

HEMIPENIAL MORPHOLOGY AND EVOLUTIONARY INFERENCES ON PYRENEAN MOUNTAIN LIZARDS (*Squamata: Lacertidae*)

Oscar J. Arribas

Avda. Fco. Cambó 23; 08003 – Barcelona (Spain)

Paraules clau: *Lacertidae*, *Lacerta*, *Iberolacerta*, *I. aranica*, *I. aurelioi*, *I. bonnali*, Peninsula Ibèrica, Pirineos, Hemipenes, Microornamentació genital.

Key words: *Lacertidae*, *Lacerta*, *Iberolacerta*, *I. aranica*, *I. aurelioi*, *I. bonnali*, Iberian Peninsula, Pyrenees, Hemipenes, Hemipenial microornamentation.

Palabras clave: *Lacertidae*, *Lacerta*, *Iberolacerta*, *I. aranica*, *I. aurelioi*, *I. bonnali*, Peninsula Ibérica, Pirineos, Hemipenes, Microornamentación genital.

Resum:

L'estudi de la morfologia i de la microornamentació de l'hemipenis mostra l'existència de diferències entre les tres espècies pirinenques de *Iberolacerta*, fet que corrobora el seu estatus com espècies diferents. A grandàries equivalents, *I. aurelioi* posseeix hemipenis sensiblement menors que les altres dues espècies, i *I. bonnali* té majors llavis externs en el *sulcus spermaticus*. Ambdues característiques deuen haver aparegut després de l'especiació a partir del seu avantpassat comú i, en el primer cas, ho interpreto com un fenomen de desplaçament divergent de caràcter induït per un contacte passat amb *I. aranica*. La microornamentació del hemipenis és clarament coroniforme en *I. aurelioi* i espiniforme en *I. aranica* i *I. bonnali*, encara que un especimen amb tubèrculs coroniformes ha estat trobat en cadascuna d'aquestes dues espècies. La microornamentació coroniforme sembla ser l'estadi apomòrfic, però l'espiniforme pot igualment aparèixer de forma secundària per reversió de la primera.

Abstract:

The study of hemipenial morphology and microornamentation shows us the existence of differences among the three species of pyrenaean *Iberolacerta*, which support their specific status. At equivalent sizes, *I. aurelioi* has a significantly smaller hemipenis than the other two species, and *I. bonnali* has larger outer lips at the *sulcus spermaticus*. Both characteristics should have arisen after speciation from their common ancestor, and in the first case, I interpret it as a phenomenon of character displacement induced by a past contact with *I. aranica*. Hemipenial microornamentation is clearly crown-shaped in *I. aurelioi* and spiny in *I. aranica* and *I. bonnali*, although a specimen with crown-shaped tubercles has been found in each of these two species. The crown-shaped microornamentation appears to be the apomorphic state, but spiny-like microornamentation could be a reversal of the first.

Resumen:

El estudio de la morfología y de la microornamentación del hemipene muestra la existencia de diferencias entre las tres especies pirenaicas de *Iberolacerta*, lo que corrobora su estatus como especies distintas. A tamaños equivalentes, *Iberolacerta aurelioi* posee hemipenes

sensiblement menors que las otras dos especies, e *I. bonnali* tiene mayores labios externos en el *sulcus spermaticus*. Ambas características deben haber aparecido después de la especiación a partir de su antepasado común y en el primer caso, lo interpreto como un fenómeno de desplazamiento divergente de carácter inducido por un contacto pasado con *I. aranica*. La microornamentación del hemipene es claramente coroniforme en *I. aurelioi* y espiniforme en *I. aranica* y *I. bonnali*, aunque un espécimen con tubérculos coroniformes ha sido encontrado en cada una de estas dos especies. La microornamentación coroniforme parece ser el estadio apomórfico, pero la espiniforme puede igualmente aparecer de forma secundaria por reversión de la primera.

INTRODUCTION

Genital morphology has long been used as a source of useful systematic characters to develop and improve phylogenetic hypothesis in a wide number of taxonomic groups (Eberhard, 1985; Böhme, 1988). Examples of this are the study of the aedeagus in insects, the baculum in mammals, the penis glans of tortoises and small mammals, the hemipenes in snakes and lizards (e.g. Wöpke, 1930; Klemmer, 1957; Burt, 1960; Dowling & Savage, 1960; Zug, 1966; Arnold, 1973, 1985; and Böhme, 1988). Genital morphology is unexpectedly variable even in externally very uniform groups, such as lacertid lizards (Arnold, 1986). The main interest of the study of genitalia resides in its supposed independence from evolutionary pressures, which are supposed to affect other morphological characters.

Closely related species are expected to share very similar genital organs. Thus, play independent from the pressures which form very different external morphologies.

The intraspecific stability of these characters would be under polygenic control and their interspecific differentiation would arise by a model of pleiotropic evolution (Arnold, 1973). According to Mayr (1969), the genital differences would accumulate slowly as pleiotropic by-products of other changes in throughout the body. However, although the mutations causing these pleiotropic changes are originally beneficial, they can cause a reduction of reproductive fitness. Arnold (1973) suggests that normalising selection returns the genital organ to near its initial level of efficiency, suppressing a great part of the pleiotropic change. This would explain similarities between the genital organs at closely related species. Simultaneously a parallel modification of female reproductive organs would balance these changes. Thus, where these changes occur, there is a return to the optimum situation of reproductive efficiency. The two types of genitals would obtain full efficiency without returning to their initial morphology (Arnold, 1983).

Although in the lacertids the hemipenes could provide interesting information, the anatomy of everted organs is very similar among species and usually does not offer diagnostic characters. Because differences in anatomy are not linked with the patterns of sexual behaviour, behaviour is not associated with changes in the morphology of the hemipenes.

A detailed study of the microornamentation of the hemipenial epithelium during the reproductive period reveals the existence of some small microscopic tubercles which can differ in form among the different species. The development of this epithelium is controlled by hormonal changes which accompany the reproductive cycle. Tiny thorns or tubercles develop, each one of which is a unique epithelial cell (Böhme, 1971, 1993) that could appear in form of a thorn more or less rounded and more or less curved (finger-shaped, hooked or spiniform microornamentation), forked (forked microornamentation), or as a small tubercle with minuscule spiniform prolongations in his apex (crown-shaped microornamentation) (Klemmer, 1957; Böhme, 1971; Arnold, 1973, 1986, 1989; Arribas, 1994). Until now, intraspecific variations were unreported and thus should be a useful systematic character (Böhme, 1993).

The use of hemipenial microornamentation for taxonomic and systematic purposes in lacertids dates back to Klemmer (1957) and Böhme (1971). The latter author give a good review of the microornamentations from a great number of species. Subsequently, other authors as Arnold (1973, 1986, 1989), Arribas (1993, 1994), Böhme (1993), and Leptien & Böhme (1994) have utilised it.

The main goals of this paper are:

1. To describe the hemipenial morphology of the Pyrenean *Iberolacerta* and to detect possible differences among these taxa, two of them recently described (Arribas, 1993, 1994, 1996).
2. To describe their genital microornamentation, intraspecific variability and interspecific differences.
3. To determine the polarity of the change between the different types of genital microornamentation.
4. To evaluate critically the utility of the hemipenial microornamentations and the validity of their use in phylogeny estimation.

MATERIAL AND METHODS

Abbreviations:

H.P.: Hautes Pyrenees, France; HU: Huesca Province, Spain; L: Lérida or Lleida Province, Spain.

Specimens studied:

The genital morphology of 22 males of Pyrenean Mountain lizards captured from the end of May (moment of the begin of activity) until the first days of July (period of the first clutches) has been studied. Specimens come from the following locations:

-*Iberolacerta bonnali* (Lantz, 1927).

Bigorre (H.P., France) (2 indiv.), Monte Perdido (Hu., Spain) (5 indiv.), Posets (Hu., Spain) (1 indiv.), Maladeta (Hu., Spain) (1 indiv.), Aigüestortes National Park (L., Spain) (1 indiv.).

-*Iberolacerta aranica* (Arribas, 1993).

Coll de Barradós (L., Spain) (6 indiv.), Port d'Orlà (L., Spain) (2 indiv.).

-*Iberolacerta aurelioi* (Arribas, 1994).

Pica d'Estats (L., Spain) (3 indiv.), Port de Rat (Andorra-Ariège) (3 indiv.).

Study of the hemipenial morphology:

In order to perform it, I proceed to the study of 'in situ' everted hemipenes from conserved specimens (general hemipenial morphology), or by means of post mortem amputation in specimens previously fixed in the field with their hemipenes everted (hemipenial microornamentation). In all cases, it has been done in adult animals captured in the reproductive period and which subsequently have been utilized also for the study of the genital microornamentation.

The general morphology of the hemipenes has been drawn by means of a Zeiss camera lucida, coupled to a binocular stereoscope.

The anatomical nomenclature of the hemipenes (after Arnold, 1973, 1986) is shown in Fig.1.

Study of the hemipenial microornamentation:

For the study of the microornamentation, I examined the hemipenes, or their lobes, by the estandar process of dehydration. The hemipenes were immersed in an ethanol series of increasing concentration (70°, 90°, 100°) for 12 hours in each. Following the dehydration, I transfered the material to xylene for 2 to 6 hours, and then to paraffined xylene during the same period. Finally, the hemipenes were immersed in fused paraffin for 8 hours.

After the imbedding, the blocks were cut, deparaffined with xylene (15 min.) and rehydrated with ethanols of decreasing graduation (100°, 90°, 70°) and finally distilled water (5 to 10 min.), prior to observation at 1000 x.

RESULTS

Hemipenial morphology:

The overall hemipenial morphology is nearly equivalent in the three Pyrenean species, and is typical of the pattern seen in all lacertids (see Arnold, 1986 for a detailed description of a typical lacertid hemipenis).

The hemipenes of the three species (Fig 2) are symmetrically bilobed, with a common basal section or pedicel, the lobed section is shorter than the basal one. These proportions are typical for most of the family, except *Podarcis*, *Gallotia*, *Psammodromus* and some species whose systematic position seems to be near to *Podarcis* (like '*L. laevis*' and '*L. danfordi*'), in which these proportions appear inverted (Arnold, 1973).

Notwithstanding this overall similarity, I have observed that for equivalent sizes, *I. aurelioi* has clearly smaller hemipenes than the other two Pyrenaean species, a phenomenon that is translated into a markedly less enlarged tail base in the males of this taxon, and is

easily visible in live specimens. In *I. bonnali* and *I. aranica* is easy to discern males from females by their enlarged tail basis, whereas in *I. aurelioi* it is not possible without a detailed examination of other sexually dimorphic characters.

The sulcus spermaticus (studied by means of a section at the height of the hemipenial bifurcation of the lobes) is clearly visible in the three species, and the lips appear asymmetrical, with the extent of development in the outer lip different between the three species. *Iberolacerta bonnali* has an external lip with noticeable development, which is much more modest in *I. aurelioi* and *I. aranica*. These lips get wider in the lobes and appear reflected towards the outer parts of the lobes, especially in *I. bonnali*. Big lips in the sulcus spermaticus are typical of *Podarcis*, '*L. danfordi*', '*L. laevis*', '*L. andreanszkyi*' and *Teira perspicillata* (Arnold, 1973, 1986).

The surface of lobes appears typically plicate from the apex towards the base, as usual in lacertids (except in *Parvilacerta parva* and *Parvilacerta fraasii*). The apex of the lobes lack papillae, thorns or tubercles of the type of those which appear in the most basal species of the group (*Gallotia*, small species of *Psammmodromus* and some *Podarcis*).

Microornamentation of the hemipenis:

Iberolacerta bonnali:

Results have been obtained in specimens of Bigorre, Monte Perdido, Maladeta and Aigüestortes, but specimens from Posets did not show any development of the epithelium. Their examined hemipenes have a spiny-like microornamentation (Arribas, 1993, 1994). One specimen from Monte Perdido has a typical, highly developed crown-shaped microornamentation (see Fig. 3).

Iberolacerta aranica:

The microornamentation in this species is spiny-like (Arribas, 1993), although one specimen had also some tubercles crown-shaped (Fig. 3).

Iberolacerta aurelioi:

In this species, the microornamentation is crown-shaped (Arribas, 1994). (Fig. 3).

DISCUSSION

-Hemipenial microornamentation.

The fact that the development of the epithelium which carries the microornamentation appears bound to the hormonal cycle implicates that fully developed hemipenial microornamentation only appears during the moment of the reproduction, between two periods of moult (Böhme, 1971). Being ectodermal tissues, all the epithelium of the hemipenis comes off during the process of ecdysis, for the one which the utility of its study is reduced by the necessity to center it in animals picked up during the reproductive period.

Outside the mating season the hemipenes decrease in size and the epidermal microornamentation is lost (Arnold, 1986).

The models of microornamentation are reduced basically to three: the forked, the spiny-like and the crown-shaped (Böhme, 1971), and it is accepted that no intra-specific variability exists (Böhme, 1993). However, it is difficult to assure which is the more primitive model, since we lack outgroup information about other saurian families. Arnold (1989) argues that it is less parsimonious to consider the model of more complex microornamentation (the crown-shaped) as the most primitive. By this, we could consider that the spiny-like is the most primitive and that from him derive the crown-shaped and other more scarce like the forked one. This theory fits well with the observations on the ontogenetic development of the hemipenial microornamentation. During this, the tubercles still not developed (for example in animals recently emerged from hibernation, previously to the reproductive period) present a similar look to the spiny-like model, for the one which one could argue that these correspond to the primitive microornamentation.

Also, by an ingroup criterion, the spiny-like microornamentation appears in some of the most basal species within the Eurasian Radiation of Lacertids (sensu Mayer & Benyr, 1994) as well as in the ones from the outgroup, like *Gallotia spp.*, *Psammodromus algirus*, *Podarcis spp.*, *Teira spp.* and *Apathya cappadocica*.

However, both types of microornamentation appear in closely related species, like *Omanosaura cyanura* versus *Omanosaura jayakari*; the species of *Algyroides*; *Archaeolacerta bedriagae* concerning most of the other european *Archaeolacertids* (s.l.) (Böhme, 1971; Leptien & Böhme, 1994), or in the pyrenaean species here studied. Also, both types appear completely blended between the different phyletic lines of the Eurasian Radiation. This has made to suggest, with certain reserves, that the crown shaped microornamentation has appeared several times in the evolution of this group of lacertids (Böhme, 1993), as well as that the hemipenial microornamentation has diagnostic utility in order to classify species but not phylogenetic in order to reconstruct their relationship (Arribas, 1994).

In view of the fact that clearly related species present different microornamentations and that both types of microornamentation appear in the same locality and in occasions in the same individual (as occurs in *Lacerta s. str.*, where both tubercle types appear in different parts of the hemipenial lobes: long and pointed - spiny-like - on the plicae covering the lobe flanks but tubercular and minutely spinose - crown-shaped - on the lobe apices - Böhme, 1971; Arnold, 1986-), one must be very cautious about the use of this character for phylogenetic reconstruction.

Moreover, I believe that a good part of the spiny microornamentations which appear in these species, and especially when both models appear blended in closely related species, could be reversals to the primitive model, that is to say, that they are apomorphic microornamentations indistinguishable from the more plesiomorphic ones. Such an

apparent change of polarity could have arisen by a mechanism of heterocrony, which could impede the complete development of the tubercles of the hemipenial microornamentation. In support of this theory subadult specimens, or adults with incomplete matured epithelies, could present spiny-like models, included in species with model usually crown-shaped. The cases of *I. bonnali* and *I. aranica* can be reversals toward the primitive model shown by *I. aurelioi*. This fact is confirmed by the find of crown-shaped tubercles in one individual of the first two species and because this ornamentation is the most widespread model in other species probably closely related to this group, like *I. monticola*, *I. cyreni*, *I. horvathi*, etc., although not in *Archaeolacerta bedriagae*, which also presents it spiniform. The fact of be in some cases species related to extreme habitats could be an indicative of a significative paper from the activity cycle reduction in this incomplete development of the microornamentation, at fewer in some cases. So then, it is also possible that the crown-shaped microornamentation could have appeared several times, but this is no parsimonious and therefore not very probable. It is possible and very probable from my point of view that a part of the spiny-like microornamentations are secondary reversals. The obtain of a robust phylogeny for this group will permit to elucidate which of these microornamentations are primitive and which the secondarily derived.

Morphology of the hemipenes.

It is suggested that some marked differences between closely related lacertids have arisen as physical isolating mechanisms. Hemipenes may sometimes differ greatly between otherwise very similar species, probably as a result of the evolution of such an isolating mechanism. These differences are often helpful in recognising new taxa and confirming that forms differing only slightly in external morphology actually deserve to be treated as separate species. Species status is given in such cases because radical differences in genitalia between the forms concerned is likely to make copulation between them difficult or impossible, thereby producing or preventing potential gene flow (Arnold, 1986). Such differences in size or asymetry and simplification have been already employed in defining species of *Acanthodactylus* (Arnold, 1983) and *Mesalina* (Arnold, 1986). In these genera it has been demonstrated that between closely related species when they meet in sympatry appear modifications which prevent the hybridization. These are the reduction in size of the male copulator organ (and therefore of the female cloacal bag where it is inserted) and the asymmetry of the hemipenes in any of the two species in question (Arnold, 1983, 1986).

Although haven't studied the female genital tracts from these species, I believe that the small hemipenes present in *I. aurelioi* would correspond to narrow entrances to female genital tracts and that these differences could have arisen during a previous period of sympatry or parapatry. Although the selective pressures that initially produced them no longer act because they are fully allopatric today, these isolation mechanisms have been retained and appear stored now in the hemipenes from these species.

The data about geographical distribution of the here studied species (Arribas, 1996, and in prep.) suggest a speciation by cyclic vicariance by alternating periods of favorable and

unfavourable climates, with resident taxa being alternately widespread during favourable periods and with restricted ranges during unfavourable periods. Restricted areas function as refugia during unfavorable periods, and probably these persist to function again and again as survival centres during successive climatic deteriorations. During unfavourable periods, the ranges of taxa are fragmented into isolated vicarages provided by the refuge, and under isolation the resulting vicars undergo differentiation that can lead to speciation. During favourable periods, the taxa become widespread by dispersal.

In the case of the Pyrenean species, *I. aranica* shows an ancient separation from the common stem. Based in electrophoretic data (Mayer & Arribas, 1996), this separation very probably dates from the Pliocene or beginning of Pleistocene (Arribas, 1997). This species has a relatively plesiomorphic and undifferentiated hemipenis and also lacks other apomorphic karyological and osteological characteristics compared to the other two Pyrenean species (Arribas, 1997, 1998 and 1999).

Differences among *I. bonnali* and *I. aurelioi* should have arisen after his speciation from their common ancestor. This speciation could be dated back to around 300.000 y.b.p., during the Mindel-Riss Interglacial (Arribas, 1996), very long and in which climate was still slightly hotter than the present one, representing still more isolated lizard populations than today. In that moment both species could have begun his speciation, appearing the bigger outer lips in the *I. bonnali* hemipenes, and the size reduction in the *I. aurelioi* ones. But, what was the cause of the hemipenial size reduction in *I. aurelioi*? In my opinion, this could be due to a phenomenon of character displacement by contact of this populations of *I. aurelioi* with populations of *I. aranica*. Although today separated by an hiatus of 20 Km of very narrow crests slightly above 2000 m (a very narrow and relatively low corridor for these lizards), this connection could have been more wide and suitable for this alpine-environment lizards before its overexcavation and erosion during Würm, and during less warm periods (alpine environments more low than today), enabling populations of both species to contact in the area between the Montroig and Mauberge massifs, and to develop isolating reproductive mechanisms. As I stated above, such a process of hemipenial differentiation has been suggested for species of *Acanthodactylus* and *Mesalina* after a secondary contact (Arribas, 1983, 1986).

Also, a robust phylogeny of the Pyrenean Mountain lizards (Arribas, 1997, 1999) shows us that there are several morphological characters in *I. aurelioi*, as the coloration of venter (lost in the other two species) which seem to revert in this taxon. Also scalation scores of neighbouring populations from *I. aurelioi* and *I. aranica* are just the more different ones from all the Pyrenean *Iberolacerta*, suggesting also the possibility of character displacement in other morphological characteristics.

CONCLUSIONS

Morphology of the hemipenis:

1. The overall morphology of the hemipenis from the Pyrenean *Iberolacerta* don't presents great intraspecific neither interespecific differences.

2. *I. bonnali* presents a notable development of the external lip of the *sulcus spermaticus*, that doesn't appear in *I. aranica* neither in *I. aurelioi*.
3. At equivalent sizes, *I. aurelioi* presents hemipenes clearly smaller than *I. bonnali* and *I. aranica*. This character could have arisen as a character displacement in a past sympatry with *I. aranica* to prevent hybridization.

Microornamentation of the hemipenis:

1. My data and the detailed analysis of the bibliography agree with the hypothesis of considering the spiny-like microornamentation as the more primitive in the Eurasian Radiation of the lacertids, and the crown-shaped as derived, the same as the forked one.
2. They frequently reverse, fact which we attribute to heterocronies which make that both models appear blended between sister species, closely related groups, and even in the same species.
3. This joint apparition of both models subtracts efficacy to the use of the hemipenial microornamentation as phylogenetic character, since it results not very feasible to a priori distinguish a primitive spiny-like microornamentation from a derived one appeared by secondary reversal. On the other hand, it has certainly importance as diagnostic character in general, and very especially as phylogenetic character in the more apomorphic and rare models, as the forked one.
4. *I. aurelioi* presents the model of microornamentation primitive (crown-shaped).
5. In *I. bonnali* and in *I. aranica*, in general appears a spiny-like microornamentation, although one could appreciate isolated crown-shaped tubercles in some individuals which indicate that it is a secondarily reversed model.

REFERENCES

- ARNOLD, E.N. (1973): Relationships of the palaeartic lizards assigned to the genera *Lacerta*, *Algyroides* and *Psammodromus* (*Reptilia: Lacertidae*). *Bulletin of the British Museum (Natural History), Zoology* 25: 289-366.
- ARNOLD, E.N. (1983): Osteology, genitalia and the relationships of *Acanthodactylus* (*Reptilia: Lacertidae*). *Bulletin of the British Museum (Natural History), Zoology* 44 (5): 291-339.
- ARNOLD, E.N. (1986): The hemipenis of lacertid lizards (*Reptilia: Lacertidae*): structure, variation and systematic implications. *Journal of Natural History* 1986, 20: 1221-1257.
- ARNOLD, E.N. (1989 a): Towards a phylogeny and biogeography of the Lacertidae: relationships within an Old-World family of lizards derived from morphology. *Bulletin of the British Museum (Natural History), Zoology* 55 (2): 209-257.

- ARRIBAS, O.J. (1993): Intraspecific variability of *Lacerta (Archaeolacerta) bonnali* Lantz, 1927 (*Squamata: Sauria: Lacertidae*). *Herpetozoa* 6 (3-4): 129-140.
- ARRIBAS, O. (1994): Una nueva especie de lagartija de los Pirineos Orientales: *Lacerta (Archaeolacerta) aurelioi* sp. nov. (Reptilia: Lacertidae). *Bolletino del Museo regionale di Scienze naturali di Torino* 412 (1): 327-351.
- ARRIBAS, O.J. (1997): *Morfología, filogenia y biogeografía de las lagartijas de alta montaña de los Pirineos*. Ph. Dr. Thesis. Universidad Autónoma de Barcelona. 353 pp. (8 pp and microfiche. Pub. U.A.B.).
- ARRIBAS, O.J. (1998): 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: Lacertidae*). *Herpetozoa, Wien*; 11(1/2): 47-70.
- ARRIBAS, O. J. (1999): Phylogeny and relationships of the mountain lizards of Europe and Near East (*Archaeolacerta* Mertens, 1921, *Sensu Lato*) and their relationships among the Eurasian Lacertid Radiation. *Russian Journal of Herpetology* 6 (1): 1-22.
- BÖHME, W. (1971): Über das Stachelepithel am Hemipenis lacertider Eidechsen und seine systematische Bedeutung. *Zeitschrift für zoologische Systematik und Evolutionsforschung* 9: 187-223.
- BÖHME, W. (1988): Zur genitalmorphologie der Sauria: Funktionelle und stammesgeschichtliche aspekte. *Bonner Zoologische Monographien* 27. 176 pp.
- BÖHME, W. (1993): Hemipenial microornamentation in *Lacerta brandtii* De Filippi, 1863: Falsification of a systematic hypothesis?. (*Squamata: Sauria: Lacertidae*). *Herpetozoa* 6 (3/4): 141-143.
- BURT, W.H. (1960): *Bacula of North American mammals*. Miscellaneous Publications from museum of Zoology of the University of Michigan 113: 1-75.
- DOWLING, H.G. & SAVAGE, J.M. (1960): A guide to the snake hemipenis: A survey of basic structure and systematic characteristics. *Zoologica (New York)* 45: 1-28.
- EBERHARD, W.G. (1985): *Sexual selection and Animal Genitalia*. Cambridge. Harvard University Press.
- KLEMMER, K. (1957): Untersuchungen zur Osteologie und Taxonomie der europäischen Mauereidechsen. *Abhandlungen von der Senckenbergisches Naturforschenden Gesellschaft (Frankfurt/Main)* 496: 1-56.
- LEPTIEN, R. & BÖHME, W. (1994) First captive breeding of *Lacerta (Omanosaura) cyanura* Arnold, 1972, with comments on systematic implications posed by the reproductive pattern and the juvenile dress (*Squamata: Sauria: Lacertidae*). *Herpetozoa* 7 (1/2): 3-9.
- MAYER, W. & BENYR, G. (1994): Albumin-Evolution und Phylogenese in der Familie *Lacertidae* (Reptilia: Sauria). *Annalen der Naturhistorisches Museum Wien* 96 B: 621-648.
- MAYER, W. & ARRIBAS, O. (1996) Allozyme differentiation and relationship among the Iberian-Pyrenean Mountain Lizards (*Squamata: Sauria: Lacertidae*). *Herpetozoa* 9 (1/2): 57-61.
- MAYER, W. & BISCHOFF, W. (1996): Beiträge zur taxonomischen Revision der Gattung *Lacerta* (Reptilia: Lacertidae). Teil 1: *Zootoca*, *Omanosaura*, *Timon* und *Teira* als eigenständige Gattungen. *Salamandra* 32 (3): 163-170.

MAYR, E. (1969): *Principles of Systematic Zoology*. Mc Graw Hill, New York.
 WÖPKE, K. (1930): Die Kloake und die Begattungsorgane der männlicher Zauneidechse (*Lacerta agilis* L.). *Jenaische Zeitschrift für Naturwissenschaft* 65: 275-318.
 ZUG, G.R. (1966): *The penial morphology and the relationships of Cryptodiran turtles*. Occasional Papers from the Museum of Zoology of the University of Michigan n° 647.

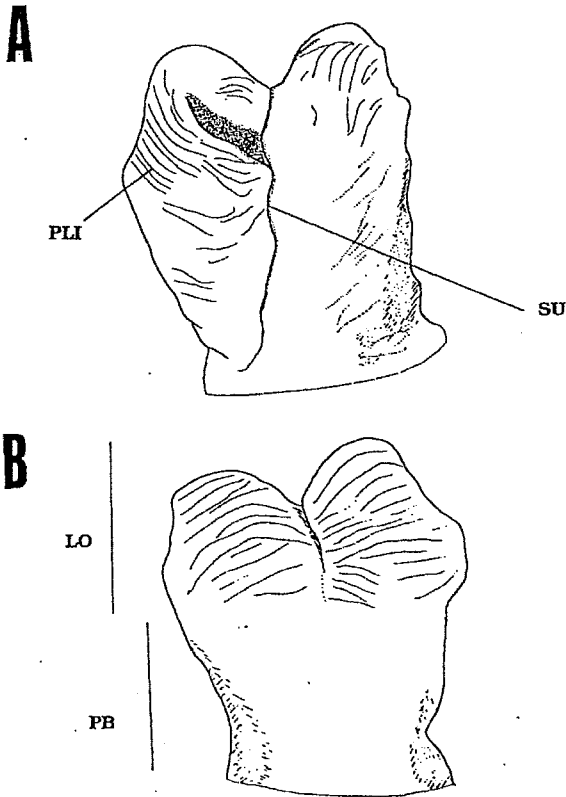


Fig 1 - Overall morphology of a Lacertid hemipenis : *I. monticola cantabrica* (Vilarello de Ancares, Lugo; EBD 25644). A: sulcal view. B: asulcal view. (PLI: plicae. SU: *sulcus spermaticus*. LO: lobes. PB: basal part or pedicel. Nomenclature from Arnold (1986).

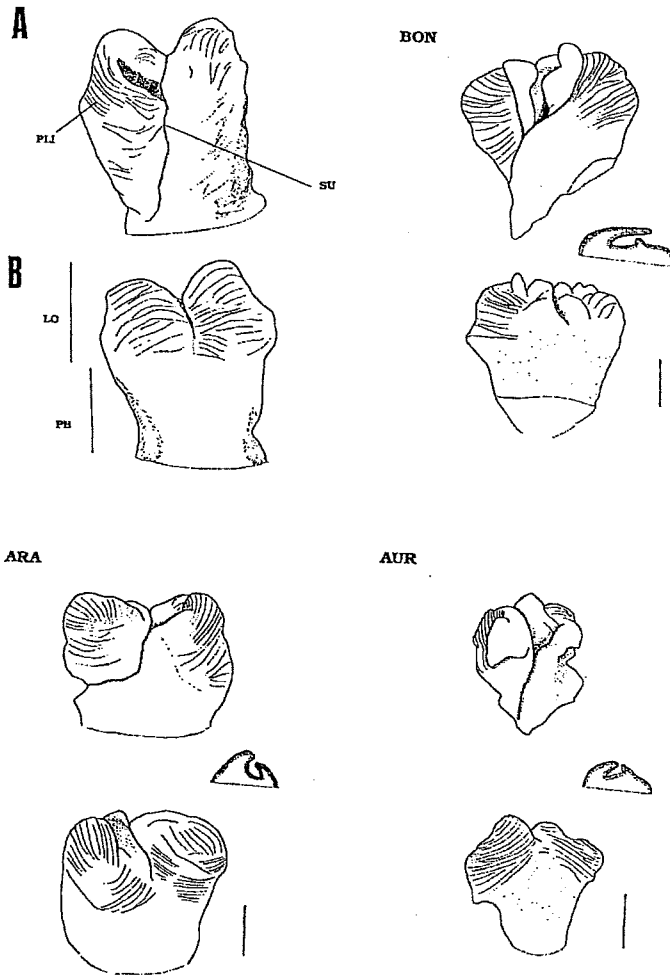


Fig 2 - Morphology the hemipenes from *I. bonnali* (BON) (Lac Bleu de Bigorre, H. Pyr.; CA 95061409), *I. aranica* (ARA) (Serra de Pica Palomera, Lérida; CA 95082703) and *I. aurelioi* (AUR) (Port de Rat, Andorra; CA 95060601). Sulcal (above) and asulcal (below) views and detail of a section of the *sulcus spermaticus* and the lips at the height of the bifurcation at the basis of the lobes. The line represents a milimeter.

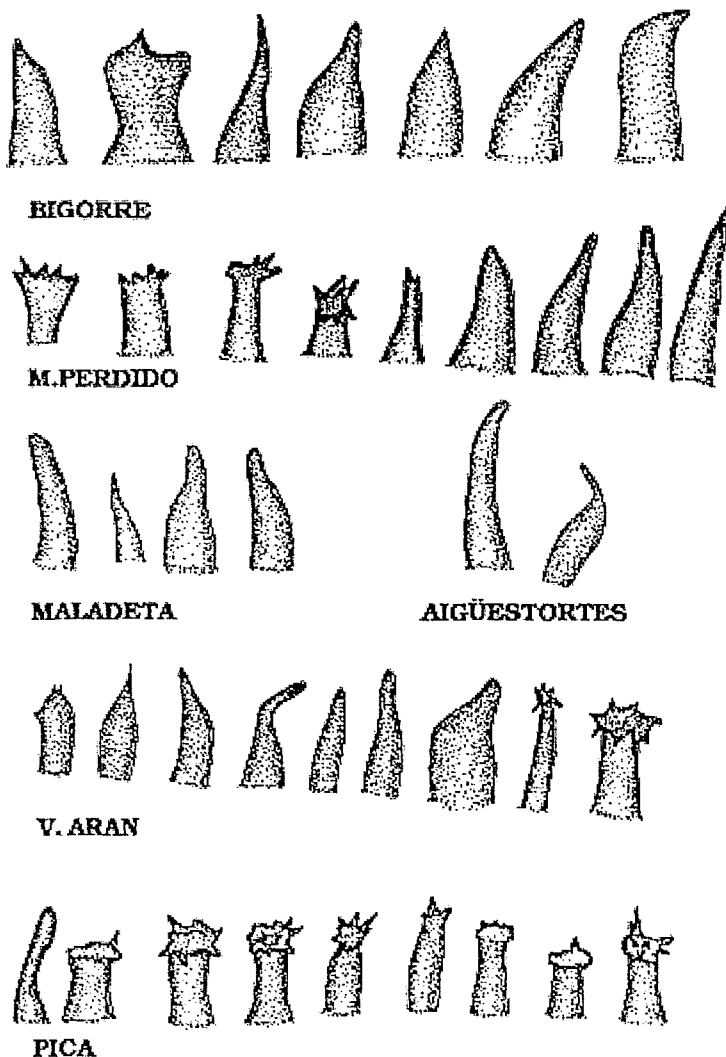


Fig 3 - Hemipenial microornamentation of the hemipenes in the three pyrenean species of *Iberolacerta*. The form of a series of epithelial cells is represented, reflecting the grade of variability. *I. bonnali* from Bigorre (CA95061404 and CA 95061409), Monte Perdido (CA 92050003 and CA 92050002), Maladeta (Llauset, CA 94071602, CA 93071703) and Aigüestortes (Muntanyó de Llacs, CA 93071602); *I. aranica* from Vall d'Aràn (CA 95061901, CA 95061902, CA95061910); and *I. aurelioi* from Pica d'Estats (CA 92070308 and CA 9107SN).