

Osteology of the Pyrenean Mountain Lizards and comparison with other species of the collective genus *Archaeolacerta* MERTENS, 1921 s. l. from Europe and Asia Minor (Squamata: Sauria: Lacertidae)

Osteologie der Pyrenäen-Gebirgseidechsen und Vergleich mit anderen Arten der
Sammelgattung *Archaeolacerta* MERTENS, 1921 s. l. aus Europa und Kleinasien
(Squamata: Sauria: Lacertidae)

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KURZFASSUNG

Die Pyrenäenarten von *Archaeolacerta* s. l. (*A. aranica*, *A. aurelioi* und *A. bonnali*) unterscheiden sich von den übrigen Arten der Eurasiatischen Radiationslinie (sensu MAYER & BENYR 1994) durch den Besitz knöcherner Rippen im Bereich des dritten Präsakralwirbels. Die drei Pyrenäenarten zeigen in der Morphologie von Postorbitale und Postfrontale jeweils osteologische Verschiedenheiten, die Artniveau erreichen und ihre zweifelsfreie Unterscheidung erlauben. Auch finden sich Unterscheidungsmerkmale im Schultergürtel (Klavikel und Sternalfontanelle).

Apomorphe Merkmale innerhalb der kaukasischen '*Lacerta*' *saxicola* - Gruppe stellen deutliche Unterschiede sowohl gegenüber den *Archaeolacerta* Europas (fast immer ein zusätzlicher Präsakralwirbel) als auch gegenüber *Apathya* (ein zusätzlicher Präsakralwirbel und eine verminderte Anzahl von Prämaxillarzähnen) dar. '*L. chlorogaster*' unterscheidet sich von den übrigen kaukasischen Formen klar durch die Zahl der Prämaxillarzähne und Form der Interklavikel. Die parthenogenetischen Taxa zeigen deutliche Ähnlichkeiten (Modalwerte der Wirbelzahl, Morphologie des Postorbitale) zu ihren Elternarten, besonders zur weiblichen Elternart.

Aufgrund der osteologischen Befunde wird deutlich, daß die europäischen, vorläufig in der Sammelgattung *Archaeolacerta* s. l. vereinigten Taxa keine natürliche Einheit darstellen. Die Formen der Pyrenäen und des Kaukasus erscheinen osteologisch deutlich differenziert, während die iberischen, balkanischen und tyrrhenischen Taxa in den untersuchten Strukturen nur symplesiomorphe Merkmalsausprägungen gemeinsam haben, die keine Aussagen über ihre Verwandtschaft ermöglichen.

ABSTRACT

The Pyrenean species of *Archaeolacerta* s. l. (*A. aranica*, *A. aurelioi* and *A. bonnali*) are different from the other species of the Eurasian radiation (sensu MAYER & BENYR 1994) by the possession of bony ribs associated with the third presacral vertebra. The three Pyrenean species can be unequivocally distinguished at a species level by the morphology of the postorbital and postfrontal bones. Other distinctive character states are found in the pectoral girdle (clavicle and sternal fontanelle).

In their apomorphic characters, the Caucasian taxa of the '*L.*' *saxicola* group present clear differences when compared to the *Archaeolacerta* of Europe (almost always an extra presacral vertebra) and to *Apathya* (an extra presacral vertebra and a minor number of premaxillary teeth). '*L. chlorogaster*' appears clearly differentiated from the other taxa of the Caucasian group by the number of premaxillary teeth and shape of interclavicle. The parthenogenetic forms present characteristic features (modal numbers of vertebrae, postorbital bone morphology) of their original parental species, the female parental species in particular.

In view of the osteological results, it becomes evident that the European species currently assigned to the collective genus *Archaeolacerta* s. l. do not constitute a natural cluster. The Pyrenean and Caucasian species are osteologically clearly differentiated while among the structures studied in the Iberian, Balcanic and Tyrrhenian taxa only symplesiomorphic character states were found which do not permit conclusions on their relationship.

KEY WORDS

Squamata: Sauria: Lacertidae; *Archaeolacerta*, *A. aranica*, *A. aurelioi*, *A. bonnali*, *A. monticola*, *A. cyreni*, *Lacerta*, Pyrenees, Iberian Peninsula, Europe, Caucasus, Asia Minor, osteology, phylogeny.

INTRODUCTION

Bibliography on lacertid osteology is scarce when compared to the number of osteological papers dedicated to other rep-

tile families of similar or even smaller range (BARBADILLO & SANZ 1983). Apart from classic works on general osteology of

the reptiles (e.g. CAMP 1923; ROMER 1956), comparatively little attention has been devoted to lacertid osteological variation of taxonomic relevance.

Standard reference publication for lacertid skull morphology is the detailed work by MÉHELY (1909) which pays special attention to the form of the postorbital and postfrontal region and the number of premaxillary, maxillary, and dentary teeth. KLEMMER'S (1957) paper highlights sexual dimorphism in the development of the skull osteoderms (crusta calcarea) and describes different degrees of platycephaly found in the various species as a function of their more or less saxicolous habitat. The outstanding publications of SIEBENROCK (1894), KÜHNE (1913), and HOFFSTETTER & GASC (1969) deal with the vertebral column while the publication of ETHERIDGE (1967) concentrates on the caudal region. More recently, ARNOLD (1973, 1989) reviewed a good number of osteological characters for a multitude of species (many of which find their first and unique osteological reference there). Together with other morphological information he util-

ized these character states for the construction of lacertid phylogenies and for definition and differential diagnosis of some genera. Further references concerning osteological characters were recently published in PÉREZ-MELLADO & al. (1993) and ARRIBAS (1993, 1994, 1996).

In the present paper the author intends to (i) indicate osteological characters of diagnostic relevance for the three Pyrenean species of *Archaeolacerta* s. l. (= *Archaeolacertae*); (ii) compare the Pyrenean species with *Archaeolacerta* s. l. species from Spain and Europe concerning the states of their osteological characters; (iii) study Caucasian species of the '*L.*' *saxicola* EVERS-MANN, 1834 group, usually assigned to *Archaeolacerta* (ARNOLD 1973, 1989; DAREVSKY 1967, 1972; MAYER & BENYR 1994) or *Apathya* (BISCHOFF 1991); the present paper submits first osteological data for a number of species; (iv) obtain a sound series of osteological characters for future phylogenetic analyses; (v) evaluate various osteological characters used for the reconstruction of lacertid phylogenies.

MATERIAL AND METHODS

Specimens studied (table 1)

As was done by ARRIBAS (1996), in the present paper the European species studied are provisionally assigned to the genus *Archaeolacerta* in a wide sense. Species of uncertain generic status, like the Caucasian ones are referred to as '*Lacerta*' sens. lat. For generic nomenclature of other taxa of the Eurasian radiation, the proposal of ARNOLD (1973, 1989), updated by MAYER & BISCHOFF (1996) is followed. *Apathya* is treated as a full genus due to its clear morphological differences to the Caucasian species of the '*L.*' *saxicola* group and the other nominal lacertid genera recognized until now. *Lacerta andreanskyi* is still assigned to '*Lacerta*' of unclear taxonomic position although MAYER & BISCHOFF (1996) classified it as belonging to the genus *Teira*.

The following taxa which are clearly different from *Archaeolacerta* s. l. were included in this study for comparison: *Lacerta agilis* LINNAEUS, 1758, *L. bilineata* DAU-

DIN, 1802, *L. schreiberi* BEDRIAGA, 1878, *Zootoca vivipara* (JACQUIN, 1787 (oviparous form)), *Podarcis muralis* (LAURENTI, 1768), *P. hispanica* STEINDACHNER, 1870, *P. bocagei* SEOANE, 1884, *P. pityusensis* BOSCA, 1883, *P. lilfordi* (GÜNTHER, 1874), *Algyroides marchi* VALVERDE, 1958, *Teira dugesii* MILNE-EDWARDS, 1829, '*Lacerta*' *andreanskyi* WERNER, 1929 and *Timon lepidus* (DAUDIN, 1802). *Gallotia galloti* (DUMÉRIL & BIBRON, 1839) and *Psammotrochus algerus* (LINNAEUS, 1758), belonging to the subfamily Gallotiinae MAYER & BENYR, 1994 were used as outgroup taxa in the discussion of the osteological characters.

Methods

X-ray photographs were taken with a Philips Super 100 cp[®] apparatus. Best results were obtained at 40 kV, 4 mA/sec., and 19 milliseconds time of exposure. X-ray photographs were used to study the number of presacral vertebrae without dis-

Table 1: Materials examined. Localities, and numbers of x-rayed and cleared specimens are indicated. (P) - Paratype(s), (p) - parthenogenetic taxon, M - male, F - female.

Tab. 1: Untersuchtes Material. Neben dem Fundort ist die Anzahl röntgenisierter und aufgehellter Exemplare angegeben. (P) - Paratyp(en), (p) - parthenogenetisches Taxon, M - Männchen, F - Weibchen.

Taxon	Locality (Province, Country) / Fundort (Provinz, Land)	X-rayed / röntgen.		cleared / aufgehell	
		M	F	M	F
' <i>A. bonnali</i> (LANTZ, 1927)	Lac Bleu de Bigorre (H. P., F)	6	12	1	3
	Monte Perdido (Huesca, E)	2	3	1	3
	Vall del Clot, Posets (Huesca, E)	-	-	-	1
	Estany de Llauset, Maladeta (Huesca, E)	-	-	1	-
	Gran Encantat, Aiguestortes (Lérida, E)	-	-	-	1
' <i>A. aranica</i> (ARRIBAS, 1993)	Coll de Barrados (Lérida, E)	6	3	2	2 (P)
	Port d'Orlà (Lérida, E)	-	-	1	1 (P)
' <i>A. aurelioi</i> (ARRIBAS, 1994)	Montroig (Lérida, E)	-	-	-	2
	Pica d'Estats (Lérida, E)	6	2	2	3 (P)
' <i>A. m. monticola</i> (BOULENGER, 1905)	Port de Rat (Andorra-Ariège, F)	-	-	-	2
	Estrela (Beira Alta, P)	5	5	3	1
' <i>A. m. cantabrica</i> (MERTENS, 1929)	Incio (Lugo, E)	-	-	1	-
	Somiedo (Asturias, E)	10	10	3	1
	Pto. de Vegarada (Leon, E)	-	-	-	2
	Pto. de las Señales (León, E)	-	-	-	1
	Vega de Enol (Asturias, E)	-	8	-	1
' <i>A. c. cyreni</i> (MÜLLER & HELLMICH, 1937)	Pto. de Navacerrada (Segovia, E)	2	4	1	1
' <i>A. c. castiliana</i> (ARRIBAS, 1996)	Circo de Gredos (Ávila, E)	2	3	3	2 (P)
' <i>A. b. bedriagae</i> (CAMERANO, 1885)	Corsica (F)	1	-	1	-
' <i>A. b. paessleri</i> (MERTENS, 1927)	Monte Limbara (Cerdeña, I)	2	1	-	-
' <i>A. horvathi</i> (MÉHELY, 1904)	Val Dogna (Udine, I)	2	1	1	2
' <i>A. masorensis</i> (KOLOMBATOVIĆ, 1886)	Durmitor Pl. (Montenegro, 'YU')	3	6	1	1
' <i>A. oxycephala</i> (DUMÉRIŁ & BIBRON, 1839)	Nicsic-Trubjela (CR)	1	-	1	-
	Terskol, Mt. Elbrus (Kabardino-Balkariya, RU)	1	-	-	-
' <i>L. alpina</i> DAREVSKY, 1967	Mt. Elbrus (Kabardino-Balkariya, RU)	2	4	1	2
	Mt. Fisht (Krasnodar, RU)	-	-	1	-
' <i>L. armeniaca</i> MÉHELY, 1909 (p)	Arpalich (Armenia)	-	6	-	3
	Gei-Gel lake (Azerbaijan)	-	-	-	1
' <i>L. caucasica</i> MÉHELY, 1909	Khvarshi (Daghestan, RU)	3	2	1	-
	Pereval (Southern Ossetia, RU)	-	-	-	1
	Canyon of the Terek river (Georgia)	-	-	-	1
' <i>L. chlorogaster</i> BOULENGER, 1908	Alexiefska (Azerbaijan)	3	3	1	1
	Guirkansky Zapovednik (Azerbaijan)	3	2	-	-
' <i>L. clarkorum</i> DAREV. & VEDMERIA, 1977	Cankurtaran Gec., Artvin (TR)	1	1	1	-
' <i>L. dahli</i> DAREVSKY, 1957 (p)	Jodieri, circa Tiflis (Georgia)	-	6	-	1
' <i>L. daghestanica</i> DAREVSKY, 1967	Khvarshi (Daghestan, RU)	10	12	-	1
	Tpig (Daghestan, RU)	-	-	1	-
' <i>L. derjugini</i> NIKOLSKY, 1898	Mlashe (Georgia)	2	2	1	1
' <i>L. lindholmi</i> LANTZ & CYRÉN, 1936	Bakhchisarai, Crimea (Ukraine)	1	1	-	1
' <i>L. mixta</i> MÉHELY, 1909	Zekari (Adjaria, Georgia)	-	-	1	1
	Baniskevi (Georgia)	1	1	-	-
' <i>L. parvula adjarica</i> DAREV. & EISELT, 1980	Chihura River (Georgia)	1	1	-	-
	Adskuri (Georgia)	3	3	1	1
' <i>L. portschinskii</i> KESSLER, 1878	Rbmoshuri (Georgia)	3	3	-	1
' <i>L. praticola</i> EVERSOMANN, 1834	Kutorskaya (Krasnodar, RU)	1	4	1	1
' <i>L. r. raddei</i> BOETTGER, 1892	Lichk (Armenia)	3	3	1	1
' <i>L. r. vanensis</i> EISELT, SCHMIDTLER & DAREVSKY, 1993	Bendimahi, Muradiye, Van (TR)	2	1	-	-(P)
	Agin (Armenia)	1	1	-	-
' <i>L. (raddei) nairensis</i> DAREVSKY, 1967	Zurnabad (Azerbaijan)	-	6	-	2
' <i>L. rostombekovi</i> DAREVSKY, 1957 (p)	Khvarshi (Daghestan, RU)	2	2	1	-
' <i>L. rudis chechenica</i> EISELT & DAREV., 1991	Achal-daba (Georgia)	3	3	1	1
' <i>L. rudis obscura</i> LANTZ & CYRÉN, 1936	30 km NW Ercis (limit Van/ Agri, TR)	-	2	-	-(P)
' <i>L. sapphirina</i> SCHMIDTLER, EISELT & DAREVSKY, 1994 (p)	Dagomys, circa Sochi (RU)	5	4	1	-
	Inguri river gorge (Georgia)	-	-	-	1
' <i>L. saxicola brauneri</i> MÉHELY, 1909	Tsomakaberd (Armenia)	-	2	-	1
' <i>L. unisexualis</i> DAREVSKY, 1966 (p)	Mt. Legli (Armenia)	-	-	-	1
' <i>L. v. valentini</i> BOETTGER, 1892	Gukasyan district (Armenia)	-	2	-	-
	Karvansaray (Armenia)	1	1	-	-
' <i>L. v. lantzicyreni</i> DAREV. & EISELT, 1967	Yükari Narlıca, Van (TR)	2	1	-	-
' <i>Apathya cappadocica wolteri</i> (BIRD, 1936)	Kirikan, Amanus Mts. (TR)	1	1	1	-

secting the specimens, as demonstrated by several authors (e. g. ARNOLD 1973).

Most specimens were preserved in 70% ethanol and thereafter cleared by means of potash lye (KOH, 1%). Bones were stained with alizarine red and transferred to glycerine for permanent storage (TAYLOR 1967; DURFORT 1978).

Characters studied

Skull characters: (i) shape of the nasal process of premaxilla, (ii) number of premaxillary teeth, (iii) number of maxillary teeth, (iv) number of dentary teeth, (v) shape of margo ocularis of maxilla ("stepped jugal" sensu ARNOLD 1989), (vi) condition of antero-distal process of the postfrontal, (vii) condition of antero-medial process of

the postorbital, (viii) length ratio of postorbital and postfrontal, (ix) degree of overlap of postorbital and squamosal, (x) condition of postorbital and postfrontal (fused or separated) at birth.

Postcranial characters: (xi) presence of visible (ossified) ribs associated with third presacral vertebra, (xii) shape of ribs associated with sixth presacral vertebra, (xiii) sternal costal formula, (xiv) number of presacral vertebrae, (xv) number of short-ribbed posterior presacral vertebrae, (xvi) expression and shape of sternal fontanelle, (xvii) shape (emarginate or not) of clavicle, (xviii) shape of interclavicle, (xix) comparative lengths of interclavicular branches, (xx) morphology of first preautotomic tail vertebrae (see ARNOLD 1973, 1989).

RESULTS AND DISCUSION

SKULL CHARACTERS

Shape of nasal process of premaxilla

In all Pyrenean species, the nasal process, extending from the premaxillary towards the nasal bones, is of elongate undifferentiated form in that its lateral margins are parallel. In the oldest specimens it sometimes appears spoon-shaped due to increased growth in the distal part above the nasals.

In the other closely related Iberian species, the nasal process can be narrow at its base and arrow-shaped in the apex. This situation is predominant in *A. cyreni*, and also appears frequently in *A. monticola monticola* and some Gallician specimens of *A. monticola cantabrica* (in one studied specimen from Incio, Lugo). Specimens studied from the other parts of the Cantabrian Mountains present undifferentiated and slender nasal processes, equaling the Pyrenean taxa. All other European species of *Archaeolacerta* as well as of the 'L.' *saxicola* group and *Apathya cappadocica* present nasal processes of undifferentiated shape, as the Pyrenean species.

From all other taxa studied, only *Timon lepidus* possesses an arrow-shaped nasal process, while in *Podarcis*, *Teira*, *Algyroides*, *Lacerta* (s. str.), *Zootoca*, *Psammo-*

dromus and *Gallotia* nasal processes are simple and undifferentiated.

The presence of an undifferentiated elongate nasal process shall be considered to be the most primitive condition. It is found in almost all outgroup species, and is the structurally most simple and widespread type in the Eurasian lacertid radiation (sensu MAYER & BENYR 1994).

Number of premaxillary teeth

It is difficult to determine the primitive number of premaxillary teeth per side in Lacertidae. The two most common numbers, 7 and 9, appear more or less mingled among the members of the Eurasian radiation. In the outgroup, both numbers appear (7 in *Gallotia*, 9 in *Psammmodromus*). In *Acanthodactylus*, a member of the African radiation, the usual number is 7, while in *Lacerta* s. str. is 9, and 7 again in *Zootoca*.

The three Pyrenean species usually develop seven premaxillary teeth. In *A. monticola cantabrica*, this number is omnipresent in all Cantabrian specimens studied (however, PÉREZ-MELLADO & al., 1993 indicated 9 and 10 as the number of premaxillary teeth in this species!), while 7 or 8 are typical to *A. monticola monticola*. *Archaeolacerta cyreni* usually presents 8 or 9 premaxillary teeth, rarely 7.

The number of 9 is found in *A. bedriagae* (9) and in *A. mosorensis* (8 or 9), while *A. horvathi* and *A. oxycephala* have 7 each. According to MÉHELY (1909), *A. mosorensis* also possesses 7 teeth, which is in discrepancy to the data of SIEBENROCK (1894), KLEMMER (1957), and of my own. The species of the 'L.' *saxicola* group usually have 7 teeth, rarely 8, except 'L.' *derjugini* (8) and the uncertain 'L.' *chlorogaster* which shows 9 or 10. *Apathya cappadocica* also has 10.

Number of maxillary teeth

In *A. bonnali* there are 15 to 18 teeth in each maxilla ($\bar{x} = 15,7$; $stD = 0,9$, $n = 19$), in *A. aranica* 14 to 17 ($\bar{x} = 15,41$; $stD = 1,18$, $n = 12$) and in *A. aurelioi* 15 to 17 ($\bar{x} = 15,95$; $stD = 0,66$, $n = 20$). Other Iberian species show numbers just slightly superior, as *A. monticola* (15 - 18, $\bar{x} = 16,41$, $n = 26$), or clearly superior, as *A. cyreni* (16 - 20, $\bar{x} = 18,07$, $n = 14$). In the other species, numbers appear rather variable and are usually higher than those found in the Pyrenean taxa.

Number of dentary teeth

The three Pyrenean species display very similar values, which are relatively low within the species studied. *Archaeolacerta bonnali* presents 17 to 21 ($\bar{x} = 19,05$; $stD = 1,20$, $n = 20$). In *A. aranica* they number from 16 to 20 ($\bar{x} = 18,58$; $stD = 1,03$, $n = 12$) and in *A. aurelioi* from 16 to 22 ($\bar{x} = 19,66$, $stD = 1,94$, $n = 18$). The lowest values are found in *A. aranica*, which proportionately has a slightly shorter head and therefore shorter maxilla and dentary.

Other closely related species, as *A. monticola* show slightly higher values (17 - 23, $\bar{x} = 20,53$, $stD = 1,49$, $n = 20$), or clearly superior ones like *A. cyreni* (20 - 24, $\bar{x} = 22,07$, $stD = 1,03$, $n = 16$). The other European species of *Archaeolacerta* also have higher numbers (21 - 23), except *A. horvathi* which is very similar to the Pyrenean species in this respect. The 'L.' *saxicola* group presents variable values: in small species, like 'L.' *derjugini*, 'L.' *dagh-estania* and 'L.' *rostombekovi* (and in the small-headed 'L.' *praticola*) numbers of

teeth are as low as in the Pyrenean species.

Within the Lacertidae there seems to be a clear positive relationship between the final size of the individual and the number of teeth in the dentary. Juveniles and adults of a given species show just small differences in the number of teeth, with higher values in adults (see e. g., ROČEK 1980). According to differences in allometric growth of the male head which is increased in almost all species, taxa can be subdivided into two types: (i) species in which males develop allometrically big heads (with more teeth), and (ii) species in which males develop relatively short or small heads (with fewer teeth). Within closely related species only one type seems to occur, indicating that this feature could be of some phylogenetic significance. However, tooth numbers are not subject to unhindered variation in Lacertidae as one can see in the large *Gallotia simonyi* (STEINDACHNER, 1889) and *T. lepidus*, in which the tooth number does not differ significantly from that found in smaller species. The numbers of premaxillary and maxillary teeth, however, do not seem to be subject to the ontogenetic variation (ROČEK 1980).

Shape of maxillary margo ocularis

The shape of the margo ocularis of the maxilla ("stepped jugal", sensu ARNOLD 1989) has been utilized as one character for the reconstruction of phylogenies. According to ARNOLD (1989), the suture between maxilla and jugal is clearly sinuous ("stepped") in *Lacerta* s. str. and *Podarcis*, and might represent the derived state of the character. However, in the sample of Ibero-balearic *Podarcis*, the above character state is not clearly more pronounced than in the rest of the Lacertidae examined. Therefore I think that the character is of limited value in phylogenetic reconstructions. In *Lacerta* s. str. the stepped route of the suture is clearly visible.

In the three Pyrenean species studied, the suture between maxilla and jugal is rather smoothly stepped, and not very pronounced. The same situation is found in all species of *Archaeolacerta* s. l. (European *Archaeolacertae*, 'L.' *saxicola* group and *Apathya cappadocica*), and in the other

lacertid species of the Eurasian radiation studied. Only in *Lacerta* s.str. this suture was strongly angulose.

Antero-distal process of postfrontal (plates 1-4)

This process is present in the majority of the Lacertidae and its lack should be considered a derived character state.

Only *A. aurelioi* lacks this process (in all specimens studied), with the unique exception of an individual from Andorra which is considered an atavistic return to the primitive character state (plate 2). In *A. bonnali*, *A. aranica*, and in all other lacertid species included in this study, this process is present and well developed. Its reduction and disappearance in *A. aurelioi* is an autapomorphy.

Antero-medial process of postorbital (plates 1-4)

The expression of this process is more subject to variation than the previous character. The presence of a well developed antero-medial postorbital process indicates the primitive character state, as is frequently found in all genera studied in which the postfrontal and postorbital are separated from birth on (e. g., most *Lacerta*, *Podarcis*, *Archaeolacerta*). In some species belonging to different phyletic lines, this process is missing or present in reduced form.

Among the Pyrenean species, the antero-medial process of the postorbital appears very well developed in *A. aranica*, while it is absent in both *A. bonnali* and *A. aurelioi*. These observations apply to all Pyrenean specimens studied and permit - in combination with the previous character - the specific distinction of all Pyrenean *Archaeolacertae* from an osteological point of view.

In most other taxa studied here, out-group taxa included, this process is clearly developed, except in some species of the '*L. saxicola* complex. It frequently lacks in '*L. mixta* and '*L. raddei*, which are maternal species of the initial crossings that led to the parthenogenetic '*L. armeniaca* (*L. valentini* M x '*L. mixta* F), '*L. dahli* (*L. portschinskii* M x '*L. mixta* F), '*L. rostrom-*

bekovi (*L. portschinskii* M x '*L. raddei* F) and '*L. unisexualis* (*L. valentini* M x '*L. raddei nairoensis* F) (UZZELL & DAREVSKY 1975; DAREVSKY & DANIELYAN 1977; DAREVSKY & al. 1985, 1986; KUPRIYANOVA 1989; MORITZ & al. 1992). As this process lacks or is extremely reduced in all these parthenogenetic species, there seems to be dominancy or at least strong maternal influence in the heredability of this character. In this respect it could be enlightening to study '*L. uzzelli*, with the same parental species like '*L. unisexualis* but with '*L. valentini* as maternal species.

Lengths of postorbital and postfrontal (plates 1-4)

In general, both bones are more or less subequal in length (primitive character state), although there is some secondary deviation in several species (e.g., in cases of reduced cranial ossification related to saxicolous life).

In the Pyrenean species *A. aurelioi* and *A. aranica*, the postorbital bone sometimes clearly surpasses the posterior end of the postfrontal. This situation should be considered the derived state, while subequal length of the elements as in *A. bonnali* would represent the secondary return to a primitive state.

In the other European *Archaeolacertae*, there are two exceptions from the rule of subequal length: *A. horvathi*, in which the postorbital is notably longer than the postfrontal, and *A. oxycephala*, in which the reverse situation is found.

In the species of the '*L. saxicola* group, however, both bones can be subequal, but there is a marked tendency towards a postorbital which is shorter than the postfrontal (*L. saxicola* ssp., '*L. lindholmi*, '*L. alpina*, '*L. daghestanica*, '*L. raddei*, '*L. parvula*, '*L. mixta*).

Overlap of postorbital and squamosal

Among the species studied, the length of the contact suture between squamosal and postorbital varies from something less than a third to near half of the length of the postorbital. In general, variation is fairly restricted within a species. It therefore

makes sense to indicate whether the length of the contact zone is closer to one half or one third of the length of the postorbital bone. The most frequently found condition is one third of overlap (as is present in the outgroup and is the most common situation in the ingroup), which is therefore considered the primitive character state.

In *A. bonnali* the length of overlap is about 1/3 of the postorbital length (20 % of the specimens approach to 1/2). In *A. aranica*, the overlap is close to 1/2 (100% of the specimens) and in *A. aurelioi* also 1/2 (30% of the specimens approach to 1/3).

Fusion or separation of postorbital and postfrontal

Depending on the species, postfrontal and postorbital are either fused or separated from birth. In species in which these bones are united from birth, they form an entire piece, possible constituents of which remain completely undifferentiable (see e.g. the development of *Z. vivipara* in RIEPPEL 1992). In all outgroup taxa, postorbital and postfrontal appear as a single element, which consequently is considered the primitive character state and the presence of separated bones as the derived one. Nevertheless, ARNOLD (1989) observed that these bones were separated in juveniles and fused in the oldest individuals of some lacertid species. By finding this, he concluded - based on an ontogenetic criterion - that the presence of two individualized bones would represent the primitive state. I think, however, that the secondary fusion mentioned is something different from having a singular bone from birth. In the first case, the suture of the bones is markedly imbricated and interdigitated. This joining process is part of the development of a robust skull (including proliferation of cranial osteoderms - *crusta calcarea*) which leaves both bones still distinguishable (coalescence of the two bones during ontogeny). This process is to be distinguished from the primordial existence of a singular bone.

All three Pyrenean species have separated bones, hatchlings as well as old individuals. A specimen of *A. aranica* presents an aberrant fusion of the bones on one side of the head, while the other side shows them perfectly separated.

All other species of *Archaeolacerta* s. l. display both bones separated, as most of the species of the Eurasian radiation do. Within the Lacertidae, the possession of bones fused from birth is found in the outgroup genera *Gallotia* and *Psammodromus*, but is also present in *Zootoca* and some *Lacerta* s. str. (e.g., *L. schreiberi*).

POSTCRANIAL CHARACTERS

Bony ribs on third presacral vertebra

According to the osteological literature on Lacertidae, the fourth presacral vertebra in the cervical region is the first to bear ribs implying that the third vertebra lacks ribs (e.g., BARBADILLO & SANZ 1983). However, I found that in those species (outgroup species included) qualified as the most primitive lacertids, small bony ribs were associated with the third presacral vertebra. In the more advanced lacertids, these ribs frequently do also exist but are not that apparent because of being reduced to their proximal part and/or not ossified.

Bony ribs associated with the third vertebra were found to be present in *Gallotia*, *Psammodromus*, *Z. vivipara* and *L. agilis*, and in the three Pyrenean *Archaeolacerta* and were found to lack in most genera of the the Eurasian radiation (*Podarcis*, *Teira*, *Algyroides*, *Archaeolacerta* s. l. - except the Pyrenean ones).

Stability of this character state is variable. In *A. aranica*, bony ribs associated with the third vertebra were expressed in 90 % of the specimens examined; in *A. aurelioi* in 70 %, and in *A. bonnali* in somewhat more than 50 %. Hence, their presence is the standard in the Pyrenean *Archaeolacertae* suggesting their close interrelationship as against the other European *Archaeolacertae* s. l.

All other Iberian and European *Archaeolacerta* s. l. as well as the species of the 'L.' *saxicola* group lack bony ribs associated with the third presacral vertebra. Very occasionally I found specimens within these taxa that presented these ribs ossified (one specimen of *A. horvathi* and one of 'L.' *unisexualis*). Both cases should be classified as atavism which was also observed in a few exceptional specimens among other

genera studied (*Podarcis*, *Teira*). In the Pyrenean species, the presence of these bony ribs could be interpreted as a secondary return as well.

Ribs of sixth presacral vertebra

The sixth presacral vertebra is the last short-ribbed vertebra previous to those that bear long ribs the first of which are not linked to the sternal apparatus. In some species (*P. algirus*, *L. agilis*, *Z. vivipara*), the ribs of the sixth vertebra are elongate and relatively undifferentiated (primitive state), while in most Lacertidae (e. g., *Archaeolacerta* s. l., *Podarcis*, *Teira*, 'L.' *saxicola* group, *Algyroides Gallotia*) these ribs are short and spoon-shaped with two small processes extending towards the suprascapula (derived state). Exceptionally, individuals can be found among them (e. g., a specimen of 'L.' *daghestanica*) which approach the primitive state.

Sternal-xiphisternal costal formula

Sternal-xiphisternal costal formula is represented by the term (x+y), where x and y are the numbers of ribs with sternal and xiphisternal contact, respectively. In Lacertidae, three sternal formulae are found: (3+1), (3+2) and (3+3), the second being the most common type. Two formulae can co-occur in one species: e. g., (3+2) [frequently] and (3+1) [more rarely] in *Gallotia* and *Zootoca* (primitive condition) or (3+2) [frequently] and (3+3) [more rarely] in all other taxa studied (derived character state).

In the three Pyrenean species, the formula is (3+2) [(3+3) in one *A. aurelioi* specimen from Montroig Massif]. The other species of *Archaeolacerta* s. l. including the Caucasian species, also present (3+2), rarely (3+3).

Number of presacral vertebrae

The majority of Lacertidae displays sexual dimorphism in the number of presacral vertebrae (primitive condition) while *Gallotia* and some *Acanthodactylus* species do not (derived condition). The modal number of vertebrae is superior in females in that they have one to three vertebrae more than males. According to ARNOLD

(1983), there is a clear although not rigid correlation between number of vertebrae and habitat: high vertebral counts are preferentially found in species colonizing mesic habitats, while low counts are typical to species from more arid, open and less vegetated places. The above author suggests that mesic habitat could require greater inflection of the body in order to move among vegetation and that a greater number of vertebrae facilitates this movement. Therefore, sexual dimorphism in the number of vertebrae would reflect differences between sexes in microhabitat selection, in that the males would spend more time in open areas due to territorial activities. An alternative theory by the same author which is more in accordance with my observations says that extra presacral vertebrae would allow expansion of the body volume in gravid females and, thus, increased clutch volume. However, I think there is an important phylogenetic background reflected by the state of this character in that the number of presacral vertebrae is similar in phylogenetically related species.

In *A. bonnali*, males always present 26, and females 27 presacral vertebrae. The same numbers apply to *A. aranica* and *A. aurelioi*, but in each of the latter two species one female was found to have 28 vertebrae. Males of some European *Archaeolacerta* s. l. (*A. monticola*, *A. cyreni*, *A. bedriagae*, *A. horvathi*) have modal counts of 26 vertebrae, while others frequently show 25 only (*A. mosorensis*, *A. oxycephala*; versus 26 found by ARNOLD 1973 from specimens of other localities). The females are more variable in this respect: 28 vertebrae are frequently encountered in *A. monticola* and *A. cyreni*, while the numbers of 26, 27 and 28 appear in *A. mosorensis*. Female *A. horvathi*, *A. oxycephala* and *A. bedriagae* usually present 27 vertebrae.

In *Podarcis* the number of presacral vertebrae is 26 or 27 in males; in *Algyroides* and *Apathya*, reduction to 25 is not rare in males, whereas all males of the 'L.' *saxicola* group present 27 (except 'L.' *raddei* which has 28). Females usually have one more vertebra than males (very rarely two or even three).

In the males of the outgroup genera (*Gallotia*, *Psammodromus*), 26 vertebrae

were observed. This number is considered to be the plesiomorphic character state, while reduction to 25 as well as increase to 27 or 28 (as found in male '*L.*' *parva* and '*L.*' *fraasi*) are apomorphic character states which evolved independently.

Number of short-ribbed posterior presacral vertebrae

ARNOLD (1989) compares the number of these posterior presacral vertebrae ("number of short free dorsal ribs") with the number of anterior dorsal ribs, and concludes that low numbers indicate the primitive state and high numbers the derived one. (i) both conditions have been found in the outgroup, and (ii) elevated numbers of short vertebrae are widespread in the most advanced species of the African radiation. To my opinion, these facts make it difficult to speculate on the direction of the evolutionary development of this character.

The Pyrenean species usually show six short-ribbed posterior presacral vertebrae in both sexes.

Archaeolacerta bonnali of Bigorre is outstanding in that it presents a constant number of five short-ribbed posterior presacral vertebrae, while the only cleared specimen of Aigüestortes has seven. Both cases refer to relatively isolated populations in which the establishment of accidental variations may be more likely. Most important, the reduction to five short-ribbed vertebrae in the posterior presacral region is not paralleled by the total number of presacral vertebrae, implying that this population is distinguished by one more long dorsal rib. Given that the long ribs are important structures in flattening the body for basking, the genetic fixation of this characteristic in the Bigorre population could constitute an adaptive advantage in thermoregulation for these individuals which live on the northern slope of the Pyrenean mountains. A detailed study of a greater sample including neighboring populations might throw more light on this topic.

All *A. aranica* and *A. aurelioi* specimens studied present 6 short-ribbed posterior presacral vertebrae, with the exception of a young male *aranica* of Port d'Orla which has 5.

In the other *Archaeolacerta* s. l., six is also the common number, e. g. in *A. monticola* and *A. cyreni* (7 in a female of Guadarrama), however, in some individuals of *A. horvathi*, *A. mosorensis* and *A. oxycephala* the number of short-ribbed posterior presacral vertebrae is 5.

Six is the usual count for the Caucasian species of the '*L.*' *saxicola* group; numbers of 5 or 7 occur less frequently. '*L.*' *portschinskii* which is distinguished by 7 short-ribbed posterior presacral vertebrae, is the parental species (with still some doubts) of the parthenogenetic '*L.*' *dahli* and '*L.*' *rostombekovi*, which frequently also present 7.

Expression and shape of sternal fontanelle

The sternal fontanelle is a foramen in the sternal plate, present from birth and found in most lacertids. Its shape can be rounded, more or less oval, slightly or clearly heart-shaped (cordiform, as in *Podarcis*, see ARNOLD, 1973, 1989). Obviously the rounded and oval, ill differentiated and very widespread types, represent the primitive character state, while the cordiform fontanelles are derived (ARNOLD, 1973, 1989). As it is not clear whether the slightly cordiform type represents an intermediate type or a secondary regression to the primitive state, this type is independently treated here, as was done by ARNOLD (1989).

In *A. bonnali* the sternal fontanelle is oval or rounded (cordiform in one specimen from Bigorre) and rounded in all *A. aranica* studied.

Almost 50 % of the *A. aurelioi* specimens (from three different massifs) lack the fontanelle, and 20 % present it reduced to a pair of small foramina, while about 30 % show the typical oval form. This absence or reduction of the fontanelle is supposed to be a secondary loss, as suggested by the fact that there is a continuous series of character states ranging from oval fontanelles through small holes to the absence of perforation. It may be allowed to speculate here, that the cordiform fontanelle could be a transitional stage to partial closing of the fontanelle.

The other European *Archaeolacerta* s. l. studied present oval fontanelles. Spo-

radically, you find individuals of *A. cyreni* and *A. horvathi* with reduced fontanelles. The fontanelle is oval in the 'L.' *saxicola* group, although reduced but still visible in some individuals (as in a specimen of 'L.' *chlorogaster*) or clearly cordiform (as in an individual of 'L.' *derjugini*, 'L.' *armeniaca* and 'L.' *mixta*, and several specimens of 'L.' *alpina*). In general, the other species including the outgroup (but with the exception of *Podarcis*, 'L.' *laevis*, 'L.' *danfordi*, some *A. moreoticus*, *A. marchi* and 'L.' *andreanskyi*) exhibit clearly oval or rounded fontanelles, wherefore this state is considered the most primitive.

Shape of clavicle (plates 5 - 10)

In general, the clavicle of Lacertidae is characterized by the presence of a great foramen in its proximal expanded part. This aperture is bordered by an anterior and a posterior clavicular branch (unmarginated or closed type). In many cases, the posterior branch is incompletely formed (emarginated or open type). Obviously, the closed type seems to be the primitive but in many species one can encounter both types. Several genera and species mainly present the closed condition (*Psammotromus*, *Gallotia*) while others the open type (e. g. *A. bedriagae*, *A. oxycephala*). Some authors (e. g. ARNOLD 1989) consider the presence of both types as the primitive situation and the exclusive presence of one or the other as the derived condition.

All *A. aranica* and *A. bonnali* specimens, except a *bonnali* hatchling from Aigüestortes (the one that has seven small-ribbed posterior presacral vertebrae), show open clavicles, while all *A. aurelioi* but one present closed clavicles. In this discordant specimen (which also has an aberrant postfrontal, plate 2) from Port de Rat (Andorra), the clavicle is open. Both peculiarities can be interpreted as atavisms in this individual.

In the other European species of *Archaeolacerta* s. l., the situation is variable. *Archaeolacerta monticola monticola* presents closed clavicles, while in *A. monticola cantabrica* there are almost twice as much open clavicles than closed (this observation is contrary to the findings of PÉREZ-MEL-

LADO & al. 1993). Clavicles are mainly closed in *A. cyreni*, open in *A. bedriagae*, *A. oxycephala* and *A. mosorensis*, and variable in *A. horvathi*. In the 'L.' *saxicola* group and in *Apathya cappadocica*, both types of clavicles appear blended in almost all species.

Shape of interclavicle (plates 5 - 10)

In all lacertids, the interclavicle is a cross-shaped (cruciform) element. The anterior process is very short in relation to the posterior one, and the lateral extensions are intermediate in length.

In general, the lateral extensions are more or less perpendicular to the antero-posterior axis; occasionally they are somewhat or clearly inclined in anterior or posterior direction. Lateral extensions which are more or less perpendicular represent the primitive character state, as present in the outgroup species and in the majority of the lacertids of the Eurasian radiation. Deviations from this most common state shall be considered as derived and are found in 'L.' *chlorogaster* (clearly directed anteriorly), *A. oxycephala* (moderately directed anteriorly), *T. dugesii*, [and *T. perspicillata* - not studied here] (clearly directed posteriorly), and 'L.' *andreanskyi* (less clearly directed posteriorly - but comp. ARNOLD 1973, 1989).

The three Pyrenean species display the primitive type, without sensible deviations. The same situation is found in all other European *Archaeolacerta* s. l., and the Caucasus and Asia Minor species, with the exception of 'L.' *chlorogaster*. I could not find large lateral processes in the interclavicle of *A. bonnali* (as described by PÉREZ-MELLADO & al. 1993) which is not different from those of the other taxa studied here (comp. plate 5).

Length of anterior and posterior interclavicular process

Proportion of the length of the anterior and posterior interclavicular process varies within and between species. In *Psammotromus algirus* for instance, the anterior process is quite long, attaining almost 50% of the length of the posterior.

Within the Pyrenean species, ratios (anterior/posterior) are 0.21-0.38 ($\bar{x} = 0.29$, StD = 0.54, $n = 6$) in *A. bonnali*, 0.20 - 0.35 ($\bar{x} = 0.26$, StD = 0.53, $n = 6$) in *A. aranica*, and 0.22 - 0.35 ($\bar{x} = 0.29$, StD = 0.39, $n = 9$) in *A. aurelioi*.

In the other *Archaeolacerta* s. l. species and *P. algirus*, ratios range from 0.25 to 0.46 and display great individual variability within populations. The index seems not to be related to the habitat type, since ground dwellers and saxicolous species can have similar values. I therefore hypothesize, that (except in very peculiar cases) the length ratio of the anterior and posterior interclavicular processes is subject to considerable variation and of little use in the study of lacertid phylogeny.

Preautotomic caudal vertebrae

ARNOLD (1973, 1989) distinguished three types of vertebrae in the immediate preautotomic caudal region: Type A shows one pair of perpendicular processes in the anterior part of the vertebra; type B with two pairs of processes, a bigger anterior and a smaller posterior one; type C displays two pairs of processes, a smaller anterior and a bigger posterior one.

Types A and B frequently co-occur and are very widespread among the Lacertidae of the Eurasian radiation, all species of *Archaeolacerta* s. l., *Apathya* included. Type C appears in *Podarcis*, some species from Asia Minor ('*L. danfordi*', '*L. anatolica*') and in the outgroup species *Gallotia* and *Psammodromus*. According to ARNOLD (1989), '*L. parva*', '*L. fraasi*', and '*L. brandtii*' are intermediate between types B and C. Although this author considers

types A and B to represent primitive character states, I think that type C as found in the outgroup taxa and the species of the African radiation (*Acanthodactylus*) should be regarded the primitive state. Nevertheless, homology and direction of evolution of the different types is not clearly understood.

The Pyrenean species *A. bonnali*, *A. aranica* and *A. aurelioi* present type A without exception.

In the other *Archaeolacertae* of the Iberian Peninsula the situation is very similar. *Archaeolacerta monticola*, *A. m. cantabrica*, and *A. cyreni* show type A vertebrae. However, in 30 % of the latter two taxa I encountered additional processes reminiscent of type B (which means that there are vertebrae of intermediate morphology between A and B, with an anterior process in one side and two processes in the other).

In the other European *Archaeolacertae* the situation is very similar. In *A. bedriagae*, and *A. horvathi* I only found type A (but this could be due to the small sample size), while *A. mosorensis*, and *A. oxycephala* present type A vertebrae with a few processes of type B in some individuals.

Apathya cappadocica shows vertebrae of type A, while in the species of the '*L. saxicola*' group, the situation is variable within the above spectrum. Vertebrae of type A (frequently associated with some of type B) are the most common combination. The reverse situation (type B vertebrae with some of type A) is found in '*L. mixta*', '*L. parvula*', '*L. praticola*', and '*L. raddei*'.

CONCLUSIONS

(i) The Pyrenean species of *Archaeolacerta* are unequivocally distinguished from all other species of the Eurasian radiation (sensu MAYER & BENYR 1994) by the possession of bony ribs associated with the third presacral vertebra. This is a plesiomorphic character state within the lacertids, but can be interpreted as a secondary return to the primitive state in this group.

(ii) Within the Pyrenean group, *A. aranica* is characterized by the presence of a well developed antero-distal process of the postfrontal as well as antero-medial process of the postorbital, and by having open (emarginated) clavicles; and oval or rounded sternal fontanelles.

(iii) Within the Pyrenean group, *A. bonnali* is characterized by the possession of the antero-distal process in the postfron-

Legends to plates 1 to 10 Legenden zu den Tafeln 1 bis 10

Plate 1 (opposite page): Dextral postfrontal and postorbital bones in *Archaeolacerta* s. l.
The part of the antero-medial postorbital process covered by the postfrontal is shown in white.

Taf. 1 (gegenüberliegende Seite): Postfrontale und Postorbitale der rechten Seite bei *Archaeolacerta* s. l.
Der vom Postfrontale verdeckte Teil des antero-medialen Postorbitalfortsatzes ist weiß dargestellt.

A. bonnali: BI - Lac Bleu de Bigorre; MP - Monte Perdido; PO - Vall del Clot, Posets; MA - Estany de Llauset, Maladeta. *A. aranica*: BA - Coll de Barradós; OR - Port d'Orlò. *A. aurelioi*: MR - Estany de Calberante, Montroig; PE - Estany de Sotllo, Pica d'Estats; AND - Port de Rat, Andorra-Ariège.

Plate 2 (plate 1 continued, page 60) / Taf. 2 (Taf. 1 fortgesetzt, Seite 60).

A. aurelioi: AND - Port de Rat, Andorra (aberrant morphology, atavism).

A. monticola cantabrica: CAN - Somiedo. *A. monticola monticola*: MON - A Torre, Estrela, Portugal.

A. cyreni castiliana: CAS - Laguna Grande, Gredos. *A. cyreni cyreni*: CYR - Pto. de Navacerrada.

A. horvathi: HOR - Val Dogna, Italy. *A. mosorensis*: MO - Zmisko Jezero, Montenegro.

A. oxycephala: OXY - Nicsic, Croatia. *A. bedriagae bedriagae*: BE - Corsica, France.

Plate 3 (plates 1 & 2 continued, page 61) / Taf. 3 (Taf. 1 & 2 fortgesetzt, Seite 61).

'*L. saxicola darevskii*': DAR - Dagomys, Sochi, Russia. '*L. saxicola brauneri*': BRA - Inguri River, Georgia.

'*L. lindholmi*': LIN - Bakhchisaray, Georgia. '*L. alpina*': ALP - Fisht Mount, Krasnodar, Russia.

'*L. caucasica*': CAU - Pereval, Southern Ossetia. '*L. daghestanica*': DAG - Khvarshi, Daghestan, Russia.

'*L. raddei raddei*': RAD - Lichk, Armenia. '*L. parvula*': PAR - Adskuri, Georgia.

'*L. portschinskii*': POR - Rbemoshuri, Georgia. '*L. mixta*': MIX - Baniskevi, Georgia.

'*L. valentini*': VAL - Legli Mt., Armenia. '*L. rudis chechenica*': CHE - Khvarshi, Daghestan, Russia.

Plate 4 (plates 1 - 3 continued, page 62) / Taf. 4 (Taf. 1 - 3 fortgesetzt, Seite 62).

'*L. rudis obscura*': OBS - Achaldaba, Georgia. '*L. praticola*': PRA - Kutorskaya,

Krasnodar, Russia. '*L. derjugini*': DER - Mlashe, Georgia. '*L. chlorogaster*': CHL - Alexiefeska, Azerbaijan.

'*L. armeniaca*': ARM - Arpalich, Armenia. '*L. dahli*': DAH - Jodieri, Georgia. '*L. rostombekovi*': ROS - Zurnabad,

Azerbaijan. '*L. unisexualis*': UNI - Tsomakaberd, Armenia. '*L. clarkorum*': CLA - Cankurtaran Gec., Turkey.

Plate 5 (page 63): Clavicle and interclavicle in *Archaeolacerta* s.l. The left ventral side of the apparatus is shown.

Taf. 5 (Seite 63): Klavikel und Interklavikel bei *Archaeolacerta* s. l. Linke Seite des Apparates von ventral.

A. bonnali: BI - Lac Bleu de Bigorre; MP - Monte Perdido; PO - Vall del Clot, Posets; MA - Estany de Llauset, Maladeta. *A. aranica*: BA - Coll de Barradós; OR - Port d'Orlò.

Plate 6 (plate 5 continued, page 64) / Taf. 6 (Abb 5 fortgesetzt, Seite 64).

A. monticola cantabrica: CAN - Somiedo. *A. monticola monticola*: MON - A Torre, Estrela, Portugal.

A. cyreni castiliana: CAS - Laguna Grande, Gredos. *A. cyreni cyreni*: CYR - Pto. de Navacerrada.

A. aurelioi: MR - Estany de Calberante, Montroig; PE - Pica d'Estats; AND - Port de Rat, Andorra-Ariège.

Plate 7 (plates 5 & 6 continued, page 65) / Taf. 7 (Taf. 5 & 6 fortgesetzt, Seite 65).

A. bedriagae bedriagae: BE - Corsica, France. *A. oxycephala*: OXY - Nicsic, Croatia.

A. horvathi: HOR - Val Dogna, Italy. *A. mosorensis*: MO - Zmisko Jezero, Montenegro, Yugoslavia.

Plate 8 (plates 5 - 7 continued, page 66) / Taf. 8 (Taf. 5 - 7 fortgesetzt, Seite 66).

Apathya cappadocica wolteri: CAP - Kirikan, Amanus Mts, Turkey. '*L. alpina*': ALP - Fisht Mt., Krasnodar, Russia.

'*L. caucasica*': CAU - Pereval, Southern Ossetia, Russia. '*L. daghestanica*': DAG - Khvarshi, Daghestan, Russia.

'*L. derjugini*': DER - Mlashe, Georgia. '*L. mixta*': MIX - Baniskevi, Georgia. '*L. parvula*': PAR - Adskuri, Georgia.

'*L. portschinskii*': POR - Rbemoshuri, Georgia.

Plate 9 (plates 5 - 8 continued, page 67) / Taf. 9 (Taf. 5 - 8 fortgesetzt, Seite 67).

'*L. praticola*': PRA - Kutorskaya, Krasnodar, Russia. '*L. rudis obscura*': OBS - Achaldaba, Georgia.

'*L. rudis chechenica*': CHE - Khvarshi, Daghestan, Russia. '*L. raddei raddei*': RAD - Lichk, Armenia.

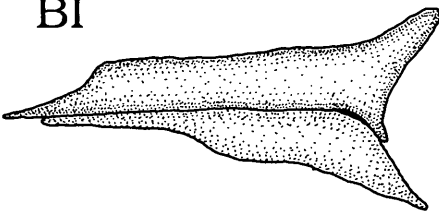
'*L. saxicola darevskii*': DAR - Dagomys, Sochi, Russia. '*L. saxicola brauneri*': BRA - Inguri River, Georgia.

'*L. lindholmi*': LIN - Bakhchisaray, Georgia. '*L. chlorogaster*': CHL - Alexiefeska, Azerbaijan.

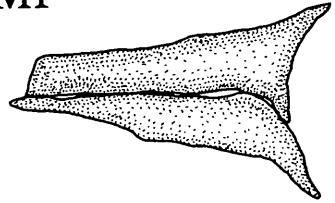
Plate 10 (plates 5 - 9 continued, page 68) / Taf. 10 (Taf. 5 - 9 fortgesetzt, Seite 68).

'*L. armeniaca*': ARM - Arpalich, Armenia. '*L. dahli*': DAH - Jodieri, Georgia. '*L. rostombekovi*': ROS - Zurnabad, Azerbaijan. '*L. unisexualis*': UNI - Tsomakaberd, Armenia. '*L. clarkorum*': CLA - Cankurtaran Gec., Turkey.

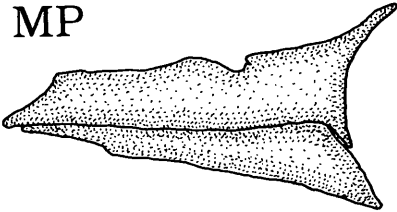
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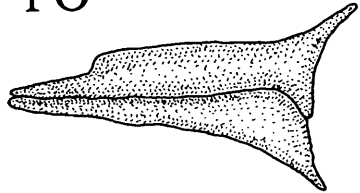
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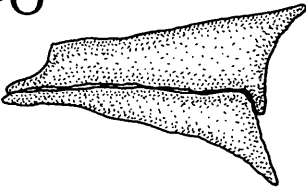
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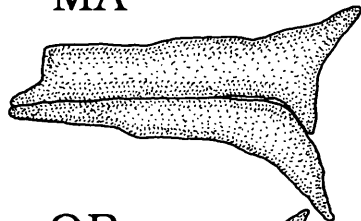
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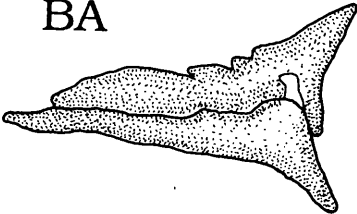
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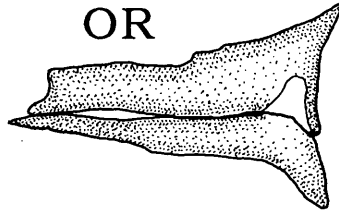
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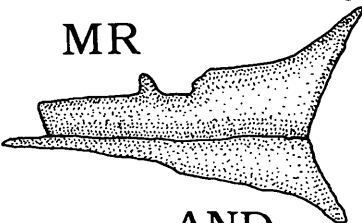
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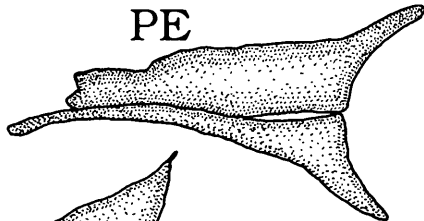
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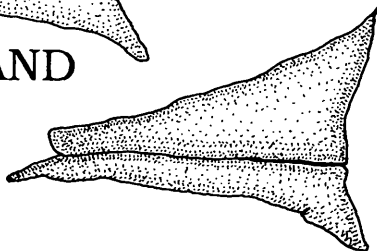
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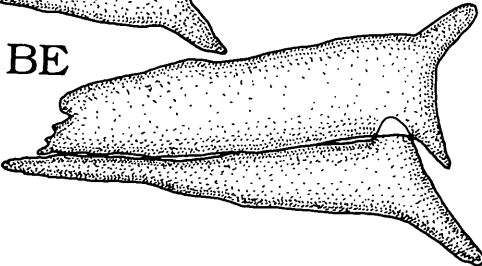
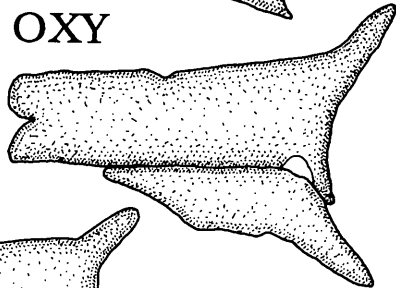
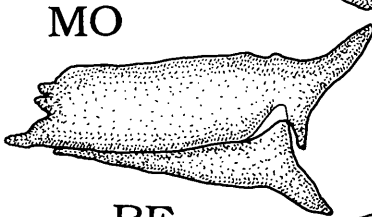
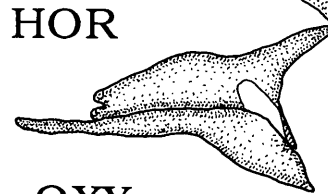
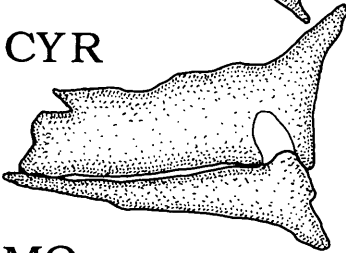
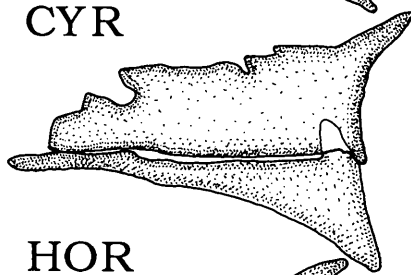
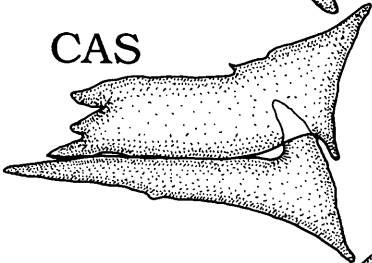
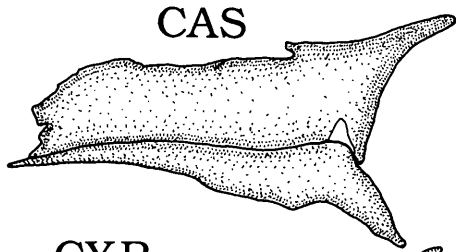
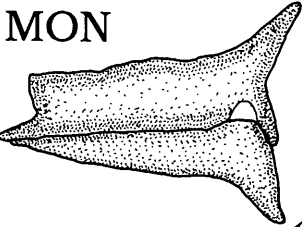
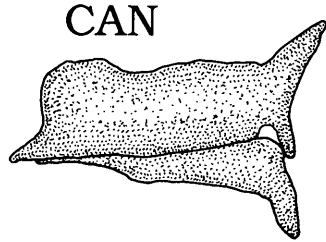
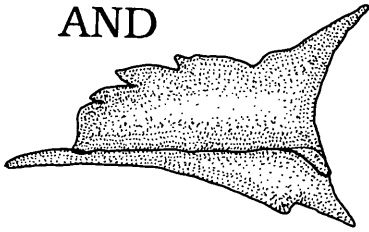


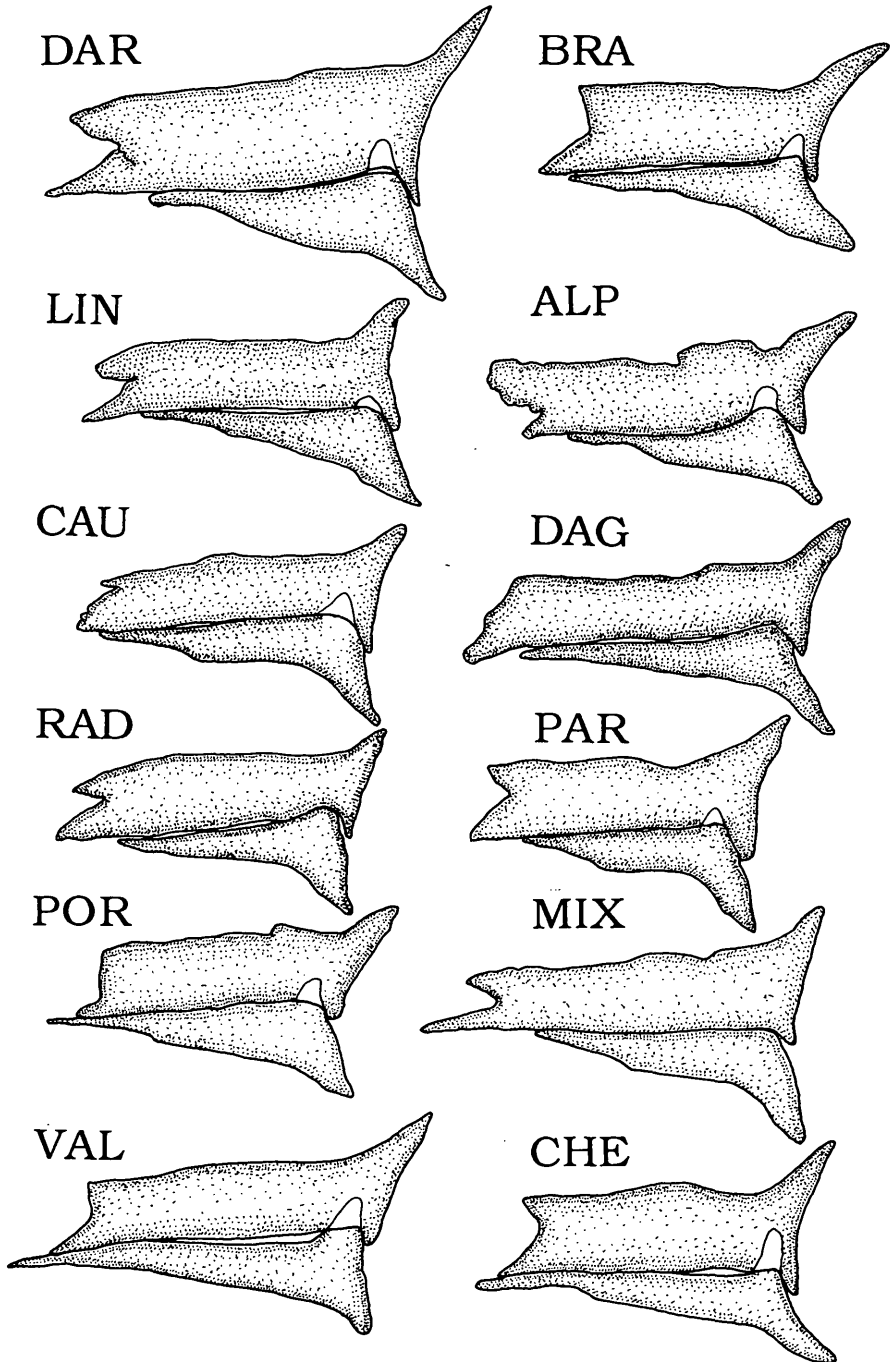
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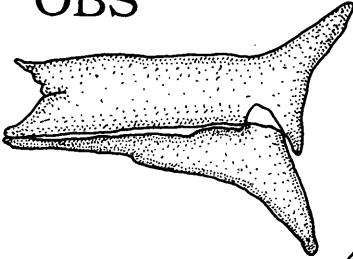
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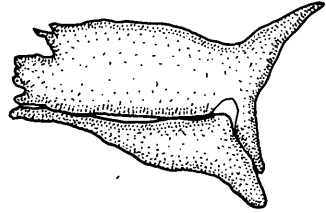




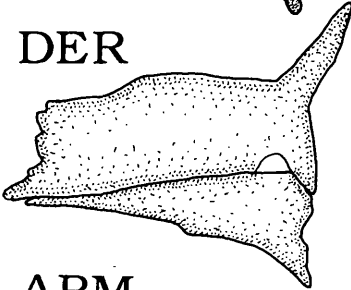
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PRA



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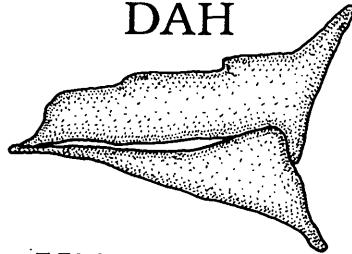
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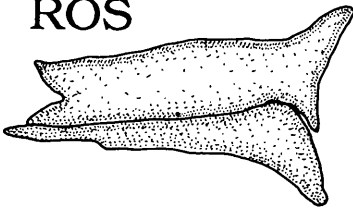
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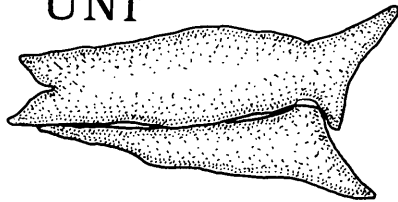
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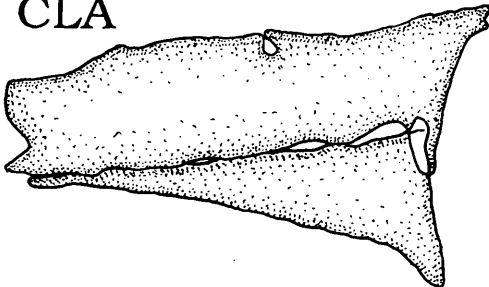
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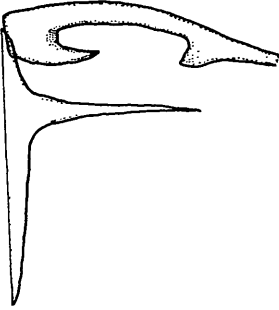
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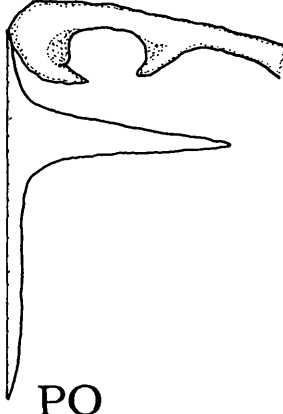
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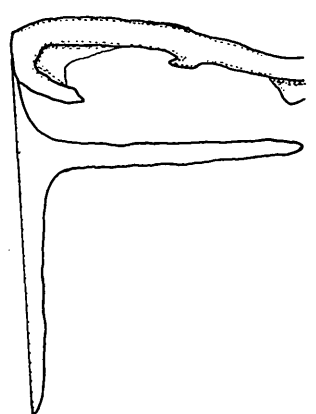
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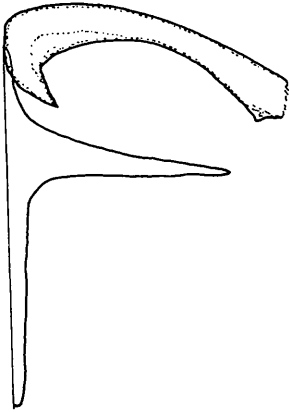
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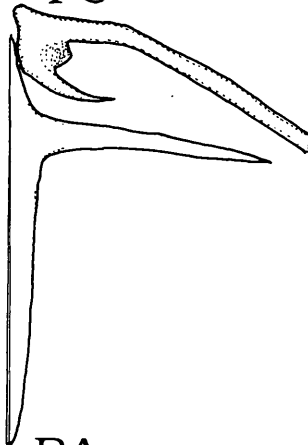
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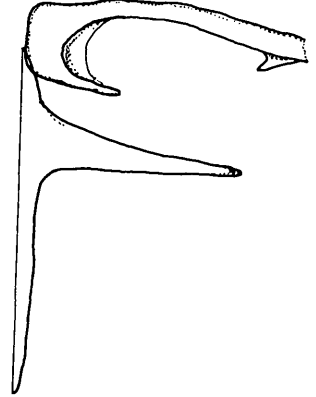
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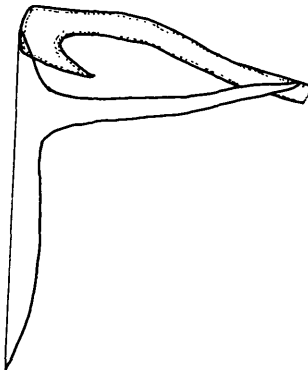
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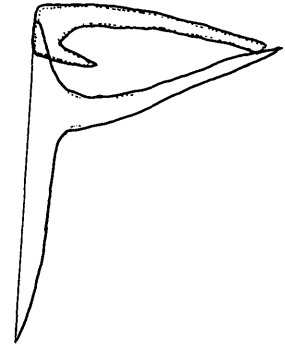
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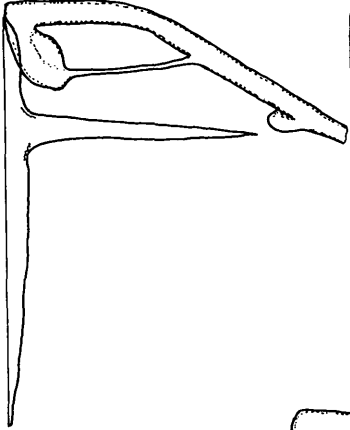
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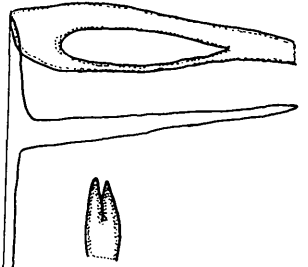
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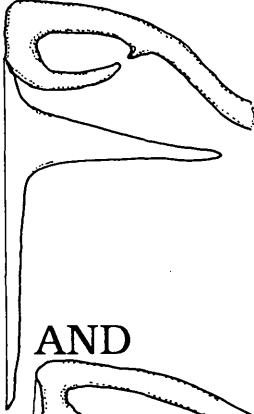
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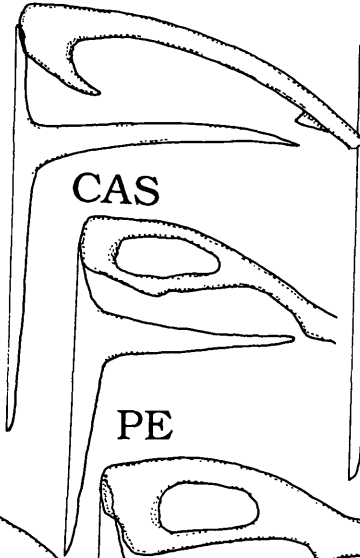
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MON



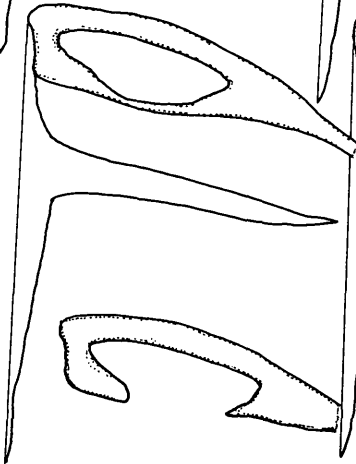
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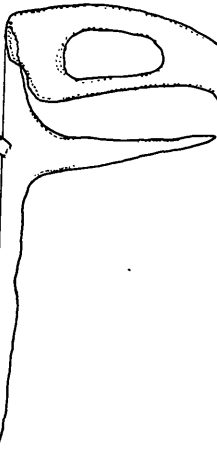
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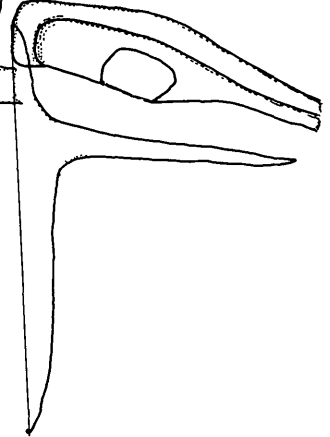
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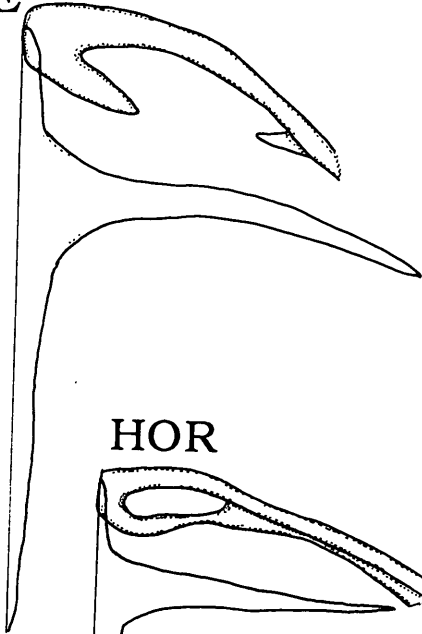
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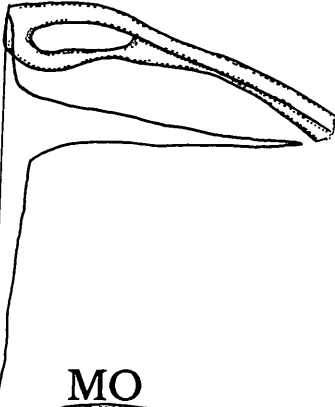
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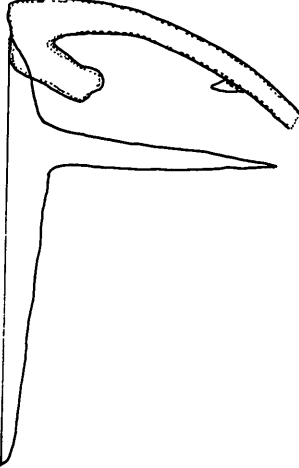
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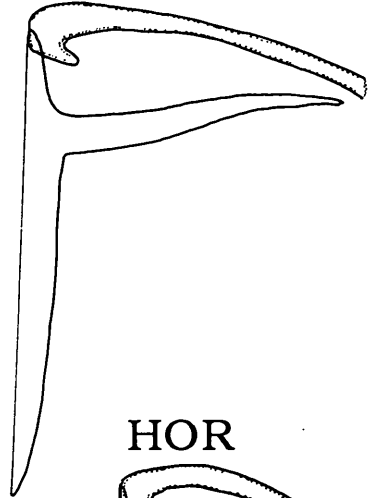
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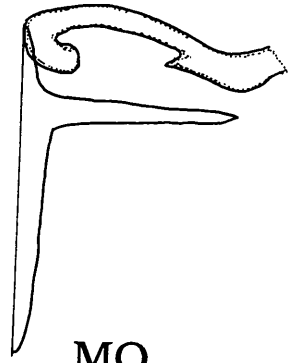
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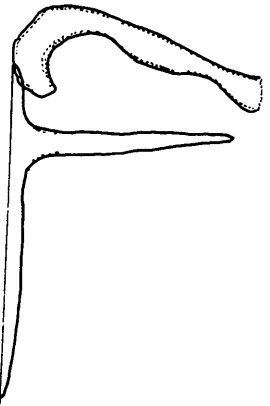
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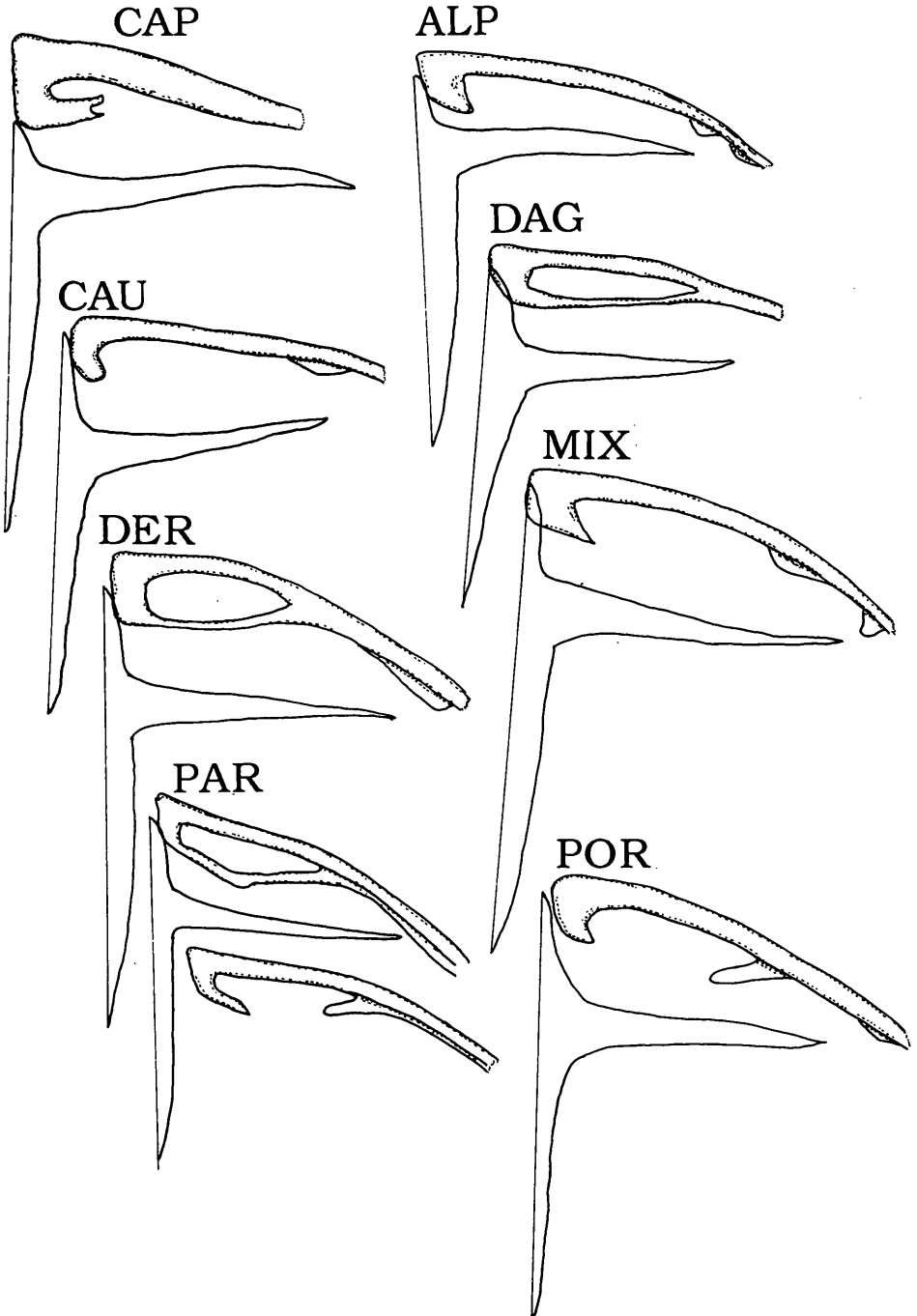


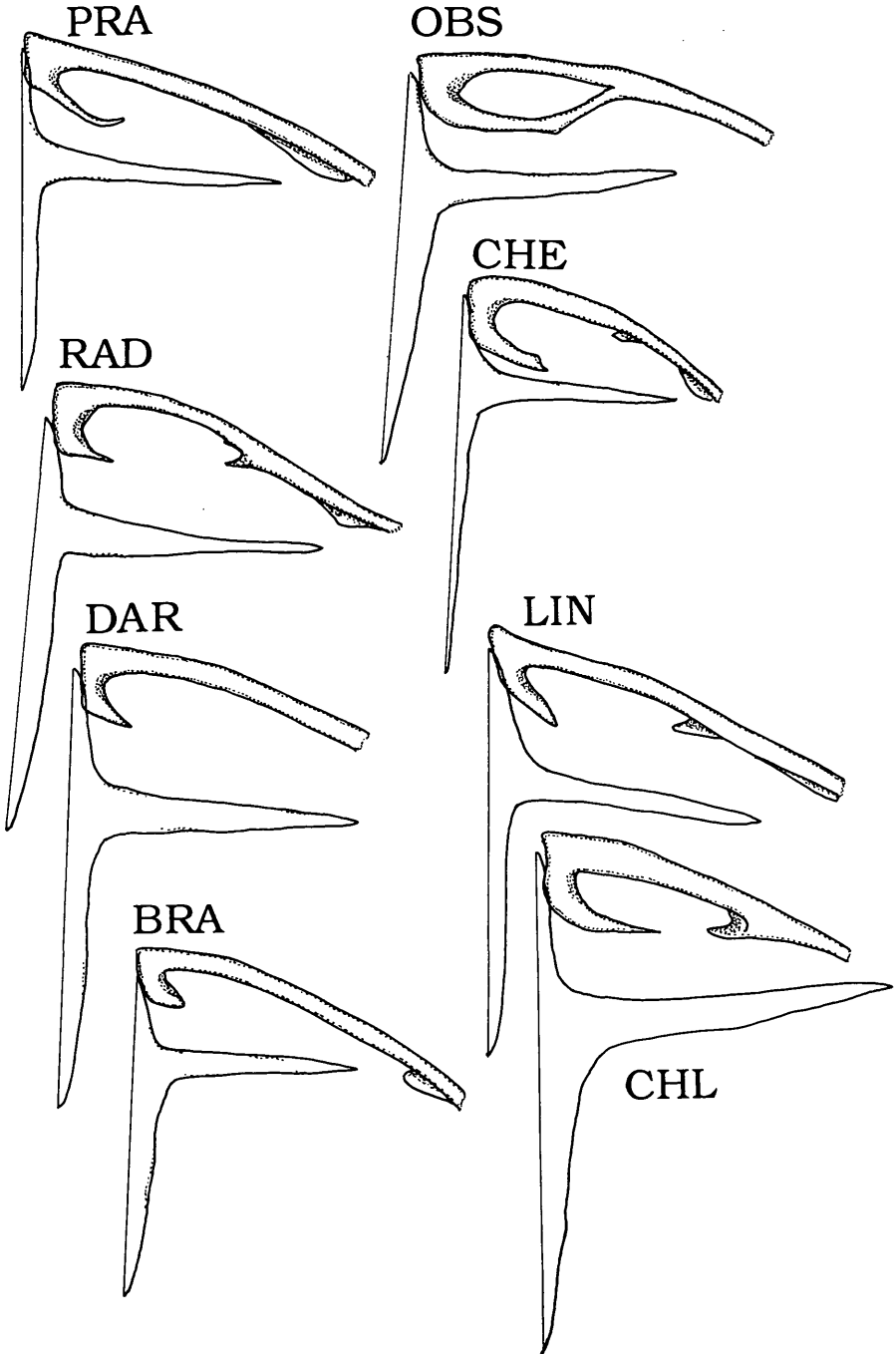
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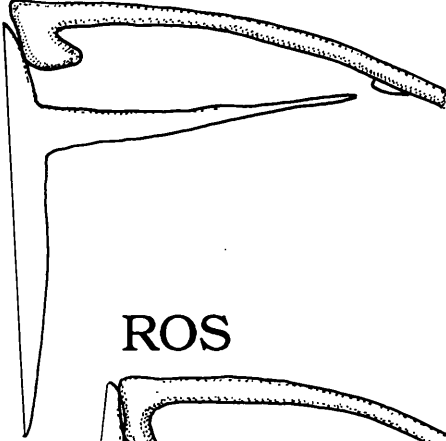
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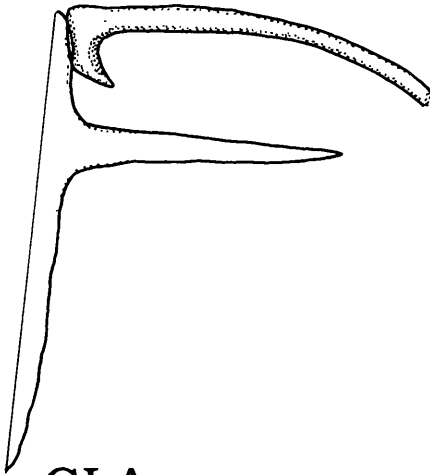




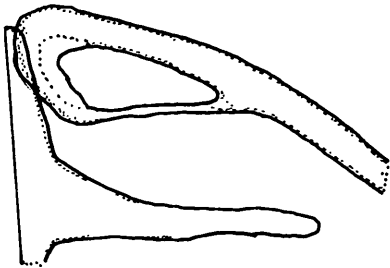
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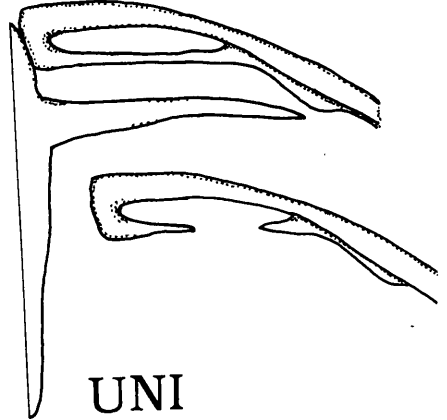
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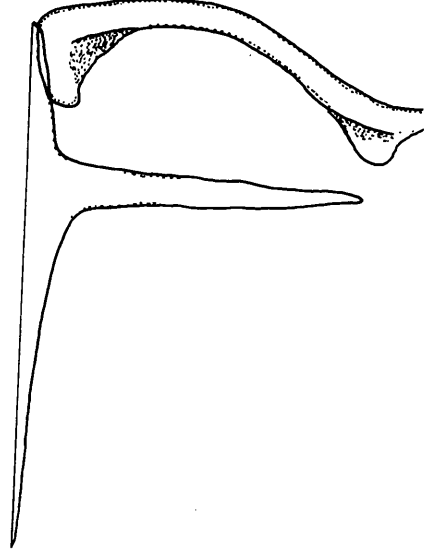
CLA



DAH



UNI



tal, and by the lack of the antero-medial process of the postorbital. The lizard has open (emarginated) clavicles and oval or rounded sternal fontanelles.

(iv) Within the Pyrenean group, *A. aurelioi* is characterized by the lack of both postfrontal and postorbital processes, by the possession of closed clavicles (unemarginated) and the frequent lack or reduction of the sternal fontanelle.

(v) All above character states are constantly expressed throughout the species' range. But we can also find characters the expression of which varies greatly, especially when peripheral or isolated populations are included, e. g., acquisition of an additional long rib in disfavour of the number of short ribs, as occurs in the Bigorre population of *A. bonnali* (but also in other species).

(vi) In view of the osteological results, it becomes clear that the European species so far assigned to *Archaeolacerta* s. l. do not constitute a natural cluster. On one hand, the Pyrenean species appear differentiated on the basis of the characters studied, while the Iberian, Balcanic and Tyrrhenic taxa share symplesiomorphic character states only which do not permit conclusions on their relationship.

(vii) The Caucasian species of the '*L. saxicola*' group, currently assigned to *Archaeolacerta* s. l., are different from the European *Archaeolacertae* by the apomor-

phic character of an extra presacral vertebra and from *Apathya* by both an extra presacral vertebra and a minor number of teeth in the premaxilla.

(viii) Within the Caucasian group, '*L. chlorogaster*' appears clearly differentiated from the other taxa by the number of premaxillary teeth and the shape of the interclavicle, which coincides with the lizard's uncertain systematic position (see BISCHOFF 1991).

(ix) The parthenogenetic Caucasian species present characteristic features of their parental species, the female parental species of the original crossing in particular. Lack or extreme reduction of the antero-medial process of the postorbital in the original maternal species '*L. raddei*' and '*L. mixta*' is also expressed in the parthenogenetic descendant species studied here. Likewise, the modal number of vertebrae of the parthenogenetic females of the '*L. raddei*' cluster is somewhat increased as compared to the other species of the '*L. saxicola*' group, with the exception of the maternal species, which also show these higher vertebral counts.

(x) '*L. portschinskii*' frequently presents the exceptional number of 7 short-ribbed posterior presacral vertebrae, which speaks in favour of this taxon to be an original parental species of the parthenogenetic '*L. dahli*' and '*L. rostombekovi*', which also present this elevated number.

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