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FRONT COVER: Viviparous lizard (Lacerta vivipara) (© Stuart Harrop)

THE MIDDLE PLEISTOCENE HERPETOFAUNA OF VALDEMINO CAVE (LIGURIA, NORTH-WESTERN ITALY)

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The herpetofauna from the Middle Pleistocene cave deposit of Valdemino (Borgio Verezzi, Liguria, north-western Italy) is represented by the following taxa: *Triturus* sp., *Speleomantes* sp., *Pelodytes punctatus, Bufo bufo, Hyla* gr. *H. arborea, Rana dalmatina, Testudo hermanni, Tarentola* cf. *T. mauritanica, Anguis fragilis, Lacerta* gr. *L. viridis,* Lacertidae indet., *Coronella* cf. *C. austriaca, Elaphe* sp., *Hierophis viridiflavus, Malpolon monspessulanus,* Colubrines indet., *Natrix natrix* and *Vipera aspis.* The most striking characteristic of the Valdemino assemblage is its modernity: all the identified taxa are members of the modern herpetofauna of western Liguria, including *Pelodytes* and *Malpolon* (identified for the first time in the Italian fossil record), that nowadays differentiate the western Ligurian herpetofauna from that of all the neighbouring Italian regions. The modernity of the herpetofauna sharply contrasts with the associated mammal fauna that still hosts, among others, Barbary ape, elephant, rhinoceros, leopard and sabre-toothed tiger. The assemblage testifies that the Ligurian herpetofauna was already established in the Middle Pleistocene and that it is not the result of post Würmian dispersal, although cyclical immigrations (from Iberian or French refugia) during warm stages, followed by extinctions during the cold ones, cannot be ruled out.

Key words: amphibians, Malpolon, Pelodytes, reptiles, Speleomantes

INTRODUCTION

The Quaternary history of the Ligurian herpetofauna is almost unknown: the only attempts to depict its evolutionary history have been made by Arillo et al. (1974) and Sindaco (1998) who expressed some considerations based almost exclusively on the modern distribution of taxa. So far, the fossil record of the Ligurian herpetofauna has been of little help, in being rather scarce and limited to a few remains found in the renowned prehistoric localities of "Arene Candide" (Morelli, 1891a; Sorrentino, 1995, 1999) and "Balzi Rossi" (Brocchi, 1879; Brocchi & Rivière, 1886; Boule, 1906, 1919), or in caves such as those of Pietra Ligure (Morelli, 1891b; Issel, 1892; Delfino, 2002), Borgio Verezzi (Issel, 1892) and Bergeggi (Morelli, 1891a). Nearly all the remains have been referred to the genus Bufo or to chelonians belonging to the genera Emys and Testudo, but since they have not been usually described or illustrated, a revision is necessary. The same can be said for reports of "Zamenis viridiflavus" and Lacerta viridis (Boule, 1906), and particularly Timon lepidus and Varanus (Morelli, 1891a, b); the Varanus dentary is unfortunately no longer available and even though it has been described by Morelli, it is not possible to refer it with confidence to any saurian (Delfino, 2002).

The only Ligurian site excavated with modern and stratigraphic criteria is the Valdemino cave, a fossiliferous locality in Borgio Verezzi (Savona Province), whose faunal list published by Tozzi (1969) comprises also a small herpetofauna represented by Bufo bufo, Testudo hermanni, Lacerta sp. and "Ophidia" indeterminate.

The present paper deals with the new and abundant amphibian and reptile remains of the Valdemino Cave that have been partly studied by Delfino (2002).

MATERIALS AND METHODS

The Valdemino Cave is located in the Borgio village (Borgio Verezzi Commune), its entrance is 25 m above the sea level and its position can be summarized as follows: I.G.M. sheet of Albenga, tablet of Loano, F° 92 II NW, Lat. 44,1633°N, Long. 12,4523°E (Tozzi, 1969; Fornasiero, 1989).

The fossil herpetofauna here described comes from three different stratigraphic units here called the Ancient, the Middle and the Recent Units. The Ancient fossil assemblage (units from 20 to 24) have been referred to the Middle Pleistocene and more in particular to the "Isernia Faunal Unit" (700,000 years before present approximately) that corresponds to the Galerian Mammal Age (for large mammal students) and to the beginning of the Toringian (for small mammal students; see Sala, 1992, and Gliozzi et al., 1997). The Recent assemblage (units 26 and 27) is relatively younger: it precedes the last glacial phase (Würmian) and therefore an early Late Pleistocene age cannot be ruled out; a precise chronological allocation is still not available and, according to Nocchi & Sala (1997), it is here considered as post-Galerian. The Middle Unit (25) is nearly sterile and its age could be similar to one of the others, or intermediate.

The remains here described have been collected during the 1989 fieldwork (Fornasiero, 1989) and are stored in the palaeontological collections of the "Museo

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Civico" of Finale Ligure with the collection numbers VAL MF 1-1549.

No distinction has been made in the section "Referred material" between perfectly preserved or fragmentary remains. The number between square brackets, that follows the section "Referred material", represents the total number of remains assigned to a given taxon.

The chelonian material is represented by few skeletal fragments and not by shell remains although abundant bony plates are stored in the same collection.

The remains are relatively well preserved and are totally disarticulated but not always completely free of the matrix, that sometimes covers the bones with a thin crust.

SYSTEMATIC STUDY

AMPHIBIA LINNAEUS, 1758

Nearly one sixth (267 remains) of the herpetofauna remains is represented by amphibians. Anurans are much more common than caudates. Altogether, six taxa (two caudates and four anurans) have been identified.

CAUDATA SCOPOLI, 1777

Caudates are very rare: only six remains belong to this order. Family Salamandridae and Plethodontidae are represented.

SALAMANDRIDAE GOLDFUSS, 1820

Triturus Rafinesque, 1815 Triturus sp. (Fig. 1)

Referred material. Ancient unit: trunk vertebra: 1. [total 1]

Vertebra. A single fragmentary vertebra (VAL MF 1) shows the following characteristics: opisthocoelous body, hint of a postcondilar constriction, prezygapophyseal facets oval-shaped and antero-laterally oriented, double rib-bearers caudally directed and linked by a bony plate, deeply concave anterior margin of the neural arch, neural spine present but (at least anteriorly) very low, subcentral foramina present although different in size and development (the left one being much wider), ventral connections between lower rib-bearer and the vertebral body not much developed on both sides. The vertebra lacks right rib-bearers, the tip of the left prezygapophyses and the posterior area of the neural arch (postzygapophyses included). The cotyle rim is partially eroded. The total centrum length can be estimated in 3.3 mm.

The morphology and the size of the vertebra match well with a caudate of the genus *Triturus* (among others: Haller-Probst & Schleich, 1994) and of *T. carnifex* (Laurenti, 1768) in particular (which lives few tens of kilometres north of the site; Raineri in Doria & Salvidio, 1994) because of the concavity of the anterior margin of the neural spine; the material is however too scarce and fragmented to allow a reliable identification at specific rank. PLETHODONTIDAE GRAY, 1850

Speleomantes Dubois, 1984 Speleomantes sp. (Fig. 1)

Referred material. Ancient unit: trunk vertebra: 4. [total 4]

Vertebra. Four vertebrae found in the same stratigraphic unit (V90 27 B/5) share the presence of a biconvex-amphicoelous centrum and only one pair of rib-bearers on each side (only one vertebra seems to show traces of a second pair of rib-bearers). In dorsal view: neural arch with a distinct interzygapophyseal constriction; anterior margin widely concave and posterior one with median concavity delimited by two pointed convexities (shorter than the posterior margins of the postzygapophyses); rib-bearers slightly bent and posteriorly directed; prezygapophyseal facets ovalshaped and antero-laterally directed. In ventral view: vertebral body hour-glass-shaped being laterally delimited by a deep furrow medially constricted; rib-bearers posteriorly connected to the vertebral body by a small lamina; prezygapophyseal facets with the same shape of the prezygapophyseal ones. In lateral view: vertebral body with a marked ventral concavity (the vertebral body is hour-glass-shaped); distinct roundish foramen located posteriorly to the rib-bearers; neural spine hardly visible although a little more pronounced in the anterior

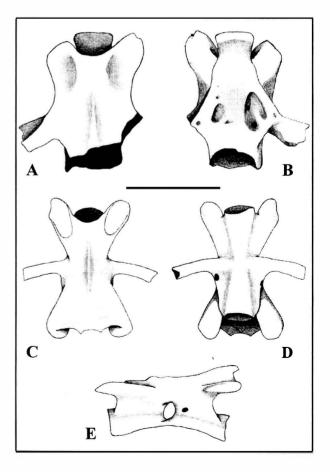


FIG. 1 *Triturus* sp., A, B: trunk vertebra (VAL MF 1), dorsal and ventral views. *Speleomantes* sp., C, D, E: trunk vertebra (VAL MF 2), dorsal, ventral and left lateral view. Scale = 2 mm.

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section. In cranial view: cotyle roundish; neural canal relatively wide; prezygapophyses nearly horizontal. In caudal view: cotyle and neural canal opening similar to the anterior ones; neural arch moderately vaulted.

The total centrum length of the best-preserved vertebra (VAL MF 2) is approximately 2.3 mm.

By the presence of amphicoelous vertebral bodies, lateral *foramina* for the intravertebral exit of spinal nerves and rib-bearers not connected to the body by wide body plates, it is possible to ascribe these vertebrae to the genus *Speleomantes*, the only European member of the family Plethodontidae (Deiana & Serra, 1978; Estes, 1981).

The taxonomy of this genus has been thoroughly discussed by Lanza *et al.* (1995) who considered seven species valid, widespread in south-western France, mainland Italy and Sardinia, that are "more differentiated at a genetic rather than morphological level" and whose "identification can be carried out also on the basis of the geographical provenience".

Unfortunately, none of the detailed osteological characters described by these authors can be applied to isolated bones or fossils. Moreover, the allocation of fossil material at specific rank based only on geographical provenience, usually inadvisable, is particularly tenuous in the case of several species with close and restricted modern ranges. The material is therefore referred at genus rank even if the only species living at present in the area is *S. strinatii* Aellen, 1958 (Salvidio in Doria & Salvidio, 1994; Lanza *et al.*, 1995).

CAUDATA INDET.

Referred material. Ancient unit: femur: 1. [total 1] A single caudate femur does not show features that allow it to be referred to the taxa identified above. It is therefore referred to Caudata indeterminate; since it could reasonably belong to these taxa, Caudata indet.

ANURA RAFINESQUE, 1815

will be not reported in the faunal list.

The majority of the amphibian fossils are anurans (261 remains; 98% of the amphibians) referable to the families Pelodytidae, Bufonidae, Hylidae and Ranidae. A relatively high number of meaningless fragments (123) has been allocated simply at order level.

PELODYTIDAE BONAPARTE, 1850

Pelodytes Fitzinger in Bonaparte, 1838 Pelodytes punctatus (Daudin, 1802) (Fig. 2)

Referred material. Ancient unit: ilium: 2. [total 2] *llium.* Two small ilia (the total length of the best preserved, almost complete, fragment is nearly 11 mm -VAL MF 3; the other is more fragmentary but should have belonged to a larger specimen -VAL MF 4) are characterized by the absence of ilial crest, preacetabular and supracetabular *fossae*, the presence of well developed dorsal and ventral acetabular expansion and of a distinct groove that separates the dorsal acetabular expansion from the ilial shaft.

All these characteristics are shared by the genera *Pelobates* and *Pelodytes*, but the weak development of the interiliac articulation (the postero-medial surface is rather smooth and not striated) and the presence of a small tubercle perceptible on the dorsal margin of the dorsal acetabular expansion, refers them to the genus *Pelodytes* (Böhme, 1977; Bailon, 1991, 1999).

Moreover, the lateral surface of the dorsal acetabular expansion laterally protrudes in caudal view as in *Pelodytes* (it does not protrude in the comparison material of *Pelobates*; compare Tab. 19 F with 19 G, H in Bailon, 1999: 36, and also Tab. 10 F, M with 10 E, L in Böhme, 1977: 296) and even though this character is not explicitly reported in literature, it could have some taxonomic weight.

The fossil material is referred to *Pelodytes punctatus*, the only modern and Quaternary European representative of the genus (not considering the Trans-Caucasian species; Kuzmin in Gasc *et al.*, 1997; Guyétant in Gasc *et al.*, 1997).

Nowadays *Pelodytes punctatus* has the eastern edge of its range in the Apennines between Liguria and Piedmont; due to its punctuated distribution (perhaps underestimated because of its secretive habits) and high human pressure, it is one of the Italian amphibians most endangered with extinction. Some small populations,

FIG. 2. *Pelodytes punctatus*, A, B, C: right ilium (VAL MF 3), lateral, caudal and medial views; D, E, F: right ilium (VAL MF 4), lateral, caudal and medial view. Scale = 2 mm.

living only few kilometers far from the site, are known (Sindaco in Doria & Salvidio, 1994).

BUFONIDAE GRAY, 1825

Bufo Laurenti, 1768 Bufo bufo Linnaeus, 1758 (Fig. 3)

Referred material. Recent unit: sphenethmoid: 1; parasphenoid: 1; humerus: 3; scapula: 1; femur: 5; tibio-fibula: 6; ilium: 8; "atlas": 1; trunk vertebra: 5; sacrum: 1; urostyle: 1. Middle unit: radio-ulna: 1. Ancient unit: humerus: 1; radio-ulna: 2; femur: 2; tibio-fibula: 5; ilium: 1; trunk vertebra: 2; urostyle: 2; indet.: 1. [total 50]

Sphenethmoid. One sphenethmoid (VAL MF 6) is relatively large and wider than long (length: 11.5 mm; width: 9.1 mm). Anthrum pro lobo olfactorio wide but not much deep and sella amplificans only slightly developed.

llium. Several ilia, some of which are very large, are devoid of either preacetabular and supracetabular *fossae* and have cylindrical ilial shafts (lacking ilial crest) and pronounced dorsal prominences (= *tuber superior*) without distinct tubercles.

Femur. The *crista femoris* is usually low and flattened proximally.

The described features unequivocally characterize the species *Bufo bufo* (Böhme, 1977; Sanchiz, 1977; Bailon, 1999). The bulk of the remains referred to this taxon are large and robust and some of them would have belonged to very large specimens: 44 mm is the maximum length for the humeri, 31.6 mm for radio-ulnae and 39.6 mm for tibio-fibulae (they all lack the articular surfaces); *B. bufo* is by far the largest Middle Pleistocene anuran of Europe. This species is at present widespread across Liguria (see map of Schiavo in Doria & Salvidio, 1994) and could be the commonest anuran.

HYLIDAE GRAY, 1825

Hyla Laurenti, 1768 Hyla gr. H. arborea (Linnaeus, 1758) (Fig. 3)

Referred material. Ancient unit: ilium: 1; trunk vertebra: 1. [total 2]

Alium. A small ilium (VAL MF 7) coming from the ancient unit differs from the rest of the ilia in having a one lobed *tuber superior* (distinct but not particularly raised) and ventral acetabular expansion developed in a relatively wide *lamina*. The preacetabular and supracetabular *fossae* and the ilial crest are lacking.

Vertebra. In the same stratigraphic unit there is a trunk vertebra (VAL MF 8) as small as the ilium; it is procoelous and devoid of neural crest, with a wide neural canal, short neural arch (in a cranio-caudal sense) showing a deep anterior concavity, condyle and cotyle roundish and characteristically small with respect to the vertebral body.

These two remains are referred to the genus *Hyla* to which the morphology fully agrees (Böhme, 1977; Bailon, 1999). Due to the poor knowledge of the osteology of the five species of Mediterranean tree frogs that are recognized at present, it is advisable not to identify fragmentary fossil remains at species rank (Delfino & Bailon, 2000); therefore the described material is referred to the *Hyla arborea* group.

Following Emanueli (in Doria & Salvidio, 1994), two species of this genus live at present in W. Liguria, *H. intermedia* Boulenger, 1882 (still included in *H. arborea* in the quoted papers) and *H. meridionalis* Boettger, 1874 but only the latter is found at present in the surroundings of the Valdemino cave and in the Mediterranean vegetational belt of Western Liguria.

RANIDAE GRAY, 1825

Rana Linnaeus, 1758

Rana dalmatina Fitzinger in Bonaparte, 1838 (Fig. 4)

Referred material. Recent unit: maxilla: 11; parasphenoid: 1; scapula: 6; coracoid: 4; humerus: 11; radioulna: 4; ilium: 9; femur: 1; tibio-fibula: 21; trunk vertebra: 3; sacrum: 3; urostyle: 4. Middle unit: scapula: 1. Ancient unit: humerus: 1; radio-ulna: 1; ilium: 2; trunk vertebra: 1. [total 84]

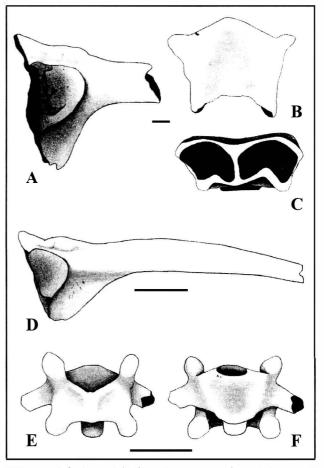


FIG. 3. *Bufo bufo*, A: right ilium (VAL MF 5), lateral view; B, C: sphenethmoid (VAL MF 6), dorsal and cranial view. *Hyla* gr. *H. arborea*, D: right ilium (VAL MF 7), lateral view; E, F: trunk vertebra (VAL MF 8), dorsal and ventral view. Scale = 2 mm.

llium. Several ilia show the characteristic morphology of the genus *Rana*: very well developed and proximally vertical ilial crest; supracetabular *fossa* generally present, preacetabular one lacking; ventral acetabular expansion relatively wide; slender *junctura*; dorsal prominence well developed and particularly elongated, forming with the dorsal acetabular expansion an angle wider than 90°, and with dorsal margin gently sloping to the ilial crest (with no sign of a step).

The slenderness of the *junctura* and the shape of the dorsal prominence allow to refer the material to *R. dalmatina* and to exclude *R. temporaria* Linnaeus, 1758 (Böhme, 1977; Bailon, 1999), the only other brown frog that inhabits W Liguria at present (Barbieri in Doria & Salvidio, 1994).

To the same taxon are tentatively referred all the *Rana* remains – although they are not diagnostic to species level, there is no evidence of the presence of different species. All the male humeri have a thin diaphysis and show a mesial crest (*crista medialis*) proximally extended and dorsally bent in a fashion that is exclusive of brown frogs (Bailon, 1991, 1999); the same can be said about the development toward the *pars suprascapularis* of the internal crest of the scapula.

ANURA INDET.

Referred material. Recent unit: humerus: 2; femur: 1; tibio-fibula: 15; ilium: 1; ischium: 1; urostyle: 1; indet.:

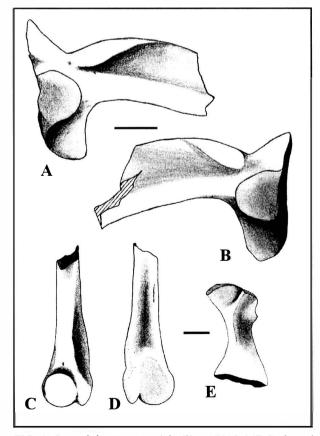


FIG. 4. *Rana dalmatina*, A: right ilium (VAL MF 9), lateral view; B: left ilium (VAL MF 10), lateral view; C, D: right male humerus (VAL MF 11), ventral and dorsal view; E: left scapula (VAL MF 12), internal view. Scale = 2 mm.

57; Middle unit: indet: 1; Ancient unit: scapula: 1; humerus: 1; radio-ulna: 4; tibio-fibula: 9; trunk vertebra: 11; indet: 18. [total 123]

Part of the anuran material has been referred to order level since it is represented by unidentifiable fragments or non-diagnostic elements. A short and stout scapula (V89 20 A) shows a developed *margo anterior* as in *Pelodytes* but it is too fragmentary to identify it with confidence. The taxon Anura indet. is not reported in the faunal list since all the undetermined material could well belong to the identified species.

Reptilia Laurenti, 1768

Reptiles are much more common than amphibians being represented by 1282 remains. Chelonians, lizards and snakes belonging respectively to 1, 4 and 7 taxa have been identified.

CHELONII BRONGNIART, 1800

Chelonians are very well represented at Valdemino and abundant are the shell fragments. The few non-shell remains here studied do not properly exemplify the chelonian abundance. Only the family Testudinidae has been identified.

TESTUDINIDAE BATSCH, 1788

Testudo Linnaeus, 1758 Testudo hermanni Gmelin, 1789

Referred material. Middle unit: scapula/acromion: 1. Ancient unit: dentary: 1; coracoid: 3; caudal vertebra: 10. [total 15]

The few chelonian remains here studied are referred to *Testudo hermanni* accordingly to Tozzi (1969) who first quoted its presence in the site. Although not diagnostic as shell elements, the remains here listed show a morphology that fits well with land tortoises (i.e. the coracoid widens caudally forming a triangle).

At present, *Testudo hermanni* can be considered as probably extinct in Liguria because of overcollection and habitat alteration or destruction; all the specimens found in the region seem to be allochthonous (Jesu in Doria & Salvidio, 1994).

LACERTILIA OWEN, 1842

Altogether, 261 remains have been referred to saurians; they belong to three families: Gekkonidae, Anguidae and Lacertidae.

Gekkonidae Gray, 1825

Tarentola Gray, 1825

Tarentola cf. T. mauritanica (Linnaeus, 1759) (Fig. 5)

Referred material. Recent unit: dentary: 2; maxilla: 1; frontal: 1. [total 4]

Maxilla. A left maxilla (VAL MF 13) is 6.7 mm long and nearly complete (only the prefrontal process is partly eroded): 31 are the teeth positions; all but one retain teeth that are pleurodont, isodont, long, slender, cylindrical with conical and smooth apices devoid of crests and accessory cusps; some of the apices of the first teeth are caudally oriented; reabsorption pits variably sized developed at the base of many teeth; external surface of the prefrontal process with seven roundish *foramina* (nearly aligned at its base) but smooth and devoid of any ornamentation; a small hole pierces the process at mid height in correspondence of the third lower *foramen*.

Dentary. Two fragmentary dentaries are characterized by a high number of teeth whose morphology is similar to that of the maxillary ones. The Meckel's groove is partially covered by the dentary and therefore it opens in a posterior position.

Frontal. A frontal (VAL MF 14) made by the complete median fusion of the two paired frontals (the suture is not visible) is associated with the described maxilla. It is characterized by: lateral margins (descending processes), ventrally folded, meet and fuse medially delimiting a relatively wide canal; dorsal surface slightly concave medially without traces of dermal ornamentations and furrows between scales; middle region of the bone with a marked interorbital constriction if seen in dorsal view.

The described tooth morphology and the unpaired (fused) and dorsally smooth frontal, as well as the size

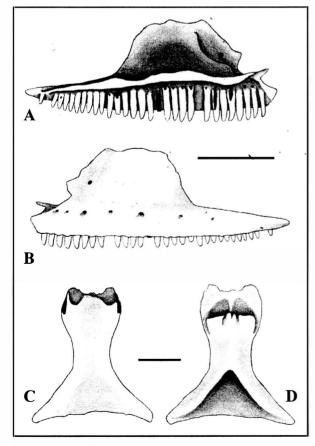


FIG. 5. *Tarentola* cf. *T. mauritanica*, A, B: left maxilla (VAL MF 13), internal and external view; C, D: frontal (VAL MF 14), dorsal and ventral view. Scale = 2 mm.

itself of the elements, clearly indicate the presence of a member of the family Gekkonidae (see summaries and literature in Estes, 1983; Bailon, 1991) of a size comparable to that of T. mauritanica or (of a large) H. turcicus. Following Bailon (1991) the degree of robustness and position of the inner premaxillary permit discrimination between T. mauritanica and H. turcicus: this process is relatively more robust and less inclined in the former species than in the second. Moreover, when observed in dorsal view, the sub-orbital region of the horizontal *lamina* is wider and more robust in *T. mauritanica* than in H. turcicus, and the prefrontal process is so dorsomedially bent in T. mauritanica that the zygomatic process is partially covered (more straight and not so covering in H. turcicus). The fossil maxilla agrees with the description of T. mauritanica but since the comparison material shows some variability, the fossil remains are tentatively referred to T. mauritanica.

This species is the only representative of the genus in Europe and the commonest gecko of Liguria where it is presently widespread in nearly all the Mediterranean belt of the region (see map in Jesu in Doria & Salvidio, 1994).

ANGUIDAE GRAY, 1825

Anguis Linnaeus, 1758 Anguis fragilis Linnaeus, 1758 (Fig. 6)

Referred material. Recent unit: dentary: 7; maxilla: 2; trunk vertebra: 3; caudal vertebra: 5. Ancient unit: trunk vertebra: 11; caudal vertebra: 1. [total 29]

Dentary. One of the most informative elements is a small left dentary (7.1 mm; VAL MF 15) that is nearly complete even if almost totally devoid of teeth and the angular process is broken off. In internal view: intramandibular septum visible inside the Meckel's groove; the latter is relatively wide in the posterior area of the dentary but very small more anteriorly (where it runs ventrally) and slightly enlarged again in the symphysary area; symphysis well defined and posteromedially directed; horizontal lamina medially inclined, showing a concave profile; it develops a small splenial spine under the ninth tooth; anterior-inferior alveolar for amen opens near the spine; most likely 10 teeth position are present (horizontal lamina has an irregular surface); three retain teeth that are subpleurodont and conical; the apices are worn or broken; the seventh and eighth teeth are strongly bent backward (and slightly lingually); the coronoid process is nearly as long as the supra-angular one but a little smaller; both have a rounded tip. In lateral view: four foramina open at mid height on the external surface of the dentary; the anterior one is the biggest.

Another left dentary (VAL MF 16) is nearly as long as the previous (7.2 mm) but more damaged in the posterior region: the angular process is broken off and the horizontal lamina is partially damaged. Its morphology is comparable to that already described with the difference that supra-angular process seems to be a little

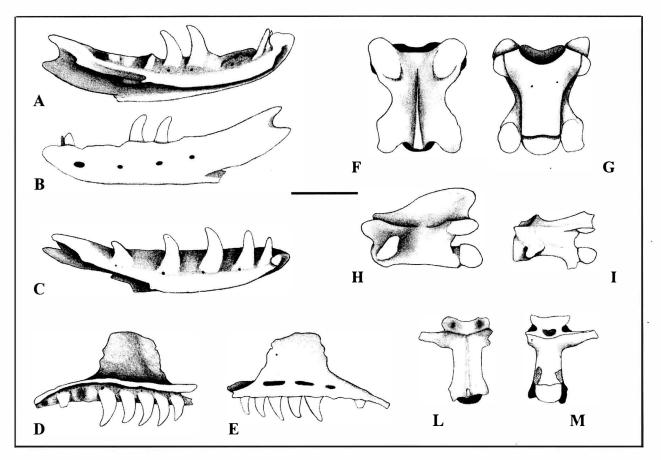


FIG. 6. Anguis fragilis, A, B: left dentary (VAL MF 15), internal and external view; C: left dentary (VAL MF 16), internal view; D, E: left maxilla (VAL MF 17), internal and external view; F, G, H: trunk vertebra (VAL MF 18), dorsal, ventral and left lateral view; I, L, M: caudal vertebra (VAL MF 19), dorsal, ventral and left lateral view. Scale = 2 mm.

longer that the coronoid one. The total number of teeth position is 10, while five are the preserved teeth.

Maxilla. The best-preserved maxilla (VAL MF 17) is 4.8 mm long: the prefrontal process seems to be slightly eroded; internal premaxillary process and the zygomatic one are partly broken; eight (or maybe nine) teeth positions are visible; six teeth are preserved; they are subpleurodont, conical, caudo-laterally bent, not striated; apices pointed (if not eroded or broken); each tooth has a small *foramen* at the base; lateral surface of the prefrontal process without any sign of dermal ossification or furrow; three wide (elongated and deep) *foramina* aligned at the base of the process.

Vertebra. A few trunk vertebrae share the following characteristics: vertebral body procoelous, moderately elongated, ventral surface flattened and with parallel margins (in the posterior section); condyle and cotyle moderately depressed; two small subcentral *foramina* usually present; prezygapophyses antero-laterally directed, dorsally tilted and devoid of processes; neural spine usually well developed and sometimes relatively high; distinct interzygapophyseal constriction in dorsal view.

Some caudal vertebrae display haemapophyses fused to the posterior ventral surface of the vertebral body, long transverse processes flattened and laterally directed, and autotomic line that separates the cotylar region from the rest of the vertebra (it runs in the anterior area of the transverse processes).

All the described characteristics are typical of the family Anguidae and of the genus Anguis in particular, the sole that shares with the fossil material the number and shape of dentary and maxillary teeth as well as the shape of the vertebrae (Klembara, 1979, 1981, 1986; Bailon, 1991). All the anguid material is referred to Anguis fragilis, the only species known in the European Quaternary because Anguis stammeri Brunner, 1954 (Middle Pleistocene of Germany) has been recently considered a large sized form of A. fragilis (Bailon, 1991; Holman, 1998). Anguis cephallonicus Werner, 1894, a living species recently revalidated (Cabela in Gasc et al., 1997), has not been taken into consideration since it is endemic to the Peloponnese and to the southern Ionian Islands and, moreover, its comparative osteology is still unknown.

A. fragilis is widespread and common in Liguria at the present time (Schiavo in Doria & Salvidio, 1994).

LACERTIDAE BONAPARTE, 1831

Lacerta Linnaeus, 1758 Lacerta gr. L. viridis (Laurenti, 1768) (Fig. 7)

Referred material. Recent unit: dentary: 19; maxilla: 6; teeth bearing bone: 1; trunk vertebra: 2; caudal vertebra: 3. Ancient unit: dentary: 6; premaxilla: 2; maxilla: 5; teeth bearing bone: 1; parietal: 1; articular: 1; humerus: 2; coxal: 1; femur: 1; trunk vertebra: 37; sacral vertebra: 3; caudal vertebra: 19. [total 110]

Dentary and maxilla. The presence of pleurodont and cylindrical teeth distinguishes some dentaries and maxillae. The teeth show usually two cusps (a very small anterior cusp and a bigger posterior one) but the anteriormost teeth are monocuspidate while the posteriormost can have three cusps. Although none of the dentaries is perfectly preserved, it is possible to state that the Meckel's groove is wide along the entire length of the dentary. The largest dentaries have a dental *lamina* of 10.5 and 11.5 mm.

Parietal. A fragmentary parietal (VAL MF 21) of medium size $(8.3 \times 6.6 \text{ mm})$ shows a dorsal surface with an evident *crusta calcarea* and the imprints of the boundaries among the frontoparietals, parietals and interparietal scales; the pineal *foramen* opens in the middle of the interparietal scale area, the shape of which is slightly irregular; it is not clear wether its asymmetric posterior prolongation represents a narrow occipital scale (without a marked interparietal-occipital boundary) or not.

Vertebra. Some trunk vertebrae show a procoelous vertebral body, moderately elongated, ventrally convex, with condyle and cotyle slightly oval or subcircular; prezygapophyses dorsally tilted (without processes) and with oval facets; neural spine high and running along almost all the neural arch (only the area between prezygapophyses is free); a sort of haemal keel well defined at least anteriorly; no traces of zygosphene-zygantrum articulations; the largest vertebra has a centrum 4.2 mm long.

By the tooth morphology (pleurodont, cylindrical, bicuspid teeth) of several teeth bearing bones it is possible to identify the family Lacertidae. The size itself of the remains allow to exclude the smallest member of the

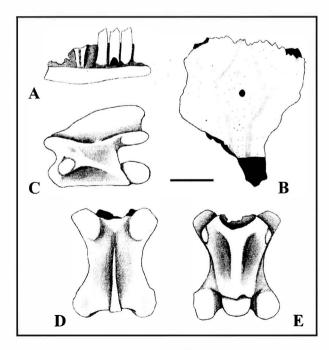


FIG. 7. *Lacerta* gr. *L. viridis*, A: right dentary fragment (VAL MF 20), internal view; B: parietal (VAL MF 21), dorsal view; C, D, E: trunk vertebra (VAL MF 22), left lateral, dorsal and ventral view. Scale = 2 mm.

family (up to the size of a big *Podarcis*) and hypothesize the presence of a medium-sized member of the genus Lacerta. The length of the dental lamina, as well as the length and width of the parietal, fall in the ranges of both L. viridis (complex) and Timon lepidus (Daudin, 1802) reported by Barahona & Barbadillo (1997; respectively bigger than 8.4 mm, 6 mm and 5.7 mm) but the centrum length of the trunk vertebrae (4.2 mm maximum) allows referral of the material to L. viridis (in the sample studied by Barbadillo & Sanz, 1983, this length is never higher than 4.38 mm in L. viridis). The allocation at species rank of these remains is therefore based on their size: unfortunately the posterior area of the parietal is damaged and it is not possible to see the occipital scale whose shape is a diagnostic morphological character (Barahona & Barbadillo, 1997).

Since the modern *L. viridis* populations have been split into two species, *L. viridis* and *L. bilineata* Daudin, 1802 (Rykena, 1991; Amann *et al.*, 1997), whose comparative osteology has not been described, the fossil material is simply referred to the *L. viridis* group that includes both.

Nowadays, L. bilineata is quite a common lizard in Liguria (Schiavo in Doria & Salvidio, 1994).

LACERTIDAE INDET.

Referred material. Recent unit: dentary: 18; premaxilla: 1; maxilla: 7; teeth bearing bone: 4. Ancient unit: dentary: 52; premaxilla: 1; maxilla: 23; teeth bearing bone: 5; parietal: 1; humerus: 1; ilium: 1; cervical vertebra: 1; caudal vertebra: 2. [total 117]

Several lacertid remains of small size are simply referred to family rank since it is not possible to identify a genus with confidence. They could either belong to fullgrown *Podarcis* or to juvenile *Lacerta* specimens as well as to different taxa. The taxon Lacertidae indet. is therefore reported in the faunal list.

SAURIA INDET.

Referred material. Ancient unit: dentary: 1. [total 1] A dentary fragments devoid of teeth cannot be allocated at a rank lower than the order.

SERPENTES LINNAEUS, 1758

Snake vertebrae are by far the most common elements of the herpetofauna and therefore this order is the best-represented (1006 remains). Seven taxa belonging to two families, Colubridae and Viperidae, have been recognised.

COLUBRIDAE OPPEL, 1811

Coronella Laurenti, 1768

Coronella cf. C. austriaca Laurenti, 1768 (Fig. 8)

Referred material. Ancient unit: trunk vertebra: 31. [total 31]

Vertebra. Some of the smallest vertebrae (2.6 mm is the centrum length of the figured one; VAL MF 23) are

characterized by: depressed neural arch whose posterior margins are sometimes nearly straight sometimes slightly curved (if seen in caudal view); condyles and cotyles slightly oval; haemal keel narrow, long and nonwell defined; prezygapophyseal facets invariably damaged but should have been oval and at least two times longer than the processes; the latter are short, pointed and with a wide and robust base; parapophyses slightly bigger than the diapophyses; anterior margin of the zygosphene is nearly straight; neural spine low and reaching anteriorly the middle of the zygosphene.

The small size of the vertebra, along with the shape of the prezygapophyseal processes and, overall, the shape of the posterior end of the neural arch, permit the material to be referred to the genus *Coronella* and more precisely to *C. austriaca* (Szyndlar, 1984). Due to the variability of these structures in the modern species (Szyndlar, 1991*a*), it is not possible to allocate this material with confidence and therefore the taxonomic particle "cf." has been introduced.

Both *C. austriaca* and *C. girondica* (Daudin, 1803) are present nowadays in Liguria (and in the area of the palaeontological site as well) but the latter is much more common in the region (Doria in Doria & Salvidio, 1994).

Elaphe Fitzinger, 1833 *Elaphe* sp. (Fig. 8)

Referred material. Recent unit: trunk vertebra: 1 [to-tal 1]

Vertebra. A trunk vertebra (VAL MF 24) is quite different from the others because it is more cranio-caudally

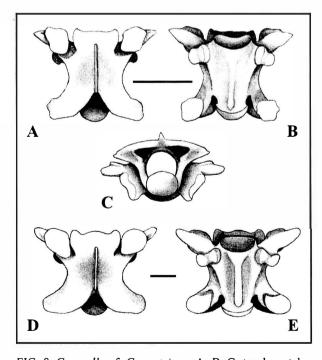


FIG. 8. *Coronella* cf. *C. austriaca*, A, B, C: trunk vertebra (VAL MF 23), dorsal, ventral and caudal view. *Elaphe* sp., D, E: trunk vertebra (VAL MF 24), dorsal and ventral view. Scale = 2 mm.

compressed and shows small prezygapophyseal processes. In dorsal view: the vertebra is "×" shaped; zygosphene crenate; prezygapophyseal facets oval (but with an anterior roundish profile); prezygapophyseal processes relatively small and with rounded tips. In ventral view: haemal keel narrow with well-defined margins, not ventrally flattened and not posteriorly widened; diapophyses bigger than the parapophyses. In cranial view: prezygapophyses nearly horizontal and zygosphene slightly convex. In caudal view: neural arch not particularly high and with straight and not vaulted dorsal margins. In lateral view: neural spine not high and overhanging posteriorly only. The centrum length is 4.4 mm.

This description fits with the morphology of the genus Elaphe (see among others, Szyndlar, 1991a; Bailon, 1991) and all the mentioned characteristics fall into the variability of either E. longissima (Laurenti, 1768) [inclusive of E. lineata (Camerano, 1891)] or E. scalaris (Schinz, 1822). Following Bailon (1991) it is possible to discriminate between these two species on the basis of the more square shape of the vertebral body of E. scalaris whose CL/NAW ratio is proximate to 1 (1.05). This ratio has a mean value of 1.15 in fossil or 1.4 in living E. longissima studied by Szyndlar (1991a). Although the ratio of the Valdemino vertebra is 1.19 (CL 4.4 mm / NAW 3.7 mm) and therefore it falls in the range of E. longissima, the material is too scarce to exclude the presence of E. scalaris, a species whose morphology and variability are largely unknown. Investigations recently carried out by Helfenberger (2001) and Utiger et al. (2002) suggest the latter species should be separated from Elaphe and included in Rhinechis Michahelles (in Wagler), 1833; such a proposal has not been taken into consideration in this work.

The Western Liguria hosts both *E. longissima* and *E. scalaris* at present, but while the former is relatively common (Poggi in Doria & Salvidio, 1994), the latter has been found only once and very close to the border with France (Ferri in Doria & Salvidio, 1994).

Hierophis Fitzinger, 1843 Hierophis viridiflavus (Lacépède, 1789) (Fig. 9)

Referred material. Recent unit: maxilla: 1; trunk vertebra: 1. Ancient unit: parabasisphenoid: 1; compound bone: 1; trunk vertebra: 19. [total 23]

Maxilla. An edentulous right maxilla (VAL MF 25) is broken at both extremities. Assuming that the first tooth position is missing, the maxilla should have had 13 teeth positions followed by a short diastema (as long as one tooth position) followed in its turn by two last positions; the prefrontal process should correspond to the 6-8 positions and the ectopterygoid process to the diastema. Dorsally to the latter process, a distinct constriction is well delimited anteriorly but weakly posteriorly.

Basiparasphenoid. Although not complete (the parasphenoid process is broken off), a basiparasphenoid

(VAL MF 26) is quite informative because its surface, ridges included, is perfectly preserved.

In external view: evident pterygoid crests, sigmoid in shape, originate from well-developed basipterygoid processes and nearly meet medially, delimiting a small central area; postpterygoid area broad and showing a very weak basisphenoid crest; wide common *foramina* (resulting from union of the posterior orifice of Vidian canal with the cerebral *foramen*) give rise to a shallow furrow postero-laterally directed; anterior orifices of the Vidian canal open anteriorly to the pterygoid crest and are much smaller than the previous; posterior margin of the bone with two lateral lobes and a median, more pronounced, one. In internal view: the foramina for the *abducens* nerve open laterally and posteriorly to a wide pituitary fossa; only the base of the frontal crest is preserved.

Vertebra. Several trunk vertebrae are robust and relatively large in size: their centrum length generally exceeds 5 mm and one reaches 6.3 mm.

In dorsal view: prezygapophyseal facets usually ovalshaped (but sometimes nearly rectangular), prezygapophyseal processes long (a little less than the facets) and pointed; anterior margin of the zygosphene straight or concave. In ventral view: the parapophyses are usually well separated from the diapophyses, the haemal keel is always well delimited, high, ventrally

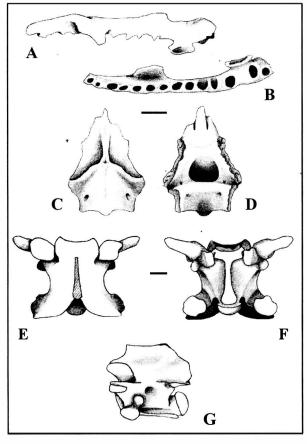


FIG. 9. *Hierophis viridiflavus*, A, B: right maxilla (VAL MF 25), medial and ventral view; C, D: basiparasphenoid (VAL MF 26), ventral and dorsal view; E, F, G: trunk vertebra (VAL MF 27), dorsal, ventral and left lateral view. Scale = 2 mm.

flattened and posteriorly expanded in a characteristic way. In cranial view: prezygapophyses approximately horizontal; dorsal margin of the zygosphene usually straight. In caudal view: neural arch high and vaulted. In lateral view: neural spine appears to be high and robust.

Some of the largest vertebrae (as the one figured) show a deeply concave zygosphene, evident epizygapophyseal spines an paracotylar tubercles, parapophyses distinctly larger than diapophyses and wide lateral foramina.

The morphology of the prezygapophyseal processes, haemal keel and posterior margin of the neural arch permits identification of *Hierophis viridiflavus* (cf. description and literature quoted in Szyndlar, 1984, 1991*a*; Bailon, 1991). Also the fossil maxilla matches well with the comparison material of this species in teeth positions numbers, presence and position of the frontal and ectopterygoid processes as well as of a short diastema. A slight difference concerns the dorsal constriction that is not so well delimited posteriorly (cf. Delfino & Bailon, 2000). The basiparasphenoid displays crests developed and located similarly to *H. viridiflavus* (cf. Bailon, 1991).

Today, *H. viridiflavus* is a very common snake in Liguria being present in all the suitable habitats (Cortesogno in Doria & Salvidio, 1994).

Malpolon Fitzinger, 1826

Malpolon monspessulanus (Hermann, 1804) (Fig. 10)

Referred material. Recent unit: trunk vertebra: 2. [to-tal 2]

Vertebra. Two large vertebrae (VAL MF 28 and 34) of the Recent unit (V91A 20B) can be grouped together on the basis of the following features. In dorsal view: zygosphene straight or slightly concave; prezygapophyseal facets oval-shaped (but the original morphology could have been different since they are eroded); the only preserved prezygapophyseal process is robust, long, apically rounded and antero-laterally directed in a characteristic fashion. In ventral view: vertebral body distinctly elongated, well delimited laterally by evident subcentral ridges; subcentral grooves well marked; haemal keel high, narrow, well delimited and, though not flattened, tends to progressively widen toward its caudal end; para- and diapophyses almost totally eroded. In cranial view: zygosphene convex and prezygapophyses horizontal. In caudal view: neural arch particularly high and with dorsal margin nearly straight (not vaulted). In lateral view: neural spine seems not to be high and overhanging on both sides (partially preserved in one vertebra only). The centrum length of the vertebrae is 6.4 and 6.5 mm (NAW is 5.1 and 5.0 respectively; CL/NAW is about 1.3 for both).

The material can be referred to *Malpolon monspessulanus* on the basis of the length and orientation of the prezygapophyseal processes, the elongation of the vertebral body, the shape of the haemal keel and of the posterior edge of the neural arch (Szyndlar, 1984, 1988; 1991*a*; Bailon, 1991).

Remarkable is the apparent absence of epizygapophyseal spines, structures regularly present in the modern comparison material ("le plus souvent presentes" following Bailon, 1991): since the vertebrae are slightly eroded and some edges smoothed, it is not know if these structures were originally present or not; even if they were absent, a proper taxonomic allocation of the two vertebrae is granted by several other reliable characters. Although it is advisable not to identify taxa on the basis of scarce and fragmentary fossil remains, as is the case of the two vertebrae here described, the morphology of this species is so characteristic that it is easily recognisable even if the material is relatively poor.

The modern range of M. monspessulanus includes W. Liguria, where the nominal subspecies reaches its eastern range limit (Ferri in Doria & Salvidio, 1994).

"COLUBRINES" INDET.

Referred material. Recent unit: trunk vertebra: 12. Ancient unit: trunk vertebra: 327. [total 339]

Vertebra. All the colubrid vertebrae, possessing haemal keel and not hypapophyses, but strongly damaged or showing mixed set of characters have been referred to the working taxon "Colubrines" indet. (*sensu* Szyndlar, 1984; Szyndlar, 1991a). Since they could belong to either the identified taxa or others, the taxon Colubrines indet. is reported in the faunal list.

Natrix (Laurenti, 1768) Natrix natrix (Linnaeus, 1758) (Fig. 11)

Referred material. Recent unit: maxilla: 1; compound bone: 1; trunk vertebra: 3. Ancient unit: compound bone: 3; trunk vertebra: 191. [total 199]

Maxilla. A right maxilla (VAL MF 29) lacks the area anterior to the prefrontal process and therefore it is not possible to estimate the teeth positions original number: 15 are those preserved, only four still host teeth (robust

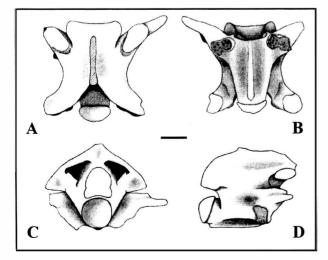


FIG. 10. *Malpolon monspessulanus*, A, B, C, D: trunk vertebra (VAL MF 28), dorsal, ventral, caudal and right lateral view. Scale = 2 mm.

and posteriorly curved); the size of the tooth sockets suggests that the last four teeth were particularly large (much larger than the preceding); both processes preserved, robust and mesio-ventrally projecting; area posterior to the ectopterygoid process dorsally bent. Maxilla "X" shaped in ventral view.

Compound bone. At least four compound bones share the following characters: medial flange hardly higher that the lateral flange (the mandibular *fossa* is therefore relatively shallow); retroarticular process robust and mesio-ventrally directed; supraangular *foramen* located far from anterior margin of the mandibular *fossa*; supraangular crest not present.

Vertebra. The morphology of many hypapophysisbearing vertebrae is rather similar.

In dorsal view: general appearance of the vertebra peculiarly elongated; anterior margin of the zygosphene slightly variable from concave to convex; prezygapophyseal processes long, particularly large, with rounded tips and often with a small anterior concavity; prezygapophyseal facets oval in shape; epizygapophyseal spines usually present. In ventral view: parapophyses well distinct (and more developed) from the diapophyses. In cranial view: prezygapophyses regularly horizontal (the ventral inclination is negligible); dorsal margin of the zygosphene variably shaped.

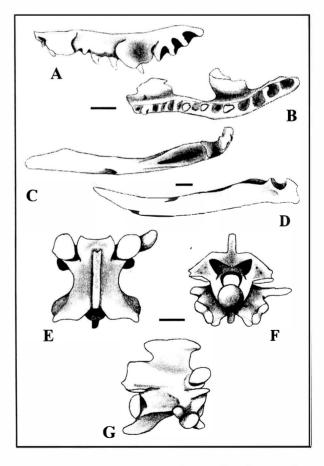


Fig. 11. *Natrix natrix*, A, B: right maxilla (VAL MF 29), medial and ventral view; C, D: left compound bone (VAL MF 30), dorsal and lateral view; E, F, G: trunk vertebra (VAL MF 31), dorsal, caudal and left lateral view. Scale = 2 mm.

In caudal view: neural arch distinctly vaulted (sometimes with an angle). In lateral view: neural spine always high and overhanging anteriorly and posteriorly; sometimes (mainly in large specimens) its dorsal edge is thickened; parapophyseal processes long, apically rounded and anteriorly directed; hypapophyses long, robust, sigmoid shaped and usually apically rounded (although pointed tips are not uncommon). Some of the vertebrae are very large: their centrum length is about 7 mm.

All of this material can be referred to the genus *Natrix* on the basis of the opisthomegadont maxilla, scarce depth of the mandibular fossa and the position of the supraangular foramen of the compound bone, and by several characteristics of the vertebrae (i.e. presence and shape of the hypapophyses as well as prezygapophyses and neural arch shape). It is possible to identify with reasonable confidence the presence of *N. natrix* on the basis of the roundish tips of the parapophyseal processes and hypapophyses (Szyndlar, 1984; 1991*b*, Holman, 1991; Ivanov, 1999*a*) although they show some variability in the fossil and modern comparative material.

All the three European species of the genus Natrix inhabit Liguria at present but only N. natrix and N. maura (Linnaeus, 1758) have been quoted in the area of the palaeontological site (Andreotti in Doria & Salvidio, 1994; Raineri in Doria & Salvidio, 1994; Salvidio in Doria & Salvidio, 1994).

VIPERIDAE LAURENTI, 1768

Vipera Laurenti, 1768 Vipera aspis (Linnaeus, 1758) (Fig. 12)

Referred material. Recent unit: trunk vertebra: 23. Ancient unit: maxilla: 1; trunk vertebra: 40. [total 64]

Maxilla. A right maxilla (VAL MF 32) is relatively well preserved: only the tip of the fang is broken off. The morphology of the fang base is masked by matrix. The prefrontal process is tall, highly developed and widens a bit apically, where it bends laterally. On the posterior surface (between the fang and the process) there is a relatively deep fossa delimited cranially by a small crest but "opened" on the sides. The fang is hollow, slender and its anterior surface shows a proximal orifice (the orifice for the venom duct) giving rise to a median line that marks the fang for its entire length. The total length of the maxilla (fang included) is 8.9 mm.

Vertebra. A peculiar set of characters allows some vertebrae to be grouped together. In dorsal view: clear interzygapophyseal constriction; prezygapophyseal facets oval and antero-laterally directed; prezygapophyseal processes very short and acute shaped; zygosphene anterior margin strongly crenate. In ventral view: parapophyses and diapophyses well separated; subcentral grooves usually more marked in the anterior area of the vertebral body. In cranial view: cotyle large and slightly depressed; paracotylar foramina present and well visible; parapophyseal processes exceeding the ventral margin of the cotyle; prezygapophyses dorsally tilted; dorsal margin of the zygosphene usually straight. In caudal view: the condyle wide and robust; the neural arch depressed and with straight dorsal margins. In lateral view: neural spine generally high (lower in posteriormost trunk vertebrae) and overhanging posteriorly only; parapophyseal processes anteroventrally directed (acute or rounded); hypapophysis usually long, robust and exceeding the condyle posteriorly. The largest vertebra is 4.2 mm long (CL).

The general morphology of the maxilla (i.e. its shortness and the presence of an hollow fang) and that of the trunk vertebrae (i.e. presence of hypapophyses, dorsally tilted prezygapophyses, ventrally directed parapophyseal processes, depressed and straight neural arch) indicates the family Viperidae, while the absence of a labial pit in the maxilla (that hosts the thermoreceptive organ) excludes the presence of the subfamily Crotalinae (Ivanov, 1999b). The general proportions of the vertebrae (among others, not particularly elongated - cf. Szyndlar & Rage, 1999) agrees with the V. aspis group, and although a distinction between adult V. aspis and subadult V. ammodytes (Linnaeus, 1758) (the two members of the group that can be reasonably taken into consideration) can be difficult, the material is abundant enough to identify with confidence the presence of V. aspis.

This species is the only viper that lives in Liguria at present (Borgo in Doria & Salvidio, 1994).

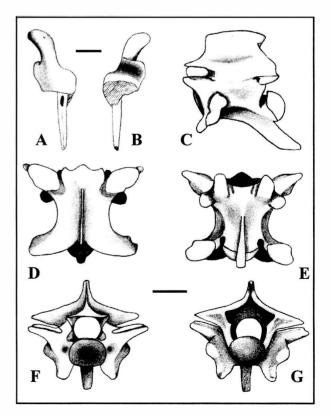


FIG. 12. *Vipera aspis*, A, B: right maxilla (VAL MF 32), antero-ventral and postero-dorsal view; C, D, E, F, G: trunk vertebra (VAL MF 33), left lateral, dorsal, ventral, cranial and caudal view. Scale = 2 mm.

SERPENTES INDET.

Referred material. Recent unit: dentary: 6; pterygoid: 2; teeth bearing bone: 5; trunk vertebra: 2; cloacal vertebra: 1; caudal vertebra: 8. Ancient unit: dentary: 6; maxilla: 4; teeth bearing bone: 1; compound bone: 9; vertebra: 155; cloacal vertebra: 1; caudal vertebra: 147. [total 347]

Several remains devoid of relevant structures because of extreme fragmentation, as well as some uninformative elements, such as caudal vertebrae, have been simply referred to order rank.

DISCUSSION

The Valdemino Cave yielded 1549 herpetofaunal remains referable to the following 18 taxa (six amphibians and 12 reptiles): Triturus sp., Speleomantes sp., Pelodytes punctatus, Bufo bufo, Hyla gr. H. arborea, Rana dalmatina, Testudo hermanni, Tarentola cf. T. mauritanica, Anguis fragilis, Lacerta gr. L. viridis, Lacertidae indet., Coronella cf. C. austriaca, Elaphe sp., Hierophis viridiflavus, Malpolon monspessulanus, Colubrines indet., Natrix natrix and Vipera aspis. This study confirms and enriches the list of the taxa identified by Tozzi (1969) and Delfino (2002): a more detailed analysis allowed the identification of Elaphe sp. and Malpolon monspessulanus, improving the allocation of some of the remains that have been previously referred to "Colubrines" by the latter author.

Among the three different units, the Ancient one shows the highest number of remains (1205) and therefore of taxa, followed by the Recent (340) and then by the Middle (four remains). The analysed samples represent two different warm stages of the Pleistocene whose herpetofaunas share some elements but differ for others. As shown in Table 1, the Ancient Unit (Galerian) hosts all the identified taxa with the exception of *Tarentola*, *Elaphe* and *Malpolon* that have been found in the Recent Unit (post-Galerian in age) only.

Altogether, the Valdemino assemblage is surprisingly rich because it contains the same number of taxa of the Gargano sites (Apulia, Early Pleistocene; Delfino & Bailon, 2000) even if the number of remains of the former is nearly one tenth of the latter; due to their high diversity, these two herpetofaunas are by far the most interesting ever found in the Italian Pleistocene. The Valdemino herpetofauna is the only one in Italy that hosts fossils of *Pelodytes* and *Malpolon*. Moreover, although relatively rare and not referred at species rank, the remains of *Speleomantes* are the only sign so far published of the ancient presence in continental Europe of this biogeographically enigmatic family.

The assemblage does not show any relevant discrepancy from the present "Ligurian Riviera" association as defined by Sindaco (1998). With the exception of *Testudo hermanni*, all the identified taxa are widespread in western Liguria at present although some of them do not live in the surroundings of the site (cf. maps in Doria & Salvidio, 1994). The Region is devoid of autochthonous population of land tortoises at present, but the fossil remains of Valdemino corroborate, along with those reported by Hervet (2000), the hypothesis (Jesu in Doria & Salvidio, 1994) that this species had a past continuous distribution between Catalunya and Southern Italy.

One of the most striking characteristics of the Valdemino assemblage is the sharp contrast between a mammal fauna that still hosts extinct taxa (among others, Barbary apes, elephants, rhinoceros, leopards and sabre-toothed tigers) and a modern herpetofauna that is entirely represented by modern taxa that nowadays are typical of a Mediterranean environment. A datum that supports, once again, the idea that the herpetofauna experienced an extraordinary evolutionary stasis during the Quaternary (cf. Holman, 1998).

Another relevant topic raised by this fossil herpetofauna is the presence of M. monspessulanus and its apparent sympatry with H. viridiflavus. The former has been considered as the only Palaearctic reptile whose distribution matches well with the average range of the Mediterranean reptiles (Saint Girons, 1982); the only exception is represented by the Italian peninsula that it inhabits only along the narrow littoral strip of the western coast of Liguria, corresponding to the meso-Mediterranean bioclimatic-zone (Salvidio et al., 1996). The two vertebrae of Valdemino referred to M. monspessulanus represent the first fossil record for this species in Italy but since they fall in the modern range of the species, they add only little information to the evolutionary history of its distribution. Its regular absence from all the Neogene and Quaternary Italian sites that yielded herpetofaunal remains (more than 300 localities so far studied), although not definitely proving its absence, seems to strongly support the fact that this large and easily recognisable snake (this is true for the fossil material also) never colonized Italy. An absence that is rather surprising since other taxa with similar modern ranges (East-West disjunct distribution are shown by the genera Mauremys and Blanus) have been recovered in Italy as fossils.

The biogeographic analysis of the north-western Italian herpetofauna carried out by Sindaco (1998) with the aid of affinity indexes based on a presence/absence matrix, showed that the Ligurian Provinces cluster together (Provinces of Savona, Genova and La Spezia) or with the French southern Departments (Provinces of Imperia), and are therefore markedly diverse from the neighbouring Piedmontese Provinces that are separated by moderately high mountain chains. The presence in the Valdemino herpetofauna of taxa as *Pelodytes* (rare and localised in Piedmont at present), *Testudo* and *Malpolon* seems to testify that such a diversification could potentially have existed during the Middle Pleistocene already.

Moreover, Sindaco (1998), discussing the origin of the herpetofauna of north-western Italy, suggested that some taxa, as *P. punctatus*, could have reached Italy

M. DELFINO

TABLE 1. The distribution of the taxa within the stratigraphic units.

	Triturus sp.	Speleomantes sp.	Caudata indet.	P. punctatus	B. bufo	H. gr. H. arborea	R. dalmatina	Anura indet.	T. gr. T. hermanni	T. cf. T. mauritanica	A. fragilis	Lacerta gr. L. viridis	Lacertidae indet.	Sauria indet.	C. cf.C. austriaca	Elaphe sp.	H. viridiflavus	M. monspessuianus	Colubrines indet.	N. natrix	V. aspis	Serpentes indet.
Recent Unit (340 remains)								\bullet			\bullet	lacksquare	ullet			ullet	lacksquare	\bullet	\bullet	\bullet	\bullet	\bullet
Middle Unit (4 remains)																						
Ancient Unit (1205 remains)																						\bullet

from Iberian or North African refugia after the Würmian cold phase (Late Pleistocene), but the Valdemino fossils pre-date its arrival in the area, although they do not exclude recurrent extinctions and recolonizations of western Liguria respectively during and after the Pleistocene climatic worsening.

At least in the late Neogene and Quaternary, the area corresponding to the present western Liguria should have been a privileged "biotic corridor" due to its physiography: a narrow E-W oriented strip of land delimited by the sea on one side, and by a mountain chain on the other. During stadial and glacial marine lowstand, the strip should have been relatively broader at least locally (because the slopes of the Maritime Alps are generally rather steep). For reasons that can probably vary for different taxa, and still need to be identified, this way of dispersal has been a "dead end" corridor indeed: none of the taxa that characterise at present the area (Hyla meridionalis, Chalcides striatus, Timon lepidus, Elaphe scalaris and Malpolon monspessulanus), are know as fossils in the rest of the peninsula even if the herpetofauna of Valdemino testify a relatively ancient presence of some of them in Liguria.

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DISTRIBUTION OF AMPHIBIAN SPECIES IN KUDREMUKH NATIONAL PARK (WESTERN GHATS, INDIA) IN RELATION TO MINING AND RELATED HABITAT CHANGES

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Amphibian communities of Kudremukh National Park in the Western Ghats, India, were examined in relation to a wide range of habitat changes associated with an active iron ore mine. Twenty-six species of amphibian were recorded, comprising 23 anurans (four families) and three apodans (two families). Based on the changes in the quality of habitat, there were considerable differences in the pattern of amphibian distribution at different locations in the National Park. Undisturbed sites yielded 96% of species recorded in the area, while the disturbed sites yielded not more than 50%. Amphibian species richness, with litter-dwelling and semi-aquatic forms predominating, was related to the richness of plant species. Changes in amphibian species-richnessand distribution were reflected in three assemblages of decreasing richness, in undisturbed, partially disturbed and heavily disturbed sites.

Key words: amphibian diversity, habitat quality, species composition

INTRODUCTION

Increasing attention is being paid to the effects of environmental changes on the persistence of animal populations at local and regional scales. Amphibians, with their biphasic life cycle and sensitive permeable skin, are considered to be very sensitive to changes in habitat quality. Thus, they are often considered as useful bioindicators of conditions of both terrestrial and aquatic habitats (Lambert, 1997a,b). Comparison of amphibian diversity and distribution has been used to assess the impact of anthropogenic disturbance to wetlands (Hecnar & M'Closkey, 1996) and primary rainforest (Kiew et al., 1996; David & Pearman, 1997). Studies pertaining to the impact of man-made activities on amphibian diversity and distribution in the Western Ghats region of India, which contains approximately 123 species, is very limited. The present study is an attempt to assess the impact of habitat changes due to iron ore mining, human habitation and dam construction on the diversity and distribution pattern of amphibians in Kudremukh National Park.

MATERIALS AND METHODS

STUDY AREA

The Kudremukh National Park (KNP) is located in the Central Western Ghats (12° N and 16° N latitude) and spreads over the Tungabhadra State Forest, Naravi and Andar Reserved Forest in Chickmagalur and Udupi Revenue districts of Karnataka State.

The National Park covers a total area of about 600 km² and comprises lowland and highland tropical ever-

green forests, shola-grassland-savanna and a mosaic of semi-evergreen forests and plantations at the periphery. Altitude of the study area ranges from 300 m (lowland forest) to 1892 m above sea level (highland forest and mountain peaks). The area receives substantial rainfall during the monsoon months of June to October (range: 1700-6350 mm) and is drained by a number of perennial streams, tributaries and rivers (Tunga and Bhadra) that flow through the valleys throughout the year. Except for a few tribal communities and the township of the Kudremukh Iron Ore Company Limited (KIOCL), a public sector enterprise, the area has no legally permanent human settlement (Hussain et al., 1999). The KIOCL township, located in the centre of the National Park, has a population of approximately 10 600 persons involved with iron ore excavation by the contour line method. A dam across the Lakya tributary retains silt generated during the processing of iron ore and supplies water used to transport the concentrated ore to the nearby Mangalore Harbour Pelletization Plant through a gravity-siphon system. This major mining operation and the associated human activities have caused a significant impact on the biota of the National Park, especially in the area immediately surrounding the mines and downstream of the river Bhadra, which flows through the mine area (Hussain et al., 1999).

We selected nine sampling sites from the range of terrestrial/semi-aquatic habitats comprising the study area (Fig. 1). Of these, Kachige Hole (Site 1), Bhagavathi Forest (Site 8) and Naravi Forest (Site 9) were undisturbed habitats, K3 Ridge (Site 2), Ridge I Valley (Site 3) and Store area (Site 4) were located within the mining area, the East shola-Sector IV (Site 5) and Sector II & III (Site 6) were in the Kudremukh township area, and Site 7 constituted the areas of the Lakya Dam (Table 1). All the sampling sites were once typical, tropical evergreen forests with a thick canopy cover. However,

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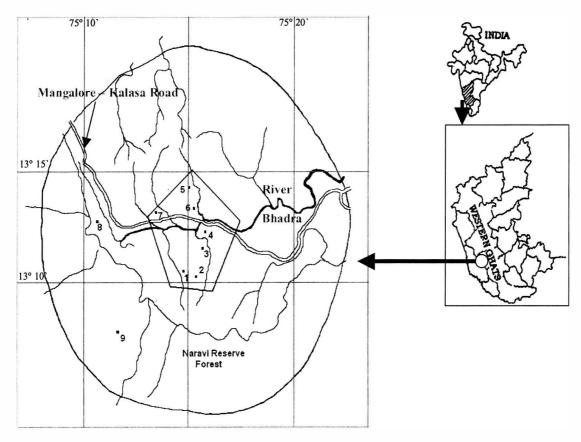


FIG 1. Map showing the study area and sampling sites (numbered 1 to 9).

subsequent to mining and related activities the canopy cover has been reduced in sampling sites 2, 3, 4, 5, 6 and 7. The sampling sites were located between 0.65 km (site 4) and 15 km (site 8) from the iron ore concentration plant. The study area ranges in altitude from 300-660 m asl (site 9: lowland forest) to 1087-1200 m asl (site 2: abandoned mine). In residential areas the canopy was made up of exotic and planted species, while in the vicinity of the mine the topsoil was heavily eroded and the canopy virtually absent.

AMPHIBIAN SAMPLING

We sampled amphibians in fixed quadrats at 30-day intervals, from the beginning of the monsoon season in 1998 until the monsoon of 1999. The size of the quadrat at each site was fixed by increasing its area until a stable number of amphibian species was recorded; this was accomplished during the monsoon, when most species are available. The quadrats covered an area of approximately one-tenth of total area in each site. Thus replicates of quadrat of varying sizes (50 × 50, 75× 100, 75 × 100, 85 × 85, 120 × 125, 120 × 125, 200 × 250, 100 \times 100 and 100 \times 100 m for site 1 to 9, respectively) were used regularly over the period of study and these quadrats were placed in such a way as to cover all possible microhabitats. Sampling was made regularly in the same place using the same quadrat defined for each site. Sampling was done at an average rate of one-man hour per 10 sq. m. The amphibian sampling in all sites was completed within three days from date of the commencement of fieldwork in each month. Searches for amphibians in each quadrat were made following the methods of Sutherland (1996). In all microhabitats "allout-search" was made by turning the rocks and boulders, scraping the litter, carefully searching the vegetation and bark of the tree, water bodies and also by digging the wet soil for apodans. Night surveys were also made using torchlight and following anuran calls. On-the-spot identifications of the amphibians were made using the field keys of Daniel (1963*a*,*b*, 1975), Daniel & Sekar (1989) and Daniels (1997*a*,*b*,*c*). The number of plant species present in each study site was counted.

DATA ANALYSIS

The similarity between survey sites were calculated in terms of the composition of amphibian assemblages using the Jaccard similarity measure. The similarity values were used to construct similarity matrices for the nine sampling sites. Based on the similarity values a phenogram was constructed using Unweighted Pair Group Method using Arithmetic Averages (UPGMA) method. The Shannon's diversity index was used to compare the sites. These analyses were made using the .programme MVSP ver. 3 for Windows (Kovach computing service). Pearson correlation coefficients were used to relate species richness to the number of plant species.

RESULTS

SPECIES COMPOSITION The highest amphibian richness was in undisturbed sampling sites, with 22, 18 and 17 species in sites 9, 1

Sampling sites	Altitude (m asl)	Direction and distance from the concentration plant	Type of terrain and details of habitat
Kachige Hole (Site 1)	890-1030	S-W 3000-3500	Undisturbed shola forest, with a small rivulet flowing in the valley. Prominent siltation on the riverbed.
K3 Ridge (Site 2)	1080-1200	S 3000-3500	Abandoned iron ore mine with exposed inner soil composite, sparsely planted with <i>Acacia</i> sp. after the mining.
Ridge I valley (Site 3)	880-1000	S 2100-2500	Remnants of shola forest and a small spring in the middle of active mine. Bed of spring stream is silted and this area is continuously exposed to the vibrations of mine blast and vehicular transport.
Store area of the mining Company (Site 4)	790-835	S-E 650-1200	Absence of natural vegetation, terrain is highly disturbed due mine vehicle activities. Site comprises two check dam to prevent the downward flow of silt during monsoon.
East-shola, Sector IV (Site 5)	770-875	1900-2700	Natural Shola Forests, and rivulets. However, margin of the forest and hill slopes are converted for human habitation (town- ship).
Sector II & III (Site 6)	780-835	N 800-1300	Part of the Kudremukh township.
Lakya Dam & Periphery (Site 7)	900-955	W 2700-3000	Area disturbed during the dam construction and subsequent dumping of the silt. The peripheral area is planted with <i>Acacia</i> sp
Bhagavathi Forest (Site 8)	900-1100	W 7000-7500	Undisturbed, thick evergreen forest.
Naravi Forest (Site 9)	500-660	S-W 14000-15000	Undisturbed lowland forest.

TABLE 1.	Description	of the study	sites.
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and 8, respectively. Of the 26 species encountered in the present study, 24 were recorded from the undisturbed habitats, 13 from residential areas, eight from around the dam (site 7) and nine from the surroundings of the mine (sites 3 and 4). Sites 3 and 4 had six and five species, respectively, while site 2 was devoid of any amphibian species. Among the three apodans recorded in the present study, two species were recorded from site 9 (Naravi) and one from site 8 (Bhagavathi Forest). The pattern of Shannon's diversity index was similar to that of species richness (Table 2). Correlations between Shannon's index and species richness was significant (r=0.90, P=0.001).

The study area is rich in flowering plants (168 species, 60 families). The undisturbed sites (S1, S8 and S9)

had 62, 70 and 76 plant species, the mine and surrounding areas (S2, S3 and S4) had 5, 40 and 39 species. The residential area (S5 and S6) had 66 and 76 species respectively and the dam and surrounding area had 42 plant species.

HABITAT FEATURES

Amphibian species were recorded in all possible microhabitats in the study area and amphibian species richness was correlated with the richness of plant species (r=0.86, P=0.003, Fig. 2). There was no significant correlation between the number of amphibian species and log area of the study sites (r=0.21, P>0.10). Based on habitat and their place of occurrence, amphibians were categorized into litter-dwelling, aquatic, semi-

Species	Habitat	Und	isturbed hal	bitats	Mining	g and surro area	ounding	Resident	ial area	Dam
		S1	S8	S9	S2	S3	S4	S5	S6	S7
ANURA: RANIDAE										
Micrixalus saxicola	LF, S-Aq	3.3 (0-7)	2.25 (1-5)	0.67 (0-2)		0.50 (0-2)		0.75 (0-3)		
Nyctibatrachus. Major	· LF, Aq		1.3 (0-4)	0.67 (0-2)						
N. aliceae	LF, Aq	1.75 (0-5)	. ,			0.83 (0-2)				
Rana aurantiaca	LF, S-Aq	1.67 (0-5)	1.08 (0-5)	0.42 (0-2)						
R. limnocharis	S-Aq	2.25 (0-6)	1.58 (0-4)	0.98 (0-3)			0.42 (0-1)	0.58 (0-2)	0.58 (0-2)	0.75 (0-3)
R. beddomii	LF, T	1.17 (0-4)	1.16 (0-4)	(0-2)			(01)	(* -)	(* -)	(0.2)
R. curtipes	LF-T	4.9 (1-12)	0.75 (0-4)	0.25 (0-2)			0.26 (0-1)	0.42 (0-2)	0.34 (0 - 2)	0.50 (0-2)
R. cyanophlyctis	Aq	1.42 (0-3)	0.5 (0-2)	0.30 (0-1)			0.16 (0-1)	(* =)	0.16	(0 -)
R. keralensis	S-Aq	1.7 (0-5)	1.17 (0-5)	0.50 (0-2)			(01)		(0-1)	
R. semipalmata	LF, S-Aq	0.75 (0-3)	1.83 (0-6)	1.33 (0-4)				0.24 (0-2)		
R. temporalis	LF, S-Aq	8.4 (4-15)	2.58 (0-6)	1.16 (0-4)				1.08 (0-3)	0.25 (0-1)	
R. tigrina	Aq	0.58 (0-3)	0.75 (0-3)	0.21 (0-2)		0.16 (0-1)		0.33 (0-2)		
Tomopterna braviceps	LF-T		. ,	0.50 (0-2)				(-)		
T. rufescense	Т	1.0 (0-5)		1.25 (0-3)						0.33 (0-1)
ANURA: RHACOPHORID	AE									
Philautus charius	А	1.5	0.33	0.42				0.41		0.17
P. femoralis	А	(0-5) 0.25	(0-2) 0.25 (0.2)	(0-2) 0.51 (0.2)				(0-2) 0.08		(0-1)
P. glandulosus	А	(0-2)	(0-2)	(0-2)		0.29 (0-1)		(0-1)		0.17
P. leucorhinus	А	1.67 (0-6)	0.83	0.33 (0-1)		(0-1)		0.16		(0-1)
P. naustus	A	(0-0)	(0-3)	(0-1)		0.41		(0-1)		0.17
Rhacophorus malabari	cus A	0.33 (0-2)	0.35 (0-2)	0.25 (0-1)		(0-1)		0.08 (0-1)		(0-1)
ANURA: BUFONIDAE										
Bufo beddomei	LF-T	1.08		1.10			0.25	0.25	0.08	0.08
B. melanostictus	LF-T	(0-3)		(0-3) 0.51 (0-1)			(0-1)	(0-1)	(0-1) 0.50 (0-2)	(0-1) 0.42 (0-1)

TABLE 2. Species composition and mean abundance (No/100 m²/month) of amphibians in different sampling sites of the study. Values in the parenthesis denote the range. Aq, Aquatic; S-Aq, Semiaquatic; T, Terrestrial; A, Arboreal; F, Fossorial; LF, Litter dwelling species.

Species	Habitat	Und	isturbed ha	bitats	Mining	g and surro area	ounding	Resident	Dam	
		S1	S8	S9	S2	S3	S4	S5	S6	S7
ANURA: MICROHYLIDAI	E									
Microhyla ornata	S-Aq	0.67 (0-3)	0.83 (0-3)	0.83 (0-2)		0.17 (0-1)	0.16 (0-1)			
APODA: Ichthyophida	E									
Ichthyophis beddomei	F, S-Aq		0.32 (0-2)							
I. bombayensis	F, S-Aq			0.25 (0-1)						
APODA: Caecilidae										
Gegeneophis carnosus	S-Aq			0.17 (0-1)						
Total abundance		34.39	17.86	13.02	0	2.36	1.25	4.88	1.91	2.59
Species richness Shannon's Index		18 2.523	17 2.639	22 2.923	0 0	6 1.160	5 1.541	11 2.146	6 1.627	8 1.878

TABLE 2. Continued...

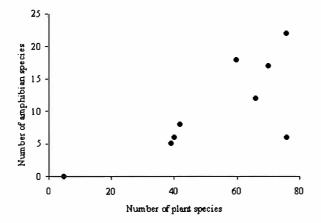


FIG. 2 Numbers of amphibian and plant species at different sampling sites.

aquatic, terrestrial, fossorial and arboreal species (Table 3). Interestingly, litter-dwelling species predominated in the undisturbed sites and accounted for 25-31% of the amphibian species richness, followed by semi-aquatic (20-32%), terrestrial (0-28.6%) and arboreal species (0-25%). Sites with undisturbed habitats (S1, S8 and S9) contained high species richness and exhibited significant similarity. Site 5 of the residential area exhibited high similarity with undisturbed habitats. Site 6 was similar to site 4 (Table 4). Other sampling sites had low species richness and the lowest similarity index. The UPGMA phenogram reveals the formation of distinct clusters of S1, S8 and S9, S6 and S4 (Fig. 3).

DISCUSSION

Because of their biphasic life style and membranous and permeable skin, amphibians are considered to be environmental indicators that can provide an early warn-

*

TABLE 3. Numbers of amphibian species in different habitats at each sampling site (total no. of species in each type of habitat is denoted in the parenthesis)

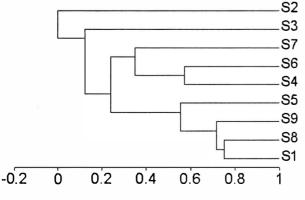
Habitat	Undisturbed habitats			Min	ne surrou	indings	Residential area		Dam area
	Site 1	Site 8	Site 9	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7
Litter $(n=11)$	8	7	10	0	2	2	5	4	3
Aquatic (n=4)	3	3	3	0	2	1	2	1	0
Semi-aquatic (n=10)	7	8	8	0	2	2	4	2	1
Terrestrial (n=6)	4	2	6	0	0	2	2	3	4
Fossorial $(n=3)$	0	1	2	0	0	0	0	0	0
Arboreal (n=6)	4	4	4	0	2	0	4	0	3

	Undisturbed habitats			Min	e surround	lings	Residen	Dam area	
	Sitel	Site 8	Site 9	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7
Site 1									
Site 8	0.750								
Site 9	0.739	0.696							
Site 2	0	0	$\overline{0}$						
Site 3	0.200	0.150	0.120	$\overline{0}$					
Site 4	0.278	0.222	0.227	0	0.100				
Site 5	0.611	0.556	0.500	0	0.133	0.231			
Site 6	0.263	0.211	0.273	0	0	0.571	0.308		
Site 7	0.238	0.136	0.250	0	0.167	0.300	0.267	0.40	

TABLE 4. Jaccard's coefficient of similarity between the sampling sites.

ing of environmental deterioration that may not be perceived by humans (Halliday & Heyer, 1997). Hence, increasing attention has been devoted to understanding the dynamics of these ecologically pivotal species (Hecnar & M'Closkey, 1996). Previous studies in relation to other taxa suggested that the loss of forest cover has led to erosion of forest species in the Western Ghats, (Daniels et al., 1995). However, in India, and especially in the Western Ghats, there is a dearth of information needed to use amphibians as a gauge for assessing habitat deterioration. Study areas in the Western Ghats have mega-hydroelectric projects, open cast-contour mining and monoculture-plantations, all reported to cause the shrinkage of habitat and decline of amphibian populations (Krishnamurthy, 1997; Gupta, 1998). The present study is an attempt to understand the impact of one such activity, open cast-contour line iron ore mining, which was initiated in 1973 at Kudremukh in a 5 km² stretch of land amidst dense moist evergreen forests.

The results of previous studies, within the vicinity (Krishnamurthy & Shakunthala, 1993; Bhatta, 1998; Krishnamurthy, 1997; 1999; Krishnamurthy & Hussain, 2000) have revealed a good number of amphibian species. In the present study, sites located in the buffer zone around the mine (undisturbed habitats) and in partially disturbed habitats were shown to have comparable species richness, whereas diversity decreased towards the active mine. Decline of amphibian populations in re-



Jaccard's Coefficient

FIG. 3. Cluster analysis of the nine sampling sites examining the similarity of their amphibian richness.

sponse to habitat degradation has been discussed for a variety of locations elsewhere (Corn & Vertucci, 1992; Daniels, 1992; Blaustein & Wake, 1995; Delis et al., 1996; Fisher & Shaffer, 1996). Delis et al., (1996) considered that differences in population structures between urban development and park were the result of habitat degradation. Hadden & Westbrooke (1996), while studying the impact of habitat alteration recorded a significant relationship between herpetofaunal richness, level of grazing pressure and vegetation understory structure and predicted amphibian richness in relation to the soil type in Victoria, Australia. Observations in the present study have revealed that habitat alteration has resulted in patchy distribution with decreased richness within a relatively small locality amidst the unique environment of moist evergreen forest. Litter-dwelling, semi-aquatic, terrestrial, arboreal and aquatic species were found in the undisturbed habitats, while aquatic and terrestrial species predominated in the residential areas. In the present study, there was a significant relationship between amphibian species richness and the number of plant species. Sites with more natural plant species were associated with rich amphibian communities. Hence the reduction in species diversity in the study area could be attributed to the development of a township around the mine, lack of topsoil and an absence of a surface litter layer. The UPGMA phenogram reflects the possibility of three assemblages of amphibian species representing undisturbed, partially disturbed and heavily disturbed habitats. Occupants of the disturbed habitats were widespread. This reflects the sharing by very few species in both assemblages and species of disturbed sites would be a subset of species complement of undisturbed sites.

The present study suggests that mining, human settlements and developmental activities have damaged habitats, resulting in the decline of amphibian populations in and around the KIOCL mine in the Kudremukh National Park.

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ECOLOGICAL MODELLING OF GENETICALLY DIFFERENTIATED FORMS OF THE IBERIAN ENDEMIC GOLDEN-STRIPED SALAMANDER, *CHIOGLOSSA LUSITANICA*

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We modelled the distribution of two genetically differentiated forms of the Golden-striped salamander, *Chioglossa lusitanica*, in Portugal with the help of a geographical information system. Models were derived with and without the assumption that the contact zone between the forms would be associated with the Mondego river valley and with and without the statistical Bonferroni correction. The modèl fit was high and ranged from kappa = 0.81-0.99. The southern form appears to live under harsher (but still tolerated) environmental conditions than the northern form (low precipitation, low air humidity, low summer temperatures, a high number of frost months, low NDVI vegetation index) and can be viewed as a mountain form. This is in line with the observation that the southern form has shorter extremities than the northern one.

Key words: amphibian distribution, GIS, Portugal, Urodela

INTRODUCTION

For many widespread animal and plant species in Europe, genetic variation is more frequently observed in or even restricted to - southern areas that remained largely unglaciated during the Pleistocene. These areas may have served as refugia during cold periods and as sources to the recolonization of Europe thereafter. The present-day general pattern of substantial genetic variation in the south and a low, depleted genetic variation in the north, is a witness to this process (Hewitt 1996, 1999). Endemic species are frequently taken as morphologically and genetically uniform. This conviction may be a priori, or be vaguely inferential, e.g. when it is suggested that a small range limits the scope for geographical subdivision and that a specialized niche limits the scope for differential adaptation. Current molecular techniques, revealing high levels of genetic variation and substantial genetic differentiation over small areas, help to demonstrate the inadequacy of these arguments. Nevertheless, patterns of genetic divergence may exist over small areas, independent of the size of the species ranges. Several case studies, including one on Chioglossa lusitanica, the Golden-striped salamander (Alexandrino et al., 2000, 2002), illustrate this point.

Chioglossa lusitanica is an Iberian endemic amphibian with a small distribution and a distinct ecological niche. Its range is restricted to the north-western corner of the Iberian peninsula. The species inhabits the banks of swiftrunning mountain streams in areas characterized by high rainfall, high topographical relief and low summer and winter temperatures (Arntzen, 1981; Teixeira *et* al., 2001; Teixeira & Ferrand, 2002). Morphological and ecological characteristics are shared with its sisterspecies, the salamandrid Mertensiella caucasica from the Caucasus and with some Nearctic plethodontid salamanders, revealing a remarkable convergent evolutionary adaptation (Arntzen, 1994). Geographic variation in C. lusitanica has been documented for several nuclear and cytoplasmic gene loci and coloration pattern. Variation at both nuclear and cytoplasmic gene loci suggests that the northern part of the distribution results from a post-glacial range expansion (Alexandrino et al., 2000, 2002, and in Teixeira & Ferrand, 2002). Furthermore, the genetic data revealed significant substructuring, warranting the recognition of a southern form as different from a northern form. The forms may have been historically separated by the Mondego river valley (Alexandrino et al., 2000, 2002; Teixeira & Arntzen, 2002). They appear to have recently resumed gene flow, at least in the western part of the Mondego area, where habitat conditions are more favourable to the species than the flat eastern Mondego range with an annual precipitation of less than 1000 mm.

The southern and northern form of *C. lusitanica* differ morphologically in the relative length of their limbs and digits. Similar morphological variation occurs gradually along a south to north axis across the species range, i.e. independent of taxonomy. The patterns of variation accumulate into a stepped cline of 'short-legged' salamanders in the south to relatively 'long-legged' salamanders in the north, with a 'step' coinciding with the Mondego valley (J. Alexandrino, unpublished data). The non-random signature of variation suggests that the morphological characters are under natural selection. We conclude that both forms are probably adapted to somewhat different environments. The agent of selection is unknown, but likely to be ecological-climatic.

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Here we model the distribution of two genetically differentiated forms of *Chioglossa lusitanica* with the help of GIS-modelling, adding a taxonomic component to spatial and spatio-temporal axes (Teixeira *et al.*, 2001; Teixeira & Arntzen, 2002).

MATERIAL AND METHODS

An extensive survey guided by the UTM-geographical system provides a sharp picture of the current range of C. lusitanica in Portugal with a 10×10 km spatial resolution (Godinho et al., 1999; Teixeira et al., 2001). Data on species absence-presence cover 281 grid cells out of 967 grid cells countrywide (29%). Perceived absences cover 74 grid cells, mostly neighbouring the recorded range. Recorded presences cover 202 grid cells, plus five grid-cells covering less than 50% of continental Portuguese that were omitted from the analysis. At this scale of observation the distribution of C. lusitanica is continuous and the ranges of the northern and the southern forms are contiguous. The contact between them may coincide with the Mondego river (Ferrand de Almeida et al., 2001). However, the observations that (1) population 5 (Várzeas), representing the southern form is situated north of the Mondego; and (2) population 6 (Buçaco) possesses both 'southern' and 'northern' cytoplasmic genetic markers, shows that the contact zone not fully and strictly coincides with the river valley (Fig. 1). A more conservative and cautious approach therefore is to recognize that the contact zone could be situated at any place in between the investigated populations 1-5 (representing the southern form) and populations 7-10 (representing the northern form). Models derived under these different considerations we refer to as model 1 and model 2, respectively.

To derive the models, the presence of one form is contrasted with the presence of the other form. Absence data are not taken into consideration and the analysis is restricted to the area covering the documented *C. lusitanica* range (Arntzen, 1999). Under model 1, data from three grid cells for which group allocation is ambiguous or mixed are omitted from the analysis, leaving 199 data points available for analysis (59 southern and 140 northern). In model 2, data from 39 grid cells for which group allocation is ambiguous are not taken into consideration, leaving 163 data points for model construction (54 southern and 109 northern).

Thirteen pre-selected environmental parameters are available as independent variables in logistic regression analysis, carried out with SPSS 10.0 for Windows (SPSS, 1999), with the distributional data as the dependent variable. Selection implied limited correlation between the environmental variables, with a Spearman correlation coefficient < 0.8 and further as in Teixeira *et al.* (2001) and 'Atlas do Ambiente' (Direcção Geral do Ambiente, 1995): acidity of the soil (pH), altitude (m), frost days (annual number), frost months (annual number), hardness of subterranean water (CaCO₃ mg l⁻¹), humidity of the air (%), insolation (h), vegetation

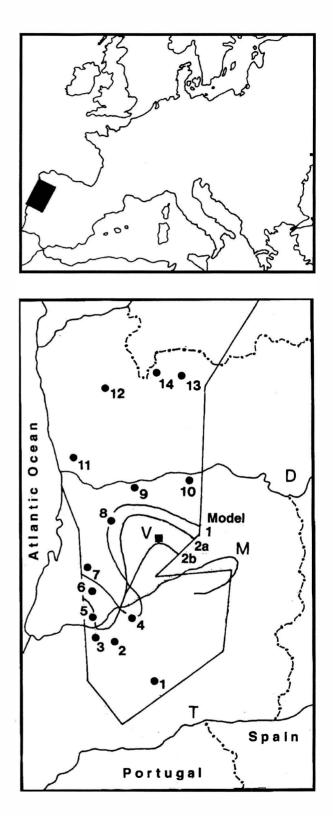


FIG. 1. Top, map of Europe with the area of interest shown in black. Bottom, the transition between northern and southern habitat types, following the GIS-models 1, 2a and 2b, are shown by curved lines. Note that models 1a and 1b are very similar in spatial terms and were merged. The range limit of *Chioglossa lusitanica* in northern Portugal is shown by straight lines (from Arntzen, 1999). Genetically studied populations are numbered 1 to 14 (from Alexandrino *et al*, 2000). D = river Douro, M = river Mondego, T = river Tejo and V = Viseu.

index (NDVI), precipitation days (d yr⁻¹), slope (%), annual mean temperature (°C) and July mean temperature (°C) as continuous variables and lithology as categorical variable (sedimentary and metamorphic versus igneous rock).

Variables were allocated to the explanatory models by a forward stepwise addition procedure, with the likelihood ratio as a selection criterion and alpha set at 0.05. Weights were applied to equilibrate the impact of differences in sample size between the northern and southern form. In the absence of significant imbalance between scores of correct and incorrect classification, the cut-off point was set at 0.5. Models were derived with and without Bonferroni correction (Holm, 1979). Models are presented on the basis of standardized continuous variables (with a mean of 0 and standard deviation of 1). The order of presentation reflects the input order of variables into the logistic equation. Model performance was evaluated with Cohen's kappa statistic. Kappa is a measure of the proportion of correct classification after accounting for chance effects. It provides a standardized, simple and effective statistic for evaluating or comparing presence-absence (and presence-presence) models (Manel et al., 2001). The closer kappa is to 1.0 the higher is the accuracy of the data.

Values of over 0.8 are considered in medical applications to indicate a near perfect model performance (Landis & Koch, 1977). For visual representation, the variables composing the models are introduced into the Geographical Information System ILWIS 2.1 (ILWIS, 1997) as raster layers with a spatial resolution of 1 km.

RESULTS

Model 1 includes three or six environmental variables. Under Bonferroni correction the probability of occurrence (P) for the southern form versus the northern form is:

Model 1a – $P = (1 / (1 + \exp(-0.730 \times \text{humidity} - 0.272 \times \text{vegetation_index} + 2.573*\text{lithology} + 85.249))).$

Without Bonferroni correction:

Model 1b –

 $P = (1 / (1 + \exp(-1.158 \times \text{humidity} - 0.499 \times \text{vegetation_index} + 2.485 \times \text{lithology} - 0.274 \times \text{precipitation} - 0.608 \times \text{July_temperature} - 0.151 \times \text{frost_months} + 224.394))).$

TABLE 1. Environmental parameters selected in logistic regression modelling of the contiguous ranges of a southern and a northern form of the Golden-striped salamander, *Chioglossa lusitanica*, in Portugal, with the mean \pm standard deviation, or the number grid cells involved. The assumption that the contact zone between the forms follows the Mondego river (model 1) is relaxed under model 2 (details see text). \dagger relative to countrywide average.

	under Bonferr	oni correction	without Bonfer	roni correction
	southern form	northern form	southern form	northern fo rm
Model 1				
Number of UTM-grid cells analysed	59	140	59	140
Allocated number of UTM-grid cells	69	133	73	129
Selected environmental parameters				
Frost months (number per year)			3.71±1.443	2.93±1.586
Humidity of the air (%)	71.1±3.15	78.5±3.03	71.5±3.35	78.5±3.23
Lithology (no. and frequency of grid cells)				
- sedimentary and metamorphic rock	57 (83%)	44 (33%)	56 (77%)	45 (35%)
 igneous rock 	12 (17%)	89 (67%)	17 (23%)	84 (65%)
Vegetation index (NDVI) †	0.938±0.0336	1.008 ± 0.0615	0.938±0.0333	1.01 ± 0.0611
Annual total precipitation (mm/year)			1256±269	1566±334
Mean July temperature (°C)			17.9±1.70	19.1±1.02
Model 2				
Number of UTM-grid cells analysed	54	109	54	109
Allocated number of UTM-grid cells	87	115	81	121
Selected environmental parameters				
Altitude (m) †			1.44±0.657	1.39 ± 0.832
Humidity of the air (%)	71.6±3.01	79.3±2.41	71.3±2.99	79.1±2.56

Kappa is 0.81 respectively 0.91. Model 2 includes one or two environmental variables. Under Bonferroni correction:

Model 2a – $P = (1 / (1 + \exp(-12.160 \times \text{humidity} - 3.298))).$

Without Bonferoni correction:

Model 2b -

 $P = (1 / (1 + \exp(-18.080 \times \text{humidity} - 2.504 \times \text{altitude} - 5.011))).$

Kappa is 0.95 respectively 0.99. The number of correctly and erroneously allocated data points across forms was not significantly out of equilibrium for either model (G-test of independence, 0.322 < G < 2.625, df=1, P > 0.05 in all four cases). The GIS spatial translation of the models is shown in Fig. 1. The area modelled as suitable for the southern form has, in climatic terms, low precipitation, low humidity, low summer temperatures and a high number of frost months, relative to the area modelled as suitable for the northern form. Also the southern area has a relatively low vegetation index, high altitude, and is mostly composed of sedimentary and metamorphic rock as opposed to igneous rock. The differential environmental characteristics of the southern and northern ranges are summarized in Table 1.

DISCUSSION

The present analysis is different from other GISmodelling exercises in that no 'false absences' (grid cells where the species occurs but has not been recorded) figure in the analysis. This is, firstly, because the distributional data set is near-complete at the 10×10 km UTM grid scale, the spatial level chosen for analysis. Secondly, the analysis does not employ any absence data, but instead contrasts the presence of one form with the presence of another. An underlying assumption of the approach is that the ranges of the forms are contiguous and non-overlapping. The available data indicate this to be the case. GIS-modelling of the Portuguese portion of the range of 12 Iberian amphibian and reptile species shows that the descriptive fit of (absence-presence based) spatial models is related to accuracy in the correct prediction of ranges in adjacent areas (J. W. Arntzen, unpublished data). In other words, species range models that show tight fit for Portugal are likely to be good predictors for the range over the remainder of the Iberian Peninsula (i.e. Spain). Therewith, the high kappa values obtained for model 1 and model 2 descriptions of genetically differentiated forms within C. lusitanica, provide confidence that the selected environmental variables are meaningful descriptors of the C. lusitanica ranges and - directly or indirectly - relevant markers for the ecology of both form. It must be kept in mind, however, that the effect of the novel 'presencepresence' approach on kappa remains to be studied.

Considering the known ecological and habitat preferences of C. lusitanica as a species (Arntzen, 1981, 1999; Teixeira et al., 2001), the parameters selected for the models can be interpreted as the southern group, stronger so than its northern counterpart, being a mountain form that is adapted to comparatively harsh environmental conditions. The possession of relatively short extremities is in line with a harsh climate (Nevo, 1972; Lee, 1993; J. Alexandrino, unpublished data). The ecological transition runs in the western part of the species range adjacent to the Mondego river. At the eastern side of the range, however, it runs up to 30-60 km north of the Mondego. The particular area around and to the south of Viseu belongs ecologically to the southern range (Fig. 1). This notion contrasts the range assumption underlying model 1, involving a contact between the forms along the Mondego river. Given the relatively harsh ecological conditions and the acknowledged effect of such an environment on the phenotype, within as well as between both forms, we predict that salamanders from this area will have shorter extremities than salamanders from populations at the same latitude at the western side of the range, or elsewhere in the northern range. Conversely, a historical biogeographical model reconstructed from genetic data and ecological modelling (Teixeira & Arntzen, 2002) predicts that the local populations belong to the northern form. This model postulates the separation of the ancestral C. lusitanica range along an east-west axis, coinciding with the Mondego river valley. Unfortunately, an adequate taxonomic description of both genetically differentiated units is not yet available and populations to the southeast of Viseu have not yet been studied. A complication is that the type locality of C. lusitanica (Buçaco, population 6) has, genetically as well as morphologically, mixed characteristics.

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THE PRESENCE OF THE GREEN SEA TURTLE, CHELONIA MYDAS, IN THE ADRIATIC SEA

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We collated and reviewed data on the green turtle in the Adriatic Sea from our own records, museum collections, and published literature. Results show overlap of records and cases of misidentification of large loggerheads as green turtles. Currently there have been twelve green turtles recorded in the Adriatic Sea. The majority of records refer to juveniles with a carapace length of 28-40 cm, recovered in the southern Adriatic. It is possible that this region contains pelagic habitats for the green turtle. It is therefore important to educate fishermen along the southern Adriatic coasts to identify and report recoveries of this endangered species.

Key words: by-catch, chelonian, marine habitats, Mediterranean

INTRODUCTION

The green turtle *Chelonia mydas* (Linnaeus 1758) is one of two species of sea turtle that reproduce in the Mediterranean basin (Broderick *et al.*, 2002). The regional population has been shown to be genetically distinct from that of the wider Atlantic (Bowen *et al.*, 1992; Encalada *et al.*, 1996), and not sustained by immigration of individuals from rookeries outside the Mediterranean. Over the past century this species has suffered heavy exploitation (Sella, 1995), which has led to a severe reduction of the population. At present, the Mediterranean green turtle population has been categorized as Critically Endangered (Hilton-Taylor, 2000), making it the most endangered green turtle population in the world (Seminoff, 2002).

The rookeries in Turkey and Cyprus contain approximately 99% of the Mediterranean nesting population (Kasparek et al., 2001). In total, between 339 and 360 green turtle females nest annually on Mediterranean beaches (Broderick et al., 2002). Although the major nesting areas of the green turtle in the region are well known (Kasparek et al., 2001), there is a paucity of data on the biology and distribution of this species in marine habitats. Post-nesting satellite tracking of six adult females has shown that the waters of Cyprus, Israel, Egypt and Libya host migratory pathways and wintering areas for adults (Godley et al., 2002). Juvenile green turtles have been recorded in the eastern and western Mediterranean (Margaritoulis et al., 1992; Laurent et al., 1997; Godley et al. 1998a,b; Gianguzza et al., 2000; Meschini, 1997; Oruç, 2001), and the Black Sea (Nankinov, 1998). Margaritoulis & Teneketzis (2001) discovered a developmental habitat for green turtles at Lakonikos Bay in the Peloponnesus, Greece. However, "at sea" recoveries of individual juveniles have yielded little solid information about the life history of green turtles away from their reproductive habitats.

The green turtle is considered to be rare in the Adriatic Sea (Stossich, 1880; Pozzi, 1966; Riedl, 1983; Bruno, 1978; Lazar & Tvrtković, 1995). The first two specimens were recovered in the western Adriatic waters, near Ancona and near Venice in Italy in 1830 and 1864 respectively (Nardo, 1864; De Betta, 1870). The first records for eastern Adriatic also date from the 19th century (Damin, 1889; Depoli, 1898). Green turtles were listed in the Catalogue of Amphibians and Reptiles of the Croatian Natural History Museum (Pavletić, 1964), and included in the indexes of the fauna of the Adriatic countries (Karaman, 1939; Pozzi, 1966; Brelih & Džukić, 1974; Bruno & Maugeri, 1979). However, most data have been published in local journals or remain unpublished, making them unavailable to the wider scientific community. This paper will review such records and present new data on green turtles in the Adriatic Sea.

MATERIALS AND METHODS

The data presented are based upon inspection of (1) museum collections, (2) literature, and (3) our personal records. We examined collections from the Croatian Natural History Museum in Zagreb, the Natural History Museum in Rijeka, the Natural History Museum in Split, the Natural History Museum in Dubrovnik, the Natural History Department of the City Museum in Zadar, the Slovenian Museum of Natural History in Ljubljana, and the Natural History Museum in Vienna. External morphological identification was carried out according to Pritchard & Mortimer (1999), whilst

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skulls identification was preformed after Wyneken (2001). We compared records from literature and care-fully avoided any possible duplication.

Data on the size (length) or weight of individuals are presented as given in the literature or reported by fishermen. The data set is, unfortunately, highly heterogeneous. It includes estimates of the total length or mass of the turtle, as well as estimates or measurements of carapace length. In the latter case, it is often unknown what precisely was measured (e.g. the curved or the straight carapace length). Therefore, these data should be considered just as an indication of the size class.

RESULTS AND DISCUSSION

From all museum collections examined, green turtles from the Adriatic were only listed in the catalogues of the Croatian Natural History Museum (CNHM). We inspected and re-identified all the sea turtles from the Herpetological Collection and the Osteological Collection of CNHM. All of the specimens listed as green turtles (CNHM 215: 589; CNHM 600: 752, 753, 2061; CNHM 216: 413) were actually large loggerheads, with a curved carapace length notch to tip (CCL_{n-l}) (Bolten, 1999) ranging from 63.0-81.4 cm.

The green turtle has been recorded on several occasions in the western Adriatic (Table 1 and references therein). However, it seems that in some cases the same specimen gave rise to several "records" in the literature. For instance, both Nardo (1864) and De Betta (1870) described the same records of two green turtles recovered in Italy, one in Ancona in 1830 and another in Malamocco in 1864 (Table 1). Stossich (1880) and Faber (1883) also mentioned that "two green turtles have been found in the Adriatic until that time", but without providing any additional information. It seems that all these records are originally based upon findings of just two specimens in Italy (Nardo, 1864). This is also the case with two turtles from Apulian Adriatic coast reported by Basso (1992), Pastorelli *et al.* (1999), and Centro Studi Cetacei (2000) (Table 1).

All literature records of green turtles in the eastern Adriatic Sea come from Croatian waters (Damin, 1889; Depoli, 1898; Hirtz, 1927; Mršić, 1987). The report of a "big turtle Chelone midas" as recorded by Hirtz (1927) and accompanied by a black and white photo of the specimen, reveals that this turtle was a loggerhead. As all of the original identifications of species turned out to be incorrect wherever we could perform re-identification, we question the identification of green turtles in the other cases where the record is not supported by some material evidence. The reason for the misidentification of sea turtles in Croatia most likely lies in the old Croatian name for C. mydas: "the huge (big) turtle". As most of loggerheads that frequent Adriatic Sea are juveniles (Affronte & Scaravelli, 2001; Lazar & Tvrtković, 1995), it seems that any "big" loggerheads were automatically and erroneously identified as C. mydas. Therefore, the record of a "big turtle" identified as C. mydas by Damin (1889), or the one identified by a local priest in 1945 and reported by Mršić (1987) are doubtful. The exception could be the record of a juvenile turtle weighting 18 kg captured in the Bay of Rijeka, Croatia (Depoli, 1898), but again, this record is not supported by any physical evidence.

In addition, we report three new recoveries of green turtles in the Adriatic Sea (Table 1, Fig 1), all incidentally captured in fishing nets. The first, with a carapace length of about 30 cm, was found in the Po River Delta in Italy in August 1985 (identification by P. Casale). Another juvenile green turtle, weighting 4 kg, was recovered in Margherita di Savoia in Italy in July 1996

TABLE 1. Records of the green turtle in the Adriatic Sea (remarks are given as presented in the papers or reported by the finders; CL - carapace length). Doubtful records are marked with an asterisk.

No.	Date	Locality	Country	Reference	Remarks
1	1830	Ancona	Italy	Nardo (1864), De Betta (1870)	Length: 45.7 cm
2	July 1864	Malamocco, Venice	Italy	Nardo(1864), De Betta (1870)	CL: 28 cm
3*	22 June 1889	Bakar Bay	Croatia	Damin (1889)	CL: 83 cm
4	9 Sept 1885	Rijeka (Fiume) Bay	Croatia	Depoli (1898)	Mass: 18 kg
5*	1945	Baška Voda, Makarska	Croatia	Mršić (1987)	"large specimen"
6	1980-1989	Unknown (south Adriatic)	Italy	Pastorelli et al. (1999),	.CL: 28-31 cm
				L. Rositani, pers. comm.	
7	August 1985	Po River Delta	Italy	This paper	CL: about 30 cm
8	July 1986	Bari	Italy	Basso (1992)	CL: 28-31 cm
	•			Pastorelli et al. (1999)	
9	1 Feb 1991	Lido S. Anna, Brindisi	Italy	Pastorelli et al. (1999)	CL: 31.5 cm
			•	Unpubl. data	
10	July 1996	Margherita di Savoia	Italy	This paper	Mass: 4 kg
11	3 April 1998	Torre a Mare, Bari	Italy	Pastorelli et al. (1999)	CL: 31 cm
	•		•	Cento Studi Cetacei (2000)	
12	14 Dec 2001	Trpanj, Pelješac Peninsula	Croatia	This paper	CL: 40 cm

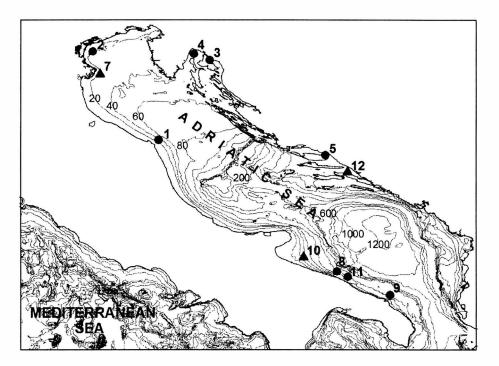


FIG. I. Distribution of recoveries of green turtle in the Adriatic Sea. (Number of the record refers to No. in Table 1. The record No. 6 with unknown locality is not shown; circles, data from literature; triangles, new data).

(identification by G. Marzano). The third specimen $(CCL_{n-t}: 40.0 \text{ cm})$ was found dead entangled in the gill net, 1 km east from the City of Trpanj, along the northeastern coast of the Pelješac Peninsula in Croatia, on the 14th December 2001 (identification by B. Lazar). The last turtle has been preserved and is kept in the herpetological collection of the CNHM in Zagreb. It is worthy of note that green turtles have not yet been recorded in Slovenia (Kryštufek & Janžeković, 1999), neither in Montenegro (Lazar & Tvrtković, 1995) nor Albania (Haxhiu, 1995). Hence, the juvenile caught in Trpanj in Croatia is the first certain record of the green turtle in the eastern Adriatic Sea.

At present, only 12 green turtles have been recorded in the Adriatic Sea (Table 1 and references therein). This is less than the number of leatherback turtles (Dermochelys coriacea) recorded in these waters (18 specimens, Casale et al., 2003). Margaritoulis & Teneketzis (2001) showed that 40.1% of turtles captured in the Lakonikos Bay in the Ionian Sea, Greece, were juvenile C. mydas, and suggested that the bay may present a developmental habitat for the species. In contrast to this, the proportion of green turtles to loggerhead turtles seems to be far lower in the Adriatic Sea. For instance, Pastorelli et al. (1999) presented recoveries of only four green turtles and at least 181 loggerheads along the southern Adriatic coast (Italy) during 1978-1998 (see Fig. 1 in Pastorelli et al., 1999). This is also reflected in the data from the eastern Adriatic, where only one out of more than 100 turtles handled was a green turtle (Lazar, personal data). However, it is possible that some of 1220 reported recoveries of unidentified turtles of the family Cheloniidae in the eastern Adriatic (Lazar & Tvrtković, 1995) belong to green turtle.

The number of green turtles in the Adriatic is low. Nevertheless, two facts should be stressed: first, the majority of turtles were small, pelagic juveniles with a carapace length ranging from 28-40 cm (Table 1), and second, most of the records come from southern Adriatic waters (Fig.1). Although these records could be incidental, individual events, it is possible that some juvenile green turtles are passively drifting into the Adriatic on the dominant surface current in the Ionian-Adriatic area. It is known that currents may affect the distribution of hatchlings and pelagic juveniles (Bolten & Balazs, 1995; Musick & Limpus, 1997; Lohmann et al., 1999). The prevailing surface current enters the Adriatic from Ionian Sea along the eastern coast moving to the north (Orlić et al., 1992). The presence of green turtles in the southern Adriatic, Italian waters in particular, could be explained by the anticlockwise gyre that branches from the main current in the southern Adriatic hence influencing the distribution of recoveries. Therefore, it is possible that southern Adriatic, with surface sea temperatures of 24-25 °C in the summer and >13 °C in the winter (Cushman-Roisin et al., 2001) contains pelagic habitats for green turtle.

The Adriatic Sea is one of the most intensively fished areas of the Mediterranean. This results in a high level of interactions between sea turtles and fisheries. It is estimated that about 2500 turtles are incidentally caught each year by the eastern Adriatic trawl fisheries (Lazar & Tvrtković, 1995) with an additional 3600 turtles caught by the western fleet (Casale *et al.*, 2001). Although we should not over-interpret the low number of records, the Adriatic fisheries seems to interact also with the critically endangered green turtle population; the extent of by-catch is, however, beyond our knowledge at the moment. Identification of critical habitats and migratory pathways are among research priorities for sea turtles (Bjorndal, 1999). In order to create an effective conservation strategy it is of the utmost importance to understand turtle movements and the relationship between habitats they utilize, particularly in the case of the critically endangered Mediterranean green turtle population. Taking this into consideration, attention should focus on the education of fishermen and local inhabitants along the southern Adriatic coasts to identify and report recoveries of this species.

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SHORT NOTES

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DIET COMPOSITION OF THE INDIAN RICE FROG, *RANA LIMNOCHARIS*, IN THE FLOODPLAIN OF THE KIZU RIVER, JAPAN

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I identified 1404 prey individuals from 57 stomachs of *Rana limnocharis* captured in the floodplain of the Kizu River, Japan. Collembolans occupied 79.8% of the total prey number. Mass consumption of collembolans occurred in late August. Pitfall trap sampling showed that collembolans increased explosively at this time of year. This synchronization suggests that the frog feeds on this tiny insect unselectively in response to the increase of its availability within the habitat. The unspecialized feeding habits may partially explain the dominant distribution of this frog in the river-floodplain, where the arthropod fauna is unpredictably devastated by inundation.

Key words: arthropod fauna, collembolans, food niche analysis

Anurans are undoubtedly the essential components of wetland ecosystems in both abundance and position in the food web as intermediate predators. Although numerous studies on their ecological roles in lentic habitats, such as ponds, marshes, and rice fields, have been conducted (e.g. Jenssen & Klimstra, 1966; Houston, 1973; Werner *at al.*, 1995; Hirai & Matsui, 1999; 2000; 2001*a*), few studies have documented their roles in river ecosystems.

In mainland Japan, 12 anuran taxa comprising 16 native species/subspecies currently use rice fields for reproduction (Maeda & Matsui, 1999). It is considered, however, that most of these anurans originally inhabited floodplains of large rivers (Moriyama, 1997). From the early 1900's, most river-floodplains in Japan were converted into rice fields through river improvement, flood control, and/or reclamation works. Consequently, rice fields have now become valuable substitutional wetland habitats for those anurans (e.g. Hasegawa, 1998).

Generally, habitat alteration in wetlands is most detrimental to anuran communities and caused the population declines in many anuran species (e.g. Beebee, 1996). Thus, the survival of frogs in riverine habitats that undergo large scale habitat alteration, followed by population recovery in the new artificially managed environments seems to be unusual phenomenon. Moriyama (1997) presumed that anurans are originally well-suited to life in rice-field habitats. This idea is based on the fact that the irrigation period in rice fields is synchronized with inundation in river plains during the rainy season, and thus their life-history requirements seem to be almost satisfied. From the viewpoint of successful spawning and larval development, this idea is very persuasive. However, some adult anurans spend prolonged periods after reproduction in rice fields, and newly recruited juveniles also remain in rice fields continuously after metamorphosis (e.g. Hirai & Matsui, 2002*a*; Hirai & Hidaka, 2002*b*). Therefore, the idea proposed by Moriyama (1997) appears to be insufficient to account for the success of anurans in rice-field habitats.

Rana limnocharis is one of the representative species of Japanese anurans inhabiting rice fields. This frog has a strong affinity for rice fields in the western part of the Mainland of Japan (Maeda & Matsui, 1999). Accordingly, available data are mostly based on observations in rice fields (e.g. Shichi *et al.*, 1988; Hata & Nagoshi, 1995; Hirai & Matsui, 2001b), and little is known about its ecology in natural wetlands such as river-floodplains.

During a herpetological survey in a river ecosystem, I had an opportunity to study a natural population of R. *limnocharis* in a river-floodplain. In this paper, I describe the diet composition of R. *limnocharis* collected in the floodplain, with reference to the arthropod fauna within this habitat. Our results would help clarify the factors that enable the frog to thrive in rice-field habitats. Based on the results, I also discussed an inherent problem in diet data analysis.

The study site is a sandbar (approximately 18 ha: 135°47'E, 34°50'N) of the Kizu River, which runs between Kyotanabe City and Jyoyou City, Kyoto Prefecture, Japan. An extensive lowland area of this sandbar is a bare sandy plain, but the riverside areas are partially covered with vine reed (*Pharagmites japonica*: Gramineae), and the inland sandhill is dominated by tall goldenrod (Solidago altissime: Compositae) and iron creeper (Humulus scandens: Moraceae). Willows are scattered within the vegetation. The sandbar is inundated several times within a year, especially during the rainy season (June to mid July) and the typhoon season (late August to September). After inundation, a number of temporal pools emerged near the shore, and foraging frogs were observed around there. I captured frogs, irrespective of species, at night usually for two hours (2100-2300 hr) because frogs are basically nocturnal predators. In order to examine seasonal variation in diet, samplings were conducted twice a month from June to October 1998.

Stomach contents of frogs were extracted by forced regurgitation with forceps immediately after collection, and preserved in 10% buffered formalin for later analyses. I recorded sex, snout-vent length (SVL), mouth width and body mass for all individual frogs. After these procedures, the frogs were released to the site of capture. The frogs were observed to jump away into the

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water or surrounding bushes, indicating that they were not adversely affected by forced regurgitation technique.

In the following year (1999), prey availability was estimated by pitfall traps for ground-surface dwelling prey and by net sweeping for aerial and plant dwelling prey. Pitfall traps were set near the water's edge for 24 hrs. Sweeps were made through the air and vegetation with an insect net continuously for 10 min. These prey samplings were made every seven days (23 May, 29 June, 24 July, 23 August, 21 September 19 October, 24 November) to examine seasonal fluctuation of prey availability within the foraging habitat of frogs. In 1999, frog diet samplings were not carried out.

In the laboratory, I analyzed samples of frog stomach contents. The methods are same as those described elsewhere (e.g. Hirai & Matsui; 1999; 2001*a*; 2001*c*). I captured a total of 86 individuals of *Rana limnocharis*, 18 of *R. nigromaculata*, three of *R. catesbeiana*, and nine of *Hyla japonica*. Seventeen adults of *R. limnocharis* had empty stomachs, and 12 juveniles (13.3-22.5 mm in SVL) were too small for forced regurgitation of stomach contents. Accordingly, I recovered 1404 prey items from 57 stomachs of *R. limnocharis* (19.2-45.8 mm in SVL) and identified 21 prey taxa (Table 1).

Arthropoda constituted the vast majority of prey, and Insecta seemed particularly important. Insecta contained ten families and made up 96.5% and 78.9% of total prey number and volume, respectively. Collembolans predominated in diet, representing 79.8% of total prey number. By volume, however, no single taxon predominated in the diet. Even the largest proportion was 16.8% of earwigs (Dermaptera), and comparable proportions were occupied by orthopterans, caterpillars (Lepidopteran larvae), and earthworms (Oligochaeta). Collembolans made up only 3.0% of total prey volume because of their tiny body size. Dipterans ranked top in frequency of occurrence, followed by collembolans and spiders (Araneae). The sole vertebrate prey was a hatchling grass-lizard (Takydromus tachydromoides) with 24.0 mm in SVL, recovered from the stomach of a male frog 37.5 mm in SVL. The frog diet composition was biased towards terrestrial arthropods. Aquatic prey occurred in 22.8% of frog stomachs, but constituted only 1.6% by number and 10.4% by volume of the total prey in diet.

The number of prey in stomachs varied seasonally and was found to be in accordance with the number of collembolans consumed (Fig. 1). Substantial numbers of collembolans was exploited on 26 August. At the maximum, 280 collembolans were recovered from a single frog stomach captured on this day. Collembolans occurred significantly higher in frequency on 26 August (59.3%) than on the other sampling days (23.3%) (χ^2 contingency table test, $\chi^2=7.5$, df=2, P<0.05).

Pitfall trap samplings showed that collembolans explosively increased in number in late August (Table 2). This insect was the most abundant prey taxon in total, TABLE 1. Diet composition of *Rana limnocharis* (1404 prey individuals from 57 stomachs, total volume 7012.5 mm³). Abbreviations: F = frequency of occurrence (the percentage of stomachs containing a particular prey taxon); N = numeric proportion; V = volumetric proportion.

Prey taxon	F	N	v
Insecta			
Hymenoptera			
Formicidae	19.3	1.1	0.2
Non-Formicidae	17.5	1.2	1.2
Coleoptera	28.1	2.8	1.7
larvae	8.8	0.6	6.3
Diptera	43.9	3.4	4.2
larvae	17.5	1.2	4.6
Lepidoptera	10.5	0.4	1.2
larvae	10.5	0.5	12.2
Neuroptera	1.8	0.1	0.1
larvae	1.8	0.1	<0.1
Hemiptera	42.1	2.7	9.7
Dermaptera	17.5	1.1	16.8
Orthoptera	26.3	1.5	12.5
Odonata nymphs	5.3	0.1	5.5
Collembola	40.4	79.8	3.0
Arachnida			
Araneae	40.4	2.9	4.0
Crustacea			
Isopoda	1.8	0.1	1.1
Amphipoda	1.8	0.1	0.2
Gastropoda	1.8	0.1	1.3
Oligochaeta	1.8	0.3	11.0
Reptilia Squamata			
Lacertidae	1.8	0.1	3.5
Plant materials	17.5	Ξ.	¥
Minerals	43.9	-	-

but the vast majority (82.7%) was collected in late August. This pattern of seasonal fluctuation is similar to that observed in frog stomachs. Dipterans were the most abundant taxon in sweeping samples in all months (Table 2) and secondarily abundant in pitfall samples. Unlike collembolans, dipterans exhibited little seasonal fluctuation.

Feeding habits of *R. limnocharis* in the floodplain could be characterized by mass consumption of collembolans. The predominance of collembolans in diet has never been observed in other ranid frogs. Even if present in diet, the numeric proportion is small. For example, the largest proportion hitherto reported for *R. limnocharis* is 1.8% in Singaporean population (Berry, 1965), and that for other ranid frogs is 18.1% of *Rana septentrionalis* (Hedeen, 1972).

On the other hand, ants were known to occur more commonly in the diet of *R. limnocharis* from rice fields of Japan (26.9%; Hirai & Matsui, 2001*a*) and China (23.4%; Liu & Chen, 1933), and swamps of Singapore (27.9%; Berry, 1965). In the present study site, ants rep-

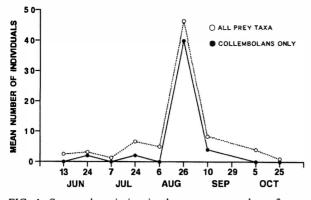


FIG. 1. Seasonal variation in the average number of prey individuals found in stomachs of *Rana limnocharis*. Diet samples were not taken on 29 September.

resented only 1.1%, or 5.3% even when calculated excluding collembolans. In fact, ants were very scarce by both pitfall and sweep sampling. Therefore, the interpopulational variation in diet of *R. limnocharis* would result from the difference of prey availability in each local habitat.

The prey availability samplings revealed that mass consumption of collembolans was synchronized with an explosive increase of this insect within the habitat. This shows that R. limnocharis feeds unselectively on prey in response to its availability within a foraging habitat. The unselective feeding habits may be advantageous in dealing with river floodplains where the arthropod fauna is unexpectedly devastated by inundation. Therefore, the feeding habits may partially explain the dominant distribution of R. limnocharis in the present study site. More importantly, the unselective feeding habits may be one of the key factors that enable the frog to survive habitat alteration and thrive in rice field habitats, where the rice-field arthropod fauna is disturbed by farming practices such as insecticide applications, ploughing, weeding, reaping, and artificial control of water status. This assumption is strengthened by the fact that prey availability – rather than prey preference – is the most important determinant of dietary composition for most other frogs inhabiting rice fields, such as R. nigromaculata (Hirai & Matsui, 1999), R. porosa

brevipoda (Hirai & Matsui, 2001*d*), and *Hyla japonica* (Hirai & Matsui, 2000). Thus, the ecological features of both breeding and non-breeding seasons should be studied to explain the patterns of distribution in anurans. Such studies would also provide useful information for the conservation of declining anuran populations.

The consumption of collembolans is more common in burrowing or ground-surface dwelling anuran species of Bufonidae (e.g. Gittins, 1987), Pelobatidae (e.g. Newman, 1999), Dendrobatidae (e.g. Donnelly, 1991), and Microhylidae (e.g. Berry, 1965). Some of these anurans exploit collembolans in a different pattern from that of R. limnocharis in the present study site. For example, the tropical litter frog, Epipedobates boulengeri, consumes a higher proportion of collembolans by frequency (about 90%) and volume (about 11%) than by number (31.9%; Caldwell, 1996), compared to R. limnocharis in the present study. These differences illustrate that numerical proportion is vulnerable to mass consumption by a small number of individuals. In many diet studies of anurans, numeric proportion has been used for calculation of food niche width, food niche overlap, or prey selection index (e.g. Toft, 1980, 1981). Thus, reanalysis with the other variables might lead us to somewhat different conclusions. Hence, diet data should be interpreted cautiously in the analysis.

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May	Jun	July	August	September	October	November	Total

TABLE 2. Seasonal variation in the number of arthropods collected by pitfall traps (Pit) and sweeps (Swp).

Prey taxon	way		Jun		July		August	September	Octobel		November		Total			
	Pit	Swp	Pit	Swp	Pit	Swp	Pit	Swp	Pit	Swp	Pit	Swp	Pit	Swp	Pit	Swp
Hymenoptera					÷											
Formicidae	0	-	2	-	0	-	1	-	0	-	0	-	0	-	3	-
Non-Formicidae	-	3	-	0	-	8	-	3	-	3	-	2	-	0	-	19
Coleoptera	33	-	44	-	44	-	23	-	95	-	0	-	1	-	240	-
Diptera	84	96	49	20	29	52	25	22	44	61	96	257	14	20	341	528
Hemiptera	1	0	1	1	11	15	1	0	0	1	0	0	0	0	14	17
Dermaptera	4	-	2	-	4	-	20	-	0	-	0	-	0	-	30	-
Collembola	25	-	75	-	79	-	2173		30	-	11	-	234	-	2627	-
Insect larvae	2	-	0	-	1	-	13	-	0	-	3	-	3	-	22	-
Araneae	31	-	13	5 - 12	75	-	17	-	8	-	6	-	1	-	151	-
Acarina	0	-	2		4	-	1	-	1	-	0	-	0	-	8	-
Miscellaneous	1	11	1	0	0	2	0	1	0	0	0	0	1	0	3	14

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FOOD HABITS AND ECOLOGY OF *PSEUDIS BOLBODACTYLA* (ANURA: PSEUDIDAE) FROM A FLOOD PLAIN IN SOUTH-EASTERN BRAZIL

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This study presents some ecological data on the aquatic frog *Pseudis bolbodactyla* (Pseudidae) of south-eastern Brazil, with emphasis on diet. Frogs ranged in size (SVL) from 33.2 to 58.0 mm and in mass from 6.2 to 28.5 g, with females larger and heavier than males. Fourteen food categories were found in the stomachs of *P. bolbodactyla*, most of them arthropods. The main prey found in the stomachs were Diptera, adult Coleoptera, Homoptera, and Araneae. Sex and size of frogs do not seem to significantly affect diet composition.

Key words: diet, frog, morphology, size

The family Pseudidae is represented by two genera (Pseudis and Lysapsus) of highly aquatic frog species that are distributed throughout most of cisandean South America (Pough et al., 2001). The larger genus, Pseudis, currently comprises six species, four of which are known only from Brazil (Kwet, 2000; Frost, 2002), and is remarkable for its giant tadpoles, which are often much larger than the adult animals (e.g. Emerson, 1988; Caramaschi & Cruz, 1998). Little has been published about the ecology of pseudid frogs, with most information referring to the widely distributed species P. paradoxa (Cei, 1980; Dixon et al., 1995; Bosch et al., 1996; Duré & Kehr, 2001; Arias et al., 2002). Pseudis bolbodactyla, the subject of this study, occurs in the Brazilian states of Minas Gerais, Espírito Santo, Goiás and Bahia (Caramaschi & Cruz, 1998). The main goal of this study was to analyze the diet of P. bolbodactyla from a site in Espírito Santo state, south-eastern Brazil. Other aspects of the ecology of the species, such as habitat use, sex ratio and sexual dimorphism are also briefly assessed.

Field work was conducted in a permanent pond (estimated area c. 750 m²; maximum depth c. 3 m) located at 19°07'S, 39°46'W within a farmland area in the lowlands of Pontal do Ipiranga, municipality of Linhares, Espírito Santo state, south-eastern Brazil. According to our surveys, P. bolbodactyla is scarce or absent in other ponds in the area. Vegetation in the pond is dominated by the cattail, Typha aff. dominguensis (Typhaceae), and comprises other plants such as Fuirena sp. (Cyperaceae), Nymphaea sp. and Cabomba sp. (Nymphaeaceae), Utricularia aff. neglecta (Lentibularianaceae), Eichornia sp. (Pontederiaceae), Polygonium sp. (Polygoniaceae), and Salvinia natans (Salviniaceae). Annual temperatures and total annual rainfall in the region of Linhares average 23.6° C and c. 1400 mm, respectively (Peixoto & Gentry, 1990).

The frogs were collected by hand from 19.00 hr through 23.00 hr, in February (n=18), April (n=17), June (n=12), August (n=9), September (n=1), and October (n=4). Due to the heavy rains, the roads were flooded during late spring and summer (November-January), which impeded us from taking samples during Soon after collections, frogs were that period. euthanased with ether and snout-vent length (SVL) measured with a caliper (0.1 mmprecision) and weighed on an electronic balance to the nearest 0.1 g. Individuals still bearing a tail were considered to be juveniles. All frogs were dissected for verification of their sex and extraction of their stomachs. Stomach contents were analyzed using a stereornicroscope. Each prey item was identified to the taxonomic level of order, measured across its longer axis with a caliper (to the nearest 0.1 mm) and weighed to the nearest 0.1 mg on an electronic balance.

A Chi-square analysis was used to test if the sex-ratio deviated from a 1:1 ratio. Differences between sexes in mean SVL and mass were tested using one-way analyses of variance (ANOVA), after testing for homogeneity of variances. The slope of the SVL/body mass relationship was compared between sexes using an analysis of covariance (ANCOVA), with SVL as the covariate. For each prey category found in the diet, we calculated the Index of Relative Importance (Ix), which was based on number of items, collective mass and frequency of occurrence (see Howard et al., 1999). Diet composition was compared (based on the Ix, which was also calculated separately for each sex) between males and females using the Kolmogorov-Smirnov two-group test (Siegel, 1956). A simple regression analysis was used to test the relationship between maximum prey size and frog SVL; maximum prey size was based on the length of the largest prey item in each stomach (only items whose original length could be accurately measured were considered). Basic statistics given throughout the text represent arithmetic means ±SD.

We examined 59 individuals of *P. bolbodactyla* (34 males, 14 females, and 11 juveniles whose sex could not be ascertained). Male/female ratio was 2.43:1, being significantly different from the expected 1:1 ratio (χ^2 =6.4, *P*<0.05). Except for one individual, found at

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the pond's edge, all frogs were collected in the water. Specimens ranged in size from 33.2 to 58.0 mm SVL (mean=40.6±5.0 mm), and in mass from 6.2 to 28.5 g (mean=11.4±4.1 g). Males ranged in size from 33.9 to 45.9 mm SVL (mean=40.1±3.1 mm), and in mass from 7.4 to 14.0 g (mean=10.6±1.9 g). Females ranged in size from 37.1 to 58.0 mm SVL (mean=45.6±6.2 mm), and in mass from 9.2 to 28.5 g (mean=15.6±6.0 g). Although females were significantly larger (ANOVA: $F_{1.46}$ =17.41, P<0.001) and heavier (ANOVA: $F_{1.46}$ =19.16, P<0.0001) than males, the slope of the SVL/body mass relationship did not differ significantly (ANCOVA: $F_{2.45}$ =1.02, P=0.317).

Of the 59 specimens examined, 56 (94.9%) had food in their stomachs. Fourteen food categories were found in the stomachs of *P. bolbodactyla*; except for Gastropoda and shed skin, all other food items were arthropods (Table 1). Overall, the most important prey categories were Diptera, adult Coleoptera, Homoptera and Araneae, in that order (Table 1). For males, the predominant items in the diet (based on values of *Ix*) were adult beetles (0.246), dipterans (0.240) and homopterans (0.215), whereas for females the most important food items were dipterans (0.365), followed by adult beetles (0.149) and homopterans (0.126). Diet composition did not differ significantly between sexes (Kolmogorv-Smirnov: D_{max} =0.165, df=2, *P*=0.97). Individual prey varied in length from 2.0 to 14.1 mm (mean= 4.8 ± 1.9 mm, n = 161). There was no significant relationship between maximum prey size and snout-vent length for *P. bolbodactyla* ($r^2=0.001$, P=0.85, n=42).

The proportion of *P. bolbodactyla* with food in their stomachs was high (56/59). Duré & Kehr (2001) found much lower proportions of stomachs with prey for *Pseudis paradoxa* (21/50) and *Lysapsus limellus* (46/75) sharing a pond in Corrientes, Argentina.

The most frequent and abundant items in the diet of *P. bolbodactyla* were dipterans (particularly mosquitoes), though coleopterans and homopterans were also frequently consumed and contributed a greater proportion of the total prey mass ingested. Dipterans (types not specified) dominated the diet of the small pseudid *Lysapsus limellus* in Corrientes, Argentina, but were not as important in the diet of the sympatric *Pseudis paradoxa*, which had a more varied diet (Duré & Kehr, 2001). In our study, the diet of *P. bolbodactyla* was also varied, with no clear dominance of a single prey type. This suggests that larger pseudids may tend to have less specialized food habits than smaller ones, since their larger size allows them to exploit a wider range of prey sizes.

According to our field observations, mosquitoes were very abundant at the study area, being found in great concentrations on and among the vegetation, including

Prey	F	%F	Ν	%N	М	% <i>M</i>	Ix
Insecta							
Coleoptera (adults)	21	37.5	32	15.8	584.4	26.4	0.220
Coleoptera (larvae)	3	5.4	3	1.5	62.4	2.8	0.026
Diptera	28	50.0	90	44.3	296.1	13.4	0.298
Hemiptera	1	1.8	7	3.4	32.1	1.4	0.020
Homoptera	17	30.4	51	25.1	199.7	9.0	0.178
Hymenoptera	2	3.6	2	1.0	4.6	0.2	0.018
Lepidoptera (larvae)	4	7.1	5	2.5	96.0	4.3	0.038
Odonata	1	1.8	1	0.5	7.1	0.3	0.006
Orthoptera	1	1.8	1	0.5	23.2	1.0	0.009
Unidentified insect	1	1.8	1	0.5	46.1	2.1	0.01
ARACHNIDA							
Araneae	5	8.9	6	3.0	709.1	32.1	0.136
Crustacea							
Isopoda	1	1.8	1	0.5	0.7	<0.1	0.006
Mollusca							
Gastropoda	3	5.4	3	1.5	71.0	3.2	0.027
Other							
Shed skin	3	5.4	-	-	77.1	3.5	0.023
 Total	-	_	203	-	2209.6	_	

TABLE 1. Food items found in the stomachs of 56 specimens of *Pseudis bolbodactyla* from Pontal do Ipiranga, south-eastern Brazil. Frequency of occurrence (F), number of individual items (N) and total ingested mass (M) are given in absolute values and proportions (%) for each prev category. Indexes of relative importance (Ix) are also given.

Typha leaves. Homopterans were also frequently seen on the leaves of *Polygonium* sp. (Polygoniaceae). *Pseudis bolbodactyla* is likely to prey mainly on insects detected above the water surface, on the leaves of plants found inside and at the margins of the pond, which the frogs may be able to do without leaving the water. This feeding behaviour was observed by Duré & Kehr (2001) for two other pseudids, *P. paradoxa* and *L. limellus*.

Shifts in diet composition according to an increase in body size have been commonly reported in anurans (e.g. Lima & Moreira, 1993; Flowers & Graves, 1995; Evans & Lampo, 1996; Giaretta *et al.*, 1998; Lima, 1998; Hirai & Matsui, 1999). However, in this study we found no relationship between prey size and frog size for *P. bolbodactyla*. This could be due to the ingestion of great quantities of relatively small items (such as mosquitoes) by many individuals, regardless of size.

The results of our study suggest that the area of Pontal do Ipiranga, found within a region subjected to periodic flooding (the Suruaca valley), represents an appropriate environment for the maintenance of a large population of P. bolbodactyla. The frogs seem to find abundant food resources and suitable habitat conditions. Nevertheless, P. bolbodactyla seems to have some specific habitat requirements, and are not found uniformly throughout the various permanent ponds. Although several ponds of various sizes were found in the study area, individuals of P. bolbodactyla were found in substantial numbers in only one, which was characterized by having denser vegetation at its margins and by the presence of Typha aff. dominguensis (not observed in the other ponds). Thus, there seems to be a close relationship between P. bolbodactyla and the plant T. aff. dominguensis at our study site, which may be due to the utility of the plant both as shelter and as oviposition sites (Pseudis paradoxa of the Argentinian Chaco is known to lay eggs among the aquatic vegetation; Dixon et al., 1995). We believe that the increase in drainage currently occurring throughout the Suruaca valley, for agricultural and developmental (i.e. opening of roads) purposes, may negatively affect the local population of P. bolbodactyla.

Acknowledgements. We thank U. Caramaschi for confirming the identity of the frog species. We are also grateful to J. Measey and an anonymous reviewer for their suggestions to improve the article. The Conselho Nacional para o Desenvolvimento Científico e Tecnológico (CNPq) provided funding to the project "Biodiversidade da Mata Atlântica do Espírito Santo" (Process # 469321/2000-8).

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CHROMOSOMAL EVIDENCE FOR THE DOUBLE ORIGIN OF VIVIPARITY IN THE EUROPEAN COMMON LIZARD, LACERTA (ZOOTOCA) VIVIPARA

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The results of a chromosomal analysis conducted in a relict, viviparous, Hungarian (Ócsa) population of *L. vivipara*, show that viviparity independently arose in this population. Chromosome characteristics of Ócsa, namely females displaying 2n=36 chromosomes with a ZW sex chromosome system and W shaped as microchromosome, are peculiar to *carniolica*, an early diversifying clade including oviparous population, and different both from oviparous Pyrenean + Aquitainean populations, whose females possess 2n=35 chromosomes with a Z_1Z_2W sex chromosome system, and W shaped as macrochromosomes.

Key words: evolution, lacertid, reptile viviparity, sex chromosomes

The European common lizard, Lacerta (Zootoca) vivipara, is unique among the lizards in reaching and crossing the Arctic polar circle, and the only lacertid species to display reproductive bimodality, so far only found in two other species of squamates. In fact, Z. vivipara possesses both widely distributed, long recognised, viviparous populations (from Central France and the British Isles up to Scandinavia and eastern Russia, until to Sakhalin Island in the Japanese Sea) and two more recently discovered groups of oviparous populations. A first group of allopatric, oviparous populations is restricted to the Pyrenees and Aquitaine in France (Braña & Bea, 1987), and the second group of oviparous populations, assigned to L. v. carniolica (Mayer et al., 2000), was found in northern Italy, southern Austria, Slovenia and Croatia (Mayer et al. 2000; Surget-Groba et al. 2002). Chromosomal analysis (Odierna et al. 2001) evidenced that oviparous populations of carniolica are karyologically differentiated from all the other populations of vivipara: females of carniolica display a chromosome complement of 2n=36 chromosomes, a ZW sex chromosome system and W shaped as microchromosome. All the other populations of vivipara, including the oviparous populations from the Pyrenees and Aquitaine, instead, display females with a complement of 2n=35 chromosomes, a Z₁Z₂W sex chromosome system, and W shaped as macrochromosomes, whose morphology and heterochromatin distribution have allowed four cytotypes to be detected (Fig. 1; refer also to Odierna et al., 2001, for further details). As shown by mtDNA analysis (Surget-Groba et al. 2001), carniolica and each of the four cytotypes of vivipara display characteristic haplotypes, allowing their identification and relationships (Fig. 1). Karyological and mtDNA results also indicate that the evolution of viviparity was a single event occurring in the clade of central European+eastern viviparous populations (Odierna et al., 2001; Surget-Groba et al., 2001). This evidence is here challenged by the results obtained from a karyological analysis performed on one male and two females of a relict, viviparous (Puky et al. 2003), Hungarian population, namely from Ócsa. Chromosomes were obtained by means of the standard air-drying method. Besides conventional staining (5% Giemsa at pH 7), Ag-NOR banding and sequential C-banding+CMA,+DAPI staining were also performed (Odierna et al., 2001). The studied male and females displayed the same number of 2n=36 chromosomes. As in all the populations studied so far (Odierna et al., 2001), NORs were on the telomeric regions of a small chromosome pair (Fig. 2A). However the male had 36 telocentric macrochromosomes, whereas the females had 34 acrocentric macroautosomes + ZW sex chromosome pair, the W being shaped as a microchromosome while Z was (tentatively) a chromosome as large as those of the sixth pair (Fig 2A). C-banding staining evidenced centromeric and telomeric C-bands on all the autosomes and on the Z chromosome. The W microchromosome was fully heterochromatic and proved DAPI positive after sequential staining of C-banding+CMA,+DAPI (Fig. 2D). This staining also revealed that centromeric C-bands were weakly DAPI positive (Fig. 2D). Telomeric regions of all autosomes were also weakly CMA, positive, except for a small autosome pair, whose telomeric NOR regions were intensely stained. Interestingly, the karyological characteristics of viviparous population of Ócsa are peculiar to the oviparous populations of Z. v. carniolica. The ZW sex chromosome system with W shaped as a microchromosome has been found in several other, unrelated, lacertid species and thought as derived from a primitive macrochromosome W, homomorphic to Z, by a multistep process, proceeding formerly by heterochromatinization and successively by progressive events of deletions (Odierna et al. 1993; Olmo et al. 1993; in den Bosch et al. 2003). In our case, this W processing might have occurred either once, consequently the Ócsa population groups within *carniolica* (our preferred hypothesis, since heterochromatin of their W is DAPI positive and Alu I resistant) or twice, then the population of Ócsa constitutes or belongs to a clade

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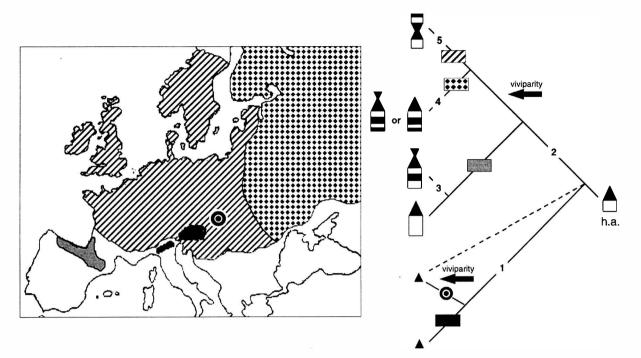
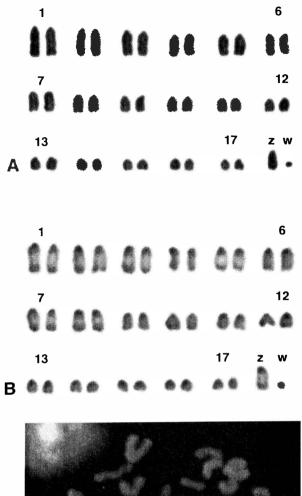
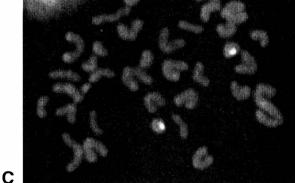


FIG. 1 Gross distribution of the five cytotypes of *L. vivipara* (Asian distribution not included) and the cladogram (modified from Odierna et al., 2001) showing their relationships and characteristics of W chromosome. Eastern viviparous populations \square ; Centroeuropean viviparous populations \square ; Pyrenean+Aquitanean oviparous populations \square ; *L. v. carniolica* oviparous populations \square ; Ócsa population \odot ; Sex chromosome differentiation, starting from a hypothetic ancestor (h.a.), possessing 2n = 36 acrocentric chromosome, a ZW sex chromosome system, W homomorphic to Z, occurred according to two different modalities: by (1) heterochromatinization of the primitive W and progressive deletion events, shaping the W as microchromosome (the hatched line considers the possibility of an independent origin of the microchromosome W in the Ócsa population); by (2) a tandem fusion of the original W with an autosome to give rise to a Z_1Z_2W sex chromosome system, W shaped as a macrochromosome; afterwards, addition of interstitial (3) and telomeric (4) heterochromatin, as well as a pericentromeric inversion (5) occurred.

distinct from carniolica (Fig. 1). However, irrespective of whether the Ócsa population does or does not group within carniolica, ours results provide evidence that viviparity independently arose twice, in the population of Ocsa and elsewhere in the clade including Pyrenean+Aquitainean, Centro-European and Eastern populations. Females of these populations possess a Z₁Z₂W sex chromosome system, which is thought derived formerly by a tandem fusion of the primitive W with an autosome and successively by heterochromatinization and/or structural rearrangements (Fig. 1) (see also Odierna et al. 1993, 2001; Olmo et al. 1993). Multiple sex chromosome systems $(Z_1Z_2W \text{ or } X_1X_2Y)$ are quite rare in vertebrates, and in lacertids, in addition to L. vivipara, have been found only in the Pyrenean populations referred to the L. bonnali complex, a group unrelated to vivipara and characterised by a number of centric fusions (Odierna et al., 1996). Then, in L. vivipara the origin of Z_1Z_2W sex chromosome system constitutes a shared derived character for the Pyrenean-Aquitainean, Centro-European and Eastern populations and splits them off from the other populations with ZW sex chromosome system (carniolica and Ócsa). On the other hand, we also exclude that the microchromosome displayed by females of Ócsa should be either a B (supernumerary) chromosome or the result of an event of centric fission occurring in the subtelocentric W disfemales of Pyrenean-Aquitenean, played by

Centro-European and Eastern populations, or a by product of the introgression of maternal markers from carniolica within a viviparous genome. B elements are randomly inherited and we found none of these elements in the Ocsa male, as well as in number of examined specimens of L. vivipara. Furthermore, supernumerary elements are quite rare among lacertids, since they have so far been found in only two species (Olmo et al. 1993). In the case of a centric fission, in addition to this kind of rearrangement we should also consider (1) the occurrence of the euchromatinization of the interstitial, heterochromatic C band that accompanies the subtelocentric W of both the clades and (2) that females of Ócsa possess a complex sex chromosome system of type Z₁Z₂W₁W₂. However, neither centric fissions nor euchromatinization of heterochromatin events have so far been noticed among lacertids (Olmo et al., 1993), while a Z₁Z₂W₁W₂ sex chromosome system would constitute a novelty not only among lacertids but in vertebrates. Lastly, in the case of introgression of carniolica maternal materials within a viviparous genome, this may only spring from hybridation between females of carniolica with viviparous males; in this case the resulting offspring should be compulsory oviparous, since cross breeding experiments between oviparous and viviparous strains of L.vivipara showed that the parental female dictate the reproductive mode of the offspring (Arrayago et al. 1996).





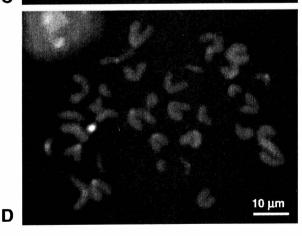


FIG. 2. Giemsa stained (A) and C-banded (B) karyotypes and a sequentially C-banding+ CMA_3 (C)+DAPI(D) stained metaphase plate of a female of L. vivipara from Ocsa.

In conclusion the adaptive value of viviparity (recently reviewed by Blackburn 2000) is further supported by our results, which point to an independent origin of viviparity in Ócsa and elsewhere in Europe.

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BOOK REVIEWS

Rödel, Mark-Oliver. Herpetofauna of West Africa, Vol 1. Amphibians of the West African Savanna. (2000). Edition Chimaira, Frankfurt am Main, Germany. ISBN 3-930612-16-x.332 pp., plus audio CD of frog calls.

This is a translated and expanded version of the author's very useful 1996 book *Amphibien der westafrikanischen Savanne*. The book is divided into three topics in six chapters. The first three chapters offer the various introductions to the West African savanna and the Comoé National Park in the Ivory Coast, where the bulk of the work reported in the book was undertaken. The second part of the book, chapter 5, covers 51 species, arranged by family. The final section considers the ecology of amphibians in the savanna. The literature is extensively cited throughout, with over 900 references.

The introduction to the Comoé National Park covers the geography and geology in detail, and the climate, illustrated with appropriate graphs of temperature and rainfall. The reader is introduced to the important amphibian habitats, such as rivers, forests and savanna. Black-and-white photographs along with details of the vegetation provide a background to the amphibians found in the area.

The species descriptions take up the bulk of the book. The information is derived from two sources; the author's observations and experimental results, followed by comparisons from the literature. The species accounts follow standard arrangements for field guides, except that extensive synonomies and discussions of taxonomy add a technical perspective that is useful for the specialist.

One of the strengths of this book is the detail accorded each species account. Many are illustrated with line drawings, photographs, and electronmicrographs of tadpole mouthparts. The discussions are suitable for the specialist, with citations from a wide variety of sources. The species accounts are enriched with 15 pages of colour. Another strength is the author's personal experience and accurate observations, drawn from a four-year field study. Africa needs more field-based works like this one.

The long lists of citations may prove too much for the non-specialist, for example the range statement for *Ptychadena oxyrhynchus* is supported by exactly 100 references. Despite the data-rich presentation, no identification keys are provided, although the author appears to be in a position to fill this gap. The difficulty of identifying amphibians, one of the reasons for writing this book, we are told, has been made a little easier, but more needs to be done.

The final chapter discussing the life histories of the savanna amphibians discusses strategies for surviving the dry season, the sharing of space, and the sharing of habitats temporally. Reproductive strategies are well studied in amphibians, and the author examines the various strategies and how these are linked to tadpole biology. Tadpoles differ in many ways between species, and this aspect is briefly considered.

The audio CD is compiled and narrated by Ulmar Grafe, and includes high quality recordings of 24 species, plus a few choruses. Anyone who has been to a frog pond at night during the breeding season, and who later listens to the choruses on this CD, will be motivated and eager to get back into the field. I know that I was.

This is overall a most valuable contribution by an active herpetologist, and deserves a space on our bookshelves.

Alan Channing University of the Western Cape

Muhammad Sharif Khan. A Guide to the Snakes of Pakistan. (2002). Edition Chimaira, Frankfurt am Main, Germany. ISBN 3-930612-44-5 265 pages, 155 figures. Euro 34.80 (cloth).

Dr Khan's book covers the 310,400 sq.km of Pakistan, bordered on the west by Iran and Afghanistan and to the east by India and China. Two-thirds of Pakistan is mountainous, from the arid Balochistan Plateau (up to 857 m elevation) to the Himalayas (up to 6714 m). The Indus plain, where most Pakistanis live, is now a totally altered, cultivated habitat with little natural forest remaining. The Indus River, which created the huge floodplain over the millennia, flows south-west from the Himalayas to the Arabian Sea. Pakistan's climate is characterized by relatively low rainfall. The northern hilly tracts receive up to 1300 mm while desert areas get no more than 40 mm and in some years, none at all. Low rainfall usually makes for a sparse snake fauna. Pakistan has about 70 species of snakes and this book covers 54 of them.

An extensive opening section takes us through the author's Introduction, Acknowledgements, the book's purpose and a concise "Survey of literature on the snakes of Pakistan." This is followed by a naturalist's description of Pakistan which gives the reader an excellent general picture of the country's habitats, ecological assemblages and distribution patterns of snakes. A short section on collecting and preserving snakes is given (but the statement "snakes do not have a homing instinct" is wrong). Advice about grasping vipers behind the head and killing specimens by injecting concentrated formalin close to the heart is rather dubious. Next follows an illustrated section on scalation, a key and up-to-date systematic checklist of the snakes of Pakistan.

The following 150 pages consists of the description, range maps plus line drawings (head details for most species) and colour plates of the 54 species covered in the book. The descriptions are adequate and the annotations helpfully include type locality and the original reference. The colour plates are good to excellent, although at least 20 are of dead specimens. Particularly useful are the various colour phases/races/subspecies depicted.

Following the species descriptions is a short note on snakebite. A 1990 estimate by the author is under 1000 deaths per year, with the Big Four: *Naja naja*, *Daboia russelii*, *Bungarus caeruleus* and *Echis carinatus* being the species responsible for most serious bites. Next is a key to the venomous snakes, some non-venomous lookalikes and how to identify a snake from its body fragments.

The 14 pages on snakes in Indian and Pakistani folklore are entertaining and reveal the conflicting emotions of deep dread and high respect snakes are given in our part of the world. The book finishes with a good, 28 page Bibliography and an Index to the scientific names.

Dr Khan is the best-known herpetologist in Pakistan. However, it is puzzling how the publishers allowed bad grammar and sentence structure to slip through the editing process. Mostly it is merely irritating and sometimes cryptic, for instance the reader is advised that "catching a hooded cobra alive needs much experience, it is advised to be killed before catching one." The misspelling and other errors could be called "typos" I guess, but where were the editors? And what was the proofreader Edward C. Sherman III doing? He certainly doesn't deserve the byline he gets. Once you encounter these anomalies, you begin to wonder if scientific accuracy has also suffered. Sure enough, there are problems and again, none that could not have been avoided by a careful edit with inputs from the herpetological community. For example, Dr Khan's treatment of the Typhlopidae had been questioned and revised by Van Wallach (2000) but this is ignored in the book (though referenced in the Bibliography). Inconsistencies between the checklist, keys and species accounts are confusing. For example in the key, Echis multisquamatus and E. pyramidium are given species status while in the species accounts, E. multisquamatus is listed as a subspecies of E. carinatus and E. pyramidium is not even mentioned. Also, some species are missing from the index and a number of references in the Bibliography do not appear anywhere in the text. I'm not familiar with some of the species described and illustrated in the book but I can say that Fig 76 on p. 144 is not Oligodon arnensis, but O. taeniolatus. Fig 122a on p. 172 is Enhydrina schistosa, not Astrotia stokesii.

Some of the other errors include: p. 9, Ashok Captain, (Poone, Arunachal Pradesh, India) should read Ashok Captain, (Pune, Maharashtra); p. 56, *Lycodon travancoricus* has paired subcaudals, not singlés and the same for *Daboia russelii*; p. 107, *Lycodon aulicus_*is described as "docile" and "does not attempt to bite." Every *L. aulicus* I've met has bitten me, but of course I've yet to pick one up in Pakistan; p. 214, in *Daboia russelii* the nostril is not crescentic - it is the supranasal that is crescentic. Distribution maps are always a vital addition to a field guide but it is unfortunate that these are peppered with crudely drawn icons to denote ranges of different species. The line drawings are copied from Smith (1943) and should have been credited to this quintessential herpetologist.

Dr Khan has made a good start toward filling the big gap in our knowledge of snakes of this region of coasts, floodplains, deserts and some of the highest mountains in the world. Pakistan is the western gateway to the Indian subcontinent and there is obviously a lot more basic snake survey work to do there. "A Guide to the Snakes of Pakistan" provides a start for the field researcher who lives in or visits Pakistan (and to some extent, northwest India and Afghanistan). This book should find a place on the bookshelf of anyone interested in snakes of our region of the world.

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Die Zauneidechse. Zwischen Licht und Schatten. Ina Blanke. (2004). 160 pp. Laurenti-Verlag, Bielefeld, Germany. Euro 20.00 (paper).

"Die Zauneidechse - zwischen Licht und Schatten" ("The sand lizard - between light and shade") appears as the seventh supplement to the Zeitschrift für Feldherpetologie (Journal for Field Herpetology), one of the publications by the German herpetological society, the DGHT. These supplements, each about 120-160 pages, contain monographic treatments of species or species groups - of the amphibians and reptiles of Germany (although the work usually covers the whole distribution of the species). In each volume, ecological, faunistic and conservation data and questions are presented and discussed. The major focus is on examples of easy methods for investigation in the field, data analysis and conservation measures. The target groups are field herpetologists and conservationists, but also include authorities and even companies in need of reliable data.

Within less than 200 pages in A5 format, not all questions can be given an equal treatment and the main focus of this book in lies with the ecology and conservation of *Lacerta agilis*. Covered extensively in other publications, the description of the species and morphometric data is kept relatively short, as is the systematics. The following chapter is on general distribution. The distribution in Germany is treated more extensively, and a more detailed view of the varied habitats occupied in different ranges and in different seasons follows. A well covered section on nutrition, feeding, predation and parasites closes with the rather surprising statement (although this is persistently true for the majority of reptiles), that there are no published data on the endoparasites of *L. agilis*. Similarly surprising is the statement, cited from other sources (Dürigen, 1897; Strijbosch, 1999), that the cartilaginous rods replacing autotomized tails have fracture planes as well and can therefore be autotomized.

In further chapters on phenology, reproductive biology and population biology a good and concise summary of current knowledge is compiled. Missing data and further resarch needed is pointed out frequently which might be useful for students in the search for a thesis, as could be the short but critical considerations of some methodologies especially for range analysis and population densities.

The book closes with sections on causes for decline and the conservation of the sand lizard. The approach is very hands-on and pleasantly critical. While most examples emanate from Germany, some examples from other countries such as the British reintroduction programme are also given. Although short, the treatment of "manipulation of populations" gives a good, down-to-earth introduction on the risks and possibilities of relocation, head-starting (e.g. unintentional genetic selection) and reintroduction. Excellent and useful for everybody wanting to preserve sand lizard habitat are the instructions for the maintenance or creation of habitats. It shows the practical measures that can be taken when the destruction of a habitat is looming, including a checklist-like guide for translocations, if these are unavoidable. It is made clear, that this would have to be only a last resort due to the high risks that most lizards will not survive, and the fact that not only the target species has to be taken into consideration. This check-list is especially useful for German readers, but the English papers cited are by Langton & Burton (1997) and Moulton & Corbett (1999), which were subsequently reviewed again for evaluating success in a non-published German diploma thesis (Thunhorst, 1999).

The book concludes with a bibliography covering a respectable 328 citations and a two-page index with 115 entries. The tables and figures are taken directly from the respective sources and are mostly reproduced in good quality. However, the quality of the pictures is not satisfactory. There are three double-pages of colour photos which are of better quality. Most of the monochromes, especially the reproduced pictures, are of poor resolution and should have been either taken again or better selected. But the low price of the book makes up for it and better pictures would probably increase costs significantly without changing the value of the comprehensive and practically instructive text.

One other point of criticism might be made. Although a scientific treatise, this book might well appeal to amateurs as well (and definitely should). For this reason, it should have been pointed out more stringently that the release or relocation of any lizards or reptile even with the best intention is highly risky. The high risks of transmitting diseases makes it a task only to be undertaken with the utmost care. If a release has to be undertaken, pre-release isolation and screening protocols of the animals to be released – as well as for populations already on site – have to be carried out very rigorously.

In sum, a recommended book and good value for money. Everybody interested in *L. agilis*, be it to get a first impression, a summary of what is already known, for further reading advice or to get involved in the conservation of the sand lizard would benefit from learning some German and reading it.

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Atlas y Libro Rojo de los Anfibios y Reptiles de Espana. (2002). Juan M. Pleguezuelos, Rafael Márquez, M. Lizana (Eds.) Ministerio de Medio Ambiente, Madrid. 587 pp.

Recent years have seen a steady stream of herpetofauna distribution atlases appear on the European market. These atlases have varied in the extent of the region covered, and in quality and detail. This spectacular book - which documents the national status (and much more) of the amphibians and reptiles of Spain sets a standard that will be difficult to match at any scale. Indeed, this is far more than a regional atlas. Its eleven chapters provide the most authoritative account of the natural history of the Spanish herpetofauna published to date. The conservation status, distribution and general ecology of every species occurring in Spain is described alongside a distribution map showing its occurrence in each 10 km² grid square within the country. Very thoughtfully, a broader scale map showing the European distribution is also provided. The maps, general text and information boxes are accompanied by some truly breathtaking colour photographs of the species concerned. However, the distribution sections dealing with the amphibians and reptiles of mainland Spain take up just over half of the 587 pages of this book. Further chapters deal with the marine turtles found around the coast, the herpetofauna of the various other Spanish territories within the Mediterranean region, conservation, regional herpetofaunas, important herpetological areas, introduced species, mapping methods and geographical information systems, and molecular approaches to systematics and phylogeny. All of this information is supported by comprehensive bibliographies, and addresses and websites of relevant organisations within the region. An undertaking of this size relies on the input of many people, and the 70 authors and consultants who have contributed to the volume underline the buoyant status of Spanish herpetology in Europe. Even if your knowledge of the Spanish language is rudimentary (as is my own) you will profit from consulting this book before any trip to the country or its associated territories. In fact, it would be worthwhile discarding most of your clothes to make room for this bulky volume in your luggage.

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INSTRUCTIONS TO AUTHORS (revised January 2004)

- 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.
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