



Relationships, evolution and biogeography of Semaphore geckos, *Pristurus* (Squamata, Sphaerodactylidae) based on morphology

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Abstract

The Sphaerodactylid gecko genus *Pristurus* has at least 20 recognised species in Arabia, the Socotra archipelago, and northeast Africa with an isolate 4500km away in Mauritania. Analysis of nineteen variable morphological characters in the Sphaerodactylidae suggests *Pristurus* is most closely related to *Quedenfeldtia* of Morocco and then successively to the Sphaerodactylini and *Saurodactylus*. This contrasts with recent studies using nuclear DNA, which place *Pristurus* in a basal polychotomy in the family. If the molecular tree is correct, there must have been considerable parallelism in anatomy in these taxa. Within *Pristurus*, parsimony analysis was carried out on a set of 72 variable morphological characters (equivalent to 86 binary ones) from external features, skeleton, musculature and behaviour. Apparent relationships are as follows: *P. celerrimus* (*P. insignis*, *P. insignoides*) (*P. guichardi* (*P. socotranus* (*P. abdelkuri* (*P. rupestris*, *P. popovi*, *P. flavipunctatus*, *P. gallagheri*, *P. adrarensis*, the *Spatalura* clade))))). Relationships within the *Spatalura* clade are: (*P. minimus*, *P. simonettai*) (*P. crucifer*, *P. phillipsi* (*P. somalicus* (*P. saada* (*P. collaris* (*P. ornithocephalus*, *P. carteri*))))). The more basal *Pristurus* were apparently primitively heliothermic rock climbers with one lineage becoming tree dwelling. These forms are now confined to the North Oman mountains of eastern Arabia and the Socotra archipelago and may have been replaced elsewhere in Arabia and perhaps northern Africa by a radiation of more morphologically advanced species. Most of these have similar niches to the more primitive forms, but one lineage that gave rise to the *Spatalura* clade became ground dwelling and partly nocturnal. Many morphological changes on the phylogeny of *Pristurus* may be functionally associated with shifts in ecology and behaviour.

Key words: *Pristurus*, Semaphore gecko, Sphaerodactylidae, evolution, biogeography

Introduction

Semaphore geckos (*Pristurus* Rüppell, 1835, type species *P. flavipunctatus*) are a discrete group of at least 21 species found in Arabia, the Socotra archipelago, and northeast Africa, with an isolated species in Mauritania (Geniez and Arnold, 2006) and another extending from Arabia to the coast of Iran and Pakistan (see Fig. 1). Unlike most other geckos they are diurnal and, as their name suggests, they are distinctive in making visual signals with the body and the tail. Here, morphological evidence for the relationships of *Pristurus* to other geckos is assessed and compared with recent results using nuclear DNA sequence (Gamble *et al.*, 2008a) and an estimate of the phylogeny of the species of *Pristurus* is also made using some 72 variable morphological characters (equivalent to 86 binary ones). In this paper, the family and tribe classification of geckos proposed by Gamble *et al.* (2008a, 2008b) is followed.

Distinctive features of *Pristurus*

Pristurus is part of the Sphaerodactylidae (Gamble *et al.*, 2008a) and possesses distinctive features that this group shares with other Sphaerodactylidae, Gekkonidae and Phyllodactylidae, namely: a single premaxilla, a large cervical extension of endolymphatic system, and more or less round eggs with calcareous shells.

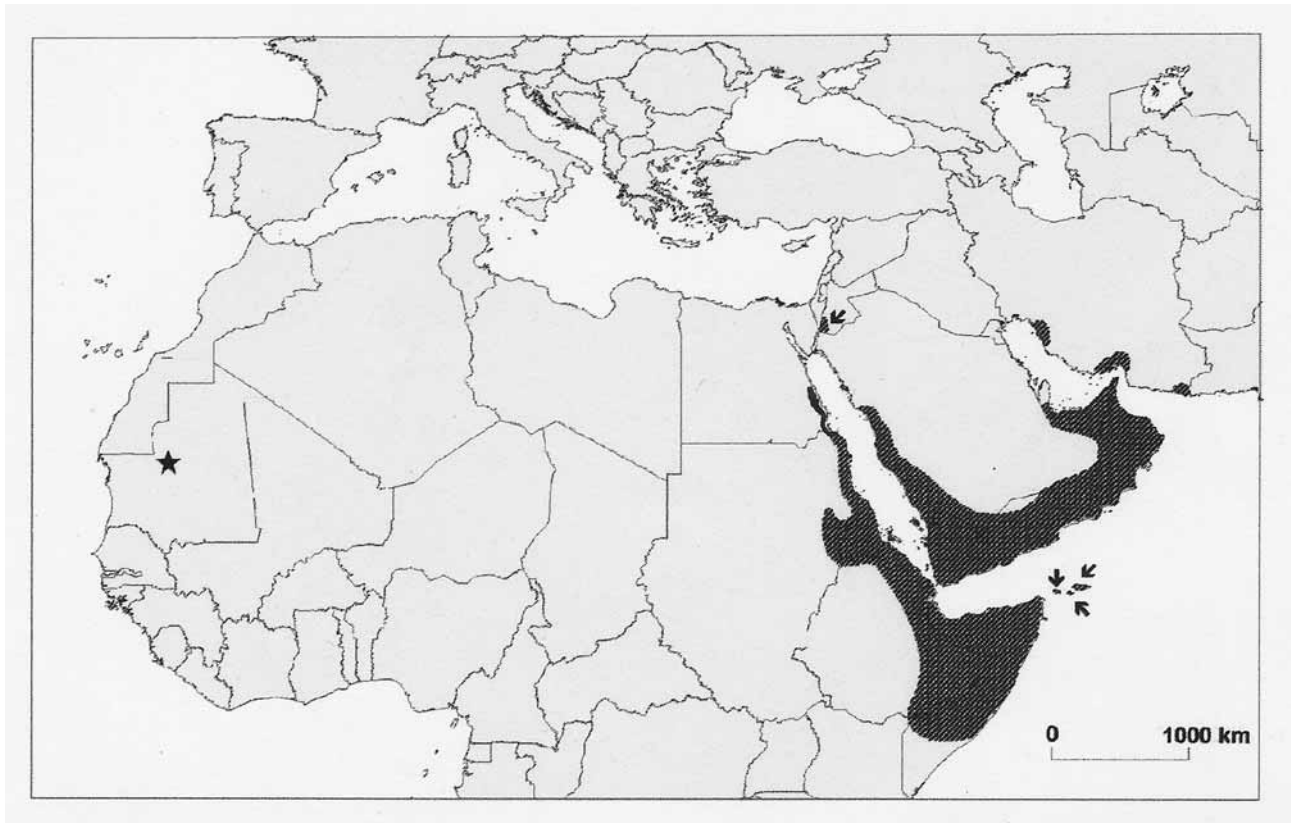


FIGURE 1. Distribution of *Pristurus*. The Socotra archipelago is indicated by arrows off the Horn of Africa, and consists, from east to west, of Socotra itself, Samhan and Darsa, and Abd al Kuri. The isolated range of *Pristurus adrarensis* in Mauretania is indicated by a star.

Other distinctive features include: dorsal process of premaxilla relatively long, nasal bones short, extent of prefrontal bone in anterior wall of orbit reduced medially*; supratemporal process of parietal bone often expanded and fully attached to exoccipital*, squamosal often short and curved*; palatine contacting vomer narrowly*, superficial posterior margin of dentary bone not obviously tridentate, the lower spur extending far backwards*. Twenty-five or fewer presacral vertebrae; toes with primitive number of phalanges (manus – 2.3.4.5.3; pes – 2.3.4.5.4); post-cloacal bones absent. Meatal closure muscle absent; anterior nuchal muscle originating mainly on second vertebra*; pectoralis muscles on each side crossing midline*, toes without complex internal musculature. Pupil approximately round with posteroventral quadrant of border less convex, or pupil vertically elliptical with un-notched borders; dorsal scaling consisting of small granules, nearly always without larger tubercles on body; preanal and femoral pores absent, cloacal tubercles and postcloacal sacs absent; toes simple without expanded adhesive pads beneath; tail strongly compressed laterally in males*, not or less so in females; in one species (*P. celerrimus*) an area of dark rugose scales in preanal region of males; flanks often with longitudinal series of short dark or reddish streaks separated by pale spots*. Largely diurnal and usually heliothermic; tail often raised and moved during intraspecific signalling*; voice little used.

*—Asterisks indicate features that are apparently largely or wholly confined to *Pristurus* among the Sphaerodactylidae, Gekkonidae and Phyllodactylidae.

Species of *Pristurus*

P. abdelkuri Arnold, 1986a—Abd al Kuri island (also Socotra, where probably introduced—Rösler and Wranik, 2000); *P. adrarensis* Geniez and Arnold, 2006 – Adrar region of Mauritania; *P. carteri* (Gray, 1863)—from central Oman westwards to North Jol in southern Yemen; *P. celerrimus* Arnold, 1977—North Oman; *P. collaris* (Steindachner, 1867)—southern Yemen, from Bal Haf eastwards to Ras Fartak; *P. crucifer* (Valenciennes, 1861)—Eritrea, Somalia, eastern Ethiopia, northern Kenya, coastal western Yemen; *P. flavipunctatus* Rüppell, 1835—southeastern Egypt, Sudan, Eritrea, eastern Ethiopia, Djibouti, Somalia, southwestern Saudi Arabia, western Yemen; *P. gallagheri* Arnold, 1986a—Jebel Akhdar region of North Oman; *P. guichardi* Arnold, 1986a—Socotra; *P. insignis* Blanford, 1881—Socotra; *P. insignoides* Arnold, 1986a—Socotra; *P. minimus* Arnold, 1977—southwest Saudi Arabia, UAE, south and central Oman; *P. ornithocephalus* Arnold, 1986a—coastal Yemen as far east as Wadi Hajr; *P. phillipsii* Boulenger, 1895—northern Somalia (Goolis and Doloh mountains); *P. popovi* Arnold, 1982—southwest Saudi Arabia (Jebel Sawdah), western Yemen; *P. rupestris* Blanford, 1874—north Somalia, Jordan, southwest and east Saudi Arabia, Yemen, Oman, UAE, Qatar, Bahrain, Kuwait, coastal Iran and Pakistan; *P. saada* Arnold, 1986a—highlands of western Yemen; *P. schneideri* Rösler, Köhler and Böhme, 2008—Hanish al-Kabir Island, Yemen; *P. simonettai* (Lanza and Sassi, 1968)—southern Somalia; *P. sokotranus* Parker, 1938—Socotra; *P. somalicus* Parker, 1932—Somalia.

P. obsti Rösler and Wranik, 1999 from Socotra and *P. samhaensis* Rösler and Wranik, 1999 from Samha and Darsa islands off Socotra, are respectively very similar in their morphology to *P. guichardi* and *P. sokotranus*. Their status needs to be assessed using molecular methods. These indicate that *P. rupestris* is really a species complex with several long-standing lineages, at least in Oman (S. Carranza and E.N. Arnold, unpublished data); there may also be a further undescribed species of *Pristurus* in Somalia similar to *P. somalicus*. Representative species of *Pristurus* are shown in Fig. 2.

Current and previous views in the relationships of *Pristurus* to other geckos

On the basis of morphology, *Pristurus* has been regarded as sister to the American sphaerodactyl geckos (Sphaerodactylini in Gamble *et al.*, 2008a) by Kluge (1987), and *Saurodactylus* and *Quedenfeldtia* were believed to be related to these (Kluge and Nussbaum, 1995). A sister relationship between *Pristurus* and *Quedenfeldtia* has also been suggested, by Arnold (1977, 1990a, 1993), with Sphaerodactylini and *Saurodactylus* as their successive closest relatives (Arnold, 1990b, 1993).

Recent investigations using nuclear DNA sequences place *Pristurus* in a newly defined family Sphaerodactylidae (Gamble *et al.*, 2008a). Here, *Pristurus* may form a polychotomy with four other units, namely *Saurodactylus* + Sphaerodactylini, *Aristelliger* + *Quedenfeldtia*, *Euleptes*, and *Teratoscincus*.

Material and methods

The morphological characters used and the data sets arising from them are given for the main taxa of Sphaerodactylidae in Appendices I and II, and for 20 species of *Pristurus* and some of its outgroups in Appendices III and IV. Data were largely obtained by examination of the large collections of *Pristurus* and related genera in the Natural History Museum, London. Material was also examined in the California Academy of Sciences, San Francisco; Museo Civico di Storia Naturale, Milan; Museo Zoologico della Specola, Università degli Studi, Florence; and the Naturhistorisches Museum, Vienna. In some cases, data were corroborated from the literature.

The data set for Sphaerodactylidae consists of 19 variable characters (equivalent to 21 binary ones). Where character states vary among the species of *Pristurus*, the primitive one was established by a separate phylogenetic analysis of these (see below) and used in the sphaerodactylid data set. Trees were rooted using a synthetic unit made up of what appear to be primitive character states in the Gekkonidae and Phyllodactylidae, which together form the sister group of the Sphaerodactylidae (Gamble *et al.*, 2008a, b).

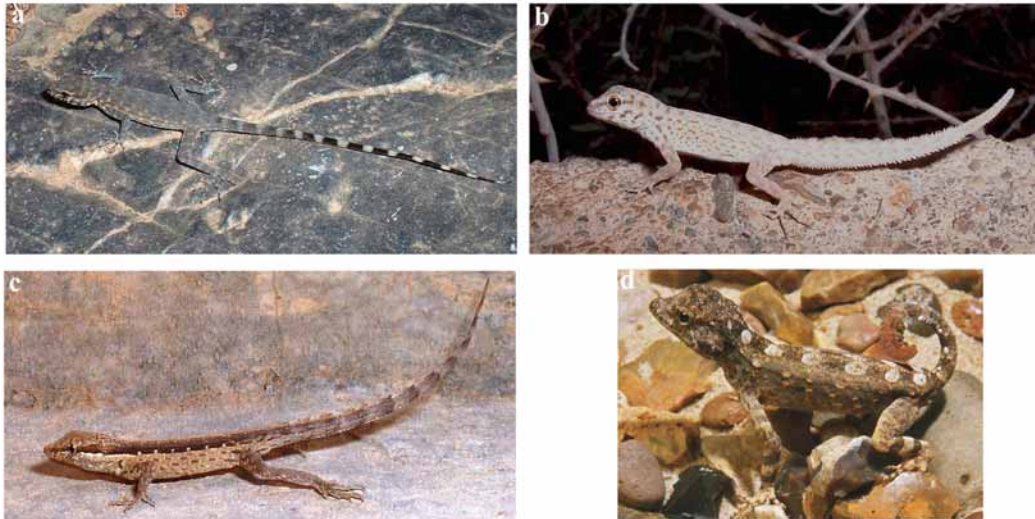


FIGURE 2. Representative species of *Pristurus*. a. *P. celerrimus* of north Oman, morphologically the most primitive member of the genus. b. *P. rupestris* from north Oman, a member of the widespread *P. flavipunctatus* assemblage. c. *P. minimus*, south Oman, a member of the *Spatalura* clade. d. *P. carteri* from south Oman, a member of the *P. carteri* group in the *Spatalura* clade. Photographs a–c taken by David Donaire.

The *Pristurus* species data set consists of 80 characters of which 72 vary within the genus (equivalent to 86 binary characters). Full data is presented for 19 species and partial data for *P. adrarensis*. Trees were rooted using three other Sphaerodactylid taxa (*Quedenfeldtia*, Sphaerodactylini and *Teratoscincus*) and a synthetic unit made up of what appear to be primitive character states in the Gekkonidae and Phyllodactylidae.

Multistate characters were treated as polymorphic, and trees were analysed by parsimony using the program PAUP* (Swofford, 2002). Both Heuristic (with TBR branch swapping) and Branch and Bound searches were conducted. As more than one tree was produced by phylogenetic analyses, the strict consensus was calculated. The robustness of the topology recovered was assessed by bootstrap analysis with 1000 replicates.

Results

Relationship of Pristurus to other sphaerodactylid geckos

Branch and bound analysis produced three trees of 29 steps with a consistency index of 0.793, a retention index of 0.786, and a homoplasy index of 0.276. The strict consensus of these is shown in Fig. 3. Bootstrap support is moderate or strong for most nodes (0.73–0.92). The results suggest that the sister group of *Pristurus* is *Quedenfeldtia* and that these two genera are successively related to Sphaerodactylini, *Saurodactylus* and *Aristelliger*. The derived states that characterise these assemblages are listed in the caption to Fig. 3.

Relationships of the species of Pristurus

Branch and bound analysis of outgroups and all *Pristurus* species except *P. adrarensis*, produced 32 trees of 175 steps with a consistency index of 0.731, retention index of 0.881, and a homoplasy index of 0.457. Inclusion of *Pristurus adrarensis* produced 96 trees of 183 steps, with a consistency index of 0.700, retention index of 0.862, and a homoplasy index of 0.480; the strict consensus of these trees is shown in Fig. 4. Exclusion of outgroups produced 24 trees of 155 steps, the consensus differing from Fig. 4 only in *Pristurus guichardi* being the sister species of *P. insignis* + *P. insignoides* (bootstrap support = 0.64).

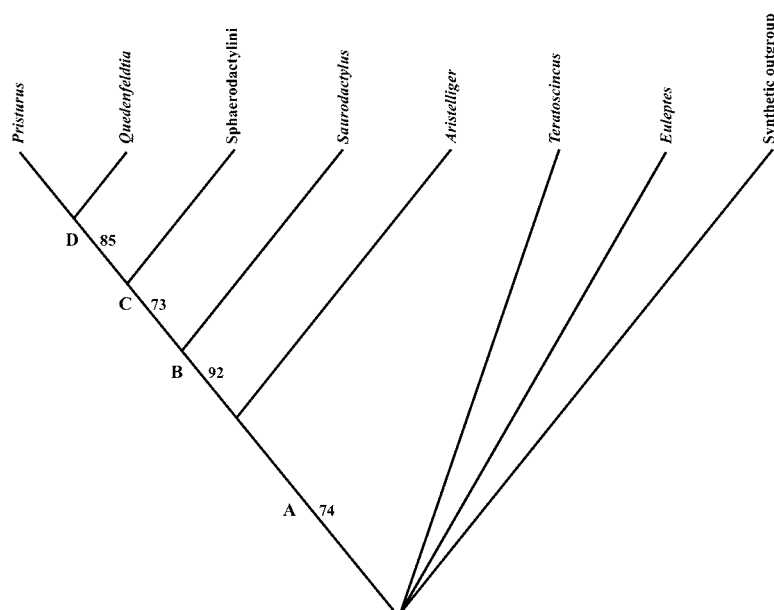


FIGURE 3. Apparent relationships of the main taxa of Sphaerodactylidae based on 19 morphological characters equivalent to 21 binary ones. The tree shown is a strict consensus of three produced by parsimony analysis; figures indicate bootstrap support for nodes based on 1000 replicates. Derived states that characterize apparent clades are as follows (character numbers are given in parentheses). A. Loss of cloacal tubercles (8), loss of cloacal sacs and bones (9, 10), clutch size reduced to a single egg (16). B. Small body size (1), voice reduced (19), active in subdued light (17-1). C. Pupil rounded but often higher than wide (6.1), sexual dichromatism often present (11), ‘escutcheon’ often present (13), active in bright light (17-2), voice reduced (19). D. Nasal bones relatively short (2), pupil round (6-2), characteristic dorsal pattern (12), ‘escutcheon’ dark (14), tail often raised as intraspecific signal (18).

Discussion

Names for units within Pristurus

It is useful to be able to refer to the more evolutionarily significant groups of species within *Pristurus*. The clade formed by *P. minimus* + *P. simonettai* plus its sister taxon is distinctive in numerous morphological synapomorphies and its behaviour, and the name *Spatalura* Gray, 1863 (type species *Spatalura carteri*) is available for it. This may be regarded as a subgenus, leaving a less derived paraphyletic unit within which formal names are not applied. Instead, the more basal species up to and including *P. abdelkuri* are referred to informally as ‘the more primitive species of *Pristurus*’, while the remaining species are called ‘the *P. flavipunctatus* assemblage’, namely *P. rupestris*, *P. popovi*, *P. adrarensis*, *P. gallagheri* and *P. flavipunctatus*. Within the *Spatalura* clade, *P. saada*, *P. collaris*, *P. ornithocephalus* and *P. carteri* also have distinctive features and are called ‘the *P. carteri* group’.

Relationship of Pristurus to other Sphaerodactylidae

The tree based on morphology is very different from that derived from nuclear DNA sequence (Gamble *et al.*, 2008a). As the latter involves far more characters and has stronger bootstrap support, it is to be preferred. If the relationships within the Sphaerodactylidae based on nuclear DNA sequence are correct, there must be considerable homoplasy in morphology in *Pristurus* and *Quedenfeldtia*, and significant though lesser amounts between these genera and Sphaerodactylini and *Saurodactylus*. It has been suggested that independent evolution of small body size may be responsible for the other supposed homoplasies (Gamble *et al.*, 2008a), which would consequently result from miniaturization (Rieppel, 1984; Hanken & Wake, 1993). Shift to

diurnality may also be relevant. But these features are not always associated with the others. Among gekkonid geckos, it is true that *Narudasia*, which is very small and active by day, has also lost femoral pores, cloacal sacs and bones, and the meatal closure muscle. But nearly all the characteristic features of small sphaerodactylids are absent in the small diurnal gekkonid *Lygodactylus* and in the very small though nocturnal *Ebanavia* and *Tropicolotes*.

Relationships of *Pristurus* species

The rooted tree shown in Fig 4 is robust with moderate and sometimes strong bootstrap support at most nodes. The relationship of *P. guichardi* to *P. insignis* + *P. insignoides* present in the unrooted tree could conceivably be real, as there are derived features shared by these three species, namely numerous scales round digits (character 58), and occasional presence of three pairs of xiphisternal ribs (character 40), and the association of *P. guichardi* with other species of *Pristurus* in the rooted tree has only limited support (bootstrap = 0.56).

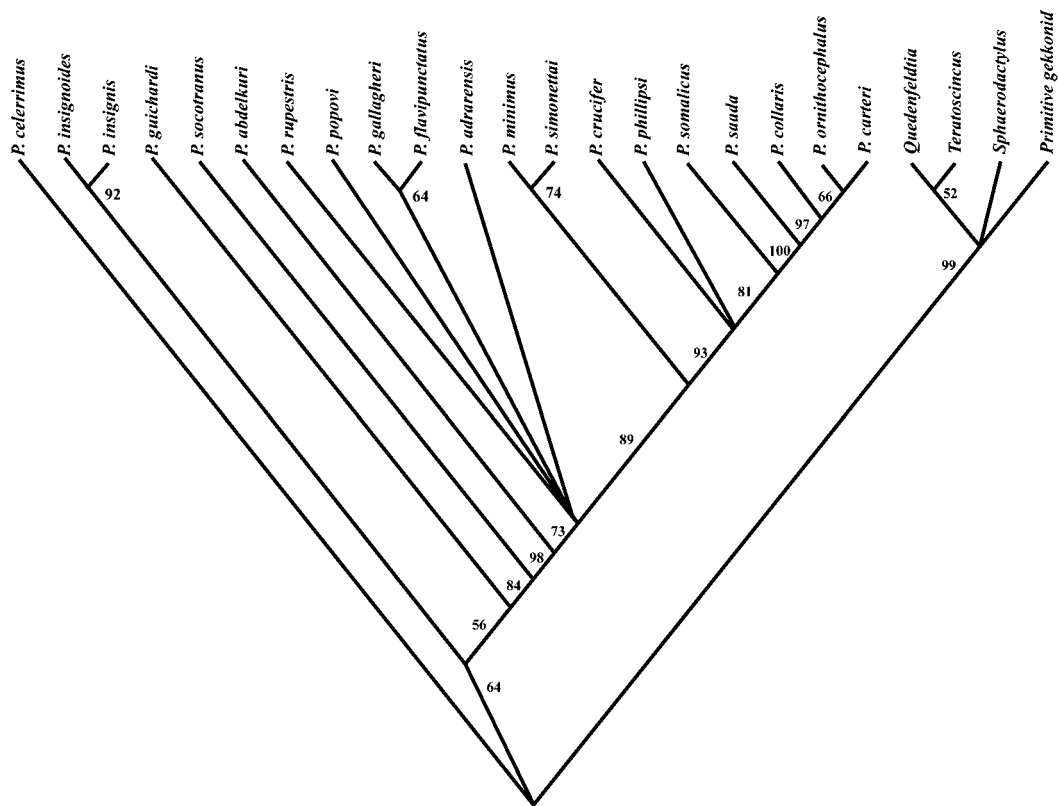


FIGURE 4. Apparent relationships of 20 species of *Pristurus* based on 72 morphological characters equivalent to 86 binary ones. The tree shown is a strict consensus of 32 produced by parsimony analysis; figures indicate bootstrap support for nodes based on 1000 replicates.

History of *Pristurus*

Information available at the time about niche and behaviour in *Pristurus* was summarized by Arnold (1993). Since then, more data have become available. Aspects of spatial niche and signalling has been noted for *P. celerrimus* (Gardner, 1993; Feulner, 2004), some Socotran species (Rösler and Wranik, 1998, 1999, 2000, 2001; Wranik, 2003), *P. gallagheri* (Gardner, 1993, 1994a), and for *P. rupestris* (Ross, 1990, Gardner, 1993). Social interactions and reproduction has also been studied in *P. socotranus* and *P. obsti* (Rösler and Wranik, 2001). Changes in some aspects of spatial niche, feeding behaviour and signalling in *Pristurus* based on these various sources are summarized in Table 1 and Fig. 5 and discussed overleaf.

Changes in spatial niche. The more primitive forms of *Pristurus* are confined to the North Oman mountains (*P. celerrimus*) and to the Socotra archipelago (*P. insignis*, *P. insignoides*, *P. guichardi*, *P. obsti*, *P. socotranus*, *P. samhaensis* and *P. abdelkuri*). They are mainly heliothermic climbers on rocky surfaces, but *P. guichardi* and *P. obsti* are arboreal on the trunks and branches of trees, and these two forms and *P. insignis* often occur in shady situations. On the mainland of Arabia and northern Africa, there appears to have been later radiation and wide spread of a clade of morphologically more advanced forms, consisting of the *P. flavipunctatus* assemblage and the *Spatalura* clade. As with the more primitive species of *Pristurus*, the great majority of the at least seven current main lineages on the mainland climb on rocks and one, or two (depending on whether *P. gallagheri* and *P. flavipunctatus* are really closely related), have moved on to trees, independently from *P. guichardi* and *P. obsti*. But one lineage, the ancestor of the *Spatalura* clade, has invaded a quite new area of niche space, becoming ground dwelling and partly nocturnal. This radiated to produce at least nine species. The radiation involved spread from relatively hard surfaces on to rather softer ground, associated with taking refuge in vegetation (in *P. minimus*-*P. simonettai*, and *P. crucifer*), and great increase in body size in the *P. carteri* group.

Foraging and diet. Apart from shifts in *spatial niche* occupied, exposure to sun and time of activity, *Pristurus* species show alterations in other behaviours. Cruising foraging, where lizards run from one feeding station to another (Regal, 1983) occurs in at least the basal *P. celerrimus*, and *P. insignis* also seems to forage actively (Wranik, 2003). But more advanced forms, such as *P. rupestris*, *P. gallagheri* and *P. flavipunctatus*, and *P. carteri* in the *Spatalura* clade, are passive foragers, spending long periods at one site, catching passing arthropods. It is not yet clear whether there was a single transition to this behaviour among the more primitive species of *Pristurus* or exactly where on the phylogeny this is situated. Prey items also vary and ants may make up more than 50% of the animals eaten in *P. celerrimus*, *P. socotranus*, *P. rupestris*, *P. popovi*, *P. flavipunctatus*, *P. collaris*, *P. ornithocephalus* and *P. carteri*. Members of the *P. carteri* group also eat many termites, a prey item that is likely to be available during their nocturnal activity. It is striking that the *P. carteri* group, the largest *Pristurus* species, take a lot of especially small food for their size, although large arthropods are also eaten.

Body temperature. The limited observations available suggest diurnal body temperatures of *Pristurus* increase along the main lineage of the genus. They are comparatively low in *P. celerrimus*, higher in *P. rupestris* and higher still in *P. carteri*, where they reach 38–40° C. However, as might be expected, *P. carteri* has much lower body temperatures during its nocturnal activity, often 20–25° C, that are similar to other nocturnal geckos in its general habitat.

Territorial signalling. Male territorial displays also vary on the phylogeny. The basal *P. celerrimus* first compresses the body from side to side and raises itself on extended limbs with the body and tail straight and sloping diagonally upwards, after which the hindquarters are lowered and the rigid straight tail flicked upwards to fall more slowly, these vertical ‘flagging’ movements being repeated a number of times (Fuelner, 1994; personal observations). In *P. guichardi*, *P. obsti*, *P. socotranus*, *P. samhaensis* and *P. abdelkuri*, flattening the body from side to side and standing high on the limbs also occurs, although the body is more horizontal and the throat is also expanded downwards; in addition, the tail is raised in an upward curve during the repeated flagging movements and is often wagged from side to side subsequently (Rösler and Wranik, 2001). In *P. rupestris*, body compression, throat extension, limb extension, tail flagging and lateral tail wagging also occur but, in flagging, the distal tail is curled tightly in the vertical plane and brought right up over the hind legs. Such signalling also occurs in at least some other members of the *P. flavipunctatus* assemblage, including *P. flavipunctatus* itself and *P. gallagheri*. Of these, at least *P. rupestris* also appears to possess additional signals (Ross, 1990). Body compression and tail signalling also occur in members of the *Spatalura* clade, such as *P. minimus* and *P. carteri*. In at least *P. rupestris*, there are minor differences in signalling between populations. In Oman, animals in the north of the country have normal flagging, but in those from Dhofar in the south the tail is more complexly twisted and is more conspicuously pale beneath (personal observations).

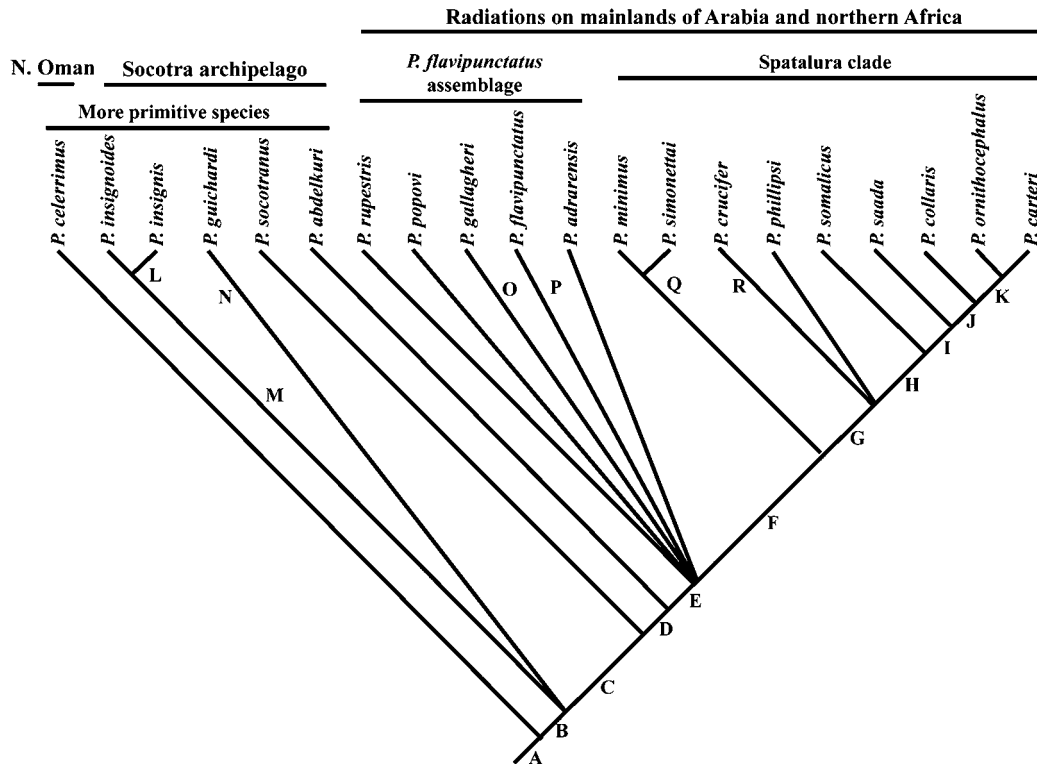


FIGURE 5. Phylogeny of *Pristurus* showing groups of species referred to in text and their broad distributions. Capital letters indicate branches where the changes in ecology, behaviour and morphology mentioned in Table 1 and in the text are likely to have taken place. The phylogeny is conservative; if *P. gallagheri* and *P. flavipunctatus* are closely related, changes at O and P could have occurred in their common ancestor.

TABLE 1. Changes in ecology, behaviour and morphology in Semaphore geckos (*Pristurus*). Letters refer to internal branches marked in Fig. 5.

Ecology and behaviour

Spatial and temporal niche. A - rock climbing and heliothermic. N, O, P – arboreal. L, N, O, P – often found in shade. F – descent to ground and shift to some nocturnal activity. H – found on firm ground surfaces. Q, R. – found on looser surfaces and vegetation.,

Foraging. A - relatively active foraging. E or earlier – shift to more passive foraging. J – prey items relatively small.

Territorial signalling. A - body compressed, then tail held straight and flagged vertically. N?, C – throat spread downwards and body laterally compressed; tail curved upwards and flagged, and subsequently wagged from side to side. E – as C, but tail tightly curled when being flagged.

Predators. H, *P. rupestris* – chigger infestation common. I – autotomy usually at base of tail.

Reproduction. R, J - sometimes clutches of two eggs.

Morphology

Spatial and temporal niche. L, N, O, P – reduction in palpebral fold in shady situations. N, O, P – change in limb proportions, arboreal colouring. F – vertically elongate pupil associated with partial nocturnality, change in limb proportions, zygapophyses on body vertebrae strongly reflexed, modified sacrum and neck muscles. Q, R - change in limb proportions, longer claws, striped pattern.

Foraging. M, I, J – increase in body size. D - shortening of body with reduction to 23 presacral vertebrae, and only one complete xiphisternal rib. F - tongue simple. I, J – increase in eye size. *P. collaris*, *P. ornithocephalus* - evolution of very pointed snout.

Territorial signalling. A - Tail laterally compressed in males. C - tail deepened by well developed fringes on tail. M – tail deepened by upward extension of neural spines. I – tail becomes shorter. D- zygapophyses on body vertebrae reflexed.

Anti-predator devices. H – mite pockets frequent. *P. carteri* – loss of autotomy planes in caudal vertebrae.

Reproduction. J – increase in mean clutch size associated with increase in body size

Changes associated with increased skull mobility. These are spread along the main lineage of *Pristurus*; change is especially marked on branches D and E in Fig. 5, where the scissor joint between anterior maxillae appeared.

Other morphological changes- A.- no splenial bone in mandible, change in origin of anterior nuchal muscles, pectoral muscles cross midline. F - change in sternum shape. I - change in clavicle.

Predation and responses to it. Several species of *Pristurus* are sometimes infested with the larvae of trombiculid mites but these micropredators are especially common in *P. rupestris*, and independently, in the clade made up of *P. somalicus* and the *P. carteri* group. In *P. carteri* itself, infestation is commonest in less dry areas, something that probably reflects the distribution of the trombiculids themselves (Arnold, 1986b). Most *Pristurus* are able to shed the tail at numerous points along its length, but in the *P. carteri* group this usually occurs only at the tail base. Basal breakage is common in gecko species that are relatively slow (Arnold, 1984), something that often appears to be true of the *P. carteri* group during their nocturnal activity. *Pristurus carteri* and perhaps other members of the *Spatalura* clade frequently close the vertically elongate pupil entirely when caught, making the eye less conspicuous.

Reproduction. Most species of *Pristurus* lay clutches of just one egg, but in *P. crucifer* and the *P. carteri* group the number sometimes increases to two.

Morphological shifts in Pristurus

Some of the more salient morphological shifts on the *Pristurus* phylogeny are summarized in Table 1 and Fig 5. These involve both characters in the data set (Appendix IV), and morphometric features concerning relative limb lengths. A proportion of these shifts appear to correlate with ones in behaviour and ecology and a case can sometimes be made that they are functionally related to these, conferring advantage in the new situations with which they are associated.

Spatial niche. Limb proportions in *Pristurus* vary according to known habitat. Species means (based on >10 individuals of nearly all of them) for the ratio of the span of the extended forelimbs to that of the extended hind limbs are around 0.85–0.86 in arboreal species, 0.80–0.82 in most rock climbers, 0.75–0.77 in ground dwellers on firm surfaces, and 0.69–0.73 in ones from generally rather softer surfaces. Relative foot size also varies being greatest in ground forms from softer surfaces. Similar differences, with the highest forelimb/hindlimb ratios in forms that climb most and the lowest in ground dwellers from soft surfaces, also occur in some other lizard groups, such as lacertids where they are related to the kind of gaits animals employ in their habitats (Arnold, 1998a). There are some exceptions in *Pristurus*. For instance *P. celerrimus* has relatively long hind legs for a rock climber (mean foreleg/hindleg ratio 0.75), but this may be because it often runs on fairly level rock surfaces.

The shifts into regular use of shady habitats involving *P. insignis*, *P. guichardi*, *P. obsti*, *P. flavipunctatus* and *P. gallagheri* are associated with reduction of the palpebral skin fold above the eye, which apparently acts as an ocular sunshade in more heliothermic species. All except *P. insignis* are arboreal and share features of their colouring that may be cryptic on bark, including the frequent presence of a broad, pale vertebral stripe on the body, often with small paired dark markings on each side of it, and dark partial cross bars on the head.

Shift to living on the ground in the ancestor of *Spatalura* (internal branch F in Fig. 5) is associated with numerous morphological changes that may be related to alterations in usual locomotion. In addition to relative lengthening of the hind legs, there are changes in the connection between the sacrum and the ilium. The muscles of the neck are also modified which may be related to the different head movements that occur when the body is habitually more or less horizontal. Members of the *Spatalura* clade that often occur on relatively soft surfaces and often take refuge in vegetation (*Pristurus minimus* + *P. simonettai*, and *P. crucifer*) have elongated claws, and dorsal colouring involves light stripes including dorsolateral ones that are likely to be cryptic in the usual habitat of these forms.

Foraging and diet. Relatively active foragers that are basal on the phylogeny, such as *P. celerrimus* and *P. insignis*, have a comparatively long and slender body, while this is short and relatively robust in most of those species that are passive foragers. Associated with this change, there is a shift to lower numbers of presacral and pygal vertebrae, the presacral ones falling from 24 or 25 to 23. The number of complete xiphisternal ribs is also reduced, from two or three to one. Such changes showing some correlation with foraging technique occur in other lizard groups including lacertids, and in the latter at least, this is correlated with reduction in vertebral number and modifications of the xiphisternal ribs (Arnold, 1989). While direct observations are not available that indicate exactly where on the phylogeny of *Pristurus* foraging mode changes, alterations in vertebrae and xiphisternal ribs suggests it may be around internal branches D and E in Fig. 5.

The shift to relatively small prey produced by increase in body size in at least the more advanced members of the *P. carteri* group is associated with the evolution of a narrow snout tip that enables them to pick up ants and termites from between the small stones often common in their habitat. The snout is particularly acute in some populations of *P. collaris* and *P. ornithocephalus*.

Territorial signalling. The evolution of frequent signalling with the tail in at least males in the ancestral lineage of living *Pristurus*, is associated with this organ becoming deeper than wide. This change places the muscles that move the tail in appropriate positions for producing vertical movements efficiently, and deepening of the tail also makes it more conspicuous from the side, the position from which it is most usually viewed by conspecifics. Later on the main lineage of the genus, depth is increased further. This is achieved in males of the sister species *P. insignis* and *P. insignoides* by upward extension of the neural spines of the tail vertebrae and of the upper margin of the tail. In contrast, in *P. socotranus* and succeeding forms deepening is produced by fringes of enlarged scales along the upper and later the lower margins of the tail. Another feature that may be associated with signalling is the way the anterior zygapophyses of body vertebrae are extended and flexed medially so they often embrace the posterior zygapophyses of the adjoining, more anterior vertebra. Experiment shows this has the effect of stiffening the backbone reducing the extent to which it can curve upwards. This may be related to resisting the action of the dorsal muscles when the tail is moved vigorously in signalling. Modified zygapophyses are best developed in the *Spatalura* clade, which raises the possibility that this emphasis is connected with a need to stiffen the backbone in rapidly running ground dwellers.

Evolutionary responses to predators. *Pristurus somalicus* and members of the *P. carteri* group that are often heavily infested with trombiculid mite larvae have mite pockets that appear to ameliorate the deleterious effects of these micropredators (Arnold, 1986b). However, pockets have not evolved in *P. rupestris*, which also often has heavy infestations, and their absence may be associated with the higher levels of mite damage found in this species (Gardner, 1994b). Restriction of autotomy to the tail base in the *P. carteri* group, may possibly be reflected in changes in the soft parts of the tail, although this has not been investigated, but adult *P. carteri* have apparently actually lost most of the autotomy planes in the vertebrae.

Reproduction. Increase in clutch size from one egg to sometimes two is associated with increased body size in the *P. carteri* group.

Increase in skull mobility. There are extensive changes in the osteology of the head that are distributed along the main lineage of the phylogeny of *Pristurus*. Up to about internal branch C in Fig. 5, the changes are relatively few and seem unlikely to affect the internal mobility of the skull much but, by branch D and especially E, there are several changes that are likely to increase this markedly. Anterior downgrowths of the frontal, that increase the rigidity of contact between this bone and the snout, disappear. On the palate, contact between the anterior maxillae behind the premaxilla becomes broad. Here the maxillae form a complex mobile scissor joint with each other and are not firmly attached to the premaxilla and this mobility enables their posterior ends to move laterally outwards. At node E the tubular frontal typical of nearly all geckos loses its lower section in all species except *P. rupestris*, so becoming an essentially flat plate; this is also likely to reduce rigidity in this area of the skull. Other changes in the head occur later on the main lineage of *Pristurus*. On branch F, the immediate ancestral lineage of the *Spatalura* clade, elongation of the dorsal spur of the premaxilla and change in scaling around and between the nostrils may also be associated with increased

mobility of the maxillae. Mobility produced by these various changes is combined with that at the frontoparietal suture and in the occipital area, which forms part of the mesokinesis common in lizards that is especially well developed in many geckos (Arnold, 1998b).

It is uncertain why these complex changes, that culminate in a skull that is more internally mobile than in many other geckos, took place. Many of them occurred at a time in the history of *Pristurus* when head and body size was very small, snout-vent distances being under 40 mm and often considerably so, and prey size was often relatively quite large. So skull mobility may possibly facilitate swallowing these comparatively larger prey, as it does in snakes and varanid lizards, and perhaps also enable this to take place more rapidly. Some of the changes also occurred around the time when there may have been a shift to more passive, sit and wait foraging, something also associated with rapid processing of prey, perhaps because the lizards concerned often forage in exposed positions where prolonged movement might attract the attention of predators. At least some of the shifts, such as the development of maxillae that meet broadly on the palate behind the premaxilla are paralleled in the southwest African *Narudasia festiva* (Kluge and Nussbaum, 1995), which is also very small and hunts in exposed situations (Branch, 1998). Whether small size in itself facilitates the evolution of the derived skull features is uncertain, but miniaturization is often associated with such radical changes in morphology (Rieppel, 1984; Hanken & Wake, 1993). Possibly some of the changes are pedomorphic. But size reduction alone is unlikely to be their cause, for many of them are lacking in the more basal *Pristurus celerrimus*, *P. guichardi* and *P. socotranus*, which are also small.

Further changes in the skull also occur. In the *Spatalura* clade, the alar projection on the prootic disappears and the epipterygoid contacts this bone low down, well away from the skull roof. Such changes are also seen in some *Stenodactylus* geckos (Arnold, 1980a) and may be associated with deeper heads with a greater mass of jaw muscles, something that again may be related to rapid prey processing. The eyes become relatively large in *P. carteri* and its close relatives, something in association with narrowing of the frontal bone between the orbits. This may be related to the very open habits of these lizards, in which they react to objects, such as prey, predators and conspecifics, at long distances. This trend is also seen in other groups where such habitats have been occupied, for example in advanced Eremiadini among lacertid lizards (Arnold, 1989).

Historical biogeography

Occurrence in the Socotran archipelago. There is evidence that the Socotra archipelago was originally attached to Arabia, in the area of Jabal Samhan in Dhofar and separated from this in the early stages of the opening of the Red Sea Gulf, in the mid-Miocene, perhaps around 20 Mya, moving southward with the African plate as the Arabian plate rotated northwards (Beydoun, 1970; Beydoun and Bichan, 1970; Samuel *et al.*, 1997). Some or all of the *Pristurus* lineages that occur in the archipelago today may possibly have been present before this event or, alternatively, colonised across the sea afterwards. At present neither fossils nor a molecular clock are available to help distinguish between these possibilities.

Several of the other reptile taxa that occur on Socotra show similarities to endemic *Pristurus* in their relatively basal positions within clades that also occur on neighbouring mainlands, or in their relatively primitive morphology, or both. These features suggest long residence on the island. The endemic chameleon, *Chameleo monachus* is basal with the respect to the other members of the *C. chamaeleon* species group in northern Africa, Arabia and India (Macey *et al.*, 2008), and the snake *Hemerophis socotrae* is basal to a widespread clade of whip snakes and their relatives (Schätti and Utiger, 2001). Socotra leaf-toed geckos, *Haemodracon*, are most closely related to *Asaccus* of the montane areas of north Oman and western Iran (Gamble *et al.*, 2008b) and are more primitive in retaining cloacal sacs and bones, and both oviducts (Arnold & Gardner, 1994). The trogonophid amphisabenian on Socotra, *Pachycalamus*, is morphologically more primitive than the related Arabian *Diplometopon* and *Agamadon* of the Arabian and northeast African mainlands (Gans, 1960). The snake, *Dityophis* also occupies an isolated position. Although the separation of *Chamaeleo monachus* has been attributed to the breaking away of Socotra (Macey *et al.*, 2008), a molecular clock estimate of the time of divergence from its relatives is not available, and the same is true for the other Socotran endemics just listed. However rough estimates have been made for the Socotran skink

Trachylepis (until recently *Mabuya*) *socotrana* (Carranza & Arnold, 2003), the gecko *Hemidactylus oxyrinus* of Abd al Kuri island and Socotran populations of *H. homoeolepis* (Carranza & Arnold, 2006; Arnold & Carranza, submitted). These indicate that colonisation by the lineages concerned was relatively recent and therefore transmarine.

The advanced mainland radiation. Primitive forms of *Pristurus* must have once been more widespread on the Arabian mainland as their range is now disjunct in north Oman and Socotra, something paralleled by leaf-toed geckos of the *Haemodracon-Asaccus* clade. In the case of primitive *Pristurus*, this may have been caused by the radiation and spread of more advanced forms in the *P. flavipunctatus* group and *Spatalura* clade. Where the ancestor of this radiation came from is not clear. It could have originated on the mainland from a more primitive lineage now extinct there, or it could conceivably have invaded from the Socotra archipelago where *P. abdelkuri*, the apparently most closely related extant species, is found. Although nearly all species in the advanced mainland radiation are confined to the periphery of Arabia and to northeast Africa, the presence of the recently discovered *P. adrarensis* in Mauritania shows that the group was once more widespread.

Red Sea Vicariance. Within the clade of advanced, mainland *Pristurus*, five units occur on both sides of the Red Sea; in southern Arabia and in northeast Africa. These are *Pristurus rupestris* s. lat., *P. flavipunctatus*, *P. minimus* and *P. simonettai*, *P. crucifer*, and *P. somalicus* + the *P. carteri* group. The absence of either fossils or a molecular clock again makes it difficult to assess whether the separation of members of each of these units was caused by vicariance when the southern part of the Red Sea opened during events related to those which separated Socotra, or if occurrence on both sides of the sea was at least sometimes the result of subsequent transmarine or overland migration. Many other squamate groups have disjunct ranges with different populations or species on each side of the southern Red Sea, including *Hemidactylus* geckos, spiny-tailed agamids, *Uromastix thomasi* and *U. princeps* (Amer & Kumazawa, 2005); *Acanthocercus* agamids, the *Chamaeleo chamaeleon* group (Macey *et al.*, 2008), *Latastia* and *Philochortus* lacertids, *Trachylepis* skinks, monitor lizards (*Varanus*), worm lizards (*Agamodon*), and puff adders (*Bitis*).

Separation within Arabia. Many relatively mesic groups show differentiation within southern Arabia, with North Oman often having different taxa from Yemen and the adjoining Dhofar region of southern Oman. This is so in *Pristurus*, with North Oman having the endemic *P. celerrimus*, the most primitive species of *Pristurus*, *P. gallagheri*, and its own group of lineages presently assigned to *P. rupestris* (S. Carranza and E. N. Arnold, unpublished data).

Island and montane restriction. While some species of *Pristurus* are restricted to islands, in the Socotran archipelago, others are limited to mountain areas. In some of these cases, an ecologically similar form occurs nearby and is the only one occurring in surrounding more lowland areas. Instances include the following (with the more lowland forms given in brackets): *P. celerrimus* and *P. gallagheri* in North Oman (*P. rupestris*), *P. insignoides* on Socotra (*P. insignis*), *P. popovi* (*P. rupestris*) and *P. saada* in west Yemen, *P. phillipsi* (*P. somalicus*) in northern Somalia. In such cases, restriction to mountains by competition from the more lowland forms is a possibility, and, once such taxa are restricted, the stability of climatic niches in mountain areas, makes it likely that they will persist (Arnold, 1981, Carranza *et al.*, 2004). Knowledge of the species of *Pristurus* and their evolution would be considerably less extensive, if it were not from the way mountains and islands have apparently maintained over half of the presently recognized species in the genus.

Concluding remarks

If the morphological estimate of phylogeny of *Pristurus* reflects reality, primitive semaphore geckos underwent extensive replacement on the mainland of Arabia, and possibly in northern Africa too, by species with similar spatial niches. Analogous events appear to have taken place in lacertid lizards in Europe and surrounding regions (Arnold, 1989, 2004; Arnold *et al.*, 2007). If such replacement has occurred, it is possible that inadvertent introduction of advanced mainland ecological analogues of the more primitive Socotran species on to the archipelago would have disastrous effects on the endemics there.

Most of the seven or so lineages in the advanced mainland radiation occupy generally similar spatial niches to the relict primitive forms, and apart from their initial advancement are not very varied in their morphology. In contrast, the ancestral lineage of the *Spatalura* clade invaded previously unexploited ecological space, evolved numerous morphological novelties, and radiated. A speculative explanation of these events is that the ancestral lineage of *Spatalura* was isolated in an atypical situation, where there were few objects to climb on, and subsequently adapted to life almost exclusively on the ground. When the lineage later became sympatric with climbing forms, competition with these may have restricted it to this spatial niche. At first sight, it is less easy to suggest why the ancestral *Spatalura* lineage broadened its temporal niche to include a degree of nocturnality, especially as there are other night-active, ground dwelling geckos within the present range of *Spatalura*, particularly members of *Stenodactylus* and *Tropicolotes*. But there may have been available niche space in the nocturnal lizard community that was not or poorly occupied by other forms. It is interesting that, at least in parts of Dhofar in southern Oman, *P. rupestris* (a member of the usually climbing *P. flavipunctatus* assemblage) is occasionally encountered on the ground, after dark, behaving much like the ancestor of *Spatalura* would be expected to have done.

The lineage leading to advanced members of the *Pristurus carteri* group in particular has apparently been eventful in both in terms of ecological and morphological change. Nocturnal geckos active at relatively low body temperatures that also probably climbed have evolved into a rough ecological analogue of some small diurnal ground-dwelling desert iguanians that are active at high temperatures. These include toad-headed agamids (*Phrynocephalus*) in Asia and gridiron-tailed phrynosomatine iguanians (*Callisaurus*) in North America (Arnold, 1990b, 1994). In the large amount of change involved, the *P. carteri* group is like *Meroles anchietae*, a member of the South African sand lizard clade (Arnold, 1990b). Both contrast with the generally smaller degree of change encountered in such speciose groups as the Lacertini (Arnold et al, 2007), where there is no main lineage on which there is steady shift towards more derived states. As suggested elsewhere (Arnold, 1990b), the robustness of some phylogenies based on morphology may often be a result of such eventfulness.

Although change in many morphological characters of *Pristurus* appears simple, being unidirectional and often without much if any homoplasy, there are exceptions. In these features, reversals may occur and sometimes more than once, especially when the ancestral lineage of the genus is also taken into account. When this is done, it is clear that body size was probably originally quite large, fell somewhere in the ancestral lineage of *Pristurus*, and increased again in the *P. carteri* group; the same is probably true of clutch size. There was also a shift to nocturnality early in the history of geckos with a reversion to diurnality within the sphaerodactylids and then one back to partial nocturnality in the *Spatalura* clade; these temporal shifts were apparently accompanied by functionally related ones in pupil shape. In addition, the frontal bone became tubular in basal gekkotans and reverted to the flat condition, likely to have been primitive for squamates in general, in most members of the *P. flavipunctatus* assemblage and in the *Spatalura* clade. Such homoplastic changes are probably commoner than they appear, as the algorithm used in phylogenetic parsimony analysis minimizes such events.

It is not yet known over what time period *Pristurus* has radiated to produce its current species, with their wide variation in ecology and behaviour, though molecular clocks based on nuclear DNA sequence suggest the group is an old one, that perhaps separated from other surviving members of the Sphaerodactylidae in the Cretaceous period 100 ± 20 My ago. (Gamble *et al.*, 2008a). While there are no procedural problems in using a phylogeny based on morphology to explore the evolution of morphological features, it is clearly desirable to test both the phylogeny and indirectly conclusions about evolution, using an independent data set. There is consequently an urgent need to investigate DNA sequence within *Pristurus*, which would also provide estimates of timings of events that have occurred in the genus.

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Appendix I. Morphological similarities between *Pristurus* and other main taxa in the Sphaerodactylidae

Nineteen characters are listed below that vary within the Sphaerodactylidae and for which *Pristurus* nearly always has the most derived condition. Distribution of the states of the characters in taxa of Sphaerodactylidae is given in Appendix II.

1. *Body size*. Usually over 50 mm from snout to vent (0); less than 50 mm from snout to vent in most cases (1).
Some *Pristurus* exceed 50 mm but analyses of species relationships in the genus indicate that this is secondary.
2. *Ascending process of premaxillary bone long and nasal bones relatively short*.
No (0); yes (1).
3. *Splénial bone*. Present (0); absent (1).
4. *Parafrontal bones*. Absent (0); present (1).
These structures have been discussed by Bauer and Russell (1989) and Gamble *et al.* (2008a)
5. *Number of presacral vertebrae*. Usually 26 (0); usually 25 or fewer (1).
6. *Shape of pupil*. Vertically elliptical and closing to a slit (0); rounded, but often somewhat higher than wide (1); more or less round, not obviously higher than wide, not closing to a slit (2).
Some *Pristurus* possess a vertically elliptical pupil that closes to a slit, but analyses of species relationships in the genus indicate that this is secondary.
7. *Preanal and femoral pores*. Often or always present (0); absent (1).
8. *Cloacal tubercles*. Present (0); absent (1).
9. *Postcloacal sacs*. Present (0); absent (1).
10. *Postcloacal bones*. Present (0); absent (1).
11. *Sexual dichromatism*. More or less absent (0); often present (1).
Many *Pristurus*, *Quedenfeldtia* and the Sphaerodactylini show some degree of sexual dichromatism, although this often involves different features.
12. *Characteristic dorsal pattern of longitudinal lines of short, dark or reddish, streaks separated by paler spots, especially on the flanks*. No (0); yes (1).
13. *An 'escutcheon' of large rugose scales in preanal and subfemoral regions of males*. No (0); yes (1).
Sphaerodactylini often have a patch of enlarged and rugose scales in the preanal region that constitutes an escutcheon generation gland (Maderson, 1972). Superficially similar patches occur in *Quedenfeldtia* and in the most primitive species of *Pristurus*, *P. celerrimus*. These have not yet been examined histologically, so it is not certain that they are strictly homologous with the condition found in Sphaerodactylini.
14. *Colouring of 'escutcheon' if present*. Light (0); dark (1).
15. *Meatal closure muscle*. Present (0); absent (1).
The meatal closure muscle of geckos, first described by Versluys (1898), was discussed in greater detail by Wever (1973, 1974, 1978) and its distribution and systematic significance considered by Kluge (1987). The muscle is absent in Sphaerodactylini, at least some *Pristurus* (*P. crucifer* and *P. phillipsi* - Kluge, 1987; *P. insignis* and *P. carteri* - personal observations). It is also lacking in *Teratoscincus*, *Euleptes*, *Sauroidacylus mauritanicus* and *Quedenfeldtia* (personal observations).
16. *Clutch size*. Usually two eggs (0); usually one egg (1).
A clutch consisting of a single egg, instead of the usual gecko number of two, occurs in *Pristurus*, *Quedenfeldtia*,

Sphaerodactylini, *Saurodactylus* and *Aristelliger* (Kluge & Nussbaum, 1995; personal observations). A few *Pristurus* species sometimes lay two eggs, but analyses of species relationships in the genus indicate that this is secondary. Production of single eggs also occurs occasionally in other non-sphaerodactylid geckos, for example in the gekkonid *Stenodactylus arabicus* (Arnold, 1984), in the phyllodactylid *Asaccus* (Arnold and Gardner, 1994), and in other forms listed by Kluge (1987).

17. Activity in light. Not usual (0); in subdued light (1); in bright light, including direct sun-light (2).
Most geckos are predominantly nocturnal, but a few are regularly active by day; some of these usually avoid the brightest conditions, for instance *Saurodactylus* is crepuscular (Bons, 1959); others, like *Quedenfeldtia* and *Pristurus* are often active in bright sunlight (Arnold, 1993)
18. Tail often raised as an intraspecific signal. No (0); yes (1).
This behaviour occurs in many *Pristurus* (Arnold & Gallagher, 1977; Arnold, 1980b, 1993) and also in *Quedenfeldtia* (Arnold, 1993).
19. Vocalisation. Usually frequent and often strong (0); infrequent, weak or absent (1).

Appendix II. Data set for main taxa of Sphaerodactylidae and its synthetic outgroup made up of what appear to be primitive states in the Gekkonidae and Phyllodactylidae, which together form the sister group of the Sphaerodactylidae. For details of characters and character states, see Appendix I

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
<i>Pristurus</i>	1	1	1	0	1	2	1	1	1	1	1	1	0/1	1	1	1	2	1	1
<i>Quedenfeldtia</i>	1	1	0	0	1	2	1	0	1	1	1	1	1	1	1	1	2	1	1
<i>Sphaerodactylini</i>	1	0	1	0	0	1	1	1	1	1	1	0	1	0	1	1	1/2	0	1
<i>Saurodactylus</i>	1	0	0	0	1	0	1	1	1	1	0	0	0	-	1	1	1	0	1
<i>Teratoscincus</i>	0	0	0	1	0	0	1	0	0	0	0	0	0	-	1	0	0	0	0
<i>Euleptes</i>	1	0	0	0	0	0	1	0	0	0	0	0	0	-	1	0	0	0	0
<i>Aristelliger</i>	0	0	0	1	0	0	1	1	1	1	0	0	0	-	0	1	0	0	0
<i>Synthetic_outgroup</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0

Appendix III. Characters and data set for phylogenetic analysis of relationships of species of *Pristurus*

Eighty characters are listed below that vary within *Pristurus* and its relatives; eight that are invariant within *Pristurus*, or likely to be so, are marked with asterisks. Distribution of the states of the characters in the species of *Pristurus* is given in Appendix IV.

Size and head proportions

1. Maximum adult size (length from snout to vent). 30-50 mm (0,0); over 50 mm (1,0); under 30 mm (0,1).
2. Head elongate. No (0); yes (1).
3. Head bulbous. No (0); yes (1).
4. Snout acutely pointed. No (0); yes (1).

Skull

5. Premaxillary foramen. Completely surrounded by bone (0); not enclosed posteriorly (1).
6. Posterior ascending process of premaxilla. Relatively short (0); longer, often more than 0.8 of distance from snout-tip to orbit (1).
7. Shape of posterior ventral border of premaxilla. Narrowed and W-shaped (0); W-shaped but not especially narrowed (1); two long rounded projections (2); two short, rounded projections (3).
8. Premaxilla and maxillae imbricate ventrally. Yes (0); no (1).
9. Exposed nasal capsule in anterior wall, of orbit calcified. Yes (0); no (1).
10. Lower part of prefrontal bone visible in anterior view of skull. No (0); yes (1).
11. Relation of dorsal spur of prefrontal bone to frontal bone. Simple contact without indentation (0); marked indentation, but outer side of prefrontal not flanked by frontal (1); strong indentation, with outer side of prefrontal partly bordered by frontal (2).

12. Contact between frontal bone and posterior surface of prefrontal bone. Simple (0); frontal notching prefrontal (1).
13. Frontal bone with downgrowths that fuse beneath olfactory tract to form tube. Yes (0); no (1).
14. Anterior descending process of frontal. Well developed (0); short (1); absent (2).
15. Frontal bone very narrow in middle compared with its posterior border. No (0); yes (1).
16. Dorsal surface of frontal bone more or less concave anteriorly. No (0); yes (1).
17. Small downward process on underside of parietal bone directed towards epipterygoid. Present (0); absent (1).
18. Shape of supraoccipital bone. Undomed, not projecting above parietals (0); domed and forming a boss projecting above level of parietals which it truncates convexly (1).
19. Relationship of supratemporal process of parietal bone to exoccipital and squamosal. Supratemporal process of parietal bone only reaching exoccipital in a point and not fully attached, squamosal bone relatively long (0); supratemporal process often expanded and fully attached to exoccipital bone, squamosal bone often short and curved (1).
20. Foramen magnum. Roughly oval, broader than high (0); more or less round (1); higher than broad (2).
21. Dorsal anterior border of maxilla. Turning forwards medially (0); not turning forwards (1).
22. Ventral contact between maxillae. None or just at a point (0); broad contact but no imbrication (1); broad contact with imbrication and usually complex interdigitation (2).
- *23. Palatine bone contacts vomer narrowly. No (0); yes (1).
24. Shape of suborbital foramen. Elongate (0); broad (1).
25. Alar projection on prootic. Present (0); absent (1).
26. Position on prootic of upper end of epipterygoid. On outer face of alar projection (0); on inner face, lower down (1).
27. Angle of supraoccipital bone. Sloping gently downwards and backwards to foramen magnum (0); more vertical (1).
28. Horizontal semicircular canal prominent and ridged, making a deep lateral hollow. No (0); yes (1).
29. Angle of upper surface of horizontal semi-circular canal to base of brain case. Small (0); large (1).

Mandible

- *30. Splenial bone. Present (0); absent (1).
- *31. Shape of posterior margin of lateral exposure of dentary bone. Tridentate (0); not obviously tridentate (1).
- *32. Posterior extent of lateral exposure of dentary bone. Scarcely extending beyond level of coronoid bone (0); extending well beyond level of coronoid bone (1).
33. Posterior surangular foramen. High (0); low (1).

Hyoid

34. Hyoid cornu. Narrow and directed laterally, or occasionally absent (0); broad (1).
35. Second ceratobranchial cartilage. Relatively long, as long as distance from its base to fork of basihyal (0); small or minute, shorter than distance from its base to fork of basihyal, often directed inwards (1).
36. Second epibranchial cartilage. Present (0); absent (1).

Postcranial skeleton

37. Usual number of presacral vertebrae. 25 (0); 24 (1); 23 (2).
38. Zygopophyses of presacral vertebrae reflexed medially. No (0); weakly reflexed in thoracic region (1); weakly reflexed in all presacral vertebrae (2); strongly reflexed in all presacral vertebrae (3).
39. Usual number of complete xiphisternal ribs. Two (0); three (1); one (2).
40. Medial section of clavicle. More or less horizontal (0); rotated forwards (1).
41. Size of interclavicle. Large (0); small (1).
42. Posterior section of sternum. Long (0); short (1).
43. Articular face on transverse processes of sacral vertebrae. Elongate (0); not so (1).
44. Usual number of pygal vertebrae. Five (0); four or less (1).
45. Zygopophyses of pygal vertebrae reflexed medially. No (0); weakly (1); strongly (2).

External features

46. Mental scale often narrower than rostral scale. No (0); yes (1).
47. Nostril separated from rostral scale by downward extension of supranasal scale and forward extension of lower postnasal scale. No (0); yes (1).
48. Lower supranasal and lower postnasal scales. Distinct from each other, even when in contact (0); confluent (1).

49. Upper postnasal scale. Present and contacting nostril (0); absent or separated from nostril (1).
50. Supranasal scale divided into upper and lower sections. No (0); yes (1).
51. Number of scales on snout separating supranasal scales from each other. One or two (0); three or more (1).
52. Upper labial scales extend back to level of posterior border of eye. No (0); yes (1).
53. Palpebral fold narrow above. No (0); yes (1).
54. Palpebral fold with enlarged scales on its edge some of which may be ciliate. No (0); yes (1).
55. Pupil shape. Not narrower than high, dorsal and ventral angulation of margin poorly marked (0); pupil narrower than high when contracted, dorsal and ventral angulation better marked (1).
56. Post-axillary mite pockets (Arnold, 1986b) present in at least some individuals. No (0); yes (1).
- *57. An enlarged cloacal tubercle on each side of tail base. Yes (0); no (1).
58. Usual number of longitudinal dorsal scale rows on distal part of fourth toe. Five (0); more than five (1).
59. Lower ungual lamellae notched. Yes (0); no (1).
60. Longest digit on manus. Fourth (0); third (1).
61. Intact tail longer than distance from snout to vent. Yes (0); no (1).
- *62. Tail laterally compressed in males. No (0); yes (1).
63. Neural spines of caudal vertebrae often reach dorsal midline of tail in males, producing a wavy upper profile. No (0); yes (1).
64. Shape of distal part of tail. Tapering steadily to a point (0); not tapering steadily and tip rounded, or only tapering abruptly at tip (1).
65. Tail with dorsal crest of clearly enlarged, pointed and usually elongate scales in males. No (0); very slight indications (1); yes (2).
66. Number of more or less complete longitudinal scale rows forming proximal dorsal crest on tail in males. One (0); two (1).
67. Tail with ventral crest of clearly enlarged scales in males that are often pointed and elongate. No (0); yes (1).
68. Caudal autotomy. General, breakage may take place through any post-pygial vertebra (0); breakage nearly always confined to tail base (1).
69. Shape of regenerated tail. Similar to original tail (0); different from original, usually short and blunt (1).
70. Pale vertebral stripe discernable on body in at least some alcohol-preserved individuals. No (0); yes (1).
71. Brightly coloured, red, orange or yellow vertebral stripe discernable in at least some live or recently preserved individuals (this may wholly or partly cover pale stripe of character 70 if present). No (0); yes (1).
72. Dark transverse collar across throat. No (0); usually weak (1); strong (2).
73. Dark pigment on posterior venter of males. None (0); in interfemoral region and on proximal tail (1)

Internal soft-part characters

74. Palatal flaps. Well developed (0); not well developed (1).
75. Notch in tongue tip. Clear (0); absent (1).
76. Distal sublingual plates. Well developed (0); reduced (1).
- *77. Anterior nuchal muscle. Originating mainly on third vertebra, with deep slip to second vertebra (0); originating mainly on second vertebra, with superior slip originating on front of third vertebra and crossing remainder more sagittally (1).
78. Origin of sternocleidomastoideus muscle. Lateral to origin of sternothyroideus (0); deep to origin of sternothyroideus (1).
- *79. Pectoralis muscles. Not reaching opposite side of sternum (0); reaching opposite side of sternum (1).
80. Window in abdominal muscles. No (0); yes (1).

Appendix IV. Data set for species of *Pristurus* and outgroups comprising the sphaerodactylid taxa *Quedenfeldtia*, *Sphaerodactylini*, *Teratoscincus*, and a synthetic outgroup made up of what appear to be primitive states in the *Gekkonidae* and *Phyllodactylidae*, which together form the sister group of the *Sphaerodactylidae*. For details of characters and character states, see Appendix III.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
<i>P. celerrimus</i>	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	-	0	0	0	1	0	0
<i>P. insignis</i>	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	1	0	0
<i>P. insignoides</i>	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	1	0	0
<i>P. guichardi</i>	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0
<i>P. socotranus</i>	0	1	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0
<i>P. abdelkuri</i>	0	1	0	0	0	0	2	1	1	0	1	0	0	1	0	0	0	0	1	0	0	1	1	1	0
<i>P. rupestris</i>	0	0	0	0	0	0	3	1	1	0	2	0	0	2	0	0/1	0	0	1	0	0	2	1	1	0
<i>P. popovi</i>	0	0	0	0	0/1	0	3	1	1	0	2	0	1	2	0	0	0	0	1	0	0	2	1	1	0
<i>P. gallagheri</i>	0	1	0	0	0	0	2	1	1	0	2	0	1	1	0	1	0	1	1	0	0	2	1	1	0
<i>P. flavipunctatus</i>	0	0	0	0	0	0	2/3	0/1	1	0	2	0	1	2	0	1	0	1	1	0	0	2	1	1	0
<i>P. adrarensis</i>	0	1	0	0	?	1	3	1	?	?	?	?	1	1	0	0	?	?	?	?	?	2	1	1	1
<i>P. minimus</i>	2	0	0	0	0	1	3	1	1	1	2	0	1	2	0	0	0	0	1	0	0	2	1	1	1
<i>P. simonettai</i>	2	1	0	0	0	1	3	1	1	1	2	0	1	2	0	0	-	0	1	0	0	2	1	1	1
<i>P. crucifer</i>	0	0	1	0	0	1	3	1	1	1	2	0	1	2	0	0	0	0	1	0	0	2	1	1	1
<i>P. phillipsi</i>	0	0	1	0	0	1	3	1	1	1	2	0	1	2	0	0	0	0	1	0	1	2	1	1	1
<i>P. somalicus</i>	0	0	1	0	0	1	3	1	1	1	2	0	1	2	0	0	0	0	1	1	0	2	1	1	1
<i>P. saada</i>	0	0	1	0	1	1	3	1	1	1	0	1	1	2	1	0	0	0	1	1	1	2	1	1	1
<i>P. collaris</i>	1	0	1	1/2	0	1	3	1	1	1	0	1	1	2	1	0	0	0	1	2	1	2	1	1	1
<i>P. ornithocephalus</i>	1	0	1	1	1	1	3	1	1	1	0	1	1	2	1	0	1	0	1	2	0	2	1	1	1
<i>P. carteri</i>	1	0	1	0	1	1	3	1	1	1	0	1	1	2	1	0	1	0	1	2	1	2	1	1	1
<i>Quedenfeldtia</i>	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Sphaerodactylini</i>	0	-	0	0	-	0	-	-	0	-	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Teratoscincus</i>	1	0	0	0	0	0	0	0	0	-	-	0	0	0	-	-	0	0	0	0	0	0	0	0	0
Synthetic outgroup	0/1	0/1	0	0	-	0	0	0	0	0	0	0	0	0/1	0	0/1	0	0	0	0	0	0	0	0	0

	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50
<i>P. celerrimus</i>	0	0	0	0	1	1	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0
<i>P. insignis</i>	0	0	0	0	1	1	1	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>P. insignoides</i>	0	0	0	0	1	1	1	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>P. guichardi</i>	0	0	0	0	1	1	1	1	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>P. socotranus</i>	0	0	0	0	1	1	1	1	0	0	1	1	1	0/1	0	0	0	0	0/1	0	0	0	0	0	0
<i>P. abdelkuri</i>	1	0	0	0	1	1	1	1	0	0	1	2	3	2	0	0	0	1	1	0	0	0	0	0	0
<i>P. rupestris</i>	0	0	0	0	1	1	1	1	0	0	1	2	2	2	0	0	0	0	1	1	0	0	0	0	0
<i>P. popovi</i>	0	0	0	0	1	1	1	1	0	0	1	2	2	2	0	0	0	0	1	2	0	0	0	0	0
<i>P. gallagheri</i>	0	0	0	0	1	1	1	1	0	0	1	2	2	2	0	0	0	0	1	1	0	0	0	0	0
<i>P. flavipunctatus</i>	0	0	0	0	1	1	1	1	0	0	1	2	2	2	0	0	0	0	1	2	0	0	0	0	0
<i>P. adrarensis</i>	1	?	?	?	1	?	?	?	?	?	2	2	2	2	0	?	?	?	1	?	0	0	0	?	?
<i>P. minimus</i>	1	0	0	0	1	1	1	0	0	1	1	2	3	2	0	0	1	1	1	1	0	1	0	0	0
<i>P. simonettai</i>	1	0	0	0	1	1	1	1	0	1	1	2	2	2	0	0	1	1	1	1	0	1	0	0	0
<i>P. crucifer</i>	1	0	0	1	1	1	1	1	0	1	1	2	3	2	0	0	1	1	1	2	0	1	1	0/1	0
<i>P. phillipsi</i>	1	0	0	1	1	1	1	1	0	1	1	2	3	2	0	0	1	1	1	2	0	1	1	0/1	0
<i>P. somalicus</i>	1	0	0	1	1	1	1	1	0	1	1	2	3	2	0	0	1	1	1	2	0	1	1	0/1	0
<i>P. saada</i>	1	0	0	1	1	1	1	1	0	1	1	2	3	2	1	1	1	1	1	2	0	1	1	0/1	0/1
<i>P. collaris</i>	1	1	1	1	1	1	1	1	0	0	1	1	2	3	2	1	1	1	1	1	2	1	1	1	0/1
<i>P. ornithocephalus</i>	1	1	1	1	1	1	1	0	0	1	1	2	3	2	1	1	1	1	1	2	1	1	1	0/1	0/1
<i>P. carteri</i>	1	1	1	1	1	1	1	0	0	1	1	2	3	2	1	1	1	1	1	2	0	1	1	0/1	0/1
<i>Quedenfeldtia</i>	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Sphaerodactylini</i>	0	0	0	0	1	0	0	-	-	-	0	0	0	0	0	0	-	-	0	-	0	0	-	0	0
<i>Teratoscincus</i>	0	-	-	0	0	0	0	0	-	-	0	0	0	0	0	0	-	0	0	0	0	0	-	0	0
Synthetic outgroup	0	0/1	0	0	?	?	?	-	-	0/1	0	0	0	0	0	0	?	0	0	?	0	0	-	0	0

	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80
<i>P. celerrimus</i>	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	-	0	0	0	0	0	0	1	0	0	0	1	0	1	0
<i>P. insignis</i>	0	0	1	1	0	0	1	1	0	0	0	1	1	0	0	-	0	0	0	0	0	0	0	0	0	0	1	0	1	0
<i>P. insignoides</i>	0	0	0	0	0	0	1	1	0	0	0	1	1	0	0	-	0	0	0	0	0	0	0	0	0	0	1	0	1	0
<i>P. guichardi</i>	0	0	1	1	0	0	1	1	0	0	0	1	0	0	1	-	0	0	0	1	-	0	0	0	0	0	1	0	1	0
<i>P. socotranus</i>	0	0	0	0	0	0	1	0	0	0	0	1	0	0	2	0/1	1	0	0	1	1	0	0	0	0/1	0	1	0	1	0
<i>P. abdelkuri</i>	0	0	0	0	0	0	1	0	0	0	0	1	0	0	2	0	1	0	0	1	-	0	0	0	1	1	1	0	1	0
<i>P. rupestris</i>	0/1	0	0	0	0	0	1	0	0	0	0	1	0	0	2	1	1	0	0	1	1	0	0	0	0/1	0	1	0	1	0
<i>P. popovi</i>	1	0	0	0	0	0	1	0	0	0	0	1	0	0	2	0	1	0	0	1	1	0	0	1	0	1	0	1	0	1
<i>P. gallagheri</i>	0	0	1	1	0	0	1	0	0	0	0	1	0	0	2	0	1	0	0	1	1	0	0	0	0/1	0	1	0	1	0
<i>P. flavipunctatus</i>	0	0	1	1	0	0	1	0	0	0	0	1	0	0	2	0	1	0	0	1	1	0	0	1	0/1	0	1	0	1	0
<i>P. adrensensis</i>	0	0	0	1	0	0	1	?	?	0	0	1	0	0	1	1	1	0	0	0	0	0	0	?	?	?	?	?	?	?
<i>P. minimus</i>	1	1	0/1	0/1	1	0	1	0	0/1	1	0	1	0	0	2	1	1	0	0	1	1	0	0	1	1	1	1	1	1	0
<i>P. simonettai</i>	1	1	0	0	1	0	1	0	1	1	0	1	0	0	1	0	0	0	0	1	-	0	0	1	1	1	1	1	1	0
<i>P. crucifer</i>	1	0	0	0	1	0	1	0	1	1	0	1	0	0	2	0	1	0	0	1	1	0	0	0	1	1	1	1	1	0
<i>P. phillipsi</i>	1	0	0	0	1	0	1	0	1	1	0	1	0	0	2	0	1	0	0	1	-	0	0	0	1	1	1	1	1	0
<i>P. somalicus</i>	1	0	0	0	1	1	1	0	1	1	0	1	0	0	2	0	1	0	0	0	0	0	0	0	1	1	1	1	1	0
<i>P. saada</i>	1	0	0	1	1	1	1	0	1	1	1	1	0	0	2	0	1	1	1	0	0	2	0	0	1	1	1	1	1	0
<i>P. collaris</i>	1	0	0	1	1	1	1	0	0/1	1	1	1	0	0	2	0	1	1	1	0	0	2	0	0	1	1	1	1	1	1
<i>P. ornithocephalus</i>	1	0	0	1	1	1	1	0	0/1	1	1	1	0	1	2	0	1	1	1	0	0	1	0	0	1	1	1	1	1	1
<i>P. carteri</i>	1	0	0	1	1	1	1	0	0	1	1	1	0	1	2	0	1	1	1	0	0	1	0	0	1	1	1	1	1	1
<i>Quedenfeldtia</i>	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>Sphaerod actylini</i>	0	-	-	0	1	-	1	-	-	0	0	0	0	0	0	-	0	0	0	-	-	0	0	-	0	0	0	0	0	0
<i>Teratoscincus</i>	0	-	0	0	0	0	0	-	0	0	1	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Synthetic outgroup	0	-	0	0	1	0	0	-	-	0/1	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0