RELATIONSHIPS OF THE PALAEARCTIC LIZARDS ASSIGNED TO THE GENERA *LACERTA, ALGYROIDES* AND *PSAMMODROMUS* (REPTILIA: LACERTIDAE)

BY

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CONTENTS

SYNOPSIS

It is pointed out that the equatorial and southern African species of *Lacerta* Linnaeus 1758 and *Algyroides* Bibron & Bory 1833 are not at all closely related to the palaearctic members of these genera. The present classification of the palaearctic species of *Lacerta, Algyroides* and

Psammodromus Fitzinger 1826 is discussed and found to be unsatisfactory in several respects. Characters available for grouping species are described, including a number of features (mainly skeletal and hemipenial) not employed before. Using ecological and functional data, an attempt is made to assess the lability of available characters : many of the external and cranial features used in ' classical ' lacertid systematics appear to be potentially labile and therefore must be given low comparative weight in judging relationships. Using this comparative weighting, it appears that *Algyroides* and *Psammodromus* are natural groups and that *Lacerta* is divisible into four main sections. Two of these will be retained in *Lacerta* (as *Lacerta* parts I and II) but the others are raised to the status of separate genera : *Gallotia* Boulenger 1916 and *Podarcis* Wagler 1830. Proposed systematic changes are listed in full on p. 357.

INTRODUCTION

AT LEAST fifty-five species are currently assigned to the genus *Lacerta*.* Of these, forty-nine are limited to a relatively small part of the southwestern Palaearctic region while two others, *L. vivipara* Jaquin and *L. agilis* Linnaeus, occur not only in this area but also range more widely in Eurasia (see Fig. 1). The remaining four members of the genus are found in Africa south of the Sahara desert. These are : *L. echinata* Cope (tropical forests of West Africa from Liberia to the eastern Congo Republic), *L. jacksoni* Boulenger (eastern Congo Republic, Uganda, Kenya and Tanganyika), *L. rupicola* Fitzsimons (Zoutpansberg, Transvaal, Republic of South Africa), and *L. australis* Hewitt (near Ceres in Cape Province, Republic of South Africa). *L. echinata* and *L. jacksoni* have strong affinities with their Central African neighbours in the genera *Algyroides*, *Bedriagaia* and *Gastropholis*, and *L. rupicola* seems to be most nearly related to *Tropidosaura*. It does not seem possible to retain these species in *Lacerta* and their precise relationships will be discussed elsewhere. *L. australis* is apparently known only from the single type specimen (which is not available to me) and is not well enough studied for its real affinities to be clear. But, on geographical grounds, it is not likely that *L. australis* is closely related to the Palaearctic species of *Lacerta* for the type locality is separated from the range of this assemblage by a hiatus of over 7000 km. In the rest of this paper, *Lacerta* will be used to refer only to the fifty-one Palaearctic species.

The classification of Palaearctic *Lacerta* has presented a number of difficulties. Many characters used in their systematics exhibit great intraspecific variation making the delimitation of species-boundaries difficult. Some of this extensive variation is geographic ; for instance, Mertens & Wermuth (1960) list no fewer than 31 subspecies of *L. erhardii*, 32 of *L. pityusensis* and 39 of *L. sicula* and many subspecies of the last have been recognized since (Brelih 1961, 1963, Lanza 1966, Lanza & Borri 1969, Mertens 1966). Many forms also show considerable intra-populational variability especially in colour and pattern. Notwithstanding this, classification at the species level is now fairly stable thanks to the investigations of a long series of workers including Eimer (1881), Bedriaga (1886), Werner (1904),

* This figure includes *Lacerta cappadocica* Werner which has sometimes been placed in a separate genus, *Apathya* Méhely, and four parthenogenetic forms allied to *L. saxicola* Eversmann, viz. *L. armeniaca* Méhely, *L. dahli* Darevsky, *L. rostombekovi* Darevsky and *L. unisexualis* Darevsky. It is very probable that several other species will eventually be recognized.

FIG. 1.   Distribution of lizards usually assigned to *Lacerta, Algyroides* and *Psammodromus*.
Black : area containing *Psammodromus*, European *Algyroides* and 51 species of *Lacerta*
(49 of which are confined to the region marked).   Diagonal hatching : distribution of
Lacerta vivipara outside the main range of Palaearctic *Lacerta*.   Broken line : distribu-
tion of *Lacerta agilis* beyond main range of Palaearctic *Lacerta* and of *L. vivipara*.
Vertical hatching : combined distribution of ' *Lacerta* ' *echinata*, ' *Lacerta* ' *jacksoni*
and the African species customarily assigned to *Algyroides*.   Solid black circle : only
known locality of ' *Lacerta* ' *rupicola*.   Black triangle : only known locality of ' *Lacerta* '
australis.

Boulenger (1905, 1913, 1916, 1920), Méhely (1907, 1909, 1910), Schreiber (1912)
and more recently Mertens (numerous publications mainly in *Senckenbergiana
Biologica*), Klemmer (1957), Peters (1962a, b) and Darevsky (1957, 1966, 1967).
   Problems still remain in defining acceptable species-groups within the genus,
despite several attempts having already been made to divide *Lacerta* into subunits,
and comprehensive schemes of classification having been put forward by Bedriaga
(1886), Werner (1904) and Boulenger (1916).   The last author divided the Palae-
arctic forms of *Lacerta* into five sections or subgenera :   I – *Lacerta* s. str., II –
Gallotia Boulenger, III – *Zootoca* Wagler, IV – *Podarcis* Wagler and V – *Thetia*
Gray which is, in fact, a junior synonym of *Scelarcis* Fitzinger.   Méhely (1907,

1909, 1910), who dealt only with the small, mainly climbing forms commonly known as Wall Lizards separated these into two groups, 'Archaeolacertae' and 'Neo-lacertae'. But Boulenger (1907, 1910) was very critical of Méhely's division and did not recognize it in his own classification when he placed all Wall Lizards in Section IV (subgenus *Podarcis*). Subsequent investigations, however, have sup-ported Méhely's division and *Podarcis* of Boulenger is now divided into the subgenera *Podarcis* s. str. and *Archaeolacerta* Mertens, which are respectively more or less equivalent to Méhely's Neo- and Archaeolacertae. A seventh subgenus, *Apathya* Méhely, is sometimes recognized for *L. cappadocica* (e.g. by Mertens 1952).

This classification is not entirely satisfactory for the borders of some subgenera are not well defined and a number of species have either never been properly assigned to a particular subgenus or their position has been recently questioned. Further-more, many of the characters by which the subgenera are distinguished are probably quite labile and on their own do not provide an adequate basis for arranging species into natural assemblages (see pp. 315). Such characters may turn out to delimit natural groups but confirmation from other features is necessary. At present, subgeneric classification is mainly based on external features plus a few variations in skull structure. It seems essential to re-assess these characters and, more im-portant, to increase the range of variables available for classifying *Lacerta* and its allies. This increase should involve not only the absolute number of characters used but also the number of sources from which they come. For this reason, I have investigated the skeletal and hemipenial morphology of these lizards.

It seems convenient to discuss the relationships of two other genera in conjunc-tion with *Lacerta*, namely *Algyroides* Bibron & Bory and *Psammodromus* Fitzinger. *Algyroides*, as presently understood, is like *Lacerta* in having a disjunct range with four species in Europe and three in central Africa (viz. *A. africanus*, *A. alleni* and *A. vauereŝelli*). As with *Lacerta*, the equatorial species have no close affinities with their Palaearctic congeners and must be removed from *Algyroides* (see Appendix I). Both *Algyroides* and *Psammodromus* (four species in northwest Africa and southwest Europe) are usually regarded as being closely related to *Lacerta*. *Algyroides* differs externally from *Lacerta* only in possessing strongly enlarged dorsal scales; *Psammodromus* also has enlarged dorsal scales but differs from both *Algyroides* and *Lacerta* in having the collar reduced or absent.

This paper consists of four sections : (i) a statement of the present classification (p. 294) ; (ii) a description of the principal characters that have either already been used to classify *Lacerta*, *Algyroides* and *Psammodromus* or that appear to be potentially useful (p. 300) ; (iii) an assessment of the relative importance of these characters (p. 315) and (iv) an attempt to revise the classification (p. 327).

THE PRESENT CLASSIFICATION OF *LACERTA*, *ALGYROIDES* AND *PSAMMODROMUS*

Genus *LACERTA* Linnaeus 1758

Until very recently, the subgeneric allocations of forty (almost 80 per cent) of the species of *Lacerta* were widely accepted and these are listed below. The characters

on which the subgenera of *Lacerta* are based are set out in Table I (p. 296) together with those of *Algyroides* (Palaearctic forms) and *Psammodromus*.

Subgenus *Lacerta* s. str. Linnaeus 1758 (type species : *L. agilis*)
   agilis Linnaeus 1758 (West and central Europe to central Asia), *schreiberi* Bedriaga 1878 (Iberian Peninsula), *strigata* Eichwald 1831 (Caucasus area ; West Iran), *trilineata* Bedriaga 1886 (Southeast Europe and Southwest Asia), *viridis* (Laurenti 1768) (central and southern Europe etc.).

Subgenus *Gallotia* Boulenger 1916 (type species : *L. galloti*)
   atlantica Peters & Doria 1882 (eastern Canary Islands), *galloti* Duméril & Bibron 1839 (western Canary Islands, not Gran Canaria), *simonyi* Steindachner 1889 (Gran Canaria, formerly Roques Zalmor off Hierro, western Canary Islands).

Subgenus *Zootoca* Wagler 1830 (type species : *L. vivipara*)
   andreanszkyi Werner 1929 (Atlas Mountains), *praticola* Eversmann 1834 (Caucasus and northern Balkan Peninsula), *vivipara* Jaquin 1787 (northern Eurasia).

Subgenus *Podarcis* Wagler 1830 (type species : *L. muralis*)
   dugesii Milne-Edwards 1829 (Madeira), *erhardii* Bedriaga 1882 (southern Balkan Peninsula and Greek Islands), *filfolensis* Bedriaga 1876 (Malta and nearby islands), *hispanica* Steindachner 1870 (Iberian Peninsula and North-west Africa), *lilfordi* (Günther 1874) (Balearic Islands), *melisellensis* Braun 1877 (eastern Adriatic region), *milensis* Bedriaga 1882 (Milos and nearby islands), *muralis* (Laurenti 1768) (South and central Europe), *pityusensis* Boscá 1883 (Ibiza and nearby islands), *sicula* Rafinesque 1810 (mainly Italy, Adriatic and Tyrrhenian areas), *taurica* Pallas 1814 (southeastern Europe), *tiliguerta* Gmelin 1789 (Corsica and Sardinia), *wagleriana* (Gistel 1868) (Sicily).

Subgenus *Archaeolacerta* Mertens 1921 (type species : *L. bedriagae*)
   armeniaca Méhely 1909 (Caucasus), *bedriagae* Camerano 1885 (Corsica and Sardinia), *caucasica* Méhely 1909 (Caucasus), *dahli* Darevsky 1957 (Caucasus), *danfordi* (Günther 1876) (western Turkey and south to Petra), *graeca* Bedriaga 1886 (southern Greece), *horvathi* Méhely 1904 (northwestern Jugoslavia), *monticola* Boulenger 1905 (Iberian Peninsula), *mosorensis* Kolombatović 1886 (southwestern Jugoslavia), *oxycephala* Duméril & Bibron 1839 (southwestern Jugoslavia), *rostombekovi* Darevsky 1957 (Caucasus), *rudis* Bedriaga 1886 (Caucasus), *saxicola* Eversmann 1834 (Caucasus etc.), *unisexualis* Darevsky 1966 (Caucasus).

Subgenus *Scelarcis* Fitzinger 1843 (type species : *L. perspicillata*)
   perspicillata Duméril & Bibron 1839 (northwestern Africa).

Subgenus *Apathya* Méhely 1907 (type species : *L. cappadocica*)
   cappadocica Werner 1902 (central Turkey to northwest Iran).

TABLE I: Characters previously used to distinguish the subgenera of *Lacerta* (*Algyroides* and *Psammodromus* are included for comparison)

	Lacerta s. str.	*Gallotia*	*Zootoca*	*Podarcis*	*Archaeolacerta*
Approximate adult body size (snout-vent)	70–160 mm	60–210+ mm	35–67 mm	45–90 mm	55–85 mm
Skull facies	Massive, deep, roof convex	Massive, deep, roof convex	Fairly light build, roof convex	Moderate-to-light build, roof usually convex	Lightly built, depressed, roof flat
Cranial osteoderms	Thick	Thick	Moderate or thin	Variable	Thin
Supraocular lamellae	Complete	Complete	Complete except in some *L. andreanszkyi*	Usually complete, exceptions in *L. dugesii* and *L. hispanica*	Incomplete in most cases
Pterygoid teeth	Usual	Usual	None	Variable	Almost always none
Micro-ornamentation of hemipenial epithelium (much data from Böhme 1971)	Lobe tips with crown-shaped tubercles. Lobe flanks with long spines, often ending in spinules	Simple, recurved spines	Crown-shaped tubercles but recurved spines in *L. andreanszkyi*	Simple recurved spines (not *L. dugesii*)	Crown-shaped tubercles, except in *L. graeca* and *L. bedriagae*
Postnasal shields	Usually two (one in some *L. agilis*)	One	One	One, in most cases	Variable
Eyelid	Scaly	Scaly	Scaly	Scaly	Scaly
First supratemporal scale emarginates parietal shield	Yes	Varies	Varies	No	Yes, exceptions in *L. bedriagae*
Dorsal scales	Raised, rather imbricate, keeled	Raised and keeled	Raised, often keeled	Usually raised, often keeled	Often flat and unkeeled
Collar	Serrated	Varies	Serrated	Serration usually weak but varies	Unserrated
Ventral scaling: shape of scales	Inclined parallelograms, strongly imbricate	As *Lacerta* s. str. but imbrication weaker	As *Lacerta* s. str., but imbrication weaker	Approximate rectangles, overlap varies	Rectangular, little imbrication
Ventral scaling: number of longitudinal rows	6–8	(8) 10–20	6	6 (8)	6–8
Subdigital tubercles	Normal	Normal	Normal	Normal	Normal
Sexual dimorphism in dorsal pattern	Frequent	Frequent	None or little	Usual	Often none
Tail brightly coloured in the young	No	No	No	In a few populations	Frequently

	Scelarcis	Apathya	Algyroides	Psammodromus
Approximate adult body size (snout–vent)	40–60 mm	50–80 mm	30–70 mm	35–80 mm
Skull facies	Moderate-to-light build, roof often flat	Lightly built, depressed, roof flat	Variable	Moderate-to-heavy build, roof convex
Cranial osteoderms	Fairly thin	Thin	Thin to moderate	Moderate to thick
Supraocular lamellae	Variable	Usually incomplete	Variable	Complete
Pterygoid teeth	None	None	Variable	Variable
Micro-ornamentation of hemipenial epithelium (much data from Böhme 1971)	Simple recurved spines	Simple recurved spines	Variable	Variable
Postnasal shields	Two	Two or three	Usually two	Usually one
Eyelid	Transparent window of one scale	Transparent window of several scales	Scaly	Scaly
First supratemporal scale emarginates parietal shield	No	Not clearly emarginated	Yes	No
Dorsal scales	Not strongly raised, unkeeled	Not strongly raised, unkeeled	Large, imbricate, keeled, often pointed	Large, imbricate, keeled and pointed
Collar	Unserrated	Unserrated	Serration variable	Collar very weak or absent
Ventral scaling: shape of scales	Rectangular, little imbrication	Rectangular, little imbrication	± as *Podarcis*	As *Lacerta* s. str. or overlap even stronger
Ventral scaling: number of longitudinal rows	10	6–8	6	6–10 (see p. 3+8)
Subdigital tubercles	Normal	Usually strongly keeled	Normal	Normal or keeled
Sexual dimorphism in dorsal pattern	None	None	None, except in *A. moreoticus*	None
Tail brightly coloured in the young	Yes	Yes	No	No

The precise systematic positions of the following eleven species are less certain.

L. lepida Daudin 1802 (southwestern Europe and northwestern Africa)
L. parva Boulenger 1887 (Turkey and Armenia)
L. princeps Blanford 1874 (eastern Turkey to southwestern Iran)
   Boulenger (1916) placed these species in the subgenus *Lacerta* s. str., but Peters (1962) believed that they had no close relationship with the other forms in this subgenus. Indeed Peters (1961) put *L. lepida* in the subgenus *Gallotia* and (1962a) suggested that the affinities of *L. parva* lie with *L. fraasii* (q.v.). More recently, Eiselt (1968) has again placed *L. princeps* close to the members of the subgenus *Lacerta* s. str.

L. fraasii Lehrs 1910 (Lebanon)
   Boulenger (1920) emphasized the similarity of this species to *L. vivipara* and even thought that the two forms might be conspecific. He consequently placed *L. fraasii* and *L. vivipara* in the subgenus *Zootoca*. Peters (1962a) disputed this close relationship and instead pointed out the likeness between *L. fraasii* and *L. parva* (see above). He suggested that, eventually, a separate subgenus might have to be created for these two species and also discussed their suitability as ancestors of the *Podarcis* group.

L. brandtii De Filippi 1863 (northwestern Iran)
   This species was regarded by Boulenger (1920) as " one of the most primitive members of the *L. muralis* group [i.e. *Podarcis* in Boulenger's sense] which it connects with *L. parva* ". Wettstein (1951), on the other hand, believed that *L. brandtii* was connected with *L. vivipara* and *L. fraasii* and allocated it to the subgenus *Zootoca*. Peters (1962) in his discussion of *L. parva* states that the possibility of a relationship with *L. brandtii* should not be dismissed, and Böhme (1971) also believes this.

L. cyanura Arnold 1972 (southeastern Arabia)
L. jayakari Boulenger 1887 (southeastern Arabia)
   In his *Monograph of the Lacertidae* (1920) Boulenger placed *L. jayakari* in *Podarcis* as he understood that subgenus, and regarded *L. laevis* as its closest relation. He suggested that both these species might have been derived from ancestral forms close to *L. brandtii*. Klemmer (1957) regarded the position of *Lacerta jayakari* as uncertain. The relationships of this form and the recently discovered *L. cyanura* have been briefly discussed in a recent paper (Arnold 1972).

L. peloponnesiaca Bibron & Bory 1833 (southern Greece)
   According to Boulenger (1920) this species is closely related to *L. taurica* which is now placed in *Podarcis* s. str. Klemmer (1957) regarded *L. peloponnesiaca* as *incertae sedis* because it has a very robust skull with heavily ossified temporal areas atypical of the subgenus *Podarcis*. But Buchholz (1960) pointed out that

this difference is not clear-cut since the degree of temporal ossification in *L. pelopon-nesiaca* is very variable.

L. derjugini Nikolsky 1898 (Caucasus)

Méhely (1909) placed *L. derjugini* in his 'Archaeolacertae' and Lantz & Cyrén (1947) followed this allocation, regarding *L. derjugini* as a member of the subgenus *Archaeolacerta*. Other authors list this species as a member of *Zootoca*, e.g. Boulenger (1920), Mertens & Müller (1928, 1940), Klemmer (1957). The last author considered that it might link *Zootoca* with *Archaeolacerta*.

L. chlorogaster Boulenger 1908 (southern Caspian region)
L. laevis Gray 1838 (East Mediterranean coastal region)

Like *L. derjugini* these two species were placed by Méhely (1909) in his 'Archaeolacertae' and most authors have followed this course. However, Mertens (1957) pointed out that *L. chlorogaster* is more like the members of the subgenus *Podarcis* in its skull and body shape and in having keeled dorsal scales and he tentatively transferred it to this subgenus. Similar arguments could be applied to *L. laevis* which resembles *L. chlorogaster* in these respects.

Genus *ALGYROIDES* Bibron & Bory 1833 (type species : *A. moreoticus*)

fitzingeri (Wiegmann 1834) (Corsica and Sardinia), *marchi* Valverde 1958 (southeastern Spain), *moreoticus* Bibron & Bory 1833 (southern Greece and Ionian Islands), *A. nigropunctatus* (Duméril & Bibron 1839) (eastern coastal area of Adriatic Sea).

Genus *PSAMMODROMUS* Fitzinger 1826 (type species : *P. hispanicus*)

P. algirus (Linnaeus 1758) (southwest Europe and northwest Africa), *blanci* (Lataste 1880) (northwestern Africa), *hispanicus* Fitzinger 1826 (southern France and Iberian Peninsula), *microdactylus* (Boettger 1881) (northwestern Africa).

Recent work

Very recently, Böhme (1971) has challenged certain aspects of the accepted classification of *Lacerta* and its allies on the basis of differences in structure of the hemipenial micro-ornamentation (see p. 309). Amongst his principal findings are the following.

1. *L. lepida* and *L. princeps* appear to be closer to the subgenus *Gallotia* than to *Lacerta* s. str.

2. *Archaeolacerta* may be an unnatural group as two species (*bedriagae* and *graeca*) have a different pattern of micro-ornamentation from the others.

3. *Archaeolacerta* (with the exception of the two species mentioned in paragraph 2) and *Zootoca* are not clearly distinguishable and should be merged.

4. *Psammodromus* and *Algyroides* are probably not natural groups.

CHARACTERS ALREADY USED OR POTENTIALLY USEFUL IN CLASSIFYING
LACERTA, ALGYROIDES AND *PSAMMODROMUS*

In these descriptions, subgeneric names refer only to those species of *Lacerta* definitely assigned on p. 295. Species of uncertain position are mentioned separately.

Osteological characters

1. *General shape of the skull* (Fig. 2)

Most lizards in the genera *Lacerta*, *Algyroides* and *Psammodromus* have a relatively deep, robust skull in which the parietal table has convex lateral edges and is domed in transverse section. But, in contrast, some species of *Lacerta* and *Algyroides* have a flattened, delicately built skull and a parietal table with concave or straight lateral borders and a flat transverse section. Many intermediates exist between these two extremes.

2. *Nasal openings of the skull* (Fig. 2)

In many species the nasal opening is small. It may expose only the external vestibule of the nasal passage but more usually allows the anterior part of the principal nasal chamber to be seen from above. In intact animals it is possible to palpate the nasal opening which in these cases either does not reach backwards under the frontonasal scute or only extends under its anterior borders. In other forms the nasal bones do not extend so far forward and the exposure of the principal nasal chamber is much greater so that the septomaxilla is visible from above. In such cases the openings may extend backwards under the posterior borders of the frontonasal scute or beyond.

3. *Development of cranial osteoderms*

Cranial osteoderms (the *crusta calcarea*) are developed mainly during the period between hatching and maturity and form a continuous layer, closely applied to the dorsal and lateral bones of the skull. They also may develop in previously unossified regions such as the skin over the orbits and in the temporal region. The cranial osteodermal layer is laid down in discrete sections each corresponding to an epidermal scute so that, as the osteoderms increase in thickness, the sutures between the scutes are left as distinct grooves. The development of osteoderms on the skull roof shows a rough correlation with the robustness of the skull ; depressed, delicately built skulls have relatively weak osteoderms.

4. *Supraocular lamellae* (Fig. 2)

The dorsal surface of the orbit is unossified in hatchling lizards but eventually is wholly or partly occupied by a series of four osteoderms (the supraocular lamellae) corresponding to the four supraocular scales. These begin to develop near the lateral borders of the frontal bones and slowly extend outwards. In adults of most species the supraocular osteoderms cover the whole orbital area but in a number of forms the second, third and sometimes the fourth osteoderms are usually
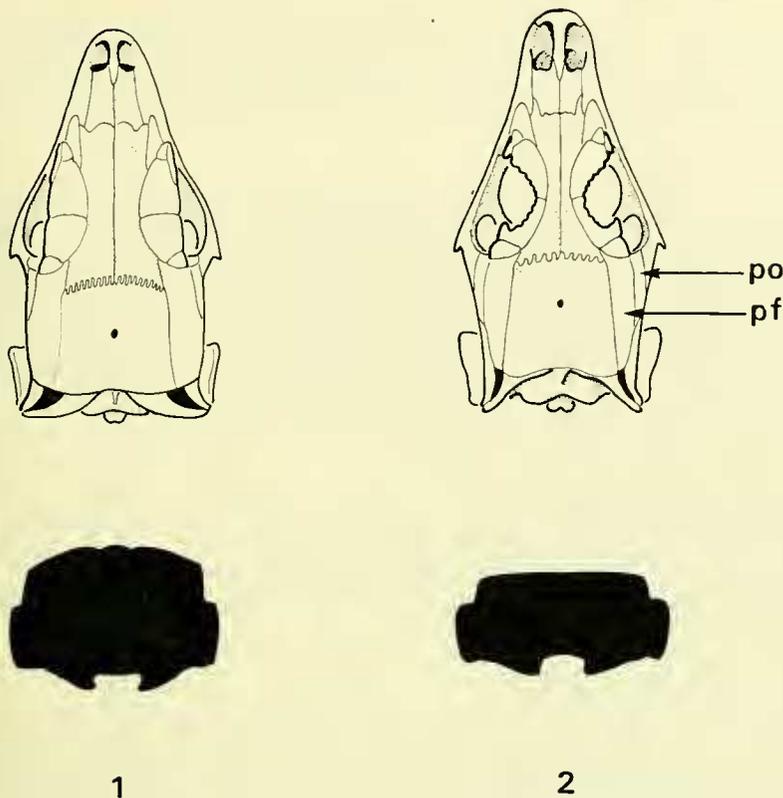
Fig. 2. Principal skull types : dorsal view and cross-profile. (1) Robust undepressed skull with small external nares, complete supraocular lamellae and transversely arched parietal region. (2) Delicately built, strongly flattened skull with large external nares, fenestrated supraocular lamellae and flat parietal region. po = postorbital bone. pf = postfrontal bone.

incomplete so that a flexible area of unossified skin remains between them. This occurs in *Algyroides fitzingeri* and *A. marchi* and in many *Archaeolacerta* spp., in *Lacerta cyanura*, *L. (Apathya) cappadocica* and some populations of *L. (Podarcis) hispanica* and *L. (Scelarcis) perspicillata*, in females of *L. (P.) dugesii* and in many *L. andreanszkyi*, *L. derjugini* and some *L. fraasii*.

5. *Ossification of the temporal region*

Osteoderms may occur in the skin covering the jaw muscles and bordered by the jugal, postorbital, squamosal and quadrate bones and the lower jaw. Such osteoderms are well developed in adults of most *Lacerta* s. str. species (not *agilis* or some populations of *trilineata*), *L. lepida*, *L. princeps*, *L. (G.) atlantica*, some

L. (G.) simonyi, and *L. peloponnesiaca* and in *Psammodromus algirus.* Minor development (particularly along the posterior border of the jugal) may occur in individuals of other species especially in *Podarcis* (commonest in *L. melisellensis* and *L. taurica*).

6. *Pterygoid teeth*

Teeth are found on the pterygoid bones of all species of the subgenera *Lacerta* s. str. and *Gallotia,* in *L. lepida, L. princeps, L. peloponnesiaca, L. brandtii, L. jayakari* and *L. laevis.* They also occur in *Psammodromus algirus* and some *Algyroides moreoticus* and *A. nigropunctatus.* Klemmer (1957) has given data for various species in the subgenus *Podarcis.* In this group, some species rarely have pterygoid teeth, in others they occur in a substantial number of individuals and in *L. (P.) milensis* and *L. (P.) taurica* they seem to be almost universally present. In *Lacerta* as a whole there appears to be an imperfect correlation between presence of pterygoid teeth and robustness of the skull.

7. *Postfrontal and postorbital bones* (Fig. 2)

These bones are separate in the hatchlings of the majority of *Lacerta* species but fused in the three members of the subgenus *Gallotia,* in *L. (Z.) vivipara* and in *L. schreiberi.* They are also fused in all four species of *Psammodromus.* In some other forms, these two elements coalesce during life, e.g. *L. lepida, L. dugesii* and in old individuals of several other species.

8. *Number of presacral vertebrae*

Presacral vertebral number varies both between species and within them (see Appendix III), the usual range for *Lacerta* being 25 to 29* vertebrae, for *Algyroides* 24 to 28 and for *Psammodromus* 26 to 28. Intraspecific variation includes geographical, sexual and intrasexual differences. In each sex of a given species, most individuals usually have the same number of presacral vertebrae (occasionally two numbers are relatively common), the remainder deviate from this figure by one or occasionally two vertebrae. Typically the total range for each sex of a species is not more than three vertebrae. The commonest presacral vertebral numbers of each sex generally differ, females usually having on average one more vertebra than males (occasionally it is two more) ; 26 and 27 are the commonest figures for males, 27 and 28 for females. The three species assigned to the subgenus *Gallotia* differ from this pattern in showing almost no sexual or individual variation in vertebral number. This condition is rare in the Lacertidae as a whole, occurring elsewhere only in a few species of *Acanthodactylus.* Of the specimens of *Gallotia* examined in this study (viz. 25 *L. atlantica,* 35 *L. galloti* and 27 *L. simonyi*), nearly all had a presacral vertebral count of 26 irrespective of sex. The exceptions were one male *L. galloti* and two female *L. simonyi* all of which had 25 presacral vertebrae.

* Two out of 32 female *L. (L.) agilis* examined had 30 vertebrae as did one out of five female *L. (Z.) praticola.*

9. *Clavicle* (Fig. 3)

Some individuals of *Lacerta*, *Algyroides* and *Psammodromus* have clavicles that correspond to the condition found in the Lacertidae as a whole. In these the clavicle is greatly expanded near the midline and the expansion is penetrated by a large foramen so that the bone in this region forms a continuous loop (Fig. 3(2)).

1   **2**
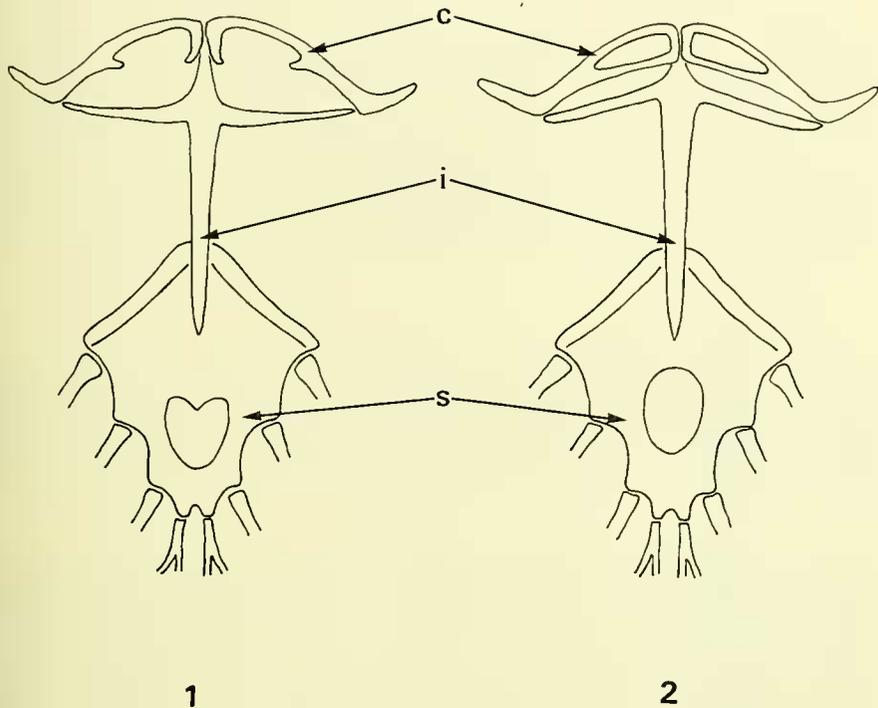
FIG. 3.   Variations in clavicle, interclavicle and sternum.   (1) Clavicle emarginated, interclavicle with lateral arms approximately at right angles to its longitudinal axis, sternum with heart-shaped fontanelle. (2) Clavicle unemarginated, interclavicle with lateral arms directed backwards, sternum with oval fontanelle. c = clavicle. i = interclavicle. s = sternum.

In other individuals the clavicle is emarginated posteriorly so that the loop is interrupted (Fig. 3(1)). This interruption may be minor or the whole posterior section may be missing. In *Psammodromus*, the species of the subgenus *Gallotia* and perhaps in *L. parva* and *L. fraasii* (the small samples available, 17 and 6 respectively, do not permit certainty) the loop of the clavicle is complete in all specimens. In most other species both the intact and emarginated conditions occur, although the proportion of each varies from species to species. In a few *Lacerta* species

only the emarginated condition was observed : these include *L. (P.) fiilfolensis, L. (P.) muralis, L. (A.) bedriagae, L. (A.) graeca, L. (A.) oxycephala, L. (S.) perspicillata* and *L. brandtii.*

10. *Sternal fontanelle* (Fig. 3)

In all species of *Lacerta, Algyroides* and *Psammodromus* the sternum usually has a distinct fontanelle penetrating its posterior area, although it may be unfenestrated in a few individuals of some species. The shape of the fontanelle is somewhat variable in most species but two main patterns are present. The majority of forms nearly always have an oval or round fontanelle while most members of *Podarcis* and *L. peloponnesiaca* have a heart-shaped (cordiform) one in which there is a well-developed, posteriorly directed process arising from the anterior border. Occasionally this extends right across the fontanelle to join its posterior margin, thus dividing it in two. Some individuals of *L. laevis, L. danfordi, L. andreanszkyi* and *Algyroides moreoticus* also have a sternal fontanelle which approaches a heart-shape but in these species the posteriorly directed process is not well developed.

11. *Interclavicle* (Fig. 3)

This element is cruciform in all species of *Lacerta, Algyroides* and *Psammodromus.* The lateral extensions of the interclavicle generally run at about 90° to the main axis of the bone although they may be directed slightly forwards or more rarely slightly backwards. *L. (P.) dugesii* and *L. (S.) perspicillata* differ in having the lateral extensions clearly directed obliquely backwards in all individuals examined.

12. *Pattern of tail vertebrae* (Fig. 4)

The systematic importance of variations in the caudal vertebrae of lizards in general has been discussed by Etheridge (1967). Three main patterns are present in the Lacertidae all of which occur in the genus *Lacerta.* Each begins with a proximal series of non-autotomic vertebrae. The number of bones in this proximal series varies from four to seven, males of any species tending to have a higher average number than females. The highest numbers encountered occur in *L. fraasii.*

Apart from the proximal series, the rest of the tail vertebrae are autotomic and the more anterior of these always bear transverse processes. It is these transverse processes which differentiate the three basic patterns (see Fig. 4).

Pattern A. All vertebrae with transverse processes have a single pair anterior to the autotomic plane.

Pattern B. The more anterior of the vertebrae with transverse processes bear two parallel pairs of which the anterior is longer. One pair lies in front of the autotomic plane, one pair behind. Normally from one to four vertebrae are involved although the number may exceptionally be up to seven. This pattern is restricted to *Lacerta* and the European species of *Algyroides.*

Pattern C. Again the more anterior autotomic vertebrae bear two pairs of transverse processes, one each side of the autotomic plane. The members of the more anterior of these pairs run laterally or occasionally are directed slightly
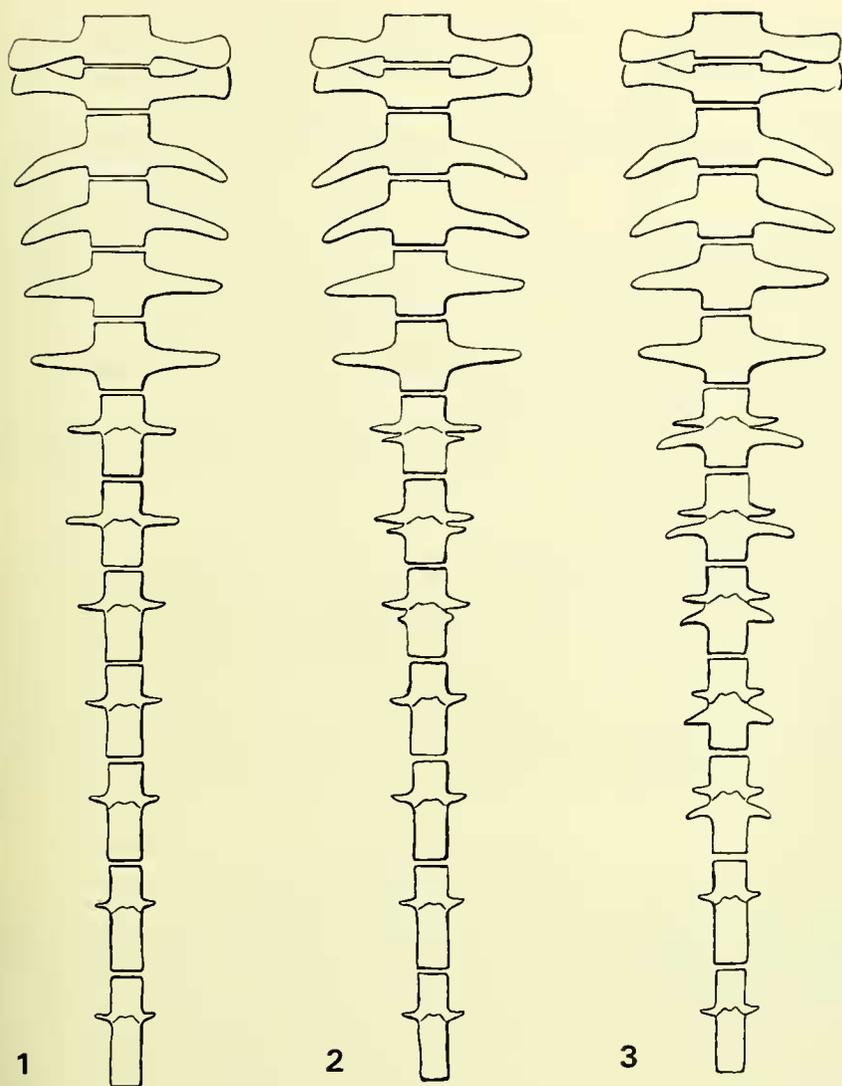
Fig. 4.   Principal patterns of caudal vertebrae.   (1) Pattern A : vertebrae with single pairs of transverse processes only.   (2) Pattern B : some anterior autotomic vertebrae with two, more or less parallel pairs of transverse processes, the posterior pair being the shorter.   (3) Pattern C : some anterior autotomic vertebrae with two diverging pairs of transverse processes, the anterior pair being the shorter.

forwards. The members of the posterior pair are often blade-like, usually longer than the front ones, and run obliquely backwards. From three to seven vertebrae are involved.

The A and B patterns are most similar, sometimes differing only in as little as the latter having secondary processes on one vertebra. Furthermore, they frequently occur together in the same population so it seems best to treat them as one class. A or B caudal patterns, or both, are found in all members of *Lacerta* s. str., most *Archaeolacerta*, the species of *Zootoca*, *L. (P.) dugesii*, *L. (S.) perspicillata*, *L. (Ap.) cappadocica*, *L. lepida*, *L. princeps*, *L. jayakari*, *L. cyanura*, *L. derjugini*, *L. laevis* and *L. chlorogaster* ; they are also found in *Algyroides*. The C pattern occurs in all members of *Gallotia*, in most members of *Podarcis* (not *L. dugesii*), in *L. peloponnesiaca*, in *L. (A.) danfordi* (in the subspecies *L. d. danfordi* and *L. d. anatolica* but not in *L. d. kulzeri*), and in *Psammodromus*.

L. parva, *L. brandtii* and *L. fraasii* have caudal patterns that are, to some extent, intermediate between the B and C types.

L. parva. Two to six vertebrae with double processes (two to four most commonly). The anterior pair is directed somewhat forwards in many individuals while the posterior pair is directed backwards ; in most cases it is larger than the anterior one but it may only be equal to it or even shorter.

L. brandtii. Four to seven vertebrae involved (six being the commonest number). The hind pair of transverse processes diverges backwards as in the C pattern but is usually not longer than the anterior one.

L. fraasii. Number of vertebrae with double processes usually two to four. The posterior pair diverges backwards and may be longer or much shorter than the hind pair.

It has not so far been possible to find any correlation between the caudal pattern and any functional parameter. The pattern does not appear to be related to the type of locomotion adopted or specialized use of the tail or to the ease with which autotomy takes place.

Hemipenial characters

The genitalia of many animals provide useful systematic characters ; for instance the baculum of mammals, the genital armature in insects, various features of the turtle penis (Zug 1966) and the hemipenis of snakes (summarized in Dowling & Savage 1960). Although not generally used, the hemipenes of lizards including lacertids can also provide helpful taxonomic information. Members of a species-group often show a similar hemipenial facies that differs from those occurring in other assemblages. The factors responsible for the evolution of different hemipenial structure in related groups are discussed on p. 324. Differences are not connected with the pattern of copulation for this does not seem to vary much in the Lacertidae. It is unlikely that the differences often function as isolating mechanisms since most sympatric lizard species appear to maintain isolation primarily by ethological means and species most likely to interbreed, that is ones which are closely related, tend to have a similar hemipenial structure.

Technique. In the overwhelming majority of specimens examined, the hemipenes had not been everted before preservation, so the following descriptions are based almost entirely on dissections of retracted organs. The ventral surface of the hemipenis is exposed and one lobe and the stem of the organ are opened by a parasagittal incision. This method of investigation is not entirely satisfactory as it is very difficult to make accurate comparative measurements of the uneverted hemipenis, but a good general impression of the morphology of the organ can be obtained by this means.

General structure of the hemipenis. The hemipenes of all species of *Lacerta*, *Algyroides* and *Psammodromus* are symmetrically bifurcate with large, usually plicate lobes. The sulcus runs along the hemipenial stem to divide into two branches each of which runs on to one of the lobes. The two lips of the stem sulcus overlap across it, but apically, where each forms the outer lip of one of the lobe sulci, they are usually enlarged and nearly always reflected outwards away from the sulcus. The inner lips of the lobe sulci are typically less developed than the outer ones and are sometimes scarcely apparent especially in the everted organ. However, their degree of development shows some correlation with that of the outer lips.

1. *The armature and the arrangement of the lobes in the retracted organ*

The hemipenes of many lacertid species are apparently different from those of most other lizards in having a clearly defined and often complex supporting structure – *the armature* (Arnold, in press). This is formed of dense connective-tissue and typically consists of a plate-like structure embedded in the dorsal surface of the *retractor magnus* muscle. The plate is attached to the cartilaginous region around the sulcus by a series of short *connectors* and may bear two, often club-shaped bodies, the *clavulae*, which lie between the retracted lobes. In forms where an armature is present, the retracted lobes are not simple sacs as in most other lizards but are flattened and complexly folded. The lobes are also peculiar in that the *retractor magnus* muscle does not insert widely over their surface but only along a narrow tract via a tendinous connexion.

Clearly armatured hemipenes with folded lobes are found in most lacertid genera but not *Takydromus*, *Platyplacopus*, *Psammodromus*, the European species of *Algyroides* and most Palaearctic *Lacerta* species. But *L. vivipara* and especially *L. cyanura* and *L. jayakari* have clearly differentiated armatures with distinct folding of the lobes. Armature development is also found in some *L. (Ap.) cappadocica*, which appear to have traces of lobar folding, and to a lesser extent in *L. (A.) graeca* where the lobes are not folded at all. Some other species of *Lacerta* have varying amounts of more diffuse connective tissue in the *retractor magnus* muscle and around the hemipenial lobes ; however, it is not differentiated enough to constitute a clear armature although it is almost certainly homologous with this structure. The wide distribution of armatured hemipenes in the *Lacertidae* may indicate that it is the primitive pattern within the family and that the condition found in other species is a secondary simplification. The sporadic occurrence of armatured hemipenes within *Lacerta* tends to support this hypothesis.

2. *Lobe proportions* (Fig. 5)

The hemipenial lobes can each be divided into two parts : an apical section from the apex to the point where the two lobes meet, and the remaining basal section. The relative lengths of these two parts vary although it is difficult to measure them accurately in the retracted hemipenis. The apical section in the majority of species is only about equal to or distinctly shorter than the basal section. In *Podarcis* (excluding *L. dugesii*) the apical portion is nearly always longer than the basal part and may at times be twice as long. This is true also of *Gallotia* (although the two sections may be subequal in *L. (G.) simonyi*), of *L. peloponnesiaca*, *L. (A.) danfordi* and to a lesser extent of *L. laevis*. The lobes are long too in *Psammodromus algirus* and in this species they are also rather narrow.
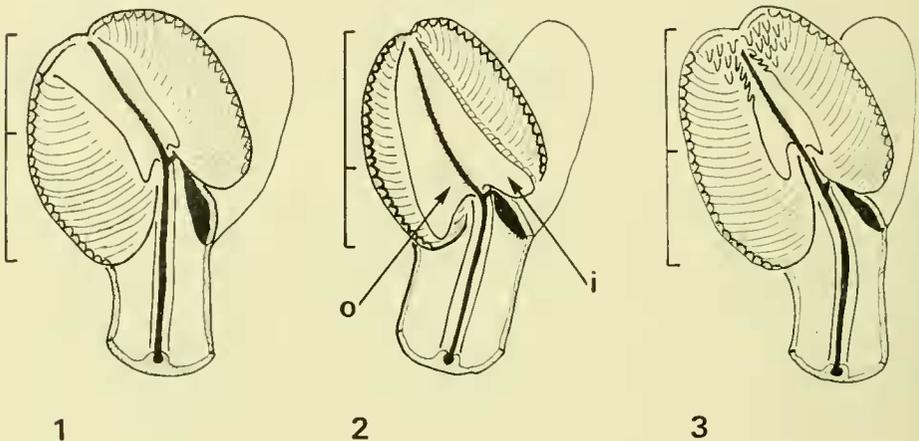
FIG. 5. Variation in hemipenis structure. Diagrams represent retracted organs viewed from below and opened by a parasagittal incision along the stem and one lobe which is spread outwards. Lines at sides indicate relative lengths of apical and basal sections of the lobes. (1) Widespread pattern in *Lacerta* : small sulcal lips, relatively short apical section, no large papillae. (2) Typical pattern in *Podarcis* : large sulcal lips, long apical region, no large papillae. (3) Typical pattern in *Gallotia* : small lips, moderate apical region, long apical papillae. o = outer lip of lobe sulcus. i = inner lip of lobe sulcus.

3. *Size of lips bordering the lobe sulci* (Figs. 5, 6)

The reflected outer sulcal lip varies considerably in size. In most species it is relatively small (Figs. 5(1), 6(1)) but it can be large especially in *Podarcis* (excluding *L. dugesii*). *L. peloponnesiaca* and some *L. (A.) danfordi* have sulcal lips that are as large as in *Podarcis* and a lesser degree of lip enlargement occurs elsewhere, for instance in *L. laevis*, *L. (S.) perspicillata* and especially *L. (Z.) andreanszkyi*. In all these forms the inner lip is also large.
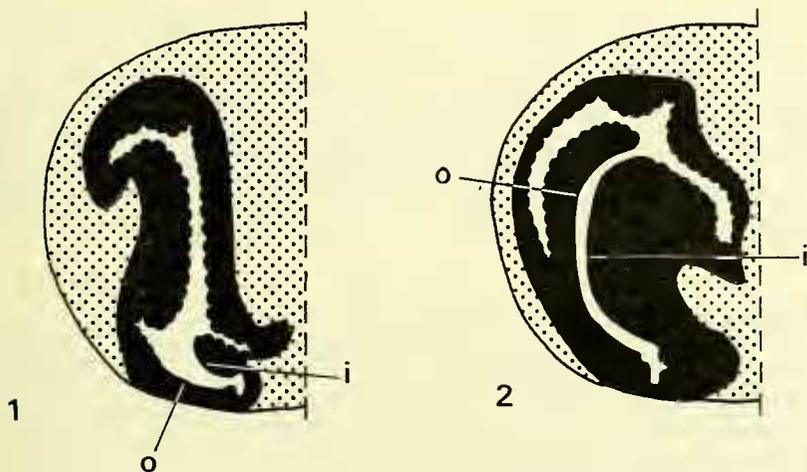
FIG. 6. Variation in hemipenis structure. Diagrams represent transverse sections of single retracted lobes just apical to the hemipenial bifurcation. (1) Small-lipped type (most *Lacerta* spp.). (2) Large-lipped type (*Podarcis*, etc.). o = outer lip. i = inner lip.

4. *Presence of plicae on the lobes*

In *Algyroides, Psammodromus* and nearly all species of *Lacerta*, the lobe surfaces have regular plicae running radially to their apicobasal axes, the only exceptions being *L. fraasii* and *L. parva*. These have the lobe surfaces irregularly folded with a series of longitudinal flaps on them.

5. *Apical papillae* (Fig. 5)

The apical region of each lobe is usually irregularly plicate, although in some members of *Podarcis* there may be a short series of small, blunt tubercles. The three species of *Gallotia* differ from the rest of *Lacerta* in having a terminal lobar area of large, pointed papillae, each of which is conical and somewhat flattened. Relatively large, pointed apical papillae also occur in *Psammodromus blanci, P. hispanicus* and *P. microdactylus*.

6. *Micro-ornamentation of the lobe surface*

Klemmer (1957) pointed out that the minute projections on the lobe plicae differed in shape between various *Lacerta* species and were potentially useful as taxonomic characters. Klemmer based his studies on fresh material (which is inevitably in rather limited supply), but it is possible to examine the pattern of micro-ornamentation in hemipenes extracted from alcohol-preserved specimens, even those over a century old provided they were killed during the mating season, which means that this character can be fairly readily surveyed. Variation in the hemipenial micro-ornamentation of lacertids has recently been studied in some

detail by Böhme (1971) and my own observations, using a scanning electron micro-
scope, appear to confirm his.

Basically there seem to be three main types of micro-ornamentation, although
intermediates do occur : (1) simple spikes or recurved spines, (2) tubercles with
a ring of spinules at their apex (crown-shaped tubercles), (3) irregular, quite often
bifurcated tubercles. As will become apparent, closely related species tend to
have a similar pattern of micro-ornamentation but there are a number of excep-
tions to this generalization.

Chromosomes

A review of the rather limited karyological data available for the Lacertidae up
to 1968 is given by Gorman (1969). Subsequently Orlova & Orlov (1969),
Kupriyanova (1968, 1969) and Gorman *et al.* (1971) have published information
on several more species. To date all the genera and species that have been investi-
gated are Palaearctic ones, viz. : *Acanthodactylus*, *Eremias* (subgenera *Eremias*
s. str. and *Mesalina*), *Lacerta*, *Ophisops*, *Psammodromus* and *Takydromus*. Nearly
all the species examined appear to have the same ' nombre fondamentale ' (i.e.
number of chromosome arms, Matthey 1949) : in the diploid state this is 38. The
commonest diploid formula is 36 acrocentric macrochromosomes plus two micro-
chromosomes. This is found in *Psammodromus algirus*, *P. hispanicus* and the
majority of *Lacerta* species investigated, viz. *armeniaca*, *agilis*, *caucasica*, *chloro-
gaster*, *dahli*, *derjugini*, *laevis*, *lilfordi*, *melisellensis*, *muralis*, *oxycephala*, *praticola*,
rostombekovi, *rudis*, *saxicola*, *sicula*, *taurica*, *trilineata*, *unisexualis* and *viridis*. *L.*
lepida, *L. vivipara* and *L. strigata* deviate slightly from the standard pattern :
L. lepida has 32 acrocentric macrochromosomes, two metacentric ones and two
microchromosomes ; *L. vivipara* lacks microchromosomes while *L. strigata*
has one of the usual pairs of acrocentric macrochromosomes replaced by a sub-
metacentric pair (Orlova & Orlov 1969). *L. parva*, while exhibiting the standard
' nombre fondamentale ', is peculiar in having only 24 chromosomes in the diploid
state : 14 metacentrics and 10 acrocentrics. A more extensive survey of the
lacertids might well reveal other variants.

External morphology and colouring

1. *Arrangement of nasal and anterior loreal scales*

The rostral scute and more frequently the first upper labial scute may contribute
to the border of the nostril in *Lacerta*, *Algyroides* and *Psammodromus*, but its greater
part is made up by scutes usually termed supranasal (lying dorsal, anterior and
sometimes ventral to the nostril) and postnasal (lying posterior to the nostril).
The scaling in this region occurs in three basic patterns : (1) Supranasal separated
from anterior loreal by a single postnasal. (2) Supranasal separated from anterior
loreal by two superposed postnasals. (3) Supranasal contacting anterior loreal
over a single postnasal. These three patterns usually occur with a single anterior
loreal but in some populations of *L. (L.) agilis* and in *L. (Ap.) cappadocica* the

scaling posterior to the nostril is very variable and there may be either one or two anterior loreals and in *L. (Ap.) cappadocica* up to three postnasals.

In fact the number of postnasals not infrequently varies within species but sometimes it is relatively stable throughout what, on other grounds, appears to be a natural species-group, e.g. there are two postnasals in most members of the subgenus *Lacerta* s. str. but only one in *Gallotia* and in the majority of individuals of *Podarcis*. Because it is so easily observed, postnasal number can be a useful, although by no means infallible, keying character.

2. *Lower eyelid*

The two monotypic subgenera of *Lacerta*, *Apathya* and *Scelarcis*, are partly based on possession of a distinctly transparent ' window ' in the lower eyelid. In *L. (Scelarcis) perspicillata* this consists of a single large scale but in *L. (Apathya) cappadocica* the window is made up of from six to eight smaller elements which have conspicuous dark borders. In fact many small lacertids without eyelid windows appear to be able to see, to some extent, through the lower eyelid which is often translucent enough in living animals for the pupil and iris to be visible when the eye is closed. In a number of species there is a series of enlarged scales in the centre of the eyelid and in *L. dugesii* these are sometimes as large as those found in *L. (Ap.) cappadocica*. Indeed the principal distinctive eyelid features of this last species are the distribution of pigment (concentrated at the scale edges) and increase in transparency rather than gross structure.

The selective forces promoting the development of eyelid windows and permanent spectacles (in which the upper and lower eyelids are fused) are probably varied. Walls (1934) thought that spectacles protect the eyes from mechanical damage, but Williams & Hecht (1955) suggest that pigmented windows may be important in cutting down the intensity of incident light and point out that many species with eyelid windows keep their eyes shut when basking. Another possibility is that eye closure reduces water loss from the corneal surface. This may be important in small heliothermic species with relatively large eyes which customarily bask in hot sun. The potential total water loss from the corneal surface may be quite large compared with the overall water balance of the animal. For instance, Reichling (1957) suggests that corneal transpiration may account for over 20 per cent of total transpirational loss in *Lacerta agilis* (a fairly small-eyed species) at normal activity temperatures. Keeping an adequate liquid film on the cornea might also present problems in these conditions. Certainly eyelid windows and spectacles are quite widespread in small heliothermic lizards, e.g. *Cabrita*, *Eremias*, *Holaspis* and *Ophisops* (Lacertidae), *Gymnophthalmus* (Teiidae), *Platysaurus* (Cordylidae), many skinks and diurnal gekkonids.

3. *Supratemporal scales and their relationship to the parietal scutes* (Fig. 7)

The shape and number of the supratemporal scales are very variable in *Lacerta*. In *Lacerta* s. str., *L. princeps*, *L. lepida*, *L. simonyi* there are usually two (or three) large, relatively deep scales, whereas in *Podarcis* the supratemporals are small,
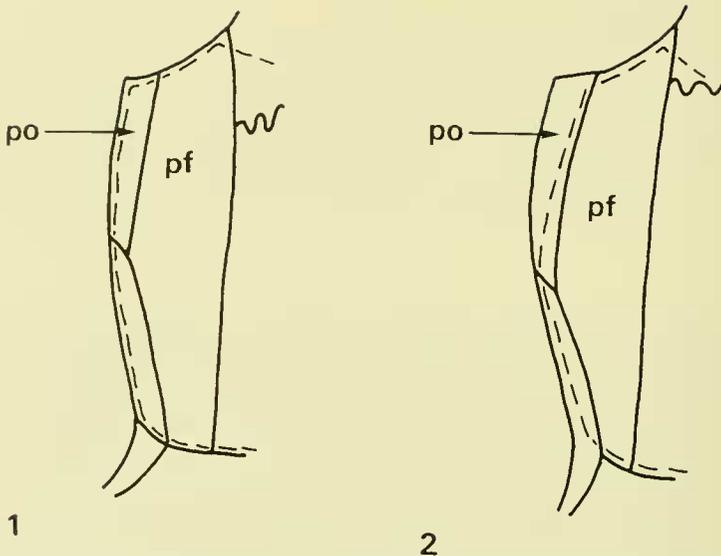
FIG. 7. Differences in relationship between the outer margin of the parietal scale and the
    underlying bones of the skull. (1) Parietal scale margin running along outer edge of
    postorbital bone. (2) Parietal scale margin close to postorbital–postfrontal suture.
    po = postorbital bone. pf = postfrontal bone.

shallow but again of about equal depth. In *L. (G.) galloti* and *L. (G.) atlantica*,
the anterior supratemporals are much shallower than the posterior ones while in
L. (S.) perspicillata and some *Podarcis* the supratemporals are scarcely distinct
from the small temporal scaling. Most other species of *Lacerta* and *Algyroides*
have a large anterior supratemporal which is both larger and deeper than those
following it. In *Psammodromus* the supratemporals may all be about the same
depth or there may be some tendency for the anterior ones to be slightly narrowed
(*P. algirus*) or enlarged.

Variation in the relationship between the anterior supratemporals and the
parietal scute was used by Méhely (1909) to define his two Wall Lizard groups
(equivalent to the subgenera *Podarcis* and *Archaeolacerta*). In the former the
outer parietal border is usually convex whereas in *Archaeolacerta* it is supposedly
emarginated by the first supratemporal. In fact, it is sometimes difficult to decide
if the parietal is emarginated and it is often easier in preserved material to see
differences in the relationship of the anterior outer border of the parietal to the
underlying bones of the skull. In the great majority of *Psammodromus*, *Podarcis*,
L. peloponnesiaca, *L. (S.) perspicillata*, *L. (Z.) andreanszkyi*, *L. (Z.) vivipara*, *L. (G.)*
atlantica and *L. (G.) galloti* the anterior border of the parietal scute with the anterior
temporal runs along the edge of the skull table (i.e. along the outer edge of the post-
orbital bone) or very close to it. In the remainder of *Lacerta* (with rare exceptions)

and in *Algyroides*, the parietal border either runs along the suture between the postorbital and postfrontal bones (if present) or fairly close to it or alternatively may run forwards from the outer edge of the postorbital to approach the postorbital–postfrontal suture anteriorly.

Méhely (1909) suggested that the peculiar arrangement of supratemporals in *L. (G.) galloti* and *L. (G.) atlantica* is a result of the original anterior supratemporals being incorporated into the parietal, the present anterior supratemporals being originally ordinary temporal scales. Some *L. (G.) galloti* have a cleft in the edge of the parietal in the position where the suture between the first and second supra-temporals would be expected to be. Possibly the parietal shields of at least some of the other forms with small apparent supratemporals also incorporate the original supratemporals.

L. (Ap.) cappadocica, *L. cyanura* and *L. jayakari* are peculiar in having all the supratemporals resting at least partly on the skull table whereas in other species some of the more central supratemporals are off it. *L. jayakari* is also singular in the adults having the posterior supratemporals diagonally elongated so that the anterior part of each lies above the posterior section of the one in front of it.

4. *Dorsal scaling*

Shape. Dorsal scales can be flat or raised, keeled or smooth, juxtaposed or imbricate. In *Lacerta* the dorsal scales are always smaller than the upper caudals but in *Algyroides* and *Psammodromus* they are nearly as large or considerably larger. In these two genera they are also strongly imbricate and keeled and are also often pointed. Scale shape may sometimes correlate with the type of habitat occupied by the species concerned (see p. 320).

Number. The number of dorsal scales in a transverse row at mid-body is a common parameter in lacertid systematics. In *Lacerta* the number varies from as low as 25 in some *L. (Z.) vivipara* to over 110 in some *L. (G.) galloti*, and the ranges in *Algyroides* and *Psammodromus* are about 21 to 31 and 15 to 28 respectively. Peters (1961) used the high dorsal count of *L. lepida* compared with its supposed relatives in the subgenus *Lacerta* s. str. as evidence that it should really be placed in *Gallotia* (where two of the three species also have fine scaling). However, there is a trend in *Lacerta* for small species and ones from moist habitats to have lower counts than large forms and ones from more arid regions. As both the fine-scaled members of the subgenus *Gallotia* and *L. lepida* are large and found in quite dry habitats, their high scale numbers might be a result of convergence.

5. *Preanal region*

Most species have a single large preanal scute bordered anteriorly by one or two semicircles of smaller scales. But in some cases the preanal is small or divided and bordered by up to four semicircles of scales. In the preanal region there is again some tendency for the larger species and those from arid regions to have higher numbers of scales.

6. *Collar*

Lacerta and *Algyroides* both have a well-defined collar. That is a backwardly directed transverse skin-fold on the lower surface of the neck, just anterior to the lateral arms of the interclavicle. The outer surface of this fold is covered by a transverse series of large plates. The posterior margins of the plates may form a regular, continuous line (collar smooth) or they may project backwards to form a free serration (collar notched). In *Psammodromus* a collar is either absent or at best very poorly defined.

7. *Ventral scaling*

Shape. There is considerable variation in the shape of the ventral scales and in their degree of overlap among the species of *Lacerta*, *Algyroides* and *Psammodromus*. As with dorsal scaling there is a marked correlation with habitat type (see p. 318).

Number of longitudinal rows. Most species have six longitudinal rows of ventrals but eight is not uncommon, and ten is the usual number in *L.* (*S.*) *perspicillata*, *L. princeps*, *L.* (*G.*) *atlantica*, *Psammodromus algirus* and some populations of *L. lepida*. *L.* (*G.*) *galloti* and *L.* (*G.*) *simonyi* have between 10 and 20 ventral rows.

8. *Keeling on subdigital lamellae*

The subdigital lamellae of nearly all *Lacerta* species are flat or tubercular, but those of the *L.* (*Ap.*) *cappadocica* examined have a single distinct central keel ; *L. cyanura* has a double row of keeled lamellae under each toe and the lamellae of *L. parva* may also occasionally bear two faint ridges (Lantz & Cyrén 1939). This character is sometimes stated or implied to be an adaptation to locomotion on loose surfaces, but its distribution in many families of lizards does not fit this hypothesis since many rock dwelling species also possess keeled lamellae, e.g. *L.* (*Ap.*) *cappadocica*, *L. cyanura*, *Platysaurus* (Cordylidae), various members of *Agama* and *Uromastyx* (Agamidae) and many skinks (e.g. *Mabuya laevis*, *M. quinquetaeniata* and *M. sulcata*). D. Western has made the more likely suggestion (personal communication) that the function of these keels is to reduce the area of contact with hot substrates and thus reduce heat flow. The toes of *Psammodromus hispanicus* are also distinctly bicarinate, while those of *P. microdactylus* and some *P. algirus* are more weakly keeled.

9. *Caudal scale whorls*

One of the characters used by Méhely (1909) to distinguish the subgenus *Archaeolacerta* from *Podarcis* is the degree of variation in the length of the caudal scale whorls. In *Archaeolacerta* the whorls are alternately long and short whereas in *Podarcis* they are said to be subequal. In fact the two conditions are not clearly separated and most members of *Algyroides*, *Psammodromus* and *Lacerta* show at least some alternation in the length of successive scale whorls and proper assessment of this feature thus requires accurate measurement of several whorls on each

individual lizard. This makes the character very time-consuming to assess and, as there is also considerable intraspecific variation, it appears to be of rather limited value except as a subsidiary character in identification.

10. *Colour and pattern*

Colour and pattern are very variable in *Lacerta* and to a much lesser extent in *Algyroides* and *Psammodromus* but two aspects In particular seem useful in defining species groups : these are the degree of sexual dimorphism in the dorsal pattern and the presence or absence of bright colour on the belly. Sexual dimorphism in dorsal pattern is well marked in most populations of *Podarcis* and *L. peloponnesiaca* and occurs also in some populations of *Lacerta* s. str. and *Gallotia*. Most other species of *Lacerta* either lack any sexual dimorphism in dorsal pattern or have it only slightly developed. This is also true of *Psammodromus* and most species of *Algyroides* (not *A. moreoticus*).

Bright, often transient ventral colouring occurs in at least some of the breeding individuals of most populations of *Lacerta*, *Algyroides* and *Psammodromus*. In the majority of these both the throat and belly are brightly coloured and the two areas may contrast with each other. However, in the subgenus *Lacerta* s. str., and in *L. jayakari*, *L. princeps* and *L. lepida* there is no bright colouring on the belly. This is true also in many populations of *L. (P.) sicula*, some *L. (P.) peloponnesiaca* (according to Buchholz 1960) and some *L. (P.) milensis*. Other individuals of the last species have bright colouring restricted to the second longitudinal rows of ventrals from the mid-line. Breeding males of *Psammodromus algirus* also have a pale belly. Other aspects of coloration are discussed elsewhere.

Hybridization

If two species are able to produce viable (although not necessarily fertile) hybrids, then a relatively close similarity in genetic material and therefore relationship is suggested. A number of cases of hybridization have been reported within *Lacerta* and most of these have been summarized by Mertens (1950, 1956, 1964, 1968, 1972). The various known or assumed crossings are shown diagrammatically in Fig. 8.

It will be seen that in nearly all cases hybridization has been within and not between accepted subgenera. Figure 8(a) involves only members of *Lacerta* s. str. ; Fig. 8(b) only members of *Podarcis* and Fig. 8(c) only members of *Archaeolacerta* plus *L. derjugini* which has been assigned to both *Archaeolacerta* and *Zootoca* (see p. 299).

RELATIVE TAXONOMIC VALUE OF CHARACTERS

Introduction

The distribution of many characters customarily used for defining intrageneric groups in *Lacerta* (see Table I) does not always correlate with that of the ' new ' osteological and hemipenial features introduced here, even although the latter tend to correlate well with each other. For instance, it is generally accepted on the
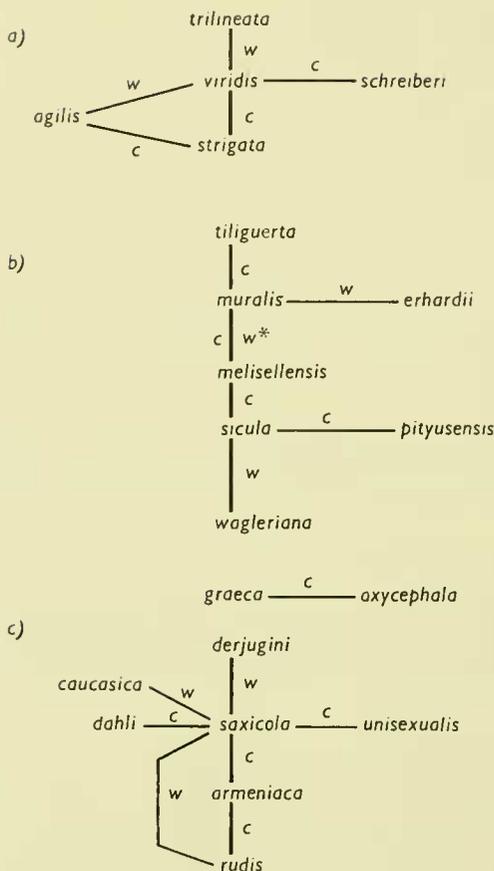
Fig. 8.   Known or assumed hybridization between species of *Lacerta*.   c indicates hybrid-
ization reported from captive animals.   w indicates hybridization assumed from morpho-
logically intermediate animals caught in areas of sympatry.   * indicates personal
observation.   For further explanation, *see* text.

evidence of the characters usually employed that *L. dugesii* is a member of the
subgenus *Podarcis* but its skeletal and hemipenial characteristics do not support
such a relationship. Similarly the lizards now separated into the subgenera
Archaeolacerta, *Lacerta* s. str. and *Zootoca* are all very similar in many features
of their hemipenes and postcranial skeletons which may suggest a closer relation-
ship than is usually acknowledged. This conflict of evidence makes it necessary
to assess what relative taxonomic weight should be given to the various characters
available. One factor that seems especially important in making this judgement is
the comparative lability of the characters concerned. Obviously, beyond certain

limits, the more labile a feature is, the less likely it is to indicate real relationships. Among the factors suggesting that a feature is highly labile are the following. (1) High intraspecific variability in a substantial number of the forms under consideration. (2) Continuous variation of the feature throughout the species group being examined (instead of the variation being separable into two or more disjunct character states). This applies specially to characters that involve very simple differences, for instance the relative size or proportions of a morphological feature. These may often be the result of quite small variations in growth pattern and be under polygenic control so that they may be likely to change fairly swiftly in response to selection pressures because there is considerable stored variability in the genotype and fresh mutation is not initially necessary. (3) The suspicion of lability is increased if, especially in the case of a large and varied genus like *Lacerta*, such contrasted characters show a close correlation with environmental parameters. Such correlation may well indicate that a selective pressure connected with the ecological parameter is responsible for the distribution. If the selective pressure and its mode of action in functional terms can be identified, then the case for assuming lability is very strong. Some examples of this sort of character assessment in *Lacerta* are given below.

Ecologically correlated characters

Sympatric species of lizards avoid competing ecologically by utilizing different food resources. But, as the majority of small lacertids are fairly general carnivores and eat whatever small, palatable animals they can overpower, this ecological separation does not usually depend on actively selecting prey species. Where more than one lizard species coexist in precisely the same habitat, separation is usually achieved either by hunting at different periods or by selecting different *sizes* of prey, in which case the coexisting species often differ in size too. But the commonest and most obvious means of dividing resources depends on each species being confined to and exploiting particular areas of the general environment. Spatial separation is common among sympatric species of *Lacerta* and their allies, the division depending on such features as humidity, degree of shade and the physical nature of the lizard's substrate. For instance in some upland areas of southwestern Yugoslavia (at about 1000 m), seven species of *Lacerta* may occur within a few hundred metres of each other. They divide the environment as follows.

Species	Size	Typical habitat
L. (A.) oxycephala	Small	Scansorial on sunny rock outcrops, pavements, boulder-screes, etc.
L. (A.) mosorensis	Small	Scansorial on moister and more shady rock areas than *oxycephala*
L. (P.) muralis	Small	Less scansorial than *oxycephala* and *mosorensis* but climbs frequently on the base of rock outcrops, on steep earth banks and on vegetated field walls and screes

Species	Size	Typical habitat
L. (P.) melisellensis	Small	Largely ground-dwelling in dry places, especially on broken terrain often with some vegetation. Rarely climbs on rocks, etc. but may occasionally climb small bushes
L. (L.) viridis	Large	In and around bushes especially brambles
L. (L.) agilis	Medium	Ground-dwelling in dry pastures often with small bushes
L. (Z.) vivipara	Small	Ground-dwelling in moist well-vegetated places often near water

It is with such differences in spatial niche that many of the characters used in defining *Algyroides*, *Psammodromus* and the subgenera of *Lacerta* can be correlated. Furthermore, they can often be interpreted as functional adaptations to survival in these niches.

Ventral scaling (Fig. 9)

Variation in ventral scaling provides an example of this type of correlation. There are two extreme conditions found in *Lacerta* which are illustrated in Fig. 9 : (1) belly scales shaped like inclined parallelograms with the posterior and lateral edges strongly overlapping ; (2) belly scales almost rectangular with little or no overlap. Many intermediates between these two conditions also occur. The most complete development of the first condition is found in the large lizards which make up the subgenus *Lacerta* s. str., and in *L. princeps* and *L. lepida*. It exists in a less extreme form in the following smaller species : *L. (Z.) vivipara*, *L. praticola*, *L. derjugini*, *L. parva*, *L. fraasii* and some species of the subgenus *Podarcis* also tend towards this condition (e.g. *L. taurica*). All these forms are largely ground dwelling in at least partly vegetated areas. If they climb, it is usually in scrub and bushes rather than on open surfaces. An even greater degree of ventral scale imbrication is found in *Psammodromus algirus* which often occurs in and around dense spiny vegetation. The second condition is best developed in the subgenus *Archaeolacerta*, *L. (S.) perspicillata*, *L. (Ap.) cappadocica* and in some *Podarcis* (populations of *L. hispanica* and *L. muralis*). In contrast to species having the first condition, these are largely scansorial and most of them climb principally on rock faces, boulders or walls but rarely in bushes.

The two conditions can be ' explained ' in functional terms. A ground-living *Lacerta* carries its viscera close to the substrate from which they are separated only by a thin body-wall. When travelling at speed, there is a considerable danger that this wall will be pierced by sharp twigs, dry grass stems or thorns pointing backwards against the direction of motion. Similar risks are faced by lizards in dense bushes. The ventral plates provide protection from such damage, having a hard, mainly β-keratin epidermis (Maderson 1964) and a tough dermal layer. However, these plates are quite rigid and, to permit the sinusoidal movements occurring in locomotion, there are transverse ' hinge ' regions housing flexible areas that allow expansion or contraction. Flexible (but non-expanding) hinges
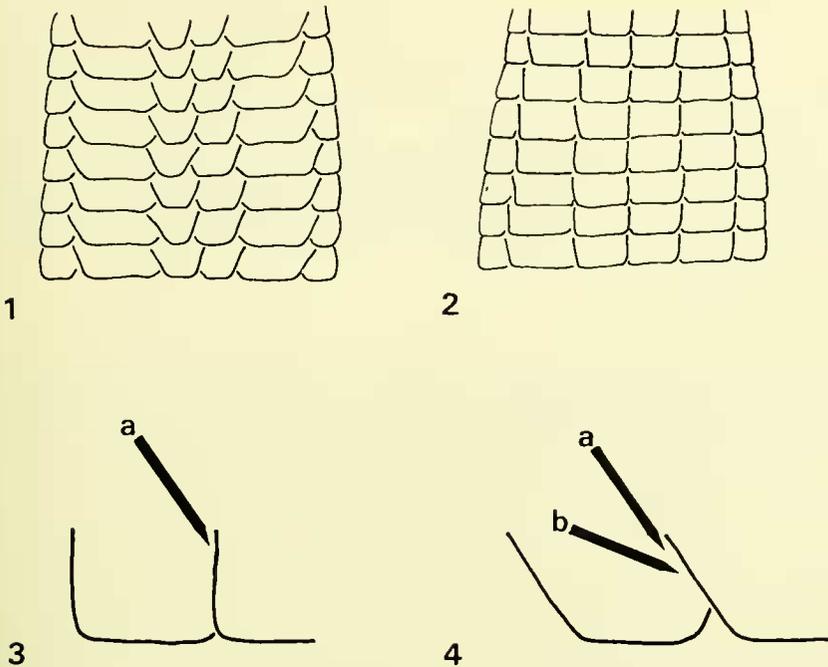
Fig. 9. Ventral scaling. (1) Strongly imbricate, most scales shaped roughly inclined like parallelograms. (2) Little imbrication, individual scales almost rectangular. (3) and (4) *see* text.

run in longitudinal series between the plates and facilitate the movements connected with respiration, lateral and dorsal compression of the body, etc. To provide the necessary flexibility these hinge regions have a thinner, less rigid epidermis largely made up of α-keratin (Maderson 1964) and a thinner dermal layer ; they consequently remain likely sites of penetration. (This can easily be confirmed on preserved material with a dissecting needle.) However, the transverse hinge regions are protected by the posterior overlap of each scale and are only exposed if the body is sharply flexed to one side. The roughly longitudinal hinge regions are also protected by imbrication but the protection is increased by the lateral scale margins being oblique. If these margins were parallel to the midline of the belly it would be possible for even slightly obliquely directed projections to penetrate under the overlap as in Fig. 9(3). The risk of damage is greatest with projections having axes approaching although not lying on a line parallel to the mid-line (Fig. 9(3a, 4a)), for at more oblique angles (Fig. 9(4b)) it is more likely that the projections will be deflected rather than penetrating. Therefore, by having the scale margins oblique, the risk of a projection entering a hinge is limited to the

potentially less damaging ones. All other things being equal, risk of damage by rigid projections increases with increase in size (since the mass and momentum of a lizard tends to increase with the cube of its linear dimensions, including skin thickness). It is therefore not unexpected that the system of overlaps should be better developed in the larger species.

Lizards habitually climbing on rock-faces are much less likely to be damaged by sharp projections and so can usually ' afford ' to do without these elaborate overlaps and their ventral scales themselves are not so resistant to penetration. (Rock-dwelling species of *Lacerta* if accidentally driven into thorn bushes during collection will sometimes get transfixed.)

Collar (Fig. 10)

When present, the collar provides an area of extension allowing movement of the gular skin during head raising. Thus when the head is thrown upwards, the collar fold is pulled out and the soft skin protected by the collar plates is extended (see Fig. 10(A), 10(B)). The various modifications of the collar that occur in *Lacerta* and related genera can, like belly scales, be interpreted as adaptations to particular structural environments. Collars with small, even-edged, only slightly imbricate plates that expose the vulnerable soft skin widely are, as might be expected, confined to habitats with few projections. In more spiky biotopes, there is a tendency for the collar plates to extend backwards to form a denticulate frill giving better protection to the soft skin (e.g. in *Lacerta* s. str.). There is also a trend in such habitats for the sites of expansion not to confined to a single vulnerable collar area but to be dispersed between a number of transverse rows of gular scales, which in the species concerned are strongly imbricate and thus cover the areas of expansion even when the skin is extended. In the most extreme cases, the collar disappears altogether (e.g. *Psammodromus algirus*), see Fig. 10(C), 10(D).

Dorsal scaling

Dorsal scales show trends in relation to habitat structure that are similar to those found in ventral scaling. Thus species in open environments tend to have small, rather convex scales with little overlap while forms living in biotopes with many projections tend to have larger, more strongly built scales with greater imbrication so that the more vulnerable interstitial skin is better protected. This process reaches its greatest development in *Psammodromus*.

Characters distinguishing the subgenus Archaeolacerta

Many of the features distinguishing the members of the subgenus *Archaeolacerta* (and *Scelarcis* and *Apathya* as well) from the rest of *Lacerta* can be interpreted as functional adaptations to the kind of spatial niche that they inhabit. As stated on p. 318, all the species assigned to *Archaeolacerta*, *L. (S.) perspicillata* and *L. (Ap.) cappadocica* are essentially rock-dwelling. (Evidence: *L. graeca, horvathi, monticola, mosorensis, oxycephala* – personal observation ; *L. bedriagae* – Lambert 1967 ; *L. danfordi* – Wettstein 1967, M. R. K. Lambert, personal communication ;
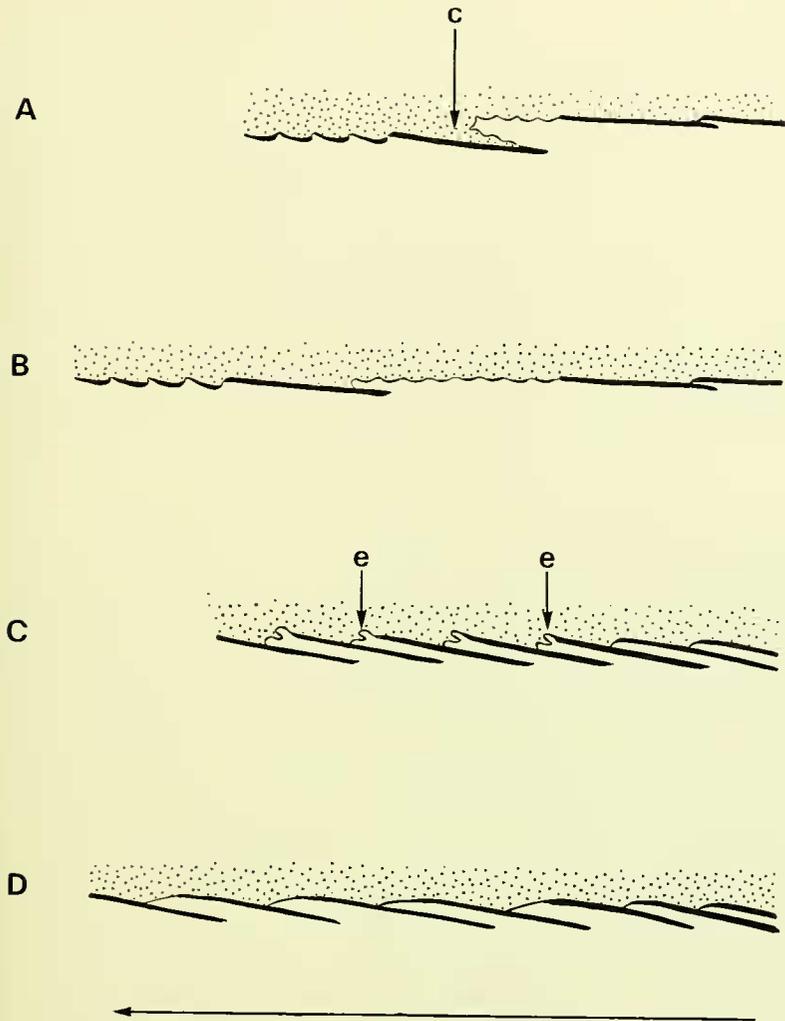
FIG. 10.   Different ways of providing elasticity in the gular skin.   A and B :   restricted area of extensible skin protected by a collar (e.g. in rock-dwelling species of *Lacerta*) ; A – skin at rest ; B – skin stretched.   C and D :   no collar, extensible skin distributed between a number of overlapping transverse gular scale rows ; C – skin at rest ; D – skin stretched.   c = collar.   e = regions of extensible skin.

L. saxicola and other Caucasian forms – Darevsky 1966 ; *L. perspicillata* – Dou-
mergue 1901 ; *L. cappadocica* – Reed & Marx 1959, Bird 1936, I. Nader, per-
sonal communication.) A more detailed account of adaptations to rock-living in
Lacerta will be published elsewhere ; the following remarks are abstracted from
this. Typical *Archaeolacerta* characters are printed in italics.

As with many lizards living in open environments, saxicolous lacertids appear to
be subjected to quite severe predator pressure, both from snakes and from birds
(shrikes, hawks, etc.). The principal means of avoiding such predators is for the
lizards to retreat deep into the narrow frost or sun-induced crevices characteristic
of many rock formations and to attach themselves firmly with their claws and by
flexing their bodies against the crevice surfaces. Birds cannot follow lizards into
such crevices and snakes have difficulty in obtaining enough purchase to extract
them. Many *Archaeolacerta* features are connected with this behaviour. The
depressed body and *low skull* make entrance into very narrow crevices possible.
The *weak ossification of the skull* with its *thin flat roof, poorly developed osteoderms*
and *large nasal openings* gives it a measure of flexibility so that the head can be
distorted and wedged into quite irregular fissures. The *flat, non-imbricate dorsal
scales, the narrow collar* and *non-overlapping ventral scutes* allow these lizards to
move as easily backwards as forwards in restricted spaces. This is advantageous
since backing out of refuges is often necessary.

Depression of the head has secondary effects, one of which involves the eyes.
An animal that depends on sight to detect prey and predators cannot ' afford '
to reduce the absolute size of its eyes, consequently in lizards with depressed heads
these project well above the level of the skull roof. But when such a lizard enters
a crevice the eyes must be accommodated within the reduced vertical dimensions
of the head. This is accomplished by some of the orbital contents passing down-
wards through the *suborbital foramen which is enlarged*, so that they project into the
buccal cavity. These movements require a much greater flexibility of the supra-
orbital region and this is provided by the *limited ossification of the supraocular plates*.

The characteristic features of rock-living *Lacerta* species often allow these lizards
to avoid predators but paradoxically make their plight worse if they cannot reach
a suitable crevice. The fragile skull is easily smashed and the absence of scale
overlaps and mechanically strong, raised scales means that the skin is more liable
to damage. Furthermore, the lowering of the skull results in the efficiency and
size of the jaw muscles being reduced so that specialized rock lizards are less able
to actively defend themselves than other species of similar size. There is conse-
quently great advantage in directing attack away from the body towards the more
expendable tail. There are often behavioural mechanisms to do this, for instance
some rock lizards switch the tail vigorously from side to side when attacked. Also
while the body is usually more or less procryptically marked, the *tail in many young
rock lizards is blue or green* and conspicuous at close quarters. In the most special-
ized rock lacertas, e.g. *L. oxycephala, L. perspicillata, L. cappadocica, L. cyanura*,
this colouring may be retained by adults too. Furthermore, the tails of rock
lizards appear to be more easily autotomized than those of other forms (well over
90 per cent of adults in some populations of *L. oxycephala* have regenerated tails).

Evolution of low autotomy thresholds is probably facilitated by the tail being of less locomotory importance in scansorial lizards than in ground dwelling ones. Y. Werner (1968) has demonstrated a similar correlation between habitat and rate of autotomy in geckoes.

Many of the characters typical of rock-dwelling lacertas also occur in saxicolous species of other families, e.g. *Afroedura*, *Ptyodactylus* and *Quedenfeldtia* (Gek-konidae) ; *Oplurus*, *Sauromalus*, *Petrosaurus* (Iguanidae) ; some *Xantusia* (Xan-tusiidae) ; *Mabuya sulcata*, *M. laevis* (Scincidae) ; *Platysaurus* (Cordylidae).

The correlation between the development of this syndrome of characters and rock-dwelling is often quite precise. Thus *L. monticola cyreni* appears to be less strictly restricted to rocks and crevices than the three Yugoslav species of *Archaeo-lacerta* (*L. horvathi*, *L. mosorensis* and *L. oxycephala*) and has the characteristic saxicole features less well developed than in these species. Similarly although most species of *Podarcis* climb to some extent, only some populations of *L. hispanica* seem to be almost exclusively rock-dwelling. These are the only members of the subgenus to show very distinct development of features supposedly characteristic of *Archaeolacerta*, etc.

Discussion

Thus the distribution of many of the characters traditionally used in the sys-tematics of *Lacerta* and allied genera can at least be tentatively related to ecological parameters and often to particular strong selective pressures. This suggests that they are rather labile, a conclusion supported by many of them being continuously variable throughout the group, in some cases by their showing some intraspecific variability and by the fact that differences between contrasted characters are often the result of quite small changes in growth pattern. For example, the supra-ocular pattern shows two characteristic adult states, viz. ' supraocular bones com-plete ' and ' supraocular bones fenestrated ' which both develop in ontogeny from an unossified juvenile condition. In most species the osteoderms develop fast, spreading outwards from the border of the frontal until the whole supraocular area is covered, but in *Archaeolacerta* and other rock species the process is much slower so that by maturity there is still an unossified (i.e. fenestrated) area. That this state is merely the result of a comparative retardation in growth rate is indicated by the occurrence of complete osteoderms in old specimens of some *Archaeolacerta* species (Klemmer 1957).

The apparent lability of the characters discussed above suggests that they should be given relatively low weight in assessing relationships although it could of course be argued that the other characters available for classifying *Lacerta* and its allies are just as likely to be labile and that this is not recognized because the selective factors responsible for their lability are unknown. This is true, but provided the possibility of high lability has been carefully considered for all features, it seems better in cases where two sets of characters suggest different classifications, to base systematic decisions on the set not known to be potentially or actually very labile. Of course, low lability does not imply that characters are non-adaptive. There are

many situations where a character may be fairly stable, yet of great functional significance.

In some cases, the contrasted characters, or systems to which they contribute, may represent different solutions to a particular problem, which are superior, in most circumstances, to intermediate conditions. They may be integral parts of complex functional systems that are unlikely to be interconvertible without dissolution of the system concerned. Thus rock lizards have different means of protecting the eyes when they enter crevices. One of these, where part of the orbital contents passes through a large suborbital foramen has already been described (p. 322). Cordylids (*Platysaurus*) use another : the suborbital foramen being small, part of the orbital contents is passed into the interpterygoid vacuity. Presumably once a rock lizard is committed to one of these methods it could not change to the other without a period of greatly reduced efficiency. Contrasted characters may represent solutions to a particular problem unconnected with the specific requirements of different niche-types. For example, Cryptodire and Pleurodire chelonians both protect the head by withdrawing it into the shell but they employ quite different means of folding the neck. Again it seems likely that the two methods are not interconvertible and the anatomical modifications connected with these methods thus make very good characters for defining the two groups. The various types of adhesive pad found on the toes of geckoes are a similar case (A. P. Russell, personal communication). While it is not yet possible to explain the stability of the lacertid characters discussed here in this way, analogous reasons for low variability seem possible.

Among the features of *Lacerta* and its allies that seem to be generally quite stable intraspecifically and for which there are no obvious external grounds for regarding as particularly labile are the following (although in the present context, stable and labile are purely relative terms since, among the species under consideration, most characters are subject to occasional exception) : postorbital–postfrontal fusion, sexually correlated variation in vertebral number, shape of the sternal foramen, caudal vertebral pattern, position of the lateral border of the parietal shield and various aspects of hemipenial structure. There are additional reasons for considering the latter to often be good indicators of relationship and these are discussed below.

Hemipenial characters

As already stated, genital characters have often been found pragmatically to be sensitive indicators of relationship (although like any other character source they are not infallible). In the lacertids, the differences between hemipenial types do not appear to be related to differing methods of copulation, or often to be isolating mechanisms. Nor is it possible at present to relate them to particular environmental selection pressures, either acting directly on the hemipenis or indirectly by producing modification of some other part of the animal which in turn causes selection to alter the form of the hemipenis itself.

Mayr (1970) suggests that genital differences might often be pleiotropic by-products of changes in the genotype induced by selection acting on other parts of the animal. This may well be so but does not entirely explain why genitals are often such particularly good indicators of relationship. The reason may be as follows. With most organ systems, any pleiotropically induced change is likely to result in a lowering of functional efficiency. However, provided this reduction in efficiency does not outweigh the original selective advantage of the genetic change concerned, the pleiotropic alteration will initially become fixed. But there will then be normalizing selection modifying the genotype further so that the pleiotropic changes will tend to be suppressed and the organ will return towards its original state and level of efficiency ; see Fig. 11(a).

One would expect rather similar events to take place when pleiotropic changes occur in the genitals but the process will not be exactly the same, since the efficiency of these organs cannot be considered in isolation but only in relation to their co-ordinated functioning with the genitals of the opposite sex which are also under selective control. (Presumably copulatory efficiency depends largely on a good physical match of the genitals rather than their absolute size and shape.)

Consequently, if there is a pleiotropic change in the male organs which reduces copulatory 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 genitals compensating for, and adapting to, the pleiotropic alterations that have already taken place in the male system. This means that the two sets of genitals may return to their previous efficiency without reverting to their original morphological state ; see Fig. 11(b). Presumably the converse situation also exists where pleiotropic changes in the female system produce compensatory alteration in the male.

The genitals are thus likely to ' store ' pleiotropic changes which in other organ systems would probably be eradicated. Furthermore, the genitals of each sex will tend to be altered not only by direct pleiotropic effects on themselves but also by those causing changes in the genitals of the opposite sex. It would consequently be expected that differences in hemipenial structure would often bear some relation to the overall genetic differences between the species compared.

Genitals, at least in lizards, are often good indicators of relationship partly because they alter in the way described above but also because their rate of change is not too fast, so that closely related forms tend to retain quite similar structural patterns. One possible reason for this is that the original extent of pleiotropic changes is reduced by compensating selection in the opposite sex.

Another possible explanation of hemipenial variability is that the female genital system in lizards is much more flexible and much less precisely structured than the hemipenis and could perhaps therefore often accommodate itself immediately, without genetic change, to slight pleiotropic alterations in the hemipenis. This would mean that such minor pleiotropic changes in the male organ would not be subject to normalizing selection or the rather more complex process described above. But if this was generally so, one would expect greater intraspecific variation than
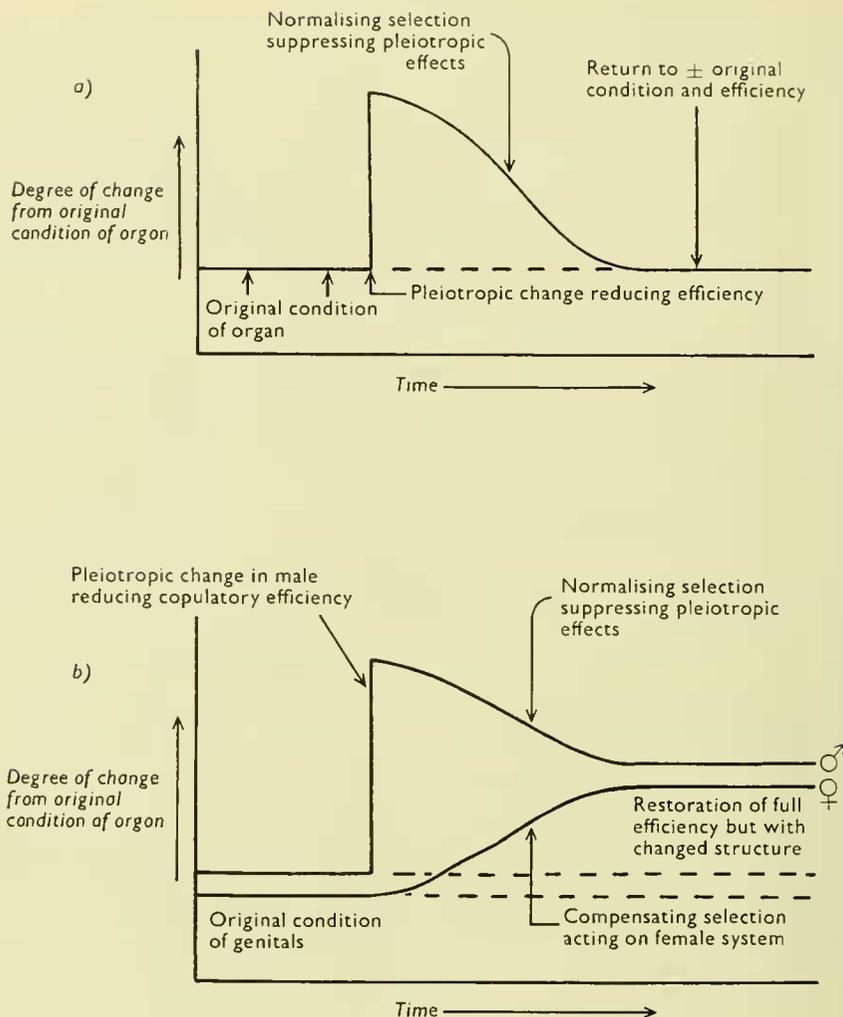
FIG. 11. For explanation *see* text.

has so far been encountered in lizard hemipenes. However, this factor may have some effect.

Although there are reasons for believing that hemipenial characters may frequently be particularly good indicators of relationship, they are not infallible pointers and must be treated with as much caution as any other type of character. For it is quite probable that they are altered by direct environmental selective

pressure on occasion. Also, as the overall form of the hemipenis is relatively simple, one must sometimes expect parallel development of similar structure in forms which are not particularly closely related, especially at the lower taxonomic levels.

Böhme (1971) has placed considerable emphasis on hemipenial micro-ornamentation as an indicator of relationship (see p. 299). However, when all available characters including other hemipenial features are taken into consideration, it appears that although hemipenial micro-ornamentation is usually similar in closely related species there are exceptions and the character consequently does not always indicate natural groupings.

RECLASSIFICATION OF *LACERTA*, *ALGYROIDES* AND *PSAMMODROMUS*

If the species of *Lacerta*, *Algyroides* and *Psammodromus* are arranged on the basis of those features listed on p. 324 as seeming relatively stable, it is found that there are a number of clearly defined species-groups, the members of each having more or less the same combination of these characters. Furthermore, some other features of less certain relative stability correlate quite well with this arrangement thus providing additional evidence that the groups are natural ones, e.g. number of postnasal scales, degree of sexual dimorphism, scale size, etc. The principal characters of the species-groups are listed in Table II.

Algyroides (excluding the African species) and *Psammodromus* appear to be natural assemblages while Palaearctic *Lacerta* can be divided into four main groups. The principal features of these taxa are given in Table II, p. 328. The *Lacerta* groupings are as follows.

1. Equivalent to the subgenus *Lacerta* s. str. including *L. princeps* and *L. lepida*.

2. Including the subgenera *Zootoca*, *Archaeolacerta*, *Scelarcis* and *Apathya* plus all species not included in other groupings.

3. Members of the subgenus *Podarcis* excepting *L. dugesii* which is placed in group 2 ; and *L. peloponnesiaca*.

4. Equivalent to the subgenus *Gallotia*.

As defined here, groups 1, 3 and 4 are relatively homogeneous while group 2 is much more varied and is in fact a polythetic assemblage. Groups 3 and 4 are quite distinct, both from each other and from groups 1 and 2 which in contrast are generally quite similar. In the interests of nomenclatorial stability it would be desirable, if possible, to retain *Lacerta* more or less as it is presently understood and recognize the groupings within it at an intrageneric level. However, this cannot easily be done for two of the groups have greater affinities with other genera than they do with the rest of *Lacerta*. Thus group 4 seems to be more nearly related to *Psammodromus* than to the other *Lacerta* groupings. Similarly there is a much closer relationship between group 2 and *Algyroides* than between groups 2 and 4 or groups 3 and 4. *Lacerta*, as it stands, is therefore a rather artificial assemblage and it seems best to divide it to produce more homogeneous entities. The most convenient way of doing this is to leave the very similar groups 1 and 2 in *Lacerta* and raise the other two groupings to the rank of full genera, group 3 becoming *Podarcis*

TABLE II : Principal features of *Algyroides*, four proposed taxa originally included in *Lacerta*, and *Psammodromus*

Proposed classification	Algyroides *Algyroides*	Lacerta				Psammodromus *Psammodromus*
		Group 1 *Lacerta* Part I	Group 2 *Lacerta* Part II	Group 3 *Podarcis*	Group 4 *Gallotia*	
Number of species	*n* = 4	*n* = 7	*n* = 28	*n* = 13	*n* = 3	*n* = 4
Osteology						
Postorbital and postfrontal bones separate at least in young	+	+ (exception)	+ (exception)	+	−	−
Sex-correlated variation in presacral vertebral no. present	+	+	+	+	−	+
Clavicle emarginated in some individuals of all or most species	+	+	+	+	−	−
Sternal fontanelle oval, not heart-shaped	+ (partial exception)	+	+ (partial exceptions)	− (in most cases)	+	+
Caudal vertebrae pattern A or pattern B	+	+	+ (exceptions)	−	−	−
Hemipenial features						
Apical portion of hemipenial lobes long	−	−	− (exceptions)	+	+ or intermediate	+/−
Lips of lobe sulci large	−	−	− (exceptions)	+	−	+/−
Long, conical papillae on lobe tips	−	−	−	−	+	+/−
Micro-ornamentation of crown-shaped tubercles	+/−	+/−	+/−	−	−	+/−

External features						
Usually two postnasals	+	+ (exceptions)	+/−	−	−	−
Parietal shield reaches outer edge of postorbital bone anteriorly	− (exception)	−	− (exceptions)	+	+/−	+
Dorsal scales relatively large	+	− (fairly large in one species)	−	− (fairly large in one species)	−	+
Collar present	+	+	+	+	+ (fairly large in one species)	− (or weak)
Number of longitudinal ventral scale rows	6	6–10	6–10	6 (8)	(8) 10–20	6, 10
Sexual dimorphism in dorsal pattern	− (exception)	+ (exceptions)	− (exceptions)	+ (few exceptions)	+	−
Belly brightly coloured in breeding males	+	−	+ (exception)	+ (exceptions)	+	+ (exception)
Adult size large (often over 100 mm snout to vent)	−	+ (exception)	− (exception)	−	+/−	−

and group 4 *Gallotia*. This would produce genera with roughly the same degree of difference that is found in other parts of the Lacertidae. Such a course will result in new name combinations for the sixteen members of groups 3 and 4. This is unfortunate but probably will not cause much confusion as the new generic names have already been widely used as subgenera. An alternative course would have been to include both European *Algyroides* and *Psammodromus* in *Lacerta*, but this would also necessitate some name changes and would result in a large and very varied genus difficult to diagnose adequately.

LACERTA Linnaeus

Linnaeus, 1758, *Syst. Nat.*, ed. 10, vol. **1** : 200.

TYPE SPECIES : *Lacerta agilis* Linnaeus.

DIAGNOSIS. Small to very large lacertids (from 35 mm to over 210 mm snout to vent). Skull shape variable, parietal foramen present, frontal bones paired throughout life, postorbital and postfrontal bones separate in young of most species but sometimes fuse during life ; clavicle strongly expanded medially, foramen either emarginated or not (the two conditions often existing within the same population) ; interclavicle cruciform, the lateral arms not strongly directed forwards ; sternal fontanelle almost invariably present, nearly always roughly oval ; sexual variation in presacral vertebral number present ; all presacral vertebrae with ribs, except the first three cervicals ; free ribs divided into two series – an anterior one of long ribs and a posterior one of short ribs ; caudal vertebrae typically of A or B pattern (rarely C). Hemipenes symmetrically bilobed. Typically armature absent and lobes not complexly folded (there are exceptions) ; lobes usually plicate, micro-ornamentation variable ; apical regions of the lobes usually short (exceptions) with small sulcal lips (exceptions) ; no large conical papillae at lobe tips. Head shields normal ; nostril usually in contact or close to the first upper labial scute, bordered posteriorly by one, two or rarely three postnasals ; lower eyelid usually scaly although a small transparent window may be present ; anteriorly parietals typically do not extend to outer margin of postorbital bone, first supratemporal scale often large ; masseteric shield often present.

Dorsal body-scales small or moderate (smaller than proximal caudals) ; collar well marked ; ventral scales smooth, truncate, strongly overlapping or not, in six to ten longitudinal rows. Toes cylindrical or compressed, usually tubercular beneath (occasionally strongly keeled) ; femoral pores present. Tail long, unmodified. Sexual dimorphism in dorsal pattern absent in most although not all species. Belly often, but not always, brightly coloured in at least the breeding males.

SPECIES REFERRED. *agilis, andreanszkyi, armeniaca, bedriagae, brandtii, cappadocica, caucasica, chlorogaster, cyanura, dahli, danfordi, derjugini, dugesii, fraasii, graeca, horvathi, jayakari, laevis, lepida, monticola, mosorensis, oxycephala, parva, perspicillata, praticola, princeps, rostombekovi, rudis, saxicola, schreiberi, strigata, trilineata, unisexualis, viridis, vivipara*.

Lacerta as defined here is an extremely varied genus within which only one species group can be clearly separated ; this is *Lacerta* part I which is more or less equivalent to *Lacerta* s. str. and will be dealt with separately ; the remainder of the genus forms *Lacerta* part II. I do not propose to use formal subgenera for these two groupings, especially as the type species of *Zootoca* (available for *Lacerta* part II) is rather anomalous.

LACERTA part I (= *Lacerta* s. str.)

SPECIES REFERRED. *agilis, lepida, princeps, schreiberi, strigata, trilineata, viridis.*

DISTINGUISHING FEATURES. A closely related group of species distinguished from the rest of *Lacerta* by possession of the following combination of characters. Body-size medium to very large (adults 70 mm to over 210 mm snout to vent) ; skull undepressed, very robust, often with ossified temporal skin. Usually two postnasal scales, dorsals strongly raised, often keeled ; collar strongly serrated, ventrals with very marked imbrication, in six to ten longitudinal rows ; sexual dichromatism in dorsal pattern quite frequent ; in young, dorsum often ocellated or with pale, narrow stripes, dorsal ground colour of adults often bright green, belly white in young, yellowish in adults, never brightly coloured.

SKELETAL FEATURES. Skull robust ; undepressed with a thick osteodermal layer. Supraocular lamellae complete in non-juvenile specimens, temporal ossification often extensive (not *agilis* or some populations of *trilineata*). Postorbital and postfrontal bones usually separate in hatchlings (not *schreiberi*) but sometimes fused in adults (always in *lepida*) ; pterygoid teeth nearly always present. Sex-correlated variation in the number of presacral vertebrae present ; commonest numbers 27 in males and 28 in females (often 28 and 29 respectively in *agilis*). Clavicle expanded medially, exists in both intact and emarginated conditions in all species. Interclavicle cruciform, lateral arms not obviously directed forwards or backwards. Sternal fontanelle oval, occasionally imperforate. Usually one, two or even three pairs of inscriptional ribs. Typically five or six non-autotomic tail vertebrae (rarely seven, four in some *agilis*). Caudal pattern most frequently B, less often A (some *agilis*, *schreiberi* and *viridis*).

HEMIPENIS. Symmetrically bilobed without an obvious armature ; lobes not folded in retracted organ, plicate. Apical sections of lobes subequal to or shorter than basal sections ; lobe tips without prominent papillae. Lips of lobe sulci small to moderate. Micro-ornamentation variable ; *L. lepida* has simple recurved spines but in most species the lobe apices have short tubercles with a fine denticulation at their tips, while the lobe flanks are covered by long, fairly straight projections that sometimes end in a point and sometimes in an irregular series of spinules. In *L. princeps* these flank spines tend to be recurved.

EXTERNAL FEATURES. Medium to large lizards (adults from about 70 mm to 210 mm snout to vent). Nostril in contact with first upper labial and usually bordered posteriorly by two postnasals (one in many *agilis*). Eyelid scaly.

Parietal shield not clearly emarginated, but its outer margin generally running medial to the postorbital–postfrontal suture if present. In most cases, two large, deep supratemporals (posterior one sometimes broken into two or three parts). Masseteric shield frequent. Dorsal scales small to moderately large, 32 to 98 across the mid-body, raised and usually strongly keeled (keeling weak or absent in *lepida*). Collar well developed, strongly serrated. Ventrals smooth, truncate, strongly imbricating, in six to ten longitudinal rows, their borders forming laterally inclined parallelograms. Preanal scale large in most cases (somewhat reduced in *L. lepida* and to a lesser extent in *L. schreiberi* and some *L. trilineata*). Toes tubercular beneath, not strongly compressed. Femoral pores usually present, each series extending to knee (except in some *L. trilineata*), 11 to 22 pores in each series. Tail long, unmodified.

COLORATION. Sexual dichromatism occurs in a number of populations and is particularly well developed in *L. schreiberi* and many *L. agilis*. In juveniles the dorsum often has up to seven light longitudinal stripes although these may be absent (especially some *lepida*, *trilineata* and *viridis* which are uniform) or replaced by ocelli (many *agilis* ; *lepida* and *schreiberi*). In adults the stripes, if originally present, are frequently lost and the dorsum becomes bright green (not in *princeps*, or some *agilis*, *lepida*, *viridis*, *schreiberi* and *strigata*). Dorsum may sometimes be heavily marked with black (especially some *agilis* and female *schreiberi*) but lizards of this group lack the dark lateral bands often found in *Lacerta* part II, *Podarcis*, *Gallotia*, *Algyroides* and *Psammodromus*. The throat is often brightly coloured in breeding males (not *L. lepida* and some populations of *agilis*, *strigata*, *trilineata* and *viridis*), but this does not apply to the belly which never contrasts strongly with the dorsum and which also always lacks blue spots on the outer ventral scales.

RELATIONSHIPS. The seven species that make up *Lacerta* part I form a tight, closely related assemblage, the members of which have a detailed morphological similarity to each other. However Peters (1961, 1962a) has suggested that *L. princeps* and *L. lepida* have no near relationship to the other species and indeed this author placed *L. lepida* in *Gallotia*. Among the grounds given for excluding *princeps* from *Lacerta* part I are (i) its large dorsal scales, (ii) lack of green pigment and (iii) the presence of ' real ' (i.e. black-bordered) blue lateral ocelli. Eiselt (1968) regards these differences as unimportant and certainly they seem rather trivial compared with the overall resemblance of *princeps* to other *Lacerta* part I lizards. Although the dorsal scales are large they are approached in size by those of some populations of *L. strigata*, a geographical neighbour of *princeps* ; also the differences in scale size within *Lacerta* part I (as defined here) are not particularly large, being considerably less than those found in *Gallotia*. Absence of green dorsal coloration is not confined to *princeps*, it occurs as well in some members of other species (see above). Similarly the presence of black-bordered, lateral ocelli is not really distinctive, indeed they do not occur in all *princeps* being typical only of the nominate subspecies ; *L. p. kurdistanica* Suchov 1936 has simple, unbordered blue spots on the flanks similar to those occurring in some *L. trilineata*. The blue ocelli of adult *L. p. princeps* appear to develop from paler ocelli in juveniles (see

photographs in Eiselt 1969) which are very similar to the ocelli found in juveniles of *L. schreiberi*.

The case for transferring *L. lepida* to *Gallotia* must also be rejected. Peters (1961) again cites the presence of blue ocelli as grounds for exclusion from *Lacerta* s. str. (= *Lacerta* part I), but as in *L. princeps*, those of *L. lepida* develop from white ocelli which are also found in juveniles of some other *Lacerta* part I species. Furthermore, some *L. lepida* have no lateral ocelli at all.

Admittedly members of *Gallotia* have bright (blue or yellow) flank spots but these are not clearly dark-edged. Bright flank-markings seem often to be sign stimuli and are likely to develop in any forms that use a lateral display in courtship or in aggressive activities ; on their own therefore they do not necessarily indicate relationship. Other resemblances between *L. lepida* and the large members of *Gallotia* pointed out by Peters are : small anal plate surrounded by many small scutes ; high counts for dorsal scales across mid-body, longitudinal rows of ventrals, gular scales between chin-symphysis and collar, caudal scales in a basal whorl and femoral pores. All these characteristics indicate a general reduction in relative scale-size. It has already been pointed out (p. 313) that this is often correlated with large body-size and dry habitats, conditions that apply both to *L. lepida* and to *Gallotia* so again this resemblance may be convergent. More important *L. lepida* agrees with the majority of species in *Lacerta* part I in a long series of characters not found in *Gallotia*, viz. postorbital and postfrontal bones separate in juveniles, sexual variation in presacral vertebral number (usually 27 in males and 28 in females as against 26 (rarely 25) in both sexes in *Gallotia*), clavicle sometimes emarginate, AB type caudal vertebrae, hemipenis without large apical papillae, two postnasals present, green dorsal colouring and no bright belly pigment. It seems certain therefore that the affinities of *L. lepida* do lie with *Lacerta* part I. Within this grouping, *L. lepida*, particularly the northwest African *L. l. pater*, has a considerable resemblance to *L. trilineata* and especially *L. schreiberi*. *L. l. pater* is similar to the latter in having eight rows of ventral shields, a small preanal, spotted juvenile livery and early fusion of the postorbital and postfrontal bones (before hatching in *schreiberi*, soon afterwards in *lepida pater*). The head shape and male colouring are also very close.

Contrary to the opinions of Boulenger (1916) *Lacerta* part I is not closely related to *Gallotia* nor does it have any clear relationship with *Podarcis*. Its members are, however, very similar in skeletal and hemipenial features to some species of *Lacerta* part II.

DISTRIBUTION (see Fig. 12). Extensive and continuous, covering much of the total range of the genus *Lacerta* (except some parts inhabited only by *L. vivipara*, some islands etc.). N.W. AFRICA : Morocco, N. Algeria, N.W. Tunisia (perhaps Rio de Oro – Valverde 1957). MAINLAND EUROPE : Southern peninsulas north to England, Denmark, Sweden, south Finland and about latitude 60° in Russia. MEDITERRANEAN ISLANDS : Sicily, Elba, islands on eastern Adriatic coast, Ionian Islands, Corfu, Crete, Cyclades, Euboa, Rhodes, Lesbos and several other Aegean islands. WESTERN ASIA : Central Asia to Turkey, east Mediterranean coast south to Israel, N. Iraq, N. and western Iran south to Shiraz and Neyriz.

BIOLOGY. *Lacerta* part I species are usually among the largest lizards occurring in their ranges. They tend to eat larger prey than other sympatric lacertid species and thus avoid competition with them. Most forms are typically associated with areas having dense bushy vegetation (or occasionally with rough grass-land). *L. agilis* is mainly ground-dwelling but the other species may climb in bushes or even trees ; they do not climb on rock surfaces to any great extent.

LACERTA part II

SPECIES REFERRED. *Lacerta* part II contains members of *Lacerta* that do not possess the combination of characters distinguishing *Lacerta* part I.

DISTINGUISHING FEATURES. Most species are under 90 mm snout to vent when adult and have brightly coloured bellies in at least the breeding males. *L. jayakari*, however, is much larger (up to 165 mm) and appears to lack a bright belly at all times ; in spite of this its affinities appear to lie with other members of *Lacerta* part II.

SKELETAL FEATURES. Skull variable, depressed and delicate in some species, very robust in others, many forms intermediate between these two extremes. Supraocular lamellae often fenestrated and external nares rather large in adults of about half the species ; temporal ossification usually absent. Postorbital and postfrontal bones usually unfused (fused in *L. vivipara*) ; pterygoid teeth usually absent (not *L. brandtii*, *L. dugesii*, *L. jayakari* and *L. laevis*). Presacral vertebral number shows sex-correlated variation : usually between 25 and 28 in males, 26 and 29 in females. Clavicle expanded medially and existing in both intact and emarginated conditions in most forms (perhaps only the intact condition present in *L. parva* and *L. fraasii*). Interclavicle cruciform with lateral arms usually not strongly directed forwards or backwards (angled distinctly backwards in *L. dugesii* and *L. perspicillata*). Sternal fontanelle usually oval. (It may approach the cordiform condition in *L. laevis, L. andreanszkyi* and *L. danfordi*.) Inscriptional ribs often absent or only one pair present. Non-autotomic caudal vertebrae most usually number 5 or 6, less commonly 4 and rarely 7. Tail vertebrae frequently B pattern or, less often, A : *L. d. danfordi* and *L. d. anatolica* but not *L. d. kulzeri* are peculiar in having C-type vertebrae while *L. brandtii, L. fraasii* and *L. parva* have caudal sequences more or less intermediate between the B and C types.

HEMIPENIS. Symmetrically bilobed ; in most cases no obvious armature and the lobes not folded in repose ; armatures and complexly folded lobes do occur in *L. vivipara, L. cyanura* and *L. jayakari* and a more limited armature development may occur in *L. cappadocica* and *L. graeca*. Outer surfaces of lobes usually regularly plicate but not in *L. parva* or *L. fraasii* where the walls of the retracted organ are arranged in irregular folds and have longitudinal flaps. Lobes without large apical papillae ; their sulcal lips usually small or very small (larger in *andreanszkyi, danfordi, perspicillata* and *laevis*).

Micro-ornamentation variable : most forms have crown-shaped tubercles but simple recurved spines occur in *andreanszkyi, bedriagae, cappadocica, graeca, jayakari*

and *perspicillata*.   *L. dugesii* has spines that at first sight appear simple but when examined with a scanning electron microscope can be seen to have a number of spinules at their tips so that they are intermediate between the two types of ornamentation mentioned so far.   *L. brandtii, L. fraasii* and *L. parva* all have irregular tubercles that seem to end in spinules.   They often appear bifurcate but this is uncertain in the case of *brandtii*. (Micro-ornamentation data from Böhme 1971, and personal observations.)

The above comments on hemipenial structure do not cover the apparently all-female parthenogenetic forms allied to *L. saxicola*, viz. *armeniaca, dahli, rostombekovi* and *unisexualis*.

EXTERNAL FEATURES.   Small to large lacertids : adults from about 35 mm (*andreanszkyi*) to 165 mm (*jayakari*) snout to vent, but most species between 50 mm and 90 mm.   Nostril usually in contact with first upper labial (often narrowly separated in some species, e.g. *andreanszkyi, brandtii, cappadocica, fraasii, monticola, parva, perspicillata, vivipara*), bordered posteriorly by one or two superposed postnasals (three in some *L. cappadocica*), usually one in about half the species, one or two in *bedriagae, fraasii* and *mosorensis*, two in the remainder, viz. *brandtii, cappadocica, cyanura, danfordi, dugesii, graeca, jayakari, laevis, oxycephala, parva* and *perspicillata*.   Eyelid fairly opaque and scaly in most forms ; a window of transparent, black-edged scales in *L. cappadocica*, a single-scaled window in *L. perspicillata*.   Anterior part of lateral border of the parietal shield often emarginated and running medial to the edge of the postorbital bone in the majority of species but along the postorbital margin in *andreanszkyi, dugesii, perspicillata, vivipara* and some *bedriagae*.   Supratemporals well developed in most cases, the first usually being longer and deeper than the rest ;   sometimes the supratemporals not easily distinguishable from temporals, e.g. particularly *dugesii, perspicillata*.   In *cappadocica, cyanura* and *jayakari* all the supratemporals rest at least partly on the bony parietal table ;   in *jayakari* the posterior supratemporals are diagonally enlarged so that the anterior of each lies above the posterior portion of the one in front.   Masseteric shield usually distinguishable in most species but not in *cappadocica, cyanura, dugesii, graeca, jayakari, perspicillata* and many *andreanszkyi, bedriagae, danfordi* and *oxycephala*.   Dorsals small, 25 (some *vivipara*) to 91 (some *jayakari*) in a transverse series at mid-body, in most species smooth or faintly keeled but more strongly so in *chlorogaster, laevis, parva, praticola, rudis* and *vivipara*.   Collar well developed, serrated or smooth. Ventrals smooth, truncate, the degree of imbrication varying with habitat (least in rock-dwellers, greatest in ground forms) ;   usually in six longitudinal rows (exceptions :   *brandtii* eight to ten, *jayakari* and *parva* eight, *perspicillata* ten ; some individuals of *cappadocica, danfordi, fraasii* and *laevis* may also have eight rows).   Preanal shield usually large, occasionally rather reduced with two or more semicircles of small scales anterior to it, e.g. *cappadocica, danfordi, fraasii, jayakari, parva*.   Toes varying in degree of compression, usually tubercular beneath but unicarinate in *L. cappadocica*, strongly bicarinate in *L. cyanura* and weakly so in some *L. parva*.   Femoral pores present, extending to, or nearly to knee ; 7 (some *vivipara*) to 31 (some *bedriagae*) in each series.   Tail long, unmodified.

COLORATION. Sexual dimorphism in dorsal patterning of adults absent in most forms (few exceptions, e.g. *L. dugesii* and to a lesser extent some populations of *L. monticola* and in *L. graeca*). Pattern very variable but most species lack the lateral pairs of *narrow*, well-defined pale stripes found in *Podarcis* and *Gallotia* (they are often present in *andreanszkyi*, *parva* and *vivipara*). Pattern usually consists of dark longitudinal stripes or series of markings which sometimes coalesce to form a reticulation (e.g. *bedriagae*, *jayakari*, *oxycephala*). In *cappadocica*, *danfordi* and *pcrspicillata* there seem to be distinct colour-morphs, the last two species including individuals with almost no markings, perhaps equivalent to the ' concolor ' morph of *Podarcis*. Venter usually brightly pigmented, particularly in breeding males although both sexes are often involved. *L. jayakari* appears to be exceptional in lacking any bright ventral coloration. The outer ventrals often have blue spots and these may extend onto the flanks in some cases.

RELATIONSHIPS. *Lacerta* part II unlike the other groupings discussed in this paper contains a very varied assemblage of species (many of their principal differences are summarized in Table III). It includes all the species originally assigned to the subgenera *Zootoca*, *Archaeolacerta*, *Apathya* and *Scelarcis* plus many of the species of uncertain position listed on pp. 298–299 and *Lacerta dugesii* which is usually classified with *Podarcis* (group 3). Many of the characters on which these subgeneric divisions were based appear to be ecologically labile and are thus relatively unimportant in assessing relationships (see pp. 315–324) ; once they are excluded from consideration, *Lacerta* part II in spite of its variability cannot be divided into discrete groups although it is often possible to suggest which forms are particularly closely related. However, for convenience, *Lacerta* part II will be discussed under a number of separate headings, even although the divisions between them are to a large extent artificial.

(a) The more typical members of *Lacerta* part II.

SPECIES DISCUSSED. *armeniaca*, *bedriagae*, *caucasica*, *chlorogaster*, *dahli*, *danfordi*, *derjugini*, *graeca*, *horvathi*, *laevis*, *monticola*, *mosorensis*, *oxycephala*, *praticola*, *rostombekovi*, *rudis*, *saxicola*, *unisexualis*.

The above species occur in a broad, but disjunct band from northern Spain and Portugal across the northern Mediterranean region to the Caucasus and south Caspian coastal area. The majority of these forms have all the features listed as characteristic of *Lacerta* part II (although this does not necessarily imply that they are primitive). This applies especially to the more northern ones ; some of the southern species are rather different, frequently having two postnasals (*danfordi*, *graeca*, *laevis*, *oxycephala* and some *bedriagae* and *mosorensis*) and the masseteric shield absent or often reduced (*bedriagae*, *danfordi*, *graeca* and *oxycephala*). These southern species are often better differentiated than the more northern ones and some possess peculiar features. For instance, some populations of *L. danfordi* have C-type caudal vertebrae and very large sulcal lips on the hemipenis ; *L. laevis* and some *L. danfordi* often have a more or less cordiform sternal fontanelle and *L. graeca* has a distinct armature development in the hemipenis and simple spines (as opposed to tubercles with a ring of spinules at their tips) on the hemipenial

	chlorogaster	praticola	derjugini	caucasica	rudis	saxicola-group	vivipara
Clear armature present .	−	−	−	−	−	−	+
Postorbital and postfrontal bones	−	−	−	−	−	−	+
No microchromosomes in karyoty	−	−	−	−	−	−	+
Parietal shield extends to outer e postorbital bone . . .	−	−	−	−	−	−	+
Lateral arms of interclavicle clear posteriorly	−	−	−	−	−	−	−
Masseteric shield absent or reduce	−	−	−	−	−	−	−
Two postnasal scales present	−	−	−	−	−	−	−
Hemipenial micro-ornamentation spines (+) or irregular often bifur tubercles (×) . . .	−	−	−	−	−	−	−
Eight or more rows of ventral sca	−	−	−	−	−	−	−
Prominent blue spots on flanks	+	−	−	−	−	(+)	−
Caudal vertebrae not of A or B ty	−	−	−	−	−	−	−
Hemipenial lobes with longitudina unplicate	−	−	−	−	−	−	−
Chromosome number greatly redu	−	−	−	−	−	−	−
Sternal fontanelle approaches hea	−	−	−	−	−	−	−
Very large body-size . .	−	−	−	−	−	−	−
Supratemporal scales diagonally e	−	−	−	−	−	−	−
Supratemporal scales all rest on s	−	−	−	−	−	−	−
Belly always pale, without bright even in breeding males . .	−	−	−	−	−	−	−
Toes carinate beneath . .	−	−	−	−	−	−	−
Lower eyelid with 'window' .	−	−	−	−	−	−	−
Strongly expanded scales under fo	−	−	−	−	−	−	−

The characters are arranged not according to anatomical proximity but so that the common features of each loose species-group can be easily appreciated. Parentheses indicate that the character is only sometimes present or present in limited form, a question-mark that no certain data are presently available.

Character	*fraasii*	*parva*	*brandtii*	*andreanszkyi*	*perspicillata*	*dugesii*	*jayakari*	*cyanura*	*cappadocica*	*laevis*	*danfordi*	*graeca*	*bedriagae*	*oxycephala*	*monticola*	*mosorensis*	*horvathi*	*chlorogaster*	*praticola*	*derjugini*	*caucasica*	*rudis*	*saxicola-group*	*vivipara*
Clear armature present	−	−	−	−	−	−	+	+	(+)	−	−	(+)	−	−	−	−	−	−	−	−	−	−	−	−
Postorbital and postfrontal bones fused	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+
No microchromosomes in karyotype	?	+	?	?	?	?	?	?	?	−	?	?	?	−	?	?	?	−	−	−	−	−	−	+
Parietal shield extends to outer edge of postorbital bone	−	−	−	+	+	+	−	−	−	−	−	−	(+)	−	−	−	−	−	−	−	−	−	−	+
Lateral arms of interclavicle clearly directed posteriorly	−	−	−	−	+	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
Masseteric shield absent or reduced	−	−	−	(+)	+	+	+	+	+	−	(+)	+	(+)	(+)	−	−	−	−	−	−	−	−	−	−
Two postnasal scales present	(+)	+	+	−	+	+	+	+	+	+	+	+	(+)	+	−	(+)	−	−	−	−	−	−	−	−
Hemipenial micro-ornamentation of simple spines (+) or irregular often bifurcate tubercles (×)	×	×	×?	+	+	(+)	+	−	+	−	−	+	+	−	−	−	−	−	−	−	−	−	−	−
Eight or more rows of ventral scales	(8)	8	8/10	−	10	−	8	−	(8)	−	(8)	−	−	−	−	−	−	−	−	−	−	−	−	−
Prominent blue spots on flanks	+	+	+	−	−	−	−	−	−	−	+	(+)	−	−	−	−	−	+	−	−	−	−	(+)	−
Caudal vertebrae not of A or B type	+	+	+	−	−	−	−	−	−	−	(+)	−	−	−	−	−	−	−	−	−	−	−	−	−
Hemipenial lobes with longitudinal flaps; unplicate	+	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
Chromosome number greatly reduced	?	+	?	?	?	?	?	?	?	−	?	?	?	−	?	?	?	−	−	−	−	−	−	−
Sternal fontanelle approaches heart-shape	−	−	−	(+)	−	−	−	−	−	+	(+)	−	−	−	−	−	−	−	−	−	−	−	−	−
Very large body-size	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
Supratemporal scales diagonally enlarged	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
Supratemporal scales all rest on skull table	−	−	−	−	−	−	+	+	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
Belly always pale, without bright colour, even in breeding males	−	(+)	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
Toes carinate beneath	−	−	−	−	−	−	−	+	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
Lower eyelid with 'window'	−	−	−	−	+	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
Strongly expanded scales under forearm	−	−	−	−	−	−	+	+	(+)	−	(+)	−	−	−	−	−	−	−	−	−	−	−	−	−

epithelium ; similar spines occur in *L. bedriagae* (Böhme 1971). Many of the northern species, on the other hand, are very similar to each other, indeed some of the key characters allegedly distinguishing allopatric forms do not always do this. This is true for *L. horvathii* and *L. mosorensis*. It seems probable that the geographical isolation of some of these northern species may be a relatively recent occurrence.

(b) *Lacerta vivipara*.

This species has an immense and largely continuous distribution mainly to the north of the area occupied by the species discussed in the last paragraph. It is probably related to the more northern of these forms but it differs from them all in a number of features : the hemipenis has a well-differentiated armature and folded lobes, the postorbital and postfrontal bones are fused even in newly deposited young, the edge of the parietal shield reaches the outer margin of the bony parietal table, one pair of microchromosomes is lacking from the usual *Lacerta* karyotype (which is present in the 12 typical members of *Lacerta* part II that have been investigated to date ; see p. 310) and unlike the rest of *Lacerta*, *L. vivipara* is ovoviviparous over most of its range.

L. vivipara is usually associated with *L. derjugini* and *L. praticola* in the subgenus *Zootoca* but there are no good grounds for doing this. The resemblance between the three species (body-shape, rather large dorsal scales, serrated collar, some overlapping of ventrals, often complete supraocular lamellae) is connected with their similar habitats – all are ground-dwelling lizards occurring most usually in rather moist herbaceous places (Lantz & Cyrén 1947). Neither *L. derjugini* nor *L. praticola* has any of the *vivipara* characters listed above, instead they are very similar to the other typical members of *Lacerta* part II in their general features and it is almost certain that this is where their close affinities lie, indeed *L. derjugini* frequently hybridizes in the wild with one of the typical species, *L. saxicola* (Darevsky 1966).

(c) Southeastern species.

SPECIES DISCUSSED. *cappadocica, cyanura, jayakari*.

These three well-defined species have some resemblance to each other. Like the more southern typical members of *Lacerta* part II they have two post-nasal scales (three in some *L. cappadocica*) and no masseteric shield. In addition all their supratemporals rest on the parietal table and they have at least some indication of an enlarged series of scales beneath the forearm. *L. cappadocica* and *L. jayakari* both have the hemipenial epithelium micro-ornamented with simple recurved spines while that of *L. cyanura* has crown-shaped tubercles.

L. cappadocica has a number of rather peculiar features : its hemipenis may have a fairly weak but definite armature and the lobes of the hemipenis may be somewhat folded, the parietal shield has a concave lateral margin, the eyelid a transparent window of black-edged scales and the digits a single row of keels beneath. Although quite distinct from it, this species probably has affinities with its geographical neighbour, *L. danfordi*, which it resembles in some features of

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head-scaling, in body proportions in similar polymorphic colour patterns and in their both often having a series of feebly enlarged scales beneath the forearm.

L. jayakari resembles *L. cappadocica* in the features common to the three south-eastern species and also in possessing a hemipenial armature and folded hemipenial lobes. However, the armature and lobe-folding are much better developed than in *L. cappadocica* and the degree of enlargement in the scales under the forearm is much greater. *L. jayakari* also differs from *L. cappadocica* and from the greater part of *Lacerta* part II in its large size, lack of belly pigment (apparently even in breeding males), diagonally elongated posterior supratemporals and its strongly keeled, straight caudal scales. In the first two characters it resembles *Lacerta* part I but does not possess the other features characteristic of the members of that group.

L. cyanura, which is sympatric with *L. jayakari* in Oman, seems to have close affinities with this species in spite of its much smaller size and possession of bright belly colouring (blue) in the male (Arnold 1972). The two species are alike in most skeletal features including the number of presacral vertebrae in females (26), most aspects of hemipenial structure, the very enlarged plates under the forearm and the strongly keeled caudal scales. The pattern of the one known juvenile has some resemblance to that found in the *wolteri* Bird 1936 form of *L. cappadocica*. Sub-digital keeling is also found in both *L. cyanura* and *L. cappadocica* but the pattern differs, *L. cyanura* having two rows of keels beneath each digit and *L. cappadocica* one.

In spite of their considerable differences it is likely that the two Oman species are closer to *L. cappadocica* than to any other member of *Lacerta*.

(d) Southwestern species.

SPECIES DISCUSSED. *andreanszkyi, dugesii, perspicillata.*

One of these species, *L. dugesii*, has usually been classified with the members of *Podarcis* but it lacks many of the features that occur in all members of that genus and to be much closer to members of *Lacerta* part II especially the other southwestern species. Among the features it possesses that do not occur in *Podarcis* are the following. (1) Interclavicle with lateral arms directed posteriorly. (2) Oval sternal fontanelle. (3) A and B pattern caudal vertebrae. (4) Hemipenis with short apical sections to the lobes and small sulcal lips. (5) Almost always two superposed postnasals. (6) No masseteric shields or well-defined supra-temporals. (7) Often a dorsal pattern including rather broad pale supraciliary stripes that become broader and fainter posteriorly (similar to that found in some members of *Lacerta* part II, e.g. *L. caucasica*) ; other specimens have a reticulated or striated pattern rather like that of some *L. perspicillata*. (8) Hemipenial orna-mentation consisting of recurved spines with minute spinules on their tips.

The three southwestern species are alike in having the parietal shield reaching the edge of the postorbital bone, in usually lacking the masseteric shield (a masseteric sometimes present in *andreanszkyi*) and in having a micro-ornamen-tation of more or less simple spines on the hemipenial plicae (distinctive pattern of *L. dugesii* is mentioned above). Each species is well differentiated from the

others and has its own peculiarities but, as with the southeastern species, each pair of the trio has features in common that, with the characters listed above, suggest that they are perhaps quite nearly related. Thus *L. perspicillata* and *L. dugesii* both have a peculiar interclavicle structure, two postnasals and similarity in dorsal patterns ; *L. andreanszkyi* and *L. dugesii* have six rows of ventrals and *L. andreanszkyi* and *L. perspicillata* share very large sulcal lips on the hemipenial lobes. *L. perspicillata* has customarily been separated from the rest of *Lacerta* in the subgenus *Scelarcis* because it has ten longitudinal rows of ventrals and a brille in the lower eyelid. Ten rows of ventrals occur elsewhere in *Lacerta* part II (in some *L. brandtii*) and, as explained on p. 311, windows in the lower eyelid are a relatively frequent development in several lines of lacertids ; indeed *L. dugesii* has a number of enlarged and translucent scales in this region. Therefore it does not seem necessary to separate *L. perspicillata* from the rest of *Lacerta* part II on these grounds.

It is uncertain how the three southwestern species relate to the rest of *Lacerta* part II. Their nearest geographical neighbour is *L. monticola* of the northern and central Iberian Peninsula but this species, which appears to have its closest affinities with the more typical members of *Lacerta* part II (see p. 336), does not resemble the southwestern species very closely. The latter have more in common with *L. danfordi* and neighbouring species in the eastern Mediterranean region. Like them they may have two postnasals, no masseteric shields and large hemipenial lips. There is also some resemblance in habitus and in dorsal patterns, especially those of *L. danfordi* to *L. dugesii* and *L. perspicillata*. Such a relationship would not be entirely unexpected as there are other cases of zoogeographical links between the eastern Mediterranean region and Northwest Africa. (The nearest relations of the following Northwest African species, *Acanthodactylus erythrurus* (Schinz) and *A. savignyi* (Audouin), *Ophisaurus koellikeri* (Günther) and *Vipera lebetina mauritanica* (Gray) seem to be respectively *Acanthodactylus tristrami* (Günther), *Ophisaurus apus* (Pallas) and *Vipera l. lebetina* (Linnaeus) which are all essentially east Mediterranean forms. The southwestern species may also have some affinities with *Podarcis*, see p. 355.)

(e) *Lacerta parva* and its relations.

SPECIES DISCUSSED. *brandtii, fraasii, parva.*

As Peters (1962) has pointed out, two of these species, namely *L. parva* and *L. fraasii*, have a considerable external resemblance to each other and this author thought that they were closely related but set somewhat apart from the rest of *Lacerta*. The close affinity of the two species is confirmed by their internal morphology. Both species have similar skeletons with most commonly 28 presacral vertebrae in males and 29 in females, unemarginated clavicles in all the specimens examined and tail vertebrae that are peculiar in being intermediate between the B and C patterns. In both, the hemipenes are unlike those of any other *Lacerta* in lacking regular plicae and having longitudinal flaps on the lobes instead. The hemipenial micro-ornamentation consists of irregular, sometimes bifurcate tubercles. *L. parva* is also singular in having a very reduced chromosomal formula ($2n = 24$)

(Gorman 1969) and is the only species of the genus known to have this degree of reduction. The karyotype of *L. fraasii* has not been investigated to date.

L. parva and *L. fraasii* would occupy an isolated place in the genus if it were not for *L. brandtii* which is morphologically intermediate between these forms and the more typical members of *Lacerta* part II. *L. brandtii* shares the following characters with *L. parva* and *L. fraasii* : tail vertebrae intermediate between the B and C patterns, two postnasals present, nostril often narrowly separated from the first upper labial, often eight longitudinal rows of ventrals, usually two well-separated series of dark markings on the perivertebral area, well-marked blue ocelli on the flanks and perhaps similar hemipenial micro-ornamentation. It differs from them in having a lower presacral vertebral count (26 in males, 27 in females), usually emarginated clavicles, and a hemipenis with clearly defined plicae on the lobes and no longitudinal flaps. In all these features it agrees with at least some of the less aberrant members of *Lacerta* part II.

DISTRIBUTION (see Figs. 12 and 13). Members of *Lacerta* part II are scattered over almost the whole range of *Lacerta*, but with the exception of *L. vivipara*, which is found over an enormous area, the species have small or disjunct ranges. This is almost certainly a relict distribution and indicates that the group has undergone considerable reduction in the area of its total range. In the more southern regions many of the allopatric species are strongly differentiated, probably indicating that their separation is of long standing but, in the north, the species are more similar to each other and here the reduction in range presumably was rather more recent. It is uncertain what caused the shrinkage in distribution ; most species are now confined to relatively moist or highland habitats (exceptions : some *L. danfordi* – Mediterranean islands ; *L. dugesii* – oceanic islands ; *L. brandtii*, *L. fraasii* and *L. parva* – steppe-type habitats) ; possibly the post-glacial temperature-increase may be important. It is difficult to assess how relevant the spread of *Podarcis* has been in this process ; these lizards seem to be better adapted to drier and warmer environments than the members of *Lacerta* part II. Where the two groups occur together, the latter seems best able to compete at high altitudes and, where the two groups are found living side by side, the *Lacerta* part II species usually occupy scansorial or moist terrestrial niches. Whether there has been active elimination of *Lacerta* part II populations by direct competition is uncertain. Certainly the expansion of *Podarcis* can only have been one of several factors in the reduction of the range of *Lacerta* part II, as the latter has undergone an apparent contraction in distribution in many areas where *Podarcis* does not occur.

BIOLOGY. The members of *Lacerta* part II are mainly small lizards that occupy a wide variety of structural niches but the great majority are adapted to living on and around rock faces, the principal exceptions being as follows. *L. chlorogaster* spends considerable amounts of time on tree-boles (Lantz & Cyrén 1947, Terentiev & Chernov 1965, Droedov 1967) and this may originally have been the main habitat of *L. laevis* (e.g. Böhme 1971, Zinner 1967). This would ' explain ' why these species lack certain of the characters of their close relatives originally placed in the subgenus *Archaeolacerta*, viz. smooth, flattened dorsal scales and strongly

depressed skull with incomplete ossification of the supraocular lamellae, these features being adaptations to utilizing rock crevices as hiding-places (see p. 320). *L. brandtii, L. fraasii* and *L. parva* all occur on the ground in relatively dry and open habitats (Lantz & Cyrén 1939, Wettstein 1928). *L. derjugini, L. praticola* and *L. vivipara* also tend to be ground-dwelling but in damp places (Lantz & Cyrén 1947). *L. andreanszkyi* does not climb high on rock faces but is at least partly saxicolous, often occurring on stones and coarse gravel in or near stream-beds (K. Klemmer, personal communication ; S. D. Busack, personal communication). *L. dugesii* is often scansorial but occupies a wide range of habitats. There is some evidence that at least the more northern species may operate at rather lower preferred temperatures than sympatric species of *Podarcis* (personal observations on *L. horvathi, L. mosorensis, L. oxycephala, L. monticola* and *L. vivipara* and on *P. melisellensis, P. muralis* and *P. sicula*).

ALGYROIDES Bibron & Bory

Bibron & Bory, 1833, *in* Bory, *Expéd. sci. Morée*, **3**, 1 : 67.

TYPE SPECIES.   *Algyroides moreoticus* Bibron & Bory.

DIAGNOSIS.   Small lacertids (adults not usually over 70 mm snout to vent). Skull fairly robust or delicate and depressed, parietal foramen present, frontal bones paired throughout life, postorbital and postfrontal bones unfused ; clavicle strongly expanded medially and exists in both emarginated and unemarginated conditions in all species ; interclavicle cruciform, the lateral arms not strongly directed forwards or backwards ; sternal fontanelle usually oval ; sexual variation in presacral vertebral count present ; all presacral vertebrae, except the first three cervicals, with ribs ; free ribs divided into two series, an anterior one of long ribs and a posterior series of short ones ; caudal vertebrae of the A or B pattern.

Hemipenis symmetrically bilobed with no obvious armature, the lobes unfolded in repose and regularly plicate with variable micro-ornamentation ; apical region of lobes short with very small sulcal lips ; no large conical papillae at lobe tips.

Head shields normal, nostril usually in contact with first labial scute, normally two superposed postnasal shields (occasionally one) ; lower eyelid scaly ; anteriorly the parietal scute does not extend to the outer margin of the postorbital bone ; first supratemporal shield large ; masseteric shield frequently present.

Dorsal body-scales large (larger than caudals in at least the mid-dorsal region), collar present and well defined ; ventral scales smooth, truncate, not overlapping very strongly, in six longitudinal rows.   Toes cylindrical or compressed, tubercular beneath, femoral pores present.   Tail unmodified.   Sexual dimorphism absent in most species.   Belly brightly coloured in breeding males.

SPECIES REFERRED.   *fitzingeri, marchi, moreoticus, nigropunctatus.*

SKELETAL FEATURES.   Skull robust in *A. moreoticus* and *A. nigropunctatus*, more delicate and depressed in *A. fitzingeri* and *A. marchi* which also have the osteodermal layer reduced and fenestrated supraocular lamellae.   No ossification

in the temporal area. Postorbital and postfrontal bones always separate, pterygoid teeth present in *A. moreoticus* and *A. nigropunctatus*. Presacral vertebrae usually 25–26 in males, 26–27 in females (total range 24–28). Clavicle exists in both intact and emarginate conditions in all species. Interclavicle cruciform, the lateral arms not strongly directed forwards or backwards. Sternal fontanelle oval (may approach cordiform condition in some *A. moreoticus*). Inscriptional ribs usually nil, occasionally one pair present. Non-autotomic caudal vertebrae four or five. Caudal pattern usually B, occasionally A.

HEMIPENIS. As diagnosis. Micro-ornamentation consists of recurved spines in *A. moreoticus* and *A. nigropunctatus* and crown-shaped tubercles in *A. fitzingeri*.

EXTERNAL FEATURES. Small lizards (adults from 30 to 70 mm snout to vent). Nostril in contact with first upper labial ; normally two postnasals present (exceptions rather frequent in *A. moreoticus*, rare in the other species). Eyelid scaly. Parietal border emarginated running medial to the outer margin of the postorbital bone (this condition least developed in *A. marchi*). Supratemporals well developed, the first larger and deeper than the rest. Masseteric shield usually well defined. Dorsal scales large (larger than the caudals), imbricate, strongly keeled (less so in *A. marchi*), either pointed (*A. fitzingeri*, *A. moreoticus*) or truncate (*A. marchi*, *A. nigropunctatus*) ; number of dorsals in a transverse series at mid-body 15 to 28. Collar well developed, fairly smooth or serrated. Ventrals truncate, smooth, without very strong overlap, in six longitudinal rows. Preanal shield large, bordered by one or (more rarely) two semicircles of small plates. Toes cylindrical or compressed, tubercular beneath. Femoral pores present, each series extending to the knee and containing 11 to 18 pores. Tail unmodified.

COLORATION. Sexual dimorphism in dorsal pattern absent except in *A. moreoticus*. Most individuals basically brown or bronze-brown above, the flanks often darker (*marchi*, *nigropunctatus*, some *fitzingeri* and male *moreoticus* ; the latter also having light spotting on the flanks). Dorsum may have irregular dark spots (*nigropunctatus*, male *moreoticus*), or a vertebral stripe (*marchi*, *fitzingeri*), or be uniform (some *fitzingeri* and *nigropunctatus*, female *moreoticus*). Male *moreoticus* have light, narrow, dorsolateral stripes. Venter brightly coloured in males, the colour extending onto the flanks in *A. nigropunctatus*. Throat and belly may contrast (blue : orange in *nigropunctatus*, blue or white : yellow in *marchi*) ; blue spots may be present on the outer ventrals.

RELATIONSHIPS. The four species of *Algyroides* are generally quite similar and they seem to constitute a natural group. They resemble each other quite closely in external morphology, osteology, and in having very small sulcal lips on the hemipenial lobes. Externally *A. nigropunctatus* seems most similar to *A. marchi* and *A. fitzingeri* to *A. moreoticus*. The first two species have small lateral scales and truncate dorsals while the last two have no differentiation between dorsals and laterals, all scales being both large and pointed. It is uncertain that these superficial resemblances indicate true relationships ; the pattern of hemipenial micro-ornamentation does not support such an arrangement since *A. moreoticus* has simple recurved spines on the lobe plicae which are like those of its geographical

neighbour *A. nigropunctatus* and unlike the crown-shaped tubercles occurring in *A. fitzingeri* (the pattern of micro-ornamentation in *A. marchi* is not yet known).

DISTRIBUTION (see Fig. 15). The four species each have relatively small ranges in southern Europe and are completely or almost allopatric (*moreoticus* and *nigropunctatus* coexist in the Ionian Islands). *Algyroides* occurs in southeastern Spain (perhaps also central Spain, see, e.g., Buchholz 1965), Corsica, Sardinia, the eastern Adriatic seaboard as far south as Epirus, the Ionian Islands and southern Greece.

BIOLOGY. There is some evidence that these small lizards were perhaps originally largely associated with semi-shaded woodland habitats (*marchi* – Klemmer 1960, personal observation ; *moreoticus* – Clarke 1970, personal observation ; *nigropunctatus* – personal observation). Populations are now found in deforested areas but some *Algyroides* occur quite frequently in and around fallen timber and others live among and climb in bushes.

PODARCIS Wagler

Wagler, 1830, *Syst Amph.* p. 154.

TYPE SPECIES. *Seps muralis* Laurenti.

DIAGNOSIS. Small, occasionally medium-sized lacertids (adults not usually over 90 mm snout to vent). Skull usually fairly robust but may be relatively depressed with a fairly thin osteodermal layer ; parietal foramen present, frontal bones paired throughout life, postorbital and postfrontal bones unfused ; clavicle strongly expanded medially, existing in both emarginated and unemarginated conditions (often within the same population) ; interclavicle cruciform, the lateral arms not strongly directed forwards or backwards ; sternal fontanelle usually heart-shaped ; sexual variation in presacral vertebral count present ; all presacral vertebrae, except the first three cervicals, with ribs ; free ribs in two series, long anterior ones differentiated abruptly from short posterior ones ; caudal vertebrae of the C pattern.

Hemipenis symmetrically bilobed with no obvious armature, the lobes unfolded in repose and regularly plicate with a micro-ornamentation consisting of simple, often recurved spines ; apical regions of the lobes relatively long (usually longer than basal portions of the lobes) with extremely large sulcal lips ; no large conical papillae at lobe tips.

Head shields normal, nostril usually in contact with first upper labial scute and usually bordered posteriorly by a single postnasal shield (occasionally two), eyelid scaly ; anteriorly the outer edge of the parietal shield runs along the lateral margin of the postorbital bone ; supratemporals present, rather narrow ; a masseteric shield frequently present.

Dorsal scales small (less than half the length of the proximal caudals) ; collar well developed ; ventral plates smooth, truncate, not strongly overlapping, in six (rarely eight) longitudinal rows. Toes somewhat compressed, tubercular beneath ; femoral pores present. Tail unmodified. Sexual dimorphism in dorsal pattern usual in most populations. Belly usually brightly coloured, at least in breeding males.

SPECIES REFERRED. *erhardii, filfolensis, hispanica,* lilfordi, melisellensis, milensis, muralis, peloponnesiaca, pityusensis, sicula, taurica, tiliguerta, wagleriana.*

SKELETAL FEATURES. Skull usually fairly robust, sometimes quite depressed with a reduced osteodermal layer, particularly in *P. hispanica*. Supraocular lamellae complete in most adults (some exceptions especially in *P. hispanica*), temporal region usually unossified (fairly extensive ossification in some *P. peloponnesiaca* and traces in individuals of some other forms, e.g. *P. taurica* and *P. melisellensis*). Postorbital and postfrontal bones always separate in hatchlings, occasionally fused in adult males, pterygoid teeth present in at least some individuals of most species (not *P. lilfordi* or *P. wagleriana* fide Klemmer 1957). Presacral vertebral number shows some correlation with sex, 27 commonest number for males (26 in *P. tiliguerta, P. filfolensis, P. muralis* and *P. pityusensis*), 28 in females (27 in *P. filfolensis, P. lilfordi, P. pityusensis* and *P. tiliguerta*) ; males occasionally have 25 presacral vertebrae, females 29. Clavicle expanded medially, most frequently emarginated but some specimens of the majority of species have the bone intact (not in *L. filfolensis* and *L. muralis*). Interclavicle cruciform, the laterally directed arms not strongly angled forward but may occasionally be angled very slightly backwards, especially in *L. wagleriana*. Sternum of most individuals with a cordiform fontanelle having a very distinct, posteriorly directed process arising from its anterior border. One inscriptional rib-pair may be present. Non-autotomic caudal vertebrae usually five or six, sometimes four. Caudal pattern always of the C type.

HEMIPENIS. Symmetrically bilobed without an obvious armature ; lobes not folded in the retracted organ, plicate. Apical sections of the lobes usually longer than basal parts, sometimes subequal ; lobe tips without prominent papillae. Lips on lobe sulci very large, the outer one varying in its mode of attachment to the lobe wall as follows.

P. hispanica, P. muralis : the outer lip is free laterally for its whole length and can be easily reflected to expose its underside which shows traces of the plication that covers the rest of the lobe wall.

All other species : here there is an obvious longitudinal fold in the lobe wall directly dorsal (in the retracted organ) to the lip which is fused to the fold apically but is free basally.

Hemipenial micro-ornamentation in *Podarcis* consists of simple recurved spines (Böhme 1971 ; personal observations).

EXTERNAL FEATURES. Small to medium-sized lizards (adults usually from 50 mm to 80 mm snout to vent, occasionally over 90 mm). Nostril in contact with first upper labial, bordered posteriorly usually by a single postnasal (occasional exceptions, especially unilateral ones). Eyelid scaly. Anteriorly the lateral border of the parietal is unemarginated, usually following or close to the outer edge of the postorbital bone. Supratemporals often distinguishable, rather narrow,

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* *P. hispanica*, as presently understood, may not be a single species (Klemmer, personal communication).

the first often the longest ; in some forms supratemporals are small and scarcely separable from the similarly sized temporals (e.g. *hispanica, lilfordi, pityusensis* and some *tiliguerta*). Masseteric present in most individuals but frequently small or absent in *P. hispanica*. Dorsals small, 42 to 90 in a transverse row across the mid-body, usually granular with a raised transverse section (fairly flat in some *P. hispanica*), sometimes smooth or faintly keeled (*erhardii, filfolensis, hispanica, lilfordi, milensis* and *pityusensis*), sometimes quite strongly keeled (*melisellensis, sicula, taurica* and *wagleriana*). Collar well developed, usually fairly smooth-edged but sometimes distinctly serrated (*P. taurica*). Ventrals smooth, truncate, degree of overlap variable but never very strong, arranged in six (rarely eight) longitudinal rows. Preanal shield with one or, more rarely, two semicircles of small scales anterior to it. Toes vary in degree of compression, tubercular beneath. Femoral pores extend to knee, 13 to 29 in each series. Tail long, unmodified.

COLORATION. Sexual dimorphism in the dorsal pattern is usual in adults. Some specimens have continuous longitudinal stripes on the body : there may be a pair of light stripes on each flank (starting from the supraciliary and supralabial regions) ; these may be separated and bordered by dark pigment and there is often a dark vertebral stripe as well. The pattern may vary, for instance particular elements may be absent or divided. In other specimens, the dark stripes are broken up into discrete, although often very irregular transverse bars which in extreme cases may coalesce to form a reticulation. In most forms, the females tend towards the striped condition while the males, by comparison, have the pattern more broken up. This does not apply to certain populations where both sexes have reticulated markings (e.g. *P. f. filfolensis, P. muralis insulanica* and *P. m. nigriventris*). Ground colour is very variable and may be brown, grey or green. In some species there may be a distinct polymorphism in dorsal pattern, some specimens having the normal dark markings while others lack them completely (usually referred to as ' concolor-mutants '). This morph occurs in *P. erhardii, P. filfolensis, P. hispanica, P. melisellensis, P. sicula, P. taurica* and *P. wagleriana*. Insular melanic populations are frequent. Ventral surface usually brightly coloured in breeding males, but not in most mainland populations of *P. sicula*, some populations of *P. peloponnesiaca* (fide Buchholz 1960) or in many *P. milensis* ; other individuals of this last species have only the second rows of ventrals from the midline brightly coloured. Throat and belly may contrast ; the outer ventrals often bear blue spots.

RELATIONSHIPS. The thirteen species of *Podarcis* form a very homogeneous assemblage. *Lacerta dugesii* which used to be classified with these forms in the sub-genus *Podarcis* in fact differs from them in many features and is more fully discussed on p. 338. Klemmer (1957) considered *Podarcis peloponnesiaca* to be *incertae sedis* because he felt that its often very robust skull and usually quite extensively ossified temporal region separated it from the other species here placed in *Podarcis*. However, *P. peloponnesiaca* possesses all the features which in combination distinguish *Podarcis* from other lacertid genera (see Diagnosis). The characters that Klemmer thought separate this species from *Podarcis* involve only relatively slight changes in degree of ossification : thus the heavy skull of *P. peloponnesiaca* is approached

by that of other *Podarcis* species such as *P. taurica*, especially its southern populations, and other members of this genus may also have some (admittedly minor) temporal ossification, e.g. individuals of *P. melisellensis* and *P. taurica*.

Because the species of *Podarcis* are all morphologically very similar, it is difficult to decide which forms are most closely related to each other. Most attempts to subdivide the group (e.g. Kopfstein and Wettstein 1921, Boulenger 1920, Klemmer 1957) have been based on external morphology, especially skull and body shape and colour pattern. Unfortunately the morphological variables are largely the sort of characters that often correlate fairly closely with the kind of niche occupied and on their own are uncertain indicators of relationship. Colour and pattern are also of rather limited use since it is often highly variable within species. The most recent subdivision of *Podarcis* was made by Klemmer (1957) who separated it into three assemblages.

1. *muralis*-group : *muralis, filfolensis, milensis, tiliguerta* and *wagleriana.*
2. *bocagei*(= *hispanica*)-group : *bocagei* (= *hispanica*), *lilfordi, pityusensis* and *dugesii.**
3. *sicula*-group : *sicula, erhardii, melisellensis* and *taurica*.

Klemmer's classification produces zoogeographically coherent groups : one in the West (*hispanica*-group), another in the East (*sicula*-group) and the third (*muralis*-group) consisting of a single, widespread continental species, *P. muralis,* and four Mediterranean island forms, all occurring south of the main range of *P. muralis,* which are presumed to have originally been connected with it either directly as in the case of *P. milensis* and *P. tiliguerta* or via another member of the group : thus Klemmer believed that *P. wagleriana* and *P. filfolensis* are closest to *P. tiliguerta.*

However, many of the characters on which Klemmer's arrangement is based are rather equivocal and a wider range of evidence will be necessary to produce a convincing theory of *Podarcis* relationships. Chemotaxonomic studies may provide useful information (G. C. Ross and Arnold, in progress). But until this and other lines of evidence are adequately surveyed, it seems best to leave the question of *Podarcis* relationships open. Comment is limited here to two minor points.

1. Gross hemipenial structure often proves to be a good indicator of lacertid relationships. *P. hispanica* and *P. muralis* are alike in having the outer sulcal lips of the hemipenis free and differ from all other *Podarcis* in this respect. This may indicate that they are fairly closely related to each other. Such free lips are found in some of the members of *Lacerta* part II that may be related to the stock from which *Podarcis* was derived (see p. 355); so it is possible that *hispanica* and *muralis* are the most primitive members of *Podarcis* in this respect.

2. *P. erhardii* and *P. peloponnesiaca* seem to be closely related. Although quite distinct on the Greek mainland, where they have a small area of sympatry, the two species are to some extent connected by island populations of *P. erhardii* that approach *P. peloponnesiaca* in build and colouring. *P. peloponnesiaca* and most populations assigned to *P. erhardii* share a similar hemipenis shape in which the outer sulcal lips are broader than in other species of *Podarcis*.

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* As stated above, *L. dugesii* is here removed from *Podarcis*; Klemmer did not include *P. peloponnesiaca* in any of his assemblages because he was uncertain whether it was related to the rest of *Podarcis*.

The neighbouring *P. taurica* might also be close to these two species, especially as some island populations usually identified as *P. erhardii* approach *P. taurica* in form and colouring. Thus the *Podarcis* population on Skyros (N. Sporades) was originally named as a subspecies of *P. taurica* (*P. taurica gaigeae* Werner 1930) but is now usually referred to *P. erhardii*. Its hemipenial lips, however, are rather narrow and tend towards the condition found in *taurica*.

DISTRIBUTION (see Fig. 14). Mainly continuous including both highland and lowland areas but limited to the western part of the total region occupied by the West Palaearctic endemic genera dealt with in this paper. N.W. AFRICA (*P. hispanica* only) : Tunisia, N. Algeria, Morocco. MAINLAND EUROPE : All southern peninsulas and northwards to S. Netherlands, Rhine Valley, Bavaria, Czechoslovakia, Hungary and Roumania ; also Northwest Black Sea coast to Crimea (*P. taurica*) and N.W. Asia Minor (*P. muralis*). MEDITERRANEAN ISLANDS : Most islands with the exception of those lying east of a line running just west of Samothraki, Limnos, Agios Evstratios, Psara, Ikaria, Kos and Kasos in the Aegean Sea.

BIOLOGY. These small lizards occupy a relatively broad spectrum of spatial niches. Most are at least partly scansorial and some spend much of their time on semi-vertical surfaces (e.g. *P. muralis* and *P. hispanica*). Others (like *P. taurica*) climb relatively little.

PSAMMODROMUS Fitzinger

Fitzinger, 1826, *Neue Classif. Rept.* : 22.

TYPE SPECIES : *Psammodromus hispanicus* Fitzinger.

DIAGNOSIS. Small lacertids (adults usually under 80 mm snout to vent). Skull moderately built or robust, not depressed, a parietal foramen present, frontal bones paired throughout life ; postorbital and postfrontal bones fused even in hatchlings ; clavicle strongly expanded medially with a large always unemarginated foramen ; interclavicle cruciform, the lateral arms not directed strongly forwards or backwards ; sternal fontanelle oval ; sexual variation in presacral vertebral count present ; all presacral vertebrae, except first three cervicals, with ribs ; free ribs in two series, long anterior ones differentiated abruptly from short posterior ones ; caudal vertebrae of the C pattern.

Hemipenis symmetrically bilobed with no obvious armature ; lobes not folded in repose, regularly plicate with variable micro-ornamentation ; apical region of lobes short or quite long with small or moderately sized sulcal lips ; fairly large conical papillae sometimes present on lobe tips.

Head shields normal, nostril usually in contact with first upper labial and bordered posteriorly by a single postnasal scale ; lower eyelid scaly ; anteriorly parietal scale borders outer margin of fused postorbital–postfrontal bone ; supratemporal scales well developed ; masseteric shield not usually discernible.

Dorsal body-scales large, pointed, strongly keeled and overlapping ; collar absent or very weakly developed ; ventral scales smooth, truncate and overlapping, often

strongly so, in six or ten longitudinal rows. Toes cylindrical or slightly compressed with smooth or keeled lamellae beneath ; femoral pores present. Tail long, unmodified. Sexual dimorphism in dorsal pattern absent. Belly usually brightly coloured in breeding males.

SPECIES REFERRED. *algirus, blanci, hispanicus, microdactylus*.

SKELETAL FEATURES. Skull undepressed, robust with a thick osteodermal layer in *P. algirus*, less so in the other species. Supraocular lamellae complete in adults, temporal region ossified in *P. algirus*. Postorbital and postfrontal bones always fused, pterygoid teeth present only in *P. algirus*. Presacral vertebrae usually 26 or 27 in males, 27 or 28 in females (total range 26 to 29). Clavicle expanded medially, always unemarginated. Interclavicle cruciform, the lateral arms not obviously directed forwards. Sternal fontanelle oval. One pair of inscriptional ribs often present (but not usual in *P. hispanicus*). Non-autotomic caudal vertebrae four or five. Caudal pattern always C.

HEMIPENIS. Symmetrically bilobed without an obvious armature ; lobes not folded in retracted organ, plicate. In *P. blanci, P. hispanicus* and *P. microdactylus* the apical parts of the lobes are short with quite large conical papillae at the tips and relatively small sulcal lips. *P. algirus* differs in having long apical sections to the lobes (twice as long as basal section) and the lobes themselves are slender with large lips that are free and expanded distally, and no conical apical papillae. Micro-ornamentation consists of simple recurved spines in *P. algirus* but in the other species the spines are irregular (and often bifurcated, Böhme 1971).

EXTERNAL FEATURES. Small lizards (adults usually 35 mm to 80 mm snout to vent). Nostril in contact with first upper labial, bordered posteriorly by a single postnasal. Eyelid scaly. Border of parietal shield unemarginated, usually running along outer margin of fused postorbital and postfrontal bones. Supratemporals well developed, the first often deepest in most species (last frequently deepest in *P. algirus*). Temporal scaling coarse, masseteric shield not clearly defined. Dorsal scales large (at least half the length of the proximal caudals), imbricate, strongly keeled and pointed. Number of dorsals in a transverse series 21 to 32. Collar very weak (*hispanicus*, some *blanci* and some *microdactylus*) or absent. Ventral plates smooth, truncate, strongly or extremely strongly imbricate (*P. algirus*), in six or ten* (*P. algirus*) longitudinal rows. Anal shield large, bordered by one or two rows of smaller plates. Toes not strongly compressed, tubercular beneath or with two series of keels (keeling strong in *P. hispanicus*, obtuse in some *P. microdactylus* and some *P. algirus*). Series of femoral pores extend to knee and consist of 10 to 21 pores in each. Tail unmodified, very long in *P. algirus*, as much as three times the snout–vent length.

COLORATION. Sexual dimorphism in dorsal pattern absent. Most individuals have light, narrow supraciliary and supralabial stripes extending along the body

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* In lacertids with large dorsal scales, it is often difficult to decide where these end and the equally large ventrals begin. But in forms with small dorsal scaling easily distinguished from the ventrals, the distribution of the latter corresponds closely with the *rectus abdominis superficialis* muscle. If this muscle is used as a criterion in defining the ventrals of *Psammodromus* species, it appears that *P. algirus* has ten longitudinal rows of ventrals rather than six as often stated (e.g. Boulenger 1921).

(these may be absent, especially in *P. blanci* and *P. microdactylus*). Other elements of the dorsal pattern rather variable. Venter brightly coloured in breeding males of the small species. *P. algirus* has a bright throat but a pale belly in breeding males.

RELATIONSHIPS. It is usually assumed that the three small species of *Psammo-dromus,* viz. *blanci, hispanicus* and *microdactylus,* are more closely related to each other than they are to *P. algirus*. This appears to be true ; *P. algirus* differs from them in several features including hemipenial structure, peculiar almost skink-like ventral scaling, extremely long tail and heavily armoured head. However, this species seems to be more closely related to the remainder of *Psammodromus* than it does to any other group of lacertids. The small species, *P. blanci* and *P. micro-dactylus,* appear to be very closely related and may even be conspecific.

DISTRIBUTION (see Fig. 15). N.W. AFRICA : Tunis, Algeria, Morocco. EUROPE : Spain, Portugal and southern France.

BIOLOGY. The three smaller species all typically occur in open areas often with low, dense vegetation in which they hunt and hide. *P. algirus* is often found in scrub regions, especially in the vicinity of bushes and shrubs. When disturbed, it retreats into the base of these and may sometimes climb in them.

GALLOTIA Boulenger

TYPE SPECIES : *Lacerta galloti* Duméril & Bibron.

DIAGNOSIS. Medium to large lacertids (adults of extant species up to 210 mm snout to vent). Skull robust, a parietal foramen present (not in the extinct *Lacerta* (= *Gallotia ?*) *maxima* according to Bravo 1953) ; frontal bones paired throughout life, postorbital and postfrontal bones fused, even in hatchlings ; clavi-cle strongly expanded medially, foramen always unemarginated ; interclavicle cruciform, the lateral arms not strongly directed forwards or backwards ; sternal fontanelle oval ; no sex correlated variation in presacral vertebral count ; all presacral vertebrae, except first three cervicals, with ribs ; free ribs in two series, long anterior ones differentiated from the short posterior ribs ; caudal vertebrae of the C pattern.

Hemipenis symmetrically bilobed with no obvious armature ; lobes not folded in repose, regularly plicate with micro-ornamentation of simple recurved spines. Apical regions of lobes usually fairly long, sulcal lips small, large conical papillae present on lobe tips.

Head shields normal, nostril in contact with first upper labial scute and bor-dered posteriorly by a single postnasal scale, eyelid scaly ; anteriorly parietal scute may or may not reach the outer margin of the fused postorbital and postfrontal bones ; supratemporals present, the anterior ones sometimes narrower than the rest ; a masseteric shield may be present.

Dorsal body-scales small or moderate sized (largest may be half the length of the proximal caudals) ; collar present and well defined ; ventral plates smooth,

truncate, not strongly overlapping, in (8) 10 to 20 longitudinal rows. Toes not strongly compressed, tubercular beneath; femoral pores present. Tail long, unmodified. Sexual dimorphism in dorsal pattern usual. Belly brightly coloured at least in breeding males.

SPECIES REFERRED. *atlantica, galloti, simonyi.*

Perhaps also the extinct *Lacerta goliath* Mertens 1942 and *Lacerta maxima* Bravo 1953.

SKELETAL FEATURES. Skull robust, undepressed with thick osteodermal layer. Supraocular lamellae complete in mature specimens, temporal ossification present in *G. atlantica* and *G. simonyi simonyi*, much reduced or absent in *G. galloti* and *G. simonyi stehlini*. Postorbital and postfrontal bones fused throughout life, pterygoid teeth present. Almost unique in the family Lacertidae in having no sex-correlated variation in the number of presacral vertebrae there being 26 in nearly all the specimens examined (occasionally 25).

Clavicle expanded medially, always unemarginated. Interclavicle cruciform, the lateral arms not directed strongly forwards, although they may be swept slightly backwards in some *G. galloti*. Sternal fontanelle oval. Most frequently one well-developed pair of inscriptional ribs in *G. galloti* and *G. simonyi* but usually none in *G. atlantica*. In most cases five non-autotomic caudal vertebrae (sometimes four in *G. galloti* and *G. atlantica* and sometimes six in *G. simonyi*). Caudal pattern always C.

HEMIPENIS. Symmetrically bilobed without an obvious armature; lobes not folded in retracted organ, plicate. Apical sections of lobes longer than basal parts or approximately equal to them; lobe tips covered by prominent papillae which are conical, rather flattened and about equal in length to the widths of two to four plicae. Lips on lobe sulci relatively small, their free edges papillate. Micro-ornamentation consists of simple recurved spines.

EXTERNAL FEATURES. Medium to large lacertids (adults from about 60 mm to 210 mm snout to vent). Nostril in contact with first upper labial, bordered posteriorly by a single postnasal. Eyelid scaly. Border of parietal shield running along the outer edge of fused postorbital and postfrontal bones in *G. atlantica* and *G. galloti*, medial to this in *G. simonyi*. Supratemporals present, the first deep in *G. simonyi*, shallow in the other two species. A masseteric shield present in many *G. galloti* and *G. simonyi*, absent in *G. atlantica*. Dorsal scales very small (*G. galloti* and *G. simonyi*) or moderately large (*G. atlantica*), 45 to 110 in a transverse row across the mid-body, distinctly keeled, very strongly so in *G. atlantica*. Collar strong; serrated or smooth. Ventrals smooth, truncate, not very strongly imbricate, arranged in 10 (rarely 8) longitudinal rows in *G. atlantica*, 10 to 14 in *G. galloti* and 16 to 20 in *G. simonyi*. Preanal shield rather small, the scales in this region rather fragmented. Toes not strongly compressed, tubercular beneath. Femoral pores extend to knee, 17 to 33 in each series. Tail unmodified.

COLORATION. Sexual dimorphism in dorsal colouring of adults present in most populations. Young typically with two pairs of light, well defined flank stripes,

one supraciliary, the other supralabial. These are usually separated and bordered by black pigment which may be either continuous or broken up. There may also be a light vertebral stripe and the pattern may be overlaid by irregular transverse rows of small white ocelli. The throat often bears a series of dark chevrons or is entirely dark. Females (and a few males of some forms) tend to retain the juvenile pattern of stripes although it may be fainter. In males (and some females, especially of *G. simonyi*) the dorsal coloration becomes more uniform (and in *G. galloti* and *G. simonyi* darker as well). Males (and females of *G. atlantica*) have prominent blue (*G. atlantica*, *G. galloti*) or yellow (*G. simonyi*) ocelli on the flanks and the outer ventrals are also often blue. In *G. g. galloti* the transverse rows of white ocelli on the back are also replaced by blue. The belly is also often brightly pigmented in adults although this colour is often largely obscured by melanin.

RELATIONSHIPS. In spite of considerable external differences, the three extant species of *Gallotia* appear to be relatively closely related to each other, albeit perhaps not as closely as the members of *Podarcis* or of *Lacerta* part I. It is generally assumed that the fossil forms discovered in Pleistocene deposits on the Canary Islands are also members of *Gallotia*. These have been found on some of the large islands in the western group (La Palma, Tenerife, perhaps Gomera) and have been named as *Lacerta* (*Gallotia*) *goliath* Mertens 1942 and *Lacerta* (*Gallotia*) *maxima* Bravo 1953. As indicated by their names, these fossil forms were larger than any extant species of lacertid, *L. maxima* having a skull length of over 120 mm and an estimated total length of 1200 mm (Bravo 1953). Insufficient data are available from the published descriptions to allow these giant forms to be firmly allocated to *Gallotia* but their skull shape and head scale impressions in the osteodermal layer resemble those of *G. simonyi*. If this indicates a real relationship, then this apparent species-group (i.e. *goliath*, *maxima* and *simonyi*) has undergone a considerable reduction in range. It does not now occur on La Palma, Tenerife or Gomera and has recently become extinct on Hierro and the nearby Roques Zalmor (Klemmer, personal communication) where it was represented by *G. simonyi simonyi*. The only known population remaining is on Gran Canaria (*G. simonyi stehlini*). On all the islands where the lizards of the putative *simonyi*-group have disappeared, *G. galloti* now exists. Possibly competitive exclusion by this species has been important in bringing about the extermination of the *simonyi*-group on some islands but it is uncertain if this was the case on Hierro. Here *G. simonyi* was represented by a very large-bodied population (adults up to 210 mm snout to vent) while the resident race of *G. galloti* (*G. galloti caesaris* (Lehrs)) is much smaller (less than 100 mm snout to vent) which suggests that the two forms were unlikely to compete directly, unless of course there was competition between the young *simonyi* and the adult *galloti*.

The three species definitely assigned to *Gallotia* have no very close relationship to the lizards assigned to *Lacerta* part I. The affinities of *Lacerta lepida* which was previously placed in *Gallotia* by Peters are discussed on p. 333.

DISTRIBUTION (see Fig. 15). Restricted to the Canary Islands.
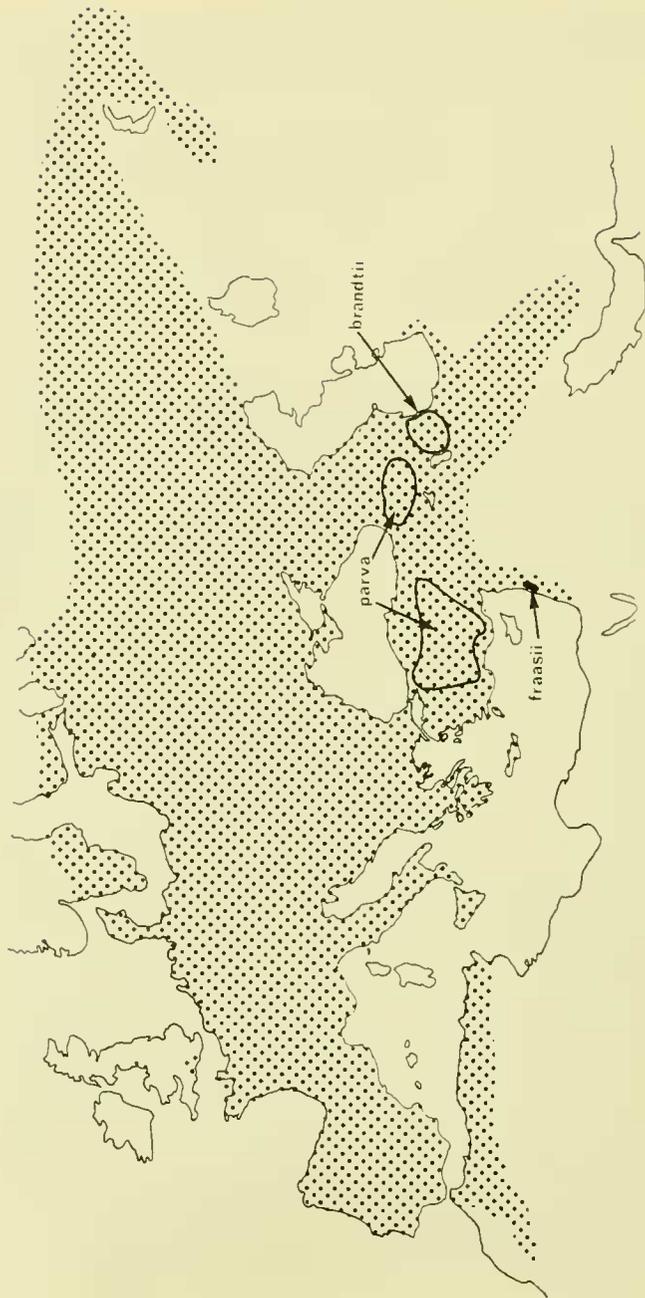
Fig. 12. Distribution of *Lacerta* part I and the *L. parva*-group of *Lacerta* part II. Stippling: approximate distribution of *Lacerta* part I. Enclosed areas: approximate distribution of the *L. parva* species group.
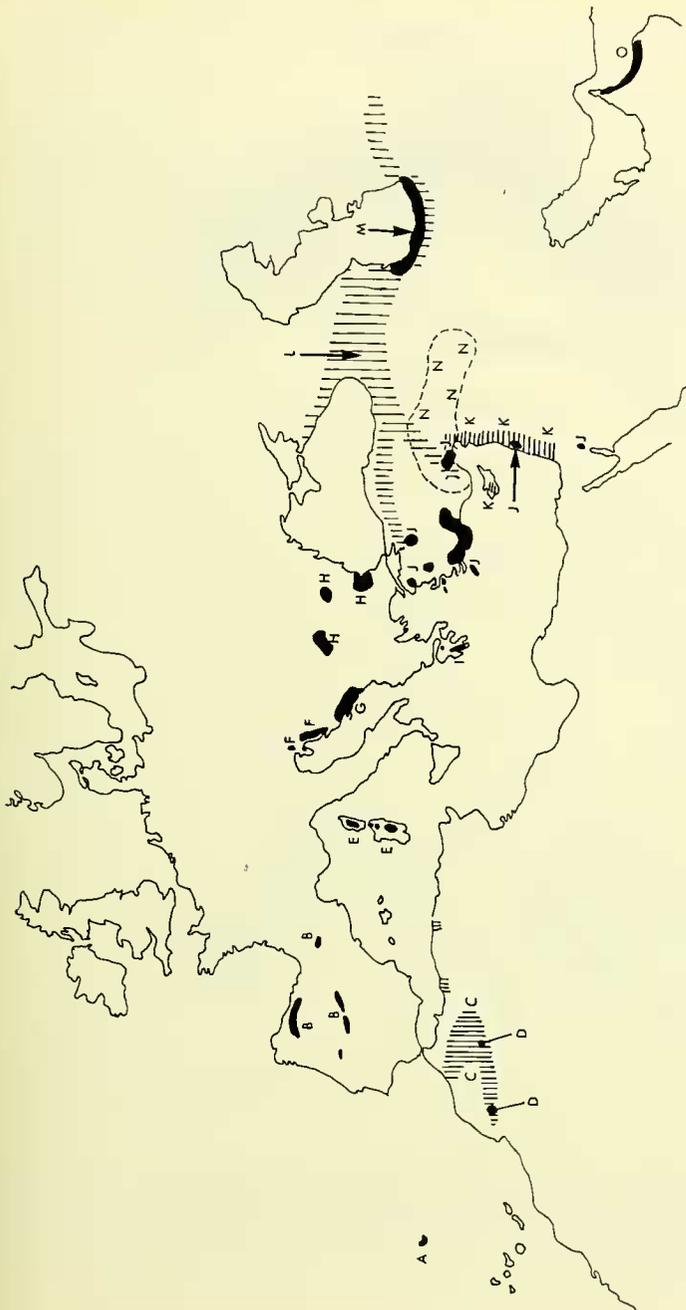
Fig. 13.   Distribution of *Lacerta* part II excluding *L. vivipara* and the *L. parva* species-group.   A : *L. dugesii*.   B : *L. monticola*. C : *L. perspicillata*.   D : *L. andreanszkyi*.   E : *L. bedriagae*.   F : *L. horvathi*.   G : *L. mosorensis* and *L. oxycephala*.   H : western populations of *L. praticola*.   I : *L. graeca*.   J : *L. danfordi*.   K : *L. saxicola* group of species ; *L. laevis*.   L : *L. saxicola* group of the Caucasus : *L. armeniaca*, *L. caucasica*, *L. dahli*, *L. derjugini*,   eastern populations of *L. praticola*, *L. rostombekovi*, *L. rudis* and *L. unisexualis*.   M : *L. chlorogaster*. N : *L. cappadocica*.   O : *L. cyanura* and *L. jayakari*.   (See Fig. 1 for *L. vivipara* and Fig. 12 for the *L. parva* species-group.)
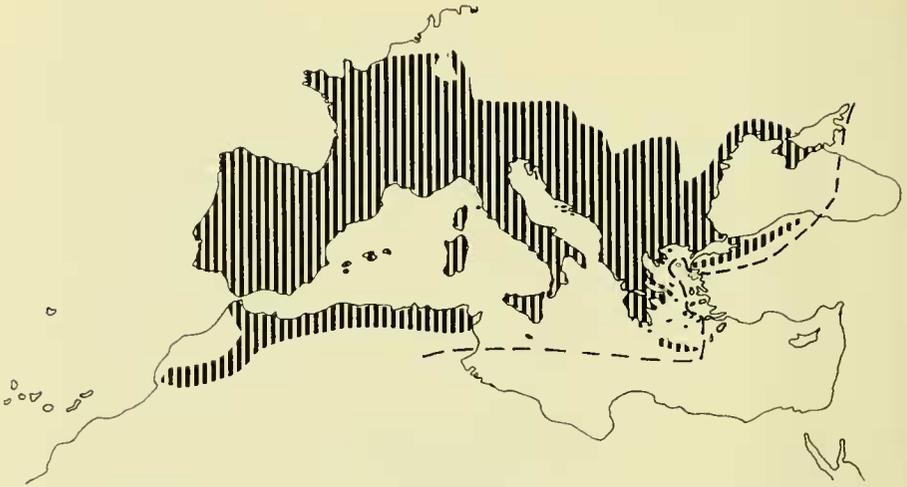
Fig. 14. Distribution of *Podarcis*. Broken line indicates eastern limit of the genus.

Fig. 15. Distribution of *Algyroides*, *Psammodromus* and *Gallotia*. Black : range of *Algyroides* (A = *A. marchi*, B = *A. fitzingeri*, C = *A. nigropunctatus*, D = *A. moreoticus*). Stipple : range of *Psammodromus*. Broken line : range of *Gallotia*.

BIOLOGY. The lizards of the genus *Gallotia* are among the largest terrestrial vertebrates native to the Canary Islands. The eastern *G. atlantica* is partly scansorial and feeds mainly on small invertebrates, while the western *G. galloti* and *G. simonyi* climb less and eat a substantial amount of vegetable food (see, e.g., Krefft 1950). These vegetarian habits are sometimes attributed to the lack of small animal prey on the islands (e.g. Peters 1961) but it may be more likely that these lizards have partly occupied plant-eating niches because, in the depauperate fauna of the Canaries, these are not completely filled by more efficient herbivores.

The species of *Gallotia* tend to produce small clutches of eggs (usually 1 to 3 – Krefft 1950) for their size. This compares with broods of 8 to 18 in species of *Lacerta* part I of equal body size (Peters 1961).

RELATIONSHIPS OF *ALGYROIDES*, *LACERTA*, *PODARCIS*, *PSAMMODROMUS* AND *GALLOTIA*

The fossil record of the Lacertidae is far too fragmentary to give any useful information about relationships within the family, so all speculation about this must be based very tentatively on comparisons of extant forms. If the groups of lizards discussed in this paper are compared with the rest of the Lacertidae, it is apparent that *Lacerta* part II has more features that are widespread in the Lacertidae as a whole than the other groups (see Table IV). *Lacerta* part II is a very varied assemblage with many, often well-differentiated species and has a complex relict distribution. These features suggest that it is long established. It could be argued from this and its greater resemblance to the rest of the family that *Lacerta* part II might be closest to the stock which gave rise to the endemic West Palae-arctic group of genera. Such a conclusion is of course highly provisional.

Lacerta part I is morphologically very like *Lacerta* part II and is separated partly because its members have a close and detailed resemblance to each other ; the actual common features that divide the species of part I from part II are relatively slight (large body-size, dorsal pattern, no bright belly colour, distinctive type of ecological niche) and it seems probable that they are a relatively recent offshoot of *Lacerta* part II although it is not possible to suggest at present what part of this assemblage gave rise to them. Comparatively recent origin, or at least recent expansion, is also suggested by the close similarity of the species in *Lacerta* part I and their continuous distribution.

Similarly *Algyroides* is also close to *Lacerta* part II, being differentiated only by large dorsal scales and to some extent by the very small size of the sulcal lips on the hemipenial lobes. This group appears to have most features in common with the more typical members of *Lacerta* part II.

In the case of the genus *Podarcis*, homogeneity and continuous (and relatively small) range indicate recent origin or expansion. Most of the characters that in combination distinguish its members occur sporadically in *Lacerta* part II, more particularly in *L. danfordi* and its closer relations, viz. *L. laevis*, *L. graeca* and the southwestern species – *L. andreanszkyi*, *L. dugesii* and *L. perspicillata*. Among these characters are large apical sections to the hemipenial lobes (*danfordi*) and

TABLE IV : Distribution of features widespread in the rest of the Lacertidae

Feature	Approximate incidence in Lacertidae excluding West Palaearctic endemic genera	Lacerta part I	Lacerta part II	Algyroides	Podarcis	Psammodromus	Gallotia
Postorbital and postfrontal bones unfused in hatchlings	Over 60% of species	+ (exception)	+ (exception)	+	+	–	–
Sexual variation in pre-sacral vertebral number	All, except a few Acanthodactylus spp.	+	+	+	+	+	–
A-type caudal vertebral pattern	Over 70% of species	Some individuals	Some individuals	Some individuals	–	–	–
Hemipenis with distinct armature	Over 80% of species	–	Some	–	–	–	–
Two superposed postnasals	80% of species	+ (exceptions)	+/–	+ (exceptions)	– (exceptions)	–	–
Margin of parietal shield does not reach edge of bony parietal table	80% to 90% of species	+	+ (exceptions)	+	–	–	+/–
Sexual dimorphism in dorsal pattern absent	Most forms	– (exceptions)	+ (exceptions)	+ (exception)	– (few exceptions)	+	–

extremely well-developed sulcal lips (*danfordi, andreanszkyi*), hemipenial micro-ornamentation of simple spines (*graeca* and the southwestern species group), C-type caudal vertebrae (some *danfordi*), sternal fontanelle approaching cordiform shape (*andreanszkyi, laevis, danfordi*), parietal shield margin reaching outer edge of postorbital bone (southwestern species group), well-developed masseteric shield in some cases (*andreanszkyi, laevis*), *Podarcis*-type dorsal pattern (*andreanszkyi*). In spite of the above individual peculiarities, all these species are closer to other members of *Lacerta* part II than they are to *Podarcis*.

Of the species cited above, *L. andreanszkyi* appears to have more in common with *Podarcis* than the others, and it may be closest to the stock that gave rise to the genus. This tentative hypothesis receives some support from the fact that one species of *Podarcis*, *P. hispanica*, can be quite similar in appearance to *L. andreanszkyi*, especially in the Atlas of Morocco where both of these forms occur. As stated (p. 346), there are reasons for believing that *P. hispanica* may be one of the more primitive members of *Podarcis*.

Boulenger (1921) thought that *Psammodromus* might be related to *Lacerta parva*. Certainly, there is an external resemblance between the smaller species of *Psammo-dromus* and this form that extends to habitus, scale-shape and coloration, although this could be convergent as these lizards occupy similar habitats. *L. parva* resembles the small *Psammodromus* species in having a rather similar, peculiar pattern of hemipenial micro-ornamentation (Böhme 1971) ; also its caudal ver-tebrae approach the C type. However, there are a number of important differences between *L. parva* and *Psammodromus* ; the latter lacks the following features that occur in *L. parva*, viz. postorbitals and postfrontals unfused, double postnasals, reduced chromosomal formula and lack of plicae on hemipenial lobes. It appears unlikely therefore that there is a very close connexion between *Psammodromus* and *L. parva* although the former may well be derived from *Lacerta* part II.

Gallotia is usually said to be closely related to *Lacerta* part I (e.g. Boulenger 1920, Peters 1961) but the two groups show many points of difference and the closest relatives of *Gallotia* appear to be the small species of *Psammodromus*. Although the more extreme forms of these two groups are superficially very different, they have many similarities especially in skeleton and hemipenis. The smallest species of *Gallotia*, *G. atlantica*, has large dorsal scales approaching those of *Psammodromus* in relative size.

SUMMARY OF PROPOSED SYSTEMATIC CHANGES

Algyroides Bibron & Bory

This genus is limited to the four European species, viz. *fitzingeri* (Wiegmann 1834), *marchi* Valverde 1958, *moreoticus* Bibron & Bory 1833 and *nigropunctatus* (Duméril & Bibron 1839). The three African species originally placed in *Algyroides* are now placed in *Adolfus* Sternfeld 1912 ; these are *africanus* Boulenger 1906, *alleni* Barbour 1914 and *vaureselli* (Tornier 1902).

Lacerta Linnaeus 1758

The central and southern African species, viz. *australis* Hewitt 1926, *echinata* Cope 1862, *jacksoni* Boulenger 1899 and *rupicola* Fitzsimons 1933, are not considered to be congeneric with the Palaearctic species of *Lacerta*. Their affinities lie with other Ethiopian lacertids and will be discussed more fully elsewhere. *L. echinata* and *L. jacksoni* are related to the Central African species placed in *Adolfus*, *Bedriagaia* and *Gastropholis*; *L. rupicola* is perhaps related to *Tropidosaura*; and the precise affinities of *L. australis* are unknown, as the type cannot be found.

Palaearctic *Lacerta*, as usually understood (and including *L. cappadocica* Werner 1902) is divided into three main groups two of which are here raised to the status of independent genera. Species are allocated as follows.

Podarcis Wagler 1830, including *erhardii* Bedriaga 1882, *filfolensis* Bedriaga 1876, *hispanica* Steindachner 1870, *lilfordi* (Gunther 1874), *melisellensis* Braun 1877, *milensis* Bedriaga 1882, *muralis* (Laurenti 1768), *peloponnesiaca* Bibron & Bory 1833, *pityusensis* Bosca 1883, *sicula* Rafinesque 1810, *taurica* Pallas 1814, *tiliguerta* Gmelin 1789, *wagleriana* Gistel 1868.

Gallotia Boulenger 1916, including *atlantica* Peters & Doria 1882, *galloti* Duméril & Bibron 1839, *simonyi* Steindachner 1889.

The remaining species are left in *Lacerta* but this is divided into two parts : *Lacerta* part I and *Lacerta* part II.

Lacerta part I contains the following species : *agilis* Linnaeus 1758, *lepida* Daudin 1802, *princeps* Blanford 1874, *schreiberi* Bedriaga 1878, *strigata* Eichwald 1831, *trilineata* Bedriaga 1886, *viridis* (Laurenti 1768).

Lacerta part II contains all other species presently assigned to *Lacerta*.

Psammodromus Fitzinger 1826

This genus is not changed and contains the four species *algirus* (Linnaeus) 1758, *blanci* (Lataste 1880), *hispanicus* Fitzinger 1826, *microdactylus* (Boettger 1881).

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APPENDIX I: RELATIONSHIPS OF THE AFRICAN SPECIES OF *ALGYROIDES*

Three Central African species of lacertid are usually placed in *Algyroides*, namely *A. africanus* Boulenger 1906, *A. alleni* Barbour 1914 and *A. vauereselli* (Tornier 1902). *A. africanus* was the first African species to be assigned to *Algyroides*. When he described it, Boulenger was struck by the superficial resemblance of this species to the European *A. nigropunctatus* and had no hesitation about regarding them as congeneric. The other African forms are much less like the European members of *Algyroides* but have fairly obvious affinities to *A. africanus*. When the two geographical groups are compared in detail it becomes apparent that they are not very similar ; the principal differences are listed below.

		European species	*African species*
1	Postnasals	Usually two	One
2	Masseteric shield	Usually present	Always absent
3	Edge of parietal shield	Does not border outer edge of postorbital bone	Borders outer edge of fused postorbital–postfrontal bones
4	Parietal foramen	Present	Absent
5	Postorbital and postfrontal bones fused	No	Yes
6	Clavicle	Strongly expanded medially, posterior margin of foramen slender, emarginated in some individuals of all species	Unexpanded (except in *A. vauereselli* where the posterior margin is very thick) ; never emarginated
7	Caudal vertebrae	Usually B pattern	Always A pattern
8	Hemipenial armature	Absent	Present
9	Lobes of retracted hemipenis complexly folded	No	Yes

All the features present in the four European species occur widely in Palaearctic *Lacerta* and many of them are found in *Podarcis*, *Psammodromus* and *Gallotia*

too. The characters typical of the African species group occur in combination in
a number of other Equatorial lacertid species (viz. *Bedriagaia tropidopholis*, *Gastro-
pholis prasinus*, *G. vittatus*, ' *Lacerta* ' *jacksoni* and ' *Lacerta* ' *echinata*). It seems
likely therefore that the superficial resemblance between *A. africanus* and *A.
nigropunctatus* is a convergent one (perhaps connected with the similar require-
ments of their original woodland or woodland-edge habitats), and that the
European and African members of the genus are unrelated. Thus the name
Algyroides must be restricted to the European forms and another one found for
the African ones ; *Adolfus* Sternfeld 1912 is available.

APPENDIX II: MATERIAL EXAMINED

Figures in parentheses indicate number of specimens examined. The first
figure denotes those investigated for osteological characters by radiography or
alizarin preparation, the second figure the number of hemipenes examined.

LACERTA part I

agilis (47 ; 7), *lepida* (17 ; 8), *princeps* (3 ; 1), *schreiberi* (16 ; 3), *strigata* (11 ; 3),
trilineata (19 ; 6), *viridis* (24 ; 6).

LACERTA part II

andreanszkyi (9 ; 2), *armeniaca* (5 ; –), *bedriagae* (25 ; 5), *brandtii* (11 ; 3), *cap-
padocica* (13 ; 5), *caucasica* (9 ; 3), *chlorogaster* (20 ; 3), *cyanura* (3 ; 1), *danfordi*
(16 ; 7), *derjugini* (9 ; 3), *dugesii* (36 ; 8), *fraasii* (6 ; 2), *graeca* (10 ; 6), *horvathi*
(21 ; 5), *jayakari* (14 ; 2), *laevis* (26 ; 4), *monticola* (25 ; 4), *mosorensis* (19 ; 6),
oxycephala (28 ; 8), *parva* (17 ; 4), *perspicillata* (22 ; 6), *praticola* (18 ; 3), *rudis*
(7 ; 2), *saxicola* (21 ; 6), *vivipara* (24 ; 7).

ALGYROIDES

fitzingeri (21 ; 2), *marchi* (10 ; 2), *moreoticus* (14 ; 3), *nigropunctatus* (18 ; 6).

PODARCIS

erhardii (45 ; 6), *filfolensis* (25 ; 2), *hispanica* (36 ; 6), *lilfordi* (20 ; 6), *melisellensis*
(28 ; 5), *milensis* (11 ; 5), *muralis* (40 ; 10), *peloponnesiaca* (20 ; 4), *pityusensis*
(17 ; 4), *sicula* (23 ; 6), *taurica* (23 ; 7), *tiliguerta* (21 ; 4), *wagleriana* (27 ; 3).

PSAMMODROMUS

blanci (6 ; 2), *hispanicus* (17 ; 3), *microdactylus* (11 ; 2).
algirus (25 ; 5).

GALLOTIA

atlantica (25 ; 6), *galloti* (35 ; 6), *simonyi* (27 ; 3).

ADOLFUS (i.e. Central African species customarily assigned to *Algyroides*)

africanus (17 ; 4), *alleni* (32 ; 6), *vauereselli* (4 ; 2).