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CHAPTER 10

ZOOGEOGRAPHIC ANALYSIS OF THE LIZARD FAUNA OF IRAN[1]

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INTRODUCTION

An understanding of present distribution patterns of organisms in South-west Asia is essential to any meaningful generalizations concerning biogeography on a world-wide basis. The vast arid physiographically complex tract stretching across all of North Africa, South-west Asia, and north-western India today forms a barrier to the exchange of faunal elements of tropical and sub-tropical Africa with Europe, south-eastern Asia, and Central Asia. The extent to which communication between these faunas may have existed at various times in the past can be postulated only on the basis of our knowledge of palaeogeography, past climatic conditions, and the distribution of living and fossil organisms.

The area covered by this paper is delimited by the political boundaries of Iran, which might be regarded as one of the most geographically complex areas of South-west Asia, and is centrally located with respect to the mingling of elements of the North African, southern Asian, Central Asian and European herpetofaunas (Anderson, 1963).

While many systematic problems remain on all levels, it is nonetheless possible to make a few generalizations regarding the zoogeography of South-west Asia, and Iran in particular. Thus far no zoogeographic analysis of the whole of South-west Asia has been attempted, and only the most cursory remarks on the zoogeography of the amphibians and reptiles of Iran have been published (Blanford, 1876; Wettstein, 1951; Anderson, 1964). In this report an effort is made to answer in the broadest sense the following questions: (1) What are the major distributional patterns? (2) What are the historical origins of these patterns?

[1] For critical reading of the manuscript in various stages of its development, I am indebted to my father, Howard T. Anderson, formerly Chief Geologist for the Iranian Oil Exploration and Producing Company, Alan E. Leviton, California Academy of Sciences, and George S. Myers, Stanford University. We have discussed the topics considered here over a period of several years, and whatever may be of value in this paper derives in large measure from these conversations.

(3) What factors determine present distributions? (4) To what extent can these generalizations be extended to the whole of South-west Asia?

The first attempt at a complete list of the herpetofauna of Iran was that of De Flippi (1865). Blanford (1876) added many species to this list as a result of his travels, and briefly discussed the zoogeography of Iran. In 1936, Werner attempted to bring the list up to date. His list was undocumented, and unfortunately contained many errors.

Material now in American museums, particularly in the California Academy of Sciences and the Field Museum of Natural History, forms a combined collection adequate as a basis for reviews of the faunistics of the South-west Asian herpetofauna. The present paper is a result of examination of this material.

Most previous work on the Iranian herpetofauna has consisted of brief reports on incidental material collected by travellers engaged in other types of work. I have drawn heavily on these reports, and in cases where identifications or localities were in doubt, I have attempted to examine either the specimens in question or other material from the particular region. In many cases such a check has not yet been possible. Also, an attempt has been made to locate every locality record in the literature, but again, this has frequently not been possible.

As a comment on the need for further investigations in Iran, it is worth remarking that only three individuals with a primary interest in reptiles and amphibians have collected in Iran: William T. Blanford in 1872; Alexander M. Nikolsky, around the turn of the century, who apparently visited the Gurgān region; and the present writer who collected in Iran during a nine-month period in 1958.

The zoogeography of any region can be viewed from three perspectives, all of which are closely interrelated.

(1) *Descriptive:* the distribution of organisms in relation to physiographic features of the region under study. This involves study of the morphology of the animals and taxonomic evaluation of available material and literature records. It is subjective in that it involves judgments based on the worker's knowledge of the groups involved, and includes all of the bias inherent in the taxonomic system employed. Obviously, it reflects the perceptiveness of the individual zoogeographer. The further he strays from familiar systematic ground, and the more he relies upon the judgment of previous workers for determination of material which he has not seen, the less reliable his zoogeographical description tends to become. The present paper is based upon

a comprehensive study of the systematics of the lizards of Iran which is in a final stage of preparation.

(2) *Ecological:* the distribution of organisms relative to environmental factors. This, too, is largely descriptive, containing many of the same pitfalls mentioned above, and usually it must be highly inferential, as available data are often diffuse and scanty, and knowledge of physiological responses to the physical factors of the environment is far from complete for any one species. Nevertheless, rough correlations are possible. These can at least prove stimulating to our speculations regarding the causes of present distribution patterns, and at times strongly indicate zoogeographical conclusions of considerable weight.

(3) *Historical:* this is often highly speculative, particularly in the absence of a fossil record. It involves a consideration of all discernible factors, in the dimension of time, which have produced present patterns of distribution. It is, therefore, an attempt to analyse observed distributional data in the light of available information regarding geomorphology, palaeogeography, palaeoclimatology, palaeoecology, and the evolutionary development of the organisms involved.

I have attempted to incorporate these three approaches in the following discussion, separating them as a matter of convenience. The third must follow as an effort at integration of the first two.

During the course of this study certain taxonomic changes have been necessary. The justification for these changes will be found in recent papers (Anderson and Leviton, 1966*a*, 1966*b*; Clark, Clark and Anderson, 1966; Anderson, 1966, 1968; Minton, Anderson and Anderson), and in the systematic treatment of the lizards now in preparation. All of the Iranian species recognized here are listed in table 6 (pp. 332–3).

Limitations of space prevent detailed discussion of the physical geography, palaeogeography, and vegetation of Iran essential to faunal analysis, and the reader is referred to the other contributions in this volume. I have drawn heavily upon the papers cited in the bibliography, and call particular attention to the following publications: Anderson (1963, 1966), Anderson and Leviton (1966*b*), Bobek (several papers), de Böckh, Lees and Richardson (1929), Butzer (several papers), Furon (1941), Hare (1961), James and Wynd (1965), Misonne (1959), Nairn (1961), Rechinger (1951), Schwarzback (1963), Shapely (1961), Stamp (1961), Walter and Lieth (1960), Wilson (1932), and Zeuner (1959).

While in Iran I was extended many courtesies by employees of the Iranian Oil Exploration and Producing Company. I particularly wish to acknowledge the friendship of William O. Williams, Dory Little, Jerry James, and Rufus Cook, who not only permitted me to accompany geological field parties under their direction, but were amiable companions in the field as well.

For several years I have had the pleasure of a lively correspondence with Mr Jeromie A. Anderson of Karachi, and with Dr Sherman A. Minton of the University of Indiana Medical Center. Both have first-hand experience with the amphibians and reptiles of West Pakistan, and our discussions have been most profitable.

DESCRIPTIVE ZOOGEOGRAPHY

Apart from those elements which it shares with other regions, South-west Asia has two major distributional components in its lizard fauna. One of these components occupies primarily the elevated regions that are generally termed the Iranian Plateau, in the broad sense of that term as defined further in this volume; and those species which occupy the Iranian Plateau may be termed the Iranian faunal element. The second major component, which may be designated as Saharo-Sindian, occupies the low desert areas from North Africa to north-western India.

Within these regions are species and associations of species with much more restricted distributional area. Only a few species of broad ecological tolerance extend throughout the greater part of either region. Also there is penetration of both areas by species characteristic of the other. Few species, however, are broadly distributed in both regions.

Entering South-west Asia on the north-west are elements with European affinities, primarily those having a Mediterranean distribution. Aralo-Caspian desert species penetrate the region on the north, and a few Oriental elements are found in the south-east.

The affinities of the lizard fauna of South-west Asia with the faunas of adjacent regions are principally at the generic level. An example of this is found in the genus *Lacerta*, the species (or subspecies) found within South-west Asia being distinct, and their distribution more or less limited to northern South-west Asia, but with near relatives in the Mediterranean countries of Europe. Where species are shared with other regions, these are usually the most widely ranging members of the genus. Examples are the agamid *Calotes versicolor*, which enters Balūchistān on the south-east and *Varanus bengalensis*, also in Balūchistān, representing the Oriental species of monitors.

Turning now to a more detailed consideration of the geography of Iranian lizards, attention will first be given to the distribution of species within the various physiographic regions of Iran.

The Central Plateau

(This term is here used to designate the internal drainage basin of the Iranian Plateau lying entirely within the confines of the Iranian borders, and rimmed by mountains.) Certain species range broadly over this entire region. These are:

Agama agilis[1]
Agama microlepis
Phrynocephalus maculatus
Phrynocephalus scutellatus
Agamura persica
Teratoscincus scincus
Eremias guttulata
Eremias velox
Eumeces schneideri
Varanus griseus

Collection has not been sufficient to permit detailed discussion of the distribution of these forms within the plateau region. *Agama microlepis* is known from the mountain slopes around the periphery of the plateau and from those ranges which cross the plateau. It probably does not stray far from large rock outcrops. *Phrynocephalus maculatus*, one of the most widely distributed members of the genus, probably occurs on sandy plains throughout the plateau; it is also one of the few lizard species to be expected in the salt depressions. *P. scutellatus* is distributed on gravel plains and slopes throughout the region. *Teratoscincus scincus* is also a sand-dwelling species, and probably occurs on the plateau wherever there are sandy soils and a sufficient beetle fauna. *Eremias guttulata* is one of the most widely distributed species of lizards in South-west Asia, the subspecies *E. g. watsonana* occurring throughout the region under consideration here. *Eremias velox* is widely distributed not only on the Iranian Plateau, but in the low deserts to the north as well; *E. v. persica* is the subspecies of the plateau. *Eumeces schneideri* has been collected in areas around the periphery of the plateau, and differs subspecifically from one area to another. It may not occur on the

[1] As used in this paper, the name *Agama agilis* Olivier covers the nominal species *A. sanguinolenta* (Pallas), *A. persica* Blanford (= *A. blanfordi* Anderson), and *A. isolepis* Boulenger. The systematic status of these forms is presently under study.

plateau proper. *Varanus griseus*, like *Eremias guttulata*, is one of a very few reptiles distributed throughout South-west Asia, in both the upland and lowland regions. *Varanus* is a genus of the Ethiopian, Oriental, and Australian tropics, *V. griseus* being the only species occurring in the intervening desert areas between the Ethiopian and Oriental Regions. The plateau form has been recognized by some as subspecifically distinct, *V. g. caspius*.

On the north and west of the plateau occur certain forms which are found also in contiguous regions. These species are:

Agama caucasica	*Lacerta saxicola*
Agama ruderata	*Ophisops elegans*
Phrynocephalus helioscopus	*Ablepharus bivittatus*
Bunopus crassicauda	*Mabuya aurata*

The plateau distribution of these species is largely confined to the inner slopes of the Zagros and Alburz Mountains bordering the plateau, and coincides with the Kurdish-Khurāsān rainfall pattern of spring and winter precipitation in excess of 200 mm.

Agama caucasica extends across the entire northern border of the plateau and into Afghanistan. It does not overlap with *A. microlepis* except in the mountains of the north-eastern corner of the plateau, where four species of large rock-inhabiting *Agama* have been recorded (but not all personally verified). *Agama ruderata* is a wide-ranging Saharo-Sindian species distributed primarily in the lowlands of western South-west Asia, but also ascending to elevations over 5,000 ft. The subspecies known from Afghanistan and Balūchistān, *A. r. baluchiana*, may not have its closest affinities with this species. *Phrynocephalus helioscopus* is essentially an Aralo-Caspian species, but perhaps more generally distributed on the plateau than indicated by the known localities. It differs ecologically from the two broadly distributed plateau species of the genus in its preference for clay soils and stony plains. *Bunopus crassicauda* presently is known only from the western part of the plateau, not extending into other areas. *Lacerta saxicola defilippii* does not occur on the plateau proper, but is the only species in the genus which crosses the passes in the Alburz Mountains and occupies the southern slopes of this range north of Tehrān. It is actually a Transcaucasian species with Mediterranean affinities. *Ophisops elegans elegans* is a lizard of lower and middle mountain slope elevations, and is found on the dry inner slopes of the northern, western and southern borders of the plateau. *Ablepharus bivittatus* has been recorded from the western part of the plateau, but the information on distribution and systematics of this genus in South-west Asia is so scanty as to render any discussion of it here meaningless. *Mabuya aurata*, a Saharo-Sindian species which also occurs in arid upland areas, may be more widely distributed on the plateau than is currently known, or at least it once may have been more widely distributed, since it is recorded also from the Transcaucasian and southern Türkmenistan regions.

Largely confined on the plateau to the south-eastern portion are several lizards, most of which occur also in the highlands of Balūchistān or in Sīstān. These are:

Agama nupta
Uromastyx asmussi
Cyrtodactylus agamuroides
Cyrtodactylus kirmanensis
Ophiomorus brevipes
Acanthodactylus cantoris
Acanthodactylus micropholis
Eremias fasciata
Ablepharus grayanus

Agama nupta is primarily a species of the southern mountains of the Iranian Plateau, distributed on the plateau only on the inner slopes of the mountains along the southern border. It is reported from a few areas within the range of *Agama microlepis*. It may also overlap *A. caucasica* in the northern extremes of its range. All three species, along with *A. erythrogastra*, reportedly occur in extreme north-eastern Iran, an unexpected circumstance. *Uromastyx asmussi* is the only species in this Saharo-Sindian genus which penetrates the plateau. Apparently its ability to burrow in gravelly soils makes this possible. The distribution of the two species of *Cyrtodactylus* is very incompletely known, as they have been rarely collected. The two species of *Acanthodactylus*, sand-inhabiting Saharo-Sindian forms, do not really penetrate the plateau, reaching only as far as Bam. *Eremias fasciata* is found on plains in the eastern plateau region; whether or not the lizard identified with this species in southern Afghanistan is actually closely related remains to be demonstrated. *Ablepharus grayanus* also occurs in West Pakistan. The distribution of *Ophiomorus brevipes* has been fully discussed elsewhere (Anderson and Leviton, 1966*b*).

A few species, mostly Aralo-Caspian in distribution, are found in the north-east of the plateau. As far as known, these are:

Phrynocephalus mystaceus
Alsophylax spinicauda
Crossobamon eversmanni
Cyrtodactylus caspius
Cyrtodactylus fedtschenkoi
Eremias nigrocellata
Eremias arguta

Alsophylax spinicauda is known only from Shāhrūd, which lies at the foot of the mountains on the north-central edge of the plateau. Whether or not this species is more widely distributed, perhaps in the mountains of Khurāsān, is not known. *Cyrtodactylus caspius* occurs in the northern mountains of Iran, being found in the plateau region on the arid inner slopes of these ranges. It is distributed in the Aralo-Caspian region along the eastern margin of the Caspian Sea. It occurs in Afghanistan, and perhaps will be found in the inner mountain ranges of the plateau in Iran. *Cyrtodactylus fedtschenkoi*, an Aralo-Caspian species, may not be on the plateau, although it has been taken in the mountains to the east. *Eremias nigrocellata* appears to be a form inhabiting the Kopet Dāgh, entering the plateau at Shāhrūd and perhaps elsewhere to the east. *Phrynocephalus mystaceus* and *Eremias arguta* are Aralo-Caspian species known only from the fringes of the plateau.

One of the least known areas of the Iranian Plateau, and yet one of the most interesting and most important faunistically, is the north–south chain of mountain masses separating the interior plateau basin from Afghanistan, including the drainages of both the Harī Rūd and the Sīstān basin. Many of the species recorded from this region are known from single records, or from a few localities all within this border district. Other species are shared with the Kopet Dāgh. Species of lizards known from this eastern region are:

Agama agilis
Agama caucasica
Agama erythrogastra
Agama microlepis
Agama nupta?
Phrynocephalus maculatus?
Phrynocephalus mystaceus
Phrynocephalus ornatus
Phrynocephalus scutellatus
Agamura persica?
Cyrtodactylus agamuroides
Cyrtodactylus caspius
Cyrtodactylus fedtschenkoi
Cyrtodactylus kirmanensis
Cyrtodactylus longipes
Stenodactylus lumsdeni
Teratoscincus bedriagai
Acanthodactylus cantoris
Acanthodactylus micropholis
Eremias arguta
Eremias fasciata
Eremias grammica
Eremias guttulata
Eremias lineolata
Eremias nigrocellata
Eremias velox
Ablepharus grayanus
Varanus griseus

Various factors account for the presence of this relatively large and varied fauna within a rather narrow strip of land. In this region several faunistically distinct areas are in contact. To the north and east, in the drainage of the Harī Rūd, various Aralo-Caspian species obviously ascend the eastern flanks of this region. Among these are *Phrynocephalus mystaceus*, *Eremias arguta*, *E. grammica*, and *E. lineolata*. These elements are largely confined to the northern half of this mountainous border zone. On the eastern slopes of the central section, certain species enter from the Helmand Basin. Most of these are Iranian faunal elements whose distribution is largely confined to the eastern half of the Iranian Plateau, that occupied by Afghanistan and upland West Pakistan. Included in this group are *Phrynocephalus ornatus*, *Stenodactylus lumsdeni*, *Teratoscincus bedriagai*, *Teratoscincus microlepis*, and *Eremias fasciata*. Entering through upland Balūchistān, and penetrating only the southern portion of this elevated border, are lowland Saharo-Sindian species such as *Acanthodactylus cantoris*, *A. micropholis*, and *Ablepharus grayanus*. Most of the species on the western flanks are wide-ranging plateau species, Iranian elements which cross the passes into Afghanistan and highland West Pakistan. Included here are *Agama agilis*, *Phrynocephalus maculatus*, *P. scutellatus*, *Agamura persica*, *Teratoscincus scincus*, *Eremias guttulata*, *E. velox*, and *Varanus griseus*. Other important Iranian elements are the mountain species, *Agama caucasica*, *Cyrtodactylus caspius*, *C. fedtschenkoi*, and *Eremias nigrocellata*, which penetrate the elevated plains and passes from the northern ranges, *Agama nupta* which enters from the south, and *Agama microlepis*, which is distributed through the elevated regions of the plateau and occupies the central area.

Of particular interest are the species apparently endemic to this region. *Agama erythrogastra* is known only from the northern part of this area, while *Cyrtodactylus agamuroides* and *Cyrtodactylus kirmanensis* have been found only in this region and similar arid mountain slope and valley situations in the southern extent of the plateau and adjacent Makrān. *Cyrtodactylus longipes* is known only from these mountains.

The road from Mashhad to Zāhidān runs the length of this border region. The terrain crossed by this road is one of plains and mountain masses, the road running through the mountains in some places, along the eastern front in others, thus traversing a considerable variety of habitats. Many of the collecting localities recorded for this region have not been precisely located on any map available to me, and I am unable to find information regarding the terrain of most localities. The best general account of this road is that given by Lay.

The majority of specimens collected in this region are deposited in the collections of the Zoological Institute at Leningrad, and were obtained by the ornithologist Zarudny at the end of the nineteenth century. The diversity of this fauna makes a detailed study of the region particularly desirable.

The Reẓā'īyeh [Urumīyeh] basin

The following lizards are known to occur in the area that drains into Lake Rezā'īyeh:

Agama caucasica
Agama ruderata
Phrynocephalus helioscopus
Apathya cappadocica
Eremias pleskei
Eremias velox
Mabuya aurata
Lacerta brandti
Lacerta strigata
Lacerta trilineata
Ophisops elegans
Ablepharus bivittatus
Eumeces schneideri

Doubtless other species, as yet unrecorded, occur on the inner slopes of the surrounding mountains; *Ophisaurus apodus*, *Cyrtodactylus caspius*, *Cyrtodactylus kotschyi*, and *Lacerta saxicola* are to be expected.

The faunal affinities of this region are with the eastern Mediterranean and Transcaucasia in the genus *Lacerta*, with Transcaucasia and Anatolia in the mountain fauna, and with the Iranian Plateau fauna in most other species. At the specific and subspecific level, however, this fauna where adequately studied, is distinctive. The subspecies *Phrynocephalus helioscopus horvathi* has been recognized by some workers, *Apathya cappadocica urmiana*, *Eremias pleskei*, *Lacerta brandti*, and *L. trilineata media* are also endemic to this basin and the contiguous areas of Transcaucasia and eastern Turkey. *Eremias velox strauchi*, a form occupying arid mountain habitats, ranges somewhat more widely, from the Armenian plateau into the Tālish Mountains, the Alburz, and the Kopet Dāgh.

The Sīstān basin

The inclusion of this portion of the Helmand drainage within the borders of Iran adds a number of interesting species to the lizard fauna of the country. The affinities of this basin are with the Iranian faunal element primarily, but exchange between the plateau and the lower eastern deserts has obviously occurred. There has also been contact with certain Aralo-Caspian species. Known from the Iranian part of the Sīstān basin are:

Agama agilis	*Cyrtodactylus zarudnyi*
Agama nupta	*Teratoscincus bedriagai*
Phrynocephalus luteoguttatus?	*Teratoscincus microlepis*
Phrynocephalus maculatus	*Teratoscincus scincus*
Phrynocephalus ornatus	*Eremias fasciata*
Phrynocephalus scutellatus	*Eremias guttulata*
Agamura persica	*Eremias velox*
Crossobamon eversmanni	*Eumeces schneideri*
Cyrtodactylus agamuroides	*Ophiomorus tridactylus*
Cyrtodactylus caspius	*Varanus griseus*
Cyrtodactylus scaber	

The majority of species belong to two basic categories: widely distributed Iranian Plateau forms, primarily occupying the uplands, and an endemic, sand-adapted Helmand fauna, having plateau affinities. *Agama agilis*, *A. nupta*, *Phrynocephalus maculatus*, *P. scutellatus*, *Agamura persica*, *Cyrtodactylus caspius*, *Teratoscincus scincus*, *Eremias guttulata*, *E. velox*, *Eumeces schneideri*, and *Varanus griseus* belong to the former category, while *Phrynocephalus luteoguttatus*, *Phrynocephalus ornatus*, *Cyrtodactylus zarudnyi*, *Teratoscincus bedriagai*, *T. microlepis*, *Eremias fasciata*, and *Ophiomorus tridactylus* represent the latter. *Crossobamon eversmanni* is an Aralo-Caspian gecko; *Cyrtodactylus agamuroides* is an apparently narrowly distributed upland Iranian form, and *Cyrtódactylus scaber* is a Saharo-Sindian element.

The Caspian region

The following lizard species have been recorded from within Iranian limits in the region of the Caspian Sea:

Agama agilis	*Eremias velox*
Agama caucasica	*Lacerta chlorogaster*
Anguis fragilis	*Lacerta saxicola*
Ophisaurus apodus	*Lacerta strigata*

From this list it is readily apparent that this small lizard fauna finds its relationships almost exclusively with Mediterranean Europe and Transcaucasia, though a few Aralo-Caspian elements are to be found along the western shore of the Caspian north of the Aras river. To the east contact is made with the Aralo-Caspian fauna in the vicinity of Gurgān and Pahlavī Dizh. Of the two Iranian elements represented, *Agama caucasica* is a species of rocky and mountainous terrain, whose range apparently extends through the passes to reach the northern slopes of the Alburz. *Eremias velox persica* may also have crossed these passes at some time, or the animals identified as this subspecies may actually be *E. v. velox*, the form found on the Türkmen Steppes. A single endemic species, *Lacerta chlorogaster*, is found along the geologically recently exposed southern Caspian coast. It is also reported from the valley of the Atrak in the Kopet Dāgh, from whence it undoubtedly moved westward as the Caspian Sea receded. *Lacerta saxicola defilippii* is a montane lizard found on both the northern and southern slopes of the Alburz. Its affinities are to the north-west.

The Khūzistān Plain and the Persian Gulf Coast

Geographically an extension of the Mesopotamian Plain, this region has a close faunal relation to lowland Iraq and northern Arabia. The Tigris has apparently served as a barrier to the distribution of some forms, however. The fauna is not uniformly distributed, certain species being reported only from the more humid gulf coastal plain. The Iranian part of the Mesopotamian lowlands has been neglected by zoological collectors, and the composition of this fauna has not been elaborated. The following lizards are known:

Agama agilis
Agama nupta
Agama ruderata
Uromastyx loricatus
Bunopus tuberculatus
Ceramodactylus affinis
Cyrtodactylus scaber
Hemidactylus flaviviridis
Hemidactylus turcicus
Pristurus rupestris
Acanthodactylus cantoris
Acanthodactylus fraseri
Eremias brevirostris
Eremias guttulata
Ophisops elegans
Ablepharus pannonicus
Chalcides ocellatus
Eumeces schneideri
Mabuya aurata
Ophiomorus blanfordi?
Scincus conirostris
Varanus griseus

With few exceptions these species may be termed Saharo-Sindian elements. *Agama agilis*, *Eremias guttulata*, *Eumeces schneideri*, *Mabuya aurata*, and *Varanus griseus* are species which are distributed widely in South-west Asia over the lowland deserts as well as across the plateau. *Ophisops elegans blanfordi* may or may not be distinct from the upland form, *O. e. elegans*. *Agama nupta* and *A. ruderata* are not widely distributed in this region, being species of the foothills and mountains. *Hemidactylus flaviviridis* is known only from Gulf ports, and its distribution is undoubtedly due to human agency. This may also be true of certain other species, such as *H. turcicus*, *Pristurus rupestris*, and *Chalcides* *ocellatus*, animals which may travel in thatch or in sand ballast used in the extensive trade by dhow. The record for *Ophimorus blanfordi* is simply "Fārs Province", and so presumably from the coastal dunes in the general area of Bushire. It, too, could have been introduced in sand ballast, but its presence in this region definitely requires confirmation.

Iranian Balūchistān and the Makrān coast

Species recorded from this region within Iranian limits are:

Agama agilis
Agama nupta
Calotes versicolor
Phrynocephalus maculatus
Phrynocephalus scutellatus
Uromastyx asmussi
Agamura persica
Bunopus tuberculatus
Ceramodactylus doriae
Cyrtodactylus agamuroides
Cyrtodactylus brevipes
Cyrtodactylus scaber
Hemidactylus flaviviridis
Hemidactylus persicus
Hemidactylus turcicus
Tropiocolotes persicus
Teratoscincus scincus
Acanthodactylus cantoris
Acanthodactylus micropholis
Eremias fasciata
Eremias guttulata
Eremias velox
Ophisops elegans
Ablepharus grayanus
Chalcides ocellatus
Eumeces schneideri
Ophiomorus blanfordi
Ophiomorus brevipes
Ophiomorus streeti
Varanus bengalensis
Varanus griseus

This somewhat large lizard fauna is made up of two main elements: an Iranian faunal element, composed of widely ranging plateau forms, most of which are here confined primarily to the rugged, folded terrain of Balūchistān, and a Saharo-Sindian faunal element, more or less confined to the coastal plain, in so far as details of distribution are known. This latter group of species can be further subdivided into those forms which apparently range no farther west than Bandar-i-Lingeh, such as *Uromastyx asmussi*, *Acanthodactylus cantoris blanfordi*, *A. micropholis*, and *Ophiomorus blanfordi* (a questionable record of this species does exist for Fārs Province, however). There are also certain species which occur in Balūchistān east of the Iranian border, for which no definite Persian records yet exist. Among these are *Agama melanura*, *Agama megalonyx*, *Agama rubrigularis*, and *Stenodactylus orientalis*. Certain other elements of the Sind fauna stop short of the Iranian border, e.g. *Uromastyx hardwicki*, *Hemidactylus brooki*, *Teratolepis fasciata*, *Mabuya macularia*, and *Ophiomorus raithmai*. It may be that the western limits of certain of these species more or less coincide with the western termination of the Balūchistān precipitation type of winter and summer rains under the influence of the monsoon.

It is only in Balūchistān and the Makrān that any Oriental elements enter Iran. *Calotes versicolor* and *Varanus bengalensis*, both wide-ranging lizards with great ecological tolerance, are known from this region.

Cyrtodactylus brevipes and *Ophiomorus streeti* are endemic species from inland Balūchistān. The extent of their distribution is not known.

An area of particular interest in this region is the extensive internal basin known as the Jāz Muriān Depression. A low basin of internal drainage, rimmed by mountains, and having extensive aeolian sand deposits on its floor, its fauna is incompletely known. Most collecting in this basin has been in the neighbourhood of Īrānshahr, near the Bampūr river in the higher eastern portion of the depression. The two endemic species, *Cyrtodactylus brevipes* and *Ophiomorus streeti*, are known only from this vicinity. *Agama agilis*, *A. nupta*, *Phrynocephalus maculatus*, *P. scutellatus*, *Uromastyx asmussi*, *Bunopus tuberculatus*, *Teratoscincus scincus*, *Acanthodactylus cantoris blanfordi*, *A. micropholis*, *Ablepharus grayanus*, *Eumeces schneideri zarudnyi*, *Ophiomorus brevipes*, *Varanus bengalensis*, and *V. griseus* are also known from the depression and the surrounding slopes.

Of particular interest in comparing the fauna of the Makrān coast with that of the western coast of the Persian Gulf is that fact that while the climatic change in the lowland region stretching from North Africa to Sind occurs east of the Iranian border, there is an additional faunal change between Bushire and Bandar-i-Lingeh. Many of the species shared by the two regions are plateau forms, not requiring a continuous coastal distribution. Of the strictly Saharo-Sindian elements, the only shared species are *Cyrtodactylus scaber*, a form which ranges into the foothills, *Bunopus tuberculatus*, in which there is some evidence of geographically correlated variation, *Acanthodactylus cantoris*, subspecifically distinct in the two areas, and *Chalcides ocellatus*, a widely distributed species known within Persian limits only from two ports, Bushire and Jāsk. The possibility of human agency as a factor in the Persian Gulf distributon of this last species cannot be discounted.

Of additional interest is the distribution of *Eremias brevirostris*, known from West Pakistan and from the western Persian Gulf, but never recorded from the Makrān coast. It is known from Qishm Island and Jazīreh-ye Tanb-i-Buzurg, islands off the Makrān coast. This suggests that these islands may have been connected with the mainland at a time when distribution of Saharo-Sindian forms was continuous along this coast. Present distribution of the Saharo-Sindian fauna along the gulf indicates that coastal environments are interrupted between Bushire and Bandar-i-Lingeh, a question which could be settled easily through observation.

The Türkmen Steppe

The contact of the fauna of the plateau with the Aralo-Caspian elements has been briefly considered in the discussion of the eastern border of the plateau. Small portions of these low plains are enclosed by Iranian borders in the north-eastern corner of the country, and in a narrow wedge east of the Caspian Sea, between the shore and the mountains. Species found in this drainage are:

Agama agilis	*Eremias arguta*
Agama caucasica	*Eremias grammica*
Agama erythrogastra	*Eremias guttulata*
Agama nupta	*Eremias intermedia*
Phrynocephalus helioscopus	*Eremias lineolata*
Phrynocephalus interscapularis?	*Eremias nigrocellata*
Phrynocephalus mystaceus	*Eremias velox*
Ophisaurus apodus	*Lacerta chlorogaster*
Crossobamon eversmanni	*Eumeces schneideri*
Cyrtodactylus caspius	*Eumeces taeniolatus*
Cyrtodactylus fedtschenkoi	*Mabuya aurata*
Teratoscincus scincus	*Varanus griseus*

Even here on the fringes of the Türkmen Steppe, only 43·5 per cent of the lizard fauna are forms which can be considered truly Aralo-Caspian, the remainder being species from the Iranian Plateau, and species confined primarily to mountain slopes, e.g. *Agama caucasica*, *A. erythrogastra*, *A. nupta*, *Ophisaurus apodus*, *Cyrtodactylus caspius*, and *Eremias nigrocellata*. The only forms which may be said to have a primarily Aralo-Caspian distribution are *Phrynocephalus interscapularis*, *P. mystaceus*, *Crossobamon eversmanni*, *Cyrtodactylus fedtschenkoi*, *Eremias arguta*, *Eremias grammica*, *Eremias intermedia*, *Eremias lineolata*, and *E. velox velox*.

The three subspecies of *E. velox* have been reported together both in the Gurgān region and in the north-eastern corner of Iran. Intermediates are said to occur in the former but not the latter region. On the basis of material that I have examined I have been unable to verify this, or even to distinguish clearly between the three forms by means of the characters usually employed.

Comparison of this Türkmen Steppe fauna with that of the Iranian Plateau indicates that the great majority of species presently capable of negotiating the passes separating the two regions are those of the plateau.

The Mughān Steppe

This region, drained by the Aras River, falls within Iranian limits only in the northernmost part of Persian Āzarbāījān. Virtually no collecting has been done in the Iranian part of this region, but the fauna of the Mughān Steppe in U.S.S.R. has been listed by Sobolevsky (1929) in his analysis of the herpetofauna of the Tālish Mountains and Lankorān lowland. He includes the following species from the Mughān Steppe:

Ophisaurus apodus
Cyrtodactylus caspius
Eremias arguta
Eremias velox
Lacerta strigata
Ophisops elegans
Eumeces schneideri?

Ophisaurus apodus and *Lacerta strigata* are species with Mediterranean affinities. *Eremias arguta* is a widely distributed Aralo-Caspian form which occurs also in Rumania, southern Russia, the Crimea, and Transcaucasia. *E. velox strauchi* and *Cyrtodactylus caspius* are lizards which occupy the intermediate upland areas between Iran and the U.S.S.R., while *Ophisops elegans* and *Eumeces schneideri* are primarily plateau forms.

Thus far the fauna has been discussed relative to the principal drainage areas of Iran, and species occupying the mountain slopes of these drainages have been included. The mountains themselves should now be discussed briefly, although our knowledge of the montane lizard fauna is very fragmentary.

The Zagros Mountains

This long mountain chain forms both a barrier between the plateau and the Mesopotamian lowlands and a corridor for the southward distribution of northern faunal elements. Unfortunately, zoological information for this range is very sketchy, though the southern extent of these northern species is known. The species known from the Zagros area itself are:

Agama agilis
Agama nupta
Agama ruderata
Ophisaurus apodus
Cyrtodactylus heterocercus
Cyrtodactylus scaber
Eremias guttulata
Lacerta princeps
Lacerta strigata
Ophisops elegans
Ablepharus bivittatus
Ablepharus pannonicus
Eumeces schneideri
Mabuya aurata
Ophiomorus persicus
Varanus griseus

Three species, *Cyrtodactylus heterocercus*, *Lacerta princeps* and *Ophiomorus persicus*, are endemic to the Zagros. The extent of their distribution is undetermined. The known fauna, is essentially that of the lower passes and consists mostly of wide-ranging South-west Asian species. These are *Agama agilis*, *A. ruderata*, *Cyrtodactylus scaber*, *Eremias guttulata*, *Ophisops elegans*, *Ablepharus pannonicus*, *Eumeces schneideri*, *Mabuya aurata*, and *Varanus griseus*, all species distributed through both lowland and arid mountain areas over much of South-west Asia. *Ophisaurus apodus* and *Lacerta strigata* are species entering from the north-west, and having Mediterranean affinities. *Agama nupta* is a species of the outer flanks of the mountains rimming the western and southern borders of the Iranian Plateau.

The western foothills of the Zagros Mountains

This area, too, has been little studied. Our limited knowledge of the fauna and general ecology of the foothills suggests that this belt should be considered separately from both the Zagros mountains proper and the Mesopotamian lowlands, although it shares species with each. The known species are:

Agama agilis
Agama nupta
Uromastyx loricatus
Cyrtodactylus scaber
Eublepharus angramainyu
Hemidactylus persicus
Hemidactylus turcicus
Tropiocolotos persicus
Varanus griseus
Phyllodactylus elisae
Ptyodactylus hasselquisti
Eremias guttulata
Ophisops elegans
Ablepharus pannonicus
Eumeces schneideri
Mabuya aurata
Scincus conirostris

The three endemic taxa of this list are of particular interest. *Eublepharus angramainyu* and *Tropiocolotos persicus helenae* both have their nearest relatives in West Pakistan and Afghanistan; *Phyllodactylus* *elisae* is probably most closely akin to the New World species of *Phyllodactylus* than to other Old World forms presently included in the genus, according to James Dixon (personal communication).

Hemidactylus persicus is a species which has been recognized only from this region, Arabia, and areas to the east, in Balūchistān and Sind.

The remaining forms are the generally distributed South-west Asian species, *Agama agilis*, *Eremias guttulata*, *Ophisops elegans*, *Ablepharus pannonicus*, *Eumeces schneideri*, *Mabuya aurata*, and *Varanus griseus*, and Saharo-Sindian elements, *Uromastyx loricatus*, *Cyrtodactylus scaber*, *Ptyodactylus hasselquisti*, and *Scincus conirostris*. *Agama nupta* is restricted to rocky outcrops through the southern and western upland regions from Iraq to Sind.

Scincus conirostris and *Uromastyx loricatus*, both narrowly distributed species, are hardly characteristic of the foothill belt, the former being found only in aeolian dunes caught in the fringes of the hills, the latter in the lower alluvial fans and valleys.

Conspicuously absent from this region are the strictly Iranian elements; that is, those characteristic of the Central Plateau. In this respect the region differs sharply from the folds of Balūchistān where such species are an important element of the lizard fauna.

The Alburz Mountains

The fauna of this range consists of two fairly well-defined segments: that of the dry southern slopes (these species having been included in the discussion of the plateau), and that of the much wetter, forested northern slopes (included in the section on the Caspian coast). A few species cross the passes; a few range along the lower crests. The known species of the Alburz are:

Agama agilis
Agama caucasica
Agama ruderata
Phrynocephalus helioscopus
Phrynocephalus scutellatus
Anguis fragilis
Ophisaurus apodus
Mabuya aurata
Cyrtodactylus caspius
Eremias nigrocellata
Eremias velox
Lacerta saxicola
Lacerta strigata
Ophisops elegans
Eumeces schneideri

Of all these species, only *Lacerta saxicola defilippii*, a montane species with Caucasian affinities, is known to occupy the mountain crests, occurring on both flanks of the range above tree line. Other species which at least cross the passes and occupy the mountain valley are *Agama caucasica*, *Ophisaurus apodus*, *Eremias velox persica*, *Lacerta strigata*, and *Mabuya aurata*. *Cyrtodactylus caspius* and *Eremias nigrocellata* are only known in the Alburz from the more arid eastern end of the range where it merges with the folds of the Kopet Dāgh. *Agama ruderata*, *Phrynocephalus helioscopus*, *P. scutellatus*, and *Ophisops elegans* are species of the southern foothills, *Agama agilis* and *Eumeces schneideri* probably ranging somewhat further up the southern flank, perhaps into the lower mountain valleys. *Anguis fragilis*, and perhaps other lowland Caspian species such as *Lacerta chlorogaster*, occur on the northern slopes.

The Kopet Dāgh

The more arid mountain folds stretching along the Iran–U.S.S.R. border east of the Alburz have not been studied in any detail, one reason being that routes crossing the border run to the west and east of these mountains. The relatively low Atrek valley divides the two main folds of the ranges, and has itself been little travelled by zoological collectors. Our scanty knowledge of the fauna suggests that transects of these ranges would yield interesting results. The known species within Iranian limits are:

Agama caucasica
Phrynocephalus helioscopus
Anguis fragilis
Ophisaurus apodus
Alsophylax spinicauda
Cyrtodactylus caspius
Eremias nigrocellata
Eremias velox
Lacerta chlorogaster
Lacerta strigata
Ablepharus bivittatus
Ablepharus pannonicus
Ablepharus persicus?

I include in this list records from Shāhrūd, on the southern flank where these mountains contact the plateau. The two endemic species *Alsophylax spinicauda* and *Ablepharus persicus* are reported from this locality. Both are of uncertain taxonomic status, particularly *A. persicus* (Werner's record of this species from Fārs can be ignored). There is a record of *Eublepharis macularius* from the Kopet Dāgh within Russian limits. In light of recent comments on the distribution and status of this species (Anderson and Leviton, 1966*a*) these specimens should be re-examined.

Phrynocephalus helioscopus, *Ophisaurus apodus*, *Cyrtodactylys caspius*, and *Lacerta chlorogaster* are known in the Kopet Dāgh from the Atrak valley.

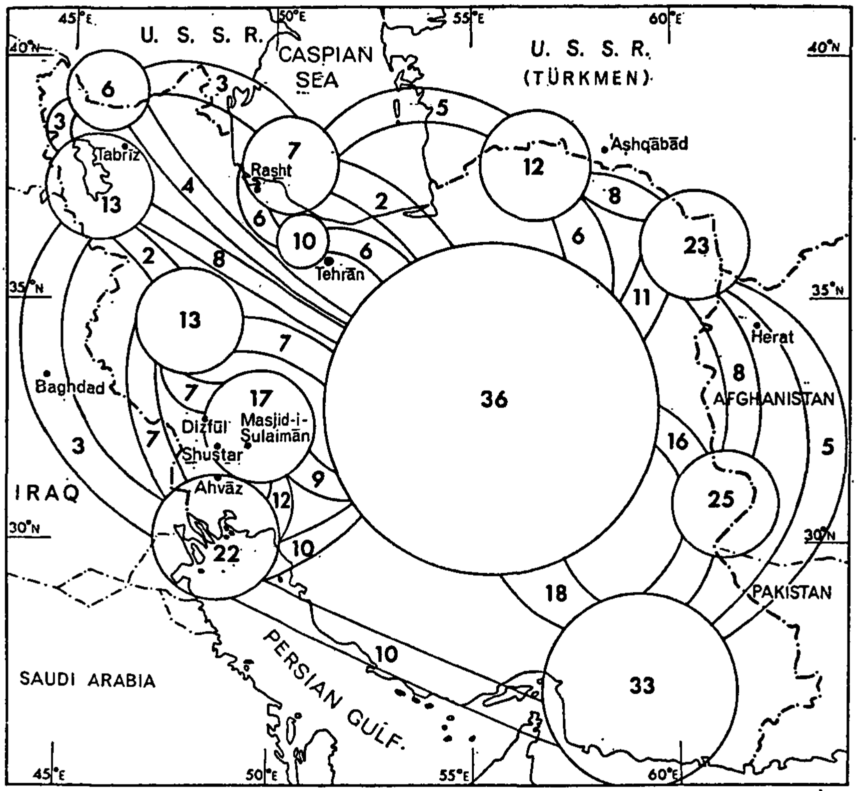


Fig. 92. Correlation of Iranian lizard fauna at the species level with physiographic regions. Figures within circles represent numbers of species recorded for the regions; figures in connecting arcs represent numbers of species in common to two regions.

Islands of the Persian Gulf

Almost nothing is known of the fauna of these islands, most of which lie close to the Iranian coast. A close study of these islands may provide an answer to some questions about earlier distributions along the gulf coasts. The few lizards known from these islands are listed here, with the island from which they were taken in parentheses:

Bunopus tuberculatus (Jazīreh-ye Tanb-i-Buzurg), *Cyrtodactylus scaber* (Bahrain Island), *Pristurus rupestris* (Jazīreh-ye Khārg; Bahrain Island), *Acanthodactylus micropholis* (Qishm Island), *Eremias brevirostris* (Qishm Island; Jazīreh-ye Tanb-i-Buzurg), *E. guttulata* (Jazīreh-ye Hingām, *Scincus conirostris* (Bahrain Island).

The distribution of turtles can be briefly considered here. *Emys* *orbicularis* is a Mediterranean species which occurs in Iran only along the Caspian coast. It ranges as far north as central Europe, and appears in the littoral fauna of north-west Africa, from Morocco to Tunisia. *Clemmys caspica* is a nearly circum-Mediterranean form, occurring in northern and western Iran, its distribution being limited to the areas where permanent streams, or at least regular and sufficient annual precipitation, occur. Thus it appears to range no further east than the extreme western portion of the plateau, or that area in which annual precipitation is in excess of 300 mm. No lizard species has a parallel distribution.

Trionyx euphraticus is a species endemic to the Mesopotamian drainage. It is the only representative of the genus (and its family) in South-west Asia, doubtless a relict of a moister period when this genus was more continuously distributed. An investigation of its affinities within the genus would prove interesting. The genus is known from the Upper Cretaceous of North America, Europe and Asia, from Africa since the Miocene, and from the East Indies since the Pleistocene (Romer, 1956).

The Mediterranean distribution of *Testudo graeca* parallels that of *Clemmys caspica*, *Testudo graeca graeca* ranging from southern Spain through North Africa, *Testudo graeca ibera* occupying the area from the Balkans east through Iran, the hiatus in the distribution of the species in southern Europe being occupied by the related *Testudo hermanni*. The form occupying the plateau region of Iran has been recognized as a distinct subspecies (or species), *T. graeca zarudnyi*, by most workers, although the distinction between the populations of *T. graeca* is not by any means great. Loveridge and Williams (1957) suggest that a continuous population of *T. graeca* formerly extended across southern Europe, the invasion of Africa taking place via Spain, with the present Iberian population constituting a relict of this former distributon.

Testudo horsfieldi, while its affinities are with the *graeca* group (Testudo *sensu stricto* of Loveridge and Williams), is quite distinct, and is an Iranian Plateau species extending into the Transcaspian region. This is the only turtle occupying the large area of South-west Asia between the range of *T. graeca* and the Indus valley, where turtles suddenly become an important faunal element.

The single amphisbaenian within Iranian limits, *Diplometopon zarudnyi*, is restricted to northern Arabia and the Mesopotamian lowlands in aeolian sand deposits. The only known member of the genus, it is the north-eastern representative of the trogonophine amphisbaenians, discontinuously distributed in the deserts of North Africa and Arabia.

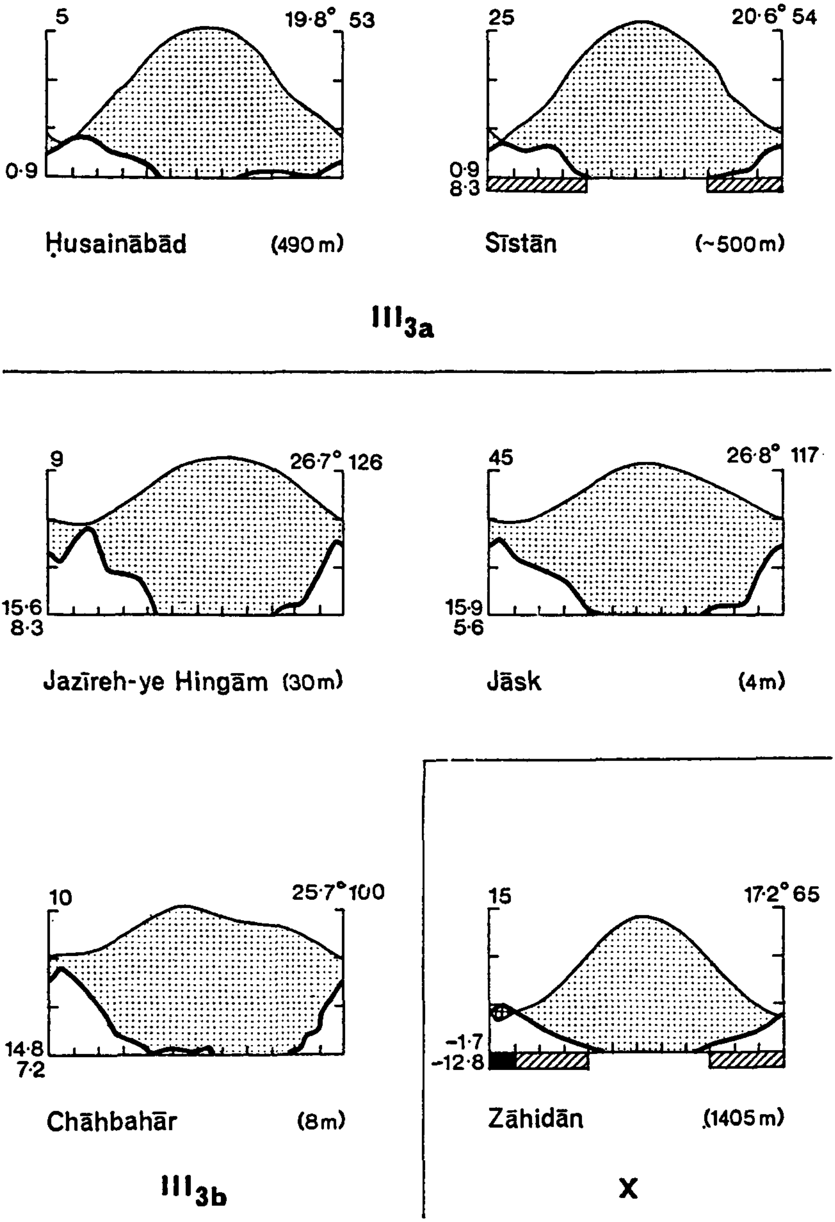


Fig. 93. (For legend see p. 329.)

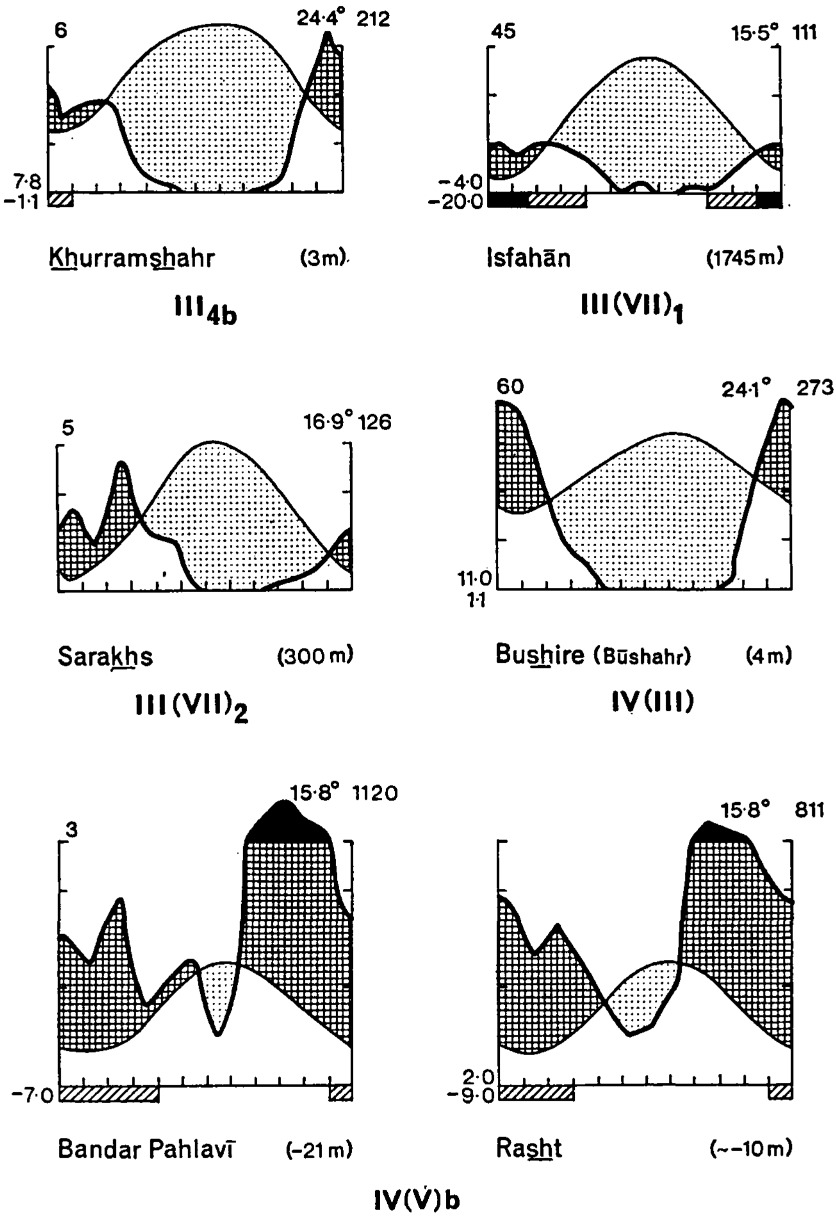

6
24·4° 212
7·8
−1·1
Khurramshahr
(3m)
III4b
45
15·5° 111
−4·0
−20·0
Isfahān
(1745 m)
III(VII)1
5
16·9° 126
Sarakhs
(300 m)
III(VII)2
60
24·1° 273
11·0
1·1
Bushire (Būshahr)
(4 m)
IV(III)
3
15·8° 1120
−7·0
Bandar Pahlavī
(−21 m)
15·8° 811
2·0
−9·0
Rasht
(∼−10 m)
IV(V)b

Fig. 93 (*cont.*)

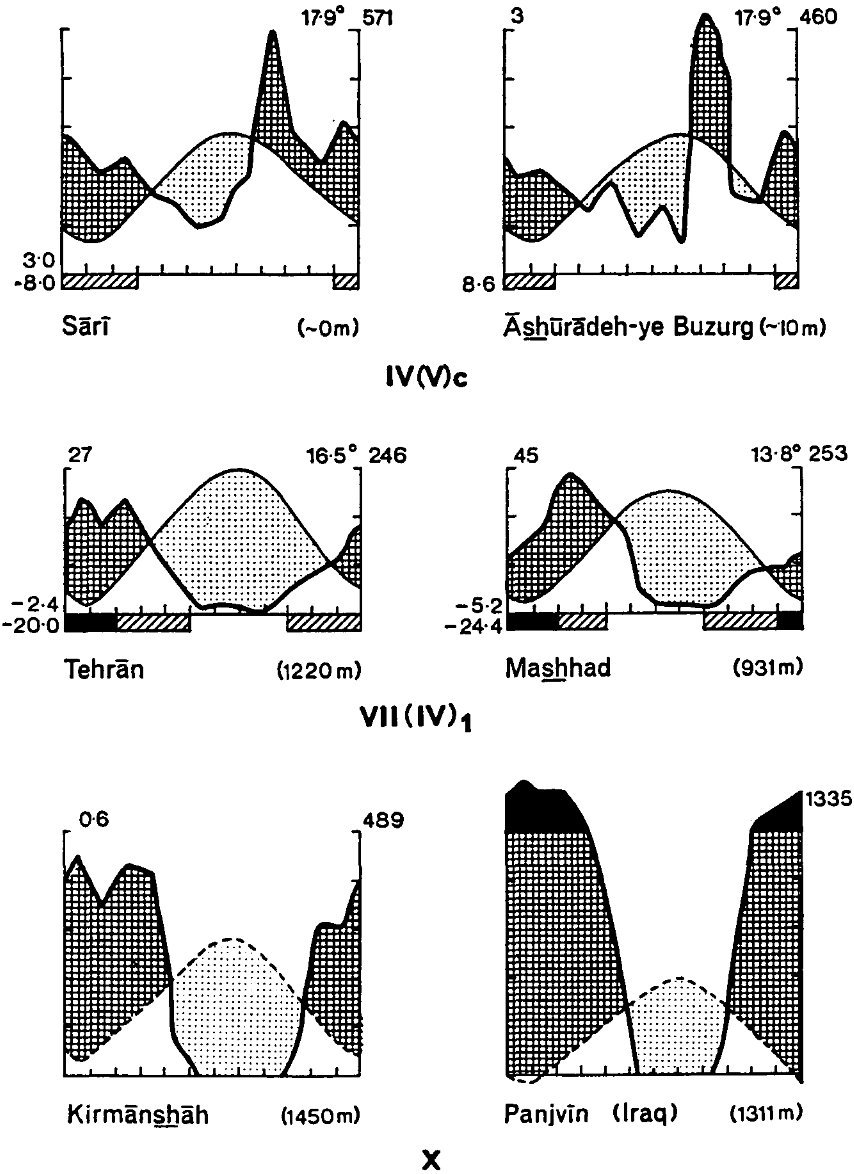
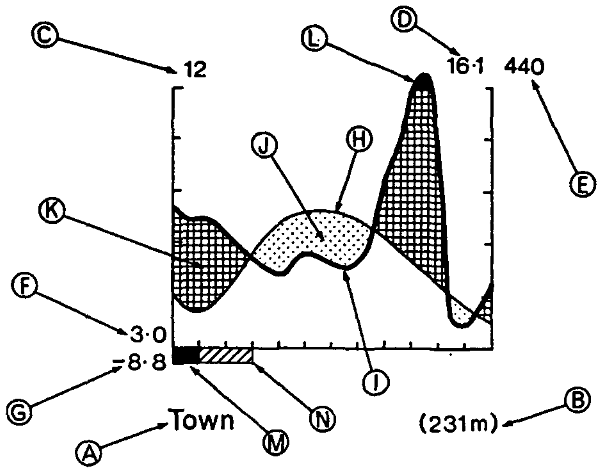

17·9°
571
3·0
-8·0
Sārī
(~0m)
3
17·9°
460
8·6
Āshūrādeh-ye Buzurg (~10 m)
IV(V)c
27
16·5°
246
-2·4
-20·0
Tehrān
(1220 m)
45
13·8°
253
-5·2
-24·4
Mashhad
(931 m)
VII (IV)1
0·6
489
Kirmānshāh
(1450 m)
1335
Panjvīn (Iraq)
(1311 m)
X

Fig. 93 (*cont.*)

Fig. 93. Climatic types in Iran (from Walter and Lieth, 1960; redrawn).

I equatorial, humid
II tropical, summer rains
III subtropical, hot and arid
IV Mediterranean, winter rains
V warm-temperate, humid
VI humid, with cold season
VII arid, with cold season
VIII boreal
IX arctic
X mountain areas in the other regions

Explanation of graphs:



A. Station.
B. Altitude.
C. Number of years observation (first figure for temperature, second for precipitation)
D. Mean annual temperature in degrees Centigrade.
E. Mean annual sum-total of precipitation in mm.
F. Mean daily minimum of coldest month.
G. Absolute minimum.
H. Monthly means of temperature (thin line).
I. Monthly means of precipitation (thick line). Both *h* and *i* stand in a fixed proportion to one another, 10° C corresponding to 20 mm precipitation.
J. Dotted area—arid period prevailing when precipitation falls below temperature curve.
K. Cross-hatched area—humid period prevailing when precipitation is above temperature curve.
L. Precipitation above 100 mm is printed in the scale of 1:10 and marked in black.
M. Black block—frost, where mean minimum of month falls below 0° C.
N. Hatched block—where absolute minimum falls below 0° C.

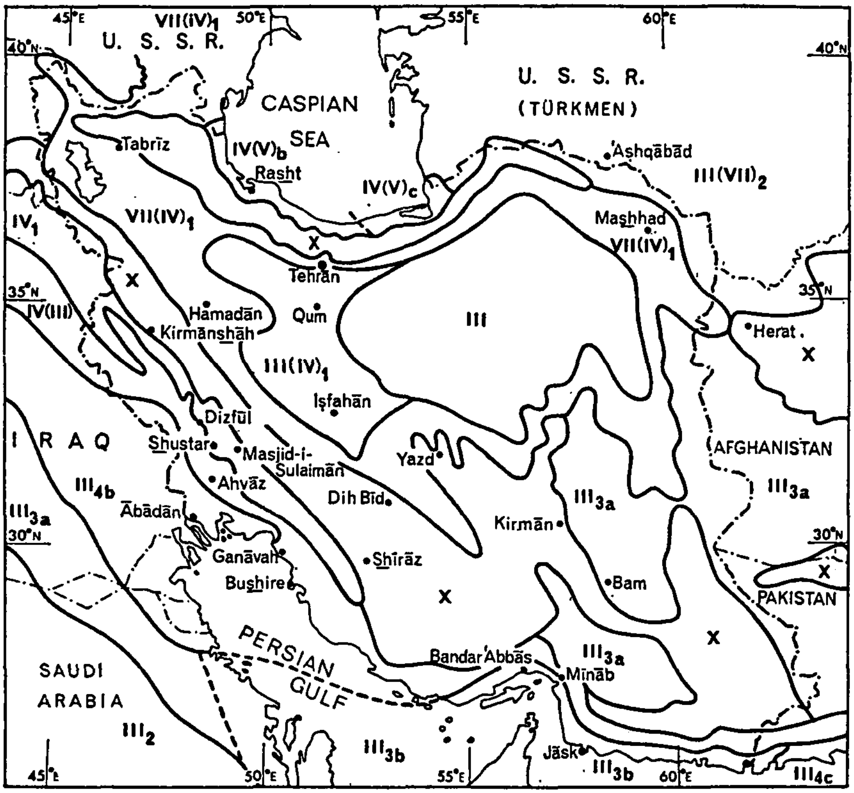


Fig. 94. Distribution of climatic types in Iran. After Walter and Lieth, 1960 (redrawn).

ECOLOGICAL ZOOGEOGRAPHY

So little is known about the Iranian lizards in nature, and information about the physical environment so lacking in detail, that only a few very general remarks can be made relative to the immediate factors determining present distributions.

One of the greatest difficulties in attempting to make ecological correlations is the fact that so little of the available climatic data is directly applicable to a consideration of the actual environmental conditions faced by small organisms. Lizards are subject to the temperatures and temperature fluctuations two in. or less above the ground, not those one metre above the ground in a sheltered meteorological screen, which is the standard basis for climatological measurement. The relative humidity affecting their lives is that to be found in burrows, under rocks, and in other areas of retreat. They may depend almost totally for water on dew, an element rarely measured in South-west Asia. By examining the gross correlations of distribution with climatic type (table 6), however, certain clues as to the direction ecological studies should take may appear, for we should expect that differences in climate over a broad area will be reflected to a considerable extent by the many microhabitats of the region.

Environmental factors influencing lizard distribution in South-west Asia

Temperature

It is now well known that lizards are able to maintain their body temperatures within a fairly narrow range. Although some physiological mechanisms, such as vasodilation and vasoconstriction, and changes in albedo (colouring) are involved, these are generally accessory to the primary, behavioural means of temperature regulation. Thus the animal's body temperature at any given time is a product of its relation to ambient temperature, and reflected radiation from substrata. For this reason, the mean air temperature, either on a daily or a seasonal basis, is less meaningful than the extremes from which the animal is unable to escape. So too, the number of hours and days during which the combination of climatic events enable the lizard to maintain a suitable activity temperature must be considered.

Temperature may be most critical to developmental stages, as the lizard must be able to place its eggs where they will be protected from lethal extremes as well as exposed to temperatures sufficiently high for development to proceed. Such species must be developmentally labile to the extent that they are able to endure the inevitable fluctuations and inconsistencies in temperature and moisture characteristic of arid regions.

The behavioural means by which temperature is regulated differs considerably from group to group. Most lizards (at least diurnal species) bask, utilizing direct insolation to raise the body temperature to the activity range. Normal activity temperatures for agamid lizards in the foothills of Khūzistān were found to lie between 38° and 43° C, the larger *Uromastyx* foraging with anal temperature as high as 44° C. A change in albedo correlated with body temperature was observed in these lizards, basking individuals being the darkest in appearance, those near or past the voluntary maximum being extremely light in

TABLE 6.

Correlation of Iranian turtles, lizards, and amphisbaenians with the climatic types of Walter and Lieth (see figs. 93 and 94). N.B.: X refers to mountain areas within the other climatic regions, and thus does not refer to a climatic type comparable in all regions.

+ = known presence within climatic type.
? = questionable presence within climatic type.
AC = Aralo-Caspian faunal element.
I = Iranian faunal element.
M = Mediterranean faunal element.
SS = Saharo-Sindian faunal element.
O = Oriental faunal element.

	Faunal class	III	III$_{2a}$	III$_{3b}$	III$_{4b}$	III (IV)$_1$	III (VII)$_3$	IV$_1$	IV (III)	IV (V)$_b$	IV (V)$_c$	VII (IV)$_1$	X
Clemmys caspica	M	.	.	.	+	+	.	+	+	+	+	+	.
Emys orbicularis	M	.	.	.	.	.	.	.	.	+	+	.	.
Testudo graeca ibera	M	.	.	.	.	+	.	+	+	+	.	+	+
Testudo graeca zarudnyi	I	+	+	.	.	+	.	.	.	.	.	+	+
Testudo horsfieldi	I	+	+	.	.	.	.	.	.	.	.	.	.
Trionyx euphraticus	SS	.	.	.	+	.	.	.	+	.	.	.	.
Agama agilis	I/SS	+	+	.	+	+	+	.	+	+	+	+	+
Agama caucasica	I	.	.	.	.	+	.	.	.	.	+	+	+
Agama erythrogastra	I	.	.	.	.	.	.	.	.	.	.	+	.
Agama kirmanensis	I	.	.	.	.	+	.	.	.	.	.	.	.
Agama megalonyx	I	.	?	.	.	.	.	.	.	.	.	.	.
Agama melanura	I	.	?	.	.	.	.	.	.	.	.	.	?
Agama microlepis	I	+	+	.	.	+	.	.	.	.	.	+	+
Agama microtympanum	?	.	.	.	.	.	.	.	.	.	.	.	.
Agama nupta	I	.	+	.	+	+	?	+	+	.	.	+	+
Agama rubrigularis	I	.	.	.	.	.	.	.	.	.	.	.	.
Agama ruderata	I/SS	.	.	.	.	+	.	.	+	.	.	+	+
Calotes versicolor	O	.	+	.	.	.	.	.	.	.	.	.	.
Phrynocephalus helioscopus	AC/I	.	.	.	.	+	+	.	.	.	.	+	.
Phrynocephalus inter-scapularis	AC	.	.	.	.	.	+	.	.	.	.	.	.
Phrynocephalus luteoguttatus	I	.	+	.	.	.	.	.	.	.	.	.	.
Phrynocephalus maculatus	I	+	+	.	.	.	.	.	.	.	.	+	.
Phrynocephalus mystaceus	AC	.	.	.	.	.	+	.	.	.	.	.	.
Phrynocephalus ornatus	I	.	+	.	.	.	.	.	.	.	.	.	.
Phrynocephalus scutellatus	I	+	+	.	+	+	.	.	.	.	.	+	+
Uromastyx asmussi	SS	+	+	.	.	.	.	.	.	.	.	+	+
Uromastyx loricatus	SS	.	.	.	?	.	.	+	+	.	.	.	.
Uromastyx microlepis	SS	.	.	.	+	.	.	.	+	.	.	.	.
Anguis fragilis colchicus	M	.	.	.	.	.	.	.	.	+	+	+	?
Ophisaurus apodus	M	.	.	.	.	.	+	.	.	+	+	+	+
Agamura persica	I	.	+	.	.	+	.	.	.	.	.	+	?
Alsophylax spinicauda	I	.	.	.	.	.	.	.	.	.	.	?	?
Bunopus crassicauda	I	.	.	.	.	+	.	.	.	.	.	.	.
Bunopus tuberculatus	SS	+	+	+	.	.	.	.	+	.	.	.	+
Ceramodactylus affinis	SS	.	.	.	.	.	.	.	+	.	.	.	.
Ceramodactylus doriae	SS	.	+	+	+	.	.	.	.	.	.	.	.
Crossobamon eversmanni	AC	.	+	.	.	.	+	.	.	.	.	.	.
Cyrtodactylus agamuroides	I	.	+	.	+	.	.	.	.	.	.	.	+
Cyrtodactylus brevipes	I	.	?	.	.	.	.	.	.	.	.	.	?
Cyrtodactylus caspius	I	+	+	.	.	.	+	.	.	.	+	+	+
Cyrtodactylus fedtschenkoi	I	.	?	.	.	.	+	.	.	.	.	+	.
Cyrtodactylus gastropholis	?	.	.	.	.	.	.	.	?	.	.	.	?
Cyrtodactylus heterocercus	I	.	.	.	.	.	.	.	.	.	.	+	?
Cyrtodactylus kirmanensis	I	.	+	.	.	.	.	.	.	.	.	.	?
Cyrtodactylus kotschyi	M	.	.	.	.	.	.	.	.	.	.	?	?
Cyrtodactylus longipes	I	.	+	.	.	.	.	.	.	.	.	.	.
Cyrtodactylus russowi	AC	.	.	.	.	.	?	.	.	.	.	.	.
Cyrtodactylus scaber	SS	.	+	+	+	.	.	+	+	.	.	.	.
Cyrtodactylus zarudnyi	I	.	+	.	.	.	.	.	.	.	.	.	.
Eublepharis angramainyu	I	.	.	.	.	.	.	+	.	.	.	.	.
Hemidactylus flaviviridis	O	.	.	+	+	.	.	.	+	.	.	.	.

TABLE 6 (*cont.*)

	Faunal class	III	III_{3a}	III_{3b}	III_{4b}	III $(IV)_1$	III $(VII)_3$	IV_1	IV (III)	IV $(V)_b$	IV $(V)_c$	VII $(IV)_1$	X
Hemidactylus persicus	SS	.	.	.	.	.	.	+	+	.	.	.	+
Hemidactylus turcicus	SS	.	.	.	.	.	.	.	+	.	.	.	?
Phyllodactylus elisae	?	.	.	.	.	.	.	+	+	.	.	.	+
Pristurus rupestris	SS	.	.	.	+	.	.	.	+	.	.	.	.
Ptyodactylus hasselquisti	SS	.	.	.	.	.	.	.	.	.	.	.	+
Stenodactylus lumsdeni	I?	.	+	.	.	.	.	.	.	.	.	.	.
Teratoscincus bedriagai	I	.	+	.	.	.	.	.	.	.	.	.	.
Teratoscincus microlepis	I	.	+	.	.	.	.	.	.	.	.	.	.
Teratoscincus scincus	I	.	+	.	.	+	+	.	.	.	.	+	?
Tropiocolotes persicus helenae	SS?	.	.	.	.	.	.	+	.	.	.	.	.
Tropiocolotes persicus persicus	SS?	.	+	.	.	.	.	.	.	.	.	.	.
Acanthodactylus cantoris blanfordi	SS	.	+	+	+	.	.	.	.	.	.	.	.
Acanthodactylus cantoris schmidti	SS	.	.	.	.	.	.	.	+	.	.	.	.
Acanthodactylus fraseri	SS	.	.	.	+	.	.	.	+	.	.	.	.
Acanthodactylus micropholis	SS	.	+	+	.	.	.	.	.	.	.	.	?
Apathya cappadocica	I	.	.	.	.	.	.	.	.	.	.	+	.
Eremias arguta	AC	.	.	.	.	.	+	.	.	.	.	+	.
Eremias brevirostris	SS	.	.	+	.	.	.	+	+	.	.	.	.
Eremias fasciata	I	.	+	.	.	.	.	.	.	.	.	+	+
Eremias grammica	AC	.	+	.	.	.	+	.	.	.	.	.	.
Eremias guttulata watsonana	I	.	+	+	+	+	+	+	+	.	.	+	+
Eremias intermedia	AC	.	.	.	.	.	+	.	.	.	.	.	.
Eremias lineolata	AC	.	.	.	.	.	+	.	.	.	.	.	.
Eremias nigrocellata	AC	+	.	.	.	.	.	.	.	.	.	+	+
Eremias pleskei	I	.	.	.	.	.	.	.	.	.	.	+	.
Eremias scripta	AC	.	?	.	.	.	+	.	.	.	.	.	.
Eremias velox persica	I	+	+	.	.	+	?	.	.	?	.	+	+
Eremias velox strauchi	I	.	.	.	.	.	.	.	.	.	?	+	+
Eremias velox velox	AC	.	.	.	.	.	+	.	.	.	+	.	.
Lacerta brandti	I	.	.	.	.	.	.	.	.	.	.	+	?
Lacerta chlorogaster	?	.	.	.	.	.	?	.	.	+	+	.	+
Lacerta princeps	I	.	.	.	.	.	.	.	.	.	.	.	+
Lacerta saxicola defilippii	I	.	.	.	.	.	.	.	.	+	.	.	+
Lacerta strigata	I/M	.	.	.	.	.	.	.	.	+	.	+	+
Lacerta trilineata media	I	.	.	.	.	.	.	.	.	.	.	+	.
Ophisops elegans blanfordi	SS	.	.	.	.	.	.	+	+	.	.	.	.
Ophisops elegans elegans	I	.	.	.	.	+	.	.	.	.	.	+	+
Ablepharus bivittatus	I	.	.	.	.	.	.	.	.	.	.	+	.
Ablepharus grayanus	I?	.	+	.	.	.	.	.	.	.	.	+	+
Ablepharus pannonicus	I	.	.	.	.	.	+	+	+	.	.	+	?
Ablepharus persicus	I	.	.	.	.	.	.	.	.	.	.	?	?
Chalcides ocellatus	SS	.	.	+	.	.	.	.	+	.	.	.	.
Eumeces schneideri	SS/I	.	+	.	.	.	+	+	+	.	.	+	+
Eumeces taeniolatus	I	.	.	.	.	.	+	.	.	.	.	.	.
Mabuya aurata	SS/I	.	.	.	.	+	+	+	+	.	.	+	?
Ophiomorus blanfordi	SS	.	.	+	?	.	.	.	.	.	.	.	.
Ophiomorus brevipes	I	.	+	+	.	.	.	.	.	.	.	.	.
Ophiomorus persicus	I	.	.	.	.	.	.	.	.	.	.	.	+
Ophiomorus streeti	I	.	+	.	.	.	.	.	.	.	.	.	.
Ophiomorus tridactylus	I	.	+	.	.	.	.	.	.	.	.	.	.
Scincus conirostris	SS	.	.	.	+	+	+	.	.	.	.	.	.
Varanus bengalensis	O	.	.	.	+	.	.	.	.	.	.	.	.
Varanus griseus	SS/I	.	+	.	?	+	+	+	+	.	.	+	+
Diplometopon zarudnyi	SS	.	+	+	+	.	.	.	+	.	.	.	.

colour. Similar activity temperatures were recorded for lacertids and for *Varanus griseus* (Anderson, 1963).

Probably most species exhibit a seasonal shift in the daily hours of activity. In Khūzistān the lizards first become active in early spring for a few hours from mid-day when temperatures are highest. As the season wears on they begin activity progressively earlier in the day and remain active longer. Eventually they seek cover during the hottest hours, and by mid-summer they are active only during the early morning and late afternoon, a reversal of this shift occurring in autumn.

Some species, such as the sand-dwelling *Ophiomorus* and *Scincus conirostris*, are able to maintain fairly constant body temperature through their burrowing habits in aeolian sand dunes. By moving on to the sand surface, or near the surface, during the warm hours they come quickly to activity temperature, while both high and low extremes are readily avoided by burrowing a few inches below the surface.

The small lacertids are able to extend their activity periods into the hottest hours of the day by utilizing the small areas of shade provided by rock or bush, making brief forays into the sunlight to catch insects.

The agamids position themselves relative to the incident sunlight so that the maximum surface area is exposed during basking, the minimum during the hottest period. The small agamids ascend low bushes at mid-day and thus escape some of the heat re-radiated from the ground. A darkly pigmented peritoneum is characteristic of diurnal species in South-west Asia, and is presumably related to the thermal environment affecting these animals.

One of the striking aspects of the lizard fauna of this desert region is the diversity of gecko species. These creatures are able to circumvent the problem of high daytime temperatures through exploitation of nocturnal activity. During the hottest season, when diurnal lizards are restricted to brief activity periods, nocturnal air temperatures remain high, due to the re-radiation from the heated ground surface. The activity of many insects and other arthropods is also largely confined to the night hours during this period. A few geckoes apparently have become secondarily diurnal, or partially so. Such behaviour is indicated for *Pristurus*, *Agamura*, and some *Cyrtodactylus* (*C. agamuroides*, *C. gastropholis*), all of which have darkly pigmented peritoneum. The habits of these lizards have not been studied, however, and only a few observations have been recorded.

Only the most cursory temperature observations have been recorded for lizards in South-west Asia (Anderson, 1963), but considerable study of thermal problems in regard to lizards of the deserts of the south-western United States has been undertaken in recent years (see particularly Cowles and Bogert, 1944; Mayhew, 1963, 1964, 1965*b*).

Mountain ranges may serve as barriers to animal distribution for several reasons, but certainly one of the most important is their imposition of a vertical temperature gradient. For instance, if continental temperature zones move southward in response to general lowering of temperatures, lizards living on the low Aralo-Caspian steppes find an increasing temperature barrier to their ascent of the passes through the east–west ranges separating the low steppes from the Iranian Plateau. Conversely, north–south ranges, such as the Zagros, may provide corridors for the southward penetration of upland northern elements. With general increase of continental temperatures, and increased aridity, some plateau species may find refuge in the higher elevations of the mountain masses present on the Iranian Plateau, while in response to climatic cooling and increased precipitation, species isolated in such mountain areas may descend to the plateau to become more widely distributed.

Precipitation and humidity

Reptiles as a group have various physiological adaptations which enable them to exploit arid environments. The more obvious of these are well known, namely, a relatively impermeable integument, excretion of uric acid, and high degree of resorption of water in the kidneys. Many other aspects of their osmoregulatory physiology remain relatively unstudied.

Certainly the amount of available water must be a limiting factor for many species in arid regions, more so perhaps than extremes in temperature. Undoubtedly behavioural adaptations play an important role in conservation of water in desert species. Many lizards spend the hours when evaporative rates are highest in burrows, where the relative humidity must be considerably higher than that of the general environment.

It has often been noted that while many desert lizards in captivity will not drink water standing in a vessel, they will, however, lap water sprayed in droplets on rocks, leaves or other objects (including other individuals) in their cages. This suggests that atmospheric water condensing as dew may be important to the survival of such species.

TABLE 7. *Elevational distribution of lizards in Iran*

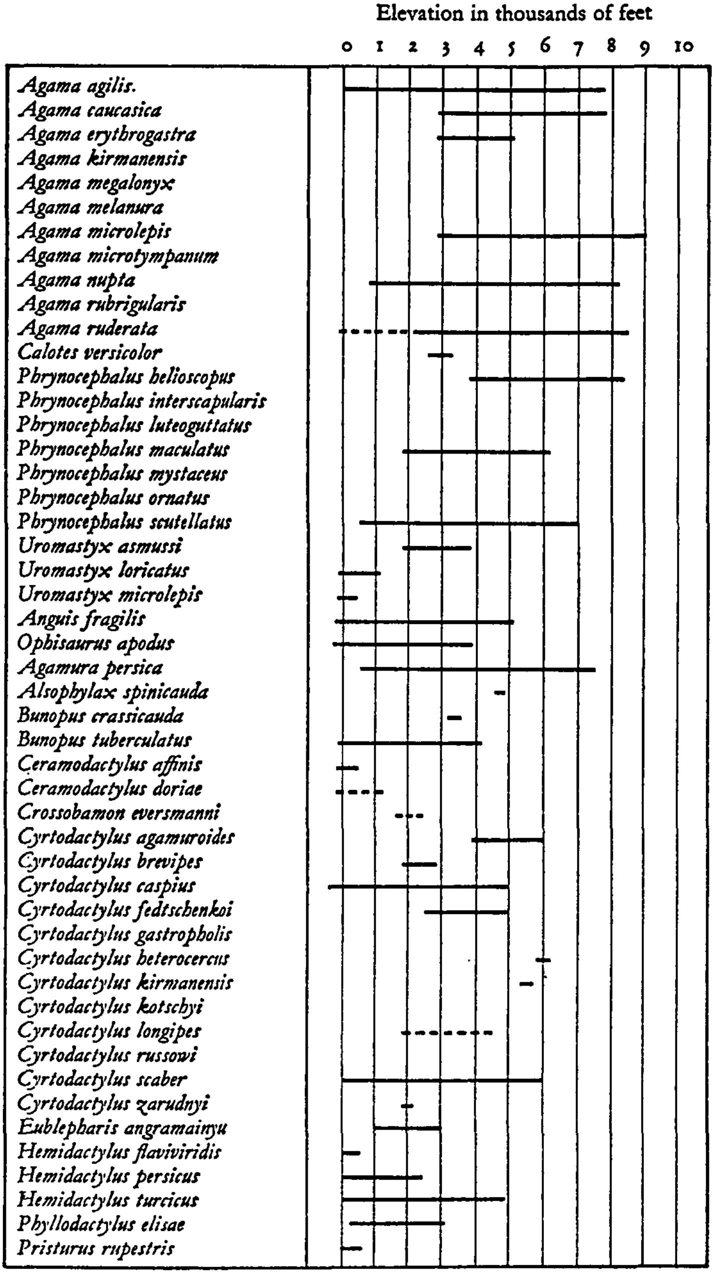
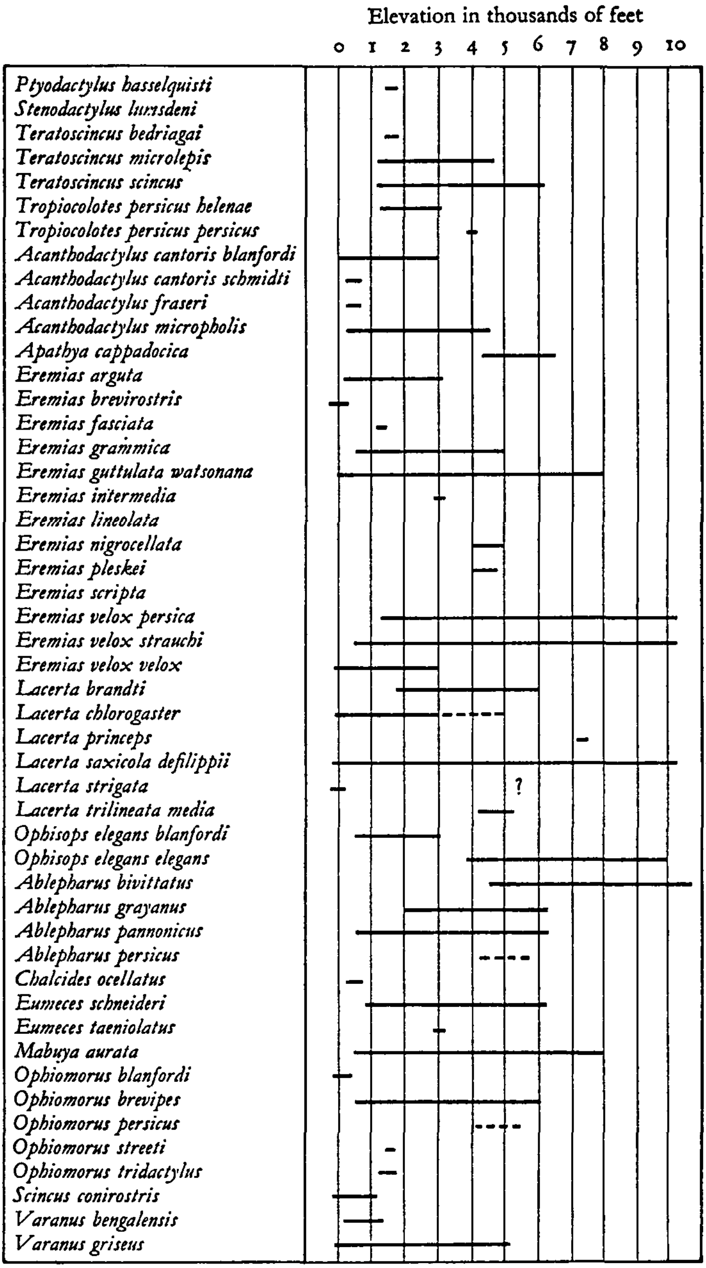


TABLE 7 (*cont.*)


Elevation in thousands of feet
0 1 2 3 4 5 6 7 8 9 10
Ptyodactylus hasselquisti
Stenodactylus lumsdeni
Teratoscincus bedriagai
Teratoscincus microlepis
Teratoscincus scincus
Tropiocolotes persicus helenae
Tropiocolotes persicus persicus
Acanthodactylus cantoris blanfordi
Acanthodactylus cantoris schmidti
Acanthodactylus fraseri
Acanthodactylus micropholis
Apathya cappadocica
Eremias arguta
Eremias brevirostris
Eremias fasciata
Eremias grammica
Eremias guttulata watsonana
Eremias intermedia
Eremias lineolata
Eremias nigrocellata
Eremias pleskei
Eremias scripta
Eremias velox persica
Eremias velox strauchi
Eremias velox velox
Lacerta brandti
Lacerta chlorogaster
Lacerta princeps
Lacerta saxicola defilippii
Lacerta strigata
?
Lacerta trilineata media
Ophisops elegans blanfordi
Ophisops elegans elegans
Ablepharus bivittatus
Ablepharus grayanus
Ablepharus pannonicus
Ablepharus persicus
Chalcides ocellatus
Eumeces schneideri
Eumeces taeniolatus
Mabuya aurata
Ophiomorus blanfordi
Ophiomorus brevipes
Ophiomorus persicus
Ophiomorus streeti
Ophiomorus tridactylus
Scincus conirostris
Varanus bengalensis
Varanus griseus

Unfortunately as we have noted, there is very little precise information regarding dew in South-west Asia, although it is well known to desert travellers that heavy dew frequently forms during late night and early morning hours, even in extremely arid areas.

The possibility exists, of course, that some lizards make use of metabolic water, as do kangaroo rats. Metabolic water may be indirectly utilized: the water which is an end-product of carbohydrate metabolism, when exhaled in the confines of a burrow, will rapidly and significantly increase the relative humidity of the atmosphere, greatly reducing the evaporative loss of water through the integument (personal communication by Tyson Roberts). Since this water is the result of carbohydrate metabolism, there may be a net gain in metabolically available water, since condensation on the burrow walls and objects in the burrow may occur as the temperature drops at night, and this can be lapped by the animal, or possibly actively absorbed through the integument. The question remains to be investigated as to whether or not the acquisition of free water through this means exceeds water loss through evaporation (since obviously there must be a net loss to the environment of *total* water: free water plus metabolically derived water). Suggestive in this regard is the fact that certain desert reptiles readily absorb water through the skin. Unless active uptake of water occurs, it would be expected that evaporation through the skin ought equally to occur, which is a peculiar adaptation for animals living in areas where little or no standing water is encountered: it is observed, for example, that the skin of a living *Varanus bengalensis* is observed to soak up water spectacularly, that of *V. griseus* showing only slightly less tendency to do so.

A salty incrustation accumulating between the eye and nostril of captive specimens of *Varanus griseus* in Iran was observed during my stay there. The possible existence of a salt-excreting gland, such as that known in the 'marine iguana', *Amblyrhynchus cristatus*, and in certain marine birds, warrants investigation.

Schmidt-Nielsen (1959) has demonstrated the role played by the blood in the water balance and metabolism of the camel. Studies along this line might well prove enlightening in other groups of desert animals as well.

Distribution of the turtle *Clemmys caspica* is definitely correlated with the occurrence of permanent water, or seasonal water which is regular and dependable from year to year.

In the case of some lizards distributed only along the coasts of the Persian Gulf in Iran, humidity may be the limiting factor. Certain species, notably geckoes, transported through human agency have become established only in coastal areas of human habitation in the areas of introduction. Humidity may play a role in these cases, although the inability of these introductions to compete successfully with existing faunal counterparts is undoubtedly the result of various factors.

Surface character

While the nature of the substrate is obviously an important factor in determining plant distribution, it has seldom been emphasized in studies of terrestrial reptile distribution. There is however considerable correlation of substrate type and local distribution of lizards in Southwest Asia, and this has distinct general significance.

Certain Iranian lizard species are adapted for life in or on aeolian sand dunes, or at least on sandy soils, and are more or less restricted to such zones. Among these are the species of *Acanthodactylus*, *Scincus*, *Teratoscincus*, *Crossobamon eversmanni*, *Phrynocephalus maculatus*, *Eremias grammica*, *E. scripta*, and several species of *Ophiomorus*. The amphisbaenian *Diplometopon zarudnyi* is also a sand-dweller. *Ophiomorus* and *Diplometopon* live beneath the surface of the sand, and their limbs have been greatly reduced, an adaptation facilitating the types of subsurface locomotion which these animals employ. The other species named above have the digits equipped with comb-like fringes of scales, an adaptation which has arisen independently in many groups in various sandy deserts throughout the world. *Scincus*, and to a lesser extent, species of *Phrynocephalus*, are adapted both for burrowing and for sand-running.

The large species of *Agama* appear to be restricted to areas such as limestone outcrops and rocky cliff faces where both basking surfaces and deep crevices for retreat are provided. Species in this group include *Agama caucasica*, *A. erythrogastra*, *A. melanura*, *A. microlepis*, and *A. nupta*. Such terrain is characteristic of the Iranian Plateau and the mountains and upland regions of its borders. The smaller species of *Agama* occur on plains, valleys and alluvial fans, on sandy, loam, clay, and gravel soils. Species specificity in regard to these different soil types has not been well established. These lizards are usually found in the vicinity of small rock piles such as those erected by local inhabitants to mark the boundaries of grain fields. Such rock piles provide vantage points and basking areas upon which the lizards are able to orient themselves relative to sunlight for temperature control. They retreat into these piles for shelter. They also ascend low shrubs, and presence or absence of low bushes may be a factor in distribution of some species. Such areas frequently interdigitate with the outcrops and boulder slides occupied by the larger species, but the occupancy of the two environments is usually sharply defined.

Species of *Phrynocephalus* and *Eremias* show distinct preferences for particular soil types. *Phrynocephalus helioscopus*, *P. ornatus*, *P. scuttulatus*, *Eremias fasciata*, and *E. guttulata* preferring open clay and gravel plains, while *Phrynocephalus interscapularis*, *P. maculatus*, *P. mystaceus*, *Eremias intermedia*, and *E. lineolata* are usually found on sandy plains and steppes. *E. pleskei* and *E. velox strauchi* apparently prefer dry mountain slopes. Local distribution of many lacertid species may be determined by the availability of cracks and holes in clay and gravel soils, or burrows in plant-stabilized sandy soil. These crevices provide a retreat from predators and from temperature extremes.

Among the geckoes, *Teratoscincus* and *Crossobamon* have been mentioned as sand-dwelling species. The various species of *Stenodactylus*, *Ceramodactylus*, and *Bunopus* also occur on sand, but to what extent they occupy substrates is not known. *Agamura*, *Pristurus*, *Tropiocolotes*, and *Cyrtodactylus* usually are collected on non-sandy substrate. The various species of *Cyrtodactylus* are found on rocky slopes and cliff faces, in crevices and caverns, and in and about places of human habitation (particularly true of *Cyrtodactylus scaber*). *Phyllodactylus elisae* is found in caverns in gypsum deposits and limestone, and occasionally as a house gecko. *Hemidactylus* and *Ptyodactylus* are similarly adapted to life on vertical surfaces. The discontinuous distribution of geckoes of the genus *Eublepharis* should be investigated from an ecological standpoint. In Khūzistān *E. angramainyu* was found only in the foothill areas where extensive gypsum deposits exist. It may be that these large geckoes are dependent upon the cavernous areas in the gypsum where water persists throughout the year and a high relative humidity may be maintained.

Man-made edifices (usually constructed from mud-brick) provide additional habitat situations not only for the geckoes mentioned above, but for the large, rock-dwelling species of *Agama* as well. These lizards are often quite numerous on walls, houses, and monuments. There is usually an abundance of insect prey in such situations, attracted by the human inhabitants and their domestic animals and cultivated plants.

The Iranian species of *Uromastyx* are confined in their local distribution to well-drained alluvial soils wherein they are able to excavate their burrows. *Uromastyx asmussi* reportedly favours gravelly alluvium, whereas *Uromastyx loricatus* prefers silty-clay soils.

The most widely ranging forms in South-west Asia are those occupying the greatest range of substrates, such as *Varanus griseus*, *Eremias velox*, *Agama agilis*, *Mabuya aurata*, *Eumeces schneideri*, or those inhabiting the most continuously distributed substrates, such as *Eremias guttulata*.

Evolution of the various lizard groups in South-west Asia may be significantly correlated with this specific affinity for substrate-type, and the discontinuous distribution of these substrates. Many populations or subpopulations may be rather effectively isolated genetically from one another over protracted periods of time. This has been discussed in the case of the obligate dune-dwelling species of *Ophiomorus* in a previous paper (Anderson and Leviton, 1966*b*). Even species physically and physiologically capable of crossing fairly narrow stretches of intervening unsuitable substrate may rarely do so.

As a casual observation, I have noticed that the greatest number of individual lizards occupying the fringe areas of a population are often juveniles. It is these animals, unable to wrest already established territories from adults, that are most easily picked off by predators. It is among these juveniles also that one expects the greatest phenotypic variation, and from this peripheral group the occasional colonizers of unoccupied habitat separated by unfavourable terrain must usually be drawn. It is thus possible to visualize these patches of discontinuously distributed substrate types as analogous to islands, and the effects of "waif disperal" and "genetic drift" readily imaginable.

Dependence on substrate may also serve as a limiting factor on one or more fronts as populations migrate in response to climatic change. Species inhabiting low sandy plains, possibly physiologically able to negotiate the temperature and/or moisture gradient imposed by a bordering mountain range, may yet fail to cross the passes when confronted by the rocky cliffs, slides, and aluvial fans along the mountain front.

Food

Food availability as a limiting factor is, of course, a reflexion of the physical factor of the environment which restricts the distribution of the food organism.

It is interesting to note that the great majority of lizard species examined in this regard exhibit a fairly wide latitude in dietary items. Most of these lizards apparently eat any small arthropod with which they come in contact and are able to capture and overcome. Vegetable matter also appears in the stomach contents of several carnivorous species, sometimes in such quantity that its ingestion incidental to capture of insects can be ruled out. Similar observations have been recorded for lizards in desert regions of North America (Banta, 1961). This non-specificity or limited specificity as to diet is obviously an important adaptation in arid regions where population densities of prey species are usually low, and the appearance of any one species of insect tends to be seasonal. Even the vegetarian *Uromastyx* are reported to take animal food in captivity, and may occasionally do so in nature as well.

Present data are insufficient to demonstrate dietary specificity in any Iranian lizard species, but it has certainly not been ruled out for some. Ants undoubtedly predominate in the stomach contents of the smaller species of *Phrynocephalus*, and in *P. ornatus* and *P. luteoguttatus* no other food material was found. This may, of course, only indicate the seasonal availability of these insects. Only beetles were found in the digestive tract of the few specimens of *Teratoscincus scincus* and *T. bedriagai* which I examined. In captivity, specimens of *Teratoscincus scincus* regurgitated mealworm larvae (*Tenebrio molitor*) and crickets, feeding successfully only on adult beetles. *Anguis fragilis* reportedly shows a preference for slugs and snails, its dentition being particularly adapted to these dietary items. It also feeds on earthworms and soft-bodied insect larvae.

The possible importance of desert locusts in the food chains of predatory animals in South-west Asia has been alluded to previously (Anderson, 1963). In the foothill belt of Khūzistān a large number of insect species and individuals appear coincident with the spring growth and bloom of annual herbaceous plants and the appearance of cultivated grain crops. The number of insects rapidly diminishes as the ephemeral vegetation dies and the crops are harvested. It is during this period that large numbers of desert locusts arrive (or so it was observed in 1958) to assist the goats in eliminating the last vestiges of vegetation from the hillsides and stream courses. These grasshoppers remain in gradually diminishing numbers, presumably making use of stored fat deposits. In the autumn as the locust population has nearly expired, there is a brief resurgence of plant growth and an attendant increase in the local insect fauna. Observation indicated that the population density of reptiles, particularly *Agama nupta*. *A. agilis*, and *Eremias guttulata watsonana* remained high throughout this period. The number of avian and mammalian predators was remarkable for such an arid region, so barren of vegetation. Large numbers of foxes (*Vulpes vulpes*), occasionally observed feeding on reptiles killed on the roads, could be seen each evening throughout the summer; wolves (*Canis lupus*), jackals (*C. aureus*), and mongooses (*Herpestes* sp.) were not uncommon, a hyena (*Hyaena hyaena*) being seen on one occasion. A large *Buteo* hawk, small owls, shrikes, and falcons were frequently observed. It seems likely that rodent populations undergo considerable cyclic fluctuation in this region, yet the reptile and predaceous mammal and bird populations remain high. One hypothesis, which suggests itself on the basis of these casual observations, is that energy is brought into the area in the form of the considerable influx of desert locusts, which sustain the commonest lizard species. These in turn provide sustenance for the secondary predators until rodent populations again increase.

Kraus (1958) briefly summarized the life-history of the desert locust and its relation to meteorological conditions. All of Iran (and indeed most of South-west Asia and all of North Africa) lies within the total invasion zone of the desert locust, and southern Iran is in the area in which breeding or swarms are to be expected in at least 50 per cent of the years. The locusts only multiply under conditions which are of rare occurrence at any one point in the great arid tract of South-west Asia and North Africa; but where successful breeding occurs, great numbers are produced, and it is their dispersal to all parts of the desert which assures their success in the next generation. They thrive best under conditions which fluctuate between great dryness and markedly seasonal or periodic rainfall. Green food is essential only in the hopper stages, the adults being able to withstand extreme dryness and heat without food for long periods. Relatively high humidity or succulent green food is necessary, however, for the locusts to attain sexual maturity.

This explanation of the life-cycle of the locust as a highly important link in the food chain is purely speculative, and based on inadequate observations. It is worthy of further investigation, however, since were it to prove correct there would be dire implications of a wider economic nature. If locusts are so reduced in numbers to the point where they no longer provide an alternative food supply for creatures that normally prey on rodents, the unchecked numbers of rodents following diminution of predators in agricultural areas may turn out to be an even greater and more general problem than the prevention of locust swarms.

Vegetation

The distribution of lizards in relation to the flora is neither a result of dependence upon common physical factors of the environment, substrate, precipitation, etc., nor a consequence of certain physical requirements provided for the lizards by the vegetation. Certain types of shrubs, for instance, stabilize dune sands and provide suitable sites for burrow excavation among their roots. These burrows may be constructed by rodents, and thus the lizards are also dependent upon the presence of these animals as well as on the plants. In the arid areas of sparse vegetation many lizards may depend for sustenance upon the insect species attracted to the vegetation, and consequently their local distribution depends upon the frequently narrowly restricted occurrence of certain plants.

The small species of *Agama* climb into the branches of low steppe and desert vegetation such as wormwood (*Artemisia*) and camel thorn (*Alhagi camelorum*) to orient themselves relative to the sun's rays and to escape the hot soil surface for temperature control. Such vantage points also enable them to survey their territories. Vegetation may play a similar role among forest species in the mountains and along the Caspian coast, the patches of alternate light and shadow enabling efficient behavioural temperature control. A few species adapted to climbing tree trunks may extend their territories vertically as well as horizontally, and the ability to move quickly around the circumference of a tree trunk offers considerable protection from the larger predators.

While the relationship of South-west Asian lizards to vegetation has been little studied, whatever dependence does exist is probably in relation to vegetation type rather than to particular species of plants.

Certainly the role of vegetation in the creation and maintenance of soil and moisture conditions and other factors of the microclimate is obvious.

Light

Light as a limiting factor in reptilian distribution has been little considered. Very few studies on the quality and quantity of light affecting the biology of reptiles exist, although it is known that reproductive cycles in some but not all lizards in temperate areas are related to photo-period (Mayhew, 1961, 1964 1965*a*). Doubtless other physiological cycles are similarly related to light.

It is possible that when continental or regional warming occurs, northward migrating species (particularly tropical elements) may find that light and photoperiodic factors rather than thermal factors become limiting.

Regional differences in qualitative and quantitative light distribution, particularly in relation to microhabitat situations, have not been studied in South-west Asia, but should be considered. Certainly cloud-cover and humidity, factors relating to this question, differ regionally as well as seasonally.

Wind

Air movement is obviously important in ecology, primarily as it affects the other physical factors of the environment. Thermal convection, rainfall distribution, and humidity are interrelated with differences in atmospheric pressure and air movement.

Analysis of the morphological adaptations for sand-dwelling in species of the skink genus *Ophiomorus* suggests that their evolution is correlated with the migration of aeolian sand dunes in a N.W.–S.E. direction due to the strong winds blowing from the north-west along the eastern borders of Iran. In this group there has been increasing specialization in certain morphological features from north-west to south-east (Anderson and Leviton, 1966*b*). Similar analysis of other groups may prove enlightening in regard to the distributional history of the organisms, as well as providing clues to the development and sequence of certain landforms. It is noteworthy in this regard that while *Ophiomorus*, an Iranian element, has moved south and east down off the plateau into coastal environments, the sand-dwelling Saharo-Sindian elements *Scincus* and *Acanthodactylus* have not penetrated the plateau. In fact, the genus *Scincus* apparently does not occur in South-west Asia east of the Persian Gulf coast in the Bushire region, in spite of the supposed record of *Scincus mitranus* from the Hab river region of West Pakistan. This Arabian species has never been collected in the West Pakistan subsequent to the original record (Murray, 1884*a*), and J. A. Anderson, who has collected extensively in this region, believes the record to be in error (personal communication), an opinion in which I fully concur.

HISTORICAL ZOOGEOGRAPHY

Analysis of the Fauna

Endemism

To be at all meaningful from the standpoint of zoogeographic analysis, the term 'endemic' must be used with reference to a geographically defined region of rather narrowly limited extent. Hence, in a state like Iran, which takes in the entirety of certain geographic regions while including small portions of others within its boundaries, it is meaningless to refer to a species as 'endemic to Iran'. Rather we must consider forms restricted to the Central Plateau, the Helmand Basin, the western foothills of the Zagros, etc. Some of these 'endemics' will consequently also be found beyond the borders of Iran.

The significance of endemic species (or subspecies) from the standpoint of historical zoogeography is threefold: (1) a narrowly restricted form may be "relictual", occupying the remaining habitable area of a once much broader distribution. Frequently its nearest relatives are to be found at some considerable distance. In continental situations this may be taken as an indication that the environment in which the animal is found was once of greater extent. The fact that adaptation to environmental change may have occurred *in situ* must not be overlooked. Nonetheless, such a situation suggests that a previously widespread environment has become discontinuously distributed, perhaps with subsequent modification even in the areas of least drastic change. *Phyllodactylus elisae* and *Trionyx euphraticus* are endemics of the above type. (2) An endemic population may be in the process of expanding its range, often at the expense of closely related neighbouring species, in response to the spread of its environmental type with climatic change. It is usually assumed that spatial isolation is necessary for the differentiation of animal populations. Endemics which are in progress of expanding their range are difficult to recognize at any one moment in time. The range of a species may be advancing on one front and retreating on another; indeed, this must be the case almost invariably, due to the climatic fluctuations that occur even within a general trend toward increased aridity, or toward increased precipitation. Certain speculations of a general nature can often be made, however. For instance, where aeolian sand dune formation has progressively increased, and dune areas are expanding and covering alluvium, we can draw the obvious conclusions that sand-dwelling populations are spreading and encroaching upon the areas inhabited by species better adapted to clay or gravel soils. Usually the changes which affect animal distribution are far more subtle, however, and our insufficient knowledge of the ecology of the species in question makes meaningful speculation impossible. With regard to lizard species, recognition of expanding populations is almost always inferential, since we have little information regarding changes in extent of distribution over even brief periods. The expansion of economically important animals is much better documented. (3) A population (most often recognized at the subspecific level) may have differentiated fairly recently out of a larger population through isolation, and may have remained relatively static in its distribution since its isolation from the parent population. With climatic change, and/or changing landform, this population will expand or contract, hence it is the incipient form of the other two categories of endemic species.

The Central Plateau

As mentioned previously, the Central Plateau region can be subdivided geographically. It consists of several drainage basins of individual character, such as the Dasht-i-Kavīr and the Dasht-i-Lūṭ. Unfortunately, our knowledge of the fauna is far too limited to enable a detailed zoogeographical analysis of the plateau region. The distribution patterns within the plateau reflect more our ignorance than our knowledge. The following species are thus far known only from the Central Plateau: *Agama kirmanensis*, *A. microlepis*, *Bunopus crassicauda*, *Cyrtodactylus kirmanensis*.

Thus four species, or 11 per cent of the fauna of the Central Plateau, are endemic, and there are taxonomic problems associated with each of these nominal species. All belong to genera well represented not merely on the Central Plateau but in the highest parts of Iran generally. It is hence not unreasonable to surmise that they are autochthonous forms which have differentiated in response to the vicissitudes of local isolation and environmental change on the plateau.

Sīstān basin

Three species endemic to this basin occur within the borders of Iran. They compose 12 per cent of the fauna of this region. They are: *Cyrtodactylus zarudnyi*, *Teratoscincus bedriagai*, and *T. microlepis*.

The remarks in regard to the endemics of the Central Plateau apply equally to these species.

Balūchistān and Makrān coast

In this region three Iranian species, *Cyrtodactylus brevipes*, *Tropiocolotes persicus*, and *Ophiomorus streeti*, or 9 per cent of the lizard fauna, are endemic. As discussed in a previous paper (Anderson and Leviton, 1966*b*), the genus *Ophiomorus* appears to have had its centre of origin on the Central Plateau, isolation through aeolian distribution of sand dunes having resulted in differentiation of several sand-dwelling species.

The problems regarding the affinities of forms here assigned to the genus *Tropiocolotes* will be discussed in forthcoming systematic studies of the lizards of South-west Asia (e.g. Minton, Anderson and Anderson). In so far as can be determined from material in collections, this group of small geckoes is discontinuously distributed through North Africa and South-west Asia, and the recognized populations may represent the fragmentation of a more continuous distribution. It is perhaps significant that none of these lizards (variously assigned to *Tropiocolotes*, *Alsophylax*, *Microgecko*) is yet known from the interior Iranian Plateau, but occurs rather along its western, southern, and northern margins. *Alsophylax pipiens* occurs at Kabul, Afghanistan, however, and *Tropiocolotes depressus* is found at 6,500 ft in northern West Pakistan. It may be that this group of small geckoes (if they are a natural group) is more continuously distributed than has yet been recognized. Unfortunately, to date nothing has been published on the ecology of these forms.

Cyrtodactylus brevipes is a member of a species-group distributed primarily on the Iranian Plateau.

South-eastern Iran

If we view the south-eastern portion of Iran from a somewhat different perspective, and include a portion of the eastern Central Plateau, including the Dasht-i-Lūṭ, a portion of Balūchistān, including the Jāz Muriān depression, and Sīstān as well, we find a number of lizards endemic to a region which approximately corresponds to the climatic type III_{3a} of Walter and Lieth (see figs. 93 and 94). These are: *Cyrtodactylus agamuroides*, *C. brevipes*, *C. kirmanensis*?, *C. longipes*, *C. zarudnyi*, *Tropiocolotes persicus persicus*, *Stenodactylus lumsdeni*, *Teratoscincus bedriagai*, *T. microlepis*, *Eremias fasciata*, *Ophiomorus brevipes*, *O. streeti*.

This is perhaps too large an area to be really meaningful; if one extends it to the east into West Pakistan and Southern Afghanistan, such species as *Phrynocephalus ornatus* and *Agamura femoralis* should be included. It is interesting, however, that all of the forms restricted to this region have their affinities with Iranian Plateau species, and not with Saharo-Sindian elements. All are adapted to live in a region with very low mean annual precipitation (under fifty-five mm) all falling during the winter months, and high daily and mean annual temperatures. Such conditions may have been more widely spread on the Central Plateau both in the recent past and at times during the Tertiary period.

Rezā'īyeh basin

Two lacertid lizards, *Apathya cappadocica urmiana* and *Eremias pleskei*, or 15 per cent of the known fauna of the Rezā'īyeh area are endemic.

If the area considered is enlarged to include adjacent areas of eastern Turkey and the southern Transcaucasian provinces of the U.S.S.R., the species *Apathya cappadocica* (*sensu lato*), *Lacerta brandti*, and L. *trilineata media*, as well as *Eremias pleskei*, may be considered "Armenian" endemics. The two forms of *Lacerta* are Mediterranean in their affinities. Representatives of this European genus probably entered Iran during the Pleistocene in a period of decreased evaporation, and may never have penetrated far into the Central Plateau. *Eremias pleskei* was regarded by Nikolsky as closely akin to *Eremias fasciata*, which is a species of the most arid region of the Central Plateau and adjacent Afghanistan and Balūchistān. It remains to be determined whether its nearest relatives are Iranian or Aralo-Caspian elements. *Apathya*, a monotypic genus, has been regarded both as a subgenus of Lacerta and as congeneric with *Latastia* by different workers. If its affinities are with the latter, its nearest relatives are now to be found in north-eastern Africa and in Arabia; if the former, it is of European or Mediterranean derivation. My limited acquaintance with these groups does not warrant the expression of an opinion in regard to its systematic position. In either case, however, *Apathya* would appear to be a relictual endemic.

No endemic lizards are recognized from the Mughān Steppe, the Caspian coast, or the Alburz mountains. *Lacerta chlorogaster*, however, occurs only on the Caspian coast and the valley of the Atrak river in the Kopet Dāgh. Since the southern coast of the Caspian Sea has only been exposed since the close of the Pleistocene as a result of continuing recession of the sea since the Chvalyn Transgression, the small lizard fauna of this region has only recently become established. The present distribution of *Lacerta chlorogaster* suggests that it may have entered Iran during the Tertiary or early Pleistocene, having been restricted to the lower elevations of the Kopet Dāgh during the Chvalyn Transgression; and it would seem at present to be extending its range with the return of favourable conditions to a more extensive area. It is quite distinct morphologically from all other Iranian species in the genus.

With the depression of snowline during the last glaciation, the Alburz Range must have been one of the areas of Iran most affected by the climatic changes of the Pleistocene. On the south slope the lizard fauna would hence have retreated to lower elevations and on to the Central Plateau. On the north flank any lizards which remained (and perhaps none did) would have been confined to a narrow belt above the more extensive Caspian Sea, and this belt would probably have had ecologically continuous connexions to the west and east. This sort of situation could not have provided the isolation conducive to the production of an endemic fauna.

Kopet Dāgh

Only two species, 17 per cent of the known fauna, may be construed as endemics to the Kopet Dāgh. This area has been very inadequately investigated, however. The two lizards, *Alsophylax spinicauda* and *Ablepharus persicus*, are of doubtful taxonomic status. Both are known with certainty only from the vicinity of Shāhrūd at the edge of the Central Plateau.

Türkmen Steppe

A single Iranian species, *Agama erythrogastra*, is endemic to the Türkmen Steppe drainage area. However, it occurs only at relatively high elevations of this drainage (3,000–5,000 ft) in the region included in climatic type VII $(IV)_1$ (Walter and Lieth, 1960), while most of the Türkmen Steppe proper has a climatic type designated III $(VII)_2$ (see figs. 93 and 94). This lizard is one of several species of large, rock-dwelling *Agama* autochthonous to the Iranian Plateau.

Zagros Mountains

Three species of lizards, *Cyrtodactylus heterocercus*, *Lacerta princeps*, *Ophiomorus persicus*, 25 per cent of the known fauna within Iranian borders, are endemic to the Zagros mountains. *Cyrtodactylus heterocercus* is a member of the South-west Asian group of the genus. According to Mertens (1952) it may be most closely allied to *C. kotschyi*, species at present having a Mediterranean distribution. This relationship is by no means certain, however. In Iran *C. heterocercus* is known only from Hamadān, the type locality. A related subspecies, *C. h. mardinensis*, is known from south-eastern Turkey, where it occurs at elevations of about 3,000 ft.

Lacerta princeps, known from the Zagros as far south as the vicinity of Shīrāz in Iran, but also reported from Iraq and south-eastern Turkey, is the only member of the genus to penetrate Iran to any extent. It is apparently restricted to the high forested areas of the Zagros, and whether or not it is continuously distributed between the recorded localities is an open question. Like *Lacerta chlorogaster*, it is a quite distinct species, and probably represents a penetration of Iran during a moister climatic regime in the Pleistocene or earlier.

Ophiomorus persicus is the least specialized member of this genus which appears to have diversified in the elevated regions of South-west Asia, the Iranian Plateau in the broadest sense. The diversification of the three western species, all of which live under rocks (the other two species occurring in Turkey, Greece, Israel and Jordan) may date from the increasing orogeny of the Tertiary, and *O. persicus* may have evolved *in situ*.

The Western Foothills of the Zagros

Of particular interest are the two species (12 per cent of Iranian lizards) endemic to the foothill belt. *Eublepharus angramainyu*, a recently described species (Anderson and Leviton, 1966*a*), long considered conspecific with *E. macularius*, is found in this region of Iran and Iraq. Its nearest relatives are found in West Pakistan, southern Afghanistan, and the Salt Range of the Punjab. *E. macularius* has also been reported from the Kopet Dāgh in the U.S.S.R., and this may prove to be yet another distinct population of the genus. There are no records of the genus as yet from the interior of the Iranian Plateau proper, the known populations occurring at localities on the periphery of the plateau. This negative evidence, and the markedly discontinuous distribution of the genus as at present constituted in Asia, suggests that these large geckoes are the remnants of an older, more continuous distribution, perhaps of considerable antiquity. Indeed, the distribution of the eublepharid geckoes as a whole (if they are a natural group) supports this hypothesis. Notably, all occur on the margins of areas with a long continental history. The relatively large size of most species and their nocturnal, ground-dwelling habit set them apart ecologically both from the active diurnal lizards and the smaller, agile geckoes of the regions they inhabit.

Interestingly enough, the second foothill endemic, *Tropiocolotes persicus* also has its nearest allies in West Pakistan (Balūchistān, Sind, and Rajasthān) and in extreme south-eastern Iran. As mentioned above, the group of small geckoes variously assigned to the genera *Tropiocolotes*, *Alsophylax*, and *Microgecko* are discontinuously distributed along the margins of the Iranian Plateau.

A third narrowly distributed species, *Phyllodactylus elisae*, also a relictual species, should perhaps be considered here, although it is also found on the Mesopotamian Plain (in the upper extent). According to Dixon (personal communication) this species is not closely related to *P. europaeus*, which is a relictual species of the Mediterranean primarily confined to islands. These two species are the only palearctic members of the genus, and *P. elisae* is more closely related to the American species than to those of Africa, Madagascar, or Australia.

Khūzistān Plain

Two species (9 per cent), *Ceramodactylus affinis* and *Acanthodactylus fraseri* are the only Iranian lizards which are known as endemics from the Khūzistān Plain (here including the western portion of the Iranian coastal plain of the Persian Gulf). Both are Saharo-Sindian derivatives. Two other Saharo-Sindian derivatives of limited distribution should also be included as endemic members of this faunal assemblage, although one (*Uromastyx loricatus*) also occurs in the foothills (only in alluvium-filled valleys) and the other (*Uromastyx microlepis*) is found along the Arabian coast of the Persian Gulf. *Acanthodactylus fraseri* is probably most closely related to other North Arabian Desert species in Syria, Jordan, Iraq, and Arabia, while *Ceramodactylus affinis* is scarcely differentiated from the more widely distributed *C. doriae*. *Uromastyx loricatus* has its nearest relative in *U. asmussi* of the eastern gulf region, and *U. microlepis* is a close ally of *U. aegyptius*. It is likely that the Khūzistān Plain became separated to a certain extent (at least ecologically) from the Mesopotamian Plain and northern Arabia at some period (or periods) of changing position and/or extent of the Persian Gulf, just as it appears to be separated at present from the coastal region east of Bandar-i-Lingeh. The valley of the Tigris, with its marshes in the lower reaches, may form a barrier of consequence to some forms at the present time. Caution is, however, necessary in assuming too readily any major change in the extent of the Persian Gulf within relatively recent times.

The Iranian faunal element

Some forty-three Iranian lizards, 46 per cent of the total Iranian lizard fauna, have a distribution largely confined to the Iranian Plateau in the broad sense. These species have been termed in this study the "Iranian" element. Other students of biogeography in South-west Asia have used the term "Irano-Turanian" for the Iranian Plateau species, and have included the Aralo-Caspian species as well. Still others have used "Eremian" to refer even more broadly to the fauna of the entire palearctic desert region. Neither of these two terms, however, has significant application to the lizard fauna.

Only three species, *Phrynocephalus helioscopus*, *Teratoscincus scincus*, and *Eremias velox* could legitimately be termed Irano-Turanian, and all seem to be subspecifically distinct in the two regions.

Eremias guttulata and *Varanus griseus* are the only species which could be termed Eremian, and here, too, there are populational differences.

Iranian elements constitute 55·5 per cent of the lizard fauna of the Central Plateau, 64 per cent of the Sīstān Basin fauna, 38·5 per cent of the Rezā'īyeh Basin fauna, 16·6 per cent of the Mughān Steppe fauna, 14·3 per cent of the Caspian coast fauna, 4·5 per cent of the Khūzistān Plain fauna, 42·4 per cent of the Balūchistān and Makrān fauna, 21·7 per cent of the Türkmen Steppe fauna, 38·5 per cent of the Zagros Mountains fauna, 17·6 per cent of the fauna of the western foothills of the Zagros, 20 per cent of the Alburz Mountains fauna, and 25 per cent of the fauna of the Kopet Dāgh.

With regard to the relationship of the Aralo-Caspian fauna to the Iranian element correlation at the generic level is particularly noteworthy. Only *Crossobamon* is not represented in the Iranian element.

A number of South-west Asian genera seem to be predominantly distributed on the Iranian Plateau: *Agama*, *Phrynocephalus*, *Agamura*, South-west Asian species of *Cyrtodactylus*, *Teratoscincus*, *Eremias*, *Ophiomorus*. It is not too unreasonable a speculation to propose the Iranian Plateau as the centre of dispersal for these groups. It is quite possible that other groups, now distributed in the Saharo-Sindian region, also had their origins on the Iranian Plateau.

On the basis of the foregoing discussion, speculation is possible regarding the Central Plateau and similar inland basins as a source of faunal origins. Surrounded by high mountains, such basins are protected from faunal invasion to a considerable extent, the only species capable of entering such regions being those with the greatest range of ecological tolerance.

Inland basins of this type in subtropical latitudes are also protected from the drastic climatic changes that affect less sheltered regions. Thus, in a region like the Central Plateau climatic change is less likely to lead to extinction or migration of an entire lizard fauna than to create local environmental situations in which isolation results in speciation.

With general lowering of temperatures, species distributed to the north of such basins are unable to move south across the elevational and temperature gradient of the mountains bordering the elevated basin on the north. Similarly, the plateau species find a barrier to their southward migration; this is of less significance for plateau species, however, since those whose ecological tolerance enables them to negotiate the southern passes are able to move to lower elevations south of the plateau. Further, the lowering of temperature is likely to be less severe in the basins than on the mountains.

As temperatures rise and aridity increases, plateau-forms again move off the interior plateau to lower elevations, but this time to the north. They also could be expected to move into the higher elevations of the internal mountain ranges, populations thus becoming discontinuously distributed. The rock-dwelling species of *Agama* may be representative of the results of just such climatic fluctuation, with certain forms distributed to the north, e.g. *A. caucasica* and *A. erythrogastra*, while *A. nupta* and *A. melanura* border the plateau on the south. The internal mountains are held by *A. microlepis*.

Species distributed immediately to the north of the Central Plateau, particularly along the outer mountain flanks, may move to higher elevations with rising temperatures, and ultimately on to the plateau, but the net faunal movement will be to the north, off the plateau, due to the greater number of reptilian forms in the warmer regions. As for the forms to the south of the plateau, again a tendency to move north and to higher elevations, hence on to the plateau, would be expected. However, such species, adapted to a maritime environment, would face the problem of moving into the more rigorous conditions of a continental climate.

In the case of the lizard faunas, movement either off or on to the plateau must (at least for many species) presuppose the existence of suitable local environments through the passes. For example, temperature conditions may prove less of a barrier to lizards native to the sandy Aralo-Caspian steppes than the terrain itself—rocky, precipitous scarps. It would appear more likely that species on the Central Plateau, with its diversified conditions of terrain, would at certain times find suitable passes to the lower elevations than the reverse.

In summary then, the plateau is expected to be a centre of evolution, the fauna being pre-adapted to move off the plateau as the climate fluctuates, to the south with general lowering of temperatures, to the north with elevation of temperature. At the same time, the plateau remains relatively sheltered, both from faunal invasion and from the extremes of climatic change. If remnants of an older plateau fauna are to be found, they must be sought on the periphery of the plateau, in the surrounding mountains (remnants of a cooler, moister period) and in the peripheral surrounding lowlands. In the isolated higher elevations of the interior mountain ranges, and in the low, hot interior basins one would expect to find isolated populations undergoing speciation.

In this regard, it is interesting that the known endemic species have been found in the regions peripheral to the Central Plateau. This picture of endemism is however undoubtedly biased by the fact that far less time has been spent by collectors in the interior mountains and basins of the plateau than in the more habitable areas on the plateau margins. The Iranian faunal element is visualized here as largely autochthonous to the Iranian Plateau.

The Aralo-Caspian faunal element

In so far as the lizards are concerned, the Aralo-Caspian faunal element seems to be derived, at least at the generic level, from the Iranian element. At the species level the lizard fauna of the Aralo-Caspian desert is at present quite distinct from that of the Iranian Plateau, with the genera of this area being nearly all represented by an even greater number and variety of forms on the Iranian Plateau. But as well, there are in this Aralo-Caspian fauna Eurosiberian elements, such as *Lacerta vivipara* and *L. agilis*, which do not enter Iran.

This element actually enters Iran only in the areas of physical extension of the Türkmen Steppe within the Iranian political boundaries. Only 8·3 per cent of the Central Plateau fauna is composed of Aralo-Caspian elements, while even in the low-lying Sīstān Basin they represent only an estimated 8 per cent of the lizard fauna. In the poorly known Kopet Dāgh 16·7 per cent of the lizard species are Aralo-Caspian forms. Even in the Iranian areas of the Türkmen steppe the Aralo-Caspian lizards constitute but 43·5 per cent of the total assemblage.

The Mediterranean faunal element

As pointed out by Heptner (1945) the Mediterranean element is probably a meaningless category in terms of faunal origin. This appears to be true for the lizards at least, since the Mediterranean area provides a mild climatic haven for the vestiges of a once more widely spread European fauna. Nonetheless, from the standpoint of present distributions, there does exist an assemblage of lizard species now confined to the Mediterranean region, and it is through this area that certain members of the allochthonous Iranian fauna entered.

Mediterranean lizards do not occur on the Central Plateau at present, but approximately 31 per cent of the species of the Rezā'īyeh Basin are either Mediterranean elements or biregional elements with their nearest relatives in the Mediterranean region. This is true of 50 per cent of the Mughān Steppe fauna and Caspian coast fauna, while about 25 per cent of the known Zagros mountains species have Mediterranean affinities. In the Alburz mountains 44·4 per cent and in the Kopet Dāgh 30·8 per cent of the lizards find their closest allies in the Mediterranean area. These percentages are somewhat misleading, as they represent not species classified here as Mediterranean elements, but for the most part species having their relationships with such elements. Some are biregional, while others are strictly Iranian in their present distribution.

The Oriental faunal element

This is a broader category than the others employed in this discussion, and would perhaps be inappropriate to regional considerations in other Asian areas. However, only three species, *Calotes versicolor*, *Hemidactylus flaviviridis*, and *Varanus bengalensis*, having their principal distribution in the Oriental region, enter Iran. *Hemidactylus flaviviridis* is found along the Persian Gulf and its occurrence here is due to human agency as it is in other coastal port areas in Asia and Africa. *Calotes versicolor* and *Varanus bengalensis* are the most widely distributed members of their respective genera and among the most widely ranging species in the Oriental region. They enter Iran through Balūchistān and are present only in the extreme south-east of the country.

The Saharo-Sindian faunal element

The Saharo-Sindian element is secondary in importance only to the Iranian element in consideration of the lizard fauna of Iran. Besides the species categorized here as Saharo-Sindian, a number of forms are regarded as bi-regional: *Agama agilis*, *Agama ruderata*, *Eremias guttulata*, *Eumeces schneideri*, *Mabuya aurata*, and *Varanus griseus* occurring widely on the Iranian Plateau as well as in the Saharo-Sindian regions. Regional population differences exist in these species, but have been inadequately studied.

While certain species, such as *Ceramodactylus doriae*, *Cyrtodactylus scaber*, *Hemidactylus turcicus*, *Acanthodactylus cantoris* (*sensu lato*), *Eremias brevirostris* occur both to the east and west of Iran as well as along the Iranian coast of the Persian Gulf, others are found only to the west or to the east. *Uromastyx loricatus*, *U. microlepis*, *Ceramodactylus affinis*, *Acanthodactylus cantoris schmidti*, *A. fraseri*, and *Scincus conirostris* apparently are encountered not much further east than Bushire, while *Uromastyx asmussi*, *Acanthodacylus cantoris blanfordi*, *A. micropholis*, and *Ophiomorus blanfordi* find their western limit at Bandar-i-Lingeh.

In so far as it has been investigated, the Persian Gulf coast of Arabia has its affinities with the western Saharo-Sindian region rather than with Balūchistān and Sind. There large numbers of Saharo-Sindian species found in North Africa and the North Arabian Desert which do not extend as far east as Iran, while several North-west Indian and West Pakistan lizards stop short of the eastern border of Iran. In short, the Saharo-Sindian element is relatively homogeneous at the generic level, but at the species level can be partitioned at least into eastern and western components, even within the borders of Iran. This is due in large part to two factors: the changes in position and extent of the Persian Gulf relative to the associated landforms, and the influence of the monsoon in the area east of Iran, adding some summer precipitation to the pattern of winter rains experienced by the western part of the Saharo-Sindian desert.

Except for those forms having a biregional distribution, the influence of the Saharo-Sindian element is little felt in the interior of Iran, even in the low Sīstān Basin. On the Khūzistān Plain, however, 82 per cent of the lizard species are either Saharo-Sindian or biregional elements, while in Balūchistān and Makrān these elements make up approximately 45 per cent of the fauna. In the western foothills of the Zagros mountains 70·6 per cent of the species are Saharo-Sindian or biregional.

In his discussion of the desert and steppe fauna of the Palearctic region, Hepter (1945), on the basis of his studies of the mammalian fauna, felt that five independent centres of origin could be distinguished: Sahara; South-west Asia (Iran and Afghanistan); Tūrān; Kazakhstān; and Mongolia. He, too, regarded the nature of the terrain as important, and felt that each of the centres had developed a fauna characteristic of the prevalent soil type, for example, 'plain deserts with compact soil' in Mongolia and Kazakhstān, sand deserts in Tūrān, 'upland deserts' in Iran and Afghanistan.

Faunal connexions with Europe

In the absence of a fossil record of any extent, past faunal connexions are largely conjectural. Present distributions indicate that there has been a faunal exchange between Iran and Europe through the Mediterranean area. Of particular note with regard to the lizards is the fact that, with the exception of *Anguis fragilis*, no Eurosiberian elements exist in Iran. This is in considerable contrast to certain other groups such as the mammals, where such forms as *Erinaceus europaeus* (hedgehog), *Talpa europaea* (mole), *Canis lupus* (wolf), *Vulpes vulpes* (fox), *Ursus arctis* (bear), *Martes foina* (marten), *Meles meles* (badger), *Lutra lutra* (otter), *Felis lynx* (lynx), *Sus scrofa* (pig), *Lepus europaeus* (hare), and *Castor fiber* (beaver) are known from Iran (several of these are subspecifically distinct in South-west Asia, however). Among the amphibia such forms as *Bufo viridis* (toad), *Hyla arborea* (tree frog), *Rana ridibunda* (frog) and *Triturus cristatus* (crested newt) are important faunal elements. *Coronella austriaca*, *Elaphe dione*, *Natrix natrix* and *Agkistrodon halys* among the snakes represent this faunal element.

There is also no indication of faunal exchange with Europe through Iran in the lizard fauna of South-east Asia, with the possible exception of the genera *Ophisops* and *Ophisaurus*. The genus *Agama* is recorded from the Eocene of Europe, however, and *Varanus* is known from the Miocene to the Pleistocene. Thus there appears to have been at least periodic faunal connexion of Europe with South-west Asia during the Tertiary either through Turkey or via Transcaucasia.

It is perhaps worth remarking that with the exception of *Tarentola* and *Chamaeleon*, which occur in Europe along the margin of the Mediterranean Sea, all of the lizard genera found in Europe are represented in Iran.

Faunal connexions with Central Asia

Iran has been connected with Central Asia continuously since the Oligocene, and at least intermittently during prior periods. The ecological relationships between the two areas have certainly differed from their present state, probably throughout much of the past. During much of the Tertiary, the climate was probably warmer than at present in Central Asia and likely more uniform between the two areas. The present contrast is a result of climatic events during the Pleistocene and later, and the Tertiary orogeny which resulted in the present elevation of the Kopet Dāgh, Hindu Kush, and Himalayas. At times the faunal exchange was undoubtedly greater than at present, but with the uplifting of the Iranian Plateau, the net faunal movement has been increasingly from the plateau to Central Asia (or is so postulated for the reasons stated above in the discussion of the Iranian faunal element).

Faunal connexions with the Oriental region

The lizards common to Iran and to Indian and other southern Asian areas, even at the generic level, occur primarily in the north-western desert of the Oriental region. The following genera occur both on the Iranian Plateau and in the Asian tropics: *Cyrtodactylus*, *Hemidactylus*, *Mabuya*, *Eumeces*, *Ophisops*, *Ophisaurus*, and *Varanus*. Of these, the South-west Asian species of *Cyrtodactylus* belong to a distinct species group which appears to have no tropical representatives. This genus is in serious need of careful revision. *Hemidactylus*, *Mabuya*, and *Eumeces* are pan-tropical genera having a few representatives in various subtropical areas of the world, while *Ophisops* and *Ophisaurus* have discontinuous distributions through eastern Europe and South-west Asia, each having two species entering the tropics. *Varanus* is now a genus of the Old World tropics, having a single species, *V. griseus*, in the intervening desert areas of South-west Asia. In the Tertiary, however, it was present in Europe, and its near relatives date back to the Cretaceous of North America. It has clearly retreated to its present range as a result of climatic change.

The distribution of the genus *Ophisaurus* is particularly interesting, for it has a living species in the southern and eastern United States (south to Veracruz, Mexico), and is known from the Oligocene to Miocene of Europe. Hence its present discontinuous distribution is the remnant of a Tertiary Holarctic distribution.

Faunal connexions with Africa

S. Bodenheimer (1938) listed several species of North African animals, including mammals, birds, beetles, butterflies, orthopterans and hemipterans which he considered the remnants of an Irano-Turanian fauna. No reptiles are included in this list however, and as regards the lizard fauna any present relationship of Iran with the North African desert is not between the Iranian Plateau and North Africa, but involves only the Khūzistān Plain and the low coastal areas of the Persian Gulf. There are a few widely distributed biregional species common to North Africa and the Iranian Plateau, but as these are more or less continuously distributed, they can scarcely be regarded as representing a relictual Iranian element in North Africa.

From his consideration of the several animal groups studied Bodenheimer draws the following conclusions:

A small, but significant relict fauna is discontinuously distributed over North Africa in such enclaves as the Hoggar and Sinai mountains. Its affinities are with the present fauna of the steppes and high plateaus of South-west and Central Asia, i.e. Irano-Turanian. Considerable remnants of this fauna are met also in all the Mediterranean islands from Cypress to Sardinia and in the steppes of Spain. It appears to represent a once continuously distributed steppe fauna.

While the present composition of the known lizard fauna contributes nothing to this hypothesis, on the other hand it offers nothing contradictory. As is apparent by comparing distribution patterns of different animal groups, different ecological factors determine distribution from group to group; hence historical events have affected lizards in a way different from that affecting mammals, birds, insects, or even other reptilian groups. We see evidences that these varying responses to historico-ecological events exist among lower taxonomic categories as well.

It is to be expected that studies of the systematic relationships between species of Saharo-Sindian lizards and Iranian species will provide evidence in regard to Bodenheimer's speculations.

The present geographic contact of South-west Asia with Africa is through Sinai. In an earlier paper Bodenheimer (1937*a*) analysed 756 species of animals known from Sinai. Of these, he regarded 13·9 per cent as Irano-Turanian faunal elements. He regarded only one snake, *Eirenis coronella*, and no lizard as Irano-Turanian. This snake occurs primarily in the higher elevations of the Sinai Massif, which Bodenheimer regards as an Irano-Turanian enclave. The Saharo-Sindian element is dominant in the northern part of the peninsula, the Tih-territory, and in the dunes and southern lowlands. This is certainly true of the lizards as well as the other groups he examined. Mediterranean elements occur on the northern dunes, in parts of north-eastern Sinai, and in the higher elevations of the Sinai Massif, being penetrants in the north, relicts in the south. This applies to the lizards, also, and Bodenheimer lists the following species from the Sinai Massif: *Agama stellio*, *Chamaeleon chamaeleon*, *Abelpharus kitaibeli*, *Chalcides ocellata*, and *Ophisops elegans*.

Bodenheimer's interpretation is that one wave of relatively recent faunal elements replaced another in Sinai, the once dominant Paleotropical fauna of the savannah being replaced by a steppe Irano-Turanian fauna contemporaneously with a period of strong Mediterranean penetration or partial dominance, until the Saharo-Sindian fauna became the most prominent element. Relics of these older faunas remain in the south and in the higher elevations.

A consideration of the fauna of Palestine (Israel and western Jordan) is interesting from the standpoint of past faunal relationships between Africa and South-west Asia. This region is one of varied environmental situations and is subject to the maritime climatic influence of the Mediterranean Sea. There probably has been at least intermittent contact between Africa and Eurasian regions through this area even during periods of greater extent of the Tethys Sea. For these reasons certain parts of Palestine might be expected to serve as refuge areas for remnants of older faunas.

Bodenheimer (1937*b*) has analysed the entire known fauna of Palestine, while Haas (1952) has considered the origins of the herpetofauna. As in Sinai, there were no tropical species of lizards still extant in Palestine. From what we have seen so far, it would appear that lizards survive less well as relicts in South-west Asia than do some other animal groups. For this reason lists of lizards at the species level of differentiation may be less useful than other groups in revealing historical faunal affinities. But once their systematic relationships are adequately known, however, they may nevertheless provide important clues. The presence of the Mediterranean species of chamaeleon, *Chamaeleon chamaeleon*, in Israel–Jordan is particularly interesting, for this is the single represenative in the Palearctic region of this now tropical family. Unlike *Varanus griseus*, it is not widely distributed but is confined to the Mediterranean margins.

The distribution of *Ptyodactylus hasselguisti* should be carefully studied in relation to past faunal history. Said to occupy a wide latitude of environmental situations, and apparently common in the countries of the eastern Mediterranean, it nonetheless has been recorded only once from Iran, in the western Zagros. It is not certain whether or not this distribution in South-west Asia is continuous. It would be interesting to know whether its presence in the arid region of the Palearctic is relictual, or represents a recent incursion. Remains of another species (of similar size, but larger teeth) occur in the Acheulean of the Judaean Desert (Haas, 1952).

Among other reptilian groups of tropical affinity, the disjunct distribution of the genus *Trionyx* has already been mentioned. *Crocodilus* existed up to the turn of the century in the Kabara swamps south of Haifa (Haas, 1952), and has survived in isolated areas of North Africa as well. As Haas points out, such aquatic animals are less subject to changing conditions of humidity than are the terrestrial groups. Two snakes are similarly noteworthy. *Micrelaps muelleri*, a nocturnal opisthoglyphous colubrid, is found at relatively high elevations with 550 mm of annual rainfall. Its only congener is in Somalia. *Atractaspis*, a tropical African genus of viperids, has a single South-west Asian member, *Atractaspis engaddensis*, known only from the En Geddi oasis in Jordan. Another species is known from southern Arabia.

Bodenheimer considers 5 per cent of the 2,852 species of the fauna of Israel–Jordan as tropical. He concludes that the effect of the glaciopluvial period was minimal on the fauna, while the most important recent event has been a "neo-Sudanian" faunal eruption on a broad front of the Saharo-Sindian region, and a subsequent penetration of this element into the southern Mediterranean area.

Faunal connexions with Arabia

The Arabian Peninsula has a large lizard fauna, many species of which are endemic. Unfortunately, this fauna is very incompletely known, and details of distribution within Arabia poorly worked out. Further collecting, particularly in the higher elevations along the coasts, will undoubtedly increase the list of species known, and will certainly increase the value of our zoogeographic speculations. In view of its long stability as a continental area and its previous connexion with Africa along its southern Red Sea coast, a study of its faunal relations with other regions should prove most enlightening.

At present, the faunal connexion of Iran with the Arabian Peninsula is through the Mesopotamian Plain at the head of the Persian Gulf. Even this contact is limited by the presence of the Tigris river. The only area of Iran having a close affinity with Arabia is the Khūzistān Plain and the associated western coastal plain of the Persian Gulf. The species shared by Iran and Arabia are either Saharo-Sindian elements, or wide-ranging biregional forms, such as *Eremias guttualata* and *Varanus griseus*.

According to Misonne (1959), the distribution of a few mammalian species indicates faunal contact of the two areas across the Strait of Hurmuz, at least three species having entered Iran by this route.

The lizard fauna provides no evidence of extensive faunal contact in the vicinity of the Strait of Hurmuz or to the east. This is somewhat surprising, in that the present position of the Persian Gulf is thought to be relatively recent, and even since its formation eustatic lowering of sea level during the Pleistocene must have established dry land contact between Iran and Arabia. Nonetheless, evidence for extensive ecological continuity across this contact is lacking. As stated previously, a faunal break for Saharo-Sindian elements is indicated on the Iranian coast of the Persian Gulf between Bushire and Bandar-i-Lingeh, and the lizard fauna of the Arabian coast is related to the Iranian fauna west of this break.

Three lizard species may have some bearing on the question of an eastern faunal contact, however; *Phrynocephalus maculatus*, an Iranian element not crossing the Zagros mountains and the western foothill belt, and not recorded from the Khūzistān Plain, is represented by a subspecies in Arabia. This species and the closely related *P. arabicus* are the only representatives of this Iranian Plateau genus in Arabia or westward. *P. maculatus* is a widely distributed sand-living form, which ranges down from the Iranian Plateau into Balūchistān on the Iranian side of the Persian Gulf.

Less certain is the distribution of *Eumeces taeniolatus*, an Iranian element distributed primarily in the eastern part of the Iranian Plateau. It has twice been recorded from Arabia, once from El Kubar in south-western Arabia (Taylor, 1935) and by Haas (1957) from twenty-three miles north of Hail, Saudi Arabia. Haas also cites a British Museum specimen from Muscat. This species does occur in the Saharo-Sindian region in lowland West Pakistan (Minton, 1962). Not having seen the Arabian material, I cannot verify that the various records refer to the same species.

Thirdly, the swimming skink, *Scincus mitranus*, an Arabian form, was reported from the Hab river region of West Pakistan by Murray (1884*a*), who recorded seven specimens (as *S. arenaria* Murray). As remarked earlier this species has never been taken again outside of Arabia, and its occurrence in West Pakistan is open to serious doubt. Indeed, this single record is the only report of this genus on the northern side of the Persian Gulf coast of Bushire.

Faunal affinities between the African and Asian tropics

There are no lizard species, apart from those distributed through human intervention, common to both the African and Asian tropics. A number of genera are found in both regions, however. These include the following: *Cnemaspis*, *Phyllodactylus*, *Hemidactylus*, *Phelsuma*, *Agama*, *Chamaeleon*, *Mabuya*, *Lygosoma*, *Leiolopisma*, *Ablepharus*, *Riopa*, *Eumeces*, and *Varanus*.

In several of these genera serious systematic problems remain, and careful study may reduce the degree of apparent correspondence at the generic level between the African and Asian tropics. Of the above genera, *Hemidactylus*, *Agama*, *Mabuya*, *Abelpharus*, *Eumeces*, and *Varanus* are now represented in South-west Asia in the region between the African and Asian tropics. *Agama* has a single, specialized species, *A. minor*, entering the Indian tropics, and the several closely related African tropical species probably represent a single radiation of savannah and forest forms. The genus appears to have had its major evolutionary centre on the Iranian Plateau. It is interesting that the Agamidae are represented in tropical Africa by this single, little-diversified genus.

With the exception of *Chamaeleon*, which has a single Mediterranean species, none of the genera show a discontinuous distribution in Asia between the two tropical areas, thus there are no relict populations of tropical genera existing on the Iranian Plateau. Most of the tropical genera which do occur in South-west Asia are represented by one or more widely distributed desert-adapted species, such as *Eumeces schneideri*, *Mabuya aurata* (and the related *M. vittata* and *M. dissimilis* to the west and east respectively) and *Varanus griseus*. *Mabuya* and *Eumeces* occur in the New World tropics, the latter having a few Neoarctic species as well. *Varanus* is known from the Tertiary of Europe, and closely related fossil genera are recorded from the Cretaceous of North America.

The relationships of the genus *Phyllodactylus* as presently constituted are being studied by James Dixon. The South-west Asian relict *Phyllodactylus elisae* appears to be related to the New World species rather than to *P. europaeus* or to the African, Malagasy, and Australian species of the nominal genus (Dixon, personal communication).

Cnemaspis is about equally represented in Africa and Asia. *Phelsuma* has a single Asian species, *P. andamanense*, found on the Andaman Islands. The other species live on Madagascar, the Comoro, Seychelles, and Mascarens Islands, but not in Africa. *Chamaeleon* is a primarily Malagasy and Africa genus, although *C. chamaeleon* is found on the eastern shores of the Mediterranean. A single species, *C. zeylanicus*, is known from Ceylon. *Riopa* has a dozen African species and an equal number of Asian members.

It is particularly interesting that most of the lizard genera residing in both the African and Asian tropics (some of them in the New World and Australia as well), but not represented in the intervening areas, nor known from the fossil record, are skinks and geckoes. The majority of these genera have island species (indeed, are often the most important elements of island lizard faunas). They represent the most successful trans-oceanic travellers among the lizards, and are the least dependent upon continuous ecological connexions for their distribution.

The explanation of faunal similarities between Africa and Asia (also Australia and the New World) through the development of land bridges and continental drift is an old story. Others would reject the theory of drift, and derive these faunal similarities solely through past continuous distribution of tropical and subtropical climatic conditions in the Holarctic Realm. Present distributions of lizards in South-west Asia contribute little to any of these hypotheses. The majority of pantropical lizard genera are represented at present in the arid regions between the tropics; hence there is faunal contact at the generic level even today. Those not represented in South-west Asia are genera which perhaps require no faunal contact for their distribution.

As we deduce from the fossil evidence and differences in present distribution, evolution proceeds neither at the same rate nor contemporaneously in all animal groups. Some modern lizard genera are also known as fossils, and reach back almost unaltered to the early Tertiary. For this reason, analogies cannot be drawn with the history of mammalian distribution.

SUMMARY

Iran comprises the most geographically complex area of South-west Asia, and is centrally located with respect to the mingling of elements of the North African, southern Asian, Central Asian, and European herpetofaunas. There are found in Iran five species of turtles in four genera and ninety-three species of lizards in thirty-two genera. A single amphisbaenian occurs within the country.

Apart from those faunal elements which it shares with other regions, South-west Asia has two major distributional components to its lizard fauna. The Iranian faunal element is viewed here as autochthonous to the Iranian Plateau, and occupies primarily the elevated regions extending from the Anatolian highlands, across the southern border of the U.S.S.R. through Afghanistan, and extending south, bordered on the west by the Zagros mountains, to the narrow coastal plain of the Persian Gulf, and east through upland Balūchistān. The Saharo-Sindian faunal element occupies the low desert areas from North Africa to north-western India. It is seen here as allochthonous to Iran, its origins probably lying in the low elevations to the south. Origins and subdivisions of this element await study of conditions in South-west Asia as a whole, and are not elaborated here. Although there is penetration of both areas by species characteristic of the other, few species are broadly distributed in both regions.

Entering South-west Asia, on the north-west are elements with European affinities, primarily those having a Mediterranean distribution. Aralo-Caspian desert species penetrate the region from the north, and a few Oriental species are found in the south-east.

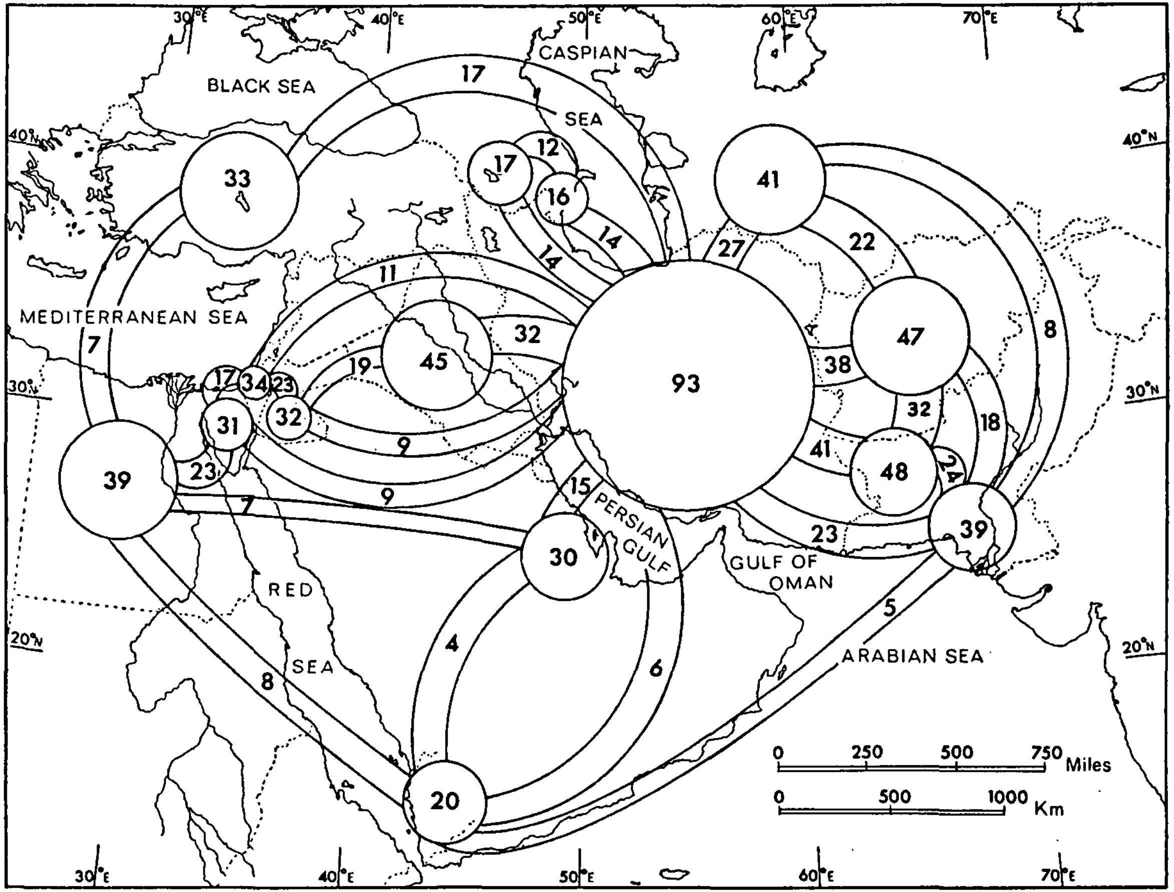


Fig. 95. Correlation of the Iranian lizard fauna at the species level with the faunas of countries elsewhere in South-west Asia. Figures within circles represent numbers of species known for the countries; figures in connecting arcs represent numbers of species common to two countries.

The affinities of the lizard fauna of South-west Asia with the faunas of adjacent regions are primarily at the generic level.

In this paper the lizard fauna of thirteen physiographic areas of Iran is examined in detail.

TABLE 8. *Summary of distribution of faunal elements in Iran*

Figures represent percent of total fauna for each physiographic region represented by each faunal element. Numbers in parentheses represent total species in fauna.

	Iranian	Saharo-Sindian	Aralo-Caspian	Mediter-ranean	Oriental	Biregional or doubtful
Central Plateau (36)	55·5	8·3	8·3	0	0	27·7
Sīstān Basin (25)	64·0	8·0	8·0	0	0	20·0
Rezā'īyeh Basin (13)	38·5	0	0	7·7	0	53·8
Mughān Steppe (6)	16·6	0	16·6	16·6	0	50·0
Caspian Coast (7)	14·3	0	0	28·6	0	57·1
Khūzistān Plain (22)	4·5	50·0	0	0	4·5	40·9
Balūchistān and Makrān Coast (33)	42·4	30·3	0	0	9·1	18·2
Türkmen Steppe (23)	21·7	0	43·5	4·3	0	30·5
Zagros Mountains (13)	38·5	7·7	0	15·4	0	38·5
Western Zagros Foothills (17)	17·6	41·2	0	0	0	41·2
Alburz Mountains (10)	20·0	0	0	20·0	0	60·0
Kopet Dāgh (12)	25·0	0	16·7	16·7	0	41·7

The Central Plateau, which has apparently existed as a terrestrial environment continuously since the Oligocene or Miocene. Encircled by developing mountain chains, the plateau has been less subject to climatic change throughout the Quaternary and much of the Tertiary than less protected continental areas. It is postulated here that such enclosed basins, containing a diversity of habitats, may be centres of origin and dispersal for many of the Asian faunal elements.

The lizard fauna of the Central Plateau is composed primarily of species belonging to the Iranian faunal element and wide-ranging biregional species (see table 8). Five patterns of distribution within the plateau are discussed.

The Sīstān Basin. The lizard fauna of this basin is derived from the Iranian faunal element and has its greatest affinities with the Central Plateau (see fig. 92).

The Rezā'īyeh [Urumīyeh] Basin. The faunal affinities are Mediterranean and Transcaucasian in the genus *Lacerta*, Transcaucasian and Anatolian in the fauna of the mountains bordering the basin, the remainder of the species being plateau-derived. Endemics account for 15 per cent of the species. The majority of the species are biregional, or belong to the Iranian faunal element (table 8).

The Caspian Coast. The emergence of this low-lying coastal zone is a post-Pleistocene phenomenon. Consequently, its small lizard fauna contains no endemic species, and has faunal relationships with Mediterranean Europe and Transcaucasia.

The Khūzistān Plain and Persian Gulf Coast. The majority of lizard species in this fauna belong to the Saharo-Sindian element, and the fauna has its greatest relationships with Mesopotamian Iraq and gulf coastal Arabia. There is a distinct break in the continuity of Saharo-Sindian species composition between Bushire and Bandar-i-Lingeh on the Persian Gulf coast. In so far as Iran is concerned, western component of this element occurs in Khūzistān, and an eastern component in Balūchistān.

Iranian Balūchistān and Makrān Coast. Almost half of the lizard species of Iranian Balūchistān belong to the Iranian faunal element, Saharo-Sindian species forming the bulk of the remainder (table 8). It is in this region that a few representatives of the Oriental element enter Iran. Three species, 9 per cent of the total fauna, are endemic to this region. If south-eastern Iran is considered more broadly, however, including part of the Central Plateau and the Sīstān Basin, we find twelve species endemic to a region approximately corresponding to climatic type III_{3a} of Walter and Lieth (see figs. 93 and 94).

Türkmen Steppe. In extreme north-eastern Iran the lizard fauna of the Tūrān lowlands of Central Asia extends into Iran. This Aralo-Caspian element is closely related to the Iranian element at the generic level, and the two elements have been considered a single faunal association, the Irano-Turanian, by most previous authors. The Central Plateau and the Tūrān lowland have had at least intermittent contact since the Eocene. It is proposed in this paper that the net faunal movement has been from the Iranian Plateau into the Tūrān lowland.

Mughān Steppe. This fauna, having species of the Mediterranean, Aralo-Caspian, and Iranian elements, has without doubt assembled since the recent regression of the Caspian Sea.

Zagros Mountains. Because of their N.W.–S.E. strike, these mountains form a distribution corridor enabling a few northern species to penetrate southward. The lizard fauna is poorly known, but does contain relictual endemics. Wide-ranging, biregional species cross the passes, and species with Mediterranean affinities are present.

Western Foothills of the Zagros Mountains. The great majority of lizards belong to the Saharo-Sindian faunal element and biregional species, although the influence of the Iranian element is also felt. In contrast with upland Balūchistān, however, the fauna of the Central Plateau is conspicuously absent, due to the intervening Zagros ranges. Relictual endemic species also occur in this area, which lies at the extreme south-western margin of the Iranian Plateau (*sensu lato*).

Alburz Mountains. Since the post-Pleistocene recession of snowline to higher elevations, the lizard fauna of the Central Plateau has invaded the dry southern slopes, while forest species with Mediterranean affinities have entered the lush vegetation on the northern flanks of the range.

Kopet Dāgh. The lizard fauna of this elevated region is little known. Some lizard species may have found a Pleistocene refuge in these drier mountains of intermediate elevation, re-invading the Caspian lowlands as the Caspian Sea receded. Iranian elements enter the ranges from the south, while Aralo-Caspian species have entered via the valley of the Atrak river.

Present distributions indicate that there has been a faunal exchange between Iran and Europe through the Mediterranean area. Strictly Eurosiberian species are notably lacking in the Iranian lizard fauna, in contrast to certain other animal groups. It is here suggested that with the uplifting of the Iranian Plateau, the net faunal movement has been from the plateau towards Central Asia. The lizards common to Iran and to India and other southern Asian areas, even at the generic level, occur primarily in the north-western desert of the Oriental region, and communication is through Balūchistān. In the lizard fauna, relationships with Africa are largely in the Saharo-Sindian element and wide-ranging biregional species. At present, the faunal connexion of Iran with the Arabian Peninsula is through the Mesopotamian Plain at the head of the Persian Gulf. Despite evidence of land connexion across the gulf during the Pleistocene, the present distribution of lizards does not indicate extensive faunal exchange between the two areas via this route.

Little ecological information is available for Iranian lizards, other than that contributed in an earlier paper (Anderson, 1963). The physical factors of the environment are briefly considered with regard to their possible effects on lizard distribution. Since there is little climatic data for South-west Asia directly applicable to microhabitats of lizards, only the broadest speculations and correlations (see table 6) can be made in regard to temperature, rainfall, humidity, light, and air movement. Examination of known distributions and gross morphological adaptation, as well as personal observation, reveals that a large number of South-west Asian lizards are rather narrowly restricted to specific types of environment, and it is suggested that this factor plays an important role in determining distribution.