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. I. 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 Archaeolacerten 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. 1. 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 synplesiomorphe Merkmalsausprägungen gemeinsam haben, die keine Aussagen über ihre Verwandtschaft ermöglichen.

ABSTRACT

The Pyrenean species of Archaeolacerta s. 1. (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 Archaeolacertae 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. I. 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 reptile 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 SIEBEN-ROCK (1894), KUHNE (1913), and HOFF-STETTER & 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 utilized 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 ARRI-BAS (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. 1. species from Spain and Europe concerning the states of their osteological characters; (iii) study Caucasian species of the 'L.' saxicola EVERSMANN, 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 AR-NOLD (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 andreansky 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 Boscá, 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 (DU-MÉRIL & BIBRON, 1839) and Psammodrommus algirus (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. Xray photographs were used to study the number of presacral vertebrae without disTable 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 (Privince, Country) / Fundort (Provinz, Land)	X-ra rönt M	ayed / gen. F	clea auf M	ared / gehellt F
A.'bonnali (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 Encantal, Alguestories (Lerida, E)	-	- 2	-	1
A. urunicu (ARRIBAS, 1995)	Port d'Orlà (Lérida E)	-	-	1	$\frac{1}{1}$ (P)
<i>A.'aurelioi</i> (ARRIBAS, 1994)	Montroig (Lérida, E)	-	-	-	2
	Pica d'Estats (Lérida, E)	6	2	2	3 (P)
	Port de Rat (Andorra-Ariège, F)	•	-	-	2
'A.'m. monticola (BOULENGER, 1905)	Estrela (Beira Alta, P)	5	5	3	1
<i>'A.'m. cantabrica</i> (MERTENS, 1929)	Incio (Lugo, E) Semiedo (Arthurian E)	-	-	1	-
	Somiedo (Asturias, E) Pto, de Vegarada (Leon, E)	10	10	3	2
	Pto de las Señales (León, E)	-	-	2	1
	Vega de Enol (Asturias, E)	-	8	-	î
'A.'c. cyreni (MÜLLER & HELLMICH, 1937)	Pto. de Navacerrada (Segovia, E)	2	4	1	1
'A.'c. castiliana (ARRIBAS, 1996)	Circo de Gredos (Avila, E)	2	3	3	2 (P)
'A.'b. bedriagae (CAMERANO, 1885)	Corsica (F)	1	-	1	-
'A.'b. paessleri (MERTENS, 1927)	Monte Limbara (Cerdeña, I)	2	1	-	-
A. norvathi (MEHELY, 1904)	Val Dogna (Udine, I)	2	Ì	1	2
4 ' orvenhala (NUMEATOVIC, 1880)	Nicsic-Trubiela (CR)	3	0	1	1
'L' alpina DAREVSKY, 1967	Terskol Mt. Elbrus (Kabardino-Balkariya, RU)	1	-	:	-
	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
'L.' caucasica MEHELY, 1909	Khvarshi (Daghestan, RU)	3	2	1	:
	Pereval (Southern Ossetia, RU)	-	-	-	1
'L' chlorogaster BOULENCEP 1908	Aleviefska (Azerbaijan)	- 2	- 2	-	1
E. Chioroguster DoolEinoEk, 1700	Guirkansky Zanoviednik (Azerbaijan)	3	2		-
L' clarkorum DAREV. & VEDMERJA, 1977	Cankurtaran Gec., Artvin (TR)	ĭ	ĩ	1	-
'L.' dahli DAREVSKY, 1957 (p)	Jodieri, circa Tiflis (Georgia)	-	6	-	1
'L.' daghestanica DAREVSKY, 1967	Khvarshi (Daghestan, RU)	10	12	-	1
	Tpig (Daghestan, RU)	-	-	1	-
L.' derjugini NIKOLSKY, 1898	Mlashe (Georgia)	2	2	1	1
L. UNANOUMI LANIZ & CYREN, 1930	Zakari (Adiaria, Georgia)	1	I	1	1
L. MIXIU MEHELI, 1909	Baniskevi (Georgia)	1	1		-
	Chihura River(Georgia)	î	î	_	-
'L.' parvula adjarica DAREV. & EISELT, 1980	Adskuri (Georgia)	3	3	1	1
L.' portschinskii KESSLER, 1878	Rbemoshuri (Georgia)	3	3	-	1
'L.' praticola EVERSMANN, 1834	Kutorskaya (Krasnodar, RU)	1	4	1	1
'L.' r. raddei BOETTGER, 1892	Lichk (Armenia)	3	3	1	1
L. r. vanensis EISELT, SCHMIDTLER & DAREVSKY, 1993	Bendimahi, Muradiye, Van (IR)	2	1	-	- (P)
L.' (raddei) nairensis DAREVSKY, 1967	Agin (Armenia)	1	Ì	-	-
L. TOSIOMOEKOVI DAREVSKY, 1957 (D)	Khyarshi (Daghertan RID	-	2	-	2
'L' rudis chechenica EBELT & DAREY., 1991	Achaldaha (Georgia)	ž	ŝ	1	1
<i>L. radis observa Eritifica</i> Official, 1990 <i>L.' sapphirina</i> SCHMIDTLER, EISELT & DAREVSKY, 1994 (p)	30 km NW Ercis (limit Van/ Agri, TR)	-	2	-	- (P)
'L.' saxicola darevskii ŠČERBAK, 1962	Dagomys, circa Sochi (RU)	5	4	1	-
L.' saxicola brauneri MEHELY, 1909	Inguri river gorge (Georgia)	-	-	-	1
'L.' unisexualis DAREVSKY, 1966 (p)	Tsomakaberd (Armenia)	-	2	-	1
'L.' v. valentini BOETTGER, 1892	Mt. Legli (Armenia)	-	-	-	1
1 Jantianani DADEU & FIOTET 1047	Gukasyan district (Armenia)	;	2	-	-
	Karvansaray (Armenia)	1	1	-	-
L. v. unizicyreni DAKEV. & EISELI, 1907 Anathya cannadocica woltari (RIBD 1036)	Kirikan Amanus Mts (TR)	1	1	1	-
ipaniya cappadocica noncri (DED, 1730)	iso many runando mila, (i K)				-

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 ("steped jugal" sensu ARNOLD 1989), (vi) condition of antero-distal process of the postfrontal, (vii) condition of antero-medial process of

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-*

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).

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 *Psammodromus*). 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 slighty 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.' daghestanica 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 (STEIN-DACHNER, 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 AR-NOLD 1989) has been utilized as one character for the reconstruction of phylogenies. According to ARNOLD (1989), the suture between maxilla and jugal is clearly sinous ("stepped") in Lacerta s. str. and Podarcis, and might represent the derived state of the caracter. However, in the sample of Iberobalearic *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, outgroup 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.' portschiskii M x 'L.' mixta F), 'L.' rostombekovi ('L.' portschinskii M x 'L.' raddei F) and 'L.' unisexualis ('L.' valentini M x 'L.' raddei nairensis F) (UZZELL & DAREVSKY 1975; DAREVSKY & DANIELYAN 1977; DA-REVSKY & 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

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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 in one side of the head, while the other side shows them perfectly separated. All other species of Archaeolacerta s. 1. 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. 1. - 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. 1.

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. 1. 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 *Algyroi*des 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. Sporadically, 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 (unemarginated 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 (Psammodromus, Gal*lotia*) 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 smallribbed 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 anteroposterior 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. Ar-NOLD 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 *Psammodromus 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. 1. 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. 1., 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 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 of '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-

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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. 1. 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. 1. 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'Orlà. 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, Éstrela, 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 - Alexiefska, 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. I. 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'Orlà.

Plate 6 (plate 5 continued, page 64) / Taf. 6 (Abb 5 fortgesetzt, Seitee 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 - Dagonys, Sochi, Russia. L' saxicola brauneri: BRA - Inguri River, Georgia. 'L' lindholmi: LIN - Bakhchisaray, Georgia. 'L' chlorogaster: CHL - Alexiefska, 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.

PLATE/TAFEL 1 (Legend/Legende p. 58) Osteology of Archaeolacerta s. l.

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PLATE/TAFEL 3 (Legend/Legende p. 58) Osteology of Archaeolacerta s. l.







PLATE/TAFEL 5 (Legend/Legende p. 58)

Osteology of Archaeolacerta s. l.

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PLATE/TAFEL 7 (Legend/Legende p. 58)





PLATE/TAFEL 9 (Legend/Legende p. 58)





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. 1. 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 premaxila.

(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 shortribbed 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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