an illustration has more than one part each should be identified as (a), (b), etc. The orientation and name of the first author should be indicated on the back. They should be supplied camera-ready for uniform reduction of one-half on A4 size paper. Line drawings should be drawn and fully labelled in Indian ink, dry-print lettering or laser printed. Illustrations produced using other types of computer printer are not usually of suitable quality. A metric scale must be inserted in micrographs etc. Legends for illustrations should be typed on a separate sheet.
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Bellairs, A. d'A. (1957). *Reptiles*. London: Hutchinson.

Boycott, B. B. & Robins, M. W. (1961). The care of young red-eared terrapins (*Pseudemys scripta elegans*) in the laboratory. *British Journal of Herpetology* 2, 206–210.

Dunson, W. A. (1969a). Reptilian salt glands. In *Exocrine glands*, 83–101. Botelho, S. Y., Brooks, F. P. and Shelley, W. B. (Eds). Philadelphia: University of Pennsylvania Press.

Dunson, W. A. (1969b). Electrolyte excretion by the salt gland of the Galapagos marine iguana. *American J. Physiol.* 216, 995–1002.
9. Final acceptance of a paper will depend upon the production by the author of a typescript, illustrations and computer diskette ready for the press. However, every assistance will be given to amateur herpetologists to prepare papers for publication.
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# THE HERPETOLOGICAL JOURNAL

Volume 10, Number 3 2000

## CONTENTS

### *Full Papers*

- |   |  |     |
|---|--|-----|
| The genus <i>Atractus</i> (Serpentes: Colubridae) in north-eastern Argentina  | A. R. GIRAUDO & G. J. SCROCCHI                         | 81  |
| Egg retention and mortality of gravid and nesting female chameleons ( <i>Chamaeleo chamaeleon</i> ) in southern Spain | M. C. BLÁZQUEZ, C. DÍAZ-PANIAGUA & J. A. MATEO         | 91  |
| Early Pleistocene herpetofauna from Cava Dell'Erba and Cava Pirro (Apulia, southern Italy)                            | M. DELFINO & S. BAILON                                 | 95  |
| Breeding migration and oviposition of the Chinhai salamander, <i>Echinotriton chinhaiensis</i>                        | F. XIE, L. FEI, C. YE, C. CAI, Z. WANG & M. SPARREBOOM | 111 |

### *Forum*

- |   |   |     |
|---|---|-----|
| Misconceptions about colour, infrared radiation, and energy exchange between animals and their environments | K. E. NUSSEAR, E. T. SIMANDLE & C. R. TRACY | 119 |
|---|---|-----|

### *Book Reviews*

123