

Why copulatory organs provide so many useful taxonomic characters: the origin and maintenance of hemipenial differences in lacertid lizards (Reptilia: Lacertidae)

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Received 16 May 1986, accepted for publication 7 August 1986

The structure of copulatory organs is used very widely in systematics, both for differentiating species and for working out relationships. Differences between taxa may arise from a variety of sources, including non-homology, differences in other parts of the animal, direct selection on copulatory organs, development of physical isolating mechanisms and pleiotropic events. Physical isolating mechanisms seem likely to account for the abrupt differences, involving size, asymmetry and simplifications, that are useful in distinguishing very similar lacertid species. Although these differences usually seem to arise at the end of a speciation event they can simultaneously be the initiating mechanism in a second one. Copulatory organs appear to have high inherent stability, probably resulting from frequent location in strongly homocostatic environments, single function, insensitivity to niche shift and inertia due to the need to conform to the genitalia of the opposite sex. This stability may be overridden at times by direct selection on the organs themselves or pleiotropic events. Such changes tend to be retained because efficiency in copulation depends not on any absolute genital architecture but on close conformity of the organs. It is the combination of relative stability and tangible input of varied change, which tends to be retained, that so often makes these structures good indicators of relationship.

KEY WORDS:—Systematics – genitalia – isolating mechanisms – speciation – phylogeny estimation – character weighting – lacertid lizards.

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INTRODUCTION

In many groups of animals, copulatory organs provide a very significant proportion of the characters used in systematic studies. This applies especially to the intromittent organs of males which are used widely in the taxonomy of, amongst others, beetles, butterflies and moths, grasshoppers, molluscs, some live-bearing fishes and elasmobranchs, snakes, lizards and some mammal groups. Indeed, so important are genital features in the first two assemblages that accounts of their variation running to hundreds of pages have been produced (Sharp & Muir, 1912; Jaennell, 1955; Higgins, 1975) and a substantial glossary of insect genitalia in general also exists (Tuxen, 1970). Large differences in male genitalia often allow otherwise very similar and, on other grounds, closely related species to be distinguished with ease. Yet, in some cases, the organs are very uniform in at least certain aspects of their morphology and are characteristic of a whole genus or other higher taxon. Where different groups have copulatory organs incorporating similar derived features, it frequently turns out, on further investigation, that they are closely related, whereas groups with markedly different genitalia often are not.

At first sight, the great difference between copulatory organs that may occur among close relatives is quite strange, since these structures perform the same rather simple function in the forms concerned, namely the transfer of sperm from the male to the female. This diverse morphology associated with uniform function contrasts with the situation in most other organ systems, which tend to be anatomically similar in close relatives unless they perform different functions or operate in conditions that put different constraints on them, for instance when the species occupy very different habitats or exploit different resources. Again, it is puzzling that features apparently capable of rapid evolutionary change, so that they may be radically different in otherwise scarcely separable sister species, are often quite constant through speciose higher groups, suggesting that change may sometimes be very slow or absent.

These apparent paradoxes raise a series of questions: (1) what are the sources of variation in copulatory organs? (2) why do the copulatory organs of close relatives often diverge so much? (3) why, on the other hand, are they sometimes quite uniform throughout large groups? and (4) why do they frequently reflect higher relationships so well? These points will be discussed with reference to squamate reptiles, particularly lacertid lizards, a group in which systematics, ecology and genital structure are quite well known.

THE COPULATORY ORGANS OF LACERTID LIZARDS

Structure and variation of male copulatory organs in lacertid lizards has been reviewed elsewhere (Arnold, 1973, 1983, 1986). Like those of all squamate reptiles they are paired structures, the hemipenes. In its functional position a hemipenis projects from the hind wall of the vent and semen is conducted along a groove on its surface, the *sulcus spermaticus*. Each, usually bilobed, organ is hollow and, when not in use, retractor muscles turn it inside out and withdraw it into the tail base. Many, although not all, lacertid hemipenes have an internal supporting structure found in no other group, the armature, which consists of dense connective tissue. This is more robust than the hemipenis and

sometimes more easily studied than the copulatory organ itself when this is retracted, the usual condition in preserved specimens.

During copulation a single hemipenis is inserted into the genital sinus (sinus génitale: Gabe & Saint-Girons, 1965) of the female, which lies above the cloaca and receives the outlets of the oviducts. The sinus of lacertids is usually a well-defined, thick-walled structure, although it must stretch and deform when eggs pass through it during oviposition. At other times it shows substantial conformation in shape and dimensions to the hemipenis of the species concerned.

As hemipenial variation in the Lacertidae has been described in detail in other publications, it will be dealt with only briefly here, although some specific examples of the kind of variation mentioned in the introductory section are discussed more fully on p. 274. Among apparently derived features of the hemipenis are the following: marked reduction in size; elongation of the lobes; reduction or absence of one lobe, and, where present, the corresponding side of the armature; coarse folding of the functional surface of the retracted hemipenis; sulcus spermaticus dividing before the bifurcation of the organ; large or very small sulcal lips; absence of fine plicae on the lobes; presence of flaps, large spines or terminal awns; various modifications of the armature including the shape of the intramuscular plate and clavulae; attachment of the clavulae directly to the lobes and the number and course of the connectors.

POSSIBLE ORIGINS OF INTERSPECIFIC DIFFERENCES BETWEEN COPULATORY ORGANS

The interspecific differences encountered in copulatory organs have been attributed to a variety of causes and, undoubtedly, more than one factor is involved. Among the possibilities are the following.

Non-homology: Copulatory organs are not all homologous. Thus, the intromittent organs of insects are quite different in form and origin from those of molluscs, as are the paired, hollow eversible hemipenes of squamates from the single, essentially solid, unversible penes found in many other amniotes.

Differences in other parts of the body: For example, as in lizards, the hemipenes of snakes are stored within the tail when not in use and, as might be expected from this, very short-tailed snakes usually possess short hemipenes. Again, snakes have different problems from limbed lizards in maintaining coition and their frequently more spiny hemipenes may reflect the difficulties of retaining effective contact without legs. Neither non-homology nor differences in other parts of the body are likely to be significant determinants of genital structure in the Lacertidae which, in most respects, is a very uniform group morphologically.

Differences in copulatory position: Variation exists in the copulatory position adopted by different kinds of lizards and it could be expected that some differences in the copulatory organs are connected with this. However, although mating postures do vary among the Lacertidae (Böhme & Bischoff, 1976), they are not obviously related to differences in the hemipenis or genital sinus.

Direct selection on copulatory organs: Direct selection may produce changes increasing the efficiency of copulatory organs in particular circumstances or increasing the efficiency of their bearer in some other way.

Differences in the opposite sex: The effectiveness of copulatory organs depends on their close physical correspondence to those of the opposite sex. Consequently,

differences arising in one sex, from causes such as change in other parts of the body, and direct selection on copulatory organs (see above) could result in selection for changes in the other that would maintain a good match between the organs (p. 272).

Development of physical isolating mechanisms: One explanation, involving direct selection on copulatory organs and differences in the opposite sex (see above), put forward to explain genital differences is that they represent physical isolating mechanisms. Species likely to interbreed may evolve genitals of different size or form, or both, so that interspecific matings are prevented or at least made more difficult. At least two arguments can be brought forward against this hypothesis as a widely applicable explanation. First, substantial differences may occur between related forms that have very sophisticated pre-mating identification mechanisms, enabling the species concerned to recognize conspecific mates with great reliability, thus excluding the need for actual physical barriers to copulation. Such devices include species-specific pheromones and pre-mating displays. Secondly, since interspecific matings are generally more likely between close relatives, it would be expected that closely related and sympatric species would show differentiation in genitalia. This certainly occurs in a number of cases but, as noted in some taxonomic assemblages, the organs are remarkably uniform among closely related species but differ between species groups. This situation is present in *Lacerta* and its allies (Arnold, 1973).

Pleiotropic effects: Many genes are pleiotropic, that is they have more than one effect on the phenotype, so that selection producing alteration in one part of an organism may have linked effects elsewhere. Mayr (1970) suggested that genital differences might often be pleiotropic by-products of changes in the genotype, produced by selection acting on other parts of the animal. Again, as a total explanation, this gives rise to problems. It might be expected, if the degree of genital difference were entirely due to pleiotropic effects, that variation would be slight between very similar forms (i.e. where little separate evolution has occurred) and great between disparate ones, yet there are many exceptions. Also, it is not immediately obvious why genitalia should be especially prone to retain such pleiotropic effects.

Thus, there are difficulties with both physical isolating mechanisms and pleiotropic effects as widespread explanations. It might be argued that both these factors are involved, the former mainly at low taxonomic levels and the latter predominantly at higher ones. But characters morphologically likely to act as isolating mechanisms are often similar to some of those separating high level categories.

THE CASE FOR PHYSICAL ISOLATING MECHANISMS IN LACERTID LIZARDS

Evidence of interspecific mating

If evolution of physical isolating mechanisms is indeed a significant source of differentiation in the copulatory organs of lacertid lizards, then some evidence that mis-matings actually occur would be expected. Some species have elaborate pre-mating behavioural displays (*Lacerta* part I: Kitzler, 1940; Weber, 1957) but others copulate with few preliminaries (*Gallotia*: Böhme & Bischoff, 1976; *Mesalina adramitana*: personal observations in the United Arab Emirates;

Acanthodactylus schmidti: observations by A. Al-Johany near Riyadh, Saudi Arabia) and in these particularly, recognition of the correct partner could be fallible. However, natural interspecific matings are undoubtedly rare in most species and, given the fact that even intraspecific copulation is only occasionally seen in the field, they are unlikely to be observed. However, there are a number of indirect indications that such events do take place. Some lacertids will copulate with other species in captivity if denied their own mates and, on occasion, produce offspring (occurrences in *Lacerta* and *Podarcis* summarized by Arnold, 1973; Bischoff, 1973; see also Nettman & Rykena, 1974; Rykena & Henke, 1978; G. Webster, pers. comm., also reports copulation between *Lacerta lepida* and *L. viridis*). Similar events might be expected among wild lizards in situations where one species is at a low density relative to a sympatric form, and wild lacertids have been found which on the basis of their intermediate morphology seem to be hybrids (members of *Acanthodactylus*, *Lacerta* and *Podarcis*: see Arnold, 1973; Mertens, 1950, 1956, 1964, 1968, 1972). Although such rare instances of hybridization are unlikely to lead to the evolution of physical isolating mechanisms, they do suggest that pre-mating isolating mechanisms are not infallible, even in instances where sympatry without general hybridization indicates that they are usually very effective.

The most probable situation in which interspecific mating would occur frequently enough to promote the evolution of a new isolating mechanism is where previously separated populations, whether derived from some immediate ancestral species or not, come into contact for the first time. In these circumstances, if the species are relatively similar they may not be able to distinguish their own mates with certainty. An indication that this can occur is that a large proportion of captive interspecific matings are between animals from allopatric (geographically non-overlapping) populations. A natural example is provided by the *Lacerta saxicola* complex in the Caucasus, which includes a number of unisexual species. There is good evidence that these are of hybrid origin and that they arose when previously isolated bisexual species came into contact (Uzzell & Darevsky, 1975).

Costs of mating with individuals of other species

The development of such independent species from hybridization is of course not usual and, far more frequently, interspecific matings produce no young at all or offspring that are weak, sterile or have reduced fertility (cases in *Lacerta* part I reported by Bischoff, 1973, 1982). As such, they decrease the effective reproductive effort of their parents and devices to avoid such wasteful miscegenation would be expected to evolve. The costs of interspecific mating are unequally shared between the sexes. Although no proper data are available for lacertids, males of at least some lizards can copulate very frequently (Crews, 1978). Consequently, provided some matings are with females of his own species a male lizard will not diminish his reproductive potential catastrophically by copulating with females of other species, although obviously some cost is involved, both in energetic terms (Dewsbury, 1982) and in increased risk of predation during coition and its preliminaries. It may well pay in normal circumstances not to be excessively discriminating and risk losing the opportunity to fertilize eggs of females that are slightly atypical in appearance, behaviour or smell.

For females, the situation is quite different. The egg or eggs to be fertilized represent a substantial energetic investment and may form a large part of an individual's total reproductive effort. In the case of the iguanid, *Anolis carolinensis*, in the southeastern U.S.A., captive males mated once every 1.28 days on average (Crews, 1978). Females, on the other hand, only produced a single egg every 10–14 days (Crews, 1980) and in the wild are estimated to lay only seven eggs a year (Gordon, 1956). The differential between the sexes is probably much greater in lizards from cooler areas, where eggs are produced in a small total number of clutches. This is true of many lacertids: for instance, *Lacerta vivipara* in southern England produces a single clutch with a mean of 7.74 eggs each year (Avery, 1975a) and usually breeds for only 3–5 years (Avery, 1975b). If, like *Anolis carolinensis*, a female only mates once before each laying (Crews, 1980), a single interspecific copulation could result in 20–33% of her total reproductive capacity being lost. Members of the *L. saxicola* group in the Caucasus also produce a single clutch annually, while even in northwestern Africa *Acanthodactylus erythrurus lineomaculatus* and *A. pardalis* have only two (Bons, 1967) and *Mesalina rubropunctata* from the Algerian Sahara has three or four (Gauthier, 1966).

How physical isolating mechanisms might arise

It is likely that evolution of isolating mechanisms would be initiated by the females as they have most to gain by preventing cross-matings. Various devices could be advantageous, including pre-mating isolating mechanisms, but in the event of these not arising selection for physical isolating mechanisms that prevent mating might well occur. The most obvious kind would be extensive divergence in overall size, or at least diameter, of the copulatory organs of the forms concerned. This would be most likely to develop if one species, A, initially had some individuals with slightly smaller copulatory organs than those found in another species, B, which mated with it (Fig. 1A). In this situation, females of species A with genitals at the lower end of the size range of this form would be capable of mating with a smaller proportion of males of species B than of their own species. Consequently, their average reproductive success, in terms of number of offspring with both parents of species A, ought to be higher than for other females. Mean size of the genital sinus should consequently fall in subsequent generations of species A (Fig. 1B). Such reduction will favour small copulatory organs in conspecific males and the size of the hemipenis should therefore track that of the genital sinus. This process of reduction in size of copulatory organs would be expected to continue until all or most males of species B are incapable of mating with females of species A (Fig. 1C). There will be no selective pressure on species B to reduce the size of its hemipenis because copulation with females of species A is not advantageous to it. Such radical differences in the size of copulatory organs between pairs of similar, often closely related, species are known among the Lacertidae (p. 275). The initial difference in size of copulatory organs may sometimes be a concomitant of overall body-size differences, which are common among congeneric lacertids and might also evolve rapidly in strict sympatry, since lizard species in these conditions often eat different sizes of prey. Physical isolating mechanisms are likely to arise most quickly if the species that reduces genital size consists of a small, isolated

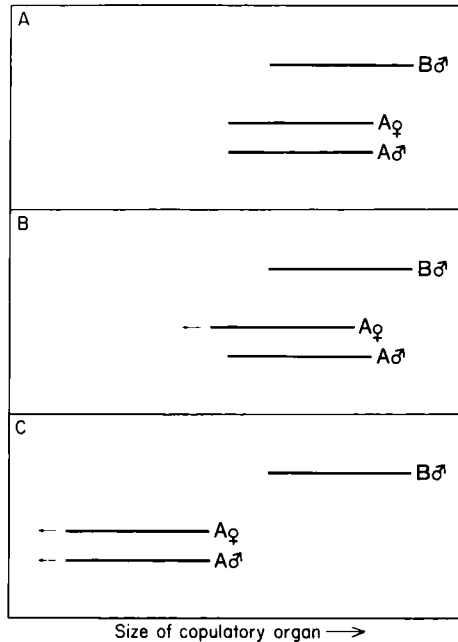


Figure 1. Possible sequence of events in the evolution of a physical isolating mechanism. A, Species A initially has some individuals with smaller copulatory organs than those of species B, which mates with it. B, Females of species A with small genitalia are more likely to mate with their own males than copulating, with less reproductive success, with males of species B. They will consequently contribute relatively more offspring to subsequent generations and average size of the female genital sinus will fall. C, This will favour small copulatory organs in conspecific males, so hemipenial size will track that of the genital sinus.

population, while the other has a larger range that entirely encompasses it. In this situation, the former is protected from gene flow from allopatric populations where there is no selection for reduction in the size of copulatory organs.

If cross-matings were reciprocal between the two species, would females of species B gain any advantage from divergence in size of the copulatory organs? This is uncertain: it seems probable that, after some reduction, the hemipenis of species A would not reach the optimal position for insemination but it might at least still be inserted into the entrance of the genital sinus of species B. In lacertid genera where divergence in genital size occurs (*Acanthodactylus*, *Eremias*, *Meroles* and *Mesalina*), the smaller organs are much below the average size for the group, whereas the larger ones are not much different. This indicates that divergence is asymmetrical, being produced by size reduction in one species without much enlargement in the other, which suggests that most advantage normally lies with the reducing species. It also supports the view that males do not initiate physical isolating mechanisms. If they did, the most probable way they would be excluded from the genital sinus of the other species would be by hemipenial enlargement and occurrence of especially large copulatory organs would be expected.

PHYSICAL ISOLATING MECHANISMS AND SPECIATION

The development of physical isolating mechanisms between sympatric species discussed above is at most the final stage of speciation, for it will only occur once

mis-mating is disadvantageous because the two forms concerned are already unable to interbreed very successfully. However, divergence in size of copulatory organs in these circumstances may be the primary factor in speciation between one of the forms concerned and another population. For instance, imagine a situation where a species has two populations, A and A', A' being a small isolate that becomes overrun by a second species, B (Fig. 2). A' might reduce genital size in response to the presence of B but, because of this reduction, also becomes incapable of breeding with the original conspecific population, A, which is likely to have retained copulatory organs of normal size. So, if A' and A subsequently come into contact, they would act as separate species.

ASYMMETRY AND SIMPLIFICATION OF THE HEMIPENIS IN LACERTID LIZARDS

In a number of diverse lacertids, the hemipenis is not regularly bilobed. Instead, one lobe is reduced or lost and the same usually applies to the armature on that side, if present. Reduction of the medial side of the hemipenis occurs in *Acanthodactylus* and *Philochortus*, while the lateral side is affected in *Eremias*, *Heliobolus*, *Latastia*, *Meroles* and *Mesalina*. Such modifications are not related to asymmetries in the female reproductive tract, but they are sometimes associated with reduced dimensions of the organ (for instance, in *Acanthodactylus maculatus* and *A. spinicauda*, *Eremias lineolata*, *Meroles suborbitalis* and *Mesalina guttulata*). It seems probable that these losses are an additional way of bringing down the size, or at least the bore, of the hemipenis in response to narrowing of the female genital sinus during the development of physical isolating mechanisms. The arbitrary way in which either side of the hemipenis may be reduced is consistent with this interpretation. Small dimensions may be associated with other

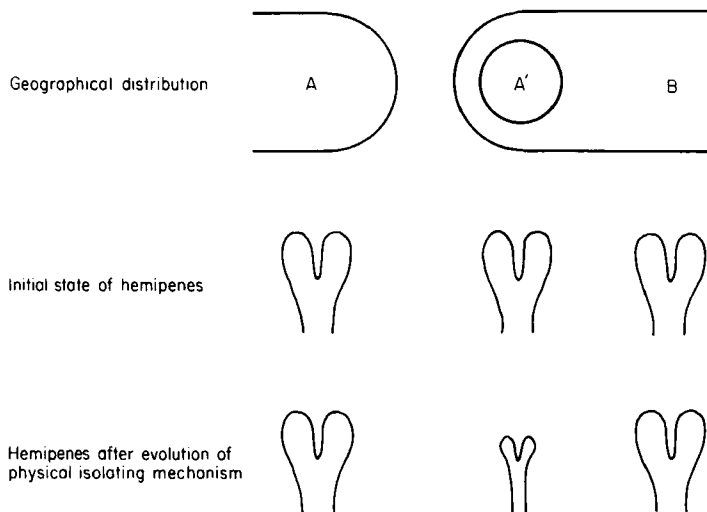


Figure 2. Example of secondary speciation caused by the development of a physical isolating mechanism. An isolated population (A') of species A becomes sympatric with species B and develops a physical isolating mechanism by reduction in the size of its genitalia. This simultaneously precludes potential interbreeding with other populations of species A which retain genitalia of normal size, like species B.

modifications, such as narrowing of the whole hemipenis, reduction in size of both lobes and simplification of their folding in the retracted organ, and total loss of the armature.

In certain cases, organs of normal dimensions show some of the features discussed here. Thus, strong asymmetry may occur in hemipenes of average size, such as in a number of *Acanthodactylus* species, *Heliobolus lugubris* and *Latastia johnstonii*. It seems possible that asymmetry has been developed during miniaturization, but the organs concerned have later reverted to full size without reconstituting the lost lobe and associated section of the armature. In these instances the remaining lobe is much bigger than usual, compensating to a large extent for the absence of its fellow. Such reversion to large size might occur after the need for a physical isolating mechanism is past, if small genitalia function less well during copulation. However, some species retain small genitalia even though there are no congeners within their range, for instance *Acanthodactylus cantoris* (p. 277). Alternatively, miniaturized copulatory organs might enlarge if the species concerned came into contact with another form possessing small genitalia and a physical isolating mechanism arose. The sequence of possible changes in the hemipenis associated with the development of physical isolating mechanisms is summarized in Fig. 3.

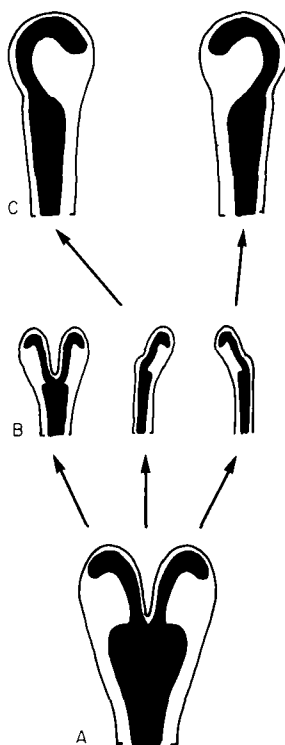


Figure 3. Possible sequence of hemipenial changes associated with the development of a physical isolating mechanism. A, Initial condition of hemipenis. B, Reduction in size during development of physical isolating mechanism by either simple miniaturization (left) or miniaturization with loss of medial or lateral lobe (centre, right). Enlargement without restoration of symmetry, either when the need for the isolating mechanism passes, or when interaction with another species possessing small genitalia occurs.

THE SPECIAL PROPENSITY OF COPULATORY ORGANS TO RETAIN CHANGES

Arnold (1973) argued that copulatory structures differed from other organ systems in their potential ability to retain changes that develop in them which might otherwise be transient. If, say, a pleiotropic alteration affects another kind of organ, it is very probable that it will reduce functional efficiency. However, provided this reduction in efficiency does not outweigh the original selective advantage of the genetic change concerned, the pleiotropic alteration will become fixed. But there will then be normalizing selection modifying the genotype further, so that the pleiotropic change will tend to be suppressed and the organ will return to its original state and efficiency (Fig. 4A).

Copulatory organs differ because, as already noted, their efficiency cannot be considered in isolation, but only in relation to their co-ordinated functioning with the organs of the opposite sex, which are also likely to be under selective control. Copulatory efficiency depends largely on a good physical match between the organs concerned, rather than on their absolute size and shape. Consequently, if there is a pleiotropic change in the male organ which reduces

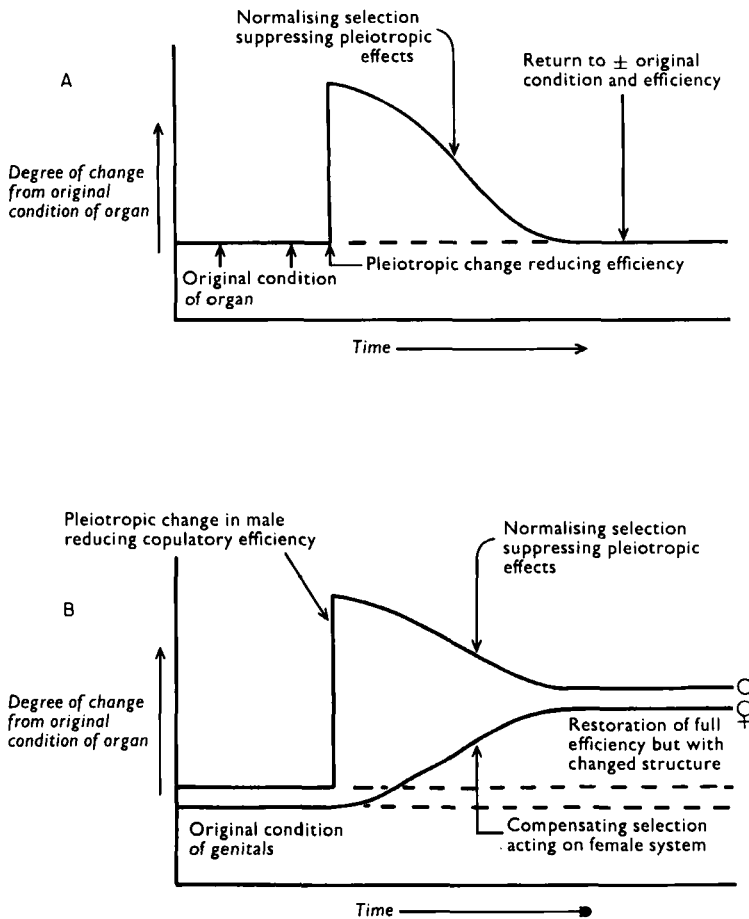


Figure 4. Potential differences in the retention of pleiotropic change between: A, most organ systems; B, genitalia; for further explanation, see text (from Arnold, 1973).

mating efficiency in some way, there will not only be normalizing selection acting on the male genotype to bring the male organ back towards its original condition, but also, simultaneously, selection acting on the female genotype to produce changes in the female genitalia compensating for, and adapting to, the pleiotropic alterations that have already taken place in the male intromittent organ. This means that the two sets of copulatory organs may return to their previous efficiency without reverting exactly to their original morphological state (Fig. 4B). So changes which would otherwise be suppressed by normalizing selection may be partly retained. Presumably, the converse situation exists, where pleiotropic changes in the female system could produce compensatory alteration in the male.

In fact, although this argument was developed with pleiotropic characters in mind, the proposed mechanism is just as likely to apply to changes arising from transient selection pressures acting directly on the copulatory organs and this would include the development of physical isolating mechanisms. The special propensity of genitals to retain features consequently allows arguments against physical isolating mechanisms being an important source of genital variation to be countered. Radical differences in size and proportion between copulatory organs need not always represent present isolating mechanisms, for they may result from previous ones. Even forms which now have sophisticated pre-mating isolating mechanisms may have gone through a stage when these were undeveloped and physical isolation advantageous. Some differences between species groups may result from similar periods of crisis in their ancestors.

FACTORS PROMOTING STABILITY IN COPULATORY ORGANS

We have seen that copulatory organs sometimes appear to alter rapidly, such as during the development of physical isolating mechanisms, and the changes may be retained more readily than in other organ systems. But lack of significant variation in these structures across some large systematic groups indicates that they are often constant for long periods. This is also suggested by studies of the amount of variation found within species. Thus, Walker (1980) showed that the genital features of a staphylinid beetle she examined have significantly lower geographical variability than other external features. Do copulatory organs then have a high inherent stability if unperturbed by things like pleiotropic change and the evolution of physical isolating mechanisms? A number of factors could contribute to such inertia.

(1) In lizards and snakes, the copulatory organs are internal structures. Even the hemipenis is but partly everted when inserted into the vent of the female and only then expands properly, so its exposure to external conditions is fleeting and incomplete. Genitals therefore exist almost entirely in internal environments which are much more constant than those of external features, whence most systematic characters are drawn.

(2) The hemipenis is an instrument dedicated to a single activity, no subsidiary use or involvement being known. In this it differs from many organs, which are involved in several functions, and are consequently liable to a wider range of selective forces.

(3) The function of copulatory organs is one that is little affected by the shift in selective regime caused by change in niche. In this it contrasts with most other parts of the body.

(4) It is to the advantage of an individual to be capable of mating with as many members of the opposite sex in its population as possible. Therefore, size and shape variation of copulatory organs, within a deme (local interbreeding unit) at least, is likely to be limited to the extent that individuals approaching one extreme could still copulate with those approaching the other. Such restricted variation will be retained because, beyond these limits, deviation will be penalized in relation to its extent.

A MODEL FOR THE ORIGIN AND MAINTENANCE OF DIFFERENCES IN THE COPULATORY ORGANS OF LACERTID LIZARDS

Surveys of the lacertid hemipenis (Arnold, 1973, 1983, 1986) and the foregoing discussion suggest the following model for hemipenial change and its maintenance in lacertids.

(1) The interacting system of male and female copulatory organs has considerable inherent stability. Among factors promoting this are: location of organs in a highly homoeostatic environment within the body; a single primary function which is not influenced by shifts in niche; and pressures resulting in a narrow range of intrapopulational variation.

(2) Differences arise relatively rarely but may result from several factors. Among the possibilities in the Lacertidae are: direct selection of unspecified origin on the hemipenis; direct selection on the genital sinus of the female which then causes change in the hemipenis; pleiotropic effects caused by selection acting elsewhere on other organ systems; and development of physical isolating mechanisms. As already noted, the latter would be likely to produce differences in dimensions and perhaps asymmetry and some simplification (pp. 268, 270). It is not liable to account for some of the other kinds of differences listed on p. 265, which are more probably attributable to other causes, such as the first three mentioned here.

(3) Copulatory organs seem more likely than other organ systems to retain pleiotropic changes and the effects of direct but transient selection, such as those causing the development of physical isolating mechanisms.

(4) Although changes tend to be retained, some may be lost when the factors that favoured their development abate if they reduce copulatory efficiency or if new selective forces supervene. This appears to sometimes be true of the small size of copulatory organs produced in the evolution of physical isolating mechanisms, but not the asymmetries and simplifications that may arise in such events (p. 271).

In summary, copulatory organs of lacertids are subject to a complex of factors. Although several of these contribute towards stability, they may at times be overridden by others which can cause fast and radical changes, in the case of the development of physical isolating mechanisms, or less spectacular ones. Such changes tend to be retained because efficiency of genitalia depends on compatibility rather than absolute configuration.

EXAMPLES OF HEMIPENIAL VARIATION AMONG LACERTID LIZARDS

Cases apparently involving physical isolating mechanisms

When a physical isolating mechanism between two lacertid species evolves, the following features are to be expected. (1) Attempts by males of at least one

species to mate with females of the other. (2) If insemination of one species by another occurs, reproductive success, or that of the offspring, will be low. (3) Development of marked differences in size and bore of the copulatory organs of the forms concerned, and perhaps asymmetry of the hemipenis in one species. (4) The distribution of the species or population with small divergent genitalia may well lie entirely within the range of the other. (5) The form with divergent genitalia may have related populations, outside the range of the second species, that are virtually identical but differ in having normal copulatory organs, because there has been no pressure on them to develop a physical isolating mechanism.

With the passage of time, some of these features may disappear. Thus the geographical ranges of the forms concerned might shift, so that the one with divergent genitalia lies wholly or partly outside the range of the other, or the latter could become extinct. Related forms with normal genitalia may become more different. Should the species remain in sympatry, isolating mechanisms of a physical type might cease to be necessary, for instance if pre-mating isolating mechanisms evolve. In this case, attempts at interspecific mating should no longer occur and later, perhaps, the difference in size and form between the two sets of genitalia may decrease, although asymmetry often remains. Examples that seem to represent some of these varied situations actually occur among lacertids.

Mesalina: Hemipenial differences in this genus have allowed a number of forms (either previously regarded only as subspecies or completely un-noticed) to be recognized as full species (Arnold, 1986). In particular, it is common for copulatory organs of otherwise quite similar populations to be very different in size (Fig. 5). In cases where two species are truly sympatric, with extensive geographical overlap rather than mere abutment, such size differences are usual, being found in nine out of 10 cases (Table 1). Forms with small genitalia do not constitute a holophyletic group and the modification appears to have arisen independently at least four times (Table 2).

Some cases of size difference may well represent active physical isolating mechanisms. Thus, *Mesalina adramitana* possesses a small hemipenis in southern Oman, where it co-exists with *M. ayunensis* which has large copulatory organs.

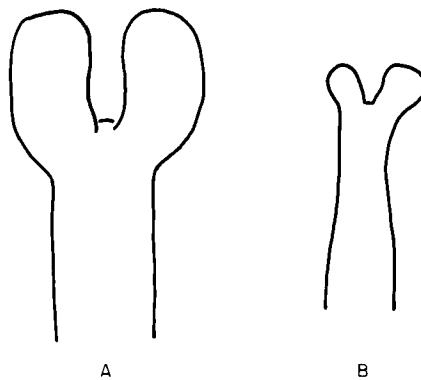


Figure 5. Hemipenes of two species of *Mesalina* sympatric in Arabia. Both organs come from animals about 50 mm from snout to vent; the one in A is 5.5 mm long. A, *M. brevisrostris*; B, *M. guttulata*.

Table 1. *Mesalina*: species-pairs that occur in sympatry (l, hemipenis large; s, hemipenis small)

Species		Area of sympatry
<i>olivieri</i> , l	<i>guttulata</i> , s	Morocco to Israel
<i>pasteuri</i> , l	<i>guttulata</i> , s	Algeria, Niger
<i>pasteuri</i> , l	<i>rubropunctata</i> , s	Algeria, Niger
<i>rubropunctata</i> , s	<i>guttulata</i> , s	Sahara
<i>martini</i> , l	<i>guttulata</i> , s	E Sudan
<i>brevirostris</i> West, l	<i>guttulata</i> , s	Iraq, N Arabia
<i>adramitana</i> , l	<i>guttulata</i> , s	South Yemen
<i>ayunensis</i> , l	<i>adramitana</i> , s	South Oman
<i>watsonana</i> , l	<i>brevirostris</i> Jerrahi, s	SW Iran
<i>watsonana</i> , l	<i>brevirostris</i> East, s	Pakistan

Outside the known range of the latter, other populations of *M. adramitana* (in northern Oman, the United Arab Emirates and the Hadhramaut), while very similar to those of southern Oman, have large genitalia. Although no observations are available from the area of sympatry, *M. adramitana* in the United Arab Emirates has been seen to copulate without obvious preliminaries (p. 266). In the *M. brevisrostris* complex western populations possess large hemipenes, but those in the highlands of southwestern Iran and in Pakistan have small ones and occur within the range of *M. watsonana* which exhibits large copulatory organs.

Other cases might represent later stages in the sequence of events that may follow the evolution of physical isolating mechanisms. Some populations of *M. guttulata*, which has small hemipenes, now occur beyond the range of species

Table 2. Hemipenis size in apparently holophyletic groups of *Mesalina* (i.e. assemblages containing all the descendants of one ancestral species) (l, hemipenis large; s, hemipenis small)

Species	Hemipenis size
1. <i>M. brevisrostris</i> West	l
<i>M. brevisrostris</i> Jerrahi	s
<i>M. brevisrostris</i> Pakistan	s
2. <i>M. rubropunctata</i>	s
3. <i>M. adramitana</i>	l
<i>M. adramitana</i> S Oman	s
<i>M. ayunensis</i>	l
4. <i>M. guttulata</i>	s
<i>M. watsonana</i>	l
5. <i>M. olivieri</i> N. Africa, Israel	l*
<i>M. olivieri</i> Jebel Akhdar (Libya)	l
<i>M. simoni</i>	l
<i>M. pasteuri</i>	l
<i>M. martini</i>	l

*Perhaps originally small (see p. 277).

with large copulatory organs, for instance in parts of the Sahara desert. *Mesalina guttulata* and *M. rubropunctata*, which also has small hemipenes, are found together over a wide area of northern Africa. This suggests that they evolved small genital size through sympatry with other *Mesalina* species, but do not need such differences to maintain isolation between themselves. *Mesalina olivieri olivieri* has a normal-sized hemipenis but its lobes are fused. As lobe modification is often associated with small dimensions, this could indicate that it has previously passed through a phase when genital size was reduced but that this has subsequently been reversed (p. 270).

Meroles: Most members of the southern African genus *Meroles* have a bilobed hemipenis of normal size, including *M. knoxii*, but the very similar *M. suborbitalis* has an extremely narrow, unlobed organ. This may represent an active physical isolating mechanism as the range of this species lies largely within that of *M. knoxii*.

Acanthodactylus: Many members of this genus possess hemipenial asymmetry and some exhibit size reduction (Arnold, 1983), but there are no cases that seem very likely to represent current physical isolating mechanisms. While the hemipenis is very reduced in *A. maculatus* and *A. spinicauda*, these species are largely allopatric from their most similar close relative, *A. pardalis*, although *A. maculatus* apparently overlaps to some extent with *A. pardalis bedriagai* in northern Algeria (Salvador, 1982). However, it could be that hemipenial size has been reduced in response to some other more fully sympatric species such as *A. scutellatus*. In *A. boueti* of western Africa the hemipenis is also small; this might arise from interaction with *A. guineensis* but the degree of sympatry is uncertain. *Acanthodactylus cantoris* has small copulatory organs as well, but its present range lies entirely outside that of other *Acanthodactylus* species.

In many cases the degree of hemipenial asymmetry is strong: for instance a lobe and corresponding side of the armature are virtually absent in *A. maculatus*, *A. spinicauda* and *A. guineensis*, in the *A. ophiodurus* and *A. scutellatus* groups and in the Arabian members of the *A. cantoris* assemblage. In all except the first two species the asymmetry is not associated with small size. This, together with the fact that holophyletic groups of species are involved, suggests that the organs of these forms bear evidence of physical isolating mechanisms in their ancestors rather than in themselves. It would seem that interactions between species of the genus, involving the development of physical isolating mechanisms, have occurred frequently over a long period.

Pedioplanis: Northern populations of the southwest African *P. undata* have developed hemipenes with extremely narrow lobes. However, there is no obvious candidate among presently sympatric lacertids that may have made such a change advantageous in terms of physical isolation.

Heliobolus, *Latastia*: In these genera a number of species have normal hemipenes, but in *H. lugubris*, *H. spekii* and *L. johnstonii* they are strongly asymmetrical. However, the organs are of normal size and the species do not co-exist with close relatives, which may indicate that these cases represent previous isolating mechanisms, rather than presently active ones.

Philochortus: In this genus all species show a degree of hemipenial asymmetry, although the organs are again of normal size. If the asymmetry is the result of previous evolution of a physical isolating mechanism, this must have pre-dated the differentiation of the present species.

Cases of hemipenial similarity throughout higher taxa

In many genera or species groups the hemipenis is quite constant in form, indicating that there has been little change since the origin of the assemblage. This is true of such taxa as *Podarcis*, *Lacerta* part I, *Nucras*, *Philochortus*, *Latastia* (with the exception of *L. johnstonii*), *Pseudieremias* and most of *Eremias*.

Cases where forms with similar hemipenial features although assigned to different groups turn out to be closely related

Species in different genera sometimes share derived hemipenial features other than those associated with physical isolating mechanisms. In a number of instances evidence from other sources has subsequently shown that they are in fact closely related. Among these are the following: *Gallotia* and *Psammodromus* (Arnold, 1973); '*Lacerta*' *jacksoni* and *Adolfus*; '*Lacerta*' *echinata*, *Bedriagaia* and *Gastropholis*; *Meroles* and *Aporosaura*; *Acanthodactylus* and '*Eremias*' *guineensis* (Arnold, 1980, 1983).

THE LIMITED OCCURRENCE OF APPARENT PHYSICAL ISOLATING MECHANISMS IN
LACERTID LIZARDS AND OTHER SQUAMATE REPTILES

The sort of abrupt difference in size and shape of the copulatory organs reported here in lacertids does not seem to have been noted among other squamates. Indeed, within the Lacertidae they are not found among primitive groups like *Lacerta* and its allies, even though interspecific mating is known to sometimes occur (p. 267). Instead they are confined to the more advanced genera which have hemipenial armatures and live in quite dry, often open habitats.

Physical isolating mechanisms depend on the hemipenis and genital sinus of sympatric species not fitting together. Such incompatibility is perhaps more easily developed when the hemipenis is firm and well-defined, as is the case in armatured organs. Again, copulation and its preliminaries may be hazardous (Crews, 1980), for in both the attention of the lizards is distracted from their surroundings and in the former they are incapacitated from immediate flight. In open situations, where lizards are especially exposed to predators, there may well be premium on initiating mating quickly, a situation where errors in identifying a conspecific mate may be made.

CORROBORATION OF HYPOTHESES ABOUT THE EVOLUTION OF COPULATORY ORGANS

The model for origin and maintenance of genital differences in lacertid lizards presented here is based largely on extrapolation from the comparative anatomy and natural history of the animals concerned. Are its component hypotheses capable of being tested? The possibility that physical isolating mechanisms are one of the main sources of genital variation would receive further support if natural situations where they certainly functioned could be found. For instance, if it could be shown that some sympatric species with divergent genitalia not only tended to copulate without many preliminaries but that actual attempts at interspecific mating took place the hypothesis would be supported. Also, it would be expected that insemination by the other species would condemn the

next clutch of a female to infertility, or result in reduced viability or fecundity or her offspring. If such insemination did not occur naturally it should be possible to confirm this point by artificial means.

Three hypotheses about copulatory organs would be difficult to test with lizards: (1) that pleiotropic events can affect genitalia; (2) that changes in the genitals of one sex may result in corresponding changes in the other; and (3) that changes produced by pleiotropic events or transient selection tend to be retained by genitalia. This is for purely practical reasons: captive lizards are not easy to maintain in large numbers and their generation times are relatively long. However, as the hypotheses would be expected to apply to other bisexual animals where there is comparatively close conformity between the genitals of the two sexes, it should be possible to test them using small, fast-breeding invertebrates such as *Drosophila*. Selection for various environmental factors might produce pleiotropic effects both in the genitals and elsewhere and it should then be possible to see whether changes appearing first in one sex were followed by correlated changes in the other. Relaxation of such selection could then perhaps demonstrate whether the changes it had produced in genitalia were retained longer than those that occurred elsewhere in the animal.

THE VALUE OF FUNCTIONAL INTERPRETATION IN CHARACTER WEIGHTING

Information about the function of characters is often wrongly dismissed as being irrelevant to phylogeny reconstruction. In the present case it at least allows us to suggest why certain kinds of derived hemipenial characters are likely to be poorer indicators of relationships than others. Thus, the radical changes, involving reduction in size and asymmetry, that occur during the development of physical isolating mechanisms will often produce misleadingly large differences between close relatives. Also, because possible ways of reducing the size and bore of intromittent organs is limited, the same modifications are likely to turn up in forms which are only distantly related. On the other hand, there are functional reasons for thinking that other hemipenial features are likely to be more useful. Pragmatic weighting assessment of the two kinds of characters (Arnold, 1981) supports this distinction.

COPULATORY ORGANS AS SOURCES OF SYSTEMATIC CHARACTERS

It is instructive to compare the copulatory organs of lacertids with a hypothetical perfect source of systematic information. The latter would provide two kinds of knowledge: the boundaries between species and the phylogeny of the studied group. In fact, these two requirements are likely to conflict because the first requires marked differentiation between closely related species, while the second needs graded differentiation with the lowest level of difference occurring between species. In a number of cases copulatory structures provide good information about species boundaries. Their inherent stability often results in intromittent organs being quite constant throughout a species and, because of the way they apparently alter during the development of physical isolating mechanisms, they are sometimes markedly different between close relatives.

A perfect anatomical source of information about phylogeny should be complex enough to allow a variety of unique character states to arise. These

should develop frequently enough for at least one to appear in each common ancestral species in the phylogeny, thereby indicating all its dichotomies, and such changes should be permanently conserved in descendants. For this to happen liability must not be too great and features should not change in response to such factors as a shift in niche. Copulatory organs obviously do not meet this stringent specification, but their frequent value as indicators of relationship seems to arise from their approaching it more closely than many other organ systems, if features associated with recent isolating mechanisms are excluded. They are often quite complicated in structure, so that a range of derived features can potentially arise and in fact do so reasonably often. The factors that seem to contribute to their stability (p. 273) and the ability of genitalia to retain changes make it more probable that such features are conserved, as does the fact that they are unlikely to be directly affected by the sort of selective pressures associated with change in niche.

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