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**Relationships of the South African lizards assigned to *Aporosaura*,
Meroles and *Pedioplanis* (Reptilia: Lacertidae)**

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Phylogenetic analyses, using parsimony and compatibility methods, were carried out on the South African lacertid lizards assigned in recent times to *Aporosaura*, *Meroles* and *Pedioplanis*. These were based on 80 primary and 102 binary morphological characters which were drawn from osteology, external features, muscles, kidneys and reproductive systems. Contrary to some previous interpretations, there are two well-defined clades: *Meroles* plus *Aporosaura*, and *Pedioplanis*; these form successive branches on the main stem of the phylogeny of advanced lacertids. The clades show considerable parallel development of derived features, presumably because they had very similar initial genetic potential. Relationships within the two groups are shown on p. 800 and p. 802. As *Aporosaura anchietae* is sister taxon to a clade consisting of three of the seven species of *Meroles*, it has been transferred to that genus. Relationships in *Meroles-Aporosaura* are very well substantiated, in contrast to the situation in *Pedioplanis*. This difference appears to be related to the different kinds of evolutionary history that the two groups have had. The *Meroles-Aporosaura* clade has spread progressively into increasingly stringent and singular aeolian sand environments which have elicited the production of many, often unique, derived character states related to the functional problems of survival in such situations. As these states are rarely duplicated in outgroups, the characters concerned are easily polarized. This, together with their abundance, means that a robust basis for phylogenetic inference is available. In contrast, *Pedioplanis* exhibits relatively limited ecological radiation of a kind that also occurs in related groups, and the functionally related derived states elicited are fewer and less distinctive. In fact, production of a phylogeny for *Pedioplanis* is very dependent on genital characters which seem to be substantially independent of the main ecological changes that have occurred in the genus. The premaxilla is embraced dorsally by the anterior processes of the maxillae in most lacertids, but the processes are less extensive in two sister species of *Pedioplanis*, *P. burchelli* and *P. laticeps*. This modified condition also occurs in the genera *Eremias*, *Acanthodactylus*, *Mesalina* and *Ophisops*, which together constitute a clade that forms the sister group of *Pedioplanis*. The modification provides extra evidence for the holophyly of the clade, even though presence in some *Pedioplanis* shows it to be homoplasious.

KEYWORDS: *Aporosaura*, *Meroles*, *Pedioplanis*, Lacertidae, cladistics, South Africa.

Namib, Namibia, dunes

Introduction

The advanced lacertid genera *Pedioplanis* Fitzinger, 1843, *Meroles* Gray, 1838 and *Aporosaura* Boulenger, 1887, contain a total of eighteen species of lizards that are

* Formerly British Museum (Natural History).

ground-dwelling in dry habitats in southern Africa (South Africa, Lesotho, Botswana, Namibia and neighbouring southern Angola). Views on the relationship of these forms have varied considerably. Boulenger (1921) regarded the species now placed in *Pedioplanis* as part of the broad genus *Eremias* Wiegmann, 1834 *sensu lato* and within this he placed them in the subgenus *Mesalina* Gray, 1838, which also includes some north African and southwest Asian species. It is now apparent that *Eremias*, as Boulenger conceived it, was paraphyletic. Indeed, most of its component subgenera have already been raised to full generic status, with *Eremias* being confined to central Eurasian forms (Shcherbak, 1974, 1975). In addition, *Mesalina* turns out to include two disparate elements (Arnold, 1980). The north African and southwest Asian forms, including the type species, *Mesalina lichtensteinii* Gray, 1838 (= *M. rubropunctata* (Lichtenstein, 1823)) differ from the south African ones in such features as having an anterolateral process on the septomaxilla, the squamosal bone being separated from the parietal, two pairs of transverse processes on the anterior autotomic caudal vertebrae, the collar being fixed on the mid-line, a well-developed thoracic fascia and a distinctive hemipenis in which the lobes are directly attached to the clavulae (Arnold, 1989a). As pointed out by Balletto (1968), the name *Pedioplanis* Fitzinger, 1843 is available for the southern African forms, which are now customarily given full generic status.

Boulenger (1921) regarded the species now assigned to the genus *Meroles* as part of an admittedly polyphyletic genus, *Scapteira* Wiegmann, 1834. This had three subgenera, *Scapteira* s. str., *Meroles* Gray, 1838 s. str. and *Saurites* Peters, 1869. The first is essentially central Asian and Boulenger thought it was derived from the sympatric *Eremias* s. str. The other two subgenera are South African and constitute the genus *Meroles* as presently understood. The relationship between Boulenger's

Table 1. Allocations of lacertid lizards originally assigned to *Eremias*, *Scapteira* and *Aporosaura* by Boulenger (1921).

Boulenger (1921)	Recent allocations
<i>Eremias</i> Wiegmann, 1834	
subgenera	
<i>Lampreremias</i> Boulenger, 1918	<i>Heliobolus</i> Fitzinger, 1843
<i>Pseuderemias</i> Boettger, 1883	<i>Pseuderemias</i> Boettger, 1883
<i>Taenieremias</i> Boulenger, 1918	<i>Acanthodactylus</i> Wiegmann, 1834 (part) (Arnold, 1980, 1983; Salvador, 1982)
<i>Mesalina</i> Gray, 1838	<i>Mesalina</i> Gray, 1838 —Saharo-Sindian forms <i>Pedioplanis</i> Fitzinger, 1843 —South African forms
<i>Eremias</i> s. str.	<i>Eremias</i> Wiegmann, 1834 (part)
<i>Scapteira</i> Wiegmann, 1834	
subgenera	
<i>Scapteira</i> s. str.	<i>Eremias</i> Wiegmann, 1834 (part)
<i>Meroles</i> Gray, 1838	<i>Meroles</i> (part) Gray, 1838
<i>Saurites</i> Peters, 1869	<i>Meroles</i> (part) Gray, 1838
<i>Aporosaura</i> Boulenger, 1887	<i>Aporosaura</i> Boulenger, 1887 —subsequently transferred to <i>Meroles</i> (this paper; Arnold, 1989a)

classification of the lizards he assigned to *Eremias* and *Scapteira* and their contemporary allocations is shown in Table 1. Boulenger believed that his subgenera, *Meroles* and *Saurites*, each originated from different species now assigned to *Pedioplanis*: *Meroles* s. str. from *P. lineocellata* and *Saurites* from *P. capensis* (= *P. laticeps*). The monotypic *Aporosaura* Boulenger, 1887 was regarded as being derived from *Saurites*.

Boulenger's view about the origin of *Scapteira* s. str. has been supported by subsequent workers (Lantz, 1928; Shcherbak, 1974) and it appears that *Scapteira* s. str., as understood by Boulenger, arose from two separate parts of Asiatic *Eremias*. All its species are now assigned to that genus in its present sense. Within *Eremias*, the species that Boulenger placed in *Scapteira* s. str. are now allocated to the subgenera *Scapteira* and *Rhabderemias* Lantz, 1928. It remains to consider whether Boulenger was also right about the southern African forms. Was *Aporosaura* derived from within *Meroles* as now understood, and did *Meroles* have a diphyletic origin from *Pedioplanis*, in the same way as *Scapteira* s. str. arose from *Eremias*? At first sight, the latter hypothesis seems a possibility, for some or all species of *Pedioplanis* and *Meroles* share many derived morphological features (p. 799). However, data from protein electrophoresis have been interpreted as suggesting that *Meroles* and *Pedioplanis* are holophyletic sister taxa and that *Aporosaura* is more distantly related (Mayer and Berger Dell'mour, 1988). In the course of a recent phylogenetic analysis of the whole of the Lacertidae based on morphology, Arnold (1989a) accepted the holophyly of *Pedioplanis* but followed Boulenger's view that *Aporosaura* was a derivative of *Meroles*.

To try to resolve these conflicts of opinion, the relationships of *Aporosaura*, *Meroles* and *Pedioplanis* have been reanalysed using a much wider range of morphological features than were available to previous workers. The detailed interrelationships of the species assigned to these genera are also considered.

The species assigned to *Aporosaura*, *Meroles* and *Pedioplanis*

The species of *Aporosaura*, *Meroles* and *Pedioplanis* that have usually been recognized in recent times are as follows: *Aporosaura anchietae* (Bocage, 1967); *Meroles ctenodactylus* (Smith, 1838); *M. cuneirostris* (Strauch, 1867); *M. knoxii* (Milne-Edwards, 1829); *M. micropholidotus* (Mertens, 1938); *M. reticulatus* (Bocage, 1867); *M. suborbitalis* (Peters, 1869); *Pedioplanis benguellensis* (Bocage, 1867); *P. breviceps* (Sternfeld, 1911); *P. burchelli* (Duméril and Bibron, 1839); *P. laticeps* (Smith, 1844); *P. lineocellata* (Duméril and Bibron, 1839); *P. namaquensis* (Duméril and Bibron, 1839) and *P. undata* (Smith, 1838). These forms have been discussed in detail by Boulenger (1921), Fitzsimons (1943) and Mertens (1955, 1971), who also list their synonyms and infraspecific taxa. A useful guide to field identification is provided by Branch (1988).

Recently, a new species of *Pedioplanis* has been described, *P. husabensis* Mayer and Berger Dell'mour (1989). In addition, the various forms originally assigned to *P. undata* have been given species status, largely on the basis of the results of protein electrophoresis (Mayer and Berger Dell'mour, 1987). These include, *P. inornata* (Roux, 1907), *P. gaerdesi* (Mertens, 1954), *P. rubens* (Mertens, 1954) and *P. undata* s. str. The distinctness of many of these forms is confirmed by differences in the hemipenis and female genital sinus and to a lesser extent by skeletal differences (Arnold, 1986a, unpublished).

Characters used to estimate phylogeny

Characters used to estimate phylogeny are listed below and their distribution summarized in Table 2. Each character or character complex is numbered. The latter,

Table 2. Distribution of character states in *Meroles*, *Aporosaura* and *Pedioplanis*. 0, Apparently primitive state, on evidence of outgroup comparison: 1, apparently derived state, on evidence of outgroup comparison: V, character variable, both 0 and 1 states present: —, no data.

Species	1	2	3	4	5	6	7	8	9	10	11.1	11.2	12	13.1	13.2	14	15	16
<i>P. benguellensis</i>	0	1	0	0	1	1	0	0	0	0	1	0	1	1	0	0	1	0
<i>P. undata</i>	0	1	0	0	1	1	0	0	0	0	1	0	1	1	0	0	1	0
<i>P. gaerdesi</i>	0	1	0	0	1	1	0	0	0	0	1	0	1	1	0	0	1	0
<i>P. rubens</i>	0	V	0	0	1	0	0	0	0	0	1	0	1	1	0	0	1	0
<i>P. husabensis</i>	0	1	0	0	1	1	0	0	0	0	1	0	1	V	0	0	1	0
<i>P. inornata</i>	0	1	0	0	1	1	0	0	0	0	1	0	1	1	0	0	1	0
<i>P. namaquensis</i>	0	1	0	0	1	1	0	0	0	0	1	0	1	1	0	0	1	0
<i>P. breviceps</i>	0	1	0	0	1	1	1	0	0	0	0	0	1	V	0	0	1	0
<i>P. lineocellata</i>	0	1	0	1	0	1	0	0	0	0	1	0	1	V	0	0	1	0
<i>P. laticeps</i>	1	1	0	1	1	1	1	0	0	0	0	0	1	0	0	0	1	0
<i>P. burchelli</i>	1	1	0	0	1	1	1	0	0	0	0	0	1	0	0	0	1	0
<i>M. knoxii</i>	0	0	0	1	1	0	0	0	0	1	1	0	0	V	0	0	0	0
<i>M. suborbitalis</i>	0	0	0	1	1	0	0	0	0	1	1	1	0	V	0	0	1	0
<i>M. reticulatus</i>	0	0	0	1	1	0	0	0	0	1	1	0	0	0	0	1	0	1
<i>M. ctenodactylus</i>	0	0	1	1	0	0	0	1	1	1	1	1	0	1	0	1	0	1
<i>M. cuneirostris</i>	0	0	1	1	0	0	0	1	1	1	1	1	0	1	1	1	0	1
<i>M. micropholodotus</i>	0	0	1	1	0	0	0	1	1	1	1	0	0	1	1	1	0	1
<i>A. anchietae</i>	0	0	1	1	0	0	0	1	1	1	1	1	0	1	0	1	0	1

Table 2 (continued).

Species	17	18	19	20	21	22	23	24	25	26.1	26.2	27	28	29.1	29.2	30	31.1	31.2
<i>P. benguellensis</i>	0	0	0	V	0	1	0	0	0	1	1	1	0	1	0	1	0	0
<i>P. undata</i>	0	0	0	V	0	0	0	0	0	1	0	1	0	1	0	1	0	0
<i>P. gaerdesi</i>	0	0	0	V	0	0	0	0	0	1	1	1	0	1	0	1	0	0
<i>P. rubens</i>	0	0	0	V	0	0	0	0	0	1	0	1	0	1	0	1	0	0
<i>P. husabensis</i>	0	0	0	V	0	0	0	0	0	0	0	1	0	1	0	1	0	0
<i>P. inornata</i>	0	0	0	V	0	0	0	0	0	1	0	1	0	1	0	1	0	0
<i>P. namaquensis</i>	0	0	0	V	0	1	0	0	0	0	0	1	0	1	0	1	0	0
<i>P. breviceps</i>	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	1	0	0
<i>P. lineocellata</i>	0	0	0	V	0	0	0	0	0	1	0	1	V	1	1	1	0	0
<i>P. laticeps</i>	0	1	0	V	0	0	1	0	0	0	0	1	V	1	1	1	0	0
<i>P. burchelli</i>	0	0	0	V	0	1	0	0	0	0	0	1	0	1	0	1	0	0
<i>M. knoxii</i>	0	0	0	V	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>M. suborbitalis</i>	0	1	0	V	0	0	0	1	0	0	0	0	0	V	0	0	V	0
<i>M. reticulatus</i>	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0
<i>M. ctenodactylus</i>	1	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	1	0
<i>M. cuneirostris</i>	1	1	0	0	1	0	1	1	1	0	0	0	1	0	0	0	1	0
<i>M. micropholidotus</i>	1	0	0	0	1	0	1	1	1	0	0	0	1	1	1	0	1	0
<i>A. anchietae</i>	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1

Table 2 (continued).

Species	32	33.1	33.2	34.1	34.2	35.1	35.2	35.3	36	37.1	37.2	38	39	40.1	40.2	41	42	43.1
<i>P. benguellensis</i>	1	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0
<i>P. undata</i>	1	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	V
<i>P. gaerdesi</i>	1	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0
<i>P. rubens</i>	1	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0
<i>P. husabensis</i>	1	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0
<i>P. inornata</i>	1	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	V
<i>P. namaquensis</i>	1	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	1
<i>P. breviceps</i>	1	0	0	1	1	1	—	0	0	0	0	0	1	0	0	0	0	V
<i>P. lineocellata</i>	1	0	0	1	1	1	—	0	0	0	0	1	1	0	0	0	0	1
<i>P. laticeps</i>	1	0	0	1	1	1	—	0	0	0	0	0	0	0	0	0	0	1
<i>P. burchelli</i>	0	0	0	1	1	1	—	0	0	0	0	0	1	0	0	0	0	1
<i>M. knoxii</i>	0	0	0	0	0	V	1	0	0	0	0	1	V	0	0	0	0	V
<i>M. suborbitalis</i>	0	1	0	V	V	V	V	0	0	0	0	1	0	0	0	0	0	1
<i>M. reticulatus</i>	0	1	0	1	1	0	1	1	0	1	0	1	0	0	0	0	0	1
<i>M. ctenodactylus</i>	0	0	0	0	0	0	1	1	1	1	1	1	0	1	0	1	0	1
<i>M. cuneirostris</i>	0	0	1	1	0	0	1	1	1	1	1	0	0	1	1	0	0	1
<i>M. micropholidotus</i>	0	0	1	1	0	0	1	1	1	1	1	0	0	1	1	0	0	1
<i>A. anchietae</i>	0	—	—	1	1	1	—	0	1	0	0	0	0	1	1	0	1	1

Table 2 (continued).

Species	43.2	43.3	43.4	44.1	44.2	45.1	45.2	46	47	48	49	50	51	52.1	52.2	53.1	53.2	54
<i>P. benguellensis</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>P. undata</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>P. gaerdesi</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>P. rubens</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>P. husabensis</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>P. inornata</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>P. namaquensis</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>P. breviceps</i>	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1
<i>P. lineocellata</i>	V	0	0	0	0	1	0	0	0	0	V	1	0	1	0	0	0	0
<i>P. laticeps</i>	1	0	0	0	0	1	V	0	1	0	1	1	0	0	0	0	0	0
<i>P. burchelli</i>	1	0	0	0	0	1	0	0	1	V	V	1	0	0	0	0	0	0
<i>M. knoxii</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
<i>M. suborbitalis</i>	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0
<i>M. reticulatus</i>	1	1	0	1	0	0	0	0	0	0	0	1	0	1	1	1	1	1
<i>M. ctenodactylus</i>	1	1	1	1	1	1	1	1	0	1	0	1	1	1	1	1	1	1
<i>M. cuneirostris</i>	1	1	1	1	1	1	1	1	0	1	0	1	1	1	1	1	1	1
<i>M. micropholidotus</i>	1	1	1	1	1	1	1	1	0	1	0	1	1	1	0	1	1	1
<i>A. anchietae</i>	1	1	1	1	1	1	1	1	0	1	0	1	1	0	0	1	1	1

Table 2 (continued).

Species	55	56.1	56.2	57.1	57.2	58	59	60.1	60.2	61	62.1	62.2	63	64	65	66	67	68
<i>P. benguellensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1
<i>P. undata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1
<i>P. gaerdesi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1
<i>P. rubens</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1
<i>P. husabensis</i>	0	0	0	0	0	0	0	0	0	0	V	V	0	0	1	1	0	1
<i>P. inornata</i>	0	0	0	0	0	0	0	0	0	0	V	V	0	0	1	1	0	1
<i>P. namaquensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1
<i>P. breviceps</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0
<i>P. lineocellata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
<i>P. laticeps</i>	0	0	0	0	0	1	V	0	0	0	0	0	0	0	1	1	0	0
<i>P. burchelli</i>	0	0	0	0	0	1	V	0	0	0	0	0	0	0	1	1	0	0
<i>M. knoxii</i>	0	0	0	0	0	0	1	1	0	1	0	0	1	0	0	0	0	0
<i>M. suborbitalis</i>	0	0	0	0	0	1	1	1	0	0	0	0	1	0	0	0	1	1
<i>M. reticulatus</i>	1	0	0	1	0	0	1	1	0	1	1	1	1	1	0	0	0	0
<i>M. ctenodactylus</i>	1	0	1	1	1	0	1	1	0	1	1	0	1	1	0	1	0	0
<i>M. cuneirostris</i>	1	0	0	1	1	0	1	1	0	1	1	1	1	1	0	1	0	0
<i>M. micropholidotus</i>	1	0	0	1	1	1	1	1	0	1	1	1	1	1	0	1	0	0
<i>A. anchietae</i>	1	1	—	0	0	1	1	1	1	1	1	1	1	1	0	1	1	0

Table 2 (continued).

Species	69.1	69.2	70	71	72	73	74	75.1	75.2	75.3	75.4	76.1	76.2	77	78	79.1	79.2	80.1	80.2
<i>P. benguellensis</i>	1	0	0	1	1	1	1	1	1	1	0	0	0	1	—	—	—	1	0
<i>P. undata</i>	1	1	1	1	1	1	0	1	1	0	0	0	0	1	—	—	—	1	1
<i>P. gaerdesi</i>	1	1	1	1	1	1	0	1	1	0	0	0	0	1	—	—	—	1	1
<i>P. rubens</i>	1	1	0	1	1	1	0	1	1	0	0	0	0	1	—	—	—	1	0
<i>P. husabensis</i>	1	0	0	1	1	0	0	1	1	0	0	0	0	1	—	—	—	1	0
<i>P. inornata</i>	0	0	0	1	1	0	1	1	0	0	0	0	0	0	0	1	1	1	0
<i>P. namaquensis</i>	1	0	0	1	1	0	0	1	1	0	0	0	0	1	—	—	—	1	0
<i>P. breviceps</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0
<i>P. lineocellata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
<i>P. laticeps</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0
<i>P. burchelli</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0
<i>M. knoxii</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>M. suborbitalis</i>	1	1	0	0	0	1	0	1	1	1	1	—	—	—	—	—	—	0	0
<i>M. reticulatus</i>	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
<i>M. ctenodactylus</i>	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	1	0
<i>M. cuneirostris</i>	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	1	0
<i>M. micropholidotus</i>	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	1	0
<i>A. anchietae</i>	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0

which have more than two states, are divided into binary characters which are designated by figures after a decimal point. Each state of a binary character is indicated by 0 or 1, the former being attached to the apparent primitive condition of the character. A total of 80 primary and 109 binary characters are used. In 102 of the binary characters, the apparent derived state occurs in more than one species and, consequently is, of direct use in assessing relationships. The remainder, in which the apparent derived state occurs in a single species, are included because they give some indication of how distinct some of the species are.

Some of the characters used involve apparent losses. Such features are often regarded as inferior indicators of relationship, on the assumption that multiple loss of a feature is more likely than multiple gain and therefore more prone to create homoplasy. The characters involved are numbers 2, 3, 5, 10, 12, 19, 23, 24, 42, 56.1, 58, 66, 71, 73 and 77. In some cases, these are only technical losses. That is, 'loss' indicates the shift of one arrangement to another, rather than real absence of a structure that was originally present. For instance, in character 19, contact between the rostral and subnasal scales is lost, but this merely means the scales concerned are separated by the development of contact between the supranasal and first upper labial scales. Characters 23 and 24 can also be interpreted in this way. Characters 42 and 56.1 are unique, being found in only one species and so do not enter into the analysis, while character 5 ultimately has its polarity reversed so that it becomes a gain rather than a loss. In fact, it turns out that the remaining loss characters do not show particularly high levels of homoplasy in analysis.

Skeleton

1. Premaxilla substantially enclosed by anterior processes of maxillae in dorsal view (Fig. 1). Yes (0); no (1).
2. Anterior projection on septomaxilla (Arnold, 1989a: Fig. 4). Present (0); absent (1).
3. Median depression on snout (Arnold, 1989a: Fig. 3). Marked (0); absent (1).
4. Postfrontal and postorbital bones. Separate (0); fused (1).
5. Pterygoid teeth. Present (0); absent (1).
6. Quadrato-jugal process on jugal bone (Arnold, 1989a: Fig. 6). Distinct (0); usually very reduced or absent (1).
7. Ectopterygoid bone exposed as a lateral facet below jugal bone. No (0); yes (1).
8. Dorso-anterior border of quadrate bone. Rounded (0); strongly angled (1).
9. Size of quadrate bone. Relatively large with big tympanic area (0); relatively small with reduced tympanic area (1).
10. Peripheral radial portion of scleral ossicle 14 (Arnold, 1989a: Fig. 8). Present (0); absent (1).
- 11.1, 11.2 Usual number of presacral vertebrae in males (Table 3: see p. 804). 25 (0, 0); 24 or less (1, 0); 23 (1, 1).
12. Ribs on last presacral vertebra. Usually present (0); usually absent or very reduced (1).
- 13.1, 13.2. Number of rib pairs attaching to sternum and xiphisternum. 5 (0, 0); 3 or 4 (1, 0); 3 (1, 1).
14. Shape of sternum (Arnold, 1989a: Fig. 10). Relatively narrow (0); broad (1).
15. Shape of sternal fontanelle (Arnold, 1989a: Fig. 10). Not heart-shaped (0); heart-shaped in at least some individuals (1).
16. Size of sternal fontanelle. Fairly large (0); very small or absent (1).
17. Length of transverse processes on proximal tail vertebrae. Relatively short (0); long (1).

External features

Lacertid head scaling is illustrated elsewhere (Arnold, 1986b: Fig. 2; 1989a: Fig. 12)

18. Contact between rostral and frontonasal scales. Absent (0); present (1).
19. Contact between rostral and lower postnasal scales. Present (0); absent (1).

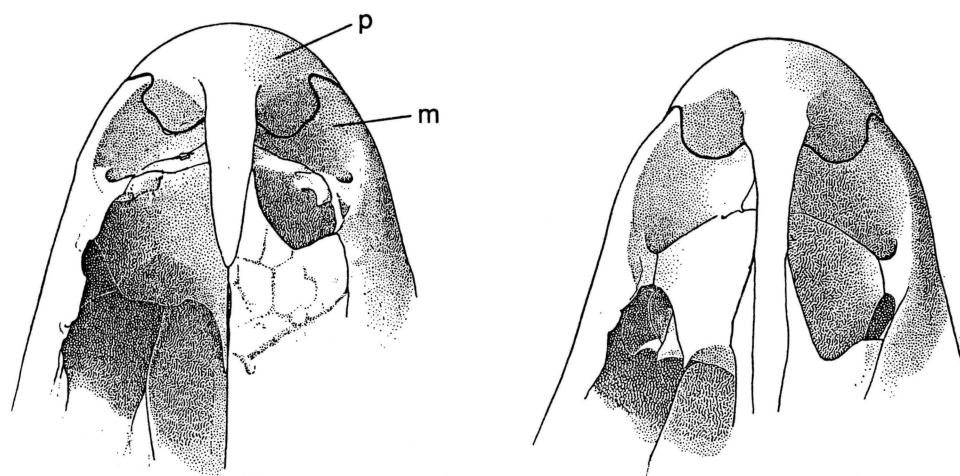


FIG. 1. Dorsal views of anterior skulls showing relationship between the premaxilla (*p*) and the maxilla (*m*). Left: *Adolfus jacksoni*, exhibiting primitive condition. Right: *Pedioplanis laticeps*, showing how the premaxilla is less enclosed by the anterior processes of the maxillae. Although restricted in *Pedioplanis*, the latter condition is widespread in the Saharo-Eurasian clade of advanced lacertids (*Eremias*, *Acanthodactylus*, *Mesalina* and *Ophisops*), and provides some additional support for the holophyly of this group.

20. Azygous scale between prefrontal scales. Absent (0); present (1).
21. Upper labial scales. Normal (0); forming a lateral ridge (1).
22. Commonest number of complete supralabial scales anterior to centre of eye. Five (0); four (1).
23. Contact between first loreal scale and upper postnasal scale. Broad (0); narrow or absent (1).
24. Subocular scale borders mouth. Yes (0); no (1).
25. Subocular scale very shallow (Fitzsimons, 1943: Fig. 248). No (0); yes (1).
- 26.1, 26.2. Transparent 'window' in lower eyelid (Mayer and Berger Dell'mour, 1987: Fig. on p. 275). Absent (0, 0); made up of two or more scales (1, 0); made up of a single scale (1, 1).
27. Size of second supraocular scale. Larger than third (0); often smaller than third (1).
28. Second and third supraocular scales in broad contact with frontal scale. Yes (0); largely or wholly separated by granules (1).
- 29.1, 29.2. Division of the first supraocular scale. Into about 1–4 elements (0, 0); into about 5–15 elements (1, 0); into 17 or more elements (1, 1).
30. Position of lateral border of parietal scale relative to parietal table of skull (Arnold, 1989a: Fig. 14). Not reaching edge of table (0); reaching edge of table and extending right across postorbital bone (1).
- 31.1, 31.2. Length of parietal scales. Normal (0, 0); some shortening (1, 0); very reduced (1, 1).
32. Size of interparietal scale. Quite small (0); often large, approaching width of one of the frontoparietal scales (1).
- 33.1, 33.2. Occipital scale. Well developed, usually in contact with interparietal or separated by an intermediate scale (0, 0); extremely small or absent (1, 0); often replaced by several granules (0, 1).
- 34.1, 34.2. Size of supratemporal scales. Large, less than four on each side (0, 0); moderate, clearly bigger than adjoining temporal scales (1, 0); very small, about the same size as adjoining temporal scales (1, 1).
- 35.1, 35.2, 35.3. Tympanic scale. Well developed and elongate (0, 0, 0); absent (1, 0, 0); rounded and raised (0, 1, 0); enlarged, rounded and raised (0, 1, 1).
36. Position of tympanum. Fairly superficial, near surface of head (0); deeply recessed (1).
- 37.1, 37.2. Ear opening. Large and unimpeded (0, 0); partly occluded by an antero-dorsal skin fold (1, 0); largely occluded by a strong diagonal skin fold (1, 1).
38. Anterior edge of ear opening. Fairly smooth (0); with a strongly denticulated fringe (1).

39. Number of pairs of chin shields. Five (0); four (1).
- 40.1, 40.2. Number of dorsal scale rows in a transverse row at mid-body. Less than 78 (0, 0); 78 to 90 (1, 0); more than 90 (1, 1).
41. Dorsal scaling on posterior body. Scales all about the same size (0); dorsolateral tracts of enlarged scales present (1).
42. Collar beneath throat (a posteriorly directed skin-fold covered externally by large scales). Present (0); absent (1).
- 43.1, 43.2, 43.3, 43.4. Number of ventral body scales in the longest row across the belly. Less than 12 (0, 0, 0, 0); 12 or more (1, 0, 0, 0); 14 or more (1, 1, 0, 0); 16 or more (1, 1, 1, 0); 22 or more (1, 1, 1, 1).
- 44.1, 44.2. Size of ventral scales in posterior thoracic region. About the same as those elsewhere (0, 0); distinctly reduced away from the mid-line (1, 0); very reduced right across thorax (1, 1).
- 45.1, 45.2. Arrangement of ventral body scales. In straight longitudinal rows (0, 0); at least partly tessellated, at sides and anteriorly (1, 0); entirely tessellated (1, 1).
46. Tail length. Usually more than 1.8 times snout-vent length (0); usually less than 1.8 times snout-vent length (1).
47. Extent of large keeled scales on dorsum of tail. Reaching level of vent, at least dorsolaterally (0); not reaching level of vent, being replaced anteriorly by smaller, usually unkeeled scales (1).
48. Size of dorsal scales on mid-line area of proximal tail. Larger than those on body (0); about the same size as those on body (1).
49. Axillary mite pockets (Arnold, 1986c). Absent (0); present (1).
50. Size of dorsal scales on upper arm. Large (0); relatively small (1).
51. Shape of dorsal scales on upper arm. Rounded (0); often pointed (1).
- 52.1, 52.2. Keeling on dorsal scales of upper arm and presence of granules below anterior ones. Absent (0, 0); keeling slight, granules present at least distally (1, 0); keeling stronger (1, 1).
- 53.1, 53.2. Number of longitudinal scale rows on the digits of forefeet (Arnold, 1986b: Fig. 16). Two (0, 0); three (1, 0); four (1, 1).
54. Number of principal keels on scales beneath digits of forefeet. More than one (0); one (1).
55. Lateral fringes of pointed scales on digits of forefeet (Arnold, 1986b: Fig. 16). No (0); yes (1).
- 56.1, 56.2. Femoral pores. Present, 25 or less under each thigh (0, 0); absent (1, 0); present, more than 25 under each thigh (0, 1).
- 57.1, 57.2. Scales on outer tibia just below knee. Unpointed and smooth (0, 0); distinctly pointed and keeled (1, 0); sharply pointed and strongly keeled (1, 1).
58. Keeling on upper tibial scales. Present, although sometimes weak (0); absent (1).
59. Pattern of subtibial scales. One very wide row of scales bordered by a narrower one (0); a less wide row bordered by more than one narrower row (1).
- 60.1, 60.2. Number of longitudinal scale rows on digits of hind feet. Two (0, 0); three (1, 0); four (1, 1).
61. Lateral fringes of pointed scales on digits of hind feet. Absent (0); present (1).
- 62.1, 62.2. Dorsal pattern. Often incorporating longitudinal stripes or rows of markings on both back and sides (0, 0); if, present, longitudinal stripes or rows of markings confined to sides (1, 0); no longitudinal stripes or rows of markings (1, 1).

Tongue colour, muscles, kidney and reproductive system

Genital features are illustrated and discussed elsewhere (Arnold, 1986a; unpublished).

63. Tongue colour. Usually pale or uniform (0); dark with a light tip (1).
64. Size and shape of kidney. With large anterior lobe, more than half the length of the kidney lying anterior to the sacrum (0); with small anterior lobe, not more than half the length of the kidney lying anterior to sacrum (1).
65. Posterior extent of kidney. Extending well posterior to level of vent (0); not extending posterior to level of vent (1).
66. Thoracic fascia connecting the *M. rectus abdominis lateralis* to the area of the lateral arms of the interclavicle. Present and well developed (0); absent or much reduced (1).
67. Lateral side of hemipenis and armature reduced. No (0); yes (1).

68. Shape of uneverted hemipenial lobes. Flattened and complexly folded (0); sac-like or tubular (1).
- 69.1, 69.2. Length of hemipenial lobes. Short (0,0); moderate (1,0); long (1,1).
70. Uneverted hemipenial lobes with a basal kink. No (0); yes (1).
71. Plicae on hemipenial lobes. Present (0); absent (1).
72. Awns present on lobe tips. No (0); yes (1).
73. Outer lip of hemipenial lobe sulcus expanded and free basally. Yes (0); no (1).
74. Flaps present on asulcate surface of stem of hemipenis. No (0); yes (1).
- 75.1, 75.2, 75.3, 75.4. Hemipenial armature. Normal (0,0,0,0); somewhat cleft and simplified (1,0,0,0), deeply cleft with, at most, very small clavulae (1,1,0,0); fragmented, often represented only by isolated minute clavulae (1,1,1,0); absent (1,1,1,1).
- 76.1, 76.2. Hemipenial clavulae. Separate (0,0); somewhat conjoined at base (1,0); strongly conjoined (1,1).
77. Outer connectors of hemipenial armature. Present (0); absent (1).
78. Form of outer connectors. Simple (0); branched (1).
- 79.1, 79.2. Origin and course of outer connectors. Originating on each side of armature and not running close to each other (0,0); originating at sides of armature and running close together dorsally; originating close to mid-line of armature and running close together dorsally or fusing with each other (1,1).
- 80.1, 80.2. Shape of female genital sinus. Simple (0,0); shallowly bilobed (1,0); sometimes very deeply bilobed (1,1).

Methods

Determination of polarities

Character polarities have been assigned largely on the basis of outgroup comparison. As the relationships of *Aporosaura*, *Meroles* and *Pedioplanis* to each other are being reconsidered here, they are analysed as a single unit and consequently, none of them can be used as outgroups in this process. A recent phylogenetic analysis of the Lacertidae (Arnold, 1989a) produces the arrangement of advanced taxa shown in Fig. 2. If it turns out that *Aporosaura* and the various species of *Meroles* form sister taxa of particular species of *Pedioplanis*, as Boulenger thought, it would be appropriate to use the Saharo-Eurasian clade (*Eremias*, *Acanthodactylus*, *Mesalina* and *Ophisops*) as the first outgroup. However, such an assumption cannot be made initially, especially as there is some evidence suggesting that the Saharo-Eurasian clade may be more closely related to the species of *Pedioplanis* than to *Meroles* and *Aporosaura* (Arnold, 1989a). It is best therefore to set the clade aside, although in fact its inclusion as an outgroup would make very little difference to the polarities actually allocated. The appropriate series of outgroups is consequently *Pseuderemias*, *Heliobolus* + *Ichnotropis*, *Latastia*, *Philochoortus* and *Nucras*.

Any character state consistently present in the two immediate outgroups of the group under study is likely to be primitive on parsimony criteria (Maddison *et al.*, 1984). In the present case, the two immediate outgroups are *Pseuderemias* and *Heliobolus* + *Ichnotropis* (the order of origin of this latter pair of genera being undetermined). In instances where both states occur in these taxa, the one that occurs widely in the broader outgroup sequence is taken as primitive. Sometimes the choice of polarity is balanced, so that the distribution of characters in immediate outgroups can either be interpreted as two forward transformations giving one polarity, or a forward transformation followed by a reversal giving the opposite polarity. In such cases, the former interpretation is preferred. Using these criteria, most characters can be polarized.

As will be shown, initial analysis confirms that *Meroles*-*Aporosaura* and *Pedioplanis* are separate entities and that there is no conflict with the relationships for

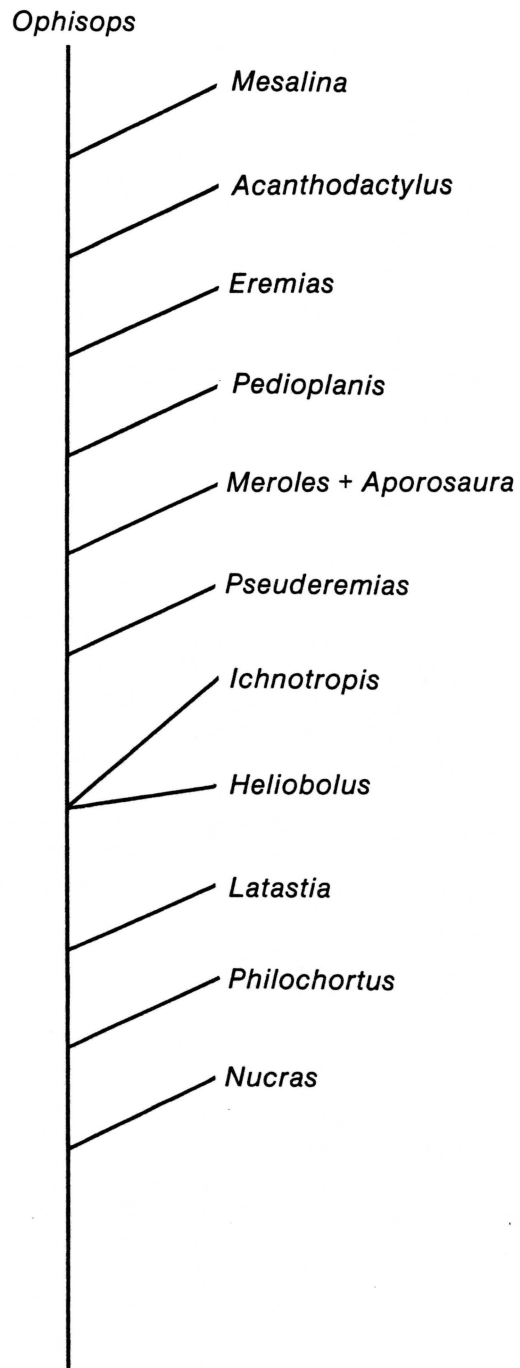


FIG. 2. Relationships of advanced lacertids based on a phylogenetic analysis of the whole family (Arnold, 1989a). All more basal genera are essentially Ethiopian, but *Eremias*, *Acanthodactylus*, *Mesalina* and *Ophisops* form a clade restricted to the Saharo-Eurasian arid regions.

advanced lacertids (Fig. 2). When *Meroles-Aporosaura* and *Pedioplanis* are analysed separately, it is appropriate in these circumstances to use a different outgroup sequence for each. For *Meroles-Aporosaura* this would be *Pedioplanis* + the Saharo-Eurasian clade, *Pseuderemias*, etc. While for *Pedioplanis* it would be the Saharo-Eurasian clade, *Meroles*, *Pseuderemias*, etc. In fact, such modifications make very little difference to the polarities already decided here.

Methods of phylogenetic analysis

Parsimony analysis was carried out using the 2.4 version of the PAUP (Phylogenetic Analysis Using Parsimony) programme of Swofford (1985). In this process, V scores were replaced by 0 scores and the optimization method used was MINF. Compatibility analysis was also carried out using the programme of Gauld and Underwood (1986) which is discussed elsewhere (Arnold, 1989a, b).

At a later stage, the results were checked using the 1.5 version of the Hennig86 programme of Farris (1988). The patterns of relationships produced were essentially like those discerned by PAUP.

Holophyletic groups

Parsimony analysis of all the species assigned to *Aporosaura*, *Meroles* and *Pedioplanis* was carried out based on 80 primary and 108 binary characters (number 22 was omitted as it became invariant once its V scores were reduced to 0). This produced four trees of 175 steps with a consistency index of 0.577, the trees differing only slightly in the placing of *Pedioplanis benguelensis*, *P. husabensis* and *P. namaquensis*. The trees contained two well-substantiated holophyletic groups, one consisting of all the species of *Pedioplanis* and the other of *Meroles* and *Aporosaura*. Within the latter, *Aporosaura* is sister taxon to the species of *Meroles* that were placed in the subgenus *Saurites*. These groupings are also produced by compatibility methods. *Pedioplanis* shares two features with the advanced Saharo-Eurasian lacertids (*Eremias*, *Acanthodactylus*, *Mesalina* and *Ophisops*), namely a reduced quadratojugal process (6) and a frequently heart-shaped sternal fontanelle (15). These features indicate that the South African advanced lacertids do not form a holophyletic group and support the pattern of relationships shown in Fig. 2.

The analyses give no support to Boulenger's hypothesis that *Meroles-Aporosaura* was derived from within *Pedioplanis*, either as a single unit or polyphyletically. On the other hand, they corroborate his view about the position of *Aporosaura* and consequently conflict with interpretations of the recent evidence from protein electrophoresis (Mayer and Berger Dell'mour, 1988). This is discussed further on p. 800.

Diagnosis of the *Meroles-Aporosaura* clade and *Pedioplanis*

Both *Meroles-Aporosaura* and *Pedioplanis* have relatively few features that are primitive within the Lacertidae. They include the following: pineal fontanelle present, lateral teeth bicuspid, no temporal ossification, sexual variation in number of presacral vertebrae, clavicle expanded medially, dorsal body scales small and a ventral collar present.

Features that are apomorphic within the Lacertidae and are shared by *Meroles-Aporosaura*, *Pedioplanis* and at least some other relatively advanced genera include: large nasal opening, septomaxilla with anterior (not *Pedioplanis*) and posterior projections and a posterolateral process, medial depression on snout primitively

strong, frontal bones fused, fronto-parietal suture bow-shaped with little interdigitation, osteoderms not extending to back of parietal bone which is relatively short, squamosal bone deep and contacting supratemporal process of parietal bone, dorsal process of maxilla narrow, lateral exposure of jugal bone large, number of short free dorsal ribs exceeds number of long, posterior border of clavicle always continuous, xiphisternal cartilages always well separated, no inscriptional ribs, caudal vertebrae with simple transverse processes (anomalous exceptions in *Pedioplanis*), lower postnasal scale contacts rostral, no masseteric scale, ten or more longitudinal rows of ventral scales, subdigital lamellae keeled, postnasal area thickened, nasal vestibule partly covers concha, hemipenial armature present, unverted hemipenial lobes complexly folded at least primitively, course of ulnar nerve deep (the 'varanide' condition, Julien and Renous-Lecuru, 1972), lateral thoracic fascia primitively present (not *Pedioplanis*), more than half of kidney primitively lying in front of sacrum (not all *Meroles*).

Among these, synapomorphies of *Meroles-Aporosaura*, *Pedioplanis* and the Saharo-Eurasian clade (*Eremias*, *Acanthodactylus*, *Mesalina* and *Ophisops*) are postnasal area thickened and nasal vestibule partly covering the concha. Most members of the above assemblage also have ten or more longitudinal rows of ventral scales, but there are exceptions and the condition also occurs occasionally in outgroups.

Distinctive features of the Meroles-Aporosaura clade

1. Postorbital and postfrontal bones fused (4).
2. Sternal fontanelle small and round, or absent (except in *M. suborbitalis*) (16).
3. Subocular scale separated from upper lip (except in *Aporosaura anchietae*) (24).
4. Three or four longitudinal rows of scales on fingers and toes (53, 60).
5. Scleral ossicle 14 with reduced peripheral radial section (10).
6. Subtibial scales small (59).
7. Fringes of pointed scales on toes (except in *M. suborbitalis*) (61).
8. Hemipenial clavulae conjoined (uncheckable in *M. suborbitalis*, which has a highly modified hemipenis) (76).
9. Tongue dark with a light tip (63).

Nearly all the above features occur in some other groups of advanced lacertids, albeit not in consistent association, only number 8 being unique to the *Meroles-Aporosaura* clade.

Distinctive features of Pedioplanis

1. Secondary absence of anterior projection on septomaxilla (2).
2. Quadrato-jugal process on jugal absent (6).
3. Last presacral vertebra with ribs absent or very reduced (12).
4. Zygous scale between prefrontal scales frequent (20).
5. First supraocular scale fragmented (29).
6. Second supraocular scale often smaller than third (27).
7. Parietal scale extends to lateral edge of parietal table of skull (30).
8. Interparietal scale usually large (32).
9. Supratemporal scales small (34).
10. Axillary mite pockets in some or all individuals of each species (49).
11. Usually only four pairs of chin shields (39).
12. Outer connectors of hemipenial armature running close together dorsally, or fused (not checkable in many species with highly modified hemipenes) (79).
13. Tongue pale (63).

As with the *Meroles-Aporosaura* clade, the great majority of derived features found in *Pedioplanis* occur in some other groups of advanced lacertids and only number 12 appears unique. It is regrettable that reduction of the armature prevents this feature being checked in many species. However, a case can be made that loss is secondary in these forms.

Parallelism between the *Meroles-Aporosaura* clade and *Pedioplanis*

Many apparently derived features appear to have originated independently in the *Meroles-Aporosaura* clade and in *Pedioplanis*. Among these are the following. Fusion of postfrontal and postorbital bones (4), presence of pterygoid teeth (5), pairs of ribs attaching to sternum and xiphisternum reduced to four (13.1), sternal fontanelle cordate (15), contact between rostral and frontonasal scales (18), azygous scale often present between prefrontal scales (20), contact between first loreal scale and upper postnasal scale (23), second and third supraocular scales largely or wholly separated from frontal scale (28), fragmentation of first supraocular scale (29.1, 29.2), lateral border of parietal scale reaching edge of parietal table of the skull (30), reduction in size of supratemporal scales (34.1, 34.2), tympanic scale lost (35.1), anterior edge of ear opening with a strongly denticulated fringe (38), number of ventral body scales in longest row across belly elevated (43.1, 43.2), ventral body scales partly tessellated (45.1), large keeled scales on dorsum of tail not reaching vent (47), size of dorsal scales on mid-line area of proximal tail reduced (48), dorsal scales on upper arm small (50) with some keeling (52.1), upper tibial scales unkeeled (58), size of subtibial scales reduced (59), dorsal stripes or longitudinal series of markings reduced (62), thoracic fascia reduced or absent (66), unverted hemipenial lobes tubular (68) and long (69.1, 69.2), outer lip of hemipenial lobe sulcus not expanded and free basally (73), hemipenial armature absent (75.1–75.4), female genital sinus bilobed (80.1).

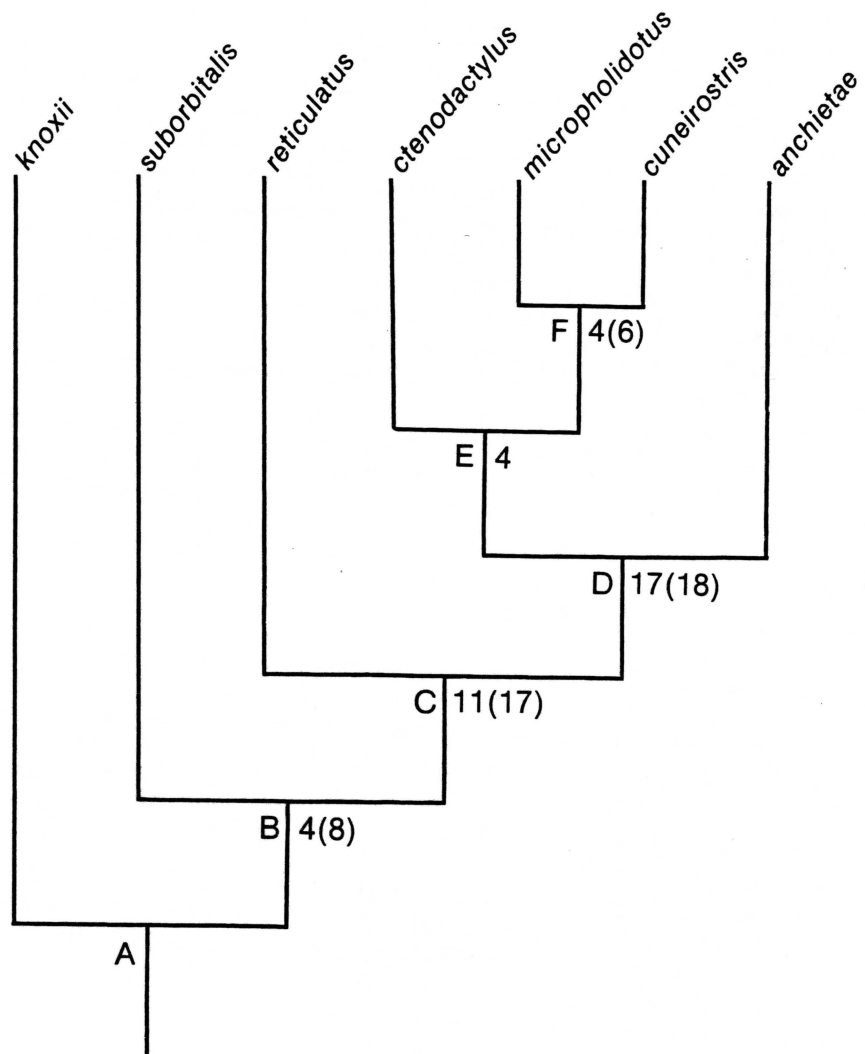
This parallel development of no less than 29 primary and 36 binary derived features is at first sight striking but perhaps not unexpected. The *Meroles-Aporosaura* clade and *Pedioplanis* are successive branches arising from the common ancestral stem of more advanced lacertids and *Pedioplanis* appears to have developed only two more derived features than the ancestor of the *Meroles-Aporosaura* clade when it diverged. The two clades would be expected to have had very similar initial gene pools and presumably very similar evolutionary potential. In fact, many of the derived features that have developed in parallel in these groups also occur sporadically in the *Saharo-Eurasian* clade, comprising *Eremias*, *Acanthodactylus*, *Mesalina* and *Ophisops-Cabrita*, which is the apparent sister group of *Pedioplanis*.

Relationships of the species of the *Meroles-Aporosaura* clade

Parsimony analysis was carried out on the 61 binary characters that vary within the *Meroles-Aporosaura* clade (after V scores eliminated) and occur in more than one species. The PAUP algorithm used was ALLTREES which considers all possible trees. This produced a single tree of 86 steps with a consistency index of 0.718. Characters are plotted on this in Fig. 3. If the polarity of characters 5 and 39 are reversed (a reasonable course as outgroup information is equivocal for them), no less than forty characters are fully compatible, showing unique transformations. Relationships within the *Meroles-Aporosaura* clade are consequently very well substantiated with an average of eight characters supporting each node (excluding the first one which is based on the common characters of the clade) and a range of 4–17. If another nine characters that show minor homoplasy are included, the figures are 9.8 and 4–18.

In compatibility analysis, the randomness ratio is 0.62 for 79 characters. The 'boil down' procedure of Gauld and Underwood (1986) produces a set of compatible characters essentially similar to the forty showing a single transformation above.

As already noted, the morphological evidence presented here places *Aporosaura anchietae* as the sister taxon to the species assigned to the subgenus *Saurites*, namely *M. ctenodactylus*, *M. cuneirostris* and *M. micropholidotus*. In contrast, evidence from protein electrophoresis (Mayer and Berger Dell'mour, 1988) suggests this species is more distantly related to the whole of *Meroles* than is *Pedioplanis*. If the second view is correct, *A. anchietae* would have evolved 28 primary and 40 binary morphological derived states in parallel to *Saurites*. Although such parallel development is possible and might be a selective product of the similar coercive aeolian sand environments in which the lizards live, this is unlikely to apply to some features, such as hemipenial structure (76.2, 78). Another apparent conflict between morphology and electrophoretic evidence involves *Meroles reticulatus*. Physical features place this as sister taxon to



Aporosaura plus the species assigned to the subgenus *Saurites*, but results of protein electrophoresis are interpreted as indicating that *M. reticulatus* is sister to the whole of *Meroles*. Again, this would involve substantial parallelism in morphology, involving 19 primary and 21 binary characters.

In fact the electrophoretic evidence for relationship may be questioned in as much as the results are based on a measure of genetic distance (Nei, 1971), and no account is taken of which electromorphs are plesiomorphic and which are apomorphic, and therefore likely to indicate genealogical relationship. Furthermore, in cases where a genetic locus shows polymorphism within a species, only the commonest electromorph is considered in calculating genetic distance. Such a course is likely to exaggerate the differences between taxa, since they may actually have electromorphs in common which are discounted in the analysis.

FIG. 3. Relationships within the *Meroles-Aporosaura* clade. Figures indicate the number of synapomorphies supporting each subclade; those in parentheses include derived character states involving some restricted homoplasy, or which are variable in some taxa. Derived character states supporting each node are listed below. As in the figure, parentheses indicate some restricted homoplasy or variability in some taxa. R indicates reversal. Node A. Distinctive features of the whole *Meroles-Aporosaura*. Node B. Fourteen or fifteen ventral scales in longest row across the belly—43.1, 43.2, dorsal scales on upper arm relatively small—50, (number of presacral vertebrae in males often reduced to 23—11.2), azygous shield between prefrontals more frequently absent—20R), (parietal scales often somewhat shortened—31.1V), (pairs of chin shields increase to five—39). Node C. Sternum broad—14, sternal fontanelle very small or absent—16, parietal scales somewhat shortened—31.1, up to 21 ventral body scales in longest row across belly—43.3, size of scales in posterior thoracic region reduced away from mid-line—44.1, four longitudinal scale rows on the digits of forefeet—53.2, only one principal keel on scales beneath digits—54, lateral fringes of pointed scales present on digits of forefeet—55, longitudinal stripes or series of markings absent on mid-back—62.1, kidney with a small anterior lobe and not more than half its length lying anterior to the sacrum—64, hemipenial clavulae strongly conjoined—76.2, (supratemporal scales somewhat reduced in size—34.1), (tympanic scale enlarged round and raised—35.3), (ear opening partly occluded by an antero-dorsal skin fold—37.1), (slight keeling on dorsal scales of upper arm—52.1), (scales on outer tibia just below knee distinctly pointed and keeled—57.1), (longitudinal stripes or series of markings absent from both back and sides—62.1). Node D. Median depression on snout absent—3, pterygoid teeth present—5R, quadrate bone relatively small with a reduced quadrate area and an angled dorso-anterior border—8, 9, transverse processes on proximal tail vertebrae long—17, upper labial scales forming a lateral ridge—21, tympanum deeply recessed—36, 78 or more dorsal scales in a transverse row at mid-body—40.1, more than 22 ventral body scales in the longest row across the belly—43.4, ventral scales in posterior thoracic region very reduced in size right across thorax—44.2, ventral body scales entirely tessellated—45.1, 45.2, length of tail usually less than 1.8 times snout-vent distance—46, dorsal scales on mid-line area of proximal tail small, about the same size as those on the body—48, dorsal scales on upper arm often pointed—51, thoracic fascia absent or much reduced—66, outer connectors of hemipenial armature branched—78, (only three or four pairs of ribs attaching to sternum and xiphisternum—13.1). Node E. Second and third supraocular scales largely or wholly separated from the frontal scale by granules—28, ear opening largely occluded by a strong diagonal skin fold—37.2, scales on outer tibia just below knee sharply pointed and strongly keeled—57.2, female genital sinus shallowly bilobed—80.1. Node F. Only three pairs of ribs attaching to the sternum and xiphisternum—13.2, contact between first loreal scale and upper postnasal scale narrow or absent—23, subocular scale very shallow—25, occipital scale often replaced by several granules—33.2, (anterior edge of ear opening without a denticulated fringe—38R), (more than 90 dorsal scales in a transverse row at mid-body—40.2).

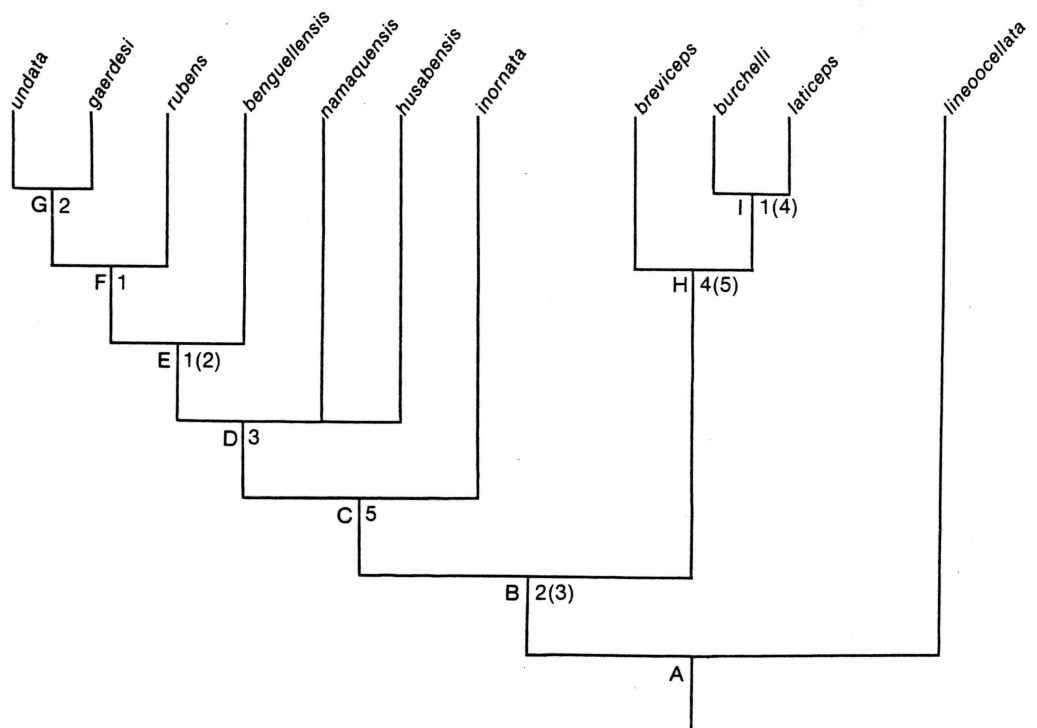
Relationships of the species of *Pedioplanis*

Parsimony analysis was carried out on the 35 binary characters that vary within *Pedioplanis* (after V scores eliminated) and occur in more than one species. The PAUP algorithm used was Branch and Bound (Hendy and Penny, 1982). This produced a tree of 55 steps and a consistency index of 0.636. Characters are plotted on this in Fig. 4. If the polarity of character 11.1 is reversed (which is reasonable as the outgroup information for it is equivocal), there are eighteen characters that have single transformations. This makes an average of two characters supporting each potential node (excluding the first which is based on the common characters of *Pedioplanis*) and a range of 0–4. If another seven characters that show limited homoplasy are included, the figures are 2.8 and 0–5. Compared with the *Meroles-Aporosaura* clade, relationships with *Pedioplanis* are not robust.

In compatibility analysis, the randomness ratio is 0.46 for 35 characters. The 'boil down' procedure produces a set of compatible characters that support the relationships shown in Fig. 4.

Node B, which puts *P. lineoocellata* basal to the other species, is supported by three features. However, one, axillary mite pockets (49), just involves a change in frequency and is paralleled elsewhere, and another, absence of pterygoid teeth (15), is of uncertain polarity as outgroup evidence for this feature is equivocal.

Relationships in the clade involving nodes C to G is based very largely on genital evidence, indeed eleven out of the seventeen characters with unique transformations in *Pedioplanis* are of genital origin. The phylogeny proposed here separates *P. inornata* from the rest of the forms that used to be assigned to *P. undata* (*P. undata*, *P. gaerdesi* and *P. rubens*). This means that the development of an eyelid window (26.1, 26.2) would have been multiple as it also occurs in *P. lineoocellata*. Parallel development of this



feature is not unexpected as such windows have evolved many times in the Lacertidae, arising independently in *Lacerta cappadocica*, *Lacerta perspicillata*, *Holaspis*, *Mesalina*, and in *Ophisops* within which they may also have originated more than once. Such multiple origin also occurs in skinks and teiids (Greer, 1983).

The clade involving nodes H and I is based on skeletal and external features and shows many parallels with *P. lineocellata*. Thus, this species shares characters 4, 28V and 29.2 with *P. laticeps*; 43.2, 45.1 and 50 with *P. laticeps* and *P. burchelli*; and 35.1 with these two and *P. breviceps*.

The relative quality of the morphological phylogenies of the *Meroles-Aporosaura* clade and of *Pedioplanis*

Although the *Meroles-Aporosaura* clade and *Pedioplanis* are successive branches on the main stem of the advanced lacertid clade with little initial differentiation between them, they differ radically in the quality of their internal phylogenies based on morphology (Table 4). In general, the phylogenetic structure of the *Meroles-Aporosaura* clade is much better substantiated than that of *Pedioplanis*. This may well be related to the different kinds of evolutionary history that the two clades have had. The *Meroles-Aporosaura* clade shows steady progression from relatively firm substrates into very stringent habitats based on loose aeolian sand. This shift appears to have elicited many novel morphological features that are necessary for survival in the extreme environments that the group has entered. As a result, there are many derived character states on which relationships can be based. Furthermore, because the stringent habitats entered are not usually occupied by members of outgroups, the new morphological features produced tend not to be duplicated there, so that polarization of characters is usually easy. In contrast, *Pedioplanis* appears to have covered a much smaller range of ecological situations and this may be responsible for the relatively

FIG. 4. Relationships within *Pedioplanis*. Figures indicate the number of synapomorphies supporting each subclade; those in parentheses include derived character states involving some restricted homoplasy, or which are variable in some taxa. Derived character states supporting each node are listed below. As in the figure, parentheses indicate some restricted homoplasy or variability in some taxa. R indicates reversal. Node A. Distinctive features of the whole *Pedioplanis* clade. Node B. Loss of pterygoid teeth—5, outer connectors arising close to mid-line of hemipenial armature and running close together or fusing with each other—79.2, (axillary mite pockets more frequent, found in nearly all individuals—49). Node C. Not more than four rib pairs attaching to sternum and xiphisternum—13.1, unverted hemipenial lobes sac-like or tubular—68, no plicae on hemipenial lobes—71, awns present on tips of hemipenial lobes—72, hemipenial armature somewhat cleft and simplified—75.1. Node D. Hemipenial lobes moderately long—69, hemipenial armature deeply cleft with, at most, very small clavulae—75.2, outer connectors of armature absent—77. Node E. Outer lip of hemipenial lobe sulcus reduced and not free basally—73, (transparent 'window' present in lower eyelid and made up of a variable number of scales—26.1). Node F. Hemipenial lobes very long—69.2. Node G. Unverted hemipenial lobes with a basal kink—70, female genital sinus sometimes very deeply bilobed—80.2. Node H. Ectopterygoid bone exposed as a lateral facet below jugal bone—7, usually 25 presacral vertebrae in males—11.1R, large keeled scales on dorsum of tail do not reach level of vent—47, upper tibial scales unkeeled—58, (tympanic scale absent—35.1). Node I. Premaxilla not markedly embraced by anterior processes of maxillae—1, (number of ventral body scales in the longest row across the belly 14 or 15—43.2), (ventral body scales partly tessellated—45.1), (dorsal scales on upper arm relatively small—50).

Table 3. Number of presacral vertebrae in *Meroles*, *Aporosaura* and *Pedioplanis*. Figures show number of individuals with particular counts; bold figures indicate majority conditions.

	Males				Females			
	23	24	25	26	23	24	25	26
<i>Meroles</i>								
<i>knoxii</i>		10	1			2	6	2
<i>suborbitalis</i>	9	1	1		3	9	1	
<i>reticulatus</i>		4	2			1	11	
<i>ctenodactylus</i>	5	1			1	2		
<i>micropholidotus</i>		2					1	
<i>cuneirostris</i>	3	3				1	5	
<i>Aporosaura</i>								
<i>anchietae</i>	3	3			1	2		
<i>Pedioplanis</i>								
<i>lineoocellata</i>	1	13	2			4	11	2
<i>breviceps</i>			3					
<i>burchelli</i>			5					2
<i>laticeps</i>		2	5	1			2	3
<i>inornata</i>	5	13	2				15	1
<i>husabensis</i>		7	1				13	2
<i>namaquensis</i>	1	14	1	2			12	2
<i>benguellensis</i>	1	5				1	6	
<i>rubens</i>		5				1	6	1
<i>gaerdesi</i>		6	1			2	8	2
<i>undata</i>		23	2				4	

Table 4. Comparison of the parameters of the phylogenies of the *Meroles-Aporosaura* clade and of *Pedioplanis*.

	<i>Meroles-Aporosaura</i> clade	<i>Pedioplanis</i>
Number of binary characters	61	35
Potential number of branching points	5	9
Fully compatible characters		
Total	40	18
Number/nodes		
Average	8	2
Range	4-17	0-4
Characters, including those showing some minor homoplasy		
Total	49	25
Number/nodes		
Average	9.8	2.8
Range	4-18	0-4
Consistency index	0.718	0.636
Randomness ratio (Gould and Underwood, 1986)	0.62	0.46

small size of the suite of morphological characters available for working out its relationships. In fact, if elucidating the phylogeny of *Pedioplanis* were entirely dependent on ecologically related features, the situation would be considerably worse, for much of the reconstruction of relationships is dependent on genital features, variation in which does not seem to be directly related to ecological shifts in the history of groups (Arnold, 1986d). These questions are discussed further elsewhere (Arnold, 1990).

Nomenclature

If the conclusions about the relationships of *Aporosaura anchietae* derived from protein electrophoresis are set aside for the reasons given, there is strong evidence that this form is more closely related to some species of *Meroles* than others, making that genus paraphyletic. It is because of this, that *Aporosaura* is transferred to *Meroles*. The matter is discussed further elsewhere (Arnold, 1989a).

The present analysis confirms Boulenger's conception of the subgenus *Saurites*; the three species, *Meroles cuneirostris*, *M. ctenodactylus* and *M. micropholidotus*, forming a holophyletic group. The subgenus *Meroles* s. str. on the other hand, which is made up of the species *Meroles knoxii*, *M. suborbitalis* and *M. reticulatus* is clearly paraphyletic. Due to this, it is probably best to abandon formal subgenera within the small genus *Meroles*. However, *Saurites* could still be used as an informal infrageneric category, if convenient.

A new synapomorphy for advanced Saharo-Eurasian lacertids

The premaxilla is embraced dorsally by the anterior processes of the maxillae in most lacertids, including primitive members of the family. In *Pedioplanis*, this condition is lost in some forms, with the anterior processes of the maxillae being less extensive (p. 793, Fig. 1). This modification occurs in *P. burchelli* and *P. laticeps*, and forms a synapomorphy for this sister pair. The anterior processes are also reduced in the members of *Eremias*, *Acanthodactylus*, *Mesalina* and *Ophisops*. These appear to form a clade which is found principally in the arid areas of north Africa and of southwest and central Asia. This Saharo-Eurasian clade is characterized by having slender squamosal bones which are separate from the supratemporal process of the parietal bone; these conditions are absent in the xeric adapted Ethiopian lacertid genera that form the immediate outgroups of the Saharo-Eurasian clade. The relationship of the maxilla and premaxilla provides another shared derived character supporting the holophyly of this group. The fact that, apparently, it has appeared separately within *Pedioplanis*, reduces its strength as an indicator of relationship, but such minor homoplasy is widespread in the Lacertidae.

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