

The Late Pliocene amphibians and reptiles from “Capo Mannu D1 Local Fauna” (Mandriola, Sardinia, Italy)

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ABSTRACT

The Late Pliocene Capo Mannu D1 Local Fauna (Mandriola, W Sardinia, Italy) produced remains of five amphibians and at least nine reptiles: *Salamandrina* sp., cf. *Ichthyosaura* sp., *Discoglossus* sp., cf. *Bufo* gr. *B. viridis* Laurenti, 1768, *Hyla* gr. *H. arborea* (Linnaeus, 1758), Gekkonidae indet., *Dopasia* sp., *Lacerta* gr. *L. viridis* (Laurenti, 1768), Lacertidae indet. (small size), *Amphisbaenia* indet., *Eryx* cf. *E. jaculus* (Linnaeus, 1758), Colubrinae indet., *Natrix* sp., and *Vipera* sp. The Capo Mannu D1 assemblage partly fills a chronological gap in the knowledge of the Sardinian herpetofauna because well-diversified herpetofaunas have been retrieved only in the Early Miocene of Oschiri and in the Pleistocene of Monte Tuttavista. It has an intermediate taxonomic composition and still shows a high rate of taxa which are now extinct on the island (*Salamandrina* sp., cf. *Ichthyosaura* sp., *Dopasia* sp., *Lacerta* gr. *L. viridis*, *Amphisbaenia* indet., *Eryx* cf. *E. jaculus*, and *Vipera* sp.). Some taxa (both extinct and extant) are present

KEY WORDS

Amphibia,
Reptilia,
Salamandrina,
Ichthyosaura,
Dopasia,
Lacerta,
Amphisbaenia,
Eryx,
Vipera,
Late Pliocene,
Sardinia.

in the three localities but none is exclusively shared by Oschiri and Monte Tuttavista. The remains of *Salamandrina* from the Capo Mannu D1 Local Fauna testify for a prolonged permanence in Sardinia of this taxon (already known from Oschiri). The absence of remains unambiguously referable to the previously reported ranids could suggest that these anurans never reached the island by natural dispersal (without human intervention). The taxonomic composition of the Capo Mannu D1 Local Fauna is overall similar to that of other west Mediterranean Pliocene herpetofaunas, and it confirms the previously reported pattern of evolution of European herpetofaunas.

RÉSUMÉ

Les amphibiens et les reptiles du Pliocène supérieur de « Capo Mannu D1 » (Mandriola, Sardaigne, Italie).

L'étude de la faune du Pliocène supérieur de Capo Mannu D1 montre la présence de cinq taxons d'amphibiens et d'au moins neuf reptiles : *Salamandrina* sp., cf. *Ichthyosaura* sp., *Discoglossus* sp., cf. *Bufo* gr. *B. viridis* Laurenti, 1768, *Hyla* gr. *H. arborea* (Linnaeus, 1758), Gekkonidae indéterminé, *Dopasia* sp., *Lacerta* gr. *L. viridis* (Laurenti, 1768), Lacertidae indéterminé (petite taille), *Amphisbaenia* indéterminé, *Eryx* cf. *E. jaculus* (Linnaeus, 1758), Colubrinae indéterminé, *Natrix* sp. et *Vipera* sp. L'ensemble de la faune de Capo Mannu D1 vient partiellement combler un vide chronologique dans la connaissance de l'herpétofaune sarde où seules les faunes du Miocène inférieur d'Oschiri et du Pléistocène de Monte Tuttavista étaient connues. Elle possède une composition taxonomique intermédiaire et montre encore un taux élevé de taxons actuellement éteints dans l'île (*Salamandrina* sp., cf. *Ichthyosaura* sp., *Dopasia* sp., *Lacerta* gr. *L. viridis*, *Amphisbaenia* indéterminé, *Eryx* cf. *E. jaculus* et *Vipera* sp.). Certains de ces taxons (éteints ou existants actuellement dans l'île), sont présents dans les trois localités mais aucun d'entre eux n'est exclusivement partagé par les sites d'Oschiri et de Monte Tuttavista. La présence de *Salamandrina* à Capo Mannu D1 (taxon déjà présent à Oschiri), témoigne d'un maintien prolongé de celui-ci en Sardaigne. D'autre part, l'absence de restes pouvant être attribués sans ambiguïté aux Ranidae, dont la présence avait été auparavant suggérée dans le site, semble indiquer que ce groupe d'anoures n'a jamais atteint l'île par une voie de dispersion naturelle (sans intervention de l'homme). La composition taxonomique de Capo Mannu D1 est globalement similaire à celle d'autres herpétofaunes pliocènes de l'ouest méditerranéen, et confirme dans ses grandes lignes le patron évolutif déjà signalé pour l'herpétofaune de l'Europe.

MOTS CLÉS

Amphibia,
Reptilia,
Salamandrina,
Ichthyosaura,
Dopasia,
Lacerta,
Amphisbaenia,
Eryx,
Vipera,
Pliocène supérieur,
Sardaigne.

INTRODUCTION

The Pliocene is an epoch of major changes in the European herpetofauna because a remarkable faunal impoverishment seems to approximately correspond to the MN 16-17 boundary (Rage 1997; Delfino *et al.* 2003; Bailon & Blain 2007), formerly considered as

the Middle-Late Pliocene boundary and now as the Plio-Pleistocene boundary (Gibbard *et al.* 2010). In Western Europe, whose palaeoherpetofaunas are the best known of the continent, during the second half of the Pliocene disappeared thermophilous families such as Varanidae Gray, 1827, Aniilidae (s.l.) Fitzinger, 1826, Boidae Gray, 1825 and Elapidae Boie,

1827. Further significant extinctions occurred during the Early Pleistocene when disappeared the scincid lizard of the *Mabuya* group, scolecophidians, and large vipers of the so-called “Oriental group”, whereas agamids, geckonids, other scincids, amphisbaenians and some colubrids apparently survived only in southern Iberia (Bailon & Blain 2007).

As far as the Italian biogeographic region is concerned, the information available at present does not allow any precise assessment because of the limited number of available herpetofaunas. Many localities yielded only one chelonian taxon (frequently a marine turtle; Delfino 2002; Chesi & Delfino 2007), whereas few others yielded diverse assemblages whose taxa have only been partly studied or simply listed. This is the case of the following sites (Fig. 1): Arondelli (Early Pliocene; Vergnaud-Grazzini 1970), Cava Sefi (Poggibonsi; Early Pliocene; Rinaldi 2003), and Capo Mannu D1 Local Fauna (Late Pliocene; Pecorini *et al.* 1974). Other sites, formerly considered as Pliocene in age but now referred to the Pleistocene (after Gibbard *et al.* 2010) could also be included in this list: Montagnola Senese (formerly Late Pliocene; Fondi 1972), Rivoli Veronese (formerly Late Pliocene; Delfino & Sala 2007), and Monte Tuttavista (formerly Plio-Pleistocene; Abbazzi *et al.* 2004; Delfino *et al.* 2008).

In order to provide updated information on the Italian Pliocene herpetofaunas, the remains of these localities are currently under revision and full description. The present paper is devoted to the description of the never described and figured amphibian and reptile remains from the Capo Mannu D1 Local Fauna, a vertebrate assemblage originally referred in the literature to the site called Mandriola (see paragraph “Age and name of the locality” in the following section). A preliminary faunal list, based on the same material described in the present paper, was already provided by Pecorini *et al.* (1974) who identified the following taxa: *Urodela* indet., *Discoglossidae* indet., *Bufonidae* indet. (cf. *Bufo*), ?*Ranidae* indet., *Gekkonidae* indet., *Lacertidae* indet., *Anguidae* indet. (legless form), *Amphisbaenia* indet., *Boidae* indet. (modern form of *Erycinae*), *Colubrinae* indet., *Natricinae* indet., and *Viperidae* indet. (cf. *Vipera*). On the basis of the same material, some identifications have been refined to *Discoglossus* sp., “*Rana*



FIG. 1. — Location of the main Italian herpetofaunistic assemblages (single findings are not shown) referred to the latest Neogene and earliest Quaternary: 1, Arondelli (Early Pliocene); 2, Cava Sefi (Early Pliocene); 3, Capo Mannu D1 Local Fauna (Late Pliocene); 4, Montagnola Senese (formerly Late Pliocene, now Early Pleistocene); 5, Rivoli Veronese (formerly Late Pliocene, now Early Pleistocene); 6, Monte Tuttavista (formerly Plio-Pleistocene, now Early Pleistocene). The star (★) indicates the Early Miocene (MN3) locality of Oschiri. Note that the late Miocene (possibly Early Pliocene) site of Monte Gargano is not listed among the Pliocene localities.

(*ridibunda*) sp.” (Sanchiz 1998 and references therein), and *Podarcis* sp. (Bailon 2004), but the description of the whole fauna was still pending.

The information provided by the amphibians and reptiles of the Capo Mannu D1 Local Fauna will be discussed in the frame of the knowledge of the evolution of the Sardinian herpetofauna and of the western European assemblages.

MATERIAL AND METHODS

ABBREVIATIONS

- | | |
|------|---|
| DSTC | Dipartimento di Scienze della Terra dell'Università di Cagliari, Italy; |
| MNCN | Museo Nacional de Ciencias Naturales, Madrid, Spain. |

REPOSITORY

The remains here described represent the fossil material on which the faunal list published by Pecorini *et al.* (1974) was based. It is now stored in the collections of the DSTC with accession numbers from DSTC 6000 to 6514.

AGE AND NAME OF THE LOCALITY

The chronological allocation of the different units of the Pliocene-Pleistocene sequence in the northern Sinis (Mandriola limestones Formation and Capo Mannu Formation) has been recently summarized by Abbazzi *et al.* (2008). Within the same sedimentary succession it is possible to distinguish two fossiliferous layers: 1) the basal Capo Mannu D1 Local Fauna (in the following paragraphs Local Fauna will be abbreviated as LF), referable to the Late Pliocene (MN15), preliminarily described by Pecorini *et al.* (1974) and subsequently often identified by the name Mandriola (as in Angelone & Kotsakis 2001); and 2) the overlaying Capo Mannu D4 LF, referable to the Early Pleistocene (MN16; described by Abbazzi *et al.* 2008 as Late Pliocene), and often, but not always, identified by the name Capo Mannu.

The present paper deals exclusively with the amphibian and reptile remains from the lower unit that, for the sake of stability, will be formally named the Capo Mannu D1 LF.

ANATOMICAL AND TAXONOMIC NOMENCLATURE

Anatomical nomenclature follows Francis (1934), Estes (1981) and Holman (2006) for caudates, Bailon (1999) and Sanchiz (1998) for anurans, Fejérváry-Láng (1932) and Estes (1983) for lacertilians and amphisbaenians, and Szyndlar (1984, 1991a, b) and Holman (2000) for snakes. In the sections "Material examined" no distinction is made between perfectly preserved skeletal elements and their fragments; the state of preservation is commented in the sections "Description" when needed.

The taxonomic nomenclature follows Sindaco *et al.* (2006) and Lanza *et al.* (2007) but the Alpine newts are referred to the genus *Ichthyosaura* Soncini & Latreille, 1801 and not to *Mesotriton* Bolckay, 1927 (see Speybroeck *et al.* 2010). The remains of the green toad are referred to the *Bufo viridis* group

on the basis of the recent molecular evidences for the presence in peninsular Italy of at least three species (Stöck *et al.* 2008) which are apparently not identifiable on a skeletal basis.

SYSTEMATIC SECTION

Class AMPHIBIA Gray, 1825
Order CAUDATA Scopoli, 1777
Family SALAMANDRIDAE Goldfuss, 1820
Genus *Salamandrina* Fitzinger, 1826

Salamandrina sp.
(Fig. 2A-I)

MATERIAL EXAMINED. — Occipito-otic unit: 3; precaudal vertebra: 16; caudal vertebra: 4.

DESCRIPTION

Two of the three occipito-otic units are relatively well preserved and allow identifying the following characters: the overall size is small and the shape is elongated (maximum length and width of about 2.1 and 1.5 mm respectively; but part of the width is due to the long *tectum synoticum*); the well-marked convexities of the dorsal surface surround an evident median concavity (in which a foramen opens in two of the three units); the medial convexity hosts, in the posterior sector, a dorsally directed small tubercle; the *tectum synoticum* narrows apically where it is naturally truncated; the axis of the *tectum synoticum* and the main axis of the capsule form an angle of approximately 60°. In medial view, the area of suture contact with the other occipito-otic unit is reduced; the endolymphatic and the perilymphatic foramina, as well as the large cavity that hosts the three acoustic nerves are visible; the latter cavity is deep and well defined; the oval fenestra is large, slightly oval in shape and with funnel-shaped rims; the lateral margin of the oval fenestra is markedly raised from the surface of the capsule; the condylar articular surface is concave; two foramina are placed laterally and lateroventrally to the occipital condyle. In lateral view, the contact area for the squamosal is small and oval-shaped.

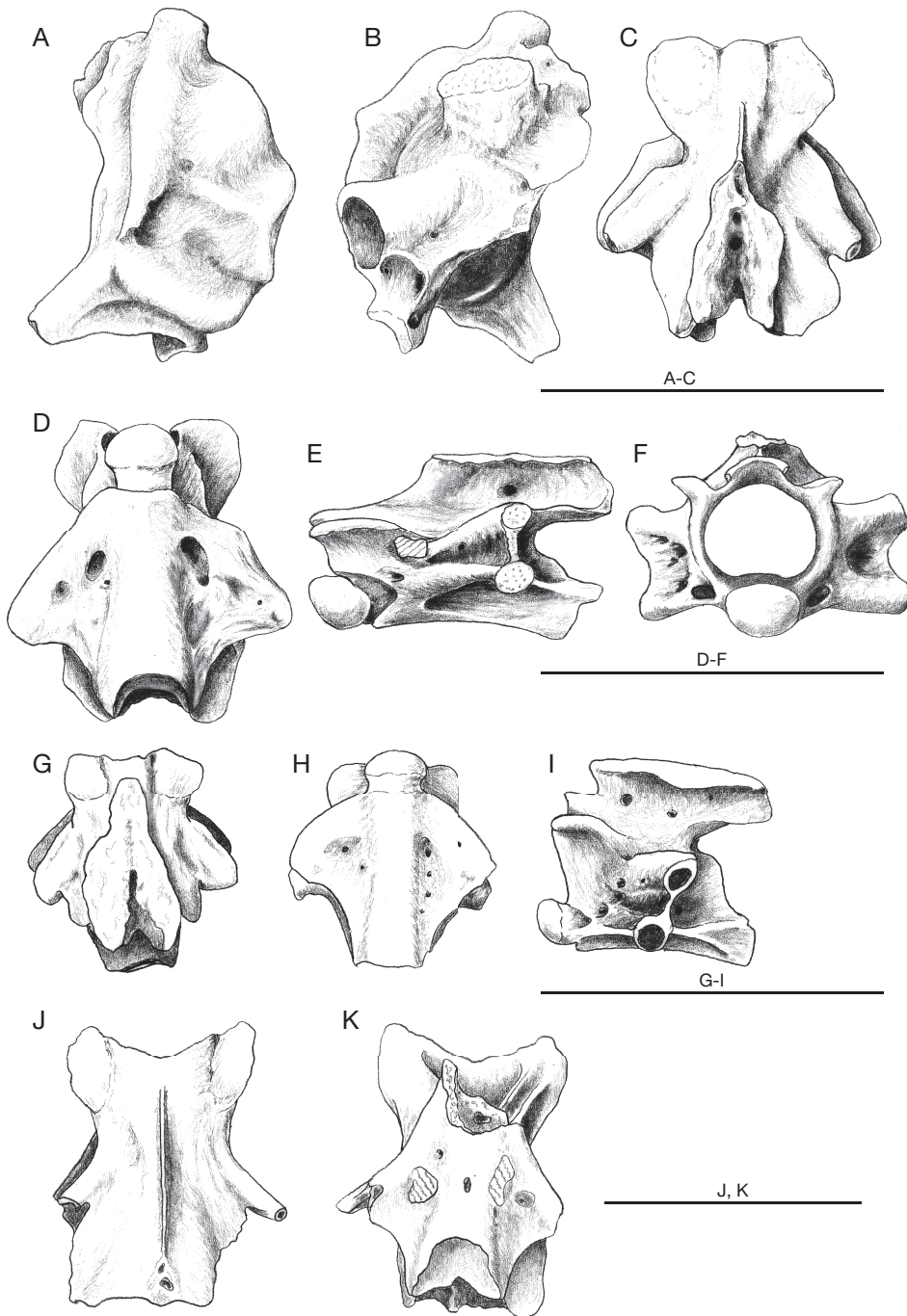


FIG. 2. — Fossil remains of amphibians from Capo Mannu D1 Local Fauna (Sardinia): **A-I**, *Salamandrina* sp.; **A, B**, right occipito-otic unit (DSTC 6000), dorsal and ventral views; **C-E**, middle trunk vertebra (DSTC 6001), dorsal, ventral, and left lateral views; **F**, trunk vertebra (DSTC 6002), anterior view; **G-I**, anterior trunk vertebra (DSTC 6003), dorsal, ventral, and left lateral views; **J, K**, cf. *Ichthyosaura* sp., trunk vertebra (DSTC 6004), dorsal and ventral views. Scale bars: 2 mm.

The precaudal vertebrae are rather small (maximum centrum length estimated at about 1.8 mm, but most of the vertebrae are much smaller). The centrum is opisthocoelous; condyle and cotyle are roundish or slightly oval in shape; an evident constriction is placed at the base of the condyle. In dorsal view, the anterior edge the prezygapophyses does not significantly surpass the neural arch. The prezygapophyseal facets are vaguely drop-shaped, longer than wide, and proportionally rather large in most of the cases (each prezygapophysis is as wide as the anterior edge of the neural arch). The lateral edge of the neural arch is distinctly constricted just anteriorly to the rib-bearers. The dorsal rib-bearer has invariably a laminar anterior edge. The rib-bearers are posterolaterally directed. A shallow groove is developed along the posterior contact between the dorsal rib-bearer and the neural arch. A deep notch is developed at the posterior edge of the neural arch; the latter does not extend beyond the posterior edge of the postzygapophyses. The neural crest has a variable length: it does not reach the anterior edge of the neural arch but it extends up to its posterior edge. It regularly bifurcates in the posterior area of the vertebra where it is apically thickened and develops laterally directed “lips”. The thickening of the crest can be present also anteriorly to the bifurcation in the most anterior vertebrae. One or few foramina can be present in the depression between the two rami just posterior to the bifurcation. In ventral view, the centrum is nearly cylinder-shaped (with a weak median constriction). The surface of the centrum is well delimited laterally, but it is covered by a bony lamina (anterior ventral crest) that extends slightly anteriorly of the rib-bearers and up to the basis of the condyle neck where it has an irregularly concave profile. The ventral rib-bearer has laminar edges both anteriorly (the above mentioned anterior ventral crest) and posteriorly (posterior ventral crest). The posterolateral edges of the lamina are variably concave. The lamina can host, posteriorly to the root of the rib-bearers, few wide depressions with foramina opening at their bottom (in some cases there are no depressions and the foramina open directly at the surface of the lamina). In lateral view, the neural crest is moderately tall in the posterior two thirds of its length. The rib-bearers are

moderately divergent but always linked by a bony lamina for their entire length. A foramen pierces the base of the lateral wall of the neural arch behind each couple of rib-bearer processes. In anterior and posterior views, the pre- and postzygapophyses are nearly horizontal. The neural canal varies in shape and size: in the vertebrae that are proportionally short and wide (therefore more anteriorly placed) it is much larger than the condyle, in the vertebrae that are relatively more elongated it is proportionally not so large. The neural arch usually shows at least a hint of zygosphenes and zygantrum.

One vertebra (DSTC 6027) referred to the precaudal section of the vertebral column could represent a sacral vertebra because of the slightly enlarged tips of the rib-bearers, and at least another one (DSTC 6028) could come from the caudo-sacral region because of the possible presence of the remnants of haemal processes.

The caudal vertebrae are smaller than the precaudal ones (the maximum length of the opisthocoelous centra is of about 1.0 mm). At least in the two better preserved vertebrae, the incomplete neural arches show the hint of zygosphenes and zygantrum and the neural crests are thickened and bifurcated. Haemal arches are regularly present and at least in one case (DSTC 6029) they develop a posteriorly bifurcated crest, hosting a foramen. At least three of the four caudal vertebrae are characterized by lateral processes forming a laid down “M” (with the base oriented towards the posterior sector of the vertebra).

DISCUSSION

The occipito-otic units can be referred to genus *Salamandrina* because of the combination of the following characters (see Pitruzzella 2008): elongated general morphology, development of the convexities and of the median depression on the dorsal surface; presence of a tubercle on the medial convexity; morphology of the bone encircling the oval fenestra.

The vertebrae can be referred to this genus on the basis of several characters (see Sanchiz 1988; Pitruzzella 2008; Pitruzzella *et al.* 2008), among which the most relevant are: the presence of zygosphenes and zygantrum; thickened and posteriorly bifurcated neural crest developing lateral “lips”; development of a ventral bony lamina covering the centrum and reaching the basis

of the condyle (in precaudal vertebrae); “M”-shaped lateral process (in caudal vertebrae).

As for the specific identification, the absence of skeletal diagnostic characters distinguishing the two extant species of this genus (Pitruzzella 2008) does not support the specific identification of the fossil remains from the Capo Mannu D1 LF. However, it is worth noting that all the remains here described are distinctly smaller than the corresponding skeletal elements of extant *Salamandrina perspicillata* (Savi, 1821) and *S. terdigitata* (Lacépède, 1788), as well as of fossil *Salamandrina* sp. from Oschiri (Pitruzzella 2008).

Genus *Ichthyosaura* Sonnini & Latreille, 1801

cf. *Ichthyosaura* sp.
(Fig. 2J, K)

MATERIAL EXAMINED. — Trunk vertebra: 3.

DESCRIPTION

These three opisthocoelous vertebrae are much larger in size than the vertebrae referred to the genus *Salamandrina*. The best preserved remain, an anterior trunk vertebra (DSTC 6030), has a centrum length of 1.8 mm, whereas the length of the other vertebrae can be assumed to slightly exceed 2 mm. DSTC 6030 is a nearly complete vertebra (damaged in the left anterior and right posterior areas). The condyle and cotyle are nearly circular. The condyle is well defined and there is a modest precondylar constriction (without the development of marked neck as in *Salamandrina*). The neural canal is particularly wide. The neural arch has a V-shaped anterior margin. The prezygapophyseal facets are anterolaterally elongated and are faintly tilted dorsally. The posterior edge of the neural arch is nearly straight; it does not surpass the postzygapophyses even if it is prolonged in a small point which extends the neural crest. The neural crest is partly broken but is clearly moderately tall, undivided (not forked) and not thickened. The rib-bearers are relatively thick and subequal in size (the ventral one is slightly thicker); they are connected to each other by a bony lamina. The bony laminae connecting the rib-bearers with the centrum are, both dorsally and ventrally, underdeveloped in

the anterior sector of the vertebra but evident in the posterior one where they have a lateral deeply concave profile. The surface of the ventral laminae hosts elongated and relatively large foramina.

The two other vertebrae have a similar morphology but are a little larger in size, with a comparatively narrower neural canal and thinner, more posteriorly directed, rib-bearers. The anteroventral edge of the ventral rib-bearers develops in both vertebrae an evident ridge. Small foramina are present on the bony laminae connecting the rib-bearers with the posterior sector of the centrum. There is no precondylar constriction in the only vertebra that preserves the anterior end of the centrum. The posterior area of the neural arch is broken off in both cases.

DISCUSSION

The width of the neural canal and the orientation of the rib-bearers indicate that DSTC 6030 is an anterior trunk vertebra, whereas the other two vertebrae come from a posterior sector of the column. The described morphology of the vertebrae is congruent with that of a newt of the genus *Ichthyosaura*, but the laminae developed anterior to the rib-bearers and the precondylar constriction are less developed in the fossils than in extant *Ichthyosaura*. Even the presence of the genus *Euproctus* Gené, 1838 (which still inhabits the island but has no fossil record yet) cannot be ruled out: a direct analysis of limited skeletal material of *E. platycephalus* (Gravenhorst, 1829) (MNCN 15981), *E. montanus* (Savi, 1838) (MNCN 15966, 15967), and *Calotriton asper* (Dugès, 1852) (MNCN 16130, 16131) revealed that these species, once grouped in a single genus, possess a vertebral morphology that is well characterized and rather variable. The region hosting the best characterizing features is the posterior area of the neural arch (the lamina developing from the dorsal rib-bearers to the postzygapophyses, and the shape of the posterior edge of the neural arch), area that is broken in the two fossil posterior trunk vertebrae.

Taking into consideration their poor preservation, the fossil remains from the Capo Mannu D1 LF are tentatively referred to cf. *Ichthyosaura* sp. Further fossil material or a detailed analysis of a larger sample of *Euproctus* vertebrae could possibly allow deepening such provisional identification.

Order ANURA Fischer von Waldheim, 1813
Family DISCOGLOSSIDAE Günther, 1859
Genus *Discoglossus* Otth, 1837

Discoglossus sp.
(Fig. 3A)

MATERIAL EXAMINED. — Humerus: 3; ilium: 6; femur: 1; atlas: 1; trunk vertebra: 15; urostyle: 1; rib: 2.

DESCRIPTION

The best preserved humerus shows an *eminentia capitata* slightly lateral to the straight shaft; the *crista radialis* is weakly bent in ventral direction; the *fossa cubitalis* is deep and wide; the olecranon scar is distinctly elongate.

None of the two right and four left ilia is completely preserved but all show an elongated *tuber superior*, a supracetabular fossa, and a laminar *crista dorsalis* curved medially; the preacetabular zone is underdeveloped so that its edge nearly coincides with the anterior acetabular rim; only in one case the acetabular region is so well preserved to show a deep interiliac groove on the medial surface.

The femur has a weak femoral crest and a well-marked sigmoid general shape.

A fragmentary atlas devoid of the neural arch shows anterior cotyles well separated by a narrow intercotylar area, a posterior cotyle elliptic in shape, and a ventral sagittal keel.

The trunk vertebrae are represented by fragments only. The vertebral centra are characteristically isolated by breakages at the level of the beginning of the neural arch (therefore it is impossible to state on a morphological basis if they were procoelous or opisthocelous); the centra are ventrally concave; cotyles are usually long and characteristically well separated from the centrum; rib bearing processes are apically flared and end with a truncated surface typical of vertebrae bearing ribs.

Two isolated ribs show a dorsal spine and an articular surface complementary to that of the rib bearing process of the vertebrae.

The proximal region of a urostyle is preserved: it shows elliptic cotyles and a couple of transverse processes.

DISCUSSION

All the described characters, the deep interiliac groove of the ilium and the ventral sagittal keel of the atlas in particular, fit well with the morphology of *Discoglossus* (Böhme 1977; Bailon 1999). A key for the identification of the extant species belonging to this genus is still not available. Clarke & Lanza (1990) discussed the distinction of the two Sardinian species *Discoglossus sardus* Tschudi in Otth, 1837 and *D. montalentii* Lanza, Nascetti, Capula & Bullini, 1984, but the osteological characters identified by them do not concern the skeletal elements preserved in the Capo Mannu D1 LF sample. The fossil remains are therefore referred to *Discoglossus* sp.

Family BUFONIDAE Gray, 1825
Genus *Bufo* Laurenti, 1768

cf. *Bufo* gr. *B. viridis* Laurenti, 1768
(Fig. 3B)

MATERIAL EXAMINED. — Ilium: 1; femur: 2.

DESCRIPTION

A tiny left ilium is characterized by a robust ilial shaft devoid of *crista dorsalis*, an elongated *tuber superior* with a relatively flattened, wide, dorsal edge, a well-marked preacetabular fossa, a uniformly thickened area for the suture with the ischium.

The best preserved femur is relatively robust in general appearance and presents a sharp, distinctly undivided *crista femoris*.

DISCUSSION

The morphology of the ilium and the femora is congruent with that of the *B. viridis* group (Böhme 1977; Sanchiz 1977; Bailon 1999). The only exception is the *tuber superior* of the ilium that is proportionally massive and does not bear the anterior tubercle typical of this species. Due to the fact that this tubercle is sometimes underdeveloped in the *B. viridis* group (Delfino pers. obs.) and taking into consideration the small size of the ilium from Capo Mannu D1 LF, these remains are here tentatively referred at species level to cf. *Bufo* gr. *B. viridis*.

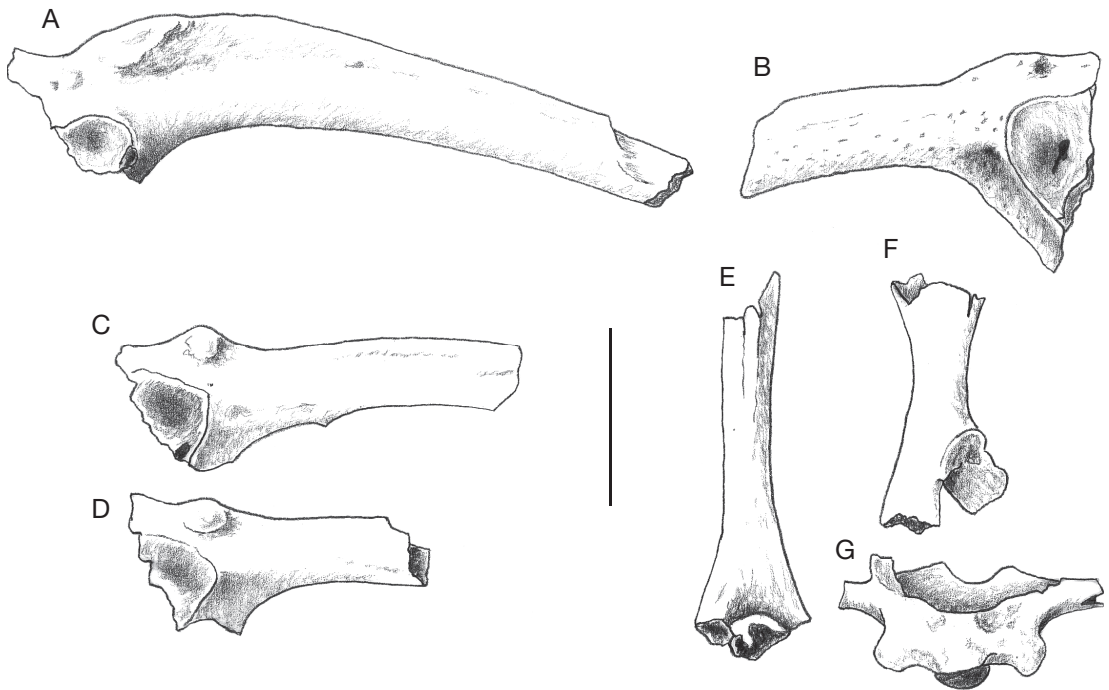


FIG. 3. — Fossil remains of amphibians from Capo Mannu D1 Local Fauna (Sardinia): **A**, *Discoglossus* sp., right ilium (DSTC 6005), lateral view; **B**, cf. *Bufo* gr. *B. viridis*, left ilium (DSTC 6006), lateral view; **C–G**, *Hyla* gr. *H. arborea*; **C**, right ilium (DSTC 6007), lateral view; **D**, right ilium (DSTC 6008), lateral view; **E**, left humerus (DSTC 6009), ventral view; **F**, left scapula (DSTC 6010), lateral view; **G**, presacral vertebra (DSTC 6011), dorsal view. Scale bar: 2 mm.

Family HYLIDAE Gray, 1825

Genus *Hyla* Laurenti, 1768

Hyla gr. *H. arborea* (Linnaeus, 1758)

(Fig. 3C–G)

MATERIAL EXAMINED. — Mandible: 1; scapula: 3; humerus: 2; ilium: 8; femur: 2; trunk vertebra: 3; sacral vertebra: 1; urostyle: 2.

DESCRIPTION

A tiny mandible is characterized by a posteriorly directed “tubercle” on the medial edge of the coronoid process.

One of the three scapulae is well preserved: it is a triradiate element with an elongated and narrow *pars suprascapularis*, and narrow subequal *pars acromialis* and *processus glenoidalis*; the inner surface of these structures is completely smooth.

The humeri fragments show a straight diaphysis with an *eminentia capitata* slightly shifted toward

the radial epicondyle; radial and epicondylar ridges are well developed; the *fossa cubitalis* is relatively deep and markedly open in lateral direction.

Seven right ilia and one left element are characterized by a *tuber superior* that develops a distinct tubercle in lateral direction and by a preacetabular zone expanded in a wide blade that involves dorsally the ilial shaft and ventrally the *pars descendens ilii*; the ilial shaft is approximately cylindrical and devoid of *crista dorsalis*.

Two fragmentary lightly-built femora show a delicate *crista femoris* in the proximal area.

All the trunk vertebrae show a remarkably wide neural canal and a proportionally tiny procoelous centrum.

The sacral vertebra is procoelous with a double posterior condyle; the partly preserved lateral apophyses clearly indicate that they were rather constricted at the base and not cylindrical; a hint of neural ridge is developed along the posterior margin of the neural arch.

Two urostyles share the presence of rounded cotylar cavities for the sacral condyles; the neural arches are broken off at the basis.

DISCUSSION

The skeletal morphology of the European tree frogs is quite characteristic and therefore their fossil remains are easily identifiable at genus rank. The morphology of the ilium (Böhme 1977; Bailon 1999), as well as of all the other skeletal elements is congruent with that of the corresponding elements of extant species of genus *Hyla*. Due to the unreliability of the osteological characters that were presumed to allow distinction among the European species, the fossil remains from the Capo Mannu D1 LF are referred only at species group rank, named after the most representative species (for a discussion see Delfino & Bailon 2000).

Anura indet.

MATERIAL EXAMINED. — Maxilla: 4; squamosal: 1; pterygoid: 2; mandible: 3; scapula: 1; clavícula: 1, coracoid: 1; humerus: 8; radioulna: 9; ilium: 5; ischium: 3; femur: 4; tibiofibula: 8; vertebra: 21; sacral vertebra: 3; urostyle: 1; indet.: 26.

DISCUSSION

The fossil remains referred at this rank are fragments devoid of diagnostic characters or skeletal elements not diagnostic even at family rank (as phalanges and metapodials). All these remains from the Capo Mannu D1 LF probably belong to the taxa reported above.

Class REPTILIA Laurenti, 1768
Order LACERTILIA Owen, 1842
Family GEKKONIDAE Gray, 1825

Gekkonidae indet. (Fig. 4A, B)

MATERIAL EXAMINED. — Maxilla: 1; ilium: 1; trunk vertebra: 3.

DESCRIPTION

A fragment of maxilla corresponding to eight tooth positions preserves only one tooth; it is

pleurodont, slender, conical, and monocusped; a cavity opens at the base of the tooth. Two rows of foramina are aligned on the outer surface of the maxilla.

A right ilium has a short but dorsoventrally expanded shaft; the anterior process is developed as a wide dorsal lamina and not as a prominent tubercle.

The largest trunk vertebra has an amphicoelous centrum slightly longer than 1 mm; the cotyles are approximately circular; the neural canal is extremely large when compared to the centrum; the prezygapophyses are nearly completely broken-off; the postzygapophyseal facets are narrow and elongated; the anterior edge of the neural arch is V-shaped; the posterior edge of the neural arch develops a process that does not significantly surpass the postzygapophyses; the neural crest is weakly developed or absent and therefore the neural arch is nearly smooth, being present only as a modest keel; the synapophyses are elongated and dorso-caudally directed; the ventral surface of the centrum is markedly concave and devoid of keels or ridges. The figured vertebra (DSTC 6012; Fig. 4A, B) has an evident tubercle on both the lateral surfaces of the neural arch.

DISCUSSION

The amphicoelous condition of the vertebra, associated to a maxilla bearing a pleurodont monocusped tooth, allows the identification of a member of Gekkonidae (see among others Bailon 1991). The absence of diagnostic characters on the skeletal elements preserved in the Capo Mannu D1 LF assemblage hinders a more precise identification.

Family LACERTIDAE Bonaparte, 1831
Genus *Lacerta* Linnaeus, 1758

Lacerta gr. *L. viridis* (Laurenti, 1768) (Fig. 4C)

MATERIAL EXAMINED. — Tooth bearing bone: 4; humerus: 1; trunk vertebra: 1; caudal vertebra: 5; rib: 1; ungual phalanx: 6.

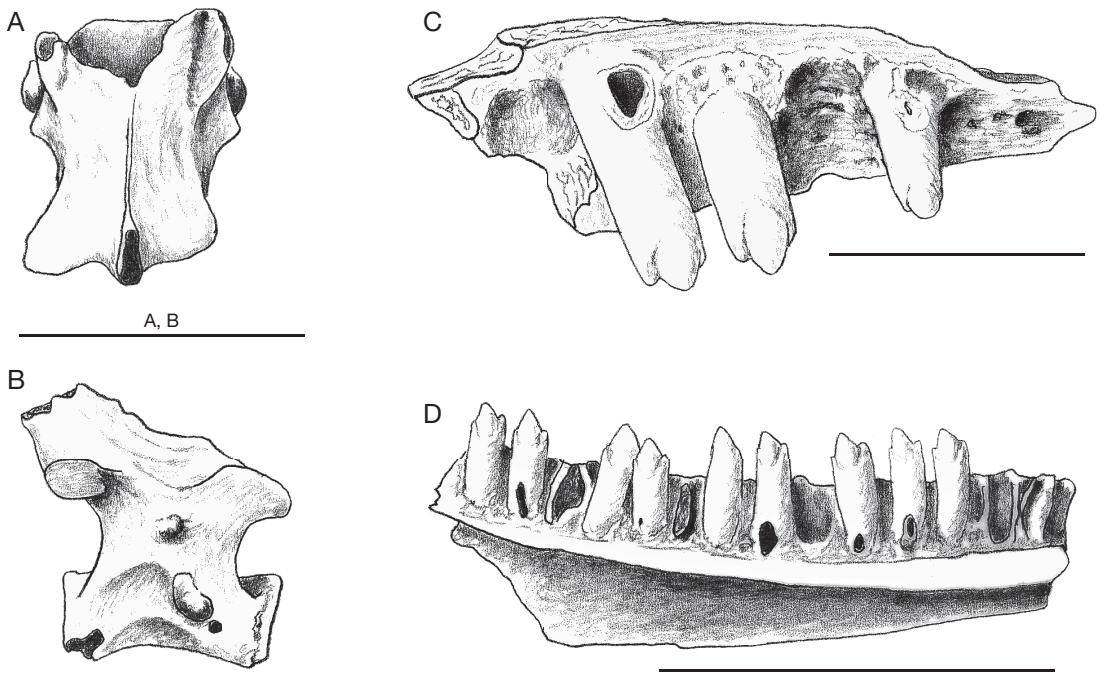


FIG. 4. — Fossil remains of reptiles from Capo Mannu D1 Local Fauna (Sardinia): **A, B**, Gekkonidae indet., trunk vertebra (DSTC 6012), dorsal and right lateral views; **C**, *Lacerta* gr. *L. viridis*, right maxilla (DSTC 6013), medial view; **D**, Lacertidae indet., fragmentary left dentary (DSTC 6014), medial view. Scale bars: 2 mm.

DESCRIPTION

The tooth bearing bones have pleurodont teeth cylindrical in shape and with a bicuspidate or tricuspidate apex; the height of the teeth does not exceed 2.5 mm approximately.

A fragmentary humerus preserves the distal region of the diaphysis and part of the epiphysis; a large foramen is present close to the epiphysis.

A trunk vertebra preserves only the triangular centrum; it shows a wide medial keel laterally bordered by two deep longitudinal grooves; cotyle and condyle are damaged but they were probably roundish in shape.

Caudal vertebrae are characterized by roundish cotyles and condyles and by the absence of any haemal process fused to the centrum.

A single rib with a circular articular surface does not show any process or keel; two longitudinal opposite grooves are developed in the proximal area (one is much shorter than the other).

A few ungual phalanges are characterized by a distal pointed end and a proximal articular surface divided into two concavities; a tubercle-like structure is developed on the ventral edge of the phalanges, close to the articular surface.

DISCUSSION

In this context, the pleurodont bicuspidate or tricuspidate teeth indicate the presence of a lacertid lizard (see Bailon 1991, and literature therein). The size and robustness of all elements described in this section clearly exceed the ones of the corresponding elements of a small lacertid lizard (as *Podarcis* spp.), and they fall in the range of an adult green lizard. The remains are referred at group rank, *Lacerta* gr. *L. viridis* (named after its most representative member) due to the absence of osteological diagnostic characters allowing a discrimination among the extant species of green lizards. The phalanges and the rib are tentatively associated to the lacer-

tid lizards, because their size matches that of the remains described above.

Lacertidae indet.
(Fig. 4D)

MATERIAL EXAMINED. — Fragmentary left dentary: 1.

DESCRIPTION

A small left dentary (total length of the fragment is about 3 mm) is preserved as a section corresponding to at least 14 tooth positions, still hosting nine pleurodont teeth. Both the anterior and the posterior ends of the dentary are missing. The teeth are cylindrical with bicuspidate or tricuspidate apices (the largest cusp is the median one). The base of the teeth can show a variably sized reabsorption pit. The Meckel's canal is particularly wide along the entire length of the preserved sector of the dentary.

DISCUSSION

This small fragmentary dentary clearly shows the typical characters of Lacertidae (as the pleurodont bicuspidate or tricuspidate teeth, and the widely open Meckel's canal; see Bailon 1991). Because of the weakly spaced teeth, it is likely that the dentary belongs to an adult of an undetermined small sized lacertid lizard and not to a juvenile of a medium sized form (as the above described *Lacerta* gr. *L. viridis*).

Family ANGUIDAE Gray, 1825
Genus *Dopasia* Gray, 1853 (sensu Augé 2005)

Dopasia sp.
(Fig. 5)

MATERIAL EXAMINED. — Maxilla: 2 ; pterygoid: 2; frontal: 2; parietal: 1 ; dentary: 1 ; cervical vertebra: 1; trunk vertebra: 30 ; caudal vertebra: 33 ; rib: 11; osteoderm: 5.

DESCRIPTION

The two fragmentary maxillae (an anterior and a posterior fragment belonging to one or two left maxillae) are characterized by canine-like teeth that

are slightly curved and have a narrow base. On one of the posterior teeth, a weak ridge is developed along the anterior edge of the apex.

The two pterygoid fragments correspond to the central area of the bone only. The palatine, transverse, and posterior processes are broken off. In ventral view, the pterygoid fragments are characterized by teeth arranged in three or four rows placed in an oval dentigerous region. The 17 or 18 teeth are weakly developed (in some cases there is just a hint of a tooth) and have blunt apices. A foramen is visible at the level of the pterygoid sulcus in one of the pterygoids.

Both frontals do not preserve the anterior region. They show an evident dermal vermicular sculpture on the dorsal surface; the sculpture does not cover the entire surface of the bone and its lateral edge is marked by a distinct step. In lateral view, the frontals have, in their anterior sector, a deep and well-delimited V-shaped groove whose rims open in anterior direction (= prefrontal impression). Posteriorly, the impression of the postfrontal is visible along the parietal-postfrontal process. The ventral frontal process is moderately prominent and has a convex ventral edge.

The fragmentary parietal is about 5 mm long and it corresponds to the right half of the element whose anterior tip and parotic process (= *processus supratemporalis sensu* Klembara 1979) are broken off. In dorsal view, this element shows a vermicular dermal ossification, the so-called sculpture, corresponding to the parietal scale; laterally, such dermal ossification develops a subtle dermal "blade" that overhangs the lateral edge, which is markedly convex and corresponds to the anterior branch of the parietal crest. The preserved portion of the parotic process has an undulated surface (clearly visible along the section): convex medially and concave laterally. In ventral view, the anterior branch of the parietal crest is distinctly convex and constitutes the lateral edge of the bone. Posteriorly, the crest becomes concave (= internal branch of the parietal crest, *sensu* Fejérváry-Lángh 1932) and it is prolonged up to the medial margin of the parotic process. The junction of this crest with the "*margo posterior of lamina parietalis*" (*sensu* Klembara 1986) constitutes a concave surface whose posterior extremity

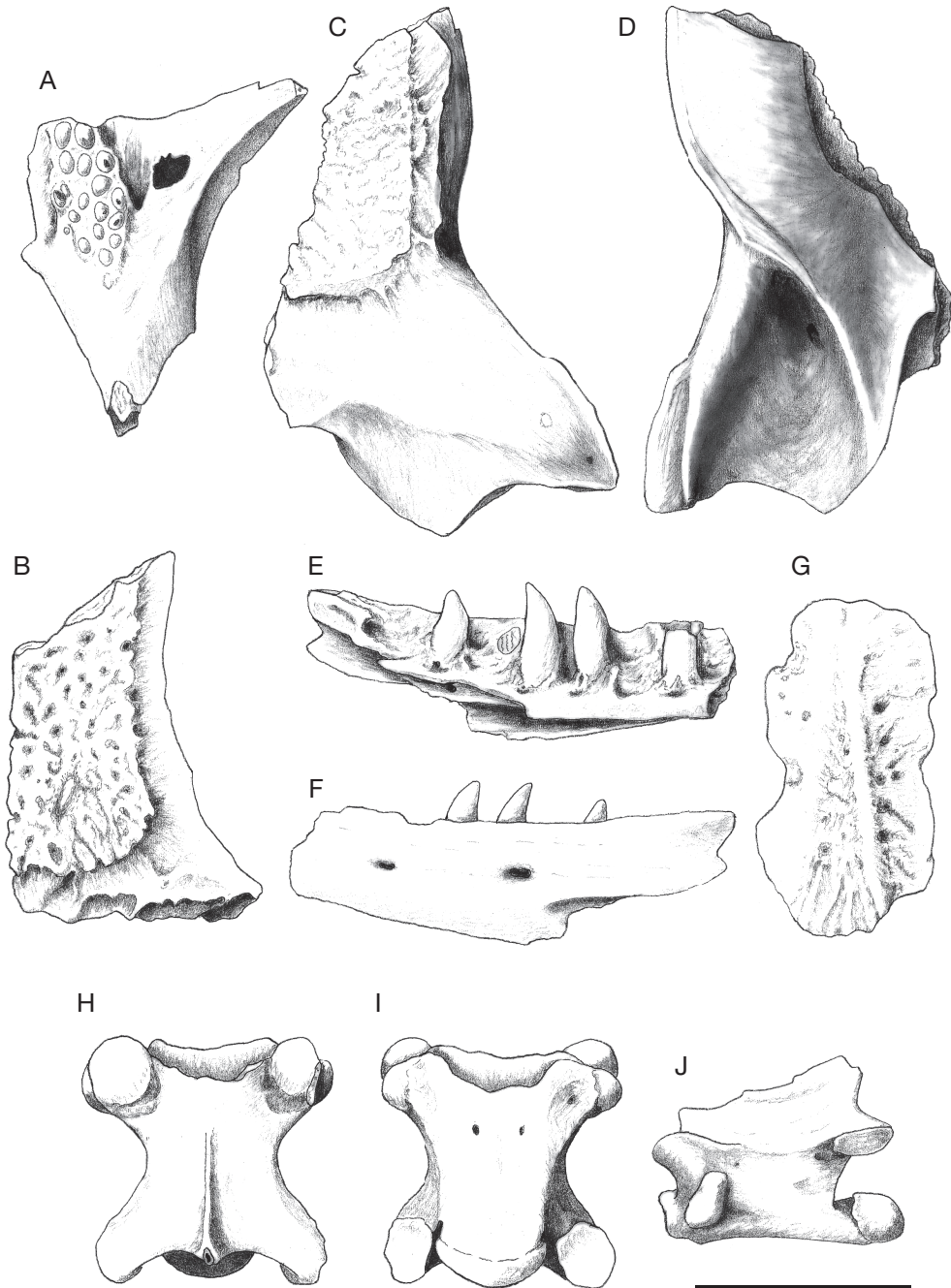


FIG. 5. — Fossil remains of reptiles from Capo Mannu D1 Local Fauna (Sardinia): *Dopasia* sp.: **A**, left pterygoid (DSTC 6015), ventral view; **B**, right frontal (DSTC 6016), dorsal view; **C**, **D**, parietal (DSTC 6017), dorsal and ventral views; **E**, **F**, left dentary (DSTC 6018), medial and lateral views; **G**, osteoderm (DSTC 6019), dorsal view; **H–J**, trunk vertebra (DSTC 6020), dorsal, ventral, and left lateral views. Scale bar: 2 mm.

extends beyond the posterior rim of the parietal fossa (that occupies about half of the total length of the parietal notch). The posterior branch of the parietal crest has a rounded section; it is more massive anteriorly, where it constitutes the lateral edge of the parotic process, and then becomes slightly thinner and runs parallel to the lateral edge.

A fragmentary left dentary is represented by approximately the posterior two thirds of the bone, likely having eight tooth positions. It is small (the fragment is about 4 mm long) and elongated (maximum height of 1.2 mm). The preserved teeth are subpleurodont, with a narrow base, canine-like and weakly hook-like, with pointed and posteromedially directed apices; they exceed the height of the lateral wall of the dentary of about one third of their height. In medial view, the Meckel's canal is partially visible posteriorly but not anteriorly, where it runs along the ventral edge of the bone and is therefore hidden by the horizontal lamina. The latter is inclined medioventrally, except at the level of the last two tooth positions where its remnants are nearly horizontal. The dental groove (*sulcus dentalis sensu* Fejérváry-Lángh 1923) is underdeveloped. The splenial spine is located under the fourth last tooth position. The splenial crest of the horizontal lamina is distinctly notched between the fourth last and the penultimate tooth positions; this notch represents the dorsal edge of the anterior inferior alveolar foramen. The posterior area of the medial edge of the horizontal blade (*carina coronoidea sensu* Fejérváry-Lángh 1923) apparently shows a process that might possibly be the result of a breakage or that might correspond to the anterior limit of the insertion area of the coronoid. The coronoid process is moderately robust and posteriorly truncated (it is not unlikely that it is apically broken); its medial surface is slightly overhanging. The coronoid process is approximately as long as the last dentary socket. The intramandibular septum is partially free ventrally. The interalveolar foramen opens under the penultimate tooth position. In labial view, the dental crest is slightly convex and posterodorsally inclined; the coronoid process is apically blunt. The angular process is only slightly shorter than the coronoid process. The coronoid notch is not symmetric and corresponds to a triangular convexity

of the lateral wall of the dentary representing the lateral facet for the attachment of the coronoid. The surangular notch reaches, anteriorly, the level of the third last tooth position. The intramandibular septum, as well as the angular process, are partially broken off.

Trunk vertebrae are small, having a centrum length not exceeding 3 mm (but the best-preserved vertebrae are much smaller). The cotyles and condyles are oval in shape; centra have a distinctly flattened ventral surface, with lateral edges anteriorly divergent, slightly concave, and with parallel sides only in the more posterior area; two distinct foramina open on the ventral surface posteriorly to the cotyle; synapophyses are oval-shaped and slightly inclined; prezygapophyses are dorsally tilted, rather large and nearly circular in shape; a laminar neural crest was present but it is invariably broken; the anterior edge of the neural arch is broken but it seems that it was convex; the posterior edge of the neural arch has a neural spine that does not extend beyond the postzygapophyses.

All the caudal vertebrae, except the best-preserved one, are represented by the posterior part of the vertebra only. The best-preserved element has a centrum length of about 1.5 mm but the size of the fragments indicates that some of the vertebrae were significantly larger. Common characters are the oval shape of condyles and cotyles; the flattening of the ventral surface of the centrum; the presence of flattened lateral processes in the anterior region of the vertebra, and of an underdeveloped neural spine that gives origin to a medial process in correspondence of the posterior edge of the neural arch; the development of two parasagittal shallow grooves in the cranial sector of the ventral surface of the centrum; the presence of haemal processes fused to the centrum; the presence of an autotomy surface that is testified by the symmetry of the breakage and its regular surface.

The ribs show an approximately rounded articular surface, a distinct tuberculiform process, and a blade-like ridge in the proximal area.

The osteoderms are lightly built and rather small: the largest is 3.2 mm long and 1.5 mm wide, but one of the fragments, 2.8 mm wide, indicates that the size could have been sensibly larger. All the os-

teoderms are characterized by an anterior smooth transversal strip followed by an ornate, vermicular, surface. A smooth sagittal keel is present in all the osteoderms except in the above mentioned large fragment.

DISCUSSION

The fossils described above, show the typical characteristics of Anguinae, and more precisely of Anguinae: the dermal ornamentation not extended on the lateral edges of the frontal; the notch of the anterior inferior alveolar foramen; the ventral edge of the intramandibular septum partially visible in labial view; the ventral position of the Meckel's canal along the anterior edge of the dentary; the surangular impression more extended than the coronoid; the trunk vertebrae with a flat or slightly convex centrum (Augé 2005, and literature therein).

Despite some contrasting results (Sullivan 1987; Sullivan *et al.* 1999), the monophyly of Anguinae seems to be confirmed from both an osteological (Augé 2005) and molecular (Macey *et al.* 1999) point of view, but the systematics of several taxa within the clade is still debated. On the basis of the parietal and tooth morphology, Klembara (1979, 1981) recognized three valid genera for the European Neogene anguids: *Pseudopus* Merrem, 1820 (for the taxa, formerly referred to *Ophisaurus*, with molariform posterior teeth and with the parietal characterized by an anterior branch of the parietal crest medially developed and without a distinct parietal notch), *Anguis* Linnaeus, 1758, and *Ophisaurus* Daudin, 1803 (including the taxa with canine-like teeth, an anterior branch of the parietal crest laterally developed and with a distinct parietal notch). According to Gauthier (1982), Sullivan (1987), and Augé (1992), two groups should be identified within the genus *Ophisaurus*; the American taxa (with teeth approximately cylindrical and with apices finely striated and slightly pointed) should be distinguished from the Euro-Asiatic taxa (characterized by canine-like teeth, with non-striated curved apices). More recently, Augé (2005) suggested to refer the Neogene and Quaternary European anguids to the genera *Anguis*, *Dopasia* and *Pseudopus* mostly on the basis of the morphology and number of teeth, as well

as the morphology of the vertebrae and of the osteoderms. *Dopasia* groups the old world species previously placed in *Ophisaurus* s.l., and therefore the name *Ophisaurus* (s.s.) should be restricted to the American representatives of *Ophisaurus* s.l. Noteworthy is that among the African and Asian taxa with canine-like teeth, only *Dopasia harti* (Boulenger, 1899) has been examined by Augé and that therefore the referral of the Old World species to the genus *Dopasia* should be confirmed by further studies; moreover, the genetic differences (mtDNA) observed by Macey *et al.* (1999) for the African *D. koellikeri* Günther, 1873 could suggest the revalidation of the name *Hyalosaurus koellikeri* and to consider the group *Ophisaurus* (including the American and Asian taxa) as a metataxon whose precise relationships are still to be defined. However, the nomenclature proposed by Augé (2005) has been adopted here.

If compared with extant genera, the fossils from Capo Mannu clearly match the morphology of the genus *Dopasia* only. *Pseudopus* is characterized by a medial position of the anterior branch of the parietal crest and by a well-developed lateral *facies muscularis* (*sensu* Féjerváry-Lángh 1923); the parietal notch is absent or weakly developed; the teeth are more numerous and the posterior ones are molariform in shape; moreover all the bones are large in size and robust (Klembara 1979, 1981). In *Anguis*, whose size is comparable to that of the fossils from Capo Mannu, the number of teeth in a similar portion of dentary is lower; the tooth morphology is more distinctly hooked; the notch of the anterior inferior alveolar foramen is located below the last two tooth positions; the ventral surface of the parietal is not intersected significantly by the arched keel, and, consequently, the parietal fossa is reduced and the parietal notch is more developed; the pterygoids are toothless; the lateral edges of the trunk vertebrae are less divergent; the osteoderms are rounded and devoid of any keel.

The parietal from Capo Mannu differs from the Early Miocene taxa from Dolnice (see Klembara 1979, 1981) *D. spinari* (Klembara, 1979) and *D. fejfari* (Klembara, 1979) (according to Estes [1983], the morphology of the parietal, that is

to say the element used for the diagnosis of these two species, does not allow to discriminate them from other anguines and therefore they should be considered as *nomina dubia*. Moreover, it differs from extinct *D. (? Anguis) robustus* (Klembara 1979) and extant *D. harti*, *D. koellikeri* (the morphology of the latter has been evaluated on the basis of the material coming from a Neolithic site in Morocco, see Stoetzel *et al.* 2008), and *Anguis fragilis* Linnaeus, 1758. The parietal crest has an anterior branch more convex and laterally placed and an inner branch slightly more concave than in *Anguis*. In dorsal view, the lateral edge (the dorsal surface of the anterior branch of the parietal crest) of the fossil fragment is well visible and convex. The median narrowing is more marked and more anteriorly placed than in the other taxa. Moreover, in *D. spinari*, *D. harti* and *D. koellikeri*, the parotic process is less divergent (this morphology resembles slightly that of *D. fejfari*, *D. [?Anguis] robustus*, and *Anguis fragilis*) and the posterior branch of the parietal crest is located on the lateral edge of the parotic process.

Following Augé (2005), the presence of several rows of teeth on the pterygoid is a character restricted to the American taxa, therefore *Ophisaurus*, whereas in *Dopasia* and *Pseudopus* only one row should be present (character 27-0; Augé 2005). However, this character seems to be highly variable and, for the time being, should not be taken into account because several rows are present in all the extant *P. apodus* at our disposal (5 specimens) and in *P. cf. P. panonicus* of the Late Pliocene of Montoussé 5, France (Bailon 1991), or in the pterygoids of the Miocene of Dolnice referred to *Ophisaurus* by Klembara (1981) and Roček (1984) (= *Dopasia* sp., this work).

The hook-like maxillary and dentary teeth (without striated apexes), is a character of the group *Anguis-Dopasia* (Augé 2005). However, the teeth are less in number, more spaced, taller and more hook-like in *Anguis* than in the fossil from Capo Mannu and in *Dopasia*.

The general shape of the teeth of the fragmentary lower jaw from Capo Mannu matches that of the material from the Early Miocene of Dolnice (*D. cf. D. spinari*; Roček 1984) and Sansan (*Dopasia* sp.

1; Augé & Rage 2000) and from the Late Miocene of Polgardi 4 and 5 (*Dopasia* sp.; Venczel 2006). In aff. "*Ophisaurus*" from the Pliocene of the Iles Medas (Bailon 1991), teeth are more cylindrical and more numerous (thus somehow recalling the American taxa; a general revision of this material is required to address this issue), whereas in *D. harti* the teeth are more robust, with a basal portion much more enlarged.

While analyzing fossil anguids from Central Europe, Böhme (2002) indicated that sharp anterior cutting edges occur on teeth of maxillae and dentaries associated with *D. fejfari* parietals, whereas teeth associated with *D. spinari* parietals do not have such a sharp cutting edge; consequently, the author identified the material from the Middle Miocene from Obergänserndorf (Austria) as *D. aff. D. fejfari*. The same taxon (identified as *D. cf. D. fejfari*) has been identified in the Early Miocene of Oschiri (Sardinia; Venczel & Sanchiz 2006). In this respect, it is worth mentioning that a keel is present on a tooth of one of the fragmentary maxillae from Capo Mannu, it is nonetheless much less developed than that shown by *D. aff. D. fejfari* (Böhme 2002: pl. I, fig. O) or *D. cf. D. spinari* (Roček 1984: pl. VIII, figs 4, 5; pl. IX, figs 2, 3). The variability of this morphology should be carefully evaluated in order to properly assess its diagnostic value for the identification of anguines.

The morphology of the fossil dentary from Capo Mannu matches well the slender dentaries referred to *D. cf. D. spinari* (Early Miocene, Dolnice; Roček 1984) and *Dopasia* sp. 1 (Early Miocene, Sansan; Augé & Rage 2000) and differs from *Dopasia* sp. from the Late Miocene of Polgardi 4 and 5 which is comparatively more robust (Venczel 2006; Fig. 2A, B). Conversely, the fragmentary parietal from Capo Mannu differs from the fossil and extant anguines we used for comparisons, possibly indicating a different specific status. However, the scarcity of the fossil material as well as the imprecise knowledge of the variability of some of the morphological characters of extant and fossil anguine taxa, does not allow any specific identification and the material from Capo Mannu is referred to *Dopasia* sp.

Lacertilia indet.

MATERIAL EXAMINED. — Maxilla: 5; dentary: 8; tooth bearing bone: 5; coronoid: 1; jugal: 1; articular: 1; scapulo-locoracoid: 2; humerus: 7; femur: 7; tibia: 1; vertebra: 42; ribs: 5.

DISCUSSION

Several poorly preserved or non diagnostic remains are referred to *Lacertilia* indet. even if they probably belong to the above mentioned taxa. The limb bones could belong to juvenile specimens of *Lacerta* but the presence of a smaller taxon of the same family cannot be ruled out.

Order AMPHISBAENIA Gray, 1844

Amphisbaenia indet. (Fig. 6A-C)

MATERIAL EXAMINED. — Trunk vertebra: 16; caudal vertebra: 1.

DESCRIPTION

The trunk vertebrae have a maximum centrum length of 1.5 mm. They show a rather uniform morphology with distinctly dorsoventrally depressed cotyles and condyles; wide oval-shaped prezygapophyses characteristically “protruding” from the rest of the vertebra in dorsal view and bearing large and short blunt processes; well-defined globular synapophyses; convex anterior and concave posterior edge of the neural arch; underdeveloped neural crest (in some cases a hint of a ridge terminating in a flattened area can be present close to the posterior end of the neural arch); depressed neural arch (when seen in posterior view); flattened ventral surface of the centrum with parallel lateral margins and two small foramina in the anterior region.

The caudal vertebra has a similar morphology but differs for the absence of prezygapophyseal processes and for the presence of anterior transverse and posterior haemal processes fused to the centrum.

DISCUSSION

The combination of the morphological characters described above allows to identify a member of the

Amphisbaenia, but due to the fact that isolated amphisbaenian vertebrae are generally not diagnostic even at genus level, a precise taxonomic allocation is not possible (see Delfino 1997, and literature therein). It is however likely that these vertebrae belong to Blanidae Kearney, 2003, the only family that has been identified so far in the European fossil record. The fossil remains are morphologically congruent with the extant genus *Blanus* Wagler, 1830 and not with, for example, *Trogonophis wiegmanni* Kaup, 1830 (Morocco) whose vertebrae are comparatively more elongated and narrow.

Noteworthy is that Venczel & Sanchiz (2006) listed the presence of *Blanus gracilis* (Roček, 1984) in the Lower Miocene Sardinian site of Oschiri. This species was originally described on the basis of isolated vertebrae which are notoriously poorly informative (Rage 1988; Delfino 1997; Augé 2005) but it seems that tooth bearing bones are present at Oschiri and that therefore a valid diagnosis of this taxon based on diagnostic characters could be possible. In any case, the absence of tooth bearing elements in the Capo Mannu D1 LF does not allow confirmation of the possible survival of this taxon in Sardinia.

Order SERPENTES Linnaeus, 1758

Family BOIDAE Gray, 1825

Subfamily ERYCINAE Bonaparte, 1831

Genus *Eryx* Daudin, 1803

Eryx cf. *E. jaculus* (Linnaeus, 1758) (Fig. 6D-G)

MATERIAL EXAMINED. — Cervical vertebra: 1; trunk vertebra: 9; caudal vertebra: 2.

DESCRIPTION

The cervical vertebra preserves only the centrum: it is very short (1.1 mm) but proportionally wide (at least as wide as long); cotyles and condyle are dorsoventrally flattened; the remnants of the hypapophysis are present.

The trunk vertebrae share the following common features (not necessarily visible on all the remains): centrum rather short but invariably wider than long (the largest well-preserved vertebra has a length of

1.4 mm and a width of 1.9 mm; some vertebral fragments belonged to vertebrae slightly larger); cotyles and condyles dorsoventrally flattened; paracotylar foramina absent; the haemal keel wide and low, with weakly defined margins; tiny subcentral and lateral foramina variably present; parapophyseal processes not developed; paradiapophyses proportionally big; dia- and parapophyseal regions not well separated from each other; pre- and postzygapophyses dorsally tilted; prezygapophyseal processes very short and pointed; neural canal proportionally large; the anterior end of neural arch slightly convex; the neural arch depressed and its dorsal edges straight to weakly convex in posterior view; the neural spine originating far from the anterior edge of the neural arch and, despite invariably broken, probably low.

The two caudal vertebrae are not complete but taken together they preserve all the vertebral structures except the neural spine. The largest vertebra has a centrum length of 2.2 mm. The caudal morphology assessed on these remains is characterized by roundish cotyles and condyles; long laminar haemapophyses and pleurapophyses; absence of subcotylar processes; neural canal rather small (smaller than the cotyle in anterior view); neural arch devoid of zygosphenes and zygantrium; postzygapophyses not developing wide wings; prezygapophyses devoid of processes and well separated from the postzygapophyses; additional process between the neural spine and the postzygapophysis developed as a spine directed anteriorly.

DISCUSSION

On the basis of the diagnostic characters discussed by Szyndlar in several papers concerning the identification of the erycine boids from the Neogene and Quaternary of Europe (among others, Szyndlar 1991a; Szyndlar & Schleich 1993, 1994), it is possible to tentatively refer the Erycinae remains from the Capo Mannu D1 LF to *Eryx jaculus*. Such identification is based on the well-developed haemapophyses that characterize the posterior caudal vertebrae of the Euro-Asiatic species of this genus and by the separation of the prezygapophysis from the postzygapophyseal wings that characterize this species. The qualifier “cf.” precedes the specific identification in order to underline that the scarcity of the remains and their imperfect preservation hinder a confident identification.

Family COLUBRIDAE Oppel, 1811

“Colubrine” type (trunk
vertebrae without hypapophysis)
(Fig. 7A-D)

MATERIAL EXAMINED. — Maxilla: 1 fragment; trunk vertebra: 21.

DESCRIPTION

The fragmentary right maxilla is represented by a posterior section of this element extending from an undetermined point following the prefrontal process (not preserved) and the tooth position following the ectopterygoid process (preserved); the ectopterygoid process corresponds to two tooth sockets, hosting the only preserved tooth, and part of the preceding socket; two more tooth sockets are placed anteriorly to the ectopterygoid process; the toothed region is preceded by a long diastema corresponding to at least two tooth positions; in ventrolateral view, an evident change of slope corresponds to the boundary between the diastema and the toothed region.

The most common vertebral morphotype is characterized by an elongated centrum (whose length can reach 2.4 mm); subcircular cotyles and condyles; parapophysis and diapophysis separated by a shallow depression; parapophysis anteroposteriorly longer than diapophysis; parapophyseal processes absent; haemal keel well defined and usually modestly widened posteriorly; pre- and postzygapophyses weakly tilted dorsally; prezygapophyseal processes slender, pointed and long up to half the width of the prezygapophyseal facet; prezygapophyseal facets drop-shaped; zygosphenes moderately convex in dorsal view; neural arch depressed and with dorsal edge modestly convex in posterior view; neural spine long and very low.

Variations of the morphology described above are mostly related to minor differences in terms of haemal keel shape (not widened posteriorly) and shape of the posterior edge of the neural arch.

DISCUSSION

The presence of a diastema is a character typical of the opisthoglyphous colubrids at our disposal for

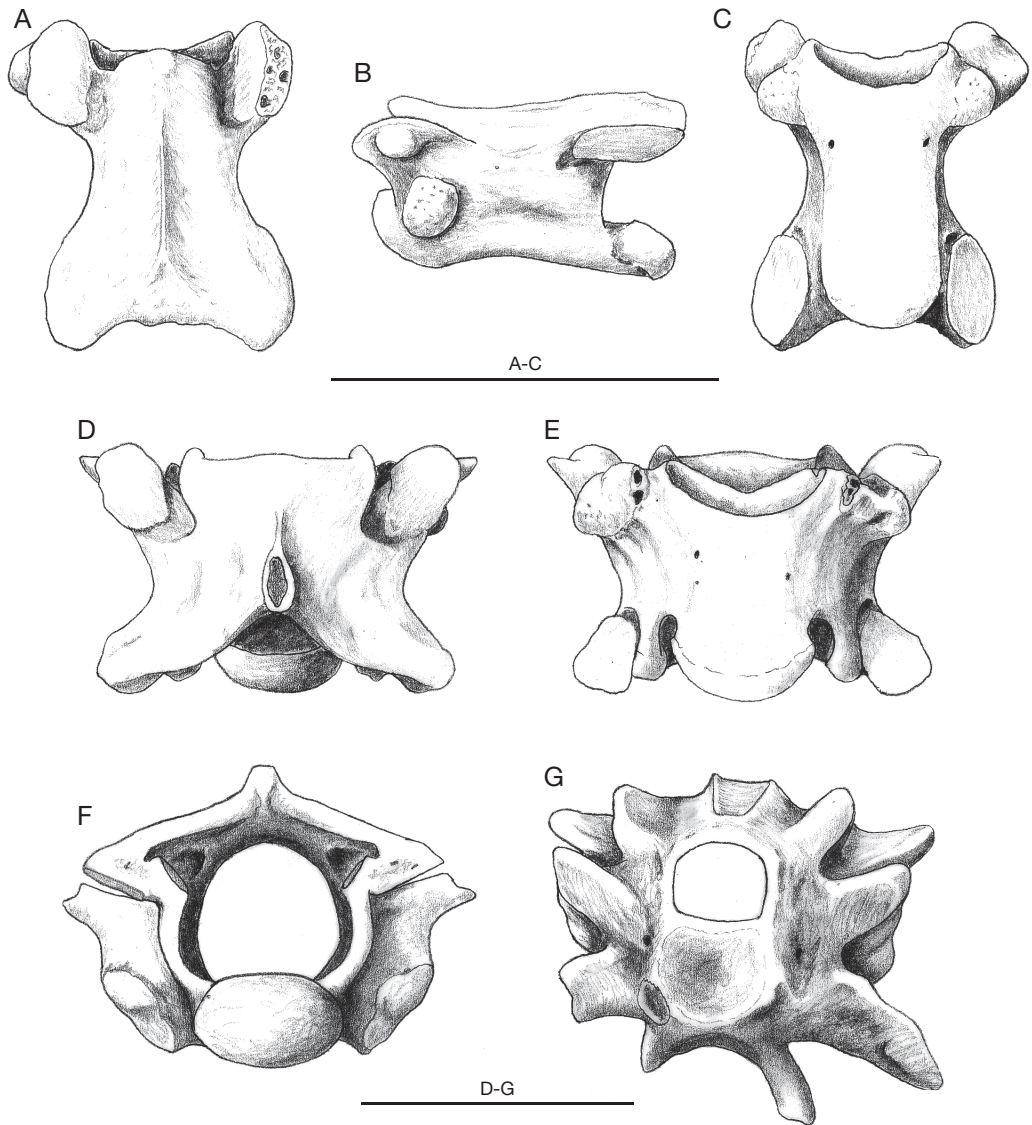


FIG. 6. — Fossil remains of reptiles from Capo Mannu D1 Local Fauna (Sardinia): **A-C**, *Amphisbaenia* indet., trunk vertebra (DSTC 6021), dorsal, left lateral and ventral views; **D-F**, *Eryx* cf. *E. jaculus*, trunk vertebra (DST 6022), dorsal, ventral and posterior views; **G**, caudal vertebra (DSTC 6023), anterior view. Scale bars: 2 mm.

comparison: *Malpolon* Fitzinger, 1826, *Telescopus* Wagler, 1830, and *Macroprotodon* Guichenot, 1850. Even if not totally congruent in morphology, the fragmentary maxilla of Capo Mannu is more similar to that of *Macroprotodon* than to those of *Malpolon* or *Telescopus*. The morphology of the fragmentary

maxilla does not match with that of any known taxon so that is not demonstrated if it belongs to a new taxon or, more likely, if it is an unusual morphology of a taxon already described.

The colubrid trunk vertebrae devoid of hypapophysis are referred to an undetermined member of

the working taxon “Colubridae” (sensu Szyndlar 1991a). The morphological uniformity of these vertebrae suggests that most of them probably belong to a single taxon, but it is not possible to exclude that some of the fragments belong to other taxa. Noteworthy is that the depressed neural arch and the long and low neural spine are two characters typical of taxa like *Coronella* Laurenti, 1768 and *Telescopus*.

“Natricine” type
(trunk vertebrae with hypapophysis)
Genus *Natrix* Laurenti, 1768

Natrix sp.

MATERIAL EXAMINED. — Trunk vertebra: 1.

DESCRIPTION

The fragmentary vertebra (not figured) has an elongate centrum whose length is of 3.0 mm; the parapophysis and diapophysis are separated by a depression and both distinctly protrude from the lateral wall of the centrum; the parapophyseal processes are horizontally oriented, long, rather wide and with a nearly rounded tip; cotyle and condyle are approximately circular; paracotylar tubercles are weakly developed; subcentral grooves are rather deep; the hypapophysis is present but only its basis is preserved; paracotylar, lateral, and subcentral foramina are small; the orientation of the only preserved postzygapophysis indicates that the missing prezygapophyseal facets were approximately horizontal; the neural arch is tall and its posterior border is nearly straight in posterior view; the neural canal is proportionally wide; the neural spine is nearly completely broken off.

DISCUSSION

The general proportions of the vertebra, the morphology of the paradiapophyses, the shape and proportions of the parapophyseal processes, the orientation of the pre- and postzygapophysis, the presence of a hypapophysis, and the height of the neural arch, indicate that this vertebra belongs to the genus *Natrix*. The absence of a complete

hypapophysis and the overall poor preservation of the vertebra hinder a specific identification, despite the roundness of the parapophyseal processes could suggest the presence of *N. natrix* (see characters discussed by Szyndlar 1984, 1991b; Holman 1991).

Family VIPERIDAE Laurenti, 1768
Genus *Vipera* Laurenti, 1768

Vipera sp.
(Fig. 7E, F)

MATERIAL EXAMINED. — Tooth: 1; trunk vertebra: 2.

DESCRIPTION

The isolated tooth is the proximal portion (2.7 mm long) of a fang which, despite the missing tip retains a distinct curvature. Part of a relatively wide, but sagittally elongated, opening of the venom canal is preserved on the convex side at the proximal end of the fragment; in correspondence of such opening the external surface is internally folded.

The two fragmentary vertebrae are characterized by being relatively short and tall (centrum length about 1.9 mm); the cotyle and condyle are rather round and proportionally large; the paracotylar foramina are fairly large and open at the bottom of a deep depression; the paradiapophyses are damaged but the only preserved parapophyseal process is long, pointed and anteroventrally directed; the preserved portion of the hypapophysis indicates that it was anteroposteriorly narrow and long; the neural canal is slightly larger than the condyle; the pre- and postzygapophyses are markedly tilted in dorsal direction; the only preserved prezygapophyseal facet is elongated and its process is rather robust but short (not exceeding the facets in dorsal view); the postzygapophyseal facets have a shape complementary to that of the prezygapophyses; the zygosphenes are convex both in anterior and dorsal view; the posterior edge of the neural arch is low and its borders are straight (to nearly concave) in posterior view; the neural spine should have been quite tall.

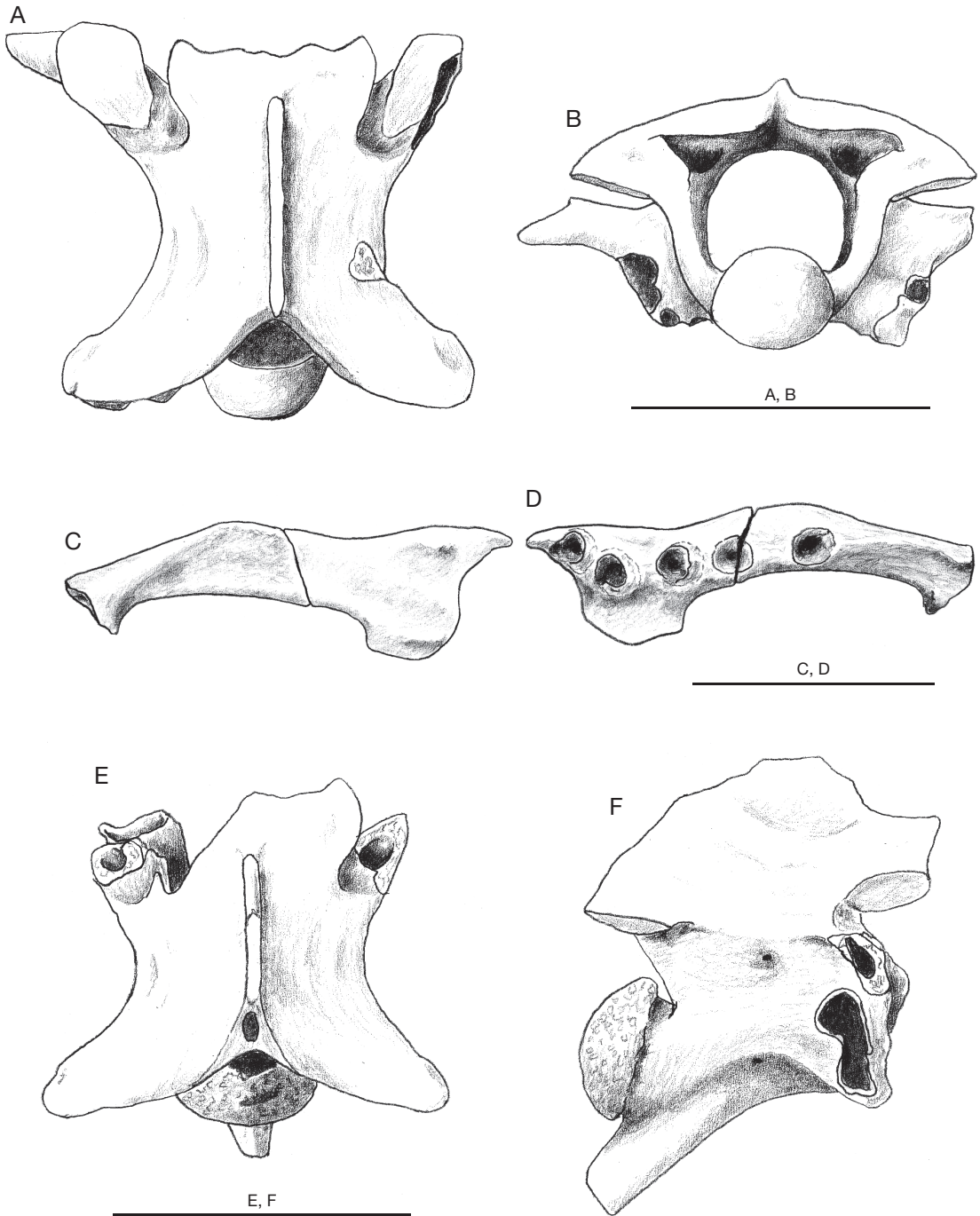


FIG. 7. — Fossil remains of reptiles from Capo Mannu D1 Local Fauna (Sardinia): **A–D**, “Colubridae” indet: **A, B**, trunk vertebra (DSTC 6024), dorsal and posterior views; **C, D**, right maxilla (DSTC 6025), medial and ventral views; **E, F**, *Vipera* sp. trunk vertebra (DSTC 6026), dorsal and right lateral views. Scale bars: 2 mm.

DISCUSSION

The isolated tooth is clearly a maxillary fang of a venomous snake matching with the solenoglyphous teeth of viperids. The vertebrae can be referred to the genus *Vipera* on the basis of the orientation of the zygapophyses, the size of the cotyles and condyles, and the shape of the hypapophysis and neural arch (Szyndlar 1984, 1991b; Szyndlar & Rage 2002). The short vertebral centrum somewhat recalls the morphology of *V. aspis*, however, due to the scarcity of the material and its preservation, the identification is limited at genus rank.

Serpentes indet.

MATERIAL EXAMINED. — Vertebra: 48; cloacal vertebra: 1; caudal vertebra: 9 (including a fused caudal tip); rib: 24.

DESCRIPTION AND DISCUSSION

Several snake ribs, fragmentary trunk vertebrae, as well as cloacal and caudal vertebrae, not showing any diagnostic character are referred to *Serpentes indet.*

DISCUSSION

Cenozoic herpetofaunal assemblages comprising small-sized taxa, i.e. not only isolated findings of crocodylians and chelonians, are not rare in Sardinia, being mentioned for the sites of Capo Mannu D1 LF, Dragonara, Grotta Corbeddu, Monte Tuttavista, Nuraghe su Casteddu, Oschiri, Porto Leccio, San Giovanni in Sinis, and Su Guanu. However, most of them date to the Late Pleistocene or Holocene (see Delfino 2002 and literature therein; Abbazzi *et al.* 2004; Venczel & Sanchiz 2006). Rare and up to now not fully studied are the pre-Quaternary assemblages (Delfino & Rook 2008).

Despite representing highly fragmented skeletal elements, the 515 remains from the Late Pliocene of the Capo Mannu D1 LF are an exception. Referred to 14 taxa, they are a relevant point of reference in the present knowledge of the evolution of the Sardinian amphibians and reptiles because they partly fill the long gap between the two most

representative Sardinian herpetofaunas: the one from the Early Miocene site of Oschiri (Venczel & Sanchiz 2006) and the one from the Pleistocene site of Monte Tuttavista (Abbazzi *et al.* 2004). Table 1 summarizes the taxa so far reported from the three sites.

Two taxa are shared only by Oschiri and by the Capo Mannu D1 LF (*Salamandrina* and *Dopasia*; both now extinct in Sardinia), three taxa are shared only by the Capo Mannu D1 LF and Monte Tuttavista (green toads, tree frogs, and green lizards; the latter taxon is now locally extinct), whereas five taxa are present in all the three localities (discoglossid frogs, geckos, amphisbaenians, natricines, and viperids; amphisbaenians and viperids are now locally extinct). Small sized lacertid lizards are also present in all the three sites, but they have been identified at different rank (indeterminate lacertids in the case of Oschiri and Capo Mannu, *Podarcis* sp. at Monte Tuttavista). No taxa are exclusively shared by Oschiri and Monte Tuttavista.

A relevant aspect of the Neogene evolution of the Sardinian herpetofauna is the prolonged permanence of the now locally extinct genus *Salamandrina*: from the Early Miocene to at least the Late Pliocene (extinction and successive re-immigration seems less likely). Among caudates, *Euproctus*, *Salamandrina*, and *Speleomantes* are ancient inhabitants of Sardinia: Miocene fossil remains are available for *Salamandrina* only, but the presence in Sardinia of the other two taxa before the onset of its Oligo-Miocene detachment from palaeo-Europe and rotation has been suggested on a phylogeographic basis by several authors and is considered as ascertained (Lanza 1983; Caccone *et al.* 1994; Lanza *et al.* 2006). There are no apparent reasons explaining why these ancient inhabitants of Sardinia had such a different fate and why only genus *Salamandrina* went extinct after such a long permanence (about 20 million years), whereas the other two caudates still inhabit the island. Noteworthy is that the *Salamandrina* skeletal elements from Capo Mannu are much smaller than those of the extant *Salamandrina* and also smaller than the fossils from the early Miocene of Oschiri (Pitruzzella 2008), possibly indicating the effect of a prolonged evolution in sub-optimal ecological conditions.

The Neogene fossil record of Sardinia testifies for a continuous presence of taxa that still inhabit the island, as discoglossids, gekkonids, lacertids, and natricine snakes, as well as of taxa that are now locally extinct as amphisbaenians and viperids.

Ranids, whose recent presence in Sardinia is due to introductions by man (Sindaco *et al.* 2006; Lanza *et al.* 2007), probably never dispersed into the island: they were listed among the amphibians of the Capo Mannu D1 LF as “?Ranidae indet.” (Pecorini *et al.* 1974) or as “*Rana (ridibunda)* sp.” (Sanchiz 1998), but the few ilium fragments that could have been the basis of the identification of a ranid taxon are here conservatively referred to Anura indet. Moreover, the remains from the Pleistocene site of Nuraghe su Casteddu, formerly referred to *Rana* sp. (Esu & Kotsakis 1979) are now considered to represent the genus *Discoglossus* (Sanchiz 1998). The interesting identification of *Rana* sp. in an archaeological context of Roman Age (II cent. A.D.; Delussu 2000), not supported by any description or figure, should be confirmed by a proper examination of the material; it could eventually represent the first evidence for the introduction of ranid frog into the island.

The herpetofaunistic assemblage of the Capo Mannu D1 LF is characterized by some taxa that were absent or rare in the fossil record of Sardinia. Not to mention the remains of *Salamandrina*, which are at present the youngest fossil evidence known in Sardinia of this extant genus (now surviving only on the Apennine Peninsula where fossils come exclusively from the Early Pleistocene of Montagnola Senese; Pitruzzella 2008), the remains referred to cf. *Ichthyosaura* sp. are of particular relevance because they could represent the first evidence for this group in an island where they are absent now (Sindaco *et al.* 2006). Interesting is also the fragmentary maxilla that could belong to an opisthoglyphous snake. Further fossil material from this locality will hopefully allow to clarify their taxonomy.

The presence of the genus *Eryx* was unknown in Sardinia, and it was previously identified in Italy only at Cava Monticino (Kotsakis 1989; Delfino 2002).

When compared to the other European Pliocene herpetofaunas (see Bailon & Blain 2007), the Capo

TABLE 1. — Summary of the herpetofauna of the three most representative Neogene and Quaternary localities of Sardinia: Oschiri (Lower Miocene; data from Venczel & Sanchiz 2006), Capo Mannu D1 LF (Late Pliocene; this work), and Monte Tuttavista (Early Pleistocene; data from Abbazzi *et al.* 2004). The taxon “*Crocodylia* indet.” has been added to the list provided by Venczel & Sanchiz (2006) on the basis of an unpublished isolated tooth stored in the collections of Utrecht University (specimen unnumbered). *, taxa now extinct at least in Sardinia.

	Oschiri	Capo Mannu D1 LF	Monte Tuttavista
Amphibians			
<i>Salamandrina</i> sp.*	✓	✓	
<i>Speleomantes</i> sp.			✓
cf. <i>Mesotriton</i> sp.*		✓	
<i>Discoglossus sardus</i> Tschudi in Otth, 1837			✓
<i>Discoglossus</i> sp.	✓	✓	
<i>Bufo viridis</i> Laurenti, 1768			✓
cf. <i>Bufo</i> gr. <i>B. viridis</i> Laurenti, 1768		✓	
<i>Hyla</i> gr. <i>H. arborea</i> (Linnaeus, 1758)		✓	✓
Reptiles			
<i>Crocodylia</i> indet.*	✓		
<i>Testudo</i> cf. <i>T. hermanni</i> Gmelin, 1789			✓
Gekkonidae indet.	✓	✓	✓
<i>Dopasia</i> cf. <i>D. fejfari</i> (Klembara, 1979)*	✓		
<i>Dopasia</i> sp.*		✓	
<i>Lacerta</i> gr. <i>L. viridis</i> (Laurenti, 1768)*		✓	✓
<i>Podarcis</i> sp.			✓
Lacertidae indet.	✓	✓	
Scincidae indet.	✓		
<i>Agama</i> s.l.*			✓
Amphisbaenia indet.*		✓	✓
<i>Blanus gracilis</i> (Roček, 1984)*	✓		
<i>Eoanilius oligocenicus</i> Szyndlar, 1994*	✓		
<i>Eryx</i> cf. <i>E. jaculus</i> (Linnaeus, 1758)*		✓	
Colubrinae indet.		✓	✓
<i>Natrix</i> sp.		✓	✓
Natricinae indet.	✓		
<i>Vipera</i> gr. <i>V. aspis</i> Linnaeus, 1758*	✓		
<i>Vipera</i> sp.*		✓	✓

Mannu D1 LF is similar to other Late Pliocene west Mediterranean faunas because it no longer hosts tropical elements (as the aniilid snake re-

ported for Oschiri; Venczel & Sanchiz 2006), but still preserves thermophilous taxa as relatively large anguid lizards (*Dopasia*) and ercycine snakes that will go extinct later on.

The Capo Mannu D1 LF significantly increases the knowledge of the Italian latest Neogene herpetofaunas, but a complete analysis of the already available materials from Arondelli and Montagnola Senese is necessary to better define the taxonomy and chronology of their late Neogene and early Quaternary evolution.

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REFERENCES

- ABBAZZI L., ANGELONE C., ARCA M., BARISONE G., BEDETTI C., DELFINO M., KOTSAKIS T., MARCOLINI F., PALOMBO M. R., PAVIA M., PIRAS P., ROOK L., TORRE D., TUVERI C., VALLI A. & WILKENS B. 2004. — Plio-Pleistocene fossil vertebrates of Monte Tuttavista (Orosei, Eastern Sardinia, Italy), an overview. *Rivista Italiana di Paleontologia e Stratigrafia* 110: 681-706.
- ABBAZZI L., CARBONI S., DELFINO M., GALLAI G., LECCA L. & ROOK L. 2008. — Fossil vertebrates (Mammalia and Reptilia) from Capo Mannu (Late Pliocene, Western Sardinia, Italy), with description of a new *Testudo* (Chelonii, Testudinidae) species. *Rivista Italiana di Paleontologia e Stratigrafia* 114 (1): 119-132.
- ANGELONE C. & KOTSAKIS T. 2001. — *Rhagapodemus azzarolii* n. sp. (Muridae, Rodentia) from the Pliocene of Mandriola (Western Sardinia, Italy). *Bollettino della Società Paleontologica Italiana* 40: 127-132.
- AUGÉ M. 1992. — Une espèce nouvelle d'*Ophisaurus* (Lacertilia, Anguidae) de l'Oligocène des Phosphorites de Quercy. Révision de la sous-famille des Anguinae. *Paläontologische Zeitschrift* 66 (1/2): 159-175.
- AUGÉ M. 2005. — Évolution des lézards du Paléogène en Europe. *Mémoires du Muséum national d'Histoire naturelle* 192: 1-369.
- AUGÉ M. & RAGE J.-C. 2000. — Les Squamates (Reptilia) du Miocène moyen de Sansan, in GINSBURG (ed.), La faune miocène de Sansan et son environnement. *Mémoires du Muséum national d'Histoire naturelle* 183: 263-313.
- BAILON S. 1991. — *Amphibiens et reptiles du Pliocène et du Quaternaire de France et d'Espagne: mise en place et évolution des faunes*. PhD thesis, Université de Paris VII, Paris, 499 p.
- BAILON S. 1999. — Différenciation ostéologique des anoures (Amphibia, Anura) de France, in DESSE J. & DESSE-BERSET N. (eds), *Fiches d'ostéologie animale pour l'Archéologie*, série C: Varia. Centre de Recherches Archéologiques-CNRS, Valbonne, 38 p.
- BAILON S. 2004. — Fossil record of Lacertidae in Mediterranean Islands: the state of the art, in PÉREZ-MELLADO V., RIERA N. & PERERA A. (eds), The biology of the lacertid lizards. Evolutionary ecology and perspectives. *Recherca* 8: 37-62.
- BAILON S. & BLAIN H.-A. 2007. — Faunes de reptiles et changements climatiques en Europe occidentale autour de la limite Plio-Pléistocène. *Quaternaire* 18: 55-63.
- BÖHME G. 1977. — Zur Bestimmung quartärer Anuren Europas an Hand von Skelettelementen. *Wissenschaftliche Zeitschrift der Humboldt-Universität zu Berlin, Mathematisch-naturwissenschaftliche Reihe* 26 (3): 283-300.
- BÖHME M. 2002. — Lower Vertebrates (Teleostei, Amphibia, Sauria) from the Karpatian of the Korneuburg Basin - palaeoecological, environmental and palaeoclimatical implications. *Beiträge Paläontologie* 27: 339-353.
- CACCONE A., MILINKOVITCH M. C., SBORDONI V. & POWELL J. R. 1994. — Molecular biogeography: using the Corsica-Sardinia microplate disjunction to calibrate mitochondrial rDNA evolutionary rates in mountain newts (*Euproctus*). *Journal of Evolutionary Biology* 7: 227-245.
- CHESI F. & DELFINO M. 2007. — The Italian fossil record of the sea turtles, in BOLOGNA M. A., CAPULA M., CARPANETO G. M., LUISELLI L., MARANGONI C. & VENCHI A. (eds), *Atti VI Congresso Nazionale della Società Herpetologica Italica (Roma, 27 settembre-1*

- ottobre 2006). Edizioni Belvedere, Latina: 95-116.
- CLARKE B. T. & LANZA B. 1990. — Notes on the morphology and distribution of the Corsican Painted Frogs: *Discoglossus sardus* Tschudi and *D. montalentii* Lanza, Nascetti, Capula & Bullini. *Bollettino del Museo regionale di Scienze naturali di Torino* 8 (2): 531-544.
- DELFINO M. 1997. — *Blanus* from the Early Pleistocene of Southern Italy: another small tessera from a big mosaic, in BÖHME W., BISCHOFF W. & ZIEGLER T. (eds), *Herpetologia Bonnensis*. Societas Herpetologica Europaea, Bonn: 89-97.
- DELFINO M. 2002. — *Erpetofaune italiane del Neogene e del Quaternario*. PhD thesis in Palaeontology, Università degli Studi di Modena e Reggio Emilia, Modena, 382 p.
- DELFINO M. & BAILON S. 2000. — Early Pleistocene herpetofauna from Cava Dell'Erba and Cava Pirro (Apulia, Southern Italy). *The Herpetological Journal* 10: 95-110.
- DELFINO M. & SALA B. 2007. — Late Pliocene Albanerpetontid (Lissamphibia) from Italy. *Journal of Vertebrate Paleontology* 27 (3): 716-719.
- DELFINO M. & ROOK L. 2008. — The fossil amphibians and reptiles of Sardinia: a summary, in CORTI C. (ed.), *Herpetologia Sardiniae*. Societas Herpetologica Italica/Edizioni Belvedere, "le scienze" 8: 192-195.
- DELFINO M., RAGE J.-C. & ROOK L. 2003. — Tertiary mammal turnover phenomena: what happened to the herpetofauna?, in REUMER J. W. F. & WESSEL W. (eds), *Distribution and migration of Tertiary mammals in Eurasia*. A volume in honour of Hans de Bruijn. *Deinsea* 10: 153-161.
- DELFINO M., KOTSAKIS T., ARCA M., TUVERI C., PITRUZZELLA G. & ROOK L. 2008. — Agamid lizards from the Plio-Pleistocene of Sardinia (Italy) and an overview of the European fossil record of the family. *Geodiversitas* 30 (3): 641-656.
- DELUSSU F. 2000. — Lo stato attuale degli studi sulle faune oloceniche della Sardegna centro-settentrionale, in *Atti 2° Convegno Nazionale Archeozoologia*. ABACO Edizioni, Forlì: 183-192.
- ESTES R. 1981. — Gymnophiona, Caudata, in *Handbuch der Paläoherpetologie*. Volume 2. Gustav Fischer Verlag, Stuttgart/New York, 115 p.
- ESTES R. 1983. — Sauria terrestria, Amphisbaenia, in *Handbuch der Paläoherpetologie*. Volume 10A. Gustav Fischer Verlag, Stuttgart/New York, 249 p.
- ESU D. & KOTSAKIS T. 1979. — Restes de vertèbres et de mollusques continentaux dans le Villafranchien de la Sardaigne. *Geobios* 12 (1): 101-106.
- FEJÉRVÁRY-LÁNGH A. M. 1932. — Beiträge zur einer Monographie der fossilen Ophisaurier. *Palaeontologia Hungarica* 1 (7): 123-220.
- FONDI R. 1972. — Fauna cromeriana della Montagnola senese. *Palaeontographia Italica* 68: 1-27.
- FRANCIS E. T. B. 1934. — *The Anatomy of the Salamander*. Clarendon Press, Oxford, XXXI + 381 p.
- GAUTHIER J. 1982. — Fossil xenosaurid and anguillid lizards from the early Eocene formation Wasatch, southeast Wyoming, and a revision of the Anguioidea. *Contribution to Geology of the University of Wyoming* 21 (1): 7-54.
- GIBBARD P. L., HEAD M. J., WALKER M. J. C. & THE SUB-COMMISSION ON QUATERNARY STRATIGRAPHY 2010. — Formal ratification of the Quaternary System/Period and the Pleistocene Series/Epoch with a base at 2.58 Ma. *Journal of Quaternary Science* 25 (2): 96-102.
- HOLMAN J. A. 1991. — Fossil history of the grass snake (*Natrix natrix*) with emphasis on the British fossil record. *British Herpetological Society Bulletin* 36: 8-11.
- HOLMAN J. A. 2000. — *Fossil Snakes of North America: Origin, Evolution, Distribution, Paleocology*. Indiana University Press, Bloomington and Indianapolis, 357 p.
- HOLMAN J. A. 2006. — *Fossil Salamanders of North America*. Indiana University Press, Bloomington and Indianapolis, 232 p.
- KLEMBARA J. 1979. — Neue Funde der Gattungen *Ophisaurus* und *Anguis* (Squamata, Reptilia) aus dem Untermiozän Westböhmens (CSSR). *Vestník Ústředního Ústavu geologického* 54: 163-169.
- KLEMBARA J. 1981. — Beitrag zur Kenntnis der Subfamilie Anguinæ (Reptilia, Anguidae). *Acta Universitatis Carolinae, Geologica* 2: 121-168.
- KLEMBARA J. 1986. — New finds of the genus *Ophisaurus* (Reptilia, Anguidae) from the Miocene of Western Slovakia (Czechoslovakia). *Acta Universitatis Carolinae, Geologica, Spinar* 2: 187-203.
- KOTSAKIS T. 1989. — Late Turolian Amphibians and Reptiles from Brisighella (Northern Italy): preliminary report. *Bollettino della Società Paleontologica Italiana* 28 (2, 3): 277-280.
- LANZA B. 1983. — Ipotesi sulle origini del popolamento erpetologico della Sardegna. *Biogeographia* 8 (n.s. 1980): 723-744.
- LANZA B., PASTORELLI C., LAGHI P. & CIMMARUTA R. 2006. — A review of systematics, taxonomy, genetics, biogeography and natural history of the genus *Speleomantes* Dubois, 1984 (Amphibia Caudata Plethodontidae). *Atti del Museo Civico di Storia Naturale di Trieste* 52 (suppl.): 5-135 (dated 2005, published 2006).
- LANZA B., ANDREONE F., BOLOGNA M. A., CORTI C. & RAZZETTI E. (eds) 2007. — *Fauna d'Italia*, Vol. XLII, *Amphibia*. Calderini, Bologna, XI + 537 p.
- MACEY J. R., SCHULTE J. A., LARSON A., TUNIYEV B. S., ORLOV N. & PAPENFUSS T. J. 1999. — Molecular phylogenetics, tRNA evolution, and historical biogeography in Anguillid lizards and related taxonomic families. *Molecular Phylogenetics and Evolution* 12 (3): 250-272.

- PECORINI G., RAGE J.-C. & THALER L. 1974. — La formation continentale de Capo Mannu, sa faune de vertébrés pliocènes et la question du Messinien en Sardaigne. *Rendiconti del seminario della Facoltà di Scienze dell'Università di Cagliari* 43 (suppl.): 305-319.
- PITRUZZELLA G. 2008. — *Anatomia scheletrica, paleontologia e paleobiogeografia del genere Salamandrina (Amphibia, Caudata)*. Master Thesis in Natural Sciences, University of Firenze, 510 p.
- PITRUZZELLA G., DELFINO M., BÖHME M. & ROOK L. 2008. — Osteology of genus *Salamandrina*: preliminary observations from a palaeontological perspective, in CORTI C. (ed.), *Herpetologia Sardiniae*. Societas Herpetologica Italica/Edizioni Belvedere, "le scienze" 8: 412-415.
- RAGE J.-C. 1988. — Le gisement du Bretou (Phosphorites du Quercy, Tarn-et-Garonne, France) et sa faune de vertébrés de l'Éocène supérieur. I. Amphibiens et Reptiles. *Palaeontographica (A)* 205: 3-27.
- RAGE J.-C. 1997. — Palaeobiological and palaeogeographical background of the European Herpetofauna, in GASC J.-P., CABELA A., CRNOBRNJIA-ISAIOVIC J., DOLMEN D., GROSSENBACHER K., HAFNER P., LESCURE J., MARTENS H., MARTINEZ RICA J. P., MAURIN H., OLIVEIRA M. E., SOFIANIDOU T. S., VEITH M. & ZUIDERWIJK A. (eds), *Atlas of Amphibians and Reptiles in Europe*. Patrimoines naturels 29. Societas Europaea Herpetologica and Muséum national d'Histoire naturelle, Paris: 23-29.
- RINALDI P. M. 2003. — *La Fauna a Micromammiferi di Cava Sefi (Borro Strolla, Poggibonsi, Siena)*. Master Thesis in Natural Sciences, University of Firenze, 59 p.
- ROČEK Z. 1984. — Lizards (Reptilia: Sauria) from the Lower Miocene locality Dolnice (Bohemia, Czechoslovakia). *Rozprawy Československé Akademie Věd* 94 (1): 1-69.
- SANCHIZ B. 1977. — La familia Bufonidae (Amphibia, Anura) en el Terciario europeo. *Trabajos Neógeno-Cuaternario* 8: 75-111.
- SANCHIZ B. 1988. — On the zygosphenes-zygantrum vertebral articulations in salamandrids. *Acta Zoologica Cracoviensia* 31 (16): 493-504.
- SANCHIZ B. 1998. — Salientia, in *Handbuch der Paläoherpetologie*. Volume 4. Verlag Friedrich Pfeil, München, 275 p.
- SINDACO R., DORIA G., RAZZETTI E. & BERNINI F. (eds) 2006. — *Atlas of Italian Amphibians and Reptiles*. Societas Herpetologica Italica-Edizioni Polistampa, Firenze, 789 p.
- SPEYBROECK J., BEUKEMA W. & CROCHET P. A. 2010. — A tentative species list of the European herpetofauna (Amphibia and Reptilia) – an update. *Zootaxa* 2492: 1-27.
- STÖCK M., SICILIA A., BELFIORE N. M., BUCKLEY D., LO BRUTTO S., LO VALVO M. & ARCULEO M. 2008. — Post-Messinian evolutionary relationships across the Sicilian channel: mitochondrial and nuclear markers link a new green toad from Sicily to African relatives. *BMC Evolutionary Biology* 8: 56-74.
- STOETZEL E., BAILON S., EL HAJRAOUI M. A. & NESPOULET R. 2008. — Apport sur les connaissances des paléoenvironnements néolithiques du Maroc à partir des amphibiens-reptiles de la couche 1 d'El Harhoura 2, Rabat-Témara. *L'Anthropologie* 112: 731-756.
- SULLIVAN R. M. 1987. — *Parophisaurus pawneensis* (Gilmore 1928) new genus of anguid lizard from the middle Oligocene of North America. *Journal of Herpetology* 21: 115-133.
- SULLIVAN R. M., KELLER T. & HABERSETZER J. 1999. — Middle Eocene (Geiseltal) anguid lizards from Geiseltal and Messel, Germany. I. *Ophisauriscus quadrupes* Kuhn 1940. *Courier Forschungsinstitut Senckenberg* 216: 97-129.
- SZYNDLAR Z. 1984. — Fossil snakes from Poland. *Acta Zoologica Cracoviensia* 28 (1): 1-156.
- SZYNDLAR Z. 1991a. — A review of Neogene and Quaternary snakes of Central and Eastern Europe. Part I: Scolecophidia, Boidae, Colubrinae. *Estudios geológicos* 47: 103-126.
- SZYNDLAR Z. 1991b. — A review of Neogene and Quaternary snakes of Central and Eastern Europe. Part II: Natricinae, Elapidae, Viperidae. *Estudios geológicos* 47: 237-266.
- SZYNDLAR Z. & SCHLEICH H.-H. 1993. — Descriptions of Miocene snakes from Petersbuch 2 with comments on the Lower and Middle Miocene ophidian faunas of Southern Germany. *Stuttgarter Beiträge zur Naturkunde (ser. B)*, 192: 1-47.
- SZYNDLAR Z. & SCHLEICH H.-H. 1994. — Two species of the genus *Eryx* (Serpentes; Boidae; Erycinae) from the Spanish Neogene with comments on the past distribution of the genus in Europe. *Amphibia-Reptilia* 15: 233-248.
- SZYNDLAR Z. & RAGE J.-C. 2002. — Fossil record of the true vipers, in SCHUETT G. W., HÖGGREN M., DOUGLAS M. E. & GREENE H. W. (eds), *Biology of the Vipers*. Eagle Mountain Publishing, Eagle Mountain, UT: 419-444.
- VENCZEL M. 2006. — Lizards from the late Miocene of Polgárdi (W-Hungary). *Nymphaea, Folia naturae Bihariae* 33: 25-38.
- VENCZEL M. & SANCHIZ B. 2006. — Lower Miocene Amphibians and reptiles from Oschiri (Sardinia, Italy). *Hantkeniana* 5: 72-75.
- VERGNAUD-GRAZZINI C. 1970. — Les Amphibiens fossiles du gisement d'Aronelli. *Palaeontographica Italica* 66 (ser. 36): 47-65.

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