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Do Ecological Analogues Assemble their Common Features in the Same Order? An Investigation of Regularities in Evolution, Using Sand-Dwelling Lizards as Examples

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Do ecological analogues assemble their common features in the same order? An investigation of regularities in evolution, using sand-dwelling lizards as examples

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CONTENTS

SUMMARY

Ecological analogues provide an opportunity to assess the regularity of the evolutionary process and some of the factors that control this. By using cladistic methods of phylogeny reconstruction, it is possible to see if two or more stocks have responded in the same way to similar environments, or whether factors such as accident, contingency and previous history have restricted such orderliness.

A method is described for comparing the sequences in which ecological analogues assemble their common traits, including ways of handling incomplete data and of testing the statistical significance of the results. The method is applied to situations that mainly involve lizard groups independently associated with aeolian sand habitats. A case where the lineages concerned are closely related is contrasted with two where this is not so.

The first instance involves an intrafamilial comparison of three members of the lacertid genera *Meroles* and *Acanthodactylus*, which show strong concordance in trait order and great similarity in their independently acquired traits. The other comparisons are of members of different families: *Meroles anchietae* (Lacertidae), *Uma* (Phrynosomatidae), *Phrynocephalus arabicus* (Agamidae) and *Pristurus carteri* (Gekkonidae). Here concordance in trait order is much lower and independently developed traits often show substantial differences in the various groups. The principal reason for the disparity in results appears to be the much longer and more varied separate histories of the lineages involved in the interfamilial comparisons before they finally entered aeolian sand. These historical differences result in particular independently acquired features developing much earlier in some lineages than others and in the development of phylogenetic constraints and proclivities that influence the detailed ways some environmental problems are solved. Finally, no evidence could be found that traits which evolve in similar sequences in different lineages are developmentally interconnected.

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1. INTRODUCTION

Ecological analogues are often allopatric taxa which have independently encountered similar environmental conditions and occupy niches with at least some similar parameters. They usually share independently acquired traits which given them performance advantages in the situations concerned and it is possible to ask: have such shared traits been assembled in the same order? Such similarity in order of trait development in the history of ecological analogues would involve considerable regularity in the evolution of the lineages concerned, for the probability that two taxa have developed n common traits in the same order due to chance is the reciprocal of n factorial ($1/n!$). For example, in the case of three characters it is $1/(3 \times 2 \times 1) = 1/6$. This value falls very rapidly as more traits are considered. Thus, it is $1/120$ for five traits, 3.6288×10^6 for ten and 1.3076×10^{12} for fifteen!

In this paper, the problem of finding whether such order exists is addressed and methods described for doing so, using phylogenies of the taxa concerned and including means of dealing with incomplete data. The methods are then applied to surface-dwelling, diurnal lizard groups independently associated with aeolian sand habitats. A case where the lineages concerned are closely related is contrasted with ones where this is not so and reasons for the differences encountered considered. Instances where shared traits differ in detail and the absence of particular traits in some comparisons are also discussed. Finally the question of whether traits appearing in the evolutionary sequences are essentially independent of each other is briefly addressed.

2. THEORY AND METHOD

(*a*) *Order of trait assembly on single lineages*

If a trait has developed just once in a phylogeny, its likely point of origin can often be established from its distribution among terminal taxa and, in complex cases, computer programmes such as PAUP (Swofford 1990) and MacClade (Maddison & Maddison 1987) can be used to estimate its position most parsimoniously. However, when a number of traits on a lineage develop in sequence, the order in which they appear can only be fully established if each is separated from the others by internal nodes, that is points where side branches originate. Thus, in figure 1*a*, on the lineage leading to taxon C there is an apparent tie between traits 5, 6, 7 and 8, so that it is impossible to establish the order in which they arose. Nevertheless, some statements about order of trait origin can still be made for this lineage. For instance, traits 1, 2, 3 and 4 arose before traits 5, 6, 7 and 8 and all these arose before traits 9, 10, 11 and 12.

It is possible to specify the extent to which trait order can be recognized on a lineage with a particular topology, that is its pattern of internal nodes relative to trait origins. This can be achieved through a simple index: the number of statements that can actually be made about the order of origin of particular traits relative to others (called here the *topological maximum*), divided by the number of statements that could be made if the order were completely specified, this fraction being expressed as a percentage. For a given number of traits, the number of possible order statements that could be made if the trait sequence were completely specified can be found from the formula $n(n-1)/2$, which produces the number of pair-wise comparisons possible for any group of entities. So, when the lineage in figure 1*a* is considered, the maximum number of order statements for 12 traits is 66, but the number that can actually be made for a lineage with this pattern of internal nodes is 48. These are made up as follows: traits 1–4 preceded traits 5–12 (32 statements); traits 5–8 preceded traits 9–12 (16 statements). So the index of recognizable order is $48/66 = 73\%$.

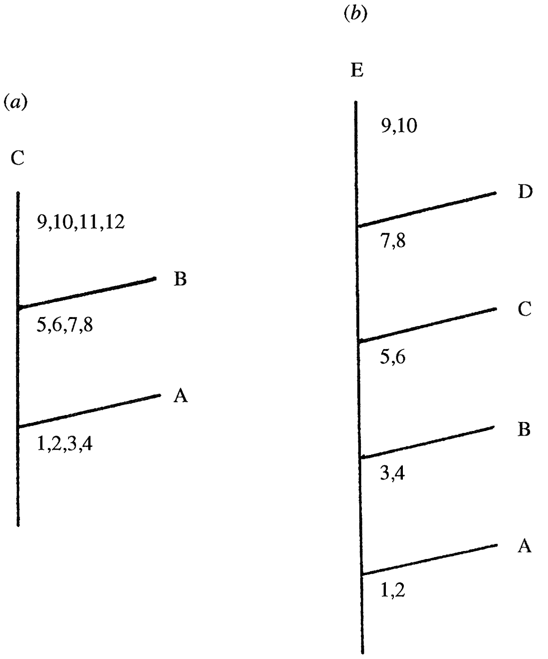

Figure 1. (*a*) A phylogeny of species A, B and C in which not all points of trait origin are separated by internal nodes but nevertheless, 73% of possible order statements on the lineage leading to C can be recognized. (*b*) A phylogeny with relatively few internal nodes may still give much information about order of trait origin. Nine branches would be needed to establish the complete order, but the four regularly distributed branches shown allow 89% of order statements to be recognized, and the remaining internal nodes would only contribute 11%.

The number of order statements that can be made for a lineage depends not only on the number of traits and the number of internal nodes, but also on the position of the latter. In a lineage with 12 trait origins, a single internal node will enable only 11 order statements to be made if it is located peripherally, either after the first or before the last origin in the sequence. However, 36 statements can be made if it is placed medially, between origins 6 and 7. In general, the more regularly internal nodes are distributed among trait origins, the higher the number of statements that can be made.

In real lineages, there are often few internal nodes relative to the number of traits and it might not seem worth making an analysis in such circumstances. However, if internal nodes are added successively to a series of trait origins, the early ones contribute many more order statements than those inserted later. For instance, in figure 1*b*, the maximum number of statements possible for 10 traits is 45 and, to specify all these, nine internal nodes would be necessary, but the four nodes shown specify 40 (89%) of the possible statements and the remaining five nodes would only contribute an additional 5 (11%) statements. Consequently, even on lineages with few internal nodes relative to the number of traits, quite a lot of statements can be made.

(*b*) *Comparing the order of trait assembly on different lineages*

If two independent lineages exhibit a number of shared traits, it is possible to compare them to see if the order of trait development varies. If this order is fully resolved, it is easy to see whether there is variation between two lineages and to assess the proportion of trait comparisons that have the same order. For instance, in figure 2, trait 2 arose before traits 3 and 4 on lineage (*a*), but after these on lineage (*b*). The maximum number of order statements that could be shared by both lineages is 10, but the actual number is 8 (80%), so the number of potentially shared statements that cannot be made is consequently 2 (20%). The proportion of order statements that are shared is affected not only by the number of traits that are differently ordered, but also by the extent to which their positions on the compared lineages differ. Thus, on lineages 2*a* and 2*c*, the origins of trait 2 are less disparate than when 2*a* and 2*b* are compared and the proportion of common statements is higher, in this case 90%.

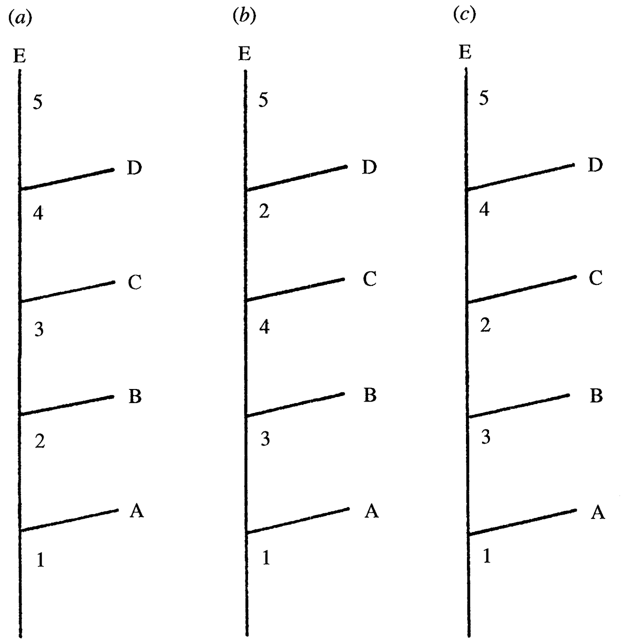

Figure 2. Phylogenies with different orders of trait origin; see text.

When real lineages are compared, the order of the origins of traits is often only partly specified, so that there are apparent ties between them and internal nodes frequently separate different numbers of trait origins and also vary in number themselves. In some cases, it is possible to arrange the shared traits in more or less the same order on the compared lineages (figure 3), which does not mean they necessarily evolved in that overall order, merely that the restricted number of internal nodes only allows a proportion of shared order statements to be confirmed and prevents any differences in order being recognized. When internal nodes are in the same position relative to the shared trait origins on each lineage, common order statements generated by such matched nodes are obvious. Thus, in figure 3, it is clear that all order statements involving traits 1–6 preceding traits 7–10 are common, as are ones involving 7–9 preceding 10. Staggered internal nodes, which are positioned differently on each lineage, may then be considered. Here shared order statements can be recognized involving traits arising before the level of the node on one lineage and after a later node on the

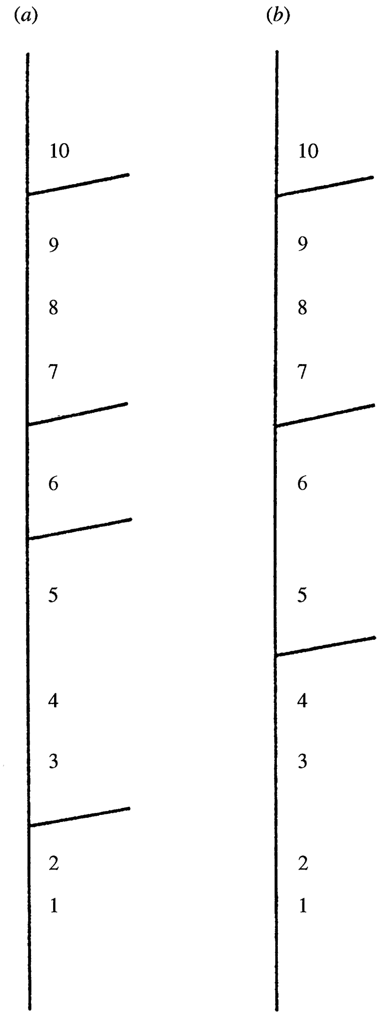

Figure 3. Compared phylogenies with restricted numbers of internal nodes in which common traits may be aranged in more or less the same order.

other, although the traits between the nodes will not have their internal order specified.

In lineage 3*a*: traits 1 2 preceded 3 4 5 6;
in lineage 3*b*: traits 1 2 3 4 preceded 5 6.

The two lineages thus share statements that 1 and 2 preceded 5 and 6. If there are more than just two internal nodes staggered relative to each other, additional shared statements may be recognizable. Thus the pattern of nodes in figure 3 also allows the shared statements 1–4 preceded 6 to be made, of which the statements 3, 4 preceded 6 have not been recognized before. However, staggered pairs of nodes that span matched pairs, or involve one member of the latter, do not add further shared statements.

If trait origins cannot be listed in more or less the same notional order on the lineages, for instance as in figures 2 and 4, they must be counted individually. In figures 4*a* and 4*b*, eight traits are shared so, if fully resolved there would be 28 order statements. The maximum number of shared order statements that could be recognized, with the patterns of internal nodes present on the lineages concerned (called here the *shared topological maximum*), can be worked out by putting the same sequence of traits on each lineage (the necessary modifications to the lineage in 4*b* are shown in 4*c*) and using the method for recognizing shared order statements described above. In the present case, this procedure shows there could be 20 shared order statements but, in fact, there are only 14 when 4*a* and 4*b* are compared: 1 preceded 3, 4, 6, 7 and 8; 2 preceded 4, 6, 7 and 8; 3 preceded 7; 4 preceded 7*; 5 preceded 6*, 7* and 8. Eleven of these statements are the same as ones that would be detected if trait origins on lineage (*b*) could be arranged in the same notional order as on lineage (*a*), but differences in relative position of traits create new possibilities and three extra statements are present; these are marked by asterisks.

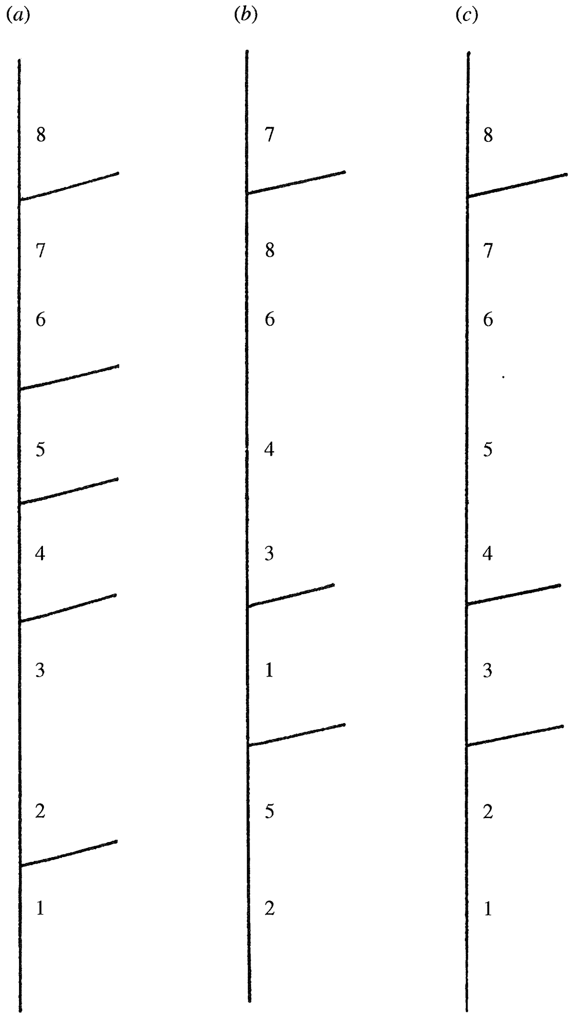

Figure 4. Phylogenies with different orders of trait origin; see text.

Pairs of traits that are ordered differently on the two lineages can also be counted. Thus the traits in the following order statements on lineage 4*b* are differently ordered on lineage 4*a*: 2 preceded 1; 5 preceded 1, 3 and 4. It will be observed that not all possible common statements for compared lineages with these topologies are recognizable in the present case as either shared or differently ordered, for two remain undetermined. This is because the branching pattern does not allow them to be confirmed, given the different positions of the relevant trait origins on each lineage. Thus 2 preceded 3 and 6 preceded 7 on lineage 4*b*, but the order of the traits in these pairs cannot be confirmed on lineage 4*a*.

It should be emphasized that the shared topological maximum only applies to the maximum number of shared order statements recognizable and excludes those that are differently ordered. In fact, the total number of order statements can sometimes exceed the shared topological maximum. Thus, in figure 5, lineages (*a*) and (*b*) are compared. The shared topological maximum can be found by putting the same sequence of traits on both lineages (necessary modifications to 5*b* are shown in 5*c*) and comparing

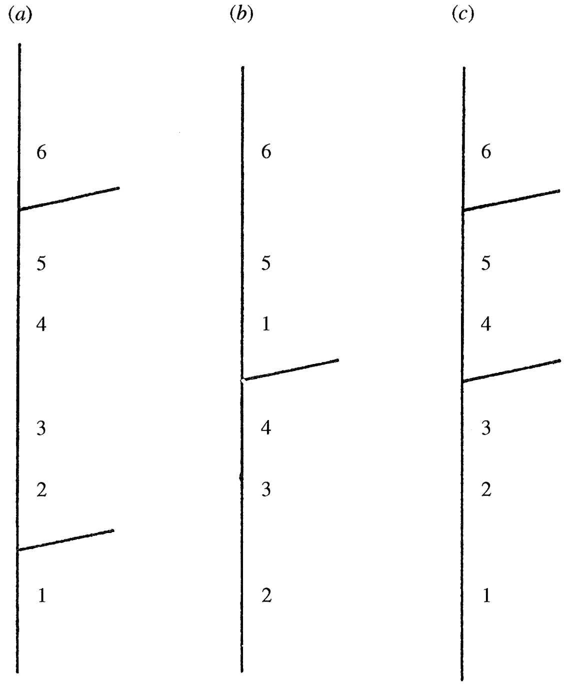

Figure 5. Total number of order statements relative to the shared topological maximum; see text.

them: common order statements are then 1 preceded 4, 5 and 6; 2 and 3 preceded 6, giving a total of five statements. However, when 5*a* and 5*b* are compared directly, the number of order statements that can be recognized as shared is three, namely 2–4 preceded 6, and the number of trait pairs recognized as differently ordered is also three, involving 2–4 and 1. Consequently there are actually 6 discernable order statements compared with a shared topological maximum of 5.

If two lineages have the same number of internal nodes which separate the same number of trait origins in the same proportions, then the shared topological maximum is the same as the topological maximum for either lineage, but when there are differences in the position of all internal nodes, then the shared topological maximum will be less than the topological maxima for either lineage. If there is a difference in number of internal nodes, the shared topological maximum cannot exceed the topological maximum for the lineage with fewer and will only reach it if all the internal nodes on this lineage are matched by some of those on the other one.

Although no certain assessments of unknown order statements can be made, node positions will place limits on what these may be. For instance, in figure 1*a*, where 48 of the 66 possible order statements can be recognized, internal nodes restrict the unknown ones to three groups of six involving traits 1–4, 5–8 and 9–12 respectively. Some idea of the overall extent of shared order might possibly be gained by extrapolation from known statements. As the origins of traits may well be independent of speciation events and the consequent development of branches and their associated internal nodes, the latter could be regarded as providing a more or less random sample of order statements. If this were so, commonality of order statements that the nodes allow to be recognized would suggest that unknown order statements were also likely to be shared. Such a conclusion might be valid if there were enough nodes and they were regularly distributed throughout the length of a considered lineage. However, the situation is likely to be potentially misleading when nodes are concentrated towards one extremity. Known order statements can only give an impression of the overall degree of order for the parts of the lineage in which they occur and are only likely to provide a reasonable estimate for the whole lineage if they are evenly distributed throughout it.

(*c*) *Parameters and indexes for compared lineages*

It is helpful to recognize the following parameters for compared lineages.

1. *a*: the maximum number of shared order statements possible, if trait order were fully resolved: $n(n-1)/2$.
2. *b*: the *shared topological maximum*. The maximum number of order statements that could be recognized as shared, given the topologies of the compared lineages.
3. *c*: the number of order statements actually recognized as shared.
4. *d*: the number of pairs of traits recognized as being differently ordered on the two lineages.

These parameters can usefully be combined into three indexes.

1. $b/a \times 100$: named here the *index of recognizable shared order*. This is the maximum proportion of potential order statements that could be recognized as shared, given the topologies of the two lineages, expressed as a percentage.
2. $c-d$: the difference between the number of order statements actually recognized as shared and pairs of traits recognized as being differently ordered. This is equivalent to the numerator, S, in Kendall's coefficient of correlation, tau (τ) (Kendall 1938), where $\tau = S/0.5N(N-1)$, where N = the number of objects or individuals ranked.
3. $c-d/b$: named here the *coefficient of assembly order*. This is the difference between the number of shared order statements and that of differently ordered pairs of traits, expressed as a proportion of the topological maximum. A score of +1 would indicate that all investigatable order statements are shared; −1 that all investigatable order statements are differently ordered; and 0 that the numbers were equal, so there is no positive or negative correlation.

The coefficient of assembly order is superior in the present context to a correlation coefficient such as Kendall's τ. This is because tau is designed to deal with cases where the order (ranking) of the components in each compared series is largely resolved so that ties are uncommon, something that is often untrue of lineages. The numerator in τ is the geometrical mean of the number of possible order statements in each of the two compared series. But as the number of order statements in the compared lineage with fewer places an upper limit on the possible number of shared statements there can be, this procedure will exaggerate the latter.

(*d*) *Testing the significance of similarities in order of trait assembly* (see Appendix)

As correlation coefficients, such as Kendall's τ, may not be suitable for many comparisons of the order of trait assembly, standard approximate methods of calculating probability based on these may also not be appropriate. However, an exact test can be carried out using the S statistics in Kendall's τ.

The traits in one lineage were numbered in their natural order and held fixed. Then all possible orders of traits were considered for the other lineage. By taking into account the observed pattern of internal nodes and therefore of ties, it was then possible to work out the number of concordant and discordant trait pairs and so determine S when each of the possible sequences for the second lineage were compared with the first.

The probability of the concordance between the two compared lineages being due to chance can then be assessed in a one sided test by counting all the possible sequences that attain the value found in the two lineages actually compared initially, or a higher one, and dividing this number by the total number of possible sequences for the second lineage.

The above operation, which can be carried out using a relatively small computer program, was applied to the various groups discussed later. These were also subjected to a standard test of significance (Siegel 1956), based on the Kendall rank correlation coefficient, to see whether, in spite of uncertainties about its appropriateness, it might in fact give similar results to the exact test in practice and so avoid the need of calculating the latter. In fact, it gave substantially different results.

3. USING THE METHOD: ORDER OF TRAIT ASSEMBLY IN DIFFERENT SAND-DWELLING LIZARDS

(*a*) *Lizard ecological analogues in aeolian sand habitats*

Ecological analogues vary in their development in terms of the number of shared independently derived traits they possess, how marked these are and how closely the traits resemble each other. In general, shared traits tend to be best developed in taxa which have entered harsh coercive environments that involve a range of severe survival problems, where existence appears to depend on solving these successfully. The performance advantages of shared traits are often easiest to comprehend when the survival problems involved are mechanical ones. Not only are these often amenable to simple analysis but the environmental situations responsible for them tend to have strong physical characteristics that are likely to produce very similar selective pressures in different geographical areas. This means that the performance of different allopatric taxa can be more directly compared. Ecological analogues are often best developed where the habitat concerned is the termination of a continuum of increasingly severe environments through which the lineages of the taxa concerned have passed. In this situation a clear series of derived traits is often produced which has the additional benefit of allowing a phylogeny to be inferred that is at least superficially robust (Arnold 1990).

One environment with these characteristics is open, arid, aeolian (wind-blown) sand, a medium which provides many physical problems of survival. At least eight diurnal, surface-dwelling lizard clades appear to have independently entered this and, in most cases, there is evidence that they passed along an environmental continuum from hard ground through firm sand habitats to reach it. The groups include *Uma* (Phrynosomatidae; southwestern United States and adjoining Mexico), some *Leiocephalus* (Tropiduridae; coastal South America), many *Phrynocephalus* (Agamidae; central and southwestern Asia), *Meroles* (Lacertidae; southwestern Africa), *Acanthodactylus* (Lacertidae; North Africa and southwest Asia); some *Eremias* (Lacertidae; central and southwest Asia); *Scincus* (Scincidae; north Africa and southwest Asia), *Angolosaurus* (Cordylidae; southwest Africa). Sources of information on the sand-dwelling habits of these forms include the following. *Uma*, Stebbins (1944), Pough (1970), Pough *et al.* (1978); *Phrynocephalus*, Minton (1966), Bannikov *et al.* (1977), Arnold (1984); *Meroles*, sources summarized elsewhere (Arnold 1990, 1994*a*); *Acanthodactylus*, Minton (1966), Arnold (1983); *Eremias*, Minton (1967), Bannikov *et al.* (1977); *Scincus*, Arnold (1984); *Angolosaurus*, Mitchell *et al.* (1987).

Note on nomenclature. Frost & Etheridge (1989) suggest the names Phrynosomatidae and Tropiduridae for clades which were previously assigned to the Iguanidae and known informally as sceloporines and tropidurines. This course is followed here but the authors' proposal to transfer lizards previously placed in the Agamidae to the Chamaeleonidae is not.

The sand-dwelling forms listed above share at least some of the following anatomical and behavioural traits that appear to be advantageous in the stringent environment in which these lizards exist. All are more or less strictly ground-dwelling with often relatively short and broad bodies and toes that are expanded laterally by fringes of pointed scales which increase efficiency in traversing loose sand (Carothers 1986). Various features exist that exclude sand from body orifices, an important function as sand tends to enter easily, is abrasive and, when in contact with moist surfaces, removes water by capillary action. Included here are valvular nostrils, fringes of pointed scales on the eyelids, a countersunk jaw and often some closure of the ear orifice. The nasal vestibule is frequently elongated, protecting the moist primary nasal chamber from the dry external environment and probably also helping to prevent the entry of sand.

Feeding is often by sit-and-wait foraging, a technique that is common in open habitats where many potential prey items tend to be infrequent and mobile. Forms that hunt actively to some extent often have pointed snouts that are used to probe the sand for prey (for instance some *Acanthodactylus* and *Meroles reticulatus*). Because it is difficult to construct permanent burrows in many aeolian substrates, a number of taxa avoid predators by burying themselves rapidly directly in the sand (Arnold 1994*a*). In association with this behaviour, the head may be streamlined and the upper lip is often keeled, which aids penetration. Respiratory movement is predominantly at the sides of the thorax in most lizards but, if they were submerged in loose sand, this would tend to fall into the lateral gaps created by exhalation, preventing further breathing. This problem is avoided in many specialized aeolian sand lizards because respiratory movements occur on the ventral surface of the thorax. Various anatomical features are connected with this (Pough 1969), often including the presence of ventrolateral ridges that prevent sand filtering laterally into the space where breathing takes place. Crypsis on more or less uniform aeolian sand tends to be achieved by uniform or dappled dorsal colouring. A number of sand lizards also signal inter- and intraspecifically with their tails (for example, *Uma*, *Meroles* and *Phrynocephalus*).

(*b*) ***Comparisons within a lizard family:* Meroles *and* Acanthodactylus *(Lacertidae)***

Meroles and *Acanthodactylus* are both advanced genera in the clade made up of Ethiopian lacertids and Saharo-Eurasian forms from arid areas (Arnold 1989). They share a large number of derived features inherited from a common ancestor and are separated by very few internal nodes in the phylogeny of their family. *Acanthodactylus* is somewhat more apomorphic than *Meroles* but has few additional derived traits (Arnold 1989), so the ancestors of each genus must have been very similar when they branched off the main stem of the lacertid phylogeny. *Meroles* has an extremely robust morphological phylogeny (Arnold 1991), but that of *Acanthodactylus* is less so (Arnold 1983). One reason for this is that the latter genus appears to have two main clades with considerable acquisition of similar non-ancestral conditions in both. However, genital features tend to confirm the separateness of these two clades, one mainly in the Saharan area and the other in southwestern Asia.

The taxa compared are *Meroles reticulatus*, *Acanthodactylus longipes* and *A. schmidti*; the last two are respectively representatives of the western and eastern clades of *Acanthodactylus*. All these forms are found on soft aeolian sand in relatively open situations with sparse vegetation. Shared traits are listed in table 1. Of these, 3 is associated with increase in eye size, a trend common in lizard groups occupying increasingly open environments; 4, 5 and 6 are functionally related to the problems of locomotion on substrates with rather soft surfaces; 10 with probing for prey in more yielding aeolian sand; 12 and 13 with travelling on this medium, and 14 with crypsis on largely bare sand environments. Performance advantages, if any, conferred by the remaining traits are not apparent, but increase in the number of longitudinal rows of ventral scales (8, 9 and 15) and their tessellation (11) is often associated with arid conditions in lacertid lizards (as well as in *Acanthodactylus* and *Meroles*, this trend occurs in *Eremias*, *Ichnotropis* and *Pedioplanis*). Phylogenies for the compared species are shown in figure 6 and on these are marked likely points of entry into sandy habitats in general and into aeolian sand. These points were decided on the basis of the habits of individual species and the development of characters giving performance advantages in these habitats.

Three pairwise comparisons are possible which are discussed in turn. The order statements listed as contributing to the shared topological maximum are based on putting the same consecutive sequence of traits on both of the compared topologies.

Table 1. *Shared traits of* Meroles *and* Acanthodactylus

1. Scleral ossicle 14 peripherally reduced
2. Occipital scale reduced or absent
3. Subocular scale usually separated from lip
4. Three longitudinal rows of scales on fingers
5. Three longitudinal rows of scales on toes
6. Lateral fringes of pointed scales on toes
7. Usually five or more upper labial scales in front of eye
8. Ventral scales in 12 or more longitudinal rows
9. Ventral scales often in 14 longitudinal rows
10. Snout very pointed
11. Ventral scales tessellated
12. Four longitudinal rows of scales on fingers
13. Lateral fringes of pointed scales on fingers
14. Young often or always without longitudinal stripes
15. Ventral scales often in 16 or more longitudinal rows

(i) *Comparison of* M. reticulatus *and* A. longipes

Fifteen traits are shared by the two clades. The maximum number of common order statements possible is consequently $15(15-1)/2=105$. The shared topological maximum is 57, made up as follows: 1–8 preceded 9–15; 9 preceded 15. The number of common order statements that can actually be recognized matches this figure and is made up in the same way; no differently ordered trait pairs can be detected. The coefficient of assembly order is 1.0, and the probability that this degree of concordance is due to chance is 0.000133. In the statistical test 45 045 possible trait sequences were recognized of which only 5 showed the same or more order than the studied case.

(ii) *Comparison of* M. reticulatus *and* A. schmidti

Again fifteen traits are shared by the two clades and the maximum number of common order statements possible is 105. The shared topological maximum is again 57, made up as follows: 1–7 preceded 9–15; 8–9 preceded 12–15. The number of common order statements that can actually be recognized is 55, made up as follows: 1–7 preceded 9–15; 8 preceded 9, 13–15; 9 preceded 14–15. The number of trait pairs recognized as differently ordered in the two phylogenies is three, namely 10–12 and 9, so overall more order statements can be recognized than the shared topological maximum. The coefficient of assembly order is 0.87, and the probability that this degree of concordance is due to chance is 0.000577. As in the previous example, 45 045 possible trait sequences were recognized in the statistical test of which 25 showed the same or more order than the studied case.

(iii) *Comparison of* A. longipes *and* A. schmidti

Here, traits 1–6 are inherited from a common ancestor, so only traits 7–15 can be compared. The maximum number of common order statements possible is therefore $9(9-1)/2=36$. The shared topological maximum is 16, made up as follows: 7 preceded 9–15; 8 preceded 12–15; 9–11 preceded 15; 12 and 13 preceded 15. The number of common order statements that can actually be recognized matches this figure and is made up as follows 7 preceded 9–15; 8 preceded 9, 13–15; 10–12 preceded 15; 9 and 13 preceded 15; no differently ordered trait pairs can be detected. Traits 10, 11 and 12 preceded 9 in *A. schmidti*, but this does not imply that the pattern is necessarily unmatched in *A. longipes*, because here the order of traits 9–14 is unknown. The coefficient of assembly order in this comparison is 1.0, and the probability that this degree of concordance is due to chance is 0.03. In the statistical test 252 possible trait sequences were recognized of which only 7 showed the same or more order than the studied case.

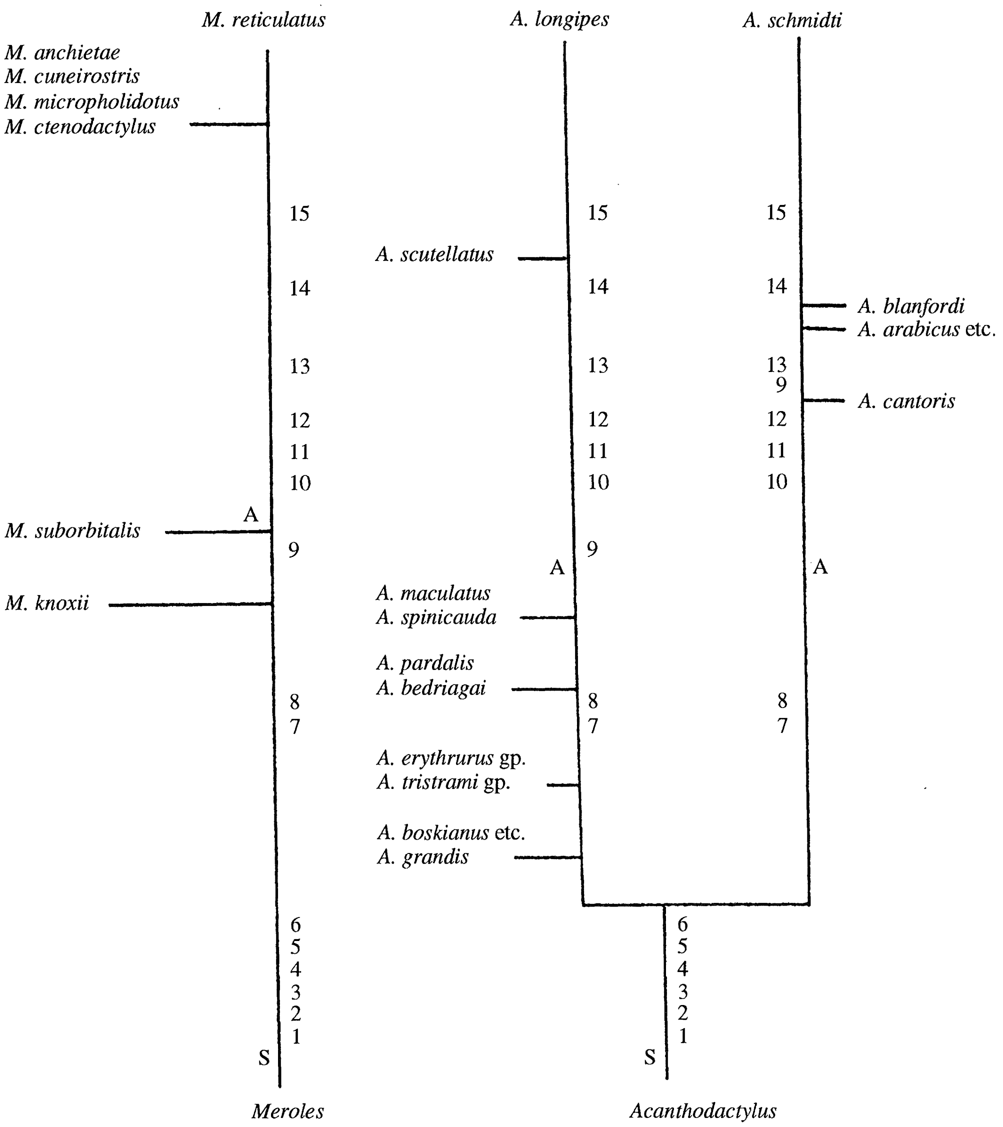

Figure 6. Phylogenies for three sand-dwelling members of the Lacertidae: *Meroles reticulatus*, *Acanthodactylus longipes* and *A. schmidti*. Figures refer to traits (see table 1). Likely points of entry into sandy habitats (S) and aeolian sand (A) are marked.

(*c*) *Comparisons between lizard families:* Meroles *(Lacertidae),* Uma *(Phrynosomatidae) and* Phrynocephalus *(Agamidae)*

Members of three families are compared that share similar aeolian sand habitats and a range of similar traits (table 2), although about half these are behavioural rather than morphological as in the previous example. The taxa are *Meroles anchietae* of southwest Africa (Lacertidae), the genus *Uma* of the southwestern U.S.A. and adjoining Mexico (Phrynosomatidae) and *Phrynocephalus arabicus* of Arabia (Agamidae). All these are found in areas of aeolian sand where they tend to be substantially sit-and-wait hunters and avoid predators by burying themselves rapidly in the sand. Phylogenies of these three taxa are shown in figure 7, together with likely points of entry into sandy habitats in general and into aeolian sand. Sources of the phylogenies are as follows: *Meroles* (Arnold 1991), *Uma* (Etheridge & De Queiroz 1988; De Queiroz 1992), *Phrynocephalus arabicus* (Arnold 1992, personal observations). In the latter instance, the phylogeny differs from that suggested by Moody (1980), but the sequence of traits would be more or less the same whichever hypothesis of relationship was used.

Table 2. *Traits shared by some or all of the following taxa:* Meroles anchietae, Phrynocephalus arabicus *and* Pristurus carteri

1. More or less consistently ground-dwelling
2. Nasal vestibule elongated
3. Nasal valve present
4. Lateral fringes of pointed scales on toes
5. Predominantly sit-and-wait foraging
6. Able to escape predators by rapidly burying in loose sand
7. Capable of breathing by vertical movements of ventral surface of thorax
8. Upper labial scales forming a lateral ridge
9. Tail lifted and moved as a signal (either intra- or interspecific); often with dark bars beneath
10. Tail autotomy reduced

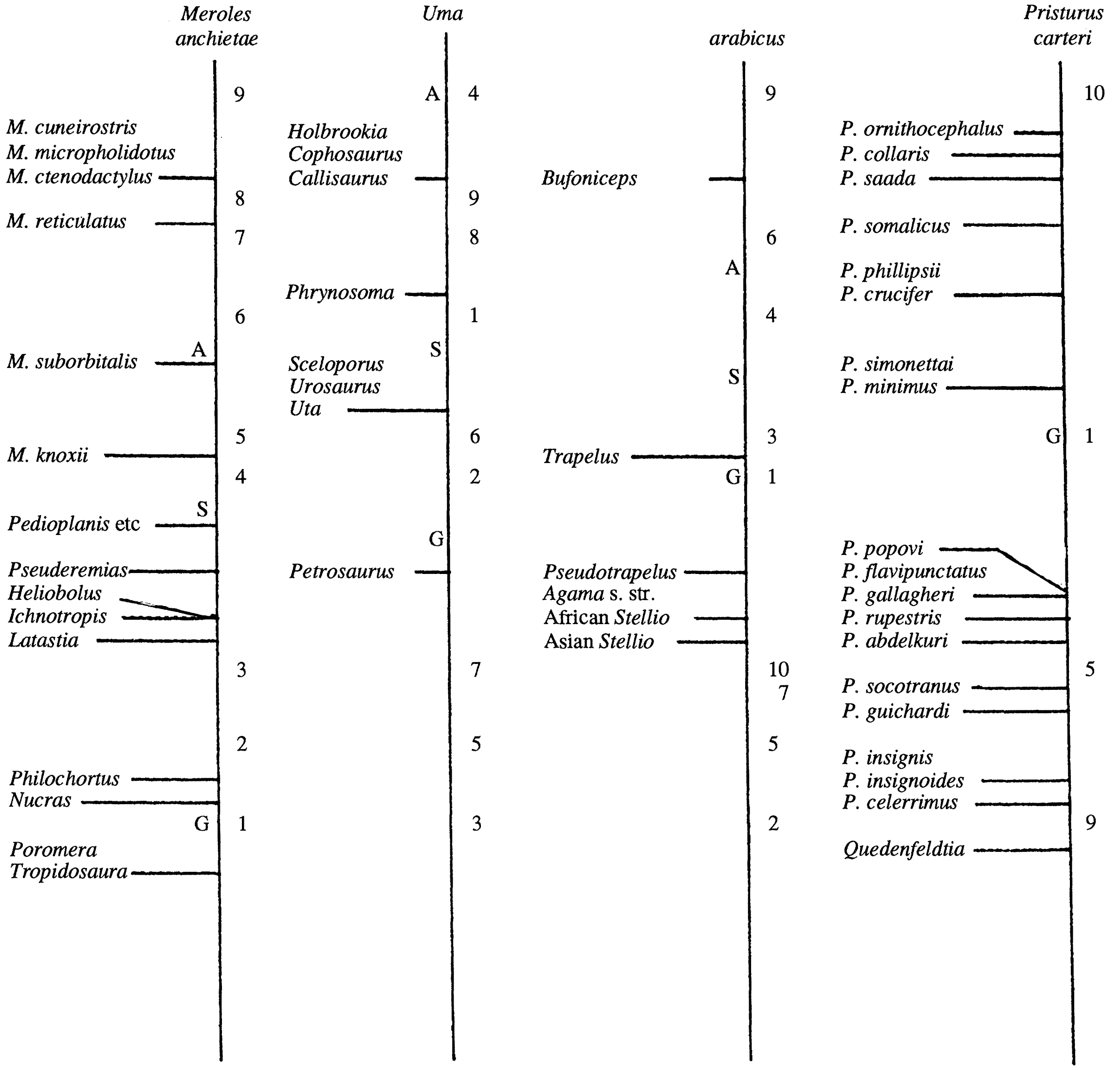

Figure 7. Phylogenies for three sand-dwelling taxa from different families, *Meroles anchietae* (Lacertidae), *Uma* (Iguanidae) and *Phrynocephalus arabicus* (Agamidae); also included is the ground-dwelling diurnal gecko, *Pristurus carteri*. Figures refer to traits (see table 2). Likely points of origin of exclusively ground-dwelling habits descent to ground (G), entry into sandy habitats (S) and aeolian sand (A) are marked.

Three pairwise comparisons are possible which are discussed in turn. The order statements listed as contributing to the shared topological maximum are based on putting the same sequence of traits on both of the compared topologies.

(i) *Comparison of* Meroles anchietae *and* Uma

Nine traits are shared by the two clades (both lack trait 10). The maximum number of order statements possible is consequently $9(9-1)/2 = 36$. The shared topological maximum is 30, made up as follows: 1–3 preceded 4–9; 4–5 preceded 6–9; 6–8 preceded 9; 6 preceded 8. The number of common order statements that can actually be recognized is 17: 1 preceded 4, 8 and 9; 2 preceded 4, 8 and 9; 3 preceded 4, 6, 8 and 9; 5 preceded 6, 8 and 9; 6 preceded 8 and 9; 7 preceded 8 and 9. The number of trait pairs recognized as differently ordered is 12: 2 and 1; 3 and 1; 5 and 1, 2, 4; 6 and 1, 4; 7 and 1, 2, 4; 8 and 4; 9 and 4. The coefficient of assembly order is 0.17, and the probability that this degree of concordance is due to chance is 0.33.

(ii) *Comparison of* Meroles anchietae *and* Phrynocephalus arabicus

Eight traits are shared by the two clades (*Meroles* lacks trait 10 and *Phrynocephalus arabicus* trait 8). The maximum number of order statements possible is consequently $8(8-1)/2 = 28$. The shared topological maximum is 22, made up as follows (on the basis of their both having the same arrangement of traits): 1–3 preceded 4–7 and 9; 4 preceded 5–7 and 9; 5–7 preceded 9. The number of common order statements that can actually be recognized is 13, made up as follows: 1 preceded 3, 4, 6 and 9; 2 preceded 4, 6 and 9; 3 preceded 9; 4 preceded 9; 5 preceded 6 and 9; 6 preceded 9; 7 preceded 9. The number of trait pairs recognized as differently ordered is 7: 2 and 1; 5 and 1, 3, 4; 7 and 1, 3, 4. The coefficient of assembly order is 0.27, and the probability that this degree of concordance is due to chance is 0.246.

(iii) *Comparison of* Uma *and* Phrynocephalus arabicus

Eight traits are shared by the two clades (*Uma* lacks

Table 3. *Comparisons of order of trait assembly within a family: the lacertid lizards.* Meroles reticulatus, Acanthodactylus longipes *and* A. schmidti

	M. retic. *A. long.*	*M. retic.* *A. schmi.*	*A. long.* *A. schmi.*
number of traits compared (n)	15	15	9
order statements			
a: maximum number recognizable as shared if trait order fully resolved: $n(n-1)/2$	105	105	36
b: maximum number recognizable as shared for given topologies (shared topological maximum)	57	57	16
proportion recognizable as shared (index of recognizable shared order): $b/a \times 100$	54%	54%	44%
c: number actually recognized as shared	57	55	16
d: number recognized as different	0	3	0
e: difference (Kendall's S): $c-d$	57	52	16
coefficient of assembly order: e/b	1.0	0.91	1.0
probability of shared order being due to chance	0.000133	0.000577	0.03

trait 10 and *Phrynocephalus arabicus* trait 8). The maximum number of order statements possible is consequently 28. The shared topological maximum is 21. The number of common order statements that can actually be recognized is 15, made up as follows: 1 preceded 4 and 9; 2 preceded 1, 4 and 9; 3 preceded 9; 5 preceded 1, 4, 6 and 9; 6 preceded 9; 7 preceded 1, 4, 6 and 9. The number of trait pairs recognized as differently ordered is 4: 3 and 1, 2; 6 and 1; 9 and 4. The coefficient of assembly order is 0.52 and the probability that this degree of concordance is due to chance is 0.23.

(*d*) *Comparisons between lizard families:* Pristurus *(Gekkonidae) and* Phrynocephalus arabicus *(Agamidae)*

Pristurus carteri is a diurnal, ground-dwelling gecko found in arid areas of southern Arabia (Arnold 1986). Although it does not occur on aeolian sand and possess the wider range of independently acquired traits often associated with this habitat, it has considerable ecological resemblance to *Phrynocephalus arabicus* (Arnold 1980). Like this taxon it is not especially fast, and is an open ground (1), sit-and-wait forager (5) that uses tail signalling (9) and has reduced tail autotomy (10). Its phylogeny is reported in detail elsewhere (Arnold 1994*c*) and is compared with that of *Phrynocephalus arabicus* in figure 7. The two taxa share four of the traits listed above. The maximum number of common order statements possible is consequently $4(4-1)/2=6$. The shared topological maximum is 5. The number of common order statements that can actually be recognized is just 1: 5 preceded 1. The number of trait pairs that can be recognized as differently ordered is 4: 9 and 1, 5; 10 and 1, 9. The coefficient of assembly order is −0.6, and the probability that this degree of concordance is due to chance is 0.92.

(*e*) *Summary of differences between comparisons of trait order made within and between families*

Parameters, indexes and probabilities of significance for the cases discussed above are summarized in tables 3 and 4. In the three comparisons made within the Lacertidae, the index of recognizable shared order is only around half that possible (44% to 54%), but coefficients of assembly order are high, ranging from 0.91 to 1.00. In the two cases where 15 traits were considered, the exact probabilities of the high number of common order statements being due to chance are

Table 4. *Comparisons of order of trait assembly between families:* Meroles anchietae *(Lacertidae),* Uma *(Iguanidae),* Phrynocephalus arabicus *(Agamidae),* Pristurus carteri *(Gekkonidae)*

	M. anchi. *Uma*	*M. anchi.* *Ph. arab.*	*Uma* *Ph. arab.*	*P. cart.* *Ph. arab.*
number of traits compared (n)	9	8	8	4
order statements				
a: maximum number recognizable as shared if trait order fully resolved: $n(n-1)/2$	36	28	28	6
b: maximum number recognizable as shared for given topologies (shared topological maximum)	30	22	21	5
proportion recognizable as shared (index of recognizable shared order): $b/a \times 100$	83%	79%	75%	83%
c: number recognized as common	17	13	15	1
d: number recognized as different	12	7	4	4
e: difference (Kendall's S): $c-d$	5	6	11	−3
coefficient of assembly order: e/b	0.17	0.27	0.52	−0.60
probability of shared order being due to chance	0.33	0.246	0.23	0.92

very low, in both cases less than 0.0006, and even in the third instance where only nine traits could be considered, the probability is 0.03 and so significant at the $p = 0.05$ level.

When more distantly related forms in different families were compared, the index of recognizable shared order is higher than in comparisons within the Lacertidae (varying from 75% to 83%), but the proportion of order statements actually shared is smaller. Coefficients of assembly order in the interfamilial comparisons of taxa found in aeolian sand are consequently lower, varying from 0.17 to 0.52. When *Phrynocephalus arabicus* was compared with the gecko *Pristurus carteri* for the four traits they share, there was a negative correlation giving a coefficient of assembly order of −0.6. In all interfamilial comparisons the probabilities of the number of common order statements being due to chance is relatively high, varying from 0.25 to 0.95.

4. DISCUSSION

Figures in parentheses are numbers assigned to traits in tables 1 and 2.

(*a*) *Differences in trait order*

As summarized above, the degree of concordance of trait origin varies considerably, with high levels of agreement in the comparisons made within the Lacertidae and substantially lower ones when members of different families are compared. When likely times of entry into sandy habitats are plotted on phylogenies, it is apparent that the independently derived traits in the comparisons among lacertids all appeared at about this time or afterwards. In contrast, when comparisons of sand dwellers from different families are made, some features that arose in association with sandy habitats in certain taxa developed much earlier in the histories of others and often in different environments. Thus, although toe fringes (4) always developed late, in association with terminal occupation of aeolian sand situations, tail signalling (9) appeared rather earlier in the *Uma* lineage than in the others. Similarly, vertical breathing movement (7), which appeared late in *Meroles* was one of the earliest features to occur in the *Uma* and *Phrynocephalus* clades.

The same phenomenon is observable in the comparison between *Phrynocephalus arabicus* and *Pristurus carteri*. Here tail signalling movements (9) have developed in association with sand in the former, whereas in *Pristurus* they appeared when the ancestors of the ground dwelling *P. carteri* were climbers on rock faces (Arnold 1993). In contrast, lack of intravertebral tail autotomy has a very long history in the *Phrynocephalus arabicus* lineage, but occurs very late in that leading to *Pristurus carteri* (Arnold 1993).

Why should order of trait assembly in ecological analogues within the Lacertidae be much more similar than when members of different families are compared? The reasons for this appear to be substantially historical. The three groups of lacertids found in aeolian sand and considered here are only likely to have separated from each other in the Neogene (Arnold 1989) and perhaps only within the last ten million years or so. Tracing character change on a phylogeny of the Lacertidae (Arnold 1989) indicates that, at the points where the ancestors of the studied taxa entered sandy habitats, they had developed relatively little morphological differentiation and were consequently generally very similar to each other. In this situation, there would be little opportunity for traits ultimately giving performance advantages in sandy habitats to develop in only one or two of the three taxa after these separated from each other but before they entered these environments. Consequently such features which include exaptations would be unlikely to disturb the common order of trait origins. Any traits antedating separation would have been present in the common ancestor of all three taxa and therefore not included in the comparison of independently acquired characters.

Again, plotting habitat information on the phylogenies indicates that the three lacertid taxa have had similar histories. The ancestors of extant *Acanthodactylus* and *Meroles* were likely to have been ground-dwellers on hard substrates. Subsequently, they each moved into firm sand habitats, where the two main clades of *Acanthodactylus* separated, and then later still on to soft, aeolian sand.

If, as seems likely, overall morphological resemblance is associated with similar evolutionary potential, the close similarity in evolution of these three forms may result from organisms with comparable propensities being exposed to a similar chronological sequence of environments that exerted similar selective forces. The fact that the changes elicited at each stage in the process resembled each other would mean that the separate lineages continued to be alike, so that similarity in evolutionary potential would probably also be maintained. Certainly the actual sequence of character development supports the hypothesis of parallel adaptation to a series of environments, since features identified as giving performance advantages respectively in dry open habitats, relatively firm sand and aeolian sand (p. 283) have developed in that sequence.

The differences in order of trait assembly between the sand-dwelling taxa from different families may also reflect their overall history. The fossil record indicates that groups to which they belong (Scincomorpha including the Lacertidae, 'Iguanidae' and Acrodonta including Agamidae) have been separate since at least the Cretaceous period (Estes 1983). Indeed, the lineage from which lacertids are descended probably diverged from the ancestors of iguanids and agamids much earlier, for in the phylogeny of lizards, geckoes separated from the ancestors of scincomorphs at a later time than this divergence (Estes *et al.* 1988) yet fossils assignable to both these latter groups are known from the middle Jurassic period over 150 million years ago (Evans & Milner 1991).

The lineages leading to the three sand dwellers from different families show some similarities in their relatively recent ecological history. They all may have passed through a climbing phase, descended to the ground (see figure 7), progressed into arid habitats and finally entered sandy environments. However, given the length of their separation, much of their individual histories is likely to have been very different. This would increase the chances of early development in one or two lineages of features that subsequently gave a performance advantage in sandy environments.

The comparison between the agamid *Phrynocephalus arabicus* and *Pristurus carteri* is similar to that between the three aeolian sand forms just discussed. As already noted, the two lineages concerned have been separated for a very long time: since the middle Jurassic or earlier. Although the *Pristurus carteri* lineage resembles that of *Phrynocephalus arabicus* in having progressed from climbing to ground dwelling and then into increasingly arid habitats, the total independent history of these two groups has been very different, for instance, agamids are essentially diurnal lizards whereas many of the ancestors of *Pristurus carteri* were habitually active at night. Consequently there has been plenty of opportunity for earlier development of a trait in one lineage than in the other.

(*b*) *Differences in the way traits manifest themselves*

In the intrafamilial comparisons within the Lacertidae, common traits are nearly identical, whereas in the comparisons involving sand-dwellers from different families this is often not so. Thus, although all three of these taxa dive beneath the surface to escape from predators (6), the method employed differs (Arnold 1994*a*). Advanced *Meroles* enter the sand by modifications of basic running movements and high-amplitude lateral undulations of the head, body and tail, while *Uma* scarcely uses the forelimbs and employs very rapid twisting motions of the head and low-amplitude vibrations of the body and tail. Unlike these forms, *Phrynocephalus* descends vertically, using lateral oscillations of the flattened trunk. Differences also exist in the way the tail is used in signalling (9) (Arnold 1984, 1993). It is also notable that some features often associated with the habitats concerned are not found in all ecological analogues in the interfamily comparisons. For instance, among the sand-dwellers, the upper labial scales of *Phrynocephalus* do not form a ridge (8), as they do in *Meroles anchietae* and *Uma*.

As with trait order, a case can be made that these differences arise from the different histories the groups have had. In association with their long separation from each other, the three sand dwelling lineages discussed here diverged very substantially in morphology and behaviour before they made their entrance into aeolian sand habitats. These differences have resulted in different evolutionary potential with respect to the problems of occupying such situations which explains why the lineages have responded to similar environments in different ways (Arnold 1994*a*,*b*). Thus, it is probable that advanced *Meroles* developed their sand-diving technique as a direct adaptation to predator avoidance in aeolian dune situations, while that of *Uma* was an exaptation of a technique that arose initially for slow burial during periods of inactivity and was then modified for rapid submergence in relatively firm substrates before being transferred to aeolian sand habitats. Finally, the vertical descent adopted by *Phrynocephalus* is probably an accommodation to its blunt, very flat-fronted snout which would make forward entry into sand difficult and arose before sand-diving in this lineage. The fact that this feature resulted in a vertical mode of sand-diving being adopted, explains why there has been no evolution in *Phrynocephalus* of the stream-lined head profile and sharp ridges on the lips that are required for efficient forward entry.

(*c*) *Are sequential traits independent in their development?*

The results presented here indicate that there may sometimes be a high degree of regularity in order of trait assembly in ecological analogues and it has been tacitly assumed that development of particular traits in a sequence constitute more or less independent events. However, the possibility must be considered that this is not so. For instance similar order of appearance of traits might result from their being developmentally linked in some way, so that the evolution of one facilitates that of the next in the series, and so on.

In fact there is not much evidence for such a phenomenon. In the interfamilial comparisons characters are seen to be relatively disparate in order, so close developmental control of sequence is unlikely here, especially as particular traits may be missing in some cases. Also, in these instances, traits may be tangibly different in detail, as in the case of sand-diving. A particularly striking example of different solutions to this functional problem involves a group outside the present comparison. In the South American tropidurid genus *Leiolaemus*, sand-diving species enter the sand forwards and like other taxa that do this, such as advanced *Meroles*, *Uma*, *Scincus* and *Angolosaurus*, have a stream-lined head with a sharp lateral ridge on the snout. However, instead of involving the upper lip, as in these taxa, the ridge of *Leiolaemus* is formed from the lower lip (R. Etheridge, personal communication). Such intrinsic differences within a particular trait make it very unlikely that its varied manifestations would facilitate the appearance of very similar following traits in two or more groups.

Character dependence seems more possible when dealing with the comparisons made within a single family where sequences of assembly are very similar and traits are very alike. But successive traits involve very disparate parts of the animal in the lacertid comparison. Thus the sequence runs through scleral ossicles, head scaling, digits, head scaling, belly scaling, snout shape, belly scaling, digits, dorsal pattern and finally belly scales. It seems improbable that such a varied sequence would involve a tight series of developmental connexions, although it would be difficult to discount the possibility of facilitation within a particular area of the body.

Another reason for doubting explanations for common sequences as a whole that involve chains of developmental facilitation is the way the lacertid sequence complies with changes in the environment (p. 283). It seems very unlikely that any developmental predisposition for order of appearance of disparate characters would fit the sequence of habitat change so well.

5. CONCLUDING REMARKS

Results show that evolution may be very regular when closely related and similar taxa enter similar sequences of environments, for they may establish extremely similar common features in very similar orders. On the other hand, although more distantly related and dissimilar taxa can exhibit common traits in similar environments, the traits may be acquired in very different orders and be very varied in detail. Individual traits may also be absent from particular lineages. In the cases investigated here, the overwhelming factor in causing such disparity is marked differences in previous histories of the compared groups. These result in some taxa developing particular traits before the shared habitats are occupied, rather than by direct adaptation to these. Historical differences also influence the way traits evolve, both through phylogenetic constraint and by providing varied opportunities for developing solutions to environmental problems.

I am very grateful to Dr Clive Moncrieff (Natural History Museum, London) for helpful and patient discussion of the statistical aspects of this paper and for writing the computer program used for carrying out an exact test of the significance of concordance in the order in which ecological analogues have assembled their common traits. Dr R. Etheridge (San Diego State University) provided information about tropidurid sand lizards.

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APPENDIX: COMMENTS ON THE STATISTICAL TEST

By C. Moncrieff

Kendall's τ is a non-parametric statistic used to test whether two orderings can be considered independent. Essentially it requires counting the pairs which are like ordered and counting those which are unlike ordered; in the absence of ties the sum of these two counts is fixed and either determines the other. Kendall's τ is essentially the difference between these counts, but appropriately scaled to obtain a value in the range $[-1, +1]$.

This is an appropriate test-statistic to use when the observations can be regarded as independent and randomly selected from a common distribution, but where this common distribution is of totally indeterminate form. In the current context the observations may be thought of as 'dendritic time', defined as the set of evolutionary events occurring before first expression of a character and with ordering defined by set-inclusion. Each phylogeny here considered consists of a linear sequence of evolutionary events occurring on a main stem with side branches leading to a single species or group of species defined by the absence of further expressions of the character under investigation. Thus any two of these characters are either ordered or 'tied'; however, in more general phylogenies two characters could have indeterminate order if they arise on separate branches, and furthermore in such phylogenies a character could arise more than once; in fact this is what occurs when the separate trees for each phylogeny are combined into a single tree!

The underlying hypothesis that the characters can be considered to have arisen independently and from a common distribution is scarcely consistent with the expression of the phylogeny as a single linear tree; furthermore there must be some subjectivity in the selection of characters; thus the use of Kendall's τ cannot be rigidly justified; nevertheless it seems a reasonable test statistic to use. Strictly the characters being considered should not have played a large role in the formation of the phylogenies but it seems unlikely that a failure of this condition would seriously affect the conclusions.

Tabulated values of Kendall's τ can easily be found. Standard adjustments can be applied to take account of ties but these are really only appropriate for a small number of ties. In the present context the number of species is fixed and as the number of characters considered increases the proportion of ties will increase towards 100% and so adjustments will progressively lose value. A one-sided test appeared reasonable as there appeared to be little scientific interest in two orderings being opposed. A FORTRAN programme was therefore written to calculate the exact proportion of orderings of characters in one genus that would lead to an equal or higher value of the test statistic than the value observed; the program chooses which phylogeny to regard as the 'fixed' one so as to minimise calculation time.

The program allows characters which are never expressed in one phylogeny either to be disregarded or to be regarded as not having yet arisen and so placed at the top of the list.

Several generalizations are possible. One would be a simultaneous multiple comparison of more than two phylogenies similar to standard generalizations of Kendall's τ. Another generalization would be to allow for more complicated phylogenies by allowing for partial orderings; this can be accommodated in the program by careful specification of the data but even greater care must be taken before use to consider the assumptions underlying such a test.