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Friedhelm Krupp, Wolfgang Schneider
and Ragnar Kinzelbach (Eds.)

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Zoogeography of the Reptiles and Amphibians of Arabia

E. N. Arnold

Abstract: Arabia, including the arid lowland regions of Jordan, Syria, Iraq and southwest Iran, has approximately 128 species of terrestrial reptiles and about 7 of amphibians. Endemicity is high, 55% of species being largely or entirely confined to the area. Abrupt faunal discontinuities are present between Arabia and neighbouring regions, namely the Horn of Africa, the Sahara desert and the relatively mesic areas to the north. However, there must have been substantial interchange with these areas in the past. Within Arabia, the main zoogeographic division is between the arid regions occupying most of the peninsula and much smaller, often more mesic areas of endemicity in the south. The former are mainly occupied by Saharo-Sindian taxa and have rather more affinities with the Sahara than to arid regions east of Arabia. Southern areas of endemicity include: 1. The southwestern coast, with affinities to the Horn of Africa and the inland deserts of Arabia. 2. The southwest and southern highlands which share a number of forms with northeast African relationships but differ significantly, the former having more, often endemic species with African affinities and a number with relatives in the Mediterranean and other northern mesic regions. The drier southern mountains have their own endemics, some of which have representatives in the Ǧiddat al-Ḥarāsīs area to the east. 3. The north Oman mountains also possess distinctive species and populations, some of which are related to forms in the less arid parts of the Iranian area. Finally there are a number of mesic forms distributed around the periphery of Arabia, and populations at oasis sites in the arid region which are probably relicts of forms more widespread in Quaternary pluvial phases.

Keywords: Reptilia, Amphibia, Arabia, zoogeography.

Introduction

Until recently, the herpetofauna of Arabia was very poorly known but, over the last 30 years, collections have accumulated which allow its zoogeography to be assessed. Zoogeography is of course dependant on knowledge of the phylogeny of the animals concerned. While this is not available in detail for all Arabian reptile groups, the nearest relations of most taxa can be identified and this enables us to examine the overall affinities of the Arabian herpetofauna and its internal relationships.

The limits of Arabia (fig. 1)

In many respects, Arabia is virtually an island. At the present time it is surrounded by sea on three sides and its northern biogeographical perimeters are defined, more or less, by geological and climatic factors. From the head of the Red Sea, Arabia is separated from Sinai and North Africa by the Gulf of Aqaba (Ḫalīǧ al-ʿAqaba) and Wādī al-ʿAraba (Arava) which represent a shear fault that runs northwards into the Lebanon highlands and on to the Taurus. In this

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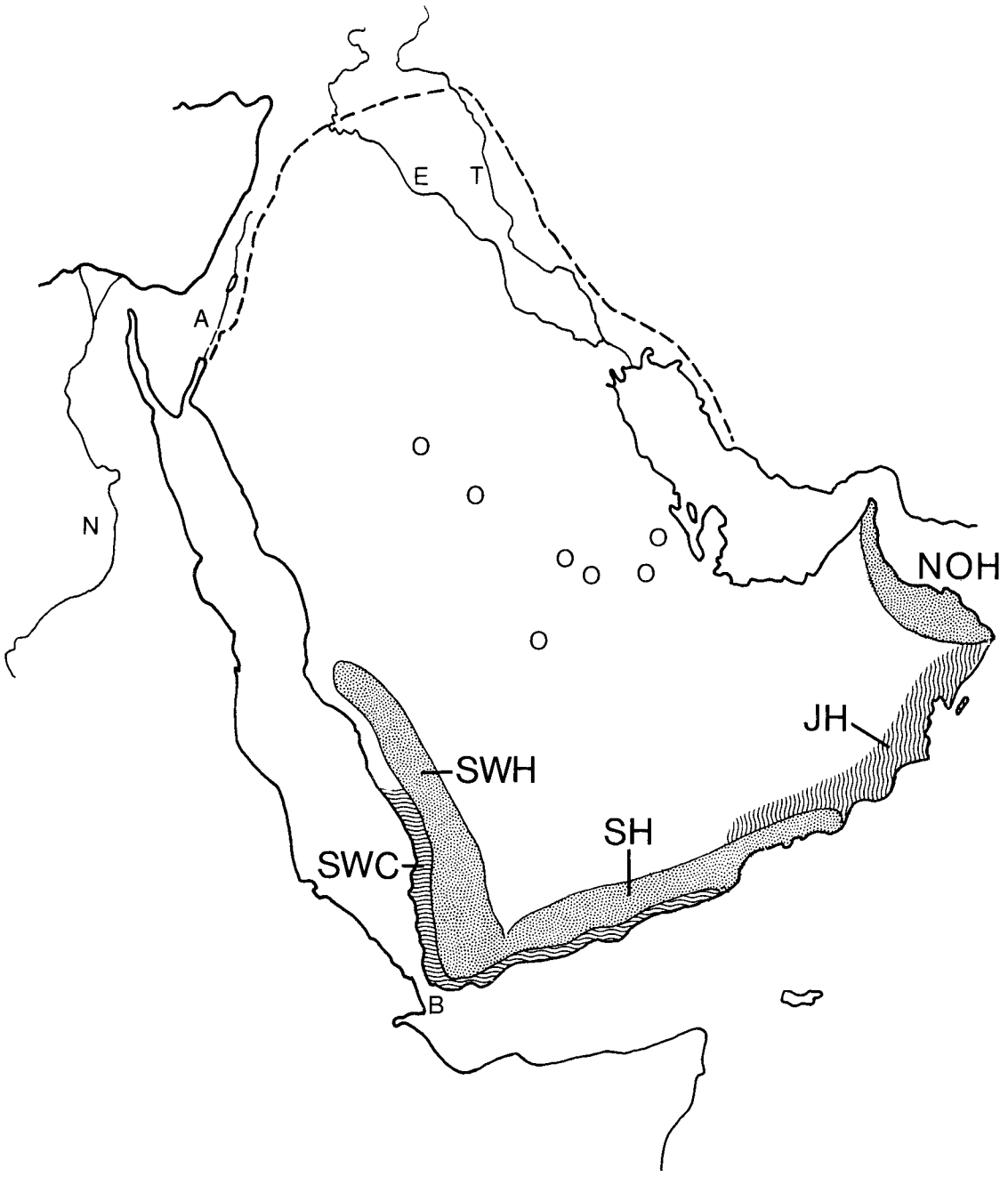

Fig. 1: Arabia. Broken line indicates approximate northern limit of Arabian region. Most of it is occupied by a widespread arid fauna but there are a number of discrete areas of high endemicity in the south: the southwestern coast (SWC), the southwestern highlands (SWH), the southern highlands (SH), the Ǧiddat (Jiddat) al-Ḥarāsīs area (JH) and the north Oman highlands (NOH). A – Wādī al-ʿAraba, B – Strait of Bāb al-Mandab, E – Euphrates, N – Nile, O – oasis sites in arid zone with mesic faunal elements, T – Tigris.

area, the moist Mediterranean coastlands provide a boundary which is continued by the relatively mesic highlands that run through southeast Turkey, north and east Iraq and adjoining Iran to embrace the north of Arabia, including Khuzestan and the northeast seaboard of the Arabian Gulf. The relatively mesic conditions in the mountains also extend into the Tigris-Euphrates area, where they form an elaborate patchwork with the arid country typical of Arabia.

History of Arabia

Twenty million years ago, Arabia was part of Africa and was separated from Eurasia by the Tethys Sea. Northward movement of Africa closed this gap and the Red Sea rift began to open. This movement, associated with Arabian plate downthrusting under the edge of Iran tilted the land mass, producing the Arabian Gulf. The history of the Red Sea has been complex, sometimes connected to the Mediterranean and sometimes to the Indian Ocean. The southern separation of Arabia and Africa at Bāb al-Mandab may have been transiently reduced in the Pleistocene period, when world falls in sea level of over 100 m occurred intermittently, or even obliterated (MILLIMAN 1977). These falls also emptied the Arabian Gulf (KASSLER 1973). Arabia may have been relatively arid from the Miocene (GLENNIE et al. 1974, WHITNEY 1983) but it is uncertain if this applied to all areas and certainly there have been broad fluctuations since, with pluvial episodes about 33,000–24,000 years B.P. and 8500–5000 years B.P. (WHITNEY 1983).

The herpetofauna of Arabia

Species from relatively mesic habitats that occur in the Tigris-Euphrates area and sometimes Jordan and Syria as well, for instance *Ophisops elegans,* are not discussed here unless they also occur further south in Arabia. The systematics of various Arabian reptile groups are discussed elsewhere (ARNOLD 1972, 1977, 1980a, 1980b, 1982, 1983, 1986a, 1986b, 1986c; ARNOLD & GALLAGHER 1977, ARNOLD & LEVITON 1977, HILLENIUS & GASPERETTI 1984, JOGER 1984, LEVITON & ANDERSON 1967). Much of the Arabian herpetofauna is listed in detail in recent and forthcoming publications (ARNOLD 1986c, GASPERETTI in preparation, BALLETTO, CHERCHI & GASPERETTI 1985) but is summarised in tabs 1 and 2. As might be expected from the aridity of Arabia, there are very few amphibians or fresh-water chelonians. Lizards outnumber snakes by

Table 1: Summary of non-marine species of reptiles and amphibians of Arabia.

	Species	Species and distinct subspecies	Endemic species	Endemic species and subspecies
Lizards and amphisbaenians	94	100	64%	69%
Snakes	32	34	31%	47%
Chelonians	2	2	0%	
Amphibians	7	7	57%	
Totals	135	143	55%	59%

Table 2: Representation of families of non-marine reptiles and of amphibians in Arabia.

	Species	Species and distinct subspecies	Endemic species	Endemic species and subspecies
LIZARDS				
Gekkonidae	37	39	62%	64%
Agamidae	13	14	62%	71%
Chamaeleonidae	3	4	67%	75%
Lacertidae	28	28	79%	86%
Scincidae	11	13	45%	54%
Varanidae	2	2	0%	
AMPHISBAENIANS				
Trogonophidae	2	2	100%	
SNAKES				
Leptotyphlopidae	3	3	33%	67%
Typhlopidae	1	1	0%	
Boidae	2	2	50%	
Colubridae	18	21	33%	43%
Elapidae	2	2	50%	100%
Viperidae	6	7	17%	
CHELONIANS				
Emydidae	1	1	0%	
Pelomedusidae	1	1	0%	
AMPHIBIANS				
Bufonidae	4	4	75%	
Hylidae	1	1	0%	
Ranidae	2	2	50%	

almost three to one and show a much higher level of endemicity. Among lizards the frequently nocturnal Gekkonidae are especially well represented with 40% of the species while the Lacertidae have 30% and a particularly high proportion of species confined to the area.

Relationships to neighbouring areas

The Horn of Africa

Bāb al-Mandab, the strait between the southernmost tip of Arabia and northeast Africa is only about 25 km across and is partly occupied by Barīm (Perim) Island on the Arabian side. In spite of the narrowness of this water barrier and the possibility of its being even smaller or absent in the recent past, it marks a very abrupt faunal change. Afro-tropical forms which predominate on the other side are in a minority in Arabia, while the reverse is true for Saharo-Sindian elements. Only 18% of 130 north Somali species also occur in Arabia, while 35% of species in the southwest of the latter area are found in northeast Africa. Afro-tropical taxa that are also present in Arabia include *Latastia, Philochortus, Mabuya brevicollis, Atractaspis, Dasypeltis, Lamprophis, Naja haje, Bitis* and *Pelomedusa.* A number of other groups, adapted to rela-

tively dry conditions, are also shared between the Horn of Africa and Arabia, such as *Pristurus*, the *Aporoscelis* section of *Uromastyx*, and *Agamadon*. The detailed phylogeny of *Pristurus* suggests there must have been multiple movements between the two regions. Reptiles with northeast African affinities are concentrated in the more mesic south and southwest of Arabia, on the southwestern coast and in the southwestern and southern highlands.

North Africa

At the present time, Arabia is largely separated from North Africa by the Red Sea and substantial discontinuities occur, in and around the narrow area of land contact through Sinai, between the desert faunas of the two regions. The most abrupt changes take place around the line of Wādī al-ʿAraba, the fault separating the African and Arabian plates. North African forms that fail to cross Wādī al-ʿAraba include *Stenodactylus petrei, S. sthenodactylus, Tarentola, Agama (Trapelus) p. pallida, A. (T.) savignyi, Uromastyx a. aegyptius, Acanthodactylus pardalis, A. s. scutellatus, Mesalina rubropunctata, Scincus s. scincus, Sphenops sepsoides, Macroprotodon, Psammophis aegyptius* and *Cerastes vipera.*

Among the Arabian forms that reach the limits of their range at or relatively near this point are *Stenodactylus doriae, S. grandiceps, Agama (Trapelus) pallida haasi, A. (T.) blanfordi, Phrynocephalus arabicus, Uromastyx m. microlepis, U. ocellatus philbyi, Acanthodactylus grandis, A. robustus, A. schmidti, A. scutellatus hardyi, Mesalina brevirostris* and *Scincus s. meccensis.* Some other eastern species extend beyond the wadi into the Negev and sometimes Sinai, but do not cross the lowland around the present Suez canal. These include *Bunopus tuberculatus, Acanthodactylus opheodurus, Atractaspis engeddensis, Coluber elegantissimus, Eirenis coronella* and *Pseudocerastes persica fieldi. Walterinnesia* and *Echis coloratus* extend further west but do not occur beyond the Nile valley. Wādī al-ʿAraba, the Suez region and the Nile are all likely to have acted as barriers to desert forms in moister periods. Indeed, during pluvial phases, it is probable that the northern border of the desert areas shifted south, so the arid regions of Arabia and North Africa would have been completely separated. Such division must have been intermittent, for many groups have close relatives on either side of the barrier region. Indeed some arid country forms go right across at the present time: *Ptyodactylus hasselquistii, Acanthodactylus boskianus, Mesalina guttulata, M. olivieri, Varanus griseus, Psammophis schokari, Malpolon moilensis, Spalerosophis diadema, Lytorhynchus diadema.* It is noteworthy that none of these is confined to soft sand habitats, as a number of species that do not traverse this region are.

Irano-Turanian area

There is an abrupt faunal discontinuity between the arid regions of Arabia and the more mesic conditions of the Turkish-Iranian mountains and the Tigris-Euphrates system. Many Arabian forms that approach this transition do not extend beyond it, e.g. *Stenodactylus, Agama (Trapelus) blanfordi, A. (T.) pallida, Uromastyx aegyptius microlepis, Acanthodactylus boskianus, A. grandis, A. schmidti, A. scutellatus, Mesalina guttulata, M. olivieri, Scincus, Diplometopon* and *Cerastes.* Conversely a number of mesic and arid taxa from Iran do not extend into Arabia (including *Eremias* sensu stricto, *Eublepharis* and *Mesalina watsonana*). In fact this discontinuity is less marked if the whole of Arabia is contrasted with Iran plus Pakistan and nearby areas, for many forms occur in both these regions but are discontinuous and are not present close to both sides of the division between them. Among these are *Rana cyanophlyctis, Eumeces taeniola-*

tus, Leptotyphlops blanfordi, all with populations in southwest Arabia and the eastern Iran-Pakistan region. *Ptyodactylus, Eublepharis, Teratoscincus, Phrynocephalus maculatus, Chamaeleo, Mesalina brevirostris* all also have disjunct distributions.

Distributional patterns within Arabia

Reptiles in Arabia show great variation in their ranges but many can be assigned to a restricted number of gross distributional patterns. The most obvious division is between taxa present in the generally arid conditions that occupy most of the peninsula, and the forms confined to small, usually more mesic areas in the south (fig. 1).

The arid regions

These include about 44 reptile species (33 lizards, 1 amphisbaenian, 10 snakes) assigned to about 21 genera. Some 24 are either confined to Arabia or largely so and there are a further six represented by endemic, or near-endemic, subspecies. Some, like the geckoes *Bunopus tuberculatus* and *Stenodactylus doriae,* have large ranges extending over 2500 km from Jordan to Oman, but others are more restricted. For instance, several otherwise widespread forms, such as *Acanthodactylus boskianus* and *A. opheodurus* avoid the Rubʿ al-Ḫālī, the great southern desert. Others, like the amphisbaenian *Diplometopon zarudnyi* and *Stenodactylus khobarensis* are confined to relatively humid situations, mainly around the Arabian Gulf but also in central Oman. The north of the arid zone with its somewhat less dry climate, has a number of endemic forms such as *Acanthodactylus grandis, A. orientalis, Stenodactylus grandiceps, Agama (Trapelus) blanfordi, A. (T.) pallida* and *Eirenis coronella.*

Ecological separation among sympatric lizard species in the arid regions depends on differences in such factors as microhabitat, especially ground type, prey size and time of activity (Arnold 1984). In some cases, forms that are similar in these parameters have largely parapatric ranges, replacing each other quite abruptly. Thus *Stenodactylus slevini, Agama (Trapelus) blanfordi* and *Mesalina brevirostris* are represented to the south by, respectively, *Stenodactylus leptocosymbotes, Agama (Trapelus) flavimaculata* and *Mesalina adramitana.*

Among the genera constituting the widespread Arabian desert fauna, only *Diplometopon* and to a large extent *Walterinnesia* are confined to it. All the others occur elsewhere in the arid Saharo-Sindian region, which extends from northwest Africa to northwest India. This is an area with a very distinctive fauna that, as an entity, cannot be easily associated with either the Palaearctic or Ethiopian biogeographic realms, although it has clear connections with both. Among the Saharo-Sindian taxa found in Arabia, *Stenodactylus, Scincus, Malpolon moilensis* and *Cerastes* occur in North Africa as well, while *Bunopus, Teratoscincus* and *Phrynocephalus* are present in Iran, Pakistan and neighbouring areas. The others nearly all occur more broadly, viz. *Ptyodactylus, Agama (Trapelus), Uromastyx, Acanthodactylus, Mesalina, Varanus (Psammosaurus), Eryx, Lytorhynchus, Psammophis* and *Spalerosophis.* Amongst these the species of *Varanus (Psammosaurus), Psammophis* and *Spalerosophis* found in Arabia occur right across the Saharo-Sindian area, those of *Ptyodactylus, Uromastyx* and *Lytorhynchus* have conspecific populations in North Africa, and the other genera, with more than one Arabian species, have relatives to the west and to the east. Overall, there are more affinities to the Sahara (about 12 apparent monophyletic units compared with 5 to the east). It seems that there has been a long

and complex interchange of fauna between the Arabian deserts and other parts of the Saharo-Sindian region, with the border areas sometimes permitting the spread of certain taxa and sometimes preventing it. In contrast there are scarcely any links with the Horn of Africa.

The southwestern coast

The dry coastal area from the Tihāma of ʿAsīr in Saudi Arabia to about Qišn (Qishn) in South Yemen has 14 species not found elsewhere in Arabia of which nine are endemic. Five are conspecific with species in the Horn of Africa (*Hemidactylus sinaitus, Pristurus crucifer, P. flavipunctatus, Mesalina martini, Echis pyramidum*), while *Bufo tihamicus, Agamodon arabicus* and possibly *Chalcides levitoni* have their nearest relatives there. Most of the remaining endemics are related to forms in the arid interior of Arabia and belong to Saharo-Sindian groups (*Stenodactylus pulcher, S. yemenensis, Acanthodactylus arabicus, Scincus hemprichii, Lytorhynchus gasperetti*). Finally *Pristurus ornithocephalus* is related to other members of the *Pristurus carteri* group which occur in the less arid parts of southern Arabia. This overall pattern suggests contact with northeast Africa over a period and previous faunal continuity between the coast and the interior desert, even though these latter areas are largely separated by high mountains. It is not certain that the southwestern coastal area is faunistically homogeneous, for some species seem restricted within it. Thus the western *Scincus hemprichii* is not known to extend beyond the Aden area, while *Stenodactylus pulcher* is possibly confined to the east.

The southwestern and southern highlands

In southern Arabia there are mountains running parallel to the coast. They can be divided into two main sections: the southwestern mountains, from around aṭ-Ṭāʾif (Taif) south to the Aden region, and the southern mountains running eastwards from here to Ẓufār (Dhofar) in southern Oman. The southwestern mountains form a seaward-facing escarpment and rise in the south to over 3000 m. They catch the monsoon and their crests may receive 500 mm of rain per annum and perhaps even 1000 mm in parts of southern North Yemen (Whitney 1983). The southern mountains are less elevated and more intermittent with lower rainfall, catching the southwest monsoon only in restricted areas, particularly Ẓufār. This whole mountain system is very different climatically from the usually arid coast and the deserts that border it inland. It has a total of some 43 species that do not seem to extend into the immediate surroundings, and of these, 26 are endemic. Because of their differences, the southwest and southern mountains are best treated separately, although there is some faunal overlap. They share five widespread species which have related populations in the Horn of Africa and are not strongly adapted to montane conditions, namely *Hemidactylus yerburii, Agama (Stellio) adramitana* (endemic), *Mabuya brevicollis, Naja haje* and *Bitis arietans. Bunopus spatalurus* and *Mabuya tessellata* occur in the southern mountains and a part of the southwestern ones, and in the north Oman mountains as well.

Southwestern highlands. These include forms with a variety of affinities.

1. Some are closely related or conspecific with forms occurring further north. Many of these have their most nearly related populations quite near at hand in the eastern Mediterranean region, including *Hyla savignyi, Rana ridibunda, Bufo viridis, Chamaeleo chamaeleon, Eirenis coronella fenelli* (endemic) and *Rhynchocalamus arabicus* (endemic). In other cases, their affini-

ties are further east. *Ablepharus pannonicus* s. lat. has conspecific populations in Iraq, while *Rana cyanophlictis ehrenbergii* (endemic), *Eumeces taeniolatus, Leptotyphlops blanfordi nursii* (endemic) have conspecifics in eastern Iran, Pakistan and India. North-south connexions are also shown by other species: *Uromastyx ornatus philbyi* is represented by other populations to the north and forms with wider ranges in the more mesic parts of Arabia, such as *Pristurus rupestris, Agama (Pseudotrapelus) sinaita, Telescopus dhara, Coluber rhodorhachis* and *Echis coloratus* also have northern extensions.

2. A number of species in the southwestern mountains have outlying populations in the Oman highlands, although they do not extend far into the neighbouring southern mountains: *Bufo arabicus, Pristurus gasperetti, Ablepharus pannonicus* and *Echis coloratus.*

3. Some forms have connexions with the Horn of Africa. A minority are apparently conspecific with African populations, such as *Varanus exanthematicus, Dasypeltis scaber* and *Pelomedusa subrufa,* but others are endemic species: *Agama yemenensis, Chamaeleo calyptratus, Latastia longicaudata andersonii, Philochortus neumanni, Coluber variabilis, Coluber manseri, Lamprophis fulginosus arabicus.* Other distinctive endemics are *Mesalina* n. sp., *Pristurus popovi* and *Pristurus saada.*

The fact that relationships with northern areas and the Horn of Africa involve both conspecific populations and well differentiated species suggests at least intermittent contacts over an extended period. In the case of more recent northern connexions, it is probable that Quaternary pluvial phases allowed these to take place. Like most massifs, the southwestern mountains have accumulated a wide range of populations that are isolated on them. Some may well be climatic relicts restricted by present dry conditions but it is possible that others have been driven into the mountains by competition (Arnold 1981). The most likely instances are where a highland species is in contact with a similar, often congeneric, form that is widely distributed at lower altitudes. Such cases occur in *Agama (Stellio), Chamaeleo* and *Mesalina.* Known ranges of many forms in the southwest mountains are very sporadic, partly due to poor collecting but also because suitable habitat is very fragmented and regional extinction likely. This is associated with local differentiation in some species.

Southern highlands. As stated, this region is drier, less elevated and far less continuous than the southwest mountains. Nevertheless it has ten endemics. There are, however, no forms with northern affinities and none connected with moist habitats. The Ẓufār mountains are very green in and after the monsoon season but have no specialised fauna, probably because the area is dry for most of the year and the forest may not have existed continuously for very long (Arnold 1980 a). Endemics occur instead in the rather drier, more extensive and probably more permanent steppe country which has forms like *Hemidactylus lemurinus, Acanthodactylus felicis, Mesalina ayunensis* and *Coluber thomasi.* Other endemics associated with the southern mountains and their periphery are *Pristurus collaris, Hemidactylus homoeolepis, Tropiocolotes scorteccii, Uromastyx benti, Chamaeleo arabicus* and *Leptotyphlops burii.* While the *Mesalina* and *Acanthodactylus* belong to essentially Saharo-Sindian groups, the latter has a close relative in the southwestern mountains, which also appears to be true of the *Chamaeleo* and *Coluber.* As in that area, the southern mountains appear to have conserved relict forms, but fragmentation and local intraspecific differentiation is even more pronounced (e. g. in *Acanthodactylus felicis, Hemidactylus homoeolepis, H. yerburii* and *Tropiocolotes scorteccii;* Arnold 1980 a).

Ğiddat (Jiddat) al-Ḥarāsīs area

This region is occupied largely by members of the neighbouring desert fauna, but along the coast the climate is less extreme being sometimes affected by the monsoon. A number of forms have the greater part of their known ranges here. One of these, *Scincus mitranus muscatensis,* is a well differentiated subspecies of an inland desert form. The others are *Pristurus minimus, P. carteri, Acanthodactylus masirae* and *Uromastyx thomasi.* The last three have close relatives in the southern mountain fauna, namely *P. collaris, A. felicis* and *U. benti.* They probably arose through geographical fragmentation within this general assemblage. All these species extend westwards, to varying degrees, north of the Ẓufār mountains and *P. carteri* reaches as far as north Ğaul (Jol) in the Ḥaḍramaut.

The north Oman highlands

This massif, which reaches 3000 m is very isolated and has some 16 species that do not extend far into the neighbouring lowlands. Four are endemic, including the most primitive member of *Pristurus, P. celerrimus,* and at least two others are represented by distinct subspecies. Some of these forms may have been competitively restricted to the mountains (ARNOLD 1981). Eight are related to taxa in the more mesic areas of Iran. Of these, five are conspecific with Iranian forms, namely *Hemidactylus persicus, Phyllodactylus elisae* sensu lato, *Ablepharus pannonicus, Echis carinatus sochureki* and *Pseudocerastes persicus,* while *Phyllodactylus gallagheri, Lacerta cyanura* and *Lacerta jayakari* are confined to the north Oman mountains. As we have seen, some forms have conspecifics in the southwestern mountains of Arabia, including *Pristurus gasperetti, Ablepharus pannonicus, Echis coloratus* and *Bufo arabicus.* Only five have their nearest related populations in the southern mountains: *Bunopus spatalurus hajarensis, Ptyodactylus hasselquistii, Mabuya tessellata, Coluber rhodorhachis* and *Telescopus dhara.* Considering that some species occur in north Oman and the distant southwestern mountains of Arabia, it is surprising that the arid Ğiddat al Ḥarāsīs area has been such an effective barrier between the herpetofauna of north Oman and the eastern end of the southern highlands in Ẓufār, only about 500 km away. Among the forms in the latter area that do not reach north Oman are *Bunopus s. spatalurus, Hemidactylus yerburii, H. lemurinus, Tropiocolotes scorteccii, Agama adramitana, Chamaeleo arabicus, Acanthodactylus felicis, Mesalina ayunensis, Mabuya brevicollis, Atractaspis microlepidota, Coluber thomasi, Naja haje, Bitis arietans* and *Echis pyramidum.* A fault runs just west of the north Oman mountains and marks the boundary of the African-Arabian plate. Sabkhas, such as the Umm as-Samīm, in this area may be remnants of incursions of the sea which could have intermittently separated Oman from the rest of Arabia.

Peripheral mesic forms

A number of reptile species typical of relatively mesic habitats occur widely in Arabia but mainly around the periphery. Some like *H. turcicus* sensu lato and *Chalcides ocellatus* extend into the moist southwestern highlands and Wādī Ḥaḍramaut but otherwise occur sporadically in coastal areas, as do *Cyrtodactylus scaber, Hemidactylus flaviviridis, Leptotyphlops macrorhynchus* and *Rhamphotyphlops braminus,* although these latter forms have one or two small inland populations as well. Most of the species have large total ranges and often occur in and around areas of human colonisation. This, together with their broken distributions suggests that they

may have been introduced by man in some places. Other mesic forms are not so widely distributed in Arabia but extend southwards from Iran and the Tigris-Euphrates area along the humid western coast of the Arabian Gulf at least as far as Bahrain. Among these are *Rana ridibunda, Mauremys caspica, Hemidactylus persicus, Mabuya aurata* and *Coluber ventromaculatus.*

Oasis relicts

Although most of inland Arabia is occupied by reptiles adapted to dry conditions, various mesic forms occur in the north and centre of Saudi Arabia at oasis sites with relatively good rainfall or ground water. These include places such as Ḥā'il, Buraida, al-Hufūf and a number of localities in the ar-Riyāḍ area. The species found include forms present in generally moister areas like the southwestern mountains, the east Mediterranean region and the Gulf coast, and there is local variation in what occurs. Thus Ḥā'il has northern forms like *Agama (Stellio) stellio* and *Mesalina olivieri* and also *Eumeces taeniolatus* and *Atractaspis.* At al-Hufūf, forms typical of the Gulf coast are present: *Cyrtodactylus scaber, Hemidactylus persicus* and *Mabuya aurata.* Finally, the ar-Riyāḍ area in its more central position has a mixture of elements: northern *Eumeces schneideri,* eastern *Cyrtodactylus scaber,* and a range of forms that occur in the southwest highlands, namely *Mabuya brevicollis, Atractaspis, Bufo arabicus, B. dhufarensis, Coluber rhodorhachis* and *Echis coloratus.* All but the first two of these are also found in the north Oman highlands.

It seems probable that these mesic forms are relicts of populations which were widespread during the pluvial phases of the Quaternary. They provide evidence that disjunct distributions of forms like *Eumeces taeniolatus* with isolated populations in southwestern Arabia and Pakistan were once continuous. Similarly, they suggest that species found in the southwestern mountains and north Oman could have been continuous through central Arabia rather than across the southern mountains and the Ǧiddat al Ḥarāsīs area.

Conclusion

It is tempting to subject the Arabian herpetofauna to a strict vicariance analysis. However, while this method works well in areas where distributions are irrevocably fragmented by permanent barriers, as for instance in the break-up of Gondwanaland to produce the southern continents, it cannot elucidate the complex situation found around and within Arabia where barriers have fluctuated, sometimes stopping movement and sometimes allowing it to take place. Such are the complexities of geological and climatic history in the area, that it is impossible to produce a detailed description of zoogeographic events, especially as there is no known fossil record of present reptiles and amphibian groups in Arabia. All that can be done is to describe patterns and mechanisms which may have produced them.

References

ARNOLD, E.N. 1972: Lizards with northern affinities from the mountains of Oman. - Zoologische Mededeelingen **47**: 111-128. Leiden.

ARNOLD, E.N. 1977: Little-known geckoes (Reptilia: Gekkonidae) from Arabia, with descriptions of two new species from the Sultanate of Oman. - The Scientific Results of the Oman Flora and Fauna Survey 1975. Journal of Oman Studies, Special Report **1**: 81-110. Muscat.

ARNOLD, E.N. 1980a: The reptiles and amphibians of Dhofar, South Arabia. - The Scientific Results of the Oman Flora and Fauna Survey 1977. Journal of Oman Studies, Special Report **2**: 273-322. Muscat.

ARNOLD, E.N. 1980b: A review of the lizard genus *Stenodactylus* (Reptilia: Gekkonidae). - Fauna of Saudi Arabia **2**: 368-404. Basle and Jeddah.

ARNOLD, E.N. 1981: Competition, evolutionary change and montane distributions. - In: The evolving Biosphere. FOREY, P.L. ed.: 217-228. London & Cambridge, British Museum (Natural History) & Cambridge University Press.

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

ARNOLD, E.N. 1983: Osteology, genitalia and the relationships of *Acanthodactylus* (Reptilia: Lacertidae). - Bulletin of the British Museum (Natural History), Zoology **44**: 291-339. London.

ARNOLD, E.N. 1984: Ecology of lowland lizards in the eastern United Arab Emirates. - Journal of Zoology **204**: 329-354. London.

ARNOLD, E.N. 1986a: A new spiny-footed lizard (*Acanthodactylus*: Lacertidae) from Saudi Arabia. - Fauna of Saudi Arabia **8**: 378-384. Basle and Jeddah.

ARNOLD, E.N. 1986b: New species of semaphore gecko (*Pristurus*: Gekkonidae) from Arabia and Socotra. - Fauna of Saudi Arabia **8**: 352-377. Basle and Jeddah.

ARNOLD, E.N. 1986c: A key and annotated check-list to the lizards and amphisbaenians of Arabia. - Fauna of Saudi Arabia **8**: 385-435. Basle and Jeddah.

ARNOLD, E.N. & M.D. GALLAGHER 1977: Reptiles and amphibians from the mountains of northern Oman with special reference to the Jebel Akhdar region. - The Scientific Results of the Oman Flora and Fauna Survey 1975. Journal of Oman Studies, Special Report **1**: 59-80. Muscat.

ARNOLD, E.N. & A.E. LEVITON 1977: A revision of the lizard genus *Scincus* (Reptilia: Scincidae) - Bulletin of the British Museum (Natural History), Zoology **31**: 187-248. London.

BALLETTO, E., M.A. CHERCHI & J. GASPERETTI 1985: Amphibians of the Arabian Peninsula. - Fauna of Saudi Arabia **7**: 318-392. Basle and Jeddah.

GASPERETTI, J. in preparation: Snakes of Arabia. - Fauna of Saudi Arabia **9**.

GLENNIE, K.W., M.W. HUGHES CLARKE, M. MOOD-STUART, W.F.H. PILAAR 1974: Geology of the Oman Mountains. - Verhandelingen van het Koninklijke Nederlandsch Geologisch Mijnbouwkundig Genootschap **31**: 1-412. s'-Gravenhage.

HILLENIUS, D. & J. GASPERETTI 1984: Chameleons of Saudi Arabia. - Fauna of Saudi Arabia **6**: 513-527. Basle and Jeddah.

JOGER, U. 1984: The venomous snakes of the Near and Middle East. - Tübinger Atlas des Vorderen Orients A (Naturwissenschaften) **12**: 1-115. Wiesbaden, Reichert.

KASSLER, P. 1973: The structural and geomorphic evolution of the Persian Gulf. - In: The Persian Gulf. PURSER, B.H. ed.: 11-32. Berlin, Springer Verlag.

LEVITON, A. E. & S. C. ANDERSON 1967: Survey of the reptiles of the Sheikhdom of Abu Dhabi, Arabian Peninsula. Part II: Systematic account of the collection of reptiles made in the Sheikhdom of Abu Dhabi by John Gasperetti. – Proceedings of the California Academy of Sciences **35**: 157–192. San Francisco.

MILLIMAN, J. D. 1977. Interstitial waters of late Quaternary Red Sea sediments and their bearing on submarine lithification. – pp. M 1–M 6. – In Red Sea Research 1970–75, Bulletin No **22**. Jiddah, Ministry of Petroleum and Mineral Resources.

WHITNEY, J. W. 1983: Erosional history and surficial geology of western Saudi Arabia. – Technical Record USGS-TR-04-1. Jiddah, Ministry of Petroleum and Mineral Resources.

Author's address: Dr. E. N. Arnold, Department of Zoology, British Museum (Natural History), Cromwell Road, London SW 7 5 BD, England.