Anurans and squamate reptiles from the latest early Pleistocene of Almenara-Casablanca-3 (Castellón, East of Spain). Systematic, climatic and environmental considerations

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ABSTRACT

The karstic fissure filling of Almenara-Casablanca-3, dated from the latest early Pleistocene, has furnished the following fauna of anurans and squamate reptiles: cf. *Discoglossus* (Alytidae), *Pelobates cultripes* (Pelobatidae), *Pelodytes* cf. *P. punctatus* (Pelodytidae), *Bufo bufo* and *Bufo* sp. (Bufonidae), *Pelophylax* cf. *P. perezi* (Ranidae), *Blanus cinereus* (Blanidae), *Chalcides* cf. *Ch. bedriagai* (Scincidae), indeterminate small lacertids (Lacertidae), *Natrix natrix, Coronella girondica, Rhinechis scalaris* and *Malpolon monspessulanus* (Colubridae) and *Vipera latasti* (Viperidae). This faunal association might have been contemporaneous with climatic conditions slightly cooler and moister than those occurring at present in the area, and it suggests an open forest environment of Mediterranean type, with some free water points.

KEY WORDS Anura, Squamata,

Squamata, early Pleistocene, Spain, palaeoclimate, palaeoenvironment.

RÉSUMÉ

Anoures et squamates du Pléistocène inférieur final d'Almenara-Casablanca-3 (Castellón, Est de l'Espagne). Considérations systématiques, climatiques et environnementales.

Le remplissage karstique d'Almenara-Casablanca-3, daté du Pléistocène inférieur final, a livré les anoures et les squamates suivants: cf. *Discoglossus* (Alytidae), *Pelobates cultripes* (Pelobatidae), *Pelodytes* cf. *P. punctatus* (Pelodytidae), *Bufo bufo* et *Bufo* sp. (Bufonidae), *Pelophylax* cf. *P. perezi* (Ranidae), *Blanus cinereus* (Blanidae), *Chalcides* cf. *Ch. bedriagai* (Scincidae), de petits Lacertidae indéterminés, *Natrix natrix, Coronella girondica, Rhinechis scalaris* et *Malpolon monspessulanus* (Colubridae), et *Vipera latasti* (Viperidae). Cette faune, dans son ensemble, pourrait être contemporaine de conditions climatiques légèrement plus fraîches et plus humides que celles qui règnent actuellement dans la région et suggère un milieu forestier ouvert de type méditerranéen, ménageant des points d'eau libre.

MOTS CLÉS Anura, Squamata, Pléistocène inférieur, Espagne, paléoclimat, paléoenvironnement.

INTRODUCTION

Almenara-Casablanca-3 (ACB-3) is a fissure filling belonging to the large karstic complex of Almenara, situated in a Triassic calcareous massif exploited by quarries, along the Mediterranean seashore between Castelló de la Plana and Valencia (East of Spain), near the city of Almenara (Fig. 1). This complex of karstic fillings consists of many deposits which correspond to precise periods of Late Neogene and Early Quaternary, immediately anterior or transitional to palaeoclimatic or palaeobiogeographic events: Almenara-Casablanca-M (Mio-Pliocene boundary, coincident with the Messinian Salinity Crisis), Almenara-Casablanca-1, -4 and -6 (late to latest Pliocene, associated with the late Plioceneearly Pleistocene climatic crisis) and the most recent Almenara-Casablanca-3, late early Pleistocene in age and close to the early-middle Pleistocene boundary (Agustí & Galobart 1986).

ACB-3 was discovered during prospections associated with the field-campaigns in 1985 and 1986, and has produced a rich micromammalian association which includes the following species: *Crocidura* sp., *Sorex* sp., *Neomys* sp., *Myotis blythi*, Chiroptera indet., *Allophaiomys chalinei, Ibero*- mys sp., Mimomys savini, Apodemus mystacinus, A. flavicollis, Castillomys rivas, Allocricetus bursae duranciensis, Eliomys quercinus helleri (Agustí & Galobart 1986; Agustí 1992; Santos-Cubedos et al. 2004; Furió et al. 2004, 2005). This association indicates a stratigraphic position intermediate between the sites of Fuente Nueva 3 and Barranco León 5 on one hand, dated about 1.3 Ma (Agustí & Madurell 2003), and those at the base of the Gran Dolina de Atapuerca section on the other hand, i.e. at about 0.8 Ma (Parés & Pérez-González 1999). Consequently, the association of Almenara-Casablanca-3 is very close to that of Cueva Victoria (Agustí 1982). Both localities are to be dated at around 1 Ma, close in age to the sites of Untermassfeld and Le Vallonet.

MATERIAL AND METHODS

The herpetofaunal samples identified consist of disarticuled bone fragments whose major part was collected from many collection campaigns conducted by the Institut de Paleontologia Miquel Crusafont teams. In addition to this material, few bones from the collection of the Museu de Geologia of Barcelona, registered as v8439 and v8440, are coming from previous collections. This assemblage includes 1888 fragments, comprising 54 elements of anurans (i.e. 2.9%) and 1834 of squamate reptiles (i.e. 97.1%). They represent six species of anurans and 10 species of squamates respectively. This material is stored in the collection of the Institut de Paleontologia Miquel Crusafont in Sabadell (Barcelona) and in the Museu de Geologia of Barcelona.

The bones were assigned to different taxa following the criteria given by Böhme (1977), Sanchiz (1977), Bailon (1991, 1999) and Sanchiz et al. (2002) for anurans, and Bailon (1986, 1991), Barbadillo (1989), Barahona & Barbadillo (1997), Szyndlar (1984) and Blain (2005) for squamates, using for comparisons the collections of dry skeletons of the Museo Nacional de Ciencias Naturales, Madrid, of the Facultad de Ciencias of the University of Granada, of the Muséum national d'Histoire naturelle, Paris, of the Laboratoire départemental de Préhistoire du Lazaret, Nice, as well as our personal collections. Accounts on the distribution and habitat of present species mainly proceed from Pleguezuelos & Martinez-Rica (1997), Salvador (1997a) and Pleguezuelos et al. (2002) for the Iberian Peninsula and Vento et al. (1991), Lacomba & Sancho (1999) and Jiménez et al. (2002) for the Community of Valencia. The taxonomic nomenclature basically follows Montori et al. (2005) and Frost et al. (2006).

All measurements have been done with a digital Measurescope Kappa MFK-II on a Wild M8 binocular to the nearest 0.01 mm or with scaled drawings.

SYSTEMATICS

Class AMPHIBIA Gray, 1825 Order ANURA Fischer von Waldheim, 1813 Family ALYTIDAE Fitzinger, 1843 Genus *Discoglossus* Otth, 1837

> cf. *Discoglossus* (Fig. 2A)

MATERIAL EXAMINED. — 1 distal fragment of left ilium.



Fig. 1. — Geographical location of Almenara-Casablanca-3 in the Community of Valencia (Spain).

DESCRIPTION

This left ilium, whose pars ascendens ilii and the major part of the *acetabulum* are not preserved, is attributed to cf. Discoglossus. Attribution to the genus Discoglossus does rest on the presence of a dorsal crest, curved medially and prolonged posteriorly by a rounded tuber superior. The angle between the pars descendens ilii and the main axis of the pars cylindriformis is slightly wider than in genus Rana Linnaeus, 1758 and Pelophylax Fitzinger, 1843. The morphological limit between the genus Discoglossus and the extinct genus Latonia Meyer, 1843 (Oligocene to Pliocene from Europe; Roček & Rage 2000; Sanchiz 1998) still remains problematic; nevertheless the small size of the ilium may be more consistent with the genus Discoglossus (Roček 1994).

CHOROLOGICAL DATA

Today, two autochthonous endemic species, Discoglossus galganoi Capula, Nascetti, Lanza, Bullini & Crespo, 1985 and Discoglossus jeanneae Busack, 1986 are present in the Iberian Peninsula. D. galganoi possesses an Iberian occidental distribution with the exception of Andalusia and Levante area. The oriental limit of the Iberian distribution of D. jeanneae in central Spain corresponds to scarce data in the provinces of Burgos, Zaragoza, Teruel, Cuenca and Requena area in Valencia (García-París 1997). On the oriental border of the Community of Valencia, D. jeanneae is reputed rare and occurs as three little isolated nuclei (Lacomba & Sancho 1999; Jiménez et al. 2002; Martínez-Solano & García-París 2002). This low and mid-lying areas species usually ranges in Iberian System from 500 to 1,200 m above sea level. In Mediterranean area, the two species are common in meso- and supramediterranean bioclimatic levels, occupying opened areas as well as "bank copse".

Family PELOBATIDAE Bonaparte, 1850 Genus *Pelobates* Wagler, 1830

Pelobates cultripes (Cuvier, 1829) (Fig. 2B-E)

MATERIAL EXAMINED. — 1 fragment of squamosal, 2 fragments of frontoparietal, 1 left ilium and 1 distal fragment of tibiofibula.

DESCRIPTION

The squamosal and frontoparietals bear an anastomosed sculpture composed of relatively dense isolated tubercles.

One fragment of frontoparietal, consisting of the right posterior part of this element, shows a relatively well developed, more or less triangular paraoccipital process. Unlike in *P. fuscus* (Laurenti, 1768), the *foramen arteriae occipitalis*, invisible in dorsal view, is situated more medially with regard to the paraoccipital process and it is present on the medial break line of this fragment. Like in *P. cultripes*, only one crest instead of two in *P. varaldi* Pasteur, 1958 (the North-African species) occurs on the dorsal surface of the paraoccipital process. On the dorsal surface, ornamentation is denser than in *P. fuscus*.

A fragment of left squamosal has been identified, corresponding to the posterior part of the *lamella alaris*. In dorsal view, the *lamella alaris* seems to be well developed and possesses a dense ornamentation like that of *P. cultripes*.

The ilium is characterized by the absence of dorsal crest, *tuber superior*, preacetabular and supracetabular fossae and by the presence of a strongly striated interiliac articulation surface and a straight dorsal limit of the *pars ascendens ilii* like in *P. cultripes*.

The tibiofibula fragment shows the general morphology of *Pelobates*.

CHOROLOGICAL DATA

The western spadefoot (*P. cultripes*) is the only representative of the Pelobatidae occurring in the Iberian Peninsula. It is a pioneer, terrestrial and fossorial Southern European species which lives in loose or sandy grounds in the vicinity of humid places. Its modern repartition seems to be restricted to thermo- and mesomediterranean bioclimatic levels, in low-lying areas with poor seasonal pluviometry. In the studied area, its distribution is discontinuous (Lacomba & Sancho 1999; Jiménez et al. 2002) and it does not seem very common, even if locally and temporarily it may be abundant some years owing to demographic explosions (Vento et al. 1991). At present, it is found principally on the coastal area, especially in sand dunes and adjacent humid areas, while inland, in littoral and pre-littoral mountains (Sierras) its distribution is conditioned by the existence of a sandy substratum. It occurs in the scrubby areas and in the hilly low-lying and dry areas if that Mediterranean vegetation is relatively open (Quercus ilex). It ranges from the sea-shore to an altitude of nearly 1,500 m (Lizana 1997a). It is probably the most adapted Iberian amphibian to xeric conditions, but it needs substantial water points, generally quiet with aquatic vegetation, due to the size of its tadpoles and to its relatively long metamorphosis period (Lizana 1997a).

> Family PELODYTIDAE Bonaparte, 1850 Genus *Pelodytes* Bonaparte, 1838



Fig. 2. – **A**, cf. *Discoglossus*, left ilium, lateral view; **B-E**, *Pelobates cultripes* (Cuvier, 1829); **B**, left squamosal, lateral view; **C**, right part of frontoparietal, dorsal view; **D**, **E**, left ilium, lateral and medial views; **F-J**, *Pelodytes* cf. *P*, *punctatus* (Daudin, 1802); **F**, **G**, left ilium, lateral and medial views; **H**, left humerus of a female, ventral view; **I**, **J**, trunk vertebra, dorsal and posterior views. Scale bars: 2 mm.

Pelodytes cf. P. punctatus (Daudin, 1802) (Fig. 2F-J)

MATERIAL EXAMINED. — 1 distal fragment of left ilium, 4 humeri, 1 trunk vertebra, 4 radio-ulnae and 1 tibiofibula.

DESCRIPTION

The ilium is characterized by the absence of a dorsal crest and of a *tuber superior*. The *pars cylindriformis* is clearly curved and the posteromedial face is smooth. According to Sanchiz *et al.* (2002), differentiation between *P. ibericus* Sánchez-Herráiz, Barbadillo, Machordom & Sanchiz, 2000 and *P. punctatus* (the two species currently occurring in the Iberian Peninsula) lies essentially in the morphology of the *pars descendens ilii* that is wider in *P. ibericus* than

in *P. punctatus* and in the weaker development of the acetabulum in *P. punctatus*. The relatively poor development of the acetabulum of the fossil ilium seems to be consistent with *P. punctatus*; the *pars descendens ilii* is broken.

The humerus possesses a straight and slender shaft, the distal condyle is spherical and slightly displaced laterally and the cubital fossa is open on the radial side.

The vertebra is procoelous, small, and it possesses a neural arch moderately long with a posterior median point slightly marked. The condyle is small and dorso-ventrally flattened; the transverse processes are quite slender and they originate below the prezygapophyses, which is characteristic of a posterior vertebra (V_5 - V_8). The sizes and morphologies of the radio-ulnae and tibiofibula are consistent with those of the genus *Pelodytes*.

The distinction between the two Iberian species on the basis of incomplete fossil bones is quite difficult. All of these elements permit undoubted attribution to the genus *Pelodytes*, but the attribution to the species *P. punctatus* rests essentially on biogeographical criteria: *P. ibericus* displays at present a southern distribution (Portugal, Extremadura and Andalusia; Sánchez-Herráiz *et al.* 2000).

CHOROLOGICAL DATA

The common parsley frog (*P. punctatus*) is a midand low-lying area Franco-Iberian species. Mainly terrestrial and nocturnal, it lives in sandy soils and beneath stones in the vicinity of water. It shows a strong tendency to dwell in cave habitats, taking refuge in substratum fissures, cavities or caves at great depth (Sánchez-Herráiz & Barbadillo 1997). In the studied area, this species is reputed common and well distributed, avoiding coastal areas and driest areas of Alicante (Lacomba & Sancho 1999; Jiménez *et al.* 2002).

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

Bufo bufo (Linnaeus, 1758) (Fig. 3B, C)

MATERIAL EXAMINED. — 2 ilia, 3 scapulas, 6 humeri, 2 vertebrae, 3 radio-ulnae and 6 tibiofibulae.

DESCRIPTION

Identification at species level is based on Böhme (1977), Sanchiz (1977), Bailon & Hossini (1990) and Bailon (1991, 1999).

As in the extant *B. bufo*, the ilia do not have a dorsal crest and possess a relatively low, rounded unilobed or slightly bilobed *tuber superior*.

The scapula is elongated dorsoventrally, with a sinuous anterior edge and a glenoid process that is strong and clearly separated from the bulk of the bone. The absence of a supraglenoid fossa permits identification as *B. bufo*.

The humeri possess a straight and relatively thick shaft, the distal condyle is slightly displaced laterally and the condyle and epicondyles are relatively little developed: these characters are consistent with *B. bufo*, as well as the size of the element, *B. bufo* being the largest bufonid in Western Europe.

Other bones (vertebrae, radio-ulnae and tibiofibulae) are very fragmentary and show the general morphology of the genus *Bufo*.

CHOROLOGICAL DATA

The common European toad (*B. bufo*) has a large Eurasian range. It lives in nearly all environments, even in dry areas. Its only requirement seems to be, during his breeding season, the presence of quiet or low energy water, preferably permanent and with vegetation (Lizana 1997b). In the studied area, its distribution is relatively continuous and it is very common, even if it seems to be rarer in the mountainous areas of the North-East of Castellón (Vento *et al.* 1991).

Bufo sp. (Fig. 3A)

MATERIAL EXAMINED. — 2 ilia.

DESCRIPTION

Among the ilia attributed to bufonids, two are characterized by the presence of a deep preacetabular fossa and a bilobed dorsal protuberance (Fig. 3A): these characters are observable in *Bufo viridis* (Laurenti, 1768), although the last one occurs irregularly (Hossini 2001), and in *Bufo mauritanicus* Schlegel, 1841. Nevertheless, in view of the absence of other bones, these ilia have been referred to as *Bufo* sp. Today *B. viridis* is absent from the Iberian Peninsula (except the Balearic Islands where it is of anthropical origin; Mayol & Román 1997; Mayol Serra 2003) and *B. mauritanicus* lives in North Africa (Morocco, Northern Algeria and Tunisia).

> Family RANIDAE Rafinesque, 1814 Genus *Pelophylax* Fitzinger, 1843



Fig. 3. – A, Bufo sp., left ilium, lateral view; B, C, Bufo bufo (Linnaeus, 1758); B, left scapula, dorso-lateral view; C, right humerus of a male, ventral view; D-G, Pelophylax cf. P. perezi Seoane, 1885; D, E, right frontoparietal, ventral and dorsal views; F, G, left ilium, lateral and distal views. Scale bars: 2 mm.

Pelophylax cf. P. perezi Seoane, 1885 (Fig. 3D-G)

MATERIAL EXAMINED. — 1 right frontoparietal, 2 mandibles, 1 sacral vertebra, 4 ilia and 1 humerus.

DESCRIPTION

Most of the bones are damaged and do not permit unquestionable specific determination. Nevertheless, the better preserved bones show the presence of a species of the "water frogs group" attributable to *Pelophylax* cf. *P. perezi*.

The frontoparietal is not fused with its homologous. In ventral view, the endocranial impression is double: the posterior one that corresponds to the mesencephalic area is closed and circular. In dorsal view, the frontoparietal does not show any occipital canal, and the prootic and occipital processes are well developed. In the genus *Pelophylax*, unlike in the genus *Rana*, the frontal area is narrower, and the crests are well marked with a parietal protuberance in central position (Bailon 1999). The medial margin is straight. The general morphology of this bone well matches *Pelophylax perezi*.

The ilium possesses a high and vertical dorsal crest on the *pars cylindriformis*. The dorsal crest shows posteriorly a globular and well differentiated *tuber superior*, typical of the genus *Pelophylax*. The angle between the anterior edge of the *tuber superior* and the dorsal edge of the *pars ascendens ilii* is slightly larger than 90°.

Other fragments (humerus, mandibles and sacral vertebra) show a size and a morphology consistent with the genus *Pelophylax*, but do not permit identification of species.

CHOROLOGICAL DATA

The southern marsh frog (*P. perezi*) is the only modern representative of the genus *Pelophylax* currently present in the region. It is a Western Mediterranean species which occurs in the whole Iberian Peninsula and in South of France. It lives in all sunny aquatic environments and its presence seems to be limited only by the absence of permanent water points. It is not sensible on water quality and tolerates sand dune and coastal sand salinity (Llorente & Arano 1997).

> Class REPTILIA McCartney, 1802 Order AMPHISBAENIA Gray, 1844 Family BLANIDAE Kearney, 2003 Genus *Blanus* Wagler, 1830

Blanus cinereus (Vandelli, 1797) (Fig. 4A-D)

MATERIAL EXAMINED. — 21 dentaries and 21 trunk vertebrae.

DESCRIPTION

The dentaries are short and strong, bearing subpleurodont and monocuspid teeth. The anterior teeth are cylindrical and inclined anteriorly whereas central and posterior teeth are cone-shaped, with a wide base and a posteromedially directed apex. All dentaries possess 8 tooth positions, the fourth tooth being the shortest whereas the first, third and fifth ones are the highest. The splenial, often preserved in anatomical connection, is small.

The trunk vertebrae show a dorsoventrally flattened neural arch, with a concave posterior end and a well marked interzygapophyseal constriction. The neural spine is lacking or is very small, and the synapophyses are globular and more or less circular or egg-shaped according to position of the vertebra in the spinal column. The ventral surface of the centrum is flat, with parallel or slightly convex margins. The prezygapophyses and postzygapophyses are well developed and inclined upward. The condyle and cotyle are flattened dorsoventrally.

The overall morphology of the dentaries and vertebrae does not differ from those of *B. cinereus*, the only current representative of the family in Western Europe.

CHOROLOGICAL DATA

The Mediterranean worm lizard (B. cinereus) is a Western Mediterranean species restricted to the Iberian Peninsula. The studied area represents the northernmost border of the modern distribution of B. cinereus on the Mediterranean coast, it being understood that it is not known with certainty beyond the Ebro delta (Gil 1997; López 2002) and shows a poor and discontinuous distribution in the province of Castellón, which seems to be connected to the difficulties of observations of this species due to its fossorial way of life (Lacomba & Sancho 1999; Vento et al. 1991). B. cinereus occurs in wet areas and in all vegetal cover types with loose or sandy and humid grounds (Pérez-Mellado 1983; Pleguezuelos 1989; Salvador 1997b). It ranges practically from the seashore to the mesomediterranean bioclimatic level in the Iberian System (Gil 1997).

Order LACERTILIA Owen, 1842

Remarks

Among the ACB-3 material, 744 fragments (mainly dentaries and maxillae) have been attributed only at the level of the order.

Family SCINCIDAE Oppel, 1811 Genus *Chalcides* Laurenti, 1768

Chalcides cf. *Ch. bedriagai* (Boscá, 1880) (Fig. 4E-I)

MATERIAL EXAMINED. — 3 dentaries and 29 vertebrae (10 trunk, 14 sacral and 5 caudal).



Fig. 4. – A-D, Blanus cinereus (Vandelli, 1797); A, right dentary, medial view; B-D, trunk vertebra, dorsal, ventral and right-lateral views; E-I, Chalcides cf. Ch. bedriagai (Boscá, 1880); E, F, right dentary, medial and lateral views; G-I, trunk vertebra, dorsal, ventral and anterior views. Scale bars: 2 mm.

DESCRIPTION

The dentaries bear pleurodont, isodont, cylindrical and monocuspid teeth with blunt apex. In lateral view, unlike in Lacertidae, the dentary lacks the impression of the coronoid. In lingual view, every tooth apex shows a more or less visible ornamentation, with vertical delicate striation limited ventrally by a transversal groove. Like in the representatives of the genus *Chalcides*, the dentaries show a Meckelian groove open in its whole length and narrower anteriorly from the eighth dental position from posterior end of the tooth row. The dentary morphology does not differ from that of the modern species *Chalcides bedriagai*, that is characterized by the presence of 17 dental positions and by a teeth width/height ratio equal to 0.3 (Barbadillo 1989).

The vertebrae are procoelous, more or less elongated and with a little deep interzygapophyseal constriction. The neural spine is long, thin and low. Posteriorly, it ends as an interzygapophyseal point which probably projects back beyond the postzygapophyses when it is not broken. In ventral view, the centrum is cylindrical with a haemal keel more or less wide and with indistinct lateral edges. The cotyle and condyle are slightly flattened dorso-ventrally.

CHOROLOGICAL DATA

The Bedriaga's skink (*Ch. bedriagai*) is an endemic Iberian species, which lives in the major part of the Iberian Peninsula with the exception of the northernmost part. For the Mediterranean coast, its present northernmost distribution border is the city of Tarragona, with a strong population density in the provinces of Valencia, Alicante and Castellón (Pollo 1997; Lacomba & Sancho 1999; Jiménez

| | Acanthodactylus erythrurus (n = 2) | | Podarcis hispanica (n = 9) | | Psammodromus algirus (n = 2) | |
|------|---------------------------------------|-------|-------------------------------|-------|---------------------------------|-------|
| | d/h | a/h | d/h | a/h | d/h | a/h |
| Ν | 31 | 31 | 124 | 124 | 45 | 45 |
| Mean | 0.280 | 0.330 | 0.269 | 0.439 | 0.301 | 0.327 |
| SD | 0.040 | 0.058 | 0.053 | 0.053 | 0.050 | 0.043 |
| Min. | 0.200 | 0.220 | 0.170 | 0.300 | 0.220 | 0.250 |
| Max. | 0.400 | 0.450 | 0.440 | 0.570 | 0.430 | 0.440 |

TABLE 1. — Ratios taken on the lacertids dentaries. Abbreviations: N, number of measured teeth; SD, standard-deviation; min., minimum; max., maximum; d, tooth diametre; h, tooth height; a, tooth height projecting beyond the dental crest. All the measurements have been made with scaled drawings.

et al. 2002). It occurs primarilly in localities with great annual pluviometry although it is present on the Almeria coast where annual precipitations are the poorest of Europe. It lives in the meadows, brushwood and forest glades, and is common in the pine forest and coastal area. It ranges from highest areas of the Community of Valencia (Penyagolosa) to the thermo- to the oromediterranean bioclimatic level (Vento *et al.* 1991).

Family LACERTIDAE Oppel, 1811

Lacertidae indet. (small lacertids) (Fig. 5)

MATERIAL EXAMINED. — Lacertid remains compose 50.6% of the fossil material (excluding "Lacertilia indeterminated" remains), with all skeleton parts represented and without any digestion marks. They are present by numerous small fragmentary remains: skull bones (8 premaxillae, 16 frontals, 6 parietals, 4 jugals, 56 maxillae, 278 dentaries and 4 quadrates) and post-cranial bones (37 humeri, 59 femora, 3 tibiae, 25 vertebrae [among which 11 dorsal and 14 caudal] and 83 hemipelves). Previously some of these remains have been attributed to *Acanthodactylus* cf. *A. erythrurus* (Schinz, 1833), *Podarcis* cf. *P. hispanica* (Steindachner, 1870) and *Psammodromus* cf. *P. algirus* (Linnaeus, 1758) (Bailon & Blain 2004; Furio *et al.* 2005; Blain 2005).

DESCRIPTION

The premaxillae show a relative variability in their size. The smallest have parallel lateral margins of the posterodorsal process, whereas in those which have a slightly larger size, this process is slightly "arrow-shaped" (*sensu* Barahona & Barbadillo 1997).

The number of tooth positions is constant and equal to 7. Such a set of characteristics is currently present in the genera *Podarcis* and *Psammodromus* and in *Lacerta bonnali* Lantz, 1927 (Barahona & Barbadillo 1997).

In their great majority the frontals are fragmentary and correspond to the central and posterior parts of the bone. Among the 16 listed fragments, 15 show the complete fusion of the two frontals, whereas the 16th corresponds to a right frontal not fused with its opposite bone. The presence of fused frontals is a characteristic constant in *Acanthodactylus* and variable in the other Iberian lacertids (Barahona & Barbadillo 1997). Nevertheless, the fossil frontals differ from those of *Acanthodactylus* by the presence of a denser dermic ornamentation, of a less marked central constriction and of a less elongated central part, thus bringing the prefrontal and postfrontal (or postorbitofrontal) impressions closer to each other.

Morphologically, the fossil frontals better compare with *Psammodromus* and *Podarcis*. In the first genus, the fusion of the frontals seems to be common (Barahona & Barbadillo 1997; Montoya *et al.* 1999; and pers. obs.), whereas in *Podarcis* the frontals are separated (Arnold 1973) or sometimes fused (Barahona & Barbadillo 1997). This characteristic suggests at first sight an assignment of the fossils to *Psammodromus*. Nevertheless, the comparisons made with 4 extant specimens of *Psammodromus algirus* (*P. hispanicus* has not been compared) show some variation within this species: the bone is less elongate posteriorly and, in ventral view, the impression of the postfrontal (or postorbitofrontal) is well marked, whereas in the fossils this impression



FIG. 5. – A-L, small lacertids; A-F, frontals, ventral and dorsal views; G, H, parietal, ventral and dorsal views; I, premaxilla, posterior view; J, K, jugal, dorsal and lateral views; L, "*Psammodromus-Acanthodactylus*" type, right dentary, medial view; M, "*Podarcis*" type, left dentary, medial view. Scale bars: 2 mm.

appears only in lateral view. According to these two characteristics, the fossils are closer to the observed specimens of *Podarcis (P. hispanica* (Steindachner, 1870), *P. muralis* (Laurenti, 1768) and *P. sicula* (Rafinesque, 1810)), even if none of them shows a fusion of the frontals.

According to all the characteristics cited above, the only unfused frontal is closer to *Podarcis* than to *Psammodromus*.

The parietals are well ossified and possess a particular morphology that prevents any precise attribution. The posterior limit of the parietal table is prolonged by a short osseous lamella that lacks any dermic ornamentation and with a medial notch. The anterior ventral crests are slightly convergent medially and reach the posterior limit of the bone. The parietal fossa is moderately short and wide and the anterior and posterior ventral crests are convergent. These characteristics suggest close relationships with *Acanthodactylus* and distinguish them from all the other adult representatives of the Iberian Peninsula (see characteristics in Barahona & Barbadillo 1997). However, these parietals differ from *Acanthodactylus* by the presence of a small occipital scale imprint, by a denser and more developed dermic ornamentation (characteristics present in *Psammodromus*, *Podarcis* and *Lacerta* s.l.) and by the weaker development of the posterior crest.

Among the Iberian lacertids, a similar condition of the ventral crests, as well as the presence of a short and wide parietal fossa and a posterior crest with a medial notch, have been observed in some sub-adult specimens (developmental stage 3, *sensu* Barahona & Barbadillo 1998) of many representatives of *Podarcis*, whereas in *Psammodromus* the parietals, at this developmental stage, have already aquired adult characteristics concerning the disposition of the ventral crests (Barahona & Barbadillo 1998).

In lateral view, the jugals show a well developed quadratojugal process, a long and narrow dorsal branch and anteriorly, a strongly developed contact surface for the maxilla. In dorsal view, the posterior part of the insertion area with the ectopterygoid forms a small medial process (called "medial process on the palatal shelf" by Barahona & Barbadillo 1997). This set of characteristics listed above permits TABLE 2. — Statistical comparisons of the ratios according to the t Student test (N = P > 0.05; S = 0.05 > P > 0.01; HS = P < 0.01).

| d/h | Podarcis hispanica | Psammodromus algirus |
|---------------|-----------------------|-------------------------|
| A. erythrurus | Ν | S |
| P. hispanica | | HS |
| a/h | | |
| A. erythrurus | HS | Ν |
| P. hispanica | | HS |

to regard the fossils closer to *Podarcis* than to any other Iberian lizards. According to Barahona & Barbadillo (1997), the presence of a medial process is a distinctive characteristic of *Psammodromus*; nevertheless, in *Podarcis* this process is also often present, although less developped, as it appears in the fossils (pers. obs.).

All the dentaries of ACB-3 are very fragmented and small-sized. They show the typical characteristics of the family: pleurodont, cylindrical, mainly mono- and bicuspid, more rarely tricuspid teeth, Meckelian groove opened in its whole length, and presence of an impression of the coronoid on the posterodorsal limit of the bone.

We have compared our material to the three most abundant and currently present species in the province of Castellón: Acanthodactylus erythrurus, Podarcis hispanica and Psammodromus algirus. The diagnostic characteristics mentioned by Barahona & Barbadillo (1997), especially the morphology of the posterior processes, being not observable due to the fossils great fragmentation, we have made a biometrical study (Tables 1; 2) on the dentary teeth of the median area of a few modern specimens stored in the collections of the Laboratoire départemental de Préhistoire du Lazaret, Nice: two A. erythrurus, two P. algirus and nine P. hispanica. These specimens all correspond to adult or subadult representatives (developmental stage 3 or 4, sensu Barahona & Barbadillo 1998).

Within the fossil material, variations suggest the presence of at least two different forms. The majority of the fossil dentaries bear teeth which do not project much beyond the dental crest (0.24 < height of the projecting part (a)/total height (h) < 0.33) and are relatively strong (0.27 < tooth diametre

(d)/total height (h) < 0.33), which may be more consistent with representatives of Psammodromus or Acanthodactylus (respectively P. algirus and A. eryth*rurus*: $a/h = 0.327 \pm 0.043$ and 0.330 ± 0.058 ; d/ $h = 0.301 \pm 0.050$ and 0.280 ± 0.040). The second form bears more projecting (0.36 < a/h < 0.42)and slightly more slender (0.24 < d/h < 0.29) teeth which is consistent with a representative of Podarcis (*P. hispanica*: mean a/h = 0.439; mean d/h = 0.269). These results seem to be relatively congruent with the descriptions made by Barbadillo (1989) for these Iberian species. Nevertheless, in view of the few observed specimens of living species and to the great variability within dentaries of small lacertids, these comparisons may be considered with the greatest caution.

Order SERPENTES Linnaeus, 1758

Remarks

Among ACB-3 material, 150 elements (mainly incomplete vertebrae) have been attributed only at the level of the order.

Family COLUBRIDAE Oppel, 1811 "Natricinae" type (trunk vertebrae with hypapophysis) Genus *Natrix* Laurenti, 1768

Natrix natrix (Linnaeus, 1758) (Fig. 6A-E)

MATERIAL EXAMINED. — 2 trunk vertebrae.

DESCRIPTION

In the genus *Natrix*, the trunk vertebrae possess a sigmoid-shaped, short and strong hypapophysis and the zygapophyseal articular surfaces are horizontal. The neural arch is vaulted posteriorly, the condyle and cotyle are small and circular and the parapophysis is provided with a parapophyseal process. In lateral view, the parapophyseal processes are strongly built. The centrum of the trunk vertebrae of *Natrix natrix* is generally flat and its lateral margins are well marked, whereas in *Natrix maura* (Linnaeus,



Fig. 6. – A-E, Natrix natrix (Linnaeus, 1758), trunk vertebra, dorsal, ventral, anterior, left-lateral and posterior views; F, G, Coronella girondica (Daudin, 1803); F, supraoccipital, dorsal view; G, left exoccipital, lateral view; H, I, Rhinechis cf. Rh. scalaris (Schinz, 1822), right articular, lateral and medial views. Scale bars: 2 mm.

1758) the centrum is slightly convex with lateral margins more or less indistinct.

CHOROLOGICAL DATA

Among representatives of the genus *Natrix*, the grass snake (*N. natrix*) is a northern mid-European species occurring in the whole Iberian Peninsula,

except large areas in the centre and in the south where the aridity may limit its extension (Santos *et al.* 1997; Braña 1997). It lives in various environments: bank grove, pinewood, oak grove and mixed grove as well as meadow and bushy areas, but always in a moist and fresh environment. *N. natrix* is less water dependant than *N. maura*.

| Coronella girondica | n | mean | median | SD | min. | max. | | |
|-------------------------|----|------|--------|------|------|------|--|--|
| CL | 88 | 2.24 | 2.29 | 0.36 | 1.48 | 3.07 | | |
| NAW | 88 | 2.08 | 2.07 | 0.34 | 1.38 | 3.09 | | |
| PR-PO | 77 | 2.73 | 2.81 | 0.44 | 1.89 | 4.03 | | |
| PO-PO | 68 | 3.25 | 3.24 | 0.58 | 2.16 | 4.61 | | |
| PR-PR | 31 | 3.27 | 3.19 | 0.51 | 2.35 | 4.34 | | |
| CNW | 88 | 0.90 | 0.89 | 0.13 | 0.59 | 1.17 | | |
| CNW/NAW | 88 | 0.43 | 0.43 | 0.03 | 0.37 | 0.50 | | |
| PR-PR/PR-PO | 31 | 1.23 | 1.24 | 0.06 | 1.11 | 1.36 | | |
| PR-PR/NAW | 31 | 1.67 | 1.66 | 0.08 | 1.48 | 1.83 | | |
| CL/NAW | 88 | 1.08 | 1.07 | 0.08 | 0.91 | 1.36 | | |
| PO-PO/NAW | 68 | 1.58 | 1.57 | 0.06 | 1.46 | 1.73 | | |
| CNW/CL | 88 | 0.40 | 0.41 | 0.03 | 0.31 | 0.47 | | |
| Rhinechis scalaris | | | | | | | | |
| CL | 28 | 2.24 | 1.94 | 0.93 | 1.41 | 5.75 | | |
| NAW | 30 | 2.20 | 1.97 | 0.83 | 1.47 | 5.43 | | |
| PR-PO | 20 | 2.84 | 2.39 | 1.24 | 1.64 | 6.94 | | |
| PO-PO | 26 | 3.23 | 3.01 | 0.85 | 2.13 | 6.33 | | |
| PR-PR | 6 | 2.87 | 2.73 | 0.48 | 2.55 | 3.83 | | |
| CNW | 29 | 1.02 | 0.93 | 0.31 | 0.64 | 2.08 | | |
| CNW/NAW | 29 | 0.47 | 0.47 | 0.05 | 0.38 | 0.59 | | |
| PR-PR/PR-PO | 6 | 1.28 | 1.27 | 0.05 | 1.21 | 1.36 | | |
| PR-PR/NAW | 6 | 1.64 | 1.62 | 0.08 | 1.58 | 1.79 | | |
| CL/NAW | 28 | 1.03 | 1.04 | 0.06 | 0.86 | 1.16 | | |
| PO-PO/NAW | 26 | 1.59 | 1.59 | 0.06 | 1.45 | 1.73 | | |
| CNW/CL | 28 | 0.46 | 0.46 | 0.05 | 0.36 | 0.57 | | |
| Malpolon monspessulanus | | | | | | | | |
| CL | 6 | 4.37 | 3.90 | 0.93 | 3.73 | 6.07 | | |
| NAW | 6 | 3.27 | 2.89 | 0.76 | 2.75 | 4.71 | | |
| PR-PO | 4 | 5.34 | 4.73 | 1.24 | 4.69 | 7.19 | | |
| PO-PO | 2 | 5.03 | 5.03 | 0.08 | 4.97 | 5.09 | | |
| PR-PR | 3 | 5.07 | 5.01 | 0.15 | 4.95 | 5.24 | | |
| CNW | 6 | 1.61 | 1.56 | 0.31 | 1.28 | 2.19 | | |
| CNW/NAW | 6 | 0.50 | 0.48 | 0.05 | 0.45 | 0.58 | | |
| PR-PR/PR-PO | 3 | 1.07 | 1.06 | 0.03 | 1.06 | 1.11 | | |
| PR-PR/NAW | 3 | 1.78 | 1.72 | 0.11 | 1.72 | 1.91 | | |
| CL/NAW | 6 | 1.34 | 1.35 | 0.04 | 1.29 | 1.37 | | |
| PO-PO/NAW | 2 | 1.78 | 1.78 | 0.10 | 1.71 | 1.85 | | |
| CNW/CL | 6 | 0.37 | 0.36 | 0.04 | 0.33 | 0.43 | | |

TABLE 3. — Measurements and ratios of trunk vertebrae of "colubrines" of Almenara-Casablanca-3. Abbreviations: see Fig. 9.

In the Community of Valencia, *N. natrix* seems to be more frequent along the coast, in marsh areas (Lacomba & Sancho 1999; Jiménez *et al.* 2002).

"Colubrinae" type (trunk vertebrae without hypapophysis)

Remarks

Only skull bones and trunk vertebrae with a good state of preservation have been used for specific identification. Unlike in Viperidae and "natricines", the trunk vertebrae belonging to "colubrines" are characterized by the absence of a hypapophysis. The "colubrines" are represented in ACB-3, principally by small-sized vertebrae



FIG. 7. – A-E, Coronella girondica (Daudin, 1803), trunk vertebra, dorsal, ventral, anterior, left-lateral and posterior views; F-J, Rhinechis scalaris (Schinz, 1822), trunk vertebra, dorsal, ventral, anterior, left-lateral and posterior views. Scale bars: 2 mm.

with a centrum length (CL) smaller than 5 mm (Table 1). Only few trunk vertebrae of *Malpolon monspessulanus* (Hermann, 1804) and *Rhinechis scalaris* (Schinz, 1822) seem to indicate the presence of adult or sub-adult specimens in the site. A biometrical study of ACB-3 fossil material (Table 3; Fig. 9) has been done in

order to attempt to separate trunk vertebrae of an adult snake such as *Coronella girondica* from those of juvenile snakes belonging to *Hemorrhois hippocrepis* (Linnaeus, 1758), *Rh. scalaris* and *M. monspessulanus*. Among the material, only 152 vertebrae have only been referred to a "colubrine" indeterminated. Genus Coronella Laurenti, 1768

Coronella girondica (Daudin, 1803) (Figs 6F, G; 7A-E)

MATERIAL EXAMINED. — 1 supraoccipital, 1 left exoccipital and 87 trunk vertebrae.

DESCRIPTION

The supraoccipital is pentagon-shaped, wider than long, short, with a posteriorly directed process. The supraoccipital area shows a convex dorsal surface which is more or less equal in size to the posterior area. On the fossil bone, the supraoccipital foramina are not visible, probably concealed by the sediment. This bone seems to show a relatively variable morphology and ornamentation, nevertheless the pronounced concavity of the anterior edge easily differentiates it from N. natrix, N. maura, Rh. scalaris and Hemorrhois hippocrepis. On the other hand, the strong development of the posterior and supraoccipital areas permits to differentiate it from *M. monspessulanus*, in which the supraoccipital area is well developed contrary to the posterior area, and from the genus Vipera Laurenti, 1768 in which, on the contrary, the posterior area is the most developed one and the supraoccipital one is almost absent. Among the available comparison material, the fossil, by its concavity, its anterior margin morphology and the relative development of its posterior and supraoccipital areas, well compares with the genus Coronella. The weak development of the sagittal and occipital crests permits to cautiously attribute it to C. girondica, which possesses less developed crests than C. austriaca Laurenti, 1768.

In lateral view, the exoccipital possesses an anterior edge with a deep and wide otic incisure. The *protuberantia postoccipitalis* is slightly marked and the moderately strong parotic process (postoccipital process) points in a postero-dorsal direction. In dorsal view, the occipital crest is well developed and extends as far as the supraoccipital. The fossil bone differs from that of *H. hippocrepis*, *Rh. scalaris* and *Vipera* by its deep and wide otic incisure and from *Natrix* and *Malpolon* by the ventrally shorter extension of the occipital crest, by a relatively long dorsal contact area between the two exoccipitals, by an exoccipital condyle relatively small, and by the postoccipital foramen position and size. The overall morphology may correspond to a representative of *Coronella*.

In the light of biometrical results obtained from modern specimens (Blain 2005), trunk vertebrae of *C. girondica* differ from juveniles of *H. hippocrepis*, Rh. scalaris and, in a lesser degree, of M. monspessulanus by a pronounced precondylar constriction (CNW/NAW and CNW/CL; Fig. 9). However, some adult trunk vertebrae of Rh. scalaris or M. monspessulanus may have such low CNW/NAW and CNW/CL ratios, but their size (CL > 5mm) and their morphology permit to distinguish them from the genus Coronella. Trunk vertebrae in the genus Coronella ever have a relatively small size (CL < 3mm) and, morphologically, the neural arch is dorso-ventrally flattened (Szyndlar 1984; Bailon 1991). Attribution to C. girondica does rest on the morphology of the proximal portion of the prezygapophysis (slender in C. girondica than in *C. austriaca*) and the relative size of parapophysis in relation to diapophysis according to Szyndlar (1984).

CHOROLOGICAL DATA

The southern smooth snake (*C. girondica*) is an ubiquitous species, occurring in the whole Iberian Peninsula. It is a thermophilous ophidian, typical of plateau and medium mountains areas (Santos & Pleguezuelos 1997; Galán 1997). It lives in various biotopes, with a preference for wooded areas and low and medium brushwood. In the Community of Valencia, it is reputed common and it ranges from the sea level to the highest summits, with a strong representation in North-East high-lying areas (Alt Maestrat, Castellón) (Vento *et al.* 1991; Lacomba & Sancho 1999; Jiménez *et al.* 2002).

Genus Rhinechis Michaelles, 1833

Rhinechis scalaris (Schinz, 1822) (Figs 6H, I; 7F-J)

MATERIAL EXAMINED. — 1 right articular *s.l.* and 30 trunk vertebrae.



Fig. 8. – A-E, Malpolon monspessulanus (Hermann, 1804), trunk vertebra, dorsal, ventral, anterior, left-lateral and posterior views; F-J, Vipera latasti Boscá, 1878, trunk vertebra, dorsal, ventral, anterior, left-lateral and posterior views. Scale bars: 2 mm.

DESCRIPTION

The fragmentary articular *s.l.* corresponds to the posterior part of this element; it lacks the lingual and coronoid processes. In lateral view, the supraangular crest is present and the retroarticular

process is strongly-built, not very long and has a rectangular-shaped posterior end. The morphology of the retroarticular process permits to distinguish the fossil from *Vipera*, *Natrix* and *H. hippocrepis*, in which the retroarticular process is quite long,

slender, with a round or oval-shaped posterior end, and from *M. monspessulanus* in which, on the contrary, the retroarticular process is very short, robust, and shows a typically L-shaped posterior end. In the comparison material, only *Rh. scalaris* and the genus *Coronella* possess a short, robust and rectangular retroarticular process. Attribution to *Rh. scalaris* essentially rests on the size and the angle between the retroarticular process and the articular *s.l.* main axis which seems smaller in *Rh. scalaris* than in *Coronella*.

The trunk vertebrae of Rh. scalaris differ from those of H. hippocrepis and particularly of M. monspes*sulanus* by a shorter centrum (CL/NAW < 1.16). Morphologically, the trunk vertebrae of Rh. scalaris and H. hippocrepis are very similar, but the biometrical results show that Rh. scalaris possesses a neural arch constriction slightly wider, in dorsal view, with regard to prezygapophyseal and postzygapophyseal (PR-PR/NAW and PO-PO/NAW; Fig. 9) widths. In the fossil material, these two ratios are low with regard to those in the few recent studied specimens of *Rh. scalaris*, but this may probably be due to a larger variability. Finally, the prezygapophyseal process, unfortunately rarely preserved on fossil vertebrae, seems to be larger in Rh. scalaris and slender in H. hippocrepis.

Genus Malpolon Fitzinger, 1826

Malpolon monspessulanus (Hermann, 1804) (Fig. 8A-E)

MATERIAL EXAMINED. — 6 trunk vertebrae.

DESCRIPTION

The trunk vertebrae of *M. monspessulanus* possess some distinctive characteristics that distinguish them from those of other species: in dorsal view, the morphology of the neural arch wings seems to be more elongated (PR-PR/PR-PO < 1.15) as well as the centrum in ventral view (CL/NAW > 1.3; Fig. 9). Morphologically, the angle between the main axis of the prezygapophysis articular surfaces seems to be wider in *C. girondica* and *Rh. scalaris* than in *H. hippocrepis* and *M. monspessulanus*. Moreover the haemal keel seems to be relatively slim in all its length with lateral edges well defined in *M. monspessulanus* and *H. hippocrepis*, whereas in *C. girondica* and *Rh. scalaris* the haemal keel is wider with indistinct lateral edges, and it is sometimes slightly spatulated in *Rh. scalaris* (Bailon 1986; Barrosso Ruiz & Bailon 2003).

CHOROLOGICAL DATA

The ladder snake (Rh. scalaris) and the Montpellier snake (M. monspessulanus) have a large and homogeneous distribution in the Iberian Peninsula (Pleguezuelos & Honrubia 1997; Carmen Blázquez 1997). In the Community of Valencia, these two species are reputed abundant, and they preferentially live in dry or occasionally mountainous moist areas, avoiding steppic areas without vegetation (Vento et al. 1991). Even if Rh. scalaris is relatively well represented, it does not seem to be locally abundant, living with M. monspessulanus, they can compete for same ecological niche occupation (Lacomba & Sancho 1999). These two species occur in the thermo-, meso- and supramediterranean bioclimatic levels (Pleguezuelos 1997a, b), although they are more abundant inland in the mesomediterranean level (Sierra of Espadà, Els Ports, Fredes and Cabanes: Castellón) than in the coastal area (Vento et al. 1991).

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

> > Vipera latasti Boscá, 1878 (Fig. 8F-J)

MATERIAL EXAMINED. — 7 trunk vertebrae.

DESCRIPTION

The trunk vertebrae show typical characters of the family: presence of a straight hypapophysis, a posteriorly depressed neural arch, a ventrally convex cross section of the centrum with indistinct lateral margins, a large condyle and cotyle, and zygapophyseal articular surfaces inclined above the horizontal. No major morphological difference can be seen between the trunk vertebrae of Almenara-Casablanca-3 and those of *V. latasti*, the only recent



FIG. 9. — Measurements of "colubrine" trunk vertebrae (from Szyndlar 1984; modified), and comparison of biometrical ratios between the Almenara-Casablanca-3 material (in black) and modern specimens (in grey) for *Coronella girondica* (Cg), *Hemorrhois hippocrepis* (Hh), *Rhinechis scalaris* (Rs) and *Malpolon monspessulanus* (Mm). Abbreviations: **CL**, centrum length; **CNW**, condyle neck width; **NAW**, centrum width; **PO-PO**, width between the outer edges of postzygapophyseal articular surface; **PR-PO**, length from the anterior edge of prezygapophyseal articular surface to the posterior edge of postzygapophyseal articular surface; **PR-PR**, width between the outer edges of prezygapophyseal articular surfaces. Data on recent specimens from Blain (2005).

representative of the family in the South-Eastern half of the Iberian Peninsula.

CHOROLOGICAL DATA

Lataste's Western nose-horned viper (V. latasti) is a discontinuously distributed Iberian and North African species that occurs principally in mountainous areas, in the meso- to oromediterranean bioclimatic levels (Pleguezuelos & Santos 1997). Common in the Community of Valencia, it preferentially lives in deteriorated scrubs and mountainous dry areas, showing special affinity for highest opened areas, like the "canchales" (places covered with stones), with few bushes where it finds refuge (Lacomba & Sancho 1999; Jiménez et al. 2002). Its most important nuclei occur in Els Ports de Morella, Penyagolosa and Alto Palancia (Castellón), but populations even exist near the littoral (Benicassim, Castellón) and in rather flat regions (Serra, Valencia) (Vento et al. 1991).

TAPHONOMIC DATA

From a taphonomic point of view, the assemblage is not homogeneous. Anuran remains seem to result from a pellet accumulation. The lack of strong intensity digestion marks, like those made by carnivores, on anuran bony remains suggests an accumulation due most probably to nocturnal birds of prey, whose gastric juices action on bones is relatively smooth (Fernández-Jalvo 1995; Pinto Llona & Andrews 1999). Among anuran identified species, representatives of genera such as *Discoglossus*, *Pelobates, Pelodytes* and *Pelophylax* are commonly predated by birds of prey (see for example Rey *et al.* 1994).

As indicated above, lacertid and snake bones do not bear any digestion marks and are the most abundant (97.1% of the total) with all skeleton parts represented. The hypothesis of a natural origin (especially for reptiles of rocky affinities) seems to be more probable, animals being dead *in situ* during their movements or during wintering.

Such considerations suggest that for quantitative palaeoclimatic and palaeoenvironmental interpretations, the "over-representation" of small lacertids with regard to other groups bias the interpretation of temperature and humidity factors as far as landscape reconstruction is concerned. In this case, only qualitative palaeoclimatic and palaeoenvironmental interpretations seem to be significant.

PALAEOBIOGEOGRAPHICAL DATA

ACB-3 documents the presence of a few taxa near the Mediterranean seashore at the end of the early Pleistocene. Recently a study has shown that this period (1 Ma) may have been the coolest for Spain during the early Pleistocene (Blain 2005).

Among the species represented in the site, only one shows a slightly different distribution than at present. As indicated above, the present distribution of the genus Discoglossus does not include the studied area. The recent representatives of this genus show a western, relatively fragmented and continental distribution inside the Iberian Peninsula (García-París 1997; Martínez-Solano & García-París 2002). During Pleistocene times, the genus seems to show a relatively great abundance in some South Iberian early Pleistocene localities (Bailon 1991; Blain 2005). Its presence on the Iberolevantine littoral may probably be due to moister and cooler climatic conditions, by the early-middle Pleistocene boundary than the present conditions.

In Spain, up to now, the western spadefoot (*P. cultripes*) was known only from the middle Pleistocene of Ambrona, Aridos 1 and Arriaga even if its presence seems to be demonstrated since the Miocene (Sanchiz 1998). Recently, some remains of *P. cultripes* have been described from the Lower Pleistocene (MmQ3) from Barranco León 5 and Fuente Nueva 3 (Blain 2003, 2005) with an age slightly older than Almenara-Casablanca-3.

Similarly the common parsley frog (*P. punctatus*) is known with certainty since the middle Pleistocene, even if its presence seems to be documented since the upper Pliocene from Sète (Bailon 1991; Sanchiz 1998) and Montoussé 5 in France (Clot *et al.* 1976a, b; Sanchiz 1998).



FIG. 10. — Percentages of the amphibians and squamate reptiles from Almenara-Casablanca-3 grouped together by climatic and environmental affinities. We have considered here some typical Mediterranean species suggesting "warm" climatic conditions (*Blanus cinereus* and *Chalcides bedriagai*), high-lying areas species suggesting "fresher" climatic conditions (cf. *Discoglossus*, *Bufo bufo*, *Na-trix natrix*, *Vipera latasti*), some aquatic or water edges species (cf. *Discoglossus* and *Pelophylax perezi*), species suggesting a some environmental humidity (cf. *Discoglossus*, *Pelodytes punctatus*, *B. bufo*, *B. cinereus*, *Ch. bedriagai*, *N. natrix*), species suggesting a dry (small lacertids, *Rhinechis scalaris*, *Malpolon monspessulanus* and *V. latasti*) or arid environment (*Pelobates cultripes*), species suggesting a more open landscape (cf. *Discoglossus*, *P. punctatus*, *B. bufo*, *B. cinereus*, *Ch. bedriagai* and *N. natrix*) and finally species suggesting a more open landscape (*P. cultripes* and *V. latasti*).

Until now, few mentions have been given of the presence of the genus *Chalcides* in the Spanish fossil record: the genus is known in the Plio-Pleistocene from Guadix-Baza (Granada; Barbadillo 1989) and from Barranco León 5, Fuente Nueva 3 and Cueva Victoria (early Pleistocene in age; Blain 2005) and Almenara-Casablanca-1 and Vallirana (late Pliocene; Blain 2005).

The other taxa are known at least since the Pliocene (Bailon 1991; Sanchiz 1998; Blain 2005).

PALAEOENVIRONMENTAL AND PALAEOCLIMATIC DATA

RECENT CLIMATIC DATA

The climate in Valencian territory is typically Mediterranean (Western Mediterranean subregion, Mediterraneo-Iberolevantine superprovince), with a dry period coinciding with summer. The particular topography of Valencian area, that is compressed between the sea and considerable altitude mountains, as well as its disposition, make that differences between parts of the area clearly occur within the Mediterranean general tendency. Autumn and to a lesser degree spring are rainy periods, which give intensive and lasting rains, especially on the half north area (Font-Tullot 2000). Spring temperatures increase on the coast, from 12-13°C in March to 16-18°C in May (Font-Tullot 2000). Temperatures increase in July and August up to 26-29°C with a minimum of 20-21°C. Sporadically but significantly, the Ponant wind which sometimes blows during the summer, causes a blazing effect with temperatures up to 40°C, and humidity rate relatively very low from 20 to 25% (Costa 1987).

All of these climatic conditions make that in the Valencian territory, practically all the bioclimatic levels are present (Rivas-Martinez 1986, 1988; Costa 1987). The mesomediterranean bioclimatic level shows the largest extent, between the thermomediterranean bioclimatic level which occurs as a narrow strip along the coast, and the supramediterranean bioclimatic level, well represented in the North in the Maestrazgo Mountains (Castellón). The oromediterranean bioclimatic level occurs punctually, but is present in Penyagolosa (Castellón) and in Rincón de Ademuz (Valencia). The crioromediterranean bioclimatic level may occur topographically in a few points of the highest mountains.

At present, the Almenara area is situated in the thermomediterranean bioclimatic level and has a mediterranean subarid, warm climate, with dry summers (Rivas-Martinez 1982, 1986, 1988). Physically, it is a coastal area in sedimentation, consisting of a sandy bar beyond which occurs a swampy depression with halophilic and freshwaters vegetal communities. Inland, the landscape comprises elm groves, presently reduced to few isolated elm (*Ulmus minor*) or replaced with fruit farming (Costa *et al.* 1986).

PALAEOCLIMATIC INTERPRETATION

At first sight (Fig. 10), the palaeoherpetofaunal assemblage suggests a temperate, dry and open environment favourable to most of the thermophilic small lacertids and snakes, anurans being very poorly represented (2.9% of the total). Even if the taphonomic study suggests that reptilian remains (especially lacertids) are over-represented, such local warm and dry conditions may certainly have occurred in the vicinity of the site.

From a qualitative point of view, the palaeoherpetofaunal assemblage seems to reveal a climate slightly cooler and more humid (subhumid mesomediterranean) than the present one on Castellón seashore (dry thermomediterranean), with presence of strictly Mediterranean thermophilic species and with species living in, or close to water. Argumentation is principally based on two points:

- the presence of taxa that principally occur at present in the area, in meso- to supramediterranean environment (*Discoglossus* sp., *P. punctatus*, *C. girondica*, *Rh. scalaris*, *M. monspessulanus* and *V. latasti*);

- the absence (subject to taphonomic bias) of typically thermomediterranean species like the gekkonids for example, as well as the absence of any reputed ubiquitous species, frequent today in the region, as for example the natterjack toad (*B. calamita* (Laurenti, 1768)), the ocellated lizard (*Lacerta* (*Timon*) *lepida* Daudin, 1802), the viperine snake (*N. maura* (Linnaeus, 1758)) and the common mid-wife toad (*Alytes obstetricans* (Laurenti, 1768)).

Intersection of the recent distributions of species occurring in the locality may indicate potential climatic conditions (Blain 2005; Martínez Solano & Sanchiz 2005). If we superimpose the recent distribution area of each species or taxon occurring in the fissure filling of Almenara-Casablanca-3, we obtain a set of nine squares UTM of 10 × 10 km, as represented in Figure 11. Such an intersection for Almenara-Casablanca-3 suggests annual mean temperatures lower than at present ($T_{ACB-3} = 14.9$ \pm 3.6°C, minimum = 8°C, maximum = 18.5°C; presently upper than 16°C: 17.1°C in the meteorological station of Castellón and 16.9-17.5°C in Valencia, recent data from Font Tullot 2000) and annual mean precipitation higher than at present $(P_{ACB-3} = 683 \pm 125 \text{ mm}, \text{min.} = 500 \text{ mm}, \text{max.} =$ 1000 mm; presently lower than 500 mm: 426 mm in the meteorological station of Castellón and 476-464 mm in Valencia, recent data from Font Tullot 2000). Mean temperature for the month of January for Almenara-Casablanca-3 is equal to 7.33 ± 3.99° C (max. = 12° C and min. = 0° C; at present 10.6°C in the meteorological station of Castellón and 10.2-11.4°C in Valencia, recent data from Font Tullot 2000) and for the month of July it is equal to 23.9 \pm 2.31°C (max. = 28°C and min. = 19°C; at present 24.3°C in the meteorological station of Castellón and 24.6°C in Valencia, recent data from Font Tullot 2000). Such climatic conditions near the seashore may be indicative of a shift toward the south or the east of the thermomediterranean bioclimatic level during the early Pleistocene and probably its disappearance along the coast of Castellón.

Such results are consistent with those obtained for Cal Guardiola (Barcelona, Spain) and Cueva Victoria (Murcia, Spain), of similar age, whose herpetofaunal remains suggest cooler mean annual temperatures (at least 1°C less in comparison with present) and slightly higher mean annual precipitation (Blain 2005).

PALAEOENVIRONMENTAL INTERPRETATION

The taphonomic study has suggested that fossil remains are coming from two main sources. The first one, by natural death may be relevant to the close environment of the site, whereas the second, by bird of prey consumption, may be relevant to a larger scale landscape probably equal to the range of an avian predator (probably a few km²).

The close vicinity of ACB-3 may have been a relatively open and sunny area, composed for a great part of rocky and scrubby biotopes. Such a type of landscape, in which the light come right to the ground was very favourable to most of lacertids and "colubrine" snakes found in the deposit, which lived preferentially on dry and warm soils. At larger scale, the landscape may have been dominated by an open Mediterranean forest. Owing to the areas less exposed to sunlight, vegetal cover as well as humidity may have been more important, thus representing predisposing factors for the presence of the Mediterranean worm lizard (B. cinereus), the Bedriaga's skinks (Ch. bedriagai) and of the Southern smooth snake (C. girondica) which primarily live in the meadows and forest glades moist soils. Presence of aquatic species such as the Southern marsh frog (*P. perezi*) or the genus *Discoglossus* strongly suggests the proximity of sunny water points with loose or sandy shores favourable to burrowing species like



FIG. 11. — Map of the Iberian Peninsula with indication of the squares UTM of 10×10 km where presently occur together all the species and taxa represented in the fissure filling of Almenara-Casablanca-3 (**m**). Square pattern corresponds to the UTM network (100×100 km). Data on recent distributions from Plegue-zuelos *et al.* 2002.

the Western spadefoot (*P. cultripes*), the common parsley frog (*P. punctatus*), the common European toad (*B. bufo*) and the Mediterranean worm lizard (*B. cinereus*).

CONCLUSION

The latest early Pleistocene karstic fissure filling of Almenara-Casablanca-3 has produced the following fauna of anurans and squamate reptiles: cf. *Discoglossus* (Alytidae), *Pelobates cultripes* (Pelobatidae), *Pelodytes* cf. *P. punctatus* (Pelodytidae), *Bufo bufo* (Bufonidae), *Pelophylax* cf. *P. perezi* (Ranidae), *Blanus cinereus* (Blanidae), *Chalcides* cf. *Ch. bedriagai* (Scincidae), small lacertids (Lacertidae), *Natrix natrix, Coronella girondica, Rhinechis scalaris* and *Malpolon monspessulanus* (Colubridae) and *Vipera latasti* (Viperidae).

Such an assemblage documents the evolution of the assemblages of amphibians and squamate reptiles as well as the evolution of climatic and environmental conditions along the Mediterranean seashore prior to the beginning of the middle Pleistocene.

The presence of *Discoglossus* demonstrates a larger distribution of this genus during the early Pleistocene, reaching the present seashore to the East.

Palaeoclimatic and paleoenvironmental reconstruction emphasises cooler and slightly moister climatic conditions than the present ones, which is consistent with the reconstruction of the environments of other sites of the same age, such as Cal Guardiola (Barcelona; Blain 2005) and Cueva Victoria (Murcia; Blain 2005). The landscape may have been a Mediterranean type open forest environment, with some free water points and moist areas of relatively denser vegetation.

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