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Historical changes in the ecology and behaviour of semaphore geckos (*Pristurus*, Gekkonidae) and their relatives

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(With 6 figures in the text)

Semaphore geckos (*Pristurus*) and their relatives have a very robust and explicit morphological phylogeny, consisting of a long pectinate tree in which the number of derived morphological states increases steadily through time. This clade consequently provides a firm base for investigating changes in ecology and behaviour. Data on these topics including diet, pattern of tail shedding and clutch size were integrated with the phylogeny and substantial regularity demonstrated in the way they have changed over time. Ancestral forms were apparently climbers on rocky surfaces and active in subdued light. There was subsequent shift into more open, sunny situations with two or three transfers into arboreal habitats which were accompanied by reversion to more shaded conditions. A change to ground-dwelling occurred perhaps twice within *Pristurus*, including the ancestor of the Spatalura clade, a group which has reverted to typical gecko nocturnality while still retaining diurnal activity. Overall, there has been a progression into hotter, drier and more open habitats.

Other shifts within the clade are adoption of passive foraging techniques, development and elaboration of intraspecific tail signalling and change in the kinds of refuges used. Clutch size fell from two eggs to one early in the clade history with subsequent partial reversion to two. Ants and sometimes termites became an important item of diet in some taxa and frequent trombiculid mite infestation appeared in the terminal group within which caudal autotomy became confined to the tail base.

Overall, the habitats occupied by morphologically advanced *Pristurus* appear more demanding, and perhaps less rewarding, than those in which their more primitive relatives live. This may result from species that did less well in competition, following each of the speciation events on the main stem of the phylogeny, being displaced into increasingly severe niches. The substantial morphological changes taking place in the evolution of the clade may be related to the problems of survival in these.

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Introduction

If phylogenetic information is available for a taxonomic group, this can be integrated with data about other aspects of the species involved, such as their ecology and behaviour, to produce at least a partial history of their adaptive radiation. It may then be possible to state what original conditions in a studied group were and how they subsequently changed. For instance, it can be shown by these methods that constriction of prey is a relatively primitive behaviour among snakes (Greene & Burghardt, 1978), the ability to shed the tail as a means of escaping from predators has been lost many times in lizards (Arnold, 1984*a*, 1988), coadaptation between optimal temperature and thermal preference breaks down in some Australian skinks (Huey & Bennett, 1987), and limb length evolves to improve locomotory performance in conjunction with habitat shift in *Anolis* lizards (Losos, 1990). More general histories of groups can also be produced and used to address such questions as whether the robustness and consistency of morphological phylogenies is related to the kind of evolutionary experiences the groups concerned have had (Arnold, 1990*a*).

For such investigations to be tenable, the phylogeny of the taxonomic group has to be relatively robust, either in whole or part. Even when this is so, the actual topology of the phylogeny may restrict what can be said and with what confidence. In general, phylogenies with numerous branches on their main stem, or stems, are likely to allow more historical statements to be made than ones where the number of branching points between the ancestral taxon and particular species is low (Arnold, 1990*a*).

The clade made up of the semaphore geckos (*Pristurus*), their sister group, the Moroccan day geckos (*Quedenfeldtia*), and related forms is of considerable interest as it shows great morphological differentiation and substantial differences in its habitats, behaviour and general mode of life. While some members of this group have life modes quite similar to many other geckos, the more extreme ones behave more like small desert agamid lizards (Arnold, 1980). With phylogenetic information, it should be possible to see how life mode, habitat and behaviour have changed in the group.

Pristurus has 19 largely diurnal species in the Arabian region and adjoining north-east Africa, while *Quedenfeldtia* has just two species. Their relationships are discussed elsewhere (Arnold, 1990*b*, subm. *a*). The clade made up of these two genera is most closely related to the Sphaerodactylini of tropical America and, with these, it may be related successively to *Saurodactylus* of north-west Africa and the south-west African *Narudasia*. The phylogeny of *Pristurus* and *Quedenfeldtia*, based on morphology, is distinctive in being robust and explicit, with most nodes supported by several derived character states (Fig. 1). It is essentially pectinate (comb-like) with many branches, each comprising one or two species, arising successively from a single stem along which the number of derived states increases steadily. As such it constitutes a firm base for making inferences about other aspects of these geckos.

Pristurus comprises a series of relatively primitive species leading to a holophyletic assemblage characterized by a wide range of derived features; this is known informally as the Spatalura clade. Within this, the four most advanced species constitute the *Pristurus carteri* group (*P. saada*, *P. collaris*, *P. ornithocephalus* and *P. carteri*).

Regrettably, few systematic studies of the ecology and behaviour of *Pristurus* and *Quedenfeldtia* have been made (Arnold & Gallagher, 1977; Arnold, 1980; Ross, 1990; Gardner, subm.). However, these can be supplemented from a number of sources. There are numerous less formal observations scattered through the herpetological literature (Blanford, 1874; Boulenger, 1903;

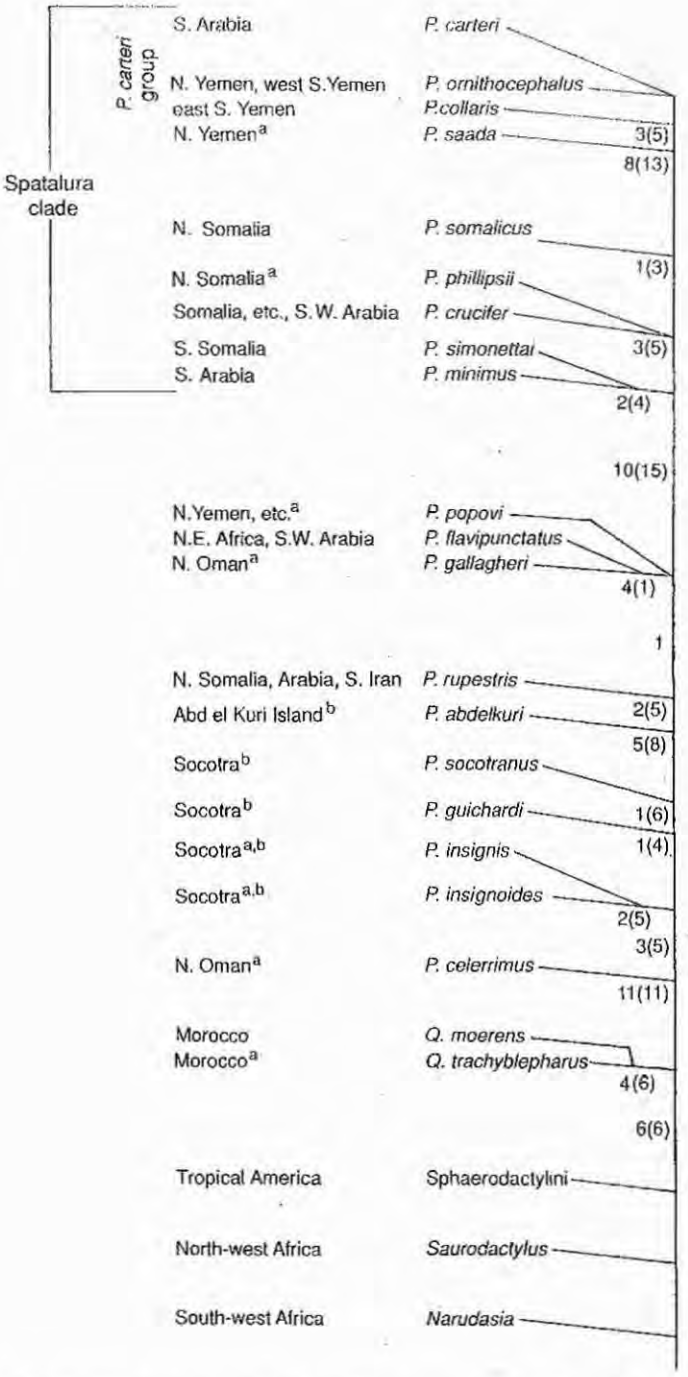

FIG. 1. Phylogeny of *Pristurus*, *Quedenfeldtia* and their presumed relatives, based on morphology, with their geographical ranges. Numbers on the phylogeny indicate the number of derived states supporting each subclade: the first denotes unique transformations, whereas that in parentheses is unique transformations plus others that involve only limited homoplasy; [a] montane distribution; [b] confined to an isolated island. The limits of the Spatalura clade of *Pristurus* and of the *Pristurus carteri* group are shown.

Steindachner, 1903; Neumann, 1905; Scortecci, 1935; Parker, 1942; Hoofien, 1960; Hoofien & Yaron, 1962; Spanò, 1963; Gans, Laurent & Pandit, 1965; Lanza & Sassi, 1968; Klemmer, 1969; Gallagher, 1971; Arnold & Gallagher, 1977; Arnold, 1982; Fritz & Schmitz, 1982; Gallagher & Arnold, 1988; Al-Safadi, In prep.; Schätti, 1989). Unpublished observations exist, made by a number of workers familiar with these geckos in the field (see Acknowledgements) and many specimens in the collection of the Natural History Museum, London have field data attached to them in the form of collector's notes. Some data on diet have been obtained by examining stomach contents of the majority of species. Where possible, pattern of tail shedding, occurrence of trombiculid mite infestations and clutch size has been assessed from preserved material. Finally, in the case of species where very little information is available, tentative inferences about ecology and behaviour have been made from their morphology.

General information on ecology and behaviour of *Quedenfeldtia* and *Pristurus*

Sources listed as 'notes' consist mainly of information attached to individual specimens in the collection of the Natural History Museum, London. A list of the specimens concerned has been deposited in the library of that institution.

Quedenfeldtia trachyblepharus (*Boettger, 1874*)
Morocco

A largely montane species extending up to 4000 m with most populations found above 1800 m. *Quedenfeldtia trachyblepharus* occurs in relatively mesic situations where it lives on rock exposures and boulders.

The following notes are based on observations by C. Weedon and J. Kuylensteirna at Imlil (about 2400 m) in August–September, 1984. At this locality, *Q. trachyblepharus* is active in the morning and again, to a lesser extent, in the late afternoon. It appears to be essentially a passive forager, perching and waiting for food animals to pass, when it will run forwards to pick them up. Pursued animals hide in crevices.

Males are very territorial and are usually about 5 m from each other. Females overlap with these and one or two may occur in the territory of a male. The species is often seen in pairs. Males stand sideways to each other, high on their legs, with the body raised, throat inflated, tail arched upwards and the forelimb nearest to the other male raised. The head may then be bobbed. Either one animal retreats, or fighting may occur, in which case the territory holder usually wins. Females may behave to each other in a similar way. Males respond to females with rapid head bobs and an inflated throat, but not usually with tail movement.

Klemmer (1969) notes that *Q. trachyblepharus* is the only lizard on vertical rock faces above 2500 m. It often reaches high population densities above 2000 m and on favourable south-facing rocks, three to five males sometimes occurring on a square metre of rock face. Territorial disputes are frequent in such situations. In late morning the lizards enter the partial shadow of crevices and may hunt there. Females lay their eggs in crevices.

Sources: C. Weedon and J. Kuylenstierna (pers. comm.); Klemmer (1969). Habitat confirmed for specimens from Asui (M. R. K. Lambert, notes), 25 miles (40 km) south of Marrakesh (N. A. Wood, notes) and Imlil (Royal Military Academy, Sandhurst Expedition, 1967, notes; also by Werner (1931).

Quedenfeldtia moerens *(Chabanaud, 1916)*
Morocco

Quedenfeldtia moerens replaces *Q. trachyblepharus* at lower altitudes. Observations by C. Raxworthy north of Taroudannt in summer, 1983 suggest its general life mode is similar to the latter species. Here it lives on large bare boulders, sometimes several metres across. While these are often near vegetation, they also occur in more open situations. The lizards bask actively. Individuals were seen every few metres and appeared solitary. The tail is raised in a gentle arc at times, especially after a lizard has halted after running.

Sources: C. Raxworthy (pers. comm.). Rocky habitat confirmed for specimens collected at Tafraoute (G. Pasteur, notes).

Pristurus celerrimus *(Arnold, 1977)*
Mountains of northern Oman and eastern United Arab Emirates

Found from sea level to 2000 m in relatively mesic situations, often with exposed water close by, or at least near the surface of the ground. A climbing species that occurs in local concentrations on large rocks, especially in boulder screes, and on smooth cliffs with deep fissures. Of 45 individuals observed in the United Arab Emirates, 16 (35%) were over a metre from the ground, often considerably more so.

Essentially diurnal, although sometimes active just after dusk, but seems to avoid direct exposure to the sun except in relatively cool periods. Body temperatures of four animals collected in the United Arab Emirates were 32°, 34°, 37·5° and 38 °C (mean 35·4 °C). *Pristurus celerrimus* is extremely swift in its movements. Hunting animals sit and observe the surrounding area, but perches are often abandoned quite quickly, the lizard frequently moving a substantial distance before pausing again. Resting animals often sit head downwards on the corner of a boulder and are thus able to scan more than one of its faces and the ground below. *Pristurus celerrimus* appear to communicate with each other by movements of the often strongly barred tail, which is held straight and rigid and flicked upwards to fall more slowly, the movement being repeated a number of times. This behaviour occurs in even quite young animals.

Pristurus celerrimus occurs in the same places as *P. rupestris* but habitually climbs higher. In contrast to *P. celerrimus*, only five (11%) out of the 46 *P. rupestris* seen in the habitats of the former were over a metre from the ground ($P < 0{\cdot}01$, χ^2 test). *Pristurus rupestris* occurs on smaller rocks than *P. celerrimus* at times, is very clearly a passive forager, and is not so local in its distribution.

Sources: Arnold & Gallagher (1977); Arnold (notes). General ecology confirmed for populations from the Jebel Akhdar region, northern Oman (Gardner, subm.). Habitat confirmed for specimens from Ruus al Jabal, Musandam (M. D. Gallagher, notes) and from Jebel Akhdar (M. D. Gallagher, P. G. White, notes).

Pristurus insignis *(Blanford, 1881)*
Socotra

A highland form. Grant, in Boulenger (1903), states that the remarks on habits he makes about *P. socotranus*, (referred to as *P. rupestris*) apply to *P. insignis* as well.

Pristurus insignoides *(Arnold, 1986)*
Socotra

A highland species. As three of the nine '*P. insignis*', collected by Grant and Forbes are actually *P. insignoides*, Grant's remarks about the former species may also apply to this one.

Pristurus guichardi *(Arnold, 1986)*
Socotra

No observations available.

Pristurus socotranus *(Parker, 1938)*
Socotra

A climbing species generally found among the larger rocks on hillsides or on large boulders in the dry beds of water courses, although one specimen came from the trunk of a tree. *Pristurus socotranus* are especially fond of cracks and fissures in the perpendicular faces of cliffs, where they may frequently be seen sunning themselves. They are extremely swift in their movements and constantly on the alert for danger. In consequence, they are very difficult to catch by hand, readily shedding the tail and taking refuge in crevices.

Sources: Grant, in Boulenger (1903, referred to as *Pristurus rupestris*). Occurrence on rocks confirmed and the presence of an individual on a tree noted for specimens from Hadibo Plain (K. M. Guichard, notes).

Pristurus abdelkuri *(Arnold, 1986)*
Abd el Kuri Island

On rocks; diurnal.

Source: K. M. Guichard (pers. comm.).

Pristurus rupestris *(Blanford, 1874)*
Periphery of Arabia; also north-east Africa—northern Somalia, Djibouti, adjoining Ethiopia; coastal Iran and Pakistan (?)

Dhofar, Southern Oman

Pristurus is by far the most widespread lizard in this area, occurring at all localities visited from sea level to over 1000 m above it. It was encountered in towns and villages, on rubbish dumps and beaches, in moist woods, grassland and in the arid country north of the mountains. In all these situations, *P. rupestris* was usually seen on rocks, stones or man-made equivalents such as concrete (83% of 184 observations) but it also occasionally occurred on earth and more or less compact

sand, although usually in the vicinity of hard objects. It has been recorded more rarely on the trunks and branches of trees, on corrugated iron buildings, on car-wrecks and on packing cases. Of 174 lizards 78% checked were perched or climbing on objects but only 22% of the 174 were more than a metre from the ground and only 8% above 1·25 m. The great majority of animals were active by day but at most sites a few individuals could be found out at night. *Pristurus rupestris* adopts a 'sit and wait' hunting strategy, often stopping in one place for long periods. Because of its very small size, no direct body temperatures could be taken, but in such a minute lizard temperature is very likely to be similar to that of the place where it is sitting. Daytime perch temperatures (°C) of 24 previously undisturbed animals were 25° (3), 28° (2), 28·5° (1), 29° (2), 31° (2), 32° (3), 32·5 (1), 33° (2), 34° (2), 34·5° (1), 35° (5). The lower readings were taken in the early morning, when lizards are usually in the sun, and the higher ones later when many individuals have moved to the shade; warm animals tend to be paler than cool ones. Two perch temperatures taken after dusk were 27 °C.

Pristurus rupestris rarely perches far from a refuge such as a crevice or interstices between stones. Of 124 individuals recorded, 54% reached a retreat within 0·5 m and 83% within a metre. Such figures apply to lizards that are hotly pursued; if mildly disturbed they may retreat less precipitately but over larger distances.

Tails, at least of males, are often raised and curled forwards and waved or shaken, either apparently spontaneously or in response to a moving object, particularly another *P. rupestris*. In one case a male curled his tail forwards and a nearby female immediately wagged hers from side to side. Another male was seen following a female and wagging his tail laterally.

North Yemen

Found up to 2500 m near Sana'a and down to about 700 m. Typically encountered in areas with a sharp day-night temperature difference where, in some days in winter, the temperature falls below freezing. Widely distributed in stony places with or without cover and usually found in the direct vicinity of rocks and stones among which it flees in time of danger. Only rarely were animals seen at heights of more than one metre above the ground, and also only exceptionally on trees. During the spring, this species was encountered at all times of day in sunny weather, but never after dark. It readily colonizes Arab graveyards, heaps of road mending material by the side of roads, ruins of abandoned houses, house foundations with fissures, dry-stone walls and abandoned irrigation systems.

Very territorial both in the wild and in the vivarium. When two animals encounter each other in captivity, the intruder is met with jerky raising of the whole body by the occupant of the territory and by separate movements of the tail. Often the tail is raised dorsally and curled. If the intruder does not flee, a fight may start, when sometimes part of the tail may be bitten off. In the terrarium, females lay single eggs during April and late summer in dry sand under stones.

Eastern Saudi Arabia

Pristurus rupestris occurs on rocks and stones close to refuges, such as crevices or gaps between stones; it occasionally also climbs on *Tamarix* shrubs. About 93% of 778 sightings were of lizards perched or climbing on objects, but only 10% involved animals more than a metre from the ground. The lizards are territorial and may frequently perch in the same small area. One individual was seen seven times in a particular 1 m^2 area in the course of a month, while another was observed

15 times in a 1·5 m^2 area over two months. In cool conditions, especially in the mornings, *P. rupestris* basks in sheltered spots. Temperatures of 20 basking places at such times were 19·5–22°C (average 20·8°C). The lizards start to move about when perch temperatures reach about 27°C. The 10 highest perch temperatures encountered were 36–37·5°C (mean 36·8°C). As elsewhere, *P. rupestris* is a passive forager in eastern Saudi Arabia. It sometimes stands by ant trails and feeds from them and was also seen foraging near mammal faeces, presumably for the insects they attracted. *Pristurus rupestris* has a large display repertoire: both males and females wave their tails and curl them forwards over their backs at times.

North Oman and montane eastern United Arab Emirates

Here, this gecko is restricted to relatively mesic areas that are sometimes close to human habitation. It is an adept climber, occurring especially on stones, scree, small rocks, low drystone walls, shaly cliff faces, walls, the footings of buildings, etc. and even old car wrecks. In most areas, *P. rupestris* is only rarely found on trees. For instance, of 23 animals from the Jebel Akhdar area, 22 were on rocks and stones and only one on a tree. In the eastern United Arab Emirates the figures were 44 and 2. In the great majority of cases, it is not found more than a metre from the ground. This was true of 39 (89%) out of 46 animals from the eastern United Arab Emirates. Although occasionally seen soon after dark, this gecko is essentially diurnal but, at least in the hotter part of the year, spends most of its time in shaded and semi-shaded positions. *Pristurus rupestris* often seems to use specific perches from which to hunt. Near Masafi, one was watched for over two and a half hours sitting on a small rock and darting forwards occasionally to chase passing insects. Two days later it was seen in the same place and remained there for nearly four hours. Males of this species occasionally curl the tail dorsally and jerk it backwards and forwards.

Central Oman

At most localities, behaviour is similar to that in other areas of Arabia, but, in the Wahiba Sands, *P. rupestris* occurs mainly on *Prosopis* trees, presumably because rocks and stones are absent from most of this area.

Other areas: In Djibouti, Ethiopia, south-western Saudi Arabia, the Kuria Muria islands, central Oman, Abu Dhabi, Qatar, Bahrain, and Kharag Island, Iran, *P. rupestris* occurs on stony surfaces, rock outcrops and on walls of buildings.

Summary for ***P. rupestris***

A widespread species of *Pristurus* found from sea level to 2000 m in northern Oman and 2500 m in North Yemen. It occurs in quite mesic places but sometimes also extends into drier areas. This gecko is nearly always found on rocky or stony surfaces, mainly within a metre of the ground. *Pristurus rupestris* is overwhelmingly diurnal and a passive forager, spending long periods at feeding perches. Body temperatures extend up to 37°C. The most usual refuges are rock crevices and the interstices between stones. Both sexes signal by curling the tail over the back.

Sources: Dhofar—Arnold (1980, pers. obs.); North Yemen—Fritz & Schütte (1987); south-west Saudi Arabia—J. Gasperetti (pers. comm.); eastern Saudi Arabia—Ross (1990, notes); North Oman and eastern United Arab Emirates—Arnold & Gallagher (1977, notes), Arnold (1984*b*, notes). Central Oman—Gallagher & Arnold (1988), Gallagher (notes); Djibouti—Hoofien (1960); Ethiopia—Hoofien & Yaron (1962); western Saudi Arabia—J. Gasperetti (pers. comm.), C. Lowe (notes); Kuria Muria islands and Central Oman—Gallagher (1971, notes); Abu Dhabi—J. N. B. Brown (notes); Qatar—Gallagher (notes); Bahrain—Arnold (notes), Gallagher (notes); Iran—Blanford (1874).

Pristurus gallagheri (*Arnold, 1986*)

Jebel Akhdar region of northern Oman, from 450 m to 1830 m.

A climbing species nearly always found on trees, such as *Moringa peregrina* and *Ficus salicifolia*, where it usually occurs on the bole rather than the branches, although sometimes the larger ones may be used. Up to five individuals may live on a single tree, often perching head down in the shade, and forage passively on passing ants. If pursued, *P. gallagheri* does not descend to the ground but runs up and down the trunk and into the branches. In response to conspecifics and observers the tail may be raised and curled sagittally and moved back and forth three or four times; there follows a series of about 12 lateral waves.

Sources: Gardner, subm.; also Arnold & Gallagher (1977); M. D. Gallagher (pers. comm.).

Pristurus flavipunctatus (*Rüppell, 1835*)

North-west Africa—Somalia, Ethiopia and south-west Sudan; Arabia—coastal areas of south-west Saudi Arabia, western North Yemen and western South Yemen.

North Somalia

This species is diurnal and occurs up to 1500 m wherever there are *Acacia*, but is also found on other kinds of trees, such as the common evergreen Agli Angel (*Mimusops angel* Chiovenda, Sapotaceae). When disturbed, it will often dodge around a trunk extremely rapidly and, if further pursued, will flee upwards among the spiny branches of acacias, or hide in crevices and under loose bark. The tail is easily shed. *Pristurus flavipunctatus* does not call when free, but will emit a guttural sound and bite if captured. Mating occurs in June and July in north-east Somalia and eggs are probably produced in August. They are laid in the forks between branches or in deep holes, and may be hidden beneath debris.

North Yemen

Found up to 500 m in the Tihama, where it is again diurnal and arboreal, occurring on the boles of such trees as date palms (*Phoenix*) and *Acacia*. Several individuals may be found on one tree, usually within 2 m of the ground. Escape behaviour is similar to that of Somali animals. At high altitudes, for instance at 1300–1400 m near Hadja and Ta'izz, *P. flavipunctatus* may occur on boulders surrounded by vegetation, as well as on trees and large shrubs.

Other areas: Arboreal on acacia trees and diurnal near Mecca and in the Jizan area of Saudi Arabia; on *Acacia* bark in the Danakil country of Ethiopia; on trunks of babool trees near Aden, South Yemen.

Sources: North Somalia—Scortecci (1935—as *P. percristatus*); Parker (1942); W. A. MacFadyen (notes) and R. H. R. Taylor (notes). North Yemen—Fritz & Schütte (1987); B. Schätti (1989, pers. comm.). Saudi Arabia—J. Gasperetti (pers. comm.), Ethiopia—M. Gajdacs (note); South Yemen—G. Yerbury (note).

Pristurus popovi (*Arnold, 1982*)
Highlands of North Yemen

This species lives on rocks, drystone walls of field terraces and on town walls. Density may be very high and 25 were seen on a 10 m length of 30 cm high wall. At Thula, *P. popovi* occupies town walls, while *P. rupestris* occurred in the surrounding stone-lined ditches. Diurnal in February and March near Sana'a, when most animals were active around midday. When disturbed, *P. popovi* flees into holes and crevices. Both sexes move the tail conspicuously. A captive female curled the organ upwards and wagged it from side to side (Arnold, 1982).

Sources: Largely from Fritz & Schütte (1987). Occurrence on rock surfaces is reported in Asir, Saudi Arabia by C. H. Lowe (notes), and confirmed near Sana'a by K. S. Al-Badry (notes).

Pristurus minimus (*Arnold, 1977*)
South and central Oman, south-west Saudi Arabia

Common in flattish areas, usually on sandy substrata or where there are sand hummocks on gravel plains, etc. Typically found in and around low shrubs, which may be dense and woody, and clumps of grass. Vegetation may include *Euphorbia*, *Leptadenia* and *Sueda*. *Pristurus minimus* is diurnal but also often active for some time after dark. It is often seen in open areas between bushes but is usually quite close to these (within about 1·5 m in Dhofar) and takes refuge in them when disturbed. The tail may be curled over the back, at least in running males.

Sources: Arnold (1980); Gallagher & Arnold (1988); Arnold (notes); Gallagher (notes); T. D. Rogers (notes).

Pristurus simonettai (*Lanza & Sassi, 1968*)
Southern Somalia

A day-active, ground-dwelling gecko found on consolidated dunes and flat sandy areas. Plant cover varies from very low and scattered vegetation to open deciduous woodland. Extremely abundant in some areas and will even enter buildings on occasion. Very fast and some individuals curl the tail upwards.

Sources: Lanza & Sassi (1968); L. Hoevers (pers. comm.).

Pristurus crucifer *(Valenciennes, 1861)*
Coastal areas of North Yemen and western South Yemen; Somalia to extreme northern Kenya

An essentially ground-dwelling gecko, generally found on sandy or other soft surfaces, but also reported on gravel and, in northern Kenya, on hard laterite with limestone (R. C. Drewes). The habitats may sometimes include low dunes or sand hummocks. Vegetation is usually present but is typically low, and fairly or very sparse. It may be bushy or thorny or, near the sea, halophytic. Exceptionally, *P. crucifer* may climb on objects, such as walls (Fritz & Schütte, 1987).

Pristurus crucifer may be active from early morning, through the middle of the day and also after dusk (Schätti, 1989). It is extremely agile and fast, and at times may appear bipedal (R. C. Drewes). In open places animals run straight, holding the tail horizontal and this may be waved when they stop abruptly. When pursued, *P. crucifer* frequently hides in isolated grass clumps or takes refuge under bushes. In Somalia, individuals may run under the broad low foliage of a spiny shrub, to emerge and flee from another point. They also use burrows dug at the base of plants, formed of interconnecting galleries with more than one small round entrance (Scortecci, 1935); in Yemen, cracks in the ground and rodent burrows are also used (Schätti, 1989). Animals do not vocalize under normal circumstances but may do so when captured. For spatial separation from *P. somalicus* see below.

Sources: General behaviour: Somalia—Scortecci (1935), North Yemen—Fritz & Schütte (1987), Schätti (1989). Additional information, mainly on habitat: North Yemen—Schmidt (1953); South Yemen—Steindachner (1903); Somalia—Neumann (1905), Gans, Laurent & Pandit (1965); R. H. R. Taylor (notes); Kenya—R. C. Drewes (pers. comm.).

Pristurus phillipsii *(Boulenger, 1895)*
Golis and Warsagli Mountains, North Somalia

Pristurus phillipsii occurs in relatively mesic montane areas at around 1800–2100 m. Taylor (1942) reported that vegetation was dense and included cedar and box in the Golis mountains, inland of Berbera and that the Warsagli mountains further east were similar.

In the Warsagli mountains, *P. phillipsii* was seen in the Daloh Forest Reserve, where the vegetation consisted of *Juniperus procera*, *Dodonea viscosa*, *Cadea purpurea*, *Osnia* sp., salvias and grasses, which grew on rich loams derived from limestone with a mixture of forest debris. Here *P. phillipsii* was rather numerous and perched on exposed small rocks. It was not seen during the cold months but appeared rapidly at the start of the first rains.

Source: A. R. Tribe (letter, 23.12.1956).

Pristurus somalicus *(Parker, 1932)*
North Somalia

A ground-dwelling form, in arid areas with little or no vegetation, that is usually encountered on hard substrata. Most specimens occur on stony or rocky ground, on plains and in fields, and along the rocky edges of canyons. *Pristurus somalicus* is replaced by *P. crucifer* in sandy areas. Both species will return to their usual habitats if displaced (Scortecci, 1935). *Pristurus somalicus* is day-active. It often stands by ant trails, dipping its head rapidly to grab the insects as they pass by and

pausing to observe its surroundings. This gecko may not run immediately when approached, but is very fast when it does so, although perhaps a little less fleet than *P. crucifer*. Fleeing animals run directly to shallow burrows under stones which may have two to four exits. At times, the throat, which has dark blotches, may be pulsated and this behaviour is more marked than in *P. crucifer*.

Sources: Behaviour largely from Scortecci (1935, referred to as *P. crucifer laticephalus*). Habitat confirmed by Gans, Laurent & Pandit (1965, referred to as *P. phillipsii*) and by R. S. R. Taylor (notes).

Pristurus saada (Arnold, 1986)
Highlands of North Yemen

Found at altitudes of around 2000 m, where it lives on arid hard ground with gravel. *Pristurus saada* is active by day but retreats during the hottest conditions and hides under stones. Tail signalling occurs and the organ may be curled upwards.

Sources: Al-Safadi (In prep., referred to as *P. mazbah*); B. Schätti (1989, pers. comm.).

Pristurus collaris (Steindachner, 1869)
Eastern South Yemen

Ground-dwelling in arid places, usually with gravel or stones. At Dek Dik and Gail Omar this species was active all through the day and was especially fast when the temperature reached a maximum of 40–45°C. It ran extremely swiftly to escape capture, not looking for refuge in the shade, and at times seemed to be bipedal.

Sources: Behavioural information from Spanò (1963); habitat confirmed for several localities by Steindachner (1903) and for Wadi Hajr by D. J. Greathead (note).

Pristurus ornithocephalus (Arnold, 1986)
Coastal western South Yemen and adjoining North Yemen

Ground-dwelling in open arid areas without vegetation or with scattered shrubs and trees, such as *Acacia tortilis* and *A. ehrenbergiana*. Usually the ground is at least partly stony or with gravel. Active by day. When fleeing, these geckos are very fast and may evade pursuit for over 100 m. They may run to vegetation and often hide under stones.

Sources: Schätti (1989, pers. comm.); Steindachner (1903); habitat confirmed near Shuqra, South Yemen by K. M. Guichard (note).

Pristurus carteri (Gray, 1863)
Inland South Yemen. South and Central Oman

In Dhofar during September and October, *P. carteri* is ground-dwelling and usually occupies open, dry, flattish areas, although occasionally it is found on slopes as well, if the gradient is not very abrupt. The substratum is nearly always hard, and may be compact sand with or without stones, crusted silt, hard ground with scattered flints, or coarse gravel. Vegetation is usually low,

most shrubs being under 0·5 m in height, and density varies, plants sometimes being extremely sparse. In such situations, *P. carteri* is abundant and the commonest lizard of its size.

The range of activity times is very broad. At all sites animals were active in the morning and there was a tendency to become less conspicuous in the afternoon, but after dusk the level of sightings rose abruptly and continued for some hours after sunset. It seems probable that activity patterns are flexible in this species and that the relative degrees of diurnality and nocturnality vary with season and temperature.

During the day, *P. carteri* is often seen sitting out in the open a long way from the nearest vegetation, distances of 5 m or more being common. Lizards will remain more or less immobile for very long periods and, on two occasions, individuals were noted very close to the same spot for over three hours. Animals often face into the wind and it appears they are hunting passively, sitting and waiting for prey to pass or be blown by. Occasionally, an individual was seen to run forwards to snap up a passing insect. This mode of foraging is particularly appropriate for habitats with relatively low productivity where exploitable prey is sparse and irregularly distributed in time and space, so that active hunting might involve the risk of expending more energy than would be recouped by captures. This may well be true of the situations in which *P. carteri* is found, which are also suitable in being very open, so that a large area can be scanned from one position.

Sitting in the open for long periods during the day must produce problems of thermoregulation, even in spring and autumn. Body temperatures of eight lizards active in the late morning were 38°, 38°, 38°, 38·5°, 39°, 39·5°, 39·5° and 40·5°C (mean 38·9°C), substantially higher than those usually reported for other geckos (see for example Werner & Goldblatt, 1978). A captive animal subjected to a temperature of 43·5°C for some minutes panted but did not collapse, so it must have been below its upper critical temperature. As well as being able to tolerate high body temperatures, *P. carteri* employs a number of strategies to reduce heat load.

Radiation input is sometimes restricted by facing the sun and exposing as small a surface to it as possible. Like many other lizards with physiological colour change, *P. carteri* is dark when it first emerges in the early morning, becoming lighter as the temperature rises and thereby probably increasing the proportion of energy in the visible part of the solar spectrum that is reflected. With increasing temperature, the lizard keeps its body as far from the hot ground as possible. This may be by posture: although animals often crouch during cool periods, they rise high on their legs in hot conditions, restricting substratum contact to finger and toe tips and one point of the tail. Alternatively, the lizard may climb on to an object: on Masirah this is often a low shrub (P. B. Mordan, pers. comm.) but in Dhofar stones and even pats of camel dung seem to be more usual; the lizard may also position itself to take full advantage of any shade the object provides. The effectiveness of reducing contact with the ground may be judged from the following observations at Ayun: at noon (12.10.77) ground temperature was 50°C, the top of a stone 5 cm high was 42°C and one 10 cm high 40°C and the air 3 cm above this 36·5°C. At night, foraging behaviour seemed similar, but the lizards moved about more. Body temperatures of 10 naturally active animals were 22°, 23°, 23·5, 24·5°, 26°, 26°, 26·5°, 27°, 28° and 29°C (mean 25·6°C).

Although no direct observations are available, it is very probable that *P. carteri*, like other small lizards that are active by day in open places, is subjected to heavy predation by visual hunters, especially birds. The extremely good match of dorsal colour to average background suggests that there is strong selective pressure for crypsis, and camouflage is certainly very effective, lizards being very difficult to detect until they move and, if still, hard to find again should observers take their eyes off them for a moment. Avoidance of detection is consequently enhanced by the long periods of inactivity already noted for *P. carteri*, and by movement being restricted to short

vigorous bursts. Lizards taking up a new foraging position abandon their original one abruptly and proceed in a series of rapid spurts, stopping suddenly at the end of each one so that human eyes, at least, tend to lose track of them. If pursued, *P. carteri* may make very long dashes to cover, runs of 10 m or even 20 m not being unusual. Refuge may be taken under stones but lizards often flee to plants, where complex shadows improve their camouflage, and may crouch there hiding their own shadow. If captured, these geckos do not bite but the tail may be shed in its entirety if handled. Also, the large pupil is contracted; possibly this makes the vulnerable eyes and head less liable to attack, as the conspicuous black pupil virtually disappears and the iris is roughly the same colour as the surrounding skin.

Males, especially, often raise and shake the tail, a gesture made conspicuous by the organ being deep, laterally flattened, fringed and often rust-coloured at the tip. This may occur when a lizard is approached by the observer but is more usual when another *Pristurus carteri* comes near or waves its own tail. It is almost certainly a social signal and does not seem to be a way of directing predators to the expendable tail, for it is not usually performed by a lizard just before or after fleeing or very often by females. However, the fact that it was also elicited by other moving objects suggests there may be a secondary function. Perhaps tail waving informs potential predators that they have been seen and that any pursuit will be of a gecko aware of its predicament and consequently costly, in terms of effort, to catch.

Pristurus carteri is one of the few lizards known to hunt regularly by day and night. Nocturnally it occupies situations similar to some exploited by the gecko *Bunopus spatalurus* in northern Oman, and its presence may well be responsible for the more restricted occurrence of this species in southern Arabia. By day it fills a niche very similar to that of members of the agamid genus *Phrynocephalus*, although this is found on a wider range of substrata including very soft aeolian sand, the preferred habitat of one of the endemic Arabian species, *P. arabicus*. However, in many other respects the ecology of this species is very like that of *Pristurus carteri*. In the eastern United Arab Emirates, it is about the same size, occupies flattish open situations away from vegetation and hunts by sitting and waiting for invertebrate prey. High body temperatures are tolerated and heat input reduced by becoming paler and adopting a high stance; predation is avoided by good camouflage, immobility, the restriction of movement to rapid dashes and often sheltering crouched in the shade of plants when pursued. As with *Pristurus carteri*, *Phrynocephalus arabicus*, from the United Arab Emirates at least, does not bite when captured and appears to communicate by conspicuous tail movements. There are differences between the two, for instance, the *Phrynocephalus* functions at markedly higher temperatures (Arnold, 1984*b*), but considering that they belong to different families, one primarily nocturnal and the other diurnal, the resemblance is surprisingly close.

Sources: Based largely on observations of over 120 animals at eight sites in southern Dhofar (Arnold, 1980, notes). Experience of collectors in central Oman is similar—Gallagher & Arnold (1988); M. D. Gallagher (notes), P. B. Mordan (notes), R. J. Parker (notes), T. D. Rogers (notes).

Diet

Some information on diet was obtained by examining stomach contents of 206 animals from 14 species of *Pristurus* and one of *Quedenfeldtia*. These were as follows (figures in parentheses indicate numbers of stomachs examined): *Quedenfeldtia trachyblepharus* (8), *Pristurus celerrimus* (12), *P. insignis* (9), *P. socotranus* (19), *P. rupestris* (42), *P. popovi* (10), *P. flavipunctatus* (25), *P. minimus*

(15), *P. crucifer* (22), *P. phillipsii* (7), *P. somalicus* (16), *P. saada* (1), *P. collaris* (8), *P. ornithocephalus* (5), *P. carteri* (20).

As results will be reported elsewhere, they will only be summarized here. About 1500 food items were identified and it appears that, like many other lizards, the species of *Pristurus* and *Quedenfeldtia* investigated are general arthropod feeders. Overall, insects are by far the most abundant component of the diet, but some arachnids are also taken. Insects include members of a wide range of orders, particularly Hymenoptera (especially ants), Isoptera, Diptera, Hemiptera, Coleoptera and Orthoptera; larvae are taken in addition to adults. Among arachnids, spiders are the most abundant element but solifugids also occasionally occur.

Some *Pristurus* eat a high proportion of worker ants. These made up over 80% of prey items in *P. popovi* and *P. flavipunctatus*; over 60% in *P. socotranus*, *P. rupestris*, *P. phillipsii*, *P. collaris*, *P. ornithocephalus* and *P. carteri*; and over 50% in *P. celerrimus*. Termites occur especially in the stomachs of members of the Spatalura clade of *Pristurus*, perhaps because these geckos are regularly active after dark, when termites are likely to be encountered on the surface. Taken together, ants and termites make up 65% of prey items in *P. carteri* and over 80% in the small number of *P. collaris* and *P. ornithocephalus* investigated.

There is considerable variation in the mean length of prey items relative to the head length or the snout-vent distance of the gecko species concerned (these two body measurements show an approximately straight-line relationship to each other in *Pristurus*). In general, the species eating comparatively small food are those that take a high proportion of ants and termites.

Pattern of tail shedding

As in most other lizards, *Quedenfeldtia* and the majority of *Pristurus* species are capable of shedding the tail anywhere along its length distal to the basal series of pygal vertebrae, and of regenerating it from whatever point fracture takes place. In *P. saada*, *P. collaris* and *P. ornithocephalus* breakage usually takes place at the tail base, so that virtually the whole organ is lost, and in *P. carteri* this is always so (Arnold, subm. *b*).

Clutch size

Little information on clutch size of the species of *Pristurus* and *Quedenfeldtia* is available from the literature and most has been derived from examination of specimens preserved in the collection of the Natural History Museum, London. Clutch size was estimated on the basis of how many large oviducal eggs were present. In most gravid females, there was only one, but in a minority two eggs were found. The often very small number of females of each species in which clutch size could be determined is given in parentheses.

Species only known to lay a single egg: *Quedenfeldtia trachyblepharus* (8), *Q. moerens* (10), *Pristurus celerrimus* (1), *P. insignis* (2), *P. insignoides* (1), *P. socotranus* (1), *P. abdelkuri* (1), *P. rupestris* (eastern United Arab Emirates—11, Arnold, 1984*b*; North Yemen—Fritz & Schütte, 1987), *P. flavipunctatus* (1; Somalia—Scortecci, 1935), *P. popovi* (5), *P. gallagheri* (1), *P. minimus* (1), *P. phillipsii* (1), *P. somalicus* (5), *P. ornithocephalus* (2).

Species known to lay two eggs sometimes: *P. crucifer* (one egg—16, two eggs—2), *P. saada* (one egg—1, two eggs—2), *P. carteri* (one egg—2, two eggs—1).

Species for which no information is available: *P. collaris*.

Ecology and behaviour of *Pristurus* inferred from morphology

Although some information on ecology and behaviour is available for most species of *Pristurus*, it is extremely sparse or non-existent for others. This is true for *Pristurus insignis*, *P. insignoides*, *P. guichardi*, *P. abdelkuri* and *P. phillipsii*. In addition, it is unknown if many other species are regularly active after dark, how they forage and what pattern of tail signalling they have, if any. However, inferences can be made about these unknown attributes from the morphology of the species concerned on the basis of what is known about related forms. This approach is discussed more fully elsewhere (Arnold, subm. *b*, In prep.).

Morphology suggests that *P. insignoides*, *P. insignis* and *P. guichardi* are all climbing forms. Of these, *P. insignis* has the anatomical features typical of a rock-dweller while those of *P. guichardi* suggest it is arboreal. *Pristurus insignis* has limb proportions characteristic of rock forms but its palpebral fold indicates it may occupy shadier situations than most other *Pristurus*. Limb proportions in *P. abdelkuri* are consistent with this form spending much of its time on the ground, rather than climbing, and the same is true of *P. phillipsii*.

There is a tendency in many lizard groups for active foragers to have relatively long, slender bodies and tails while passive; sit-and-wait foragers are often more robust with shorter bodies and tails (Vitt & Congdon, 1978). This is generally so among the few species of *Pristurus* and its relatives where foraging technique has been observed. Thus *Gonatodes* and *Pristurus celerrimus*, which appear to be quite active when hunting are slender, while *P. rupestris* and *P. carteri* are plump with fewer presacral vertebrae. If this regularity tends to hold, primitive *Pristurus* would be expected to hunt more actively than the more advanced forms.

Caudal structure is consonant with these species using the tail for mobile signalling, rather than simply raising it, and suggests that at least *P. abdelkuri* and *P. phillipsii* curl the tail forwards over the back. This is also true of various other species, such as *P. socotranus*, *P. gallagheri* and the numerous species of the Spatalura clade where direct observations on tail signalling have not been made. Pupil shape suggests that substantial nocturnal activity is widespread in the Spatalura clade, but not in other forms.

Heavy infestations by chiggers, the larvae of trombiculid mites, occur in some populations of *P. rupestris*, *P. saada* and *P. carteri*. As in many other lizard groups, this is associated with the presence of mite pockets, structures which may ameliorate the deleterious effects of the chiggers (Arnold, 1986); these are situated in the axillary region in *Pristurus*. Presence of large mite pockets in many *P. somalicus* and *P. collaris*, and smaller ones in some *P. ornithocephalus* indicate that these species too may be subject to trombiculid infestation.

Ecology and behaviour of related groups

As already noted, the successive outgroups of the *Pristurus–Quedenfeldtia* clade appear to be the Sphaerodactylini, *Saurodactylus* and *Narudasia*. Brief summaries of what is known about the ecology of these taxa are given below.

Sphaerodactylini—*Gonatodes*

This is the most primitive component of the Sphaerodactylini. Its members are essentially forest and forest-edge forms that are scansorial, usually climbing on trees but also sometimes on rocks. The group appears to be primitively diurnal, its members typically being found in or close to shade,

although apparently secondary nocturnality also occurs. Body temperatures of active animals range up to about 31 °C. Some species at least are active foragers. Intraspecific signalling involves the head and bright markings on the flanks. The tail may be brightly coloured in juveniles, but this seems to be used for predator deflection. As in other Sphaerodactylini, clutches consist of a single egg.

Sources: Rivero-Blanco (1979), Hoogmoed (1973); C. Mattison (pers. comm.); G. Underwood (pers. comm.).

Other Sphaerodactylini

Species of *Sphaerodactylus* are often found on the ground among litter, although they may climb to some extent. They are often active by day in shade, or are crepuscular (G. Underwood, pers. comm.). *Coelodactylus* and *Pseudogonatodes* are rainforest floor forms that are active by day in shade (Vanzolini, 1968*a*, *b*; Hoogmoed, 1973).

Saurodactylus

Saurodactylus mauritanicus and *S. fasciatus* are found in stony areas where they have refuges under rocks and stones, on which they may sometimes climb. Activity has been observed in *S. mauritanicus* at dawn and dusk, and at dusk in *S. fasciatus brosseti*.

Sources: Bons (1959*a*,*b*); Bons & Pasteur (1957*a*,*b*); Werner (1931).

Narudasia

The single species, *N. festiva*, is rock-dwelling, being found on the walls of ravines, on boulders and on low outcrops, where it takes refuge in crevices and beneath stones. It is substantially diurnal, although frequently avoiding strong sunlight and is often active mainly in the early morning and in the evening. Clutches consist of two eggs.

Sources: Branch (1988); Arnold (pers. obs.).

Interspecific variation in ecology and behaviour

The main ecological and behavioural parameters of the clade consisting of *Pristurus*, *Quedenfeldtia* and their immediate relatives, for which information is available are listed below. Their known distribution among the species is set out in Figs 2–5.

General environment. There is considerable variation in the general environments in which *Pristurus* and its relatives live. Some, especially high altitude species, occur in relatively mesic situations where rainfall is fairly high and where water is often available, whereas others inhabit more arid places. For convenience, because detailed information is usually lacking, they will be assigned to three broad categories. 1. Montane, fairly mesic, or both. 2. Intermediate, if mesic or montane then also extending into drier habitats. 3. Arid areas, mainly or entirely in lowlands, not found in moister areas.

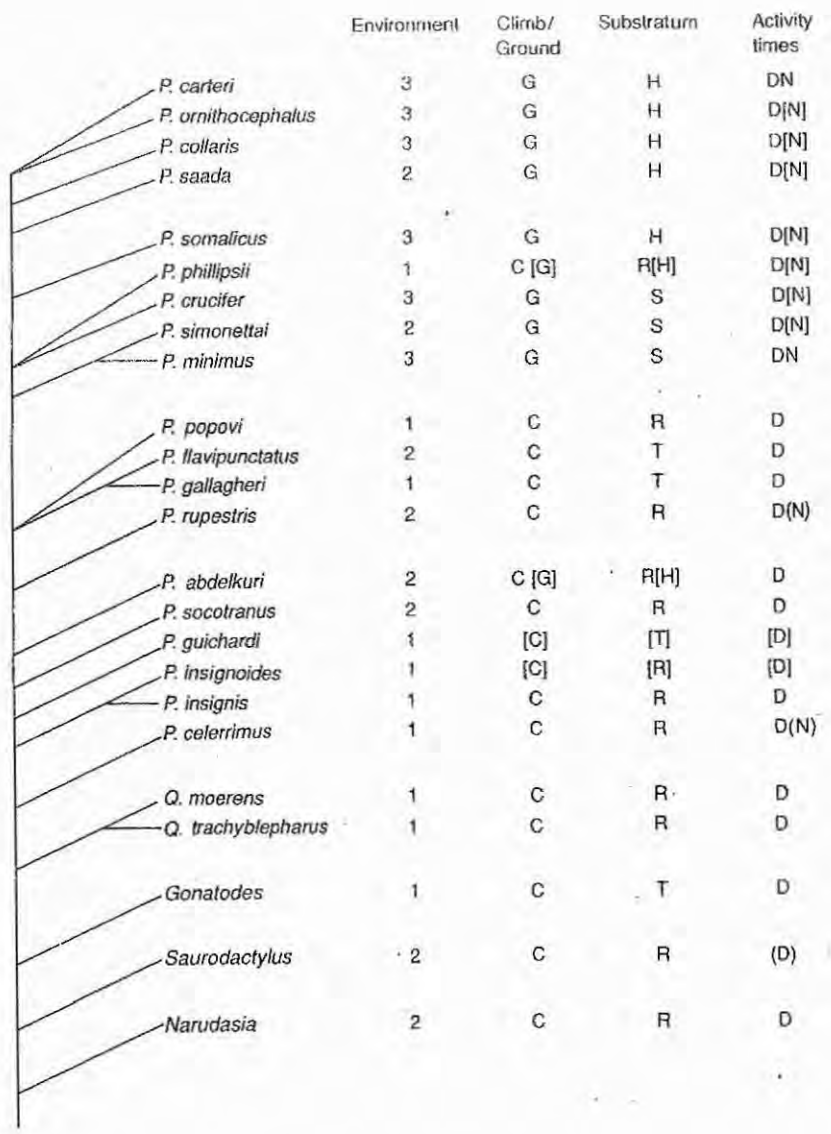

FIG. 2. Interspecific variation in ecological and behavioural parameters. Environment: 1—mesic; 2—intermediate; 3—arid lowland. Climbing/ground: C—climbing; G—ground-dwelling. Usual substratum: R—rock; T—arboreal; S—sandy ground; H—hard ground, e.g. gravel or rocky surfaces. Times of activity: D—generally diurnal; nocturnal activity: N—frequent; (N)—occasional. Square brackets indicate extrapolations from morphology rather than direct observation; round brackets denote limited occurrence.

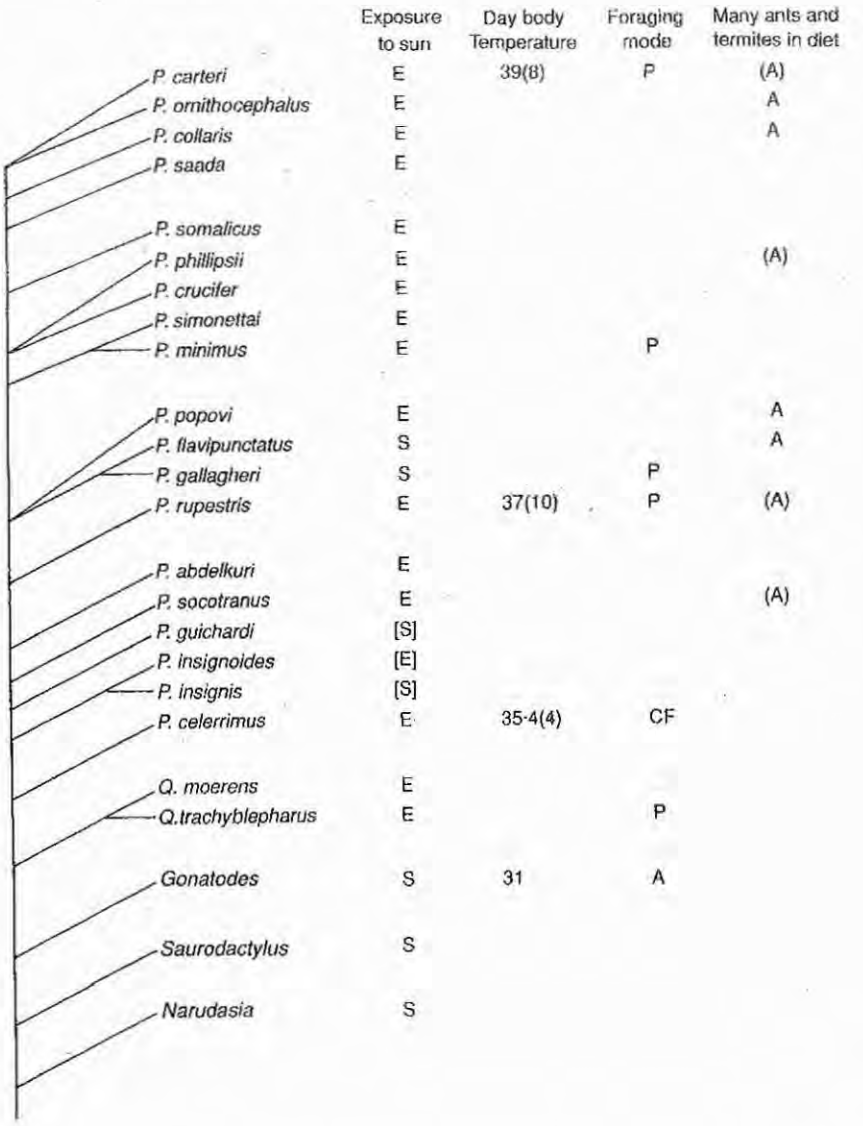

FIG. 3. Interspecific variation in ecological and behavioural parameters (*cont.*). Exposure to sun: often in shade—S; often exposed to full sun—E. Body temperature: body temperature of animals normally active by day expressed as mean with sample size in parentheses. Foraging mode: A—active; CF—cruising forager; P—passive (sit and wait). Ants and termites in diet: A—over 80% of prey items; (A)—over 60% of prey items. Square brackets indicate extrapolations from morphology rather than direct observation (suppositions about foraging mode are not shown).

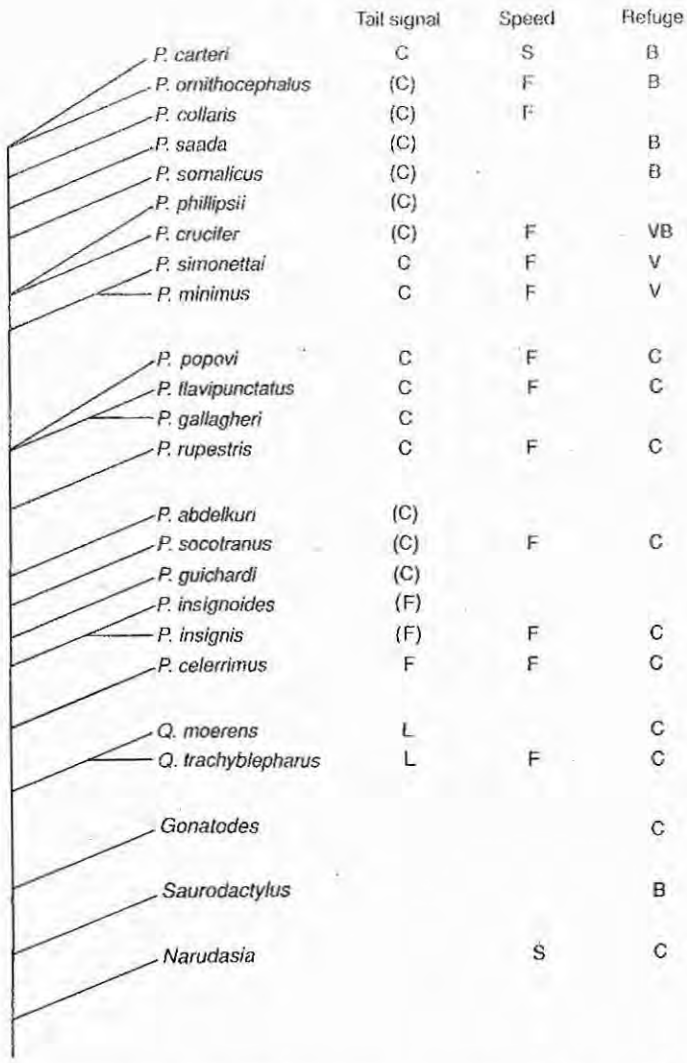

FIG. 4. Interspecific variation in ecological and behavioural parameters (*cont.*). Tail signal: L—tail lifted up but not moved; F—tail flagged, i.e. held straight and moved up and down; C—tail curled; (F), (C)—flagging and curling assumed on the basis of morphology. Speed: F—fast; S—slow. Refuge: C—crevices in rocks or in trees; V—vegetation; B—burrow.

Climbing or ground-dwelling. Most species are either predominantly climbers (C) or ground dwellers (G).

Usual substratum. Among climbers most forms occur on rock faces, boulders and stones (R) but there are a minority that habitually occur on trees (T). Most ground-dwelling *Pristurus* are found on relatively hard substrata, which are occasionally rather sandy, but typically consist largely of

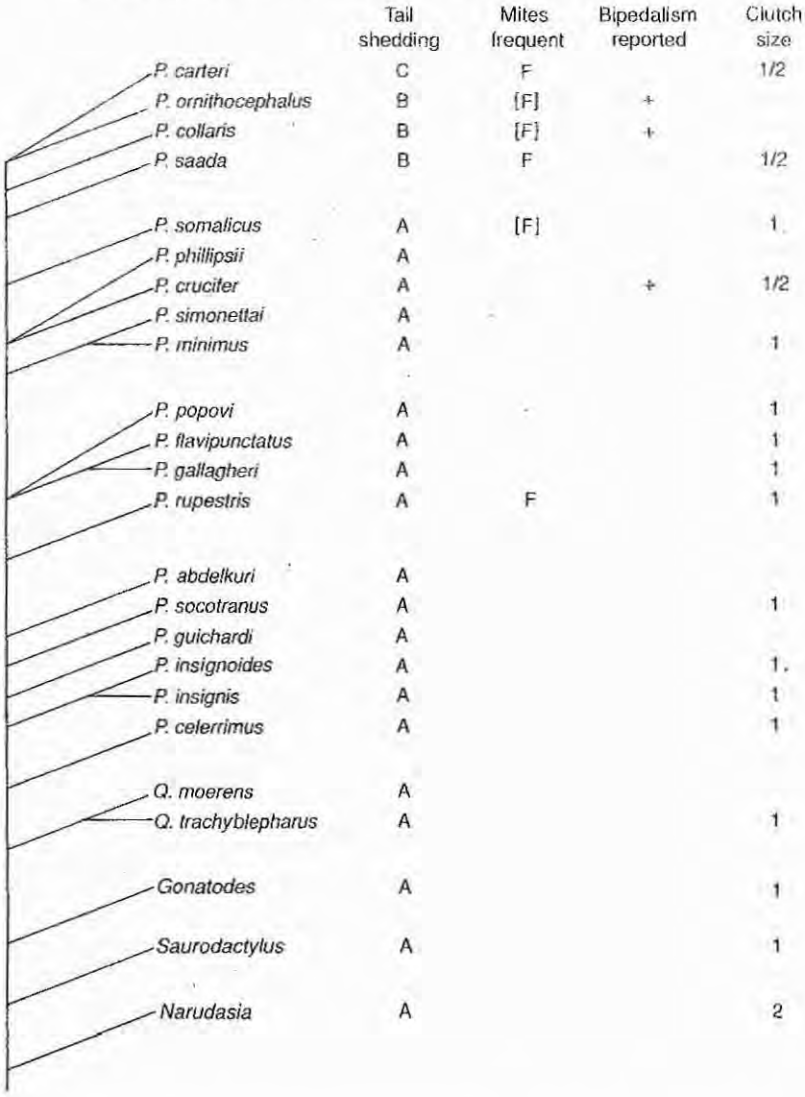

FIG. 5. Interspecific variation in ecological and behavioural parameters (concluded). Tail shedding: A—breakage occurs anywhere; B—breakage usually only at base; C—breakage always at base, most autotomy planes fused. Mites: F—frequent infestation of trombiculids. Bipedalism: +—reported to run on hind legs. Clutch size: see text. Square brackets indicate extropolations from morphology.

gravel and stones (H); in contrast, three ground-dwelling species habitually occur on fairly soft, sandy ground (S).

Times of activity. Pristurus and nearly all its relatives for which information is available appear to be active by day (D), but some species are also regularly abroad after dark as well (N).

Exposure to sun. Some forms frequently perch in full sun, at least outside the hottest part of the day (E), while others do so less frequently, or not at all, and are often found in shade (S).

Body temperatures of diurnally active animals. Few data are available, but some exist for *Gonatodes*, *P. carteri*, *P. rupestris* and *P. celerrimus*.

Foraging mode. Foraging technique clearly varies. *Gonatodes* appears to hunt actively, moving frequently and semi-continuously (A). *Pristurus celerrimus* is also quite active, but runs from one feeding station to another, pausing at each to scan its surroundings for prey (CF). This behaviour fits the definition of a cruising forager (Regal, 1983). Finally, some other species, like *Pristurus rupestris* and *P. carteri*, forage passively, sitting and waiting for prey to pass by (P).

Diet. The most obvious variation in diet is in the proportion of prey items that are ants or termites. This may exceed 80% in some cases (A) and 60% in several others ((A)).

Tail signalling. There is considerable variation in the way the tail may be used in signalling. The organ may simply be lifted obliquely and held still (L.). It may be used more vigorously for instance in flagging, where it is held straight, raised obliquely and then lowered, these movements being repeated several times (F). Finally, the tail may be curled forwards sagittally (C). Other movements occur, especially in forms employing the last method (see Ross, 1990), but these are not considered here.

Speed. No objective information exists about the speed of *Pristurus* and *Quedenfeldtia*, but observers often comment on how fast many species are (F). In contrast, at least one form, *Pristurus carteri* is relatively slow and easy to catch (S).

Refuges. Many climbing species use crevices or holes in rocks and trees as a refuge (C), while some ground-dwellers flee into vegetation (V), although they may subsequently enter holes or burrows or retreat under stones (B), as do at least some other ground-dwellers that do not habitually use plants for cover.

Tail shedding. All or part of the tail may be shed, usually in response to a predator. In most species the tail can break at any point (A), but in some advanced *Pristurus* fracture usually takes place at the base, so that the whole organ is shed (B), and in one species, *Pristurus carteri*, this is always so (C).

Mites. Some of *Pristurus* frequently have high levels of infestation by the larvae of trombiculid mites (F), whereas in others it is relatively rare.

Bipedality. No firm evidence of bipedality exists, but its possible occurrence has been reported in three species of *Pristurus*.

Clutch size. Clutches usually consist of one egg but, in a minority of forms, two eggs are produced at least sometimes.

Areas of sympatry

In a number of regions, members of the *Pristurus–Quedenfeldtia* clade occur in sympatry. In such cases, their niche characteristics are not the same. There is a variety of parameters that may differentiate species. First, they can be divided into forms that climb on objects and those that are ground-dwelling. Climbers can be separated into rock- and tree-dwellers. Sympatric rock species may be further differentiated on one or more parameters, including height from the ground when first seen, altitudinal range, body size (which may be associated with maximum prey size), hunting technique, and whether they regularly occur in full sun or not. Sympatric ground-dwellers divide into hard- and soft-ground forms and the former may exhibit differences in altitudinal range and body size.

Climbing and ground-dwelling taxa will be dealt with separately in the following summary.

Climbing species

Morocco. Quedenfeldtia trachyblepharus is an essentially highland form, whereas *Q. moerens* largely replaces it at lower altitudes (Arnold, 1990*b*).

Socotra. All four Socotran species appear to be climbers. *Pristurus insignis* and *P. insignoides* are large and montane, while the *Pristurus socotranus* and *P. guichardi* which are smaller have been found at a wide range of altitudes. How *P. insignoides* and *P. insignis* separate ecologically is unknown, but morphology suggests the former is a rock-dweller in exposed places, while *P. insignis* may occur in shadier situations. *Pristurus socotranus* is also rock-dwelling, while *P. guichardi* may well be arboreal.

North Yemen. This region has three small climbing forms: *P. flavipunctatus*, *P. rupestris* and *P. popovi*. The latter is found on trees in areas of sympatry, while the others are rock-dwellers. *Pristurus rupestris* occurs from as low as 700 m up to 2500 m, while *P. popovi* is confined to the higher part of this altitudinal range. There is a substantial difference in body size, *P. popovi* being larger, and where the two occur together, this species may climb higher than *P. rupestris*.

North Somalia, western South Yemen. Here *P. rupestris* and *P. flavipunctatus* are sympatric, being found, respectively, on rocky surfaces and on trees.

North Oman. Pristurus gallagheri, *P. celerrimus* and *P. rupestris* coexist. The former occurs on trees while the others are rock dwellers. *Pristurus celerrimus* is confined to more mesic places than *P. rupestris*, where it climbs higher and hunts more actively.

Ground-dwelling species

Abd el Kuri Island. Pristurus abdelkuri may well be largely ground-dwelling. It is not sympatric with any other *Pristurus*.

South Somalia. Pristurus simonettai is also not known to be sympatric with other *Pristurus* species.

North and Central Somalia. Two certain ground-dwellers occur, both of which are small:

P. somalicus and *P. crucifer*. These are widespread at a range of altitudes and differ clearly in the substratum on which they are found, living, respectively, on hard and soft surfaces. *Pristurus crucifer* appears regularly to take refuge in vegetation, unlike *P. somalicus*. A third species, *P. phillipsii*, also occurs in northern Somalia, but only at high altitudes and in generally more mesic environments than the other two. Morphology suggests it too is a ground-dweller, on relatively hard surfaces. It is also reported to perch on stones, as some other ground-dwelling *Pristurus* do at times.

Southern Arabia

The members of the *Pristurus carteri* group, namely *P. saada*, *P. collaris*, *P. ornithocephalus* and *P. carteri*, have essentially allopatric ranges in South Arabia. *Pristurus saada* is a high altitude form confined to the North Yemen highlands, while the other three are largely found at lower elevations. All these forms are relatively large and are ground-dwellers on hard substrata.

Pristurus crucifer occurs with *P. ornithocephalus* in western coastal areas of Yemen but is smaller and occurs on soft rather than hard ground. The same kind of relationship is found between the diminutive *P. minimus* and the large *P. carteri*, which are found together from northern Oman probably as far as south-western Saudi Arabia.

History of ecological and behavioural parameters

Using the information in Figs 2–5, it is possible to reconstruct the likely history of aspects of the ecology and behaviour of *Pristurus* and its relatives. Such statements are based initially on parsimony with the number of evolutionary events being minimized, that is the number of changes in the aspect being considered. For instance, in a pectinate phylogeny like that of the *Pristurus–Quedenfeldtia* clade, if three or more consecutive branches arising from the main stem have a condition that does not occur in branches arising before or after them, it is more parsimonious to assume this condition was originally present on the main stem of the phylogeny and then lost, than to assume it has developed independently on each branch. With two branches, the case is equivocal and, with one branch, origin on the branch itself is the most parsimonious interpretation.

If a condition appears on the lowest branches of the known phylogeny, its successive presence on only two of them is sufficient to establish its occurrence on the stem as the most parsimonious interpretation. With more complex distributions, optimization programmes may be used to establish likely conditions on the main stem (for instance that of Farris, 1970). However, it must be borne in mind that some of these programmes are designed primarily to minimize the number of changes (steps) and will not necessarily give all possible alternative patterns of change. Once the most parsimonious explanation has been determined, its strength may be assessed. Thus, the more branches there are bearing the studied condition, the more likely it is that this was really present on the stem.

It might be argued that ecological and behavioural features should not merely be plotted on an already available phylogeny, but should be regarded as primary data contributing to it, that is they should be integrated with other variables, such as morphological ones, into the data set used to establish the phylogeny. This can certainly be done, but there may be practical difficulties. For instance, ecological and behavioural information is often incomplete when compared with morphology. The variables concerned are frequently continuous ones and, as such, are not always easy to incorporate into cladistic approaches to phylogeny reconstruction (Pimentel & Riggins,

1987). Again, while behaviour can be regarded as an integral part of the organism and is therefore likely to reflect its phylogenetic history, this may not apply to some ecological parameters. For instance, dietary composition and habitat are not integral properties of a species unless they are substantially the result of some inherent preference. They are not so if they merely reflect what is available to the taxon concerned, either because nothing more suitable exists in its environment or because competing species pre-empt resources it would have otherwise used.

However, in the present instance, there is no problem about whether ecological and behavioural information should be integrated into the data set used to establish phylogeny. For, when this is done, relationships remain unchanged.

General environment

There was an overall shift during the history of *Pristurus* and its relatives into drier more demanding habitats. However, some mesic montane distributions of primitive forms may be secondary (Arnold, 1981, subm. *a*).

Climbing or ground dwelling

Clearly, the clade made up of *Pristurus* and its relatives was originally scansorial, for most of the first 12 branches of the phylogeny involve taxa that climb or, in the case of the Sphaerodactylini, probably did so primitively (as *Gonatodes* still does). The only possible exceptions are *Saurodactylus* which may spend substantial time on the ground, and *Pristurus abdelkuri* which has not been observed directly but possesses morphological features usually associated with ground-dwelling. Apart from these unconfirmed cases, ground-living appears to have arisen at least once within the Sphaerodactylini, and again in the Spatalura clade. In none of these cases is there any evidence of reversion to climbing.

Usual substratum

Among the climbing forms, the original usual substratum was rocky surfaces. From this there may have been three separate transfers to the boles and branches of trees as the commonest kind of structural niche: in *Gonatodes*, possibly in *P. guichardi*, and in the ancestor of the *P. gallagheri*–*P. flavipunctatus* clade.

In the Spatalura clade of *Pristurus*, ground-dwelling forms can occur on relatively hard or on soft substrata. Most species are found on relatively hard ground and there are only three soft-ground species, two of which form a single clade, *P. minimus* and *P. simonettai*. The third species, *P. crucifer*, is more derived than the others and, in the phylogeny of the group, forms an unresolved trichotomy with *P. phillipsii* and with the more advanced members of the Spatalura clade. This gives three possible alternative relationships: 1. *P. crucifer* may form a separate branch that arose after that leading to *P. minimus* and *P. simonettai* but before *P. phillipsii*; 2. the *P. crucifer* and *P. phillipsii* branches may be reversed; or 3. *P. crucifer* may share a common ancestor with *P. phillipsii*.

If only the different ground types occupied within the Spatalura clade are considered, it is more parsimonious to consider soft ground the primitive habitat in alternative 1, but alternatives 2 and 3 would be equivocal on this point. However, if, instead of ground type, surface texture is considered throughout the studied group, hard surfaces would not only include harder ground types but also

the rock and tree-bole situations in which more primitive forms of the *Pristurus* clade are found. If these are contrasted with soft surfaces occupied by the *P. minimus*–*P. simonettai* clade and by *P. crucifer*, it is more parsimonious overall to consider hard surfaces primitive to soft ones in alternatives 2 and 3 while alternative 1 is equivocal.

However, as applied here, parsimony aims merely to minimize evolutionary events and no distinction is made between forward transformations and reversals. If the latter are considered less likely, hard surfaces as the primitive condition would be chosen in version 1. This may well be the case for, if soft surfaces were primitive in the Spatalura clade, there would not only be reversal in the texture of the surface occupied, but also in a number of functionally associated morphological features (Arnold, subm. *b*). A further indication that hard surfaces are primitive within the Spatalura clade is provided by *P. abdelkuri* which may have become ground-dwelling independently of this group and, so far as it can be inferred from morphology, is likely to occupy hard ground.

Time of activity and exposure to sun

It seems likely that the studied clade abandoned primitive gecko nocturnality and became at least partly diurnal at a very early stage in its history. However, the earliest forms were probably inhabitants of subdued light and relatively cool microhabitats, as *Narudasia* and *Saurodactylus* and the Sphaerodactylini substantially still are. After this, there was a shift into brighter, warmer conditions with regular exposure to direct sunlight and to fairly strict diurnality. Reversion to shadier microhabitats has occurred in the *P. flavipunctatus*–*P. gallagheri* clade and perhaps in *P. insignis* and *P. guichardi* too. The Spatalura clade has returned to regular nocturnality, but this is an addition to activity in bright hot conditions rather than a substitute for them.

Foraging mode

The limited data available suggests there was a shift on the main stem of the *Pristurus* clade from relatively active to very passive foraging techniques, although this may also be paralleled in *Quedenfeldtia*.

Diet

When cases where there are high proportions of ants and termites as prey items are plotted on the phylogeny of the *Pristurus*–*Quedenfeldtia* clade, their occurrence is rather sporadic. However, apart from *P. celerrimus* and *P. socotranus*, they occur in the sequence of branches involving *P. rupestris*, *P. flavipunctatus* and *P. popovi*, and again in the *P. carteri* group. Prey size varies largely in correlation with this. The more primitive species, with the exception of *P. insignis* and *P. socotranus*, tend to eat relatively large prey, but size falls in *P. rupestris*, *P. flavipunctatus* and *P. popovi*, rises again among the small members of the Spatalura clade and then falls once more in the *P. carteri* group.

Tail signalling

Interspecific tail signalling is likely to have first developed in the ancestor of the *Pristurus*–*Quedenfeldtia* clade. After this, there seems to have been a progression from simply lifting the tail, to flicking the organ obliquely up and down, and then to curling it forwards in the sagittal plane.

This stage is likely to have been reached quite early in the history of *Pristurus*, for morphology suggests it is present in *P. socotranus*, which constitutes one of the more basal branches of the clade, and in virtually all the species that evolved subsequent to this. The range of signals used also appears to have become greater (see Ross, 1990, for *P. rupestris*) and sexual differences have become marked.

Refuges

Refuges reflect the kind of habitat occupied. Crevices and holes in rocky places appear to have been the initial common place of safety with some later transfers to similar cavities in the trunks and boles of trees. Forms that moved on to relatively hard ground surfaces took to hiding in burrows and under stones, while those that eventually occupied softer ground-types utilize vegetation to a significant degree as well.

Pupil closure

It is not known exactly how widespread is almost complete closure of the pupil in response to capture. However, this response necessitates a vertically elliptical pupil, so within *Pristurus* it cannot have developed before the origin of the Spatalura clade.

Tail shedding

There is a change in the history of the clade made up of *Pristurus* and its relatives from being able to shed the tail anywhere along its length to usually shedding virtually the whole organ and finally in *P. carteri* to always doing so.

Mites

Infestation by the larvae of trombiculid mites appears to be commonest in the more recently evolved branches of the clade.

Clutch size

The standard gecko clutch size of two eggs fell to one, presumably before the evolution of *Saurodactylus*. However, the ability to produce two eggs has reappeared in some of the members of the Spatalura clade.

Possible interactions between ecological and behavioural changes

The ancestors of the clade made up of *Pristurus* and its relatives were probably nocturnal climbers like most gekkonids. The main alterations in ecology and behaviour which have occurred since then are shown in Fig. 6. One of the possible changes has been in becoming active in places with subdued light and then moving into sunlight in often very open situations. Within *Pristurus*, there has been a shift into arboreal habitats by *Gonatodes*, and on one or two occasions within *Pristurus* with a reversion to lower light intensities. A change to ground-dwelling has occurred perhaps twice, once possibly in *P. abdelkuri* and again certainly in the Spatalura clade. In these

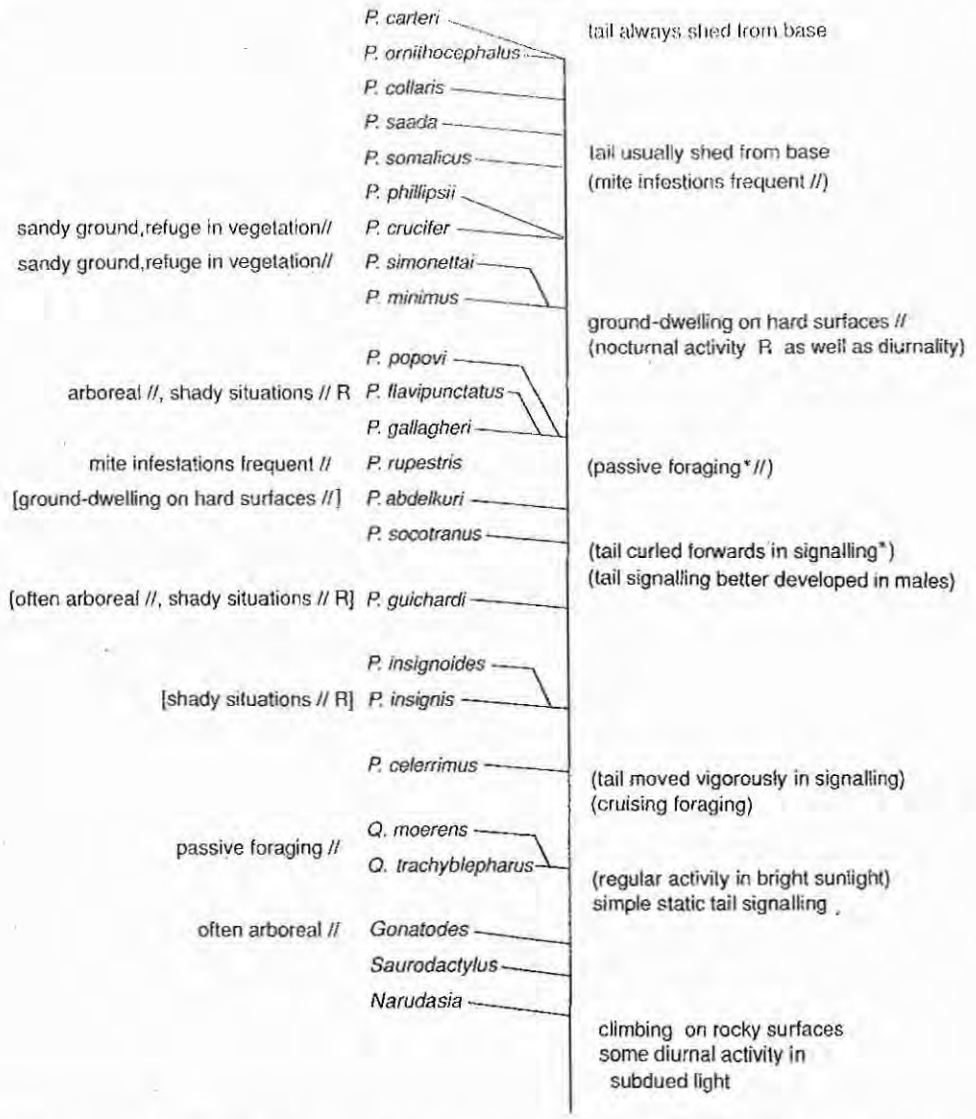

FIG. 6. Summary of some of the ecological and behavioural changes that have occurred in the history of *Pristurus* and its relatives. //—parallel changes within studied clade; R—reversals within studied clade; [ ]—based on morphological inference; ( )—based partly on morphological inference; *—actual position of change uncertain.

cases, it is most likely that relatively hard substrata were occupied initially, but that there appear to have been two invasions of soft substrata in the Spatalura clade. The latter group also reverts to nocturnality in addition to its diurnal activity. Overall, there is a tendency to progress into hotter, drier habitats which, in the case of the *P. carteri* group, become very open and bare.

Are there likely to be any functional correlations among the main shifts in time of activity and in structural niche and other parameters which change during the history of the clade? The limited information on body temperature available suggests that movement into more open habitats and then on to the ground is associated with apparent increase in diurnal temperatures of active animals. Open habitats are more exposed to the sun and flat areas tend to be hotter than semi-vertical surfaces, because the sun reaches them for longer and strikes them at steeper angles during the hotter part of the day. Secondary reversion to some nocturnality in the Spatalura clade may be related to occupying warmer diurnal habitats. Although nocturnality certainly occurs in addition to day-time activity, most observations on this point have been made in the autumn. At hotter times of the year nocturnality may perhaps largely replace diurnal activity. In southern Oman at least, there are a number of climbing geckos that might compete with climbing *Pristurus* if these were nocturnal, but far fewer ground-dwelling ones (Arnold, 1980). This may mean there are more resources available to nocturnal *Pristurus* on the ground.

Change in the kinds of refuges used also seems to reflect general habitat. It might also be thought this was true of the incidence of trombiculid infestation, but there are no data on the relative abundance of these micro-predators in the habitats concerned. There is also evidence that degree of infestation is often associated with changes in susceptibility of taxa rather than with mite abundance (Arnold, 1986).

The apparent shift to more passive foraging modes may be associated with more open situations. In such places it is easier to see prey without actively searching for it and generally lower prey levels may also favour passive foraging, which has low energy costs (Anderson & Karasov, 1981). In addition, animals in open situations are potentially more visible and predation risks may consequently be higher, placing a premium on relative immobility.

The development of intraspecific tail signalling also seems to be associated with more exposed habitats, where distant visual signals are likely to be easily seen. In *Pristurus*, the appearance of more elaborate signalling may show rough correlation with the appearance of passive foraging and it might be thought that this would confer greater advantages to animals that were more static and widely distributed. However, the simplest signalling occurs in *Quedenfeldtia* which also appear to be passive foragers. Possibly, more detailed knowledge of the habits of these animals will show whether their life modes are really similar.

Making the eye less conspicuous after capture by closing the pupil is a late development within the clade made up of *Pristurus* and its relatives. As already noted, it depends on the pupil being vertically elliptical so that it can contract to a narrow slit, something that is also characteristic of forms that are active both by night and day. This being so, protective closure could be an exaptation of increased pupil lability first developed in association with the secondary acquisition of nocturnal activity in the Spatalura clade. However, it is not possible to confirm this, unless protective closure can be shown to have developed subsequent to pupil modification associated with nocturnality. At present, this cannot be checked as the distribution of both protective closure and of certain nocturnal activity within the Spatalura clade is still incompletely known.

Basal tail shedding is something that often seems to be associated in geckos with inability to reach refuges quickly, either because the species concerned are slow or because refuges are widely spaced, or both. In these circumstances, where capture is likely, shedding the whole tail may increase the chances of escape by leaving a pursuer with a worthwhile distraction (Arnold, 1984*a*, 1988). Information on these points is not available for most species, but *P. carteri*, which has autotomy confined to the tail base and so loses the whole organ, appears to be relatively slow and lives in usually very open habitats with only widely scattered plant cover, where it often runs long

distances to shelter (p. 366). In contrast, *P. rupestris*, which can shed its tail at any point, is fast and is typically close to a refuge (p. 359).

The reduction of clutch size to a single egg and then its reversion to two in some individuals of the Spatalura clade shows a rough correlation with body size and this might be thought a determining factor. However, although many of the forms laying single eggs are very small, this is also true of some geckos that usually lay two, such as *Nàrudasia* and *Lygodactylus*. Similarly, while some of the advanced *Pristurus* that sometimes lay two eggs are large, one of them, *P. crucifer*, is as small as many of the apparently consistent producers of single eggs.

Concluding remarks

There are some non-ancestral resemblances produced by changes in the ecology and behaviour of the clade made up of *Pristurus* and its relatives. Most of these involve forward transformations but there are also a couple of reversals. Non-ancestral resemblances through forward transformations include the shift from climbing to ground-dwelling (perhaps three times); rock-dwelling to arboreality (three times); gravel to sand (probably twice); active to passive foraging (perhaps twice); heavy trobiculid mite infestation (twice). Reversals include a partial return to nocturnality and partial reversion to the primitive gecko clutch size of two eggs.

At present, it is not easy to put a time-scale on the ecological and behavioural changes that have occurred within *Pristurus* and its relatives. However, Socotra and Abd el Kuri islands are believed to have separated from southern Arabia in the mid-Miocene (Beydoun, 1970; Beydoun & Bichan, 1970). If the division between the most advanced forms presently occurring on these islands (*P. socotranus* and *P. abdelkuri*) and the more advanced mainland forms pre-date this occurrence, ecological and behavioural changes occurring before the division must have happened over 15 million years ago.

Overall, there has been a shift in the clade made up of *Pristurus* and its relatives from fairly mesic situations with an abundance of refuges to ones which are hot and arid with little cover from predators and few places of retreat. If sit and wait foraging is associated with low levels of prey acquisition (Anderson & Karasov, 1981), then derived forms are also likely to have restricted food intake, and they are also prone to trobiculid infestation. It seems at first sight paradoxical that the most derived forms in a clade which has undergone great morphological change should end up in situations that appear more demanding and less rewarding than those occupied by the primitive forms that gave rise to them. Possibly, this results from evolution driven by failure in competition, where forms that do least well competitively, following each of a sequence of speciation events, are pushed into harsher niches (Arnold, 1981).

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REFERENCES

Al-Safadi, M. M. (In prep.). A new species of semaphore gecko (*Pristurus*: Gekkonidae) from the Yemen Arab Republic.

Anderson, R. A. & Karasov, W. H. (1981). Contrasts in energy intake and expenditure in sit-and-wait and widely foraging lizards. *Oecologia* **49**: 67–72.

Arnold, E. N. (1980). The reptiles and amphibians of Dhofar, Southern Arabia. *J. Oman Stud. Spec. Rep.* No. 2: 273–332.

Arnold, E. N. (1981). Competition, evolutionary change and montane distributions. In *The evolving biosphere*: 217–228. Greenwood, P. H. & Forey, P. L. (Eds). London and Cambridge: British Museum (Natural History) and Cambridge University Press.

Arnold, E. N. (1982). Reptiles of Saudi Arabia. A new semaphore gecko (*Pristurus*: Gekkonidae) and a new dwarf snake (*Eirenis*: Colubridae) from southwestern Arabia. *Fauna Saudi Arabia* **4:** 468–477.

Arnold, E. N. (1984*a*). Evolutionary aspects of tail shedding in lizards and their relatives. *J. nat. Hist.* **18:** 127–169.

Arnold, E. N. (1984*b*). Ecology of lowland lizards in the eastern United Arab Emirates. *J. Zool., Lond.* **204:** 329–354.

Arnold, E. N. (1986). Mite pockets of lizards, a possible means of reducing damage by ectoparasites. *Biol. J. Linn. Soc.* **29:** 1–21.

Arnold, E. N. (1988). Caudal autotomy as a defense. In *Biology of the Reptilia* **16:** 235–273. Gans, C. & Huey, R. B. (Eds). New York: Alan R. Liss.

Arnold, E. N. (1990*a*). Why do morphological phylogenies vary in quality? An investigation based on the comparative history of lizard clades. *Proc. R. Soc. Lond.* (*B*) **240:** 135–172.

Arnold, E. N. (1990*b*). The two species of Moroccan day-geckos, *Quedenfeldtia* (Reptilia: Gekkonidae). *J. nat. Hist.* **24:** 757–762.

Arnold, E. N. (subm. *a*). Systematics, phylogeny and biogeography of the Semaphore geckoes, *Pristurus* (Reptilia: Gekkonidae).

Arnold, E. N. (subm. *b*). Evolution of Semaphore geckoes *Pristurus* (Reptilia: Gekkonidae).

Arnold, E. N. & Gallagher, M. D. (1977). Reptiles and amphibians from the mountains of Oman with special reference to the Jebel Akhdar region. *J. Oman Stud. Spec. Rep.* No. 1: 59–80.

Beydoun, Z. R. (1970). Southern Arabia and northern Somalia: comparative geology. *Phil. Trans. R. Soc.* (*A*) **267:** 267–292.

Beydoun, Z. R. & Bichan, H. R. (1970). The geology of Socotra Island, Gulf of Aden. *Q. J. Geol. Soc.* **125:** 413–446.

Blanford, W. T. (1874). Descriptions of two lizards from Persia and Baluchistan. *Ann. Mag. nat. Hist.* (*4*) **13:** 453–455.

Bons, J. (1959*a*). Les lacertiliens du Sud-Ouest marocain. *Trav. Inst. scient. chérif. (Gen.)* **18:** 1–130.

Bons, J. (1959*b*). Sur la faune herpétologique des Doukkala. *Bull. Soc. Sci. nat. Maroc* **39:** 117–128.

Bons, J. & Pasteur, G. (1957*a*). Récentes captures de *Saurodactylus fasciatus* Werner et nouvelles observations sur le genre *Saurodactylus* (Gekkonidés). *Bull. Soc. Sci. nat. Maroc* **37:** 57–65. [English summary].

Bons, J. & Pasteur, G. (1957*b*). Nouvelles remarques sur les Saurodactyles, avec description de *Saurodactylus mauritanicus brosseti* ***n. subsp.*** *Bull. Soc. Sci. nat. Maroc* **37:** 175–195. [English summary].

Boulenger, G. A. (1903). Reptiles. In *The natural history of Sokotra and Abd-el-kuri*: 75–96. Forbes, H. O. (Ed.). Liverpool: The Free Public Museums.

Branch, W. R. (1988). *Field guide to the snakes and reptiles of Southern Africa.* Cape Town: Struik Publishers.

Farris, J. S. (1970). Methods for computing Wagner trees. *Syst. Zool.* **19:** 83–92.

Fritz, J. P. & Schütte, F. (1987). Geckos der Gattung *Pristurus* Rüppell, 1835 aus der Arabischen Republik Yemen. *Bonn. Zool. Beitr.* **38:** 47–57.

Gallagher, M. D. (1971). *The amphibians and reptiles of Bahrain.* Bahrain.

Gallagher, M. D. & Arnold, E. N. (1988). Reptiles and amphibians from the Wahiba Sands, Oman. *J. Oman Stud. Spec. Rep.* No. 3: 405–413.

Gans, C., Laurent, R. F. & Pandit, G. (1965). Notes on a herpetological collection from the Somali Republic. *Ann Mus. r. Afr. cent.* No. 134: 1–93.

Greene, H. W. & Burghardt, G. M. (1978). Behaviour and phylogeny: constriction in ancient and modern snakes. *Science, Wash.* **200:** 74–77.

Hoofien, J. H. (1960). A collection of gekkonid lizards from French Somaliland. *Ann. Mag. nat. Hist.* (*13*) **3:** 493–495.

Hoofien, J. H. & Yaron, Z. (1962). A collection of reptiles from the Dhalak Archipelago (Red Sea). *Israel South Red Sea Expedition, 1962, Reports* **4:** 35–40.

Hoogmoed, M. S. (1973). *Notes on the herpetofauna of Surinam* **4.** *The lizards and amphisbaenians of Surinam.* The Hague: Dr W. Junk b.v., Publishers.

Huey, R. B. & Bennett, A. F. (1987). Phytogenetic studies of coadaptation: preferred temperatures versus optimal performance temperatures of lizards. *Evolution* **41:** 1098–1115.

Klemmer, K. (1969). Beobachtungen an den Hochgebirgsreptilien *Quedenfeldtia trachyblepharus* (Gekkonidae) und *Lacerta andreanskyi* (Lacertidae) des Hohen Atlas Marokko. *Verh. dt. zool. Ges.* **1968:** 325–327.

Lanza, B. & Sassi, A. R. (1968). On a new genus and species of gekkonid lizard from Somalia. *Monit. zool. ital.* (*N.S.*) (*Suppl.*) **2:** 17–26.

Losos, J. B. (1990). The evolution of form and function: morphology and locomotor performance in West Indian *Anolis* lizards. *Evolution* **44:** 1189–1203.

Neumann, O. (1905). Über nordost-afrikanische und arabische Kreichtiere. *Zool. J. Syst.* **22:** 389–404.

Parker, H. W. (1942). The lizards of British Somaliland. *Bull. Mus. comp. Zool. Harv.* **91:** 1–101.

Pimentel, R. A. & Riggins, R. (1987). The nature of cladistic data. *Cladistics* **3:** 201–209.

Regal, P. J. (1983). The adaptive zone and behaviour of lizards. In *Lizard ecology: studies of a model organism*: 105–118. Huey, R. B., Pianka, E. R. & Schoener, T. W. (Eds). Cambridge, Massachusetts and London: Harvard University Press.

Rivero-Blanco, C. (1979). *The neotropical lizard genus* ***Gonatodes***. PhD thesis, Texas A & M University.

Ross, W. (1990). Notes on the behaviour of *Pristurus rupestris* (Reptilia: Gekkonidae) with special reference to tail signalling. *Fauna of Saudi Arabia* **11:** 300–305.

Schätti, B. (1989). Amphibien und Reptilien aus der Arabischen Republic Jemen und Djibouti. *Rev. suisse Zool.* **96:** 905–937. [English summary].

Schmidt, K. P. (1953). Amphibians and reptiles of Yemen. *Fieldiana (Zool.)* **34:** 253–261.

Scortecci, G. (1935). Il genere *Pristurus* delle Somalia italiana. *Atti Soc. ital. Sci. nat.* **74:** 118–156.

Spanò, S. (1963). Nota su *Pristurus carteri collaris* (Steindachner). Spedizione Scortecci nell'Hadramaut (1962). *Boll. Musei Ist. biol. Univ. Genova* **32:** 35–41.

Steindachner, F. (1903). Batrachier und Reptilien aus Südarabien und Sokòtra. *Sber. Akad. Wiss. Wien* **112:** 7–14.

Taylor, R. H. R. (1942). Appendix on topography and climate. *Bull. Mus. comp. Zool. Harv.* **91:** 92–96.

Vanzolini, P. E. (1968*a*). Lagartos Brasileiros da familia Gekkonidae (Sauria). *Archos Zool. Est. S Paulo* **17:** 1–84.

Vanzolini, P. E. (1968*b*). Geography of the South American Gekkonidae (Sauria). *Archos Zool. Est. S Paulo* **17:** 85–112.

Vitt, L. J. & Congdon, J. D. (1978). Body shape, reproductive effort, and relative clutch mass in lizards: resolution of a paradox. *Am. Nat.* **112:** 595–608.

Werner, F. (1931). Ergebnisse einer zoologischen Forschungsreise nach Marokko. III. Amphibien und Reptilien. *Sber. Akad. Wiss. Wien* **140:** 270–318.

Werner, Y. L. & Goldblatt, A. (1978). Body temperature in a basking gekkonid lizard, *Ptyodactylus hasselquistii* (Reptilia, Lacertilia, Gekkonidae). *J. Herpet.* **12:** 408–411.