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Hemipenial morphology and microornamentation in *Iberolacerta* Arribas, 1997 (Squamata: Lacertidae)

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RESUM

S'ha estudiat l'hemipenis de totes les espècies d'*Iberolacerta*. La morfologia general és molt similar entre les diferents espècies. Els hemipenis són simètrics i bilobulats, amb la secció apical més curta que la basal (*I. galani*, *I. cyreni*, *I. monticola monticola, I. horvathi*, *I. bonnali*, *I. aranica* i *I. aurelioi*), subigual o amb proporcions lleugerament invertides (*I. m. astur* i *I. martinezricai*). Tots tenen una talla similar i proporcional a la mida de l'animal (LCC), excepte en *I. aurelioi* (i pot ser de forma menys marcada a *I. horvathi*) que tenen hemipenis notablement petits. Pel que respecta a la microornamentació genital, totes les *Iberolacerta* s. str. (*I. monticola*, *I. galani*, *I. martinezricai*, *I. cyreni* i *I. horvathi*) tenen microornamentació genital coroniforme, es a dir, composta per tubercles més o menys allargats amb una corona d'espínules al seu àpex. Enmig d'aquests poden aparèixer tubercles aïllats d'altres formes rares, probablement corresponent a estadis no prou madurats. Les espècies del Pirineu (subgènere *Pyrenesaura*) són variables: *Iberolacerta bonnali* i *I. aranica* tenen principalment tubercles espiniformes (entre els quals poden aparèixer alguns coroniformes aïllats en algun exemplar), mentre que *I. aurelioi* té microornamentació coroniforme (amb alguns tubercles espiniformes aïllats, tal I com succeeix a altres espècies d'*Iberolacerta*). La meva hipòtesi es que els models coroniformes són derivats (més madurats, seguint un criteri ontològic) respecte als espiniformes, encara que alguns espiniformes (o digitiformes) poden ser reversions secundàries per maduració incomplerta. Aquests models secundàriament derivats i els primitius són impossibles o molt difícils de distingir. Fenòmens com les heterocronies podrien estar al darrere de aquestes aparents reversions o maduracions incomplertes.

PARAULES CLAU: Lacertidae; *Iberolacerta; I. monticola; I. m. astur; I. galani; I. martinezricai; I. cyreni; I. horvathi; I. bonnali; I. aranica; I. aurelioi*; Península Ibèrica; Hemipenis; microornamentació genital.

ABSTRACT

The hemipenis of all the *Iberolacerta* species is studied. Overall morphology is very similar among the different species. Hemipenes are symmetrically bilobed, with the apical section shorter than the basal one (*I. galani*, *I. cyreni*, *I. monticola monticola, I. horvathi*, *I. bonnali*, *I. aranica* and *I. aurelioi*) or subequal or with slightly inverted proportions (*I. m. astur* and *I. martinezricai*). All are similarly sized and proportional to the animal's SVL, except in *I. aurelioi* (and perhaps to a lesser extent in *I. horvathi*) that have notably small hemipenes. Concerning the hemipenial microornamentation, all the *Iberolacerta* s. str. (*I. monticola*, *I. galani*, *I. martinezricai*, *I. cyreni* and *I. horvathi*) have hemipenial microornamentation of crown-shaped tubercles, more or less elongated with a series or a crown of small spinules in their apex. Among these, isolate odd shaped tubercles can appear, probably corresponding to immature states that do not reach their complete development. The Pyrenean species (subgenus *Pyrenesaura*) are variable. *Iberolacerta bonnali* and *I. aranica* have mainly spiny-like tubercles (among which some crown shaped can appear), whereas *I. aurelioi* presents crown-shaped microornamentation (with scattered spiny-like, as occur in other *Iberolacerta* species). Our hypothesis is that crown shaped models are derived (or more mature, following an ontogenetic criterion) in respect to the spiniform ones, but some spiny (or finger-shaped) can be secondary reversals by incomplete maturation. These secondary derived and the original primitive spiny-shaped ones are very difficult if not impossible to distinguish. Phenomena as the heterochronies could be beneath these reversals in maturation.

KEY WORDS: Lacertidae; *Iberolacerta; I. monticola; I. m. astur; I. galani; I. martinezricai; I. cyreni; I. horvathi; I. bonnali; I. aranica; I. aurelioi*; Iberian Peninsula; Hemipenial microornamentation.

RESUMEN

Se han estudiado los hemipenes de todas las especies de *Iberolacerta*. La morfología general es muy similar entre ellas. Los hemipenes son simétricamente bilobulados, con la sección apical más corta que la basal (*I. galani*, *I. cyreni*, *I. monticola monticola, I. horvathi*, *I. bonnali*, *I. aranica* e *I. aurelioi*), o bien subigual o de proporciones ligeramente invertidas (*I. m. astur* e *I. martinezricai*). Todos tienen hemipenes de tallas similares y proporcionadas al tamaño del animal (LCC), excepto en *I. aurelioi* (y quizá, aunque en menor medida en *I. horvathi*) que tiene hemipenes notablemente menores. Por lo que respecta a su microornamentación, todas las *Iberolacerta* s. str. (*I. monticola*, *I. galani*, *I. martinezricai*, *I. cyreni* e *I. horvathi*) tienen microornamentación de tubérculos coroniformes, más o menos elongados y con una serie o una corona de pequeñas espínulas en su ápice. Entre estos, pueden aparecer tubérculos de formas aberrantes, probablemente correspondientes a estados inmaduros que no han alcanzado su desarrollo completo. Las especies pirenaicas (subgenero *Pyrenesaura*) son variables: *Iberolacerta bonnali* e *I. aranica* tienen principalmente tubérculos espiniformes (entre los cuales pueden aparecer algunos coroniformes), mientras que *I. aurelioi* presenta microornamentación coroniforme (con algunos espiniformes dispersos), tal como ocurre en otras *Iberolacerta* s. str. Mi hipótesis es que los modelos coroniformes son derivados (o más maduros, siguiendo un criterio ontogénico) respecto a los espiniformes, pero algunos espiniformes (o digitiformes) podrían ser reversiones secundarias por una maduración incompleta. Estas microornamentaciones espiniformes secundariamente derivadas y las espiniformes primitivas son muy difíciles si no imposibles de distinguir. Fenómenos como las heterocronías podrían estar detrás de estas reversiones en la maduración.

PALABRAS CLAVE: Lacertidae; *Iberolacerta; I. monticola; I. m. astur; I. galani; I. martinezricai; I. cyreni; I. horvathi; I. bonnali; I. aranica; I. aurelioi*; Península Ibérica; Hemipenes; microornamentacion genital.

INTRODUCTION

Hemipenes are the paired and eversible copulatory organs of male Squamates. These organs are symmetrically bilobed, with a common basal section or pedicel, and an apical section corresponding to the lobes. Hemipenes also have an outer groove called the *sulcus spermaticus*, which transports sperm through the outside face, rather than the inside of the organ. Hemipenes are everted by the contraction of a propulsor muscle and the simultaneous relaxation of the retractor ones, as well by the entry of fluid in the tissues (blood and lymph sinuses of the hemipenis wall) (RAXWORTHY, 2012).

Edward Drinker Cope first draw attention to the importance of the hemipenes in taxonomy (COPE, 1895) but other much authors have used them in Squamate systematics, especially in some groups as Anoles, Chameleons and Snakes (SMITH, 1943; EBERHARD, 1985; BÖHME, 1988; MYERS & CADLE, 2003; KLACZKO *et al*.,2015). The genital morphology has been utilized from time ago as a source of useful systematic characters to develop and improve phylogenetic hypothesis in a wide number of taxonomic groups. 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, etc. (e.g. WÖPKE, 1930; KLEMMER, 1957; BURT, 1960; DOWLING & SAVAGE, 1960; ZUG, 1966; ARNOLD, 1973, 1986; and BÖHME, 1988, among much others). They are especially interesting in sibling species which happen to be difficult to discriminate externally, and in some group as the Anolines seem to evolve faster than the external morphological characters (KLACZKO *et al*., 2015; D'ANGIOLELLA *et al.,* 2016).

It is believed that closely related species share very similar genital organs, independently from the evolutive pressures which make very different their external morphologies, and conversely, that genital morphology is different even in externally very uniform groups as the lacertids (ARNOLD, 1986). The main interest of the study of genitalia resides in his supposed independence from evolutive pressures which affect other morphological characters.

Hemipenes are supposed to fit following the model of the "Lock and Key mechanism", first enunciated by the French entomologist León Dufour (DUFOUR, 1844) that postulated that the male genitalia fit into the female ones (of the same species) in this way, and imperfectly in other species, thus preventing or difficulting interspecific copulation. Hence, species with bifurcated hemipenes have females with bifurcated cloacae; species with hemipenial spikes have females with thicker cloacal walls, and species with different sized hemipenis have females with the same proportional genitalia.

The function of the macroscopic ornamentation of the hemipenes (i. e. spines) is explained by the "Sexual Conflict Theory" that postulates that spines (and other structures) in hemipenes are traits to assist in longer and more successful reproduction for males. Such hemipenial structures are suggested thus to play a functional role in couple-anchoring during copulation. Females, however avoid excessive long copulations with strong vaginal contractions that prevent longer mating.

Also SALES-NUNES *et al*. (2014) finds a relationship between the development of spines and the limb reduction in Gymnophtalmids.

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 be gone accumulating slowly as a pleiotropic by-product of other changes in diverse parts of the body. However, although the mutations that give place to these pleiotropic changes are originally beneficial, they can imply a reduction of the reproductive fitness, for the one which ARNOLD (1973) supposes that a normalizing selection exists that returns the genital organ to near its initial level of efficiency, suppressing great part of the pleiotropic change produced. This would explain the similarities between the genital organs in closely related species. Also, simultaneously it would take place a parallel adaptation of the female reproductive organs that would be selected in order to balance these changes. Because of this, in the population where these changes occur, there is a return to the optimum situation of reproductive efficiency. This means that the two types of genitals would return to their full efficiency but without returning to their initial exact morphology (ARNOLD, 1983).

Although in the lacertids the hemipenes could provide interesting information, the habitus of everted organs in this group is very similar and usually doesn't offer many diagnostic characters, since differences in connection with the pattern of sexual behaviour and the female reproductive organs don't exist, and don't condition changes in the morphology of the hemipenes.

Also, the detailed study of the micro-ornamentation of the hemipenial epithelium during the reproductive period reveals the existence of microscopic tubercles which can differ in form between the different species. The development of this epithelium is controlled by hormonal changes which accompany the reproductive cycle. This epithelium develops in the form of tiny thorns or tubercles, each one of which is a unique epithelial cell (BÖHME, 1971, 1993) that could appear in the form of a thorn finished in a point more or less rounded and more or less curved (finger-shaped, hooked or spiniform microornamentation), forked (forked micro-ornamentation), or as a small tubercle with minuscule spiniform prolongations in his apex (crown-shaped micro-ornamentation) (KLEMMER, 1957; BÖHME, 1971;

ARNOLD, 1973, 1986, 1989; ARRIBAS, 1994, 2001). This epithelium and its microornamentation are shed almost every day during the breeding period (In den BOSCH, 2001). Until the date, it has been admitted that intraspecific variations in mature epithelia don't exist, turning the thorny epithelium of the hemipenis in a useful systematic character (BÖHME, 1993).

The use of hemipenial microornamentation with taxonomic and systematic purposes in Lacertids goes back to the work of KLEMMER (1957), and above all, to BÖHME (1971), which gives a good revision of the microornamentations coming from a great number of species. Also, other authors have utilized it subsequently, as ARNOLD (1973, 1986, 1989), ARRIBAS (1993, 1994, 2001), BÖHME (1993), and LEPTIEN & BÖHME (1994). Data on the Pyrenean species of *Iberolacerta* are in ARRIBAS (2001). In this paper hemipenes of the other *Iberolacerta* (s str.) species are described.

MATERIAL AND METHODS

Specimens studied:

The genital morphology of *Iberolacerta* s. str. has been studied, as well as their hemipenial microornamentation. Specimens come from the following locations:

-*Iberolacerta monticola monticola* (Boulenger, 1905):

Vilarello de Ancares (Lugo, Spain) (EBD 25644).

Vega de Enol (Asturias, Spain) (OA86072401).

-*Iberolacerta monticola astur* Arribas & Galan, 2014:

Salientes (León, Spain) (OA08080706)

-*Iberolacerta galani* Arribas, Carranza & Odierna, 2006:

Laguna de los Peces (Zamora, Spain) (OA04082504)

El Teleno, Corporales (León, Spain) (OA08071001)

-*Iberolacerta martinezricai* (Arribas, 1996):

Peña de Francia (Salamanca, Spain) (OA07070602)

-*Iberolacerta cyreni cyreni* (Müller & Hellmich, 1937):

Puerto de Navacerrada (Madrid-Segovia, Spain) (OA89082702, OA93090007)

-*Iberolacerta c. castiliana* (Arribas, 1996):

Candelario (Salamanca, Spain) (OA08072303)

-*Iberolacerta horvathi* (Méhely, 1904):

Pian dei Spadovai (Udine, Italy) (OA90070701)

The three Pyrenean species of *Iberolacerta* (subgenus *Pyrenesaura* Arribas, 1999) were studied in ARRIBAS (2001) and were from:

-*Iberolacerta bonnali* (Lantz, 1927):

Bigorre (H.P., France) (OA95061404, OA95061409), Monte Perdido (Hu., Spain) (OA92050002, OA92050003; and 3 specimens without number), Posets (Hu., Spain) (OA95070805), Maladeta (Hu., Spain) (OA95090101), Aigüestortes National Park (L., Spain) (OA93071601.).

-*Iberolacerta aranica* (Arribas, 1993):

Coll de Barradós (L., Spain) (OA95082703; OA95061901; OA95061902; OA95061910), Port d'Orlà (L., Spain) (OA95070108, OA95070111).

-*Iberolacerta aurelioi* (Arribas, 1994):

Pica d'Estats (L., Spain) (OA93070405; OA93070401; OA93081001), Port de Rat (Andorra-Ariège) (OA95060601, OA95060608; OA95060601).

Study of the hemipenial morphology:

In order to perform it, we proceed to the study of 'in situ' everted hemipenes from conserved specimens (general hemipenial morphology) by post mortem amputation in specimens previously fixed in the field with their hemipenes everted (hemipenial microornamentation). In all cases, this 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 Camera Lucida of Zeiss type coupled to a binocular stereoscope and from photographs.

The anatomical nomenclature of the hemipenis follows ARRIBAS (2001).

<u>Study of the hemipenial microornamentation</u>:

For the study of the microornamentation, we underwent the hemipenes or their lobes to a standard process of dehydration by means of immersion in an alcohol (ethanol) series of increasing graduation (70°, 90°, 100°) during periods of 12 hours in each one of them. Subsequently we finished the dehydration introducing the material in xylene during 2 to 6 hours and in paraffined xylene during the same period. Finally, it was included in fused paraffin during 8 hours. These blocks can be stored indefinitely until their study.

After the inclusion, the resulting blocks were cut, deparaffined with xylene (15 min.) and rehydrated with alcohols of decreasing graduation (100°, 90°, 70°) and finally distilled water (5 to 10 min. in each one of them), previous to the observation in an optic microscope at 400 x.

RESULTS AND DISCUSION

-<u>Considerations about methodology</u>:

Hemipenis extraction is a delicate question, as both an overinflating as underinflating result in deformed hemipenis and thus the samples become incomparable.

In conserved specimens, it is impossible to evert hemipenis, as the Retractor Magnus muscle retains the organ inside the body. Hemipenis can be dissected and compared directly as can be seen in ARNOLD (1986).

Usually, the procedure to fix everted hemipenis consists into injecting preservative fluid in the lower surface of the tail basis. This emulates the natural fluids during the hemipenis eversion under natural circumstances. When the hemipenis is considered sufficiently everted, the animal shall be put carefully in the fixative, avoiding the contact with other thigs in order not to deform its fixation. This is the method used here. I recommend photographing the hemipenes recently everted, previously to their fixation. This last process can deform the structures due to contact with other specimens or to shrinkage.

Another method suitable, used for the endophallus of beetles (MEURGUES & LEDOUX, 1966) can be applied easily for hemipenis in fresh specimens to be fixed. With a syringe the hemipenis is filled up from the tail basis (as described above for ethanol fixation) with a mixture of hot glycerine and gelatine. When the mixture is cooled, it maintains the shape. This avoids the danger of deformation during the fixation.

Another system is an adaptation of the BERLOV (1992) procedure. Hemipenis is filled with sufficiently fluid toothpaste, and then dried with a glow-lamp, depending the time of the size of the hemipenis. These substances usually do not shrink after the drying process. Also, light-curing dental composites as those used in stomatology can be used, but they have a high price and they are not ever available. Hence, toothpaste is a good alternative. Time resistance of these preparations is variable. With beetle endophallus some of them resist more than a decade, whereas others became damaged by the growth of salt crystals (JANOVSKA *et al.,* 2013).

-<u>*Iberolacerta* hemipenial morphology</u>:

Size and shape:

The overall hemipenial **morphology and proportions** in *Iberolacerta* (s. str.) is, as in the Pyrenean species, nearly equivalent in all of them, showing the typical pattern seen in all the lacertids (see ARNOLD, 1986 for a detailed description of a typical lacertid hemipenis) (Figs. 1 & 2).

The hemipenes are symmetrically bilobed, with a common basal section or pedicel, and the proportions between the apical section (that is to say, the part corresponding to the lobes) and the basal part, variable. The apical section of each hemipenis is shorter than the basal one in *I.*

galani, *I. cyreni*, *I. monticola monticola* and *I. horvathi*. Also these same proportions were found in the three Pyrenean species (ARRIBAS, 2001). However, in the samples studied, their proportions can be subequal or even apparently inverted in *I. m. astur* and *I. martinezricai*. Apical part shorter than the basal one is typical for most of the Lacertidae, except *Podarcis*, *Anatololacerta*, *Iranolacerta* (almost in *I. zagrosica*), *Phoenicolacerta* (to a lesser extent), and is variable (as in *Iberolacerta*) in *Tachydromus*, all of them among the Lacertini. In the Gallotiinae as *Gallotia* and *Psammodromus* these proportions appear to be inverted (ARNOLD, 1973; ARNOLD *et al.*, 2007).

Concerning **size**, in Pyrenees *I. aurelioi* was found to have clearly smaller hemipenes than the other two Pyrenean species (Fig. 1), a phenomenon that is translated into a markedly less enlarged tail basis in the males of this taxon, easily visible in live specimens (ARRIBAS, 2001). In *I. bonnali* and *I. aranica* it is easy to discern males from females by their enlarged tail basis, as it is usual in Lacertids, whereas in *I. aurelioi* this is not possible without a detailed examination of other sexually dimorphic characters of the specimens (as the pattern of coloration and femoral pores). In the Iberian *Iberolacerta* (s. str.) all the hemipenes studied were “big”, namely, normally in proportion to the animal size. In *I. horvathi* the hemipenes of the only studied specimen (a young male) were very small, similar to the *I. aurelioi* ones. However, due to the size and age of the studied *I. horvathi*, the results must be taken with caution.

Some marked differences between closely related lacertids have arisen as physical isolating mechanisms, as also was suggested by ARNOLD (1983) in *Acanthodactylus,* and ARNOLD (1986) in *Mesalina*. In these genera, it has been demonstrated that in sympatry between closely related species, modifications appear which prevent the hybridization. These modifications are the reduction in size of the male copulatory 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). ARRIBAS (2001) suggested that the differences in hemipenis size in *I. aurelioi* could be a case of character displacement caused by past contact with *I. aranica*. In the case of *I. horvathi*, if the relative small size is confirmed, it would bemore difficult to explain, as this is the only *Iberolacerta* in their area where is largely sympatric only with *P. muralis*, that belongs to a well different genus and with which it do not hybridizes. However, other *Iberolacerta* are largely sympatric (not syntopic) or parapatric with *P. muralis* and this phenomenon is not observed.

All the *Iberolacerta* species have hemipenial **lobes** with plicae. The lobes surface appears typically plicate from the apex towards the base, as is habitual in the whole of the Lacertidae (except in *Parvilacerta*). The apex of the lobes lack macroscopic papillae, thorns or tubercles of the type of those which appear in the most primitive species of the group (*Gallotia*, *Psammodromus* spp. -the small species of the genus- and some *Podarcis*). There is no armature or folding of lobes in retracted hemipenis.

The **sulcal lips** are variable in size. The sulcus spermaticus is clearly visible in all the species with a level of development in the outer lip different between the species. It is fairly big in *I. horvathi*, moderately big in *I. m. astur* and *I. martinezricai*, and moderately small or small in *I. galani*, *I. m. monticola* and *I. cyreni*. In the *Pyrenesaura* is also variable: *I. bonnali* presents an external lip with a noticeable development, but this is much more modest in *I. aurelioi* and *I. aranica*. Big lips in the sulcus spermaticus appear typically in *Podarcis*, *Anatololacerta*, *Phoenicolacerta*, *Scelarcis*, *Atlantolacerta* and some *Takydromus* (where also, as in *Iberolacerta*, is variable) whereas especially small lips appear in *Algyroides* (ARNOLD, 1973, 1986; ARNOLD *et al*, 2007).

- Hemipenial microornamentation:

The microornamentation of all the *Iberolacerta* s. str. here studied coincides with data known from bibliography. *Iberolacerta martinezricai* and *I. galani* had crown shaped tubercles, as those already known from *I. horvathi*, *I. monticola* and *I. cyreni*. In the Pyrenean species *I. aurelioi* also shares this model, whereas *I. aranica* and *I.*

bonnali present mainly spiniform (also called digitiform) tubercles (ARRIBAS, 2001) (but see below) (Figs. 1 & 2, right side).

Spiniform microornamentation appears in *Apathya*, *Archaeolacerta*, *Hellenolacerta*, *Podarcis*, *Scelarcis*, *Timon* and all the Eremiadini studied. They are more rod-like in *Takydromus* (although still often recurved at their tips) and can be considered as a microvariant of this same model. In many other forms of the Lacertini the tubercles are crown-shaped, being blunt but with a number of spinules at their tips. In *Lacerta* s. str. the lobe flanks are covered by long and fairly straight (not recurved as the spiniform model) projections that end in a point or in a series of spinules (as the crown-shaped) (BÖHME 1971), thus coexisting both models. The same seems to occur in *Timon princeps*, but here the projections tend to curve towards the base of the organ (ARNOLD *et al*. 2007). *Parvilacerta* is distinctive in having a proportion of tubercles that are forked (these forked or similar ones can appear isolate in specimens of other genera- see for instance in *I. martinezricai* and *I. m. astur* here represented; Fig. 2).

Both main types of microornamentation appear in closely related (congeneric) species, like *Omanosaura cyanura* and *Omanosaura jayakari* (ARNOLD, 1973), or the Western versus Eastern Mediterranean species of *Algyroides* (BÖHME, 1971; ARRIBAS, 2012), and even coexist together in different parts of the same hemipenis as in *Lacerta* s. str. or *Timon princeps* (see above): long and pointed – digitiform - on the plicae covering the lobe flanks but tubercular and minutely spinose - crown-shaped - on the lobe apices; BÖHME, 1971; ARNOLD, 1986; ARNOLD *et al.* 2007). Also inside *Iberolacerta*, and more in concrete inside *Pyrenesaura*, both models coexist in different closely related species.

Also, both microornamentation types appear to be completely blended between the different otherwise internally homogeneous genera of the Lacertini. This has led 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). Theoretically this assumption of BÖHME (1993) seems correct, as it is more reliable that the spiniform model, the ontogenetically primitive, in some species reaches its full development (crown-shaped) whereas in others it stops its development in an earlier phase (spiniform) (ARRIBAS, 1997, 2001). This occurs independently in every genus or even in every species, leading to the confuse distribution of both models currently found among the Lacertini. In support of this comes the observation that in every specimen of the crown-shaped species, there appear scattered, here and there, some “immature” finger (or spiny) shaped ones. Thus, we find now that a part of the spiny-like microornamentations could be secondary reversals due to the lack of complete development, and that are virtually indistinguible from the primitive spiniform ones (ARRIBAS, 2001).

A good part of the spiny microornamentations that appear in these species, and especially when both models appear blended in closely related species, could be reversals to the primitive model, namely, they are apomorphic spiny microornamentations indistinguishable from the in theory more plesiomorphic ones. Such an evolutive apparent change of character polarity could have been arisen by a mechanism of heterochrony, which could have impeded the complete development of the tubercles of the hemipenial microornamentation to its more developed state (the crown-shaped one). In support of this theory comes the fact that subadult specimens or adults with incomplete matured epithelia, included in species with model usually crown-shaped, present spiny-like models. The cases of *I. bonnali* and *I. aranica* can be reversals or underdeveloped microornamentations regarding the primitive crown-shaped (among the *Pyrenesaura*) model shown by *I. aurelioi*. This fact is confirmed by the find of some crown-shaped tubercles fully developed in individuals of the first two species (*I. aranica* and *I. bonnali*) usually with spiniform microornamentation, and because the crown-shaped micrornamentation is the most widespread model in other species closely related to this group, like all the *Iberolacerta* (s. str.) here studied. In these *Iberolacerta* s. str. (as in *I. galani* and *I. martinezricai*; Fig. 2) among the crown-shaped tubercles (mature) there appear also some immature finger-shaped or even forked-like ones. In the case of the Pyrenean species, linked to extreme habitats, the predominance of the spiny or finger-shaped models could be an indicative of a significant paper from the activity cycle reduction in this incomplete development (heterochrony?) of the microornamentation.

CONCLUSIONS

Morphology of the hemipenis:

1.- Hemipenis overall morphology from all the *Iberolacerta* is very similar among the different species and with other small Lacertini.

2.- Hemipenes are symmetrically bilobed, with the apical section shorter than basal one in *I. galani*, *I. cyreni*, *I. monticola monticola, I. horvathi*, *I. bonnali*, *I. aranica* and *I. aurelioi*. The proportions can be subequal or even slightly inverted (apical part greater than the basal one) in *I. m. astur* and *I. martinezricai*.

3.- All the hemipenes are similarly sized and proportional to the animal's SVL, except in *I. aurelioi* that has notably small hemipenes, and therefore less bulky tail basis in males. This character could have arisen as a character displacement in a past sympatry with *I. aranica* to prevent hybridization. *Iberolacerta horvathi* also seems to have relatively small hemipenes.

4.- The development of the sulcal lips is similarly variable in all the species. The most developed external lips appear in *I. bonnali* and *I. horvathi*.

Microornamentation of the hemipenis:

5.- All the *Iberolacerta* s. str. (*I. monticola*, *I. galani*, *I. martinezricai*, *I. cyreni* and *I. horvathi*) have hemipenial microornamentation of crown-shaped type, this is blunt tubercles, more or less elongated with a series or a crown of small spinules in their apex. Among these, isolate odd shaped tubercles can appear: finger (or spiny-like) or bifurcated ones, probably corresponding to immature states that do not reach their complete development.

6.- The Pyrenean species (subgenus *Pyrenesaura*) are variable. *Iberolacerta bonnali* and *I. aranica* have mainly spiny-like tubercles (among which some crown shaped can appear), whereas *I. aurelioi* presents crown-shaped microornamentation (with scattered odd-shaped ones -for instance spiny-like-, as it happens in other *Iberolacerta* species).

7.- The presence of scattered spiniform (or digitiform) tubercles among the crown shaped ones in *Iberolacerta* (s. str.) suggests that the later are the mature ones, and the former the immature ones.

8.- On the contrary, in *Iberolacerta* (*Pyrenesaura*), the occasional presence of some crown-shaped tubercles among the spiniform ones (in *I. bonnali* and *I. aranica*) suggests that in fact their microornamentation was originally similar to the other *Iberolacerta*, but simply the epithelia do not reach the mature stage (a state that is reached in *I. aurelioi*).

9.- This complete or incomplete maturation of the hemipenial microornamentation could be linked, in the case of *Iberolacerta* (and especially in *Pyrenesaura*) to heterochronies and/or to the duration of the annual cycle.

10.- Our hypothesis is that crown shaped models are derived (or more mature, following an ontogenetic criterion) with regard to the spiniform ones, but some spiny (or finger-shaped) can be secondary reversals by incomplete maturation. These secondary derived and the original primitive spiny-shaped ones are very difficult if not impossible to distinguish.

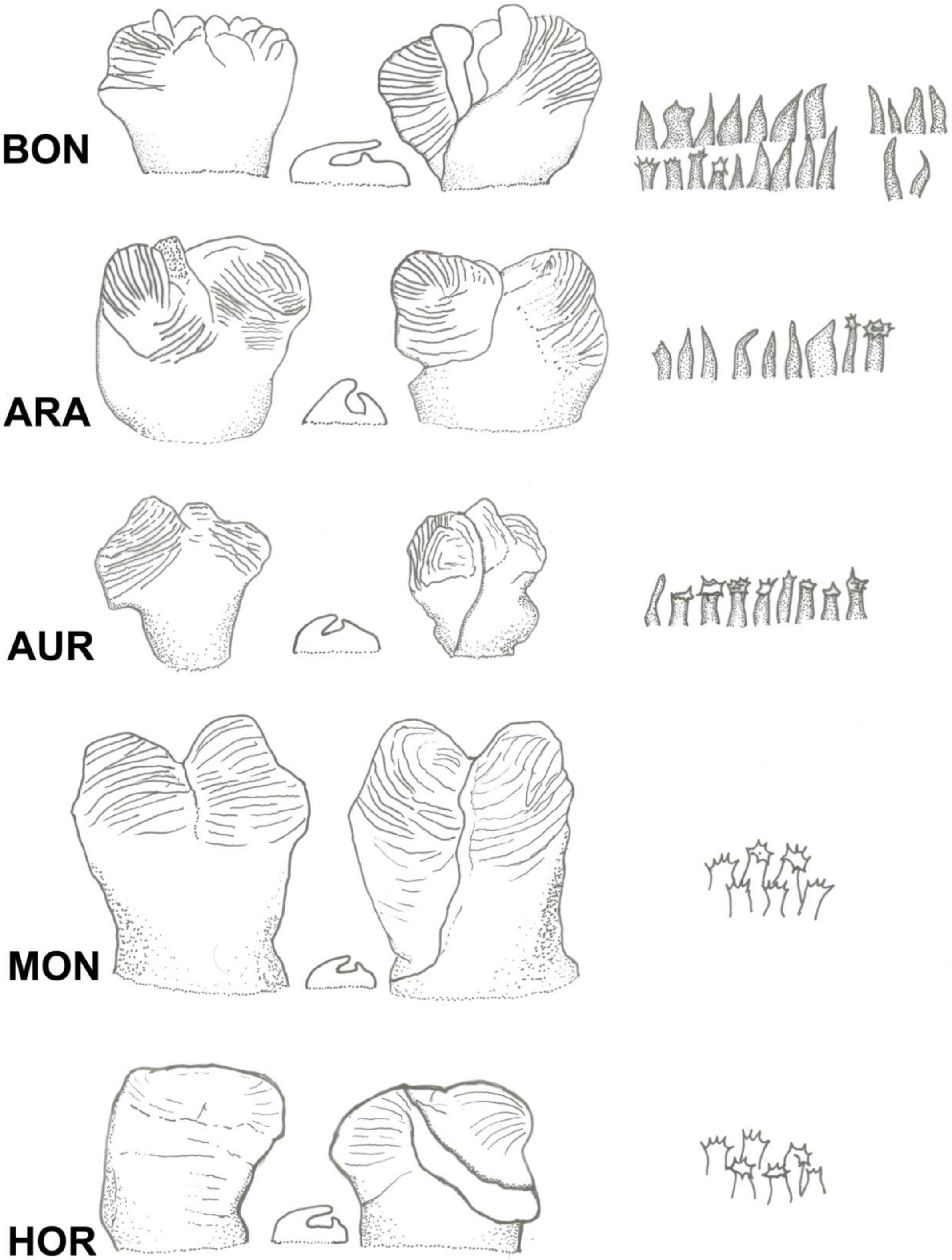

Fig.1 - Morphology the hemipenes and hemipenial microornamentation. From left to right: Asulcal view of hemipenis, section of the Sulcal Lips, Sulcal view of hemipenis (the basal origin of the sulcus is lateral-posterior in the hemipenis everted position) and hemipenial microornamentation of the lobes from (from top to bottom): *Iberolacerta bonnali* (Lantz, 1927) **[BON]** from Bigorre, Hautes Pyrénées, France [microornamentation. Upper left: Bigorre, Hautes Pyrénées, France; Upper right: Maladeta, Huesca, Spain (=S); Lower left: Monte Perdido, Huesca, S; Lower right: Aigüestortes, Lleida, S]; *Iberolacerta aranica* (Arribas, 1993) **[ARA],** Serra de Pica Palomera, Lleida, S; *Iberolacerta aurelioi* (Arribas, 1994) **[AUR]**, Port de Rat, Andorra [microornamentation from Pica d'Estats, Lleida, S]; *Iberolacerta monticola monticola* (Boulenger, 1905) **[MON],** Vilarello de Ancares, Lugo, S; *Iberolacerta horvathi* **[HOR]** (Méhely, 1904), Pian dei Spadovai, Udine, Italy. Microornamentation: tubercles stippled (BON, ARA, AUR) from Arribas (2001) and only outlined ones (MON, HOR) from Böhme (1971).

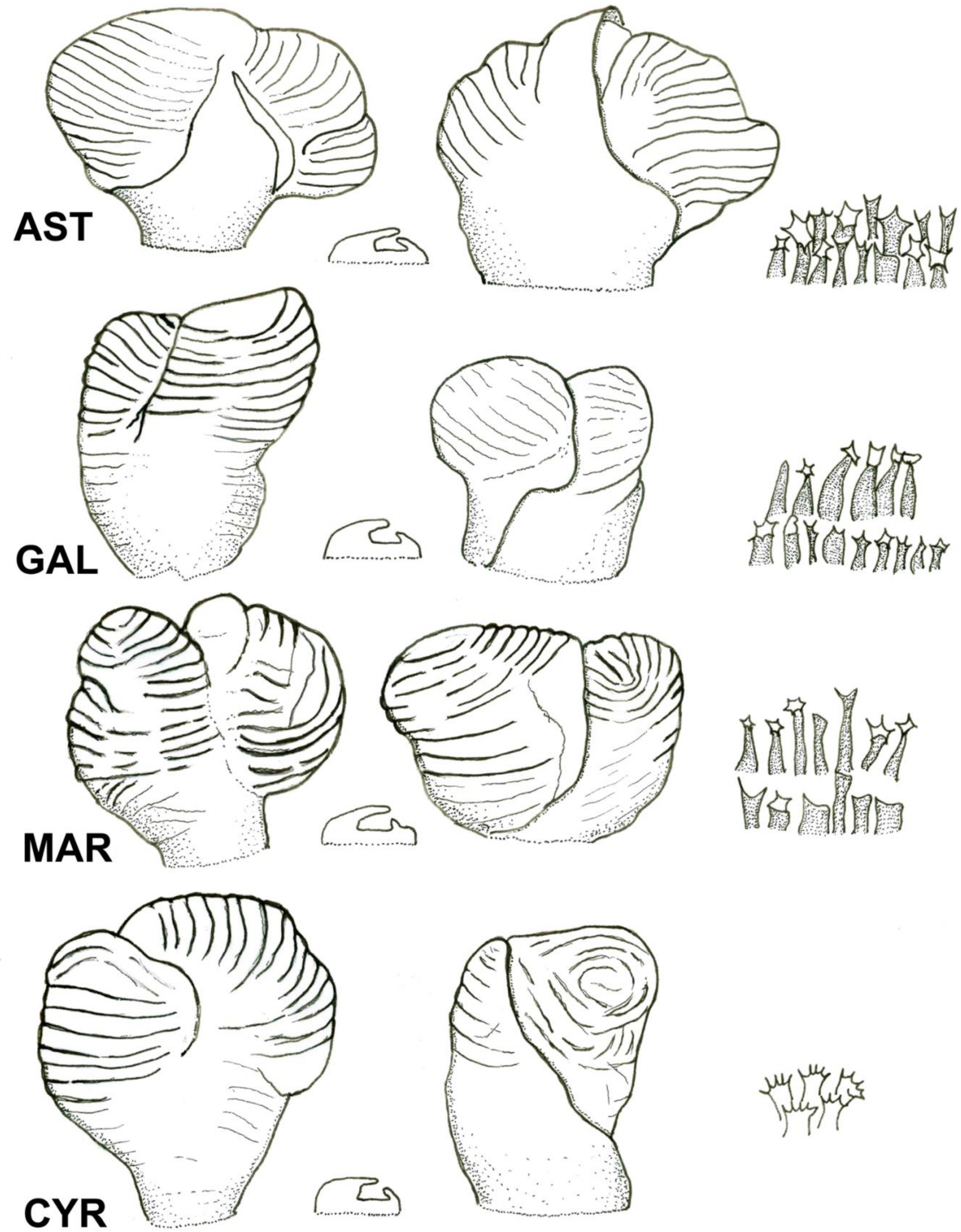

Fig.2 - Morphology the hemipenes and hemipenial microornamentation. As in Fig 1. (from top to bottom): *Iberolacerta monticola astur* Arribas & Galán, 2014 **[AST],** Salientes (León, Spain); *Iberolacerta galani* Arribas, Carranza & Odierna, 2006 **[GAL],** Laguna de los Peces (Zamora, Spain) [microornamentation from El Teleno (Corporales, León, Spain)]; *Iberolacerta martinezricai* (Arribas, 1996) **[MTN],** Peña de Francia (Salamanca, Spain); *Iberolacerta cyreni* (Müller & Hellmich, 1937) **[CYR],** Puerto de Navacerrada (Madrid-Segovia, Spain). Microornamentation: tubercles stippled (AST, GAL, MTN) original (this paper) and only outlined one (CYR) from Böhme (1971).

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