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

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An Interpretation of Reptile Zoogeography in Arabia, with Special Reference to Arabian Herpetofaunal Relations with Africa

U. Joger

Abstract: The Afrotropical element in the Arabian herpetofauna is concentrated in the southwestern mountainous region, whereas everywhere else in the peninsula the reptile fauna is Saharo-Sindian. There is a high degree of correspondence between the reptile faunas of the Yemens and Somalia. A remarkable faunistic resemblance also exists between the relict faunas of SW Arabia and Morocco.

Three evolutionary levels can be distinguished among Ethiopian taxa in Arabia and are interpreted as evidence of different times of faunal contact: 1. Old relicts (genus level) of a Palaeogene (pre continental drift) Arabian/North African fauna (*Pristurus,* Trogonophidae); 2. Endemic species closely related to East African species (most probably Miocene); 3. Species distributed on both sides of the Bāb al-Mandab (Pleistocene). Contrary to the Saharo-Sindian faunal elements, there is good evidence that groups 2 and 3 used a landbridge across the Bāb al-Mandab for faunal exchange: the Miocene closure of the southern outlet of the Red Sea and a Pleistocene land connection due to eustatic sea level change.

Keywords: Reptile distribution, herpetofaunal relations, historical biogeography, Saharo-Sindian, Ethiopian, endemism, invasion routes, continental drift, land bridges.

1. Introduction

The aim of this study is to interpret recent reptile distribution patterns in Arabia as results of the biogeographic history of the region.

Northeast Africa and most of the Arabian peninsula were once united geologically in the Nubo-Arabian Shield, a part of the African continental plate (Wolfarth 1987). The Red Sea, now being the principal migration barrier between Arabia and tropical Africa, is comparatively young. It was born in the mid-Tertiary as a tectonic crack in the north-eastern corner of the central piece of former Gondwanaland, which had been torn apart by continental drift. During the Oligocene, from 42 to 30 mybp, this crack slowly progressed from the Gulf of Aden to the area north of as-Suwais (Girdler 1984). However, only the southern third of this predecessor of the Red Sea experienced a marine transgression at the time. The northern part was a mainly terrestrial valley comparable to today's East African Rift Valley.

25 or 26 mybp, at the border between Oligocene and Miocene, more intensive tectonic movements began, giving birth to the Gulf of al-ʿAqaba and Dead Sea and considerably widening and deepening the Red Sea graben (Girdler, l.c.). A marine fauna of mediterranean affinities documented as far south as the Danakil Depression suggests that a marine connection with the aged Tethys Ocean in the north existed at that time (Gohar 1955, Hutchinson & Engels 1970), whereas a land barrier blocked the Strait of Bāb al-Mandab (Girdler 1969).

A period of tectonic rest followed from 16 to 8 mybp; extensive sea level changes and drying up of huge portions of the Red Sea are documented by thick Miocene salt deposits.

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At the start of the Pliocene, further continental drift resulted in the breaking of the Bāb al-Mandab barrier about 7–5 mybp, filling the Red Sea and the Danakil Depression with Indian Ocean water (Girdler 1984).

Whether the Bāb al-Mandab fell dry again during the eustatic sea level changes of the Pleistocene is not certain. As the minimum depth of the sea floor between Eritrea and the Yemen (137 m, Werner & Lange 1975) is approximately equal to the maximum lowering of the sea level during the glacials (120 m, as recorded on the Lebanon coast), a short-time Pleistocene southern land connection across that area is not improbable.

Today's faunal similarities between Arabia and Africa could thus have the following origins:

1) old relicts of the early Tertiary Afro-Arabian fauna;
2) witnesses of the southern land connection of Miocene age;
3) remnants of a possible Pleistocene southern landbridge;
4) invaders of a more or less recent age, which used the northern pathway across the Sinai Peninsula, originating either from Africa or from Arabia.

2. General zoogeography of reptiles in Arabia

A zoogeographic division of Arabia widely used is that of Bodenheimer (1956, cited from Haas & Werner 1969). Arabia is mainly classified as a part of the Saharo-Sindian Subregion of the Palaearctic Region, whereas the extreme Southwest is part of the Ethiopian[1] Subregion of the Palaeotropic Region.

Reptile distribution patterns seem to agree with Bodenheimer's classification. About one fourth of the reptile genera in Arabia are Ethiopian (tab. 1); they are distributed only in the Southwest of the peninsula (southern al-Hiğāz to Ẓufār) and are not found elsewhere in Asia. The only exceptions are the burrowing vipers, *Atractaspis* Smith, which also occupy isolated territories in Sinai and in the Jordan valley.

Based on distribution, nearly half of the Arabian reptile genera must be classified Saharo-Sindian: *Acanthodactylus* Wiegmann, 1834, *Mesalina* Gray, 1838, *Chalcides* Laurenti, 1786, *Scincus* Laurenti, 1786, *Stenodactylus* Fitzinger, 1826, *Ptyodactylus* Goldfuss, 1820, *Tropiocolotes* Peters, 1880, *Trapelus* Cuvier, 1817, *Uromastyx* Merrem, 1820, *Eryx* Daudin, 1803, *Malpolon* Fitzinger, 1826, *Lytorhynchus* Peters, 1862, *Spalerosophis* Jan, 1865, *Telescopus* Wagler, 1830, *Cerastes* Laurenti, 1768, and *Echis* Merrem, 1820. However, the specialists of sandy deserts among these genera do not reach further east than Ḫūzestān (= ʿArabestān). On the other hand, Irano-Turanian genera come to Arabia from the East: *Asaccus* Dixon & Anderson, 1973, *Bunopus* Blanford, 1874, *Teratoscincus* Strauch, 1863, *Phrynocephalus* Kaup, 1825, *Ablepharus* Fitzinger, 1823, and *Pseudocerastes* Boulenger, 1896.

Most other genera are either widespread with tropical origin (*Mabuya* Fitzinger, 1826, *Hemidactylus* Oken, 1817, *Varanus* Merrem, 1820, *Leptotyphlops* Fitzinger, 1843), or of Holarctic origin (*Lacerta* Linnaeus, 1758, *Eumeces* Wiegmann, 1834, *Coluber* Linnaeus, 1758, *Natrix* Laurenti, 1768).

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[1] The terms Ethiopian and Afrotropical are used here as synonyms.

Table 1: Genera with endemic species in peninsular Arabia (excl. NArabia).

Tropiocolotes (*T. scorteccii*)
* *Hemidactylus* (*H. homoeolepis, H. lemurinus*)
* *Pristurus* (*P. popovi, P. minimus, P. celerrimus, P. carteri*)
Asaccus (*A. gallagheri*)
Stenodactylus (*S. yemenensis, S. pulcher, S. khobarensis, S. arabicus*)
Bunopus (*B. spatalurus*)
* *Chamaeleo* (*C. calyptratus, C. calcarifer*)
Trapelus (*T. jayakari*)
(*) *Stellio* (*S. yemenensis, S. adramitana*)
* *Mabuya* (*M. tesselata*)
Chalcides (*C. levitoni*)
Scincus (*S. mitranus, S. hemprichi*)
Uromastyx (*U. benti, U. thomasi*)
* *Philochortus* (*P. neumanni*)
Acanthodactylus (*A. yemenicus, A. felicis, A. masirae, A. gongrorhynchus, A. haasi*)
Phrynocephalus (*P. arabicus*)
Mesalina (*M. adramitana, M. ayunensis, M.* sp.)
* *Lacerta* (*L. jayakari, L. cyanura*)
* *Agamodon* (*A. arabicus*)

(*) *Leptotyphlops* (*L. nursi, L. yemenicus?*)
Eryx (*E. jayakari*)
Lytorhynchus (*L. gasperettii*)
(*) *Coluber* (*C. thomasi, C. variabilis*)

* non-saharosindian genera
(*) widespread genera

The phylogenetic relations of the Saharo-Sindian genera are either Palaearctic or Palaeotropic, with a slight dominance of the relations to the Afrotropical Realm. Therefore it should not be regarded as a subregion of the Palaearctic.

Based on reptile endemism at the generic level, the Saharo-Sindian should be recognized as a distinct zoogeographical region, equivalent to (though intermediate between) and necessarily overlapping with the Palaearctic, the Afrotropical and the Oriental Region. The Irano-Turanian should be classified as a subregion of the Saharo-Sindian. The western half of the Saharo-Sindian Region, including the Sahara and most of Arabia, could be called the Saharo-Arabian Subregion. The Saharo-Arabian could be further divided into an Arabian and a Saharan zone, yet with a broad transition area between them, stretching from Wādī al-ʿAraba to the Nile (see also WERNER 1987).

The influences of neighbouring zoogeographic zones on the Arabian herpetofauna are documented in the fact that Arabia has no endemic reptile genus. The amphisbaenian *Diplometopon* Nikolsky, 1907, in the East, the agamid lizard *Pseudotrapelus* Fitzinger, 1843, in the West, and the elapid snake *Walterinnesia* Lataste, 1887, in the northern and central part of Arabia are nearly endemic, as they reach only limited parts of adjacent territories of Egypt/Sudan or Iran, respectively. The monotypic gekkonid genera *Trachydactylus* Haas & Battersby, 1959, and *Trigonodactylus* Haas, 1957, which were endemic to Arabia, have been synonymized with *Stenodactylus* (ARNOLD 1980).

3. Evolutionary history of certain reptile genera

3.1 *Stenodactylus* and *Ptyodactylus*

These two genera of desert geckos have been found to be part of the African gekkonine radiation, and to be fairly closely related to the northern African genus *Tarentola* Gray, 1826 (Joger 1985). According to immunological data, their ancestors could have lived in Arabia since the early Tertiary. Their evolutionary centre is clearly in Arabia (northern Arabia for *Ptyodactylus*, southern Arabia for *Stenodactylus*). Their reinvasion of North Africa seems to be rather recent (Arnold 1980, Heimes 1982).

3.2 *Uromastyx*

This genus is an example of an invader from the opposite direction, i.e., from the East. Its nearest relative is the Southeast Asian *Leiolepis*, its most primitive species the Pakistani *U. hardwickii* Gray, 1827 (Moody 1980). The immunologically based phylogeny of the genus (Joger

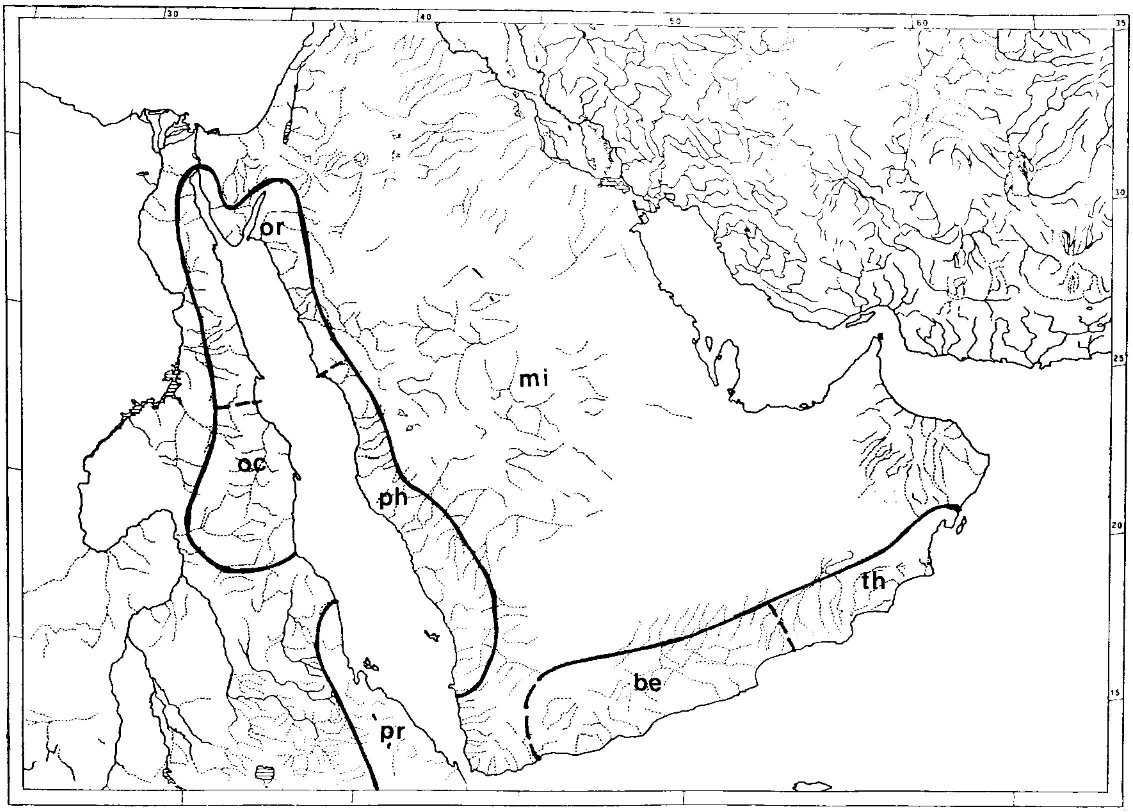

Fig. 1: Approximate distribution of Arabian *Uromastyx* (Agamidae); oc = *U. ocellatus ocellatus*; or = *U. ocellatus ornatus*; ph = *U. ocellatus philbyi*; pr = *U.* (*Aporoscelis*) *princeps*; be = *U.* (*Aporoscelis*) *benti*; th = *U.* (*Aporoscelis*) *thomasi*; mi = *U. microlepis* (synonymus with *U. aegyptius* and distributed in the whole of the Arabian Peninsula and in Egypt).

1986) suggests that the primitive eastern group gave rise to an Arabian group, which must have invaded Arabia at the time of the closure of the Tethys Sea in the middle Miocene, about 18 mybp. It contains today two polytypic species: *U. aegyptius* Forskål, 1775 (= *U. microlepis* Blanford, 1874), and *U. ocellatus* Lichtenstein, 1823, which is distributed around the northern two thirds of the Read Sea, and is joined here by the two former species *U. ornatus* Heyden, 1827, and *U. philbyi* Parker, 1938, as subspecies.

A very distinctive group of *Uromastyx* is found in the area south of *U. ocellatus,* again on both sides of the Red Sea, and extending east to Ẓufār: These two to four species are sometimes united under the name *Aporoscelis* Boulenger, 1885 (see fig. 1).

3.3 *Stellio* Laurenti, 1768

This agamid genus, formerly incorporated in the collective genus *Agama* Daudin, 1802, is composed of more than 20 species, most of which are distributed in Central Asia and in the Irano-Turanian, although there is a group of five species centered around *S. atricollis* A. Smith, 1851, which inhabits East Africa from Ethiopia and Somalia to Natal. There is a vast distribution gap between the Ethiopian species of the genus and the nearest population of *Stellio stellio* in Lower Egypt.

In Southwest Arabia however, there are two species, *Stellio adramitana* Anderson, 1896, and *S. yemenensis* Klausewitz, 1954, which KLAUSEWITZ (1954) regards as subspecies of *S. cyanogaster* Rüppell, 1835, from Ethiopia. ARNOLD (1980) gives evidence that *S. adramitana* and *S. yemenensis* are not conspecific. New biochemical data (Joger, unpublished) justify their inclusion in the *atricollis* group.

As *Stellio* is lacking in Northern Africa except in Mediterranean Egypt, it seems not improbable that in this case the Yemen served as the starting point for the invasion of a genus into tropical Africa.

The vicariant event of rifting apart of the Nubo-Arabian Shield separated the Arabian and the African portions of *Stellio* from each other. However, if one of the species, *S. adramitana* or *S. yemenensis,* is still conspecific with *A. cyanogaster,* a secondary Pleistocene crossing of the Strait of Bāb al-Mandab must be postulated.

3.4 *Echis*

This viperid genus is supposed to be related to the African Viperidae (GROOMBRIDGE 1980) and is now distributed over the whole Saharo-Sindian region and adjacent tropical territories. Of the six or seven species, three occur in Arabia: *E. coloratus* Günther, 1878, around the Red Sea from NE Sudan to S Yemen, with isolated populations around ar-Riyāḍ and in the Oman Mts., *E. carinatus* Schneider, 1801, an eastern species which reaches Arabian territory only in the Oman area, and *E. pyramidum* (Geoffroy, 1809), an African species which shares with many other Aethiopian forms the typical distribution pattern in SW Arabia from the southern al-Hiǧāz to Ẓufār (fig. 2). It is important to note that the three species who meet or nearly meet in Oman belong to three different radiations within the genus (see JOGER 1984).

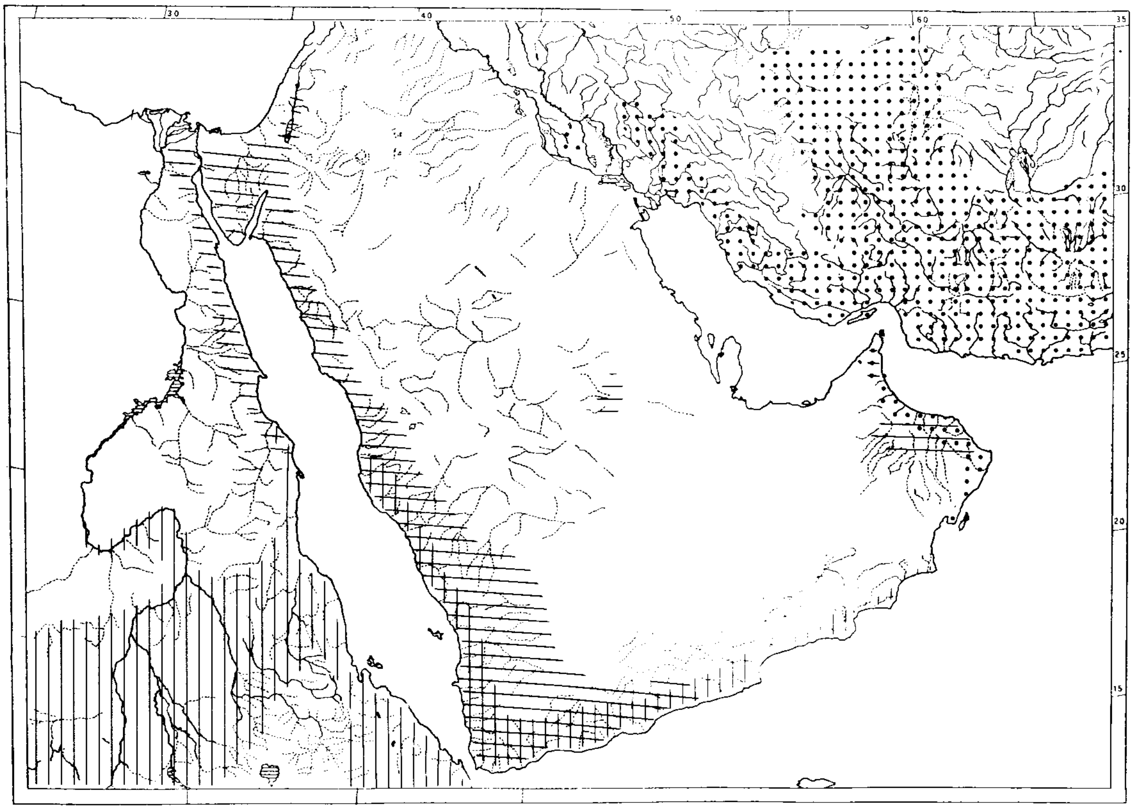

Fig. 2: Approximate distribution of Arabian *Echis* (Viperidae). Vertical bars: *E. pyramidum*; horizontal bars: *E. coloratus*; dots: *E. carinatus*. After Joger (1984).

3.5 *Naja* Laurenti, 1768, and *Chamaeleo* Laurenti, 1768

These two genera have more in common than one would expect at first glance. They are both of Ethiopian origin but have also reached the Indian subcontinent. However they are absent from the territories between Ẓufār and Balūčestān and are confined in the Arabian Peninsula to the mountainous region in the southwest, as with so many other Ethiopian immigrants. Ecologically dependent on relatively humid conditions, their limited distribution in the Middle East is not astonishing. However, their presence in India suggests that a passage across this arid belt was possible in the past, when conditions were more favourable (for example in the middle Miocene, when a subhumid tropical coastal climate prevailed on the now hyperarid eastern Arabian coast (Whybrow & McClure 1980/81). They may have been widely distributed over the Nubo-Arabian Shield when its northern extension, the Zagros Plate, collided with central Iran in the Miocene (Stoneley 1981), and migrated by the same routes as *Uromastyx* did, but in the opposite direction. This timing is consistent with the degree of differentiation between the respective Ethiopian and Oriental species of the genera concerned.

It could be suspected that the Indian chameleons were Gondwana relicts of the time when India was connected to Africa via Madagascar. However morphologically they are not closely related to the Madagascaran chameleons, but are members of the *Chamaeleo chamaeleon* group (*Chamaeleo* s.str.), which is a derived group comprising many African and all Arabian *Chamaeleo* species (KLAVER & BÖHME, 1986)

Elapids have never been present in Madagascar, but they are common in Indoaustralia. An Asian origin of *Naja* (and of other African elapids) cannot be completely excluded.

3.6 Pristurus and the Trogonophidae

These taxa. also belonging to very different reptile groups, show some outstanding biogeographic peculiarities:

- They do not follow general zoogeographic patterns. The rock living gecko *Pristurus* is distributed from Somalia to S Iran, regardless of ocean or desert barriers, but always near the coast. Its greatest species density is reached on both sides of the Gulf of Aden (fig. 3). The Arabian Amphisbaenians of the family Trogonophidae (sensu GANS 1967) are composed of *Diplometopon zarudnyi* Nikolsky, 1907, which goes from Mesopotamia down the Gulf

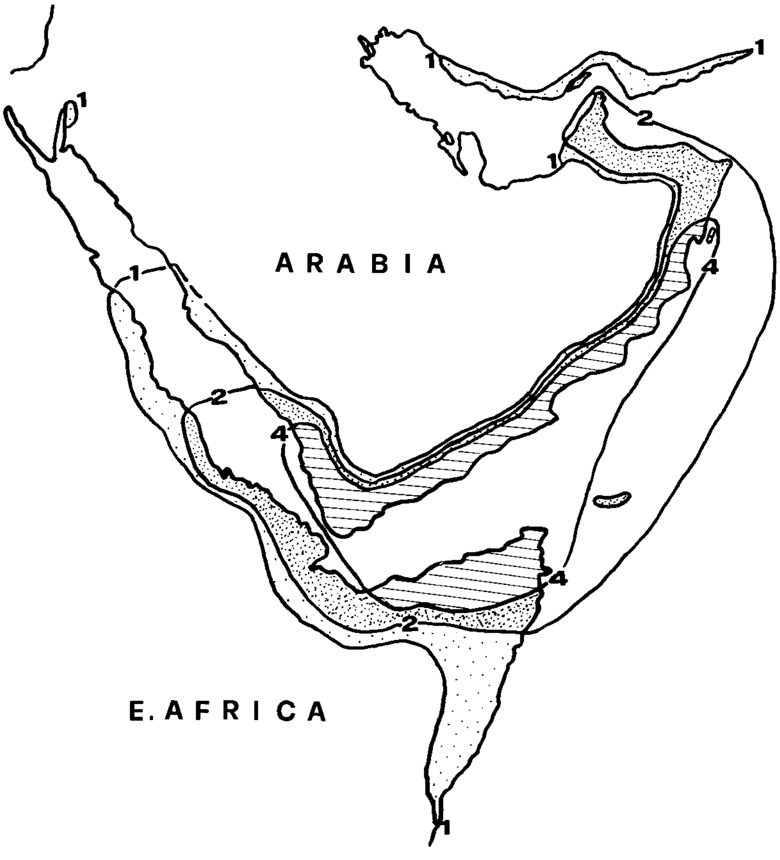

Fig. 3: Approximate distribution and regional species numbers of *Pristurus* (Gekkonidae),

4. A zoogeographic analysis of the southern Arabian reptile fauna

If the importance of the Afrotropical element in the Arabian herpetofauna is to be evaluated with special regard to possible immigration routes, caution is necessary to distinguish between Saharo-Sindian and Ethiopian taxa. Saharo-Sindian species coexist with Ethiopian ones in East Africa (Sudan to Somalia/N Kenya) as well as in SW Arabia. One main character of the Saharo-Sindian fauna is high capability of west-east migration within the Old World arid belt. However, Ethiopian taxa are less capable to withstand arid conditions. For them, the Arabian deserts are a highly effective barrier today.

East of Ẓufār, the hyperarid desert belt reaches the coast of the Arabian Sea, putting an end to the continuous distribution of Afrotropical elements in SW Arabia. In the Oman Mountains, no tropical reptiles are found anymore, though the local climatic conditions are often not worse than in Ẓufār. If tropical species still lived in the Oman at the end of the Tertiary, they were probably replaced during the cold periods of the Pleistocene by the better adapted Irano-Turanian species which we know from there now.

Of the 52 reptile species known from northern Oman and from the United Arab Emirates, 36 are shared with SW Arabia. 15 of these 36 species originate from SW Iran, which also has nine other species in common with the Oman region (fig. 5, tab. 2). This eastern Arabian area has only seven endemic reptile species (all of them lizards), of which four are sister-species to Iranian-Omani species, whereas *Lacerta jayakari* Boulenger, 1887, and *L. cyanura* Arnold, 1972, (O in fig. 5) have no close relatives in Iran (Bischoff, pers. comm.) and *Pristurus celerrimus* Arnold, 1975, is a primitive form of its genus (Arnold, pers. comm.). Altogether, more than half of the reptile species in the Oman area have their nearest relative in neighbouring Iran.

Table 2: Reptile species of Iran also found in the Oman region.

a) Species not found in other parts of Arabia
* *Teratoscincus scincus*
* *Asaccus elisae*
* *Pseudocerastes p. persicus* (*P. p. fieldi* in N Arabia)
Echis carinatus sochureki

b) Species also found in NE Arabia
Cyrtodactylus scaber
Hemidactylus persicus
Mesalina brevirostris
Acanthodactylus blanfordi, A. schmidti
Diplometopon zarudnyi
Lytorhynchus gaddi

c) Species also found in SW Arabia
Stenodactylus doriae
Hemidactylus flaviviridis, H. turcicus
Bunopus tuberculatus
Pristurus rupestris
Varanus griseus
Uromastyx microlepis
* *Phrynocephalus maculatus*
Chalcides ocellatus
* *Ablepharis pannonicus*
Eumeces taeniolatus
(*Scincus scincus conirostris*)
Coluber rhodorhachis
Spalerosophis diadema
Malpolon moilensis
(*Cerastes cerastes*)

d) East Arabian endemics closely related to Iranian species (in bracket)
* *Asaccus gallagheri* (*A. elisae*)
Acanthodactylus gongrorhynchus, A. haasi (*A. blanfordi*)
* *Phrynocephalus arabicus* (*P. maculatus*)

* Irano-Turanian genus

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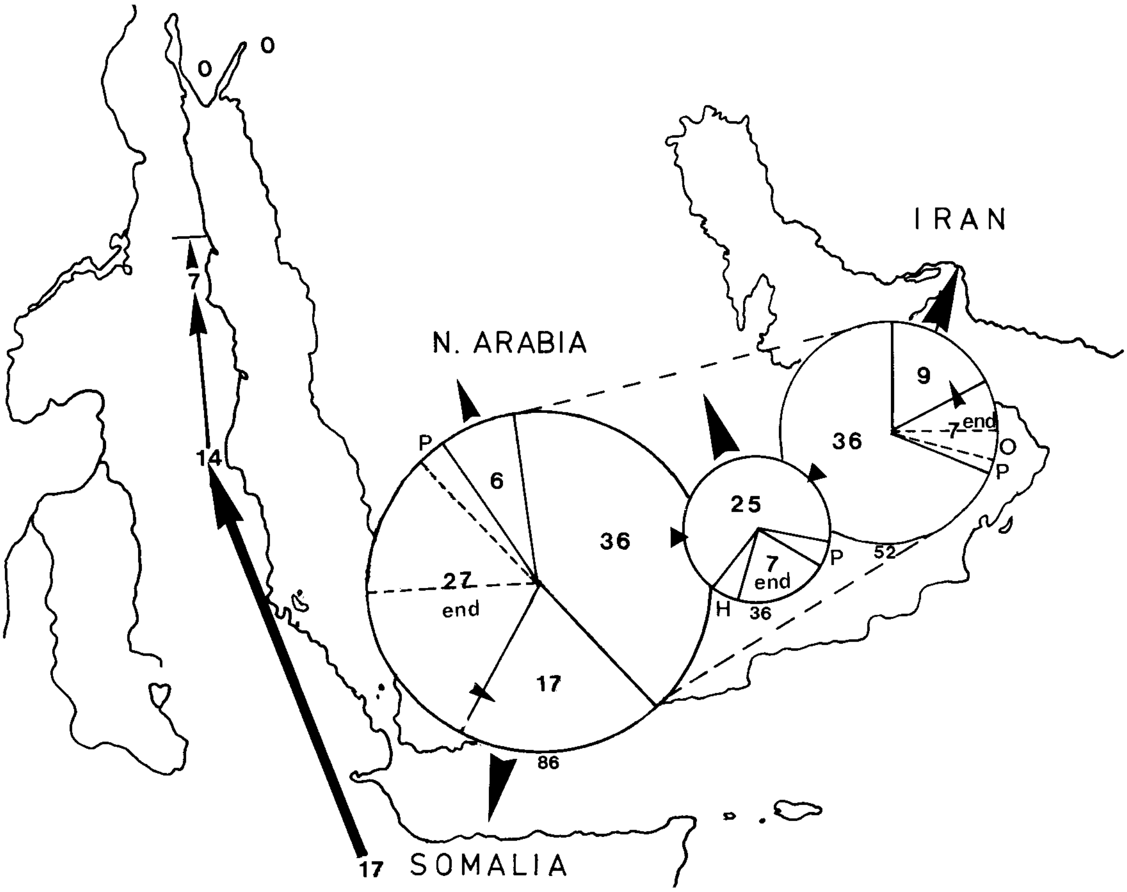

Fig. 5: Biogeographic affiliations of the South Arabian reptile fauna. The composition of Southeast and Southwest Arabian reptile faunas are depicted separately. The 36 species shared by both of these areas are shown in more details in the intermediate circle. Circle diameters and dimensions of circle sections correspond to species numbers. Arrows indicate faunal relations.
Special cases: H = widespread *Hemidactylus* species (*H. turcicus, H. flaviviridis*); P = *Pristurus* species; O = Omani *Lacerta* species. For further explanation see text.

It is important to remember here that the Zagros Plate is regarded a former part of the Afro-Arabian Plate which was moved north by continental drift. Moreover, the Arabian Gulf certainly fell dry at minimum sea levels during the Pleistocene.

The 36 species distributed over vast parts of the southern Arabian Peninsula can be subdivided as follows:

- 25 are also present in northern Arabia and elsewhere in the Middle East or North Africa. These are true Saharo-Sindian species, which had no difficulty in using the northern desert route for immigration.
- Two *Hemidactylus* species [*H. turcicus* (Linnaeus, 1758), *H. flaviviridis* Rüppell, 1835] are widely distributed in coastal regions of the Indian Ocean and the Red Sea and are easily introducable by man.

Table 3: Reptile species of Eritrea/Somalia also found in SW Arabia.

a) Species not found in other parts of Arabia

Hemidactylus sinaitus, H. yerburii
Pristurus crucifer
* *Pseuderemias mucronata*
* *Latastia longicaudata*
Mesalina olivieri martini
Mabuya brevicollis
* *Panaspis wahlbergi*
Varanus exanthematicus (new record)
Psammophis cf. *sibilans* (new record)
* *Lamprophis lineatus*
* *Dasypeltis scabra*
Naja haje
* *Bitis arietans*
Echis pyramidum
* *Atractaspis microlepidota*
* *Pelomedusa subrufa*

b) Species also found in northern or eastern Arabia

Hemidactylus turcicus parkeri, H. flaviviridis
Ptyodactylus hasselquistii
Pristurus rupestris, P. flavipunctatus
Chalcides ocellatus
Leptotyphlops macrorhynchus
Psammophis schokari
Coluber rhodorhachis
Telescopus dhara

c) Species with close relatives (in brackets) in SW Arabia

Hemidactylus laevis (*H. homoeolepis*)
Pristurus spp. (*P. popovi, P. minimus*)
Stellio phillipsi, S. annectens (*S. yemenensis, S. adramitana*)
Uromastyx (*Aporosaura*) *princeps* (*U. thomasi, U. benti*)
Chamaeleo africanus (*C. calyptratus*)
* *Agamodon anguliceps, A. compressus* (*A. arabicus*)
Coluber brevis (*C. thomasi, C. variabilis*)
Lytorhynchus diadema (*L. gasperettii*)
* *Philochortus* spp. (*P. neumanni*)

* Ethiopian genus

- *Pristurus rupestris* Blanford, 1874, is known from Somalia to S Iran, and *P. flavipunctatus* Rüppell, 1835, occurs on both sides of the Red Sea and along the South Arabian coast.
- Seven species are endemic to the South Arabian coastal region (see Arnold 1987).

The complicated biogeographic interpretation of the 86 reptile species known from SW Arabia (southern al-Hiǧāz to Ẓufār) is facilitated if we take out the 36 species shared with northern Oman. The remaining species can be grouped into three fractions (see fig. 5 and tab. 3):

- 17 species shared with Somalia and Eritrea;
- 27 endemics, at least half of which have their nearest relative in Somalia;
- only 6 invaders from northern Arabia [*Natrix tesselata* (Laurenti, 1768) (see Leviton 1977) *Eirensis coronella* (Schlegel, 1837) (see Arnold 1982), *Chamaeleo chamaeleon* (linnaeus, 1758), *Pseudotrapelus sinaitus* (Heyden, 1827), *Trapelus flavimaculatus* (Rüppell, 1835), and *Uromastyx ornatus*. The latter three species share a similar distribution pattern around the northern two-thirds of the Red Sea].

The question whether the 17 species occuring both in SW Arabia and in NE Africa (but not in the Oman area) have come to Arabia directly across the Strait of Bāb al-Mandab or indirectly via the Sinai Peninsula, is most interesting with respect to the uncertainty whether there existed during the Pleistocene a continuous land connection across the southern edge of the Red Sea. 14 of the 17 species also reach the Sudanese Red Sea coast, and seven go down to the Ğabal Alba region in SW Egypt. But further north none of these species prevails. They are not found in Sinai, Israel or Jordan (fig. 5).

Nevertheless, the last-named countries have some refugial areas for tropical faunal relicts, e.g., Wādī Fairān in Sinai, Wādī al-ʿAraba and the adjacent Rift Valley. Here the Afrotropical genus *Atractaspis,* for instance, subsists with its species *A. engaddensis* Haas, 1950. However, *Atractaspis* is not found in Egypt west of the Suez Canal. It is likely that this genus came to the north along the Arabian side of the Red Sea coast, whereas we have some evidence now that the 17 species in question (one of them is *Atractaspis microlepidota* Günther, 1866) reached Arabia directly from Eritrea via a Pleistocene landbridge across the Bāb al-Mandab.

5. Concluding discussion

The presence of tropical African (Somalian) reptile species in Southwest Arabia and their absence in Sinai and adjacent areas led us to the conclusion that these reptiles reached the Arabian Peninsula from the South during a Pleistocene lowering of the sea level. Further questions arise:

- Why didn't the Ethiopian species reach Arabia by sea rafting? The ability of different reptiles to cross sea straits is not the same, as can be seen from the reptile fauna of oceanic islands like the Canaries, which were colonized from Northwest Africa. One genus each of gekkonid, scincid and lacertid lizards reached this archipelago, whereas about 90% of the recent Moroccan lizard genera and all snakes failed to do so. Snakes are generally very poor conquerors of oceanic islands. Yet of the 16 Somalian squamate species in tab. 3, seven are snakes, which is even more than the normal proportion of snake species in savanna reptile communities. This gives a clear indication of a former land connection.
- Why didn't the species discussed above march around the northern coast of the Red Sea during wetter times? There is some evidence that the tropical savanna conditions required by the Afrotropical species have never been present continuously throughout the whole west coast of the Red Sea during the Quaternary. In glacial periods like the last one which was at its maximum about 18,000 ybp, the Sahara still acted as a barrier but was merely dislocated further south (Nicholson & Flohn 1980). Fossil dunes all over the central part of Sudan are still witnesses of the more southerly position of the desert belt. Even the White Nile was blocked by sand dunes. As this time was also the time of lowest sea-level, an immigration of Ethiopian animals into southern Arabia was favoured rather than a migration to Egypt.

The wetter periods of the Quaternary were associated with the interglacials. The last such period, the so-called post-Pleistocene climatic optimum about 6,000 ybp, led to a continuous connection of the West African savanna belt to Morocco along the Atlantic coast (Lauer & Frankenberg 1979). However, at the same time in the East, the climatic conditions did not improve to the same degree. In Butzer's (1959) reconstruction of the Red Sea coast 5,000 to 7,000 years ago, areas of less than 100 mm annual precipitation still interrupt the better irrigated regions. Thus we can perhaps assume that the ecological circumstances did not allow a savanna fauna to use the northern route around the Red Sea to Arabia during the Quaternary.

It may be of interest that five of the seven Ethiopian snake species which managed to reach SW Arabia and survive there – *Lamprophis lineatus* (Dum. & Bib., 1854), *Dasypeltis scabra*

(Linnaeus, 1758), *Naja haje* (Linnaeus, 1758), *Bitis arietans* (Merrem, 1820), and *Echis pyramidum* – are also the only tropical snake relicts in Morocco (SAINT-GIRONS 1956, STEMMLER 1971). The importance of these two distant but ecologically similar parts of the Saharo-Sindian belt for the survival of tropical relicts is thus once more shown.

My speculations about the time of the last faunal exchange with tropical Africa (6,000 ybp for Morocco, 18,000 ybp or little less for SW Arabia) agree with the level of differentiation reached by these recent invaders, as the Arabian populations of some of the species in question have already reached subspecies level (*Naja haje arabica* Scortecci, 1932, *Atractaspis microlepidota andersoni* Boulenger, 1905, probably also *Bitis arietans, Echis pyramidum, Varanus exanthematicus* and others).

However, other Ethiopian invaders to SW Arabia have already reached species level, although they are still close to their African relatives. These species must be colonists from a slightly earlier period, probably from one of the first Pleistocene glaciations, or from the Miocene land connection. During the Miocene, the increasing strength of the Saharo-Arabian desert belt as an ecological barrier is already noted (THOMAS 1979).

It is admitted that the herpetofaunal history outlined here is still rather speculative. Further insights into the historical biogeography of the Arabian reptiles can certainly be gathered by thorough phylogenetic analyses of key genera, such as the agamid lizard *Trapelus* or the colubrid snake *Coluber.*

Note added in proof

After this paper had been submitted for publication, three important papers by Arnold were published in Fauna of Saudi Arabia 8 (1986): 352–377, 378–384, 385–435. Arnold described six new *Pristurus* species, two from Suquṭrá, one from ʿAbd al-Kūrī Island, two from the Yemens and one from southern Saudi Arabia and Oman (probably also occurring in the area in between). Moreover, a new *Acanthodactylus* has been described from central Saudi Arabia, and *Panaspis wahlbergi* from Asir is reidentified as *Ablepharus pannonicus.*

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Author's address: Dr. Ulrich Joger, Hessisches Landesmuseum, Zoologische Abteilung, Friedensplatz 1, 6100 Darmstadt, West Germany.