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STUDIES IN THE FLORA OF ARABIA XI*:

Some Historical and Geographical Aspects of a Principal Floristic Frontier

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ABSTRACT. Fossil evidence suggests that a proto-Sudanian Tertiary vegetation characteristic of the Arabian-Nubian Shield extended over much of central and eastern Arabia before the marine incursions and increasing aridity of the Middle-Late Miocene. Subsequent desert conditions led to the development of Saharo-Arabian vegetation and an entry of Irano-Turanian derivatives; this was followed by a selective reintroduction of Sudanian elements from the western highlands into the east along major drainage channels. The composition of the present-day flora of the Tuwayq highlands and adjacent lands suggests that the borderlands of Sudanian vegetation might be placed as far north as the 26th parallel in the central Peninsula.

INTRODUCTION

Virtually all plant geographers who have dealt with North Africa and the Middle East have recognized a latitudinal division of this greater area into two basic floristic zones: one southern and essentially semi-tropical; the other northern, extra-tropical and desertic. The boundary between them has often been placed near the Tropic of Cancer, extending over 90° of longitude from the Atlantic coast of Africa, through the Arabian Peninsula, to the northwestern corner of the Indian subcontinent.

This frontier has a real climatic basis; it marks the southern edges of the Trade Wind belt with its descending, adiabatically dried circulation—a major factor in the genesis of the Saharo-Sindian desert—and the beginning of a climate shift to tropical patterns. It lies near the summer and northernmost latitude of the intertropical convergence zone which, beginning here and to the south, brings rising air and summer or random rain patterns. Also to the south, around the Indian Ocean, the monsoon circulation strongly affects climate.

The distribution of plants in Arabia, while certainly conditioned by these climatic influences, has also been affected by long-period geological

*See p. 15 for a list of previous parts in the series.
**Aramco Box 1912, Dhahran, Saudi Arabia.

and topographical changes. These, as I will attempt to show, must be given significant, and sometimes dominant, weight in interpreting the patterns of today's vegetation.

The views expressed here about plant-geographical boundaries arise from field impressions gained over 35 years' residence in Saudi Arabia, and after travel and plant collecting in most countries and regions of the Peninsula. I want to stress, however, that they are not based on a systematic or quantitative analysis of distributions; they are working ideas to be tested more rigorously as fuller data become available.

A few of the more frequently mentioned localities are shown in Figs. 2 & 3; for others, latitude/longitude co-ordinates are given. Other localities mentioned in the text can be found in *The Times Atlas of the World.*

History of Regional Concepts and Terminology

The Arabian Peninsula, excepting a few coastal fringes, was virtually unexplored botanically until the mid-20th Century and presented a data vacuum to early regional botanists. Boissier (1867) divided Arabia arbitrarily along the Tropic of Cancer into his 'Région du Dattier' in the north and a tropical half in the south. Grisebach (1872) followed an approach based on climate and vegetation physiognomy rather than floristic analysis. He put all of the Arabian Peninsula except the southern two-thirds of the Red Sea coast and the south coastal zones around to the vicinity of Muscat in tropical territory. Blatter (1919, 1921) reverted to a line along the Tropic in dividing Arabia into two tropical and two extra-tropical quadrants. He considered his boundaries to be essentially 'natural', but they were drawn when most of Arabia was still unstudied scientifically.

Important foundations for plant-geographical studies in the Middle East were laid by Eig and Zohary, of the Jerusalem school. Eig's work (1931–1932) was focused on Palestine although necessarily involving surrounding regions, while Zohary (1940, 1963, 1973) extended these analyses to the Middle East in a broad sense. By the mid-20th Century, following this work, the major floristic regions in North Africa and Southwestern Asia were generally being described along the lines shown in Fig. 1. The Arabian Peninsula proper included portions of two of these: the 'Saharo-Sindian Region' to the north and, in the south, the 'Sudano-Deccanian Region', each variously subdivided. Zohary, in his later writings (1963, 1973), revised his concept of the Saharo-Sindian region in regard to both its eastern limits and its boundaries in the Arabian Peninsula, where he attempted to take into account more recent but still scanty data. He assigned north-western India and adjacent coasts to a revised Sudanian region and discarded Eig's term 'Saharo-Sindian' in favour of 'Saharo-Arabian'.

Meher-Homji (1965) defended the earlier extension of this Saharan region into northern India on the basis of the desertic climate there and of Saharo-Sindian species proportions of 21·5% and 16·1%, respectively, in the Indus Delta and the Thar Desert. Hedge & Wendelbo (1978), describing distribution patterns in Iran, rejected Zohary's Sudanian label for some vegetation there, also preferring to treat it within the broader earlier framework of a Saharo-Sindian region. Such an extended concept

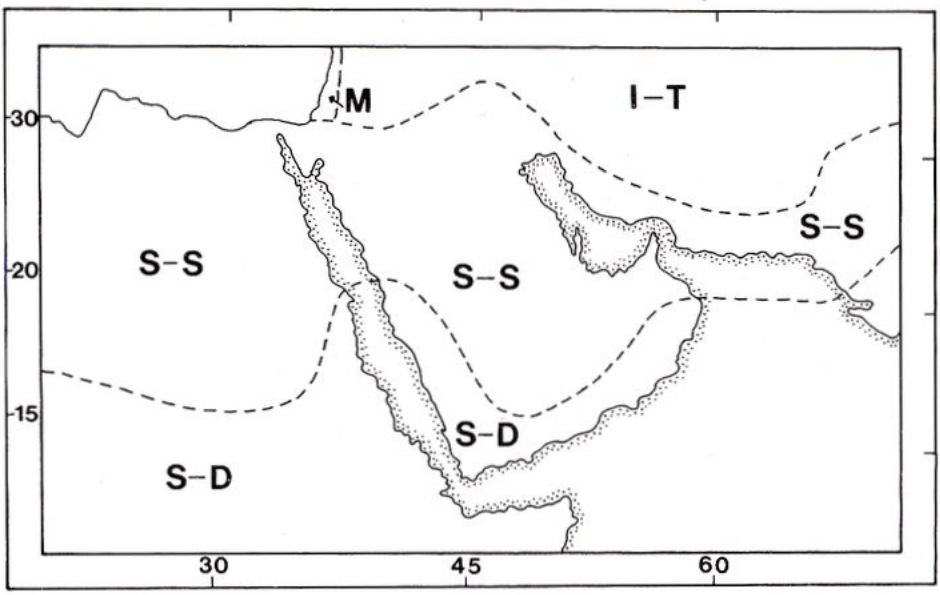

FIG. 1. Principal phytochoria of the Middle East as outlined by Guest (1966) following Eig and the earlier works of Zohary: M = Mediterranean, I-T = Irano-Turanian, S-S = Saharo-Sindian, S-D = Sudano-Deccanian.

is indeed convenient for referring to this great desert biome with a more or less uniform climate, topography, and vegetation physiognomy; as so adopted it should be divided into northern and southern subregions according to local Mediterranean or Sudanian floristic tendencies. Zohary's treatment of these extra-Arabian reaches as Sudanian territory will be followed here, and thus also his term 'Saharo-Arabian'.

The Saharo-Arabian region is certainly less well defined floristically than adjacent phytochoria. It is weak in endemics at all taxonomic levels and hardly has a well-defined core of native genera with local centres of origin or diversity. In this sense it is more like a *mélange* of elements from adjacent regions, highly selected by the desert environment. Yet it does contrast with adjacent Sudanian territory by the absence of genera characteristic of subtropical Africa, particularly such dominant ones as *Acacia*. Monod (1957) clearly recognized this in making Saharo-Sindian territory in Arabia a sub-unit of his Mediterranean Region.

A major problem in comparing earlier portrayals of Sudanian frontiers in Arabia has been the confusion of physiognomic with floristic approaches to their definition. Applying ideas of 'semi-tropical highlands and 'savannah parklands', or eliminating highly arid zones, leads to a much more restricted view of what Sudanian territory in Arabia should be. This vegetation-type approach was generally followed before the work and publications of the Jerusalem school, if only because knowledge of the Arabian vegetation was of the roughest reconnaissance quality.

Floristic methods, themselves, range from strict 'numerical taxonomy', integrating distribution boundaries of all species in a region, to more subjective systems following indicator species. The first extreme is probably of limited utility, at least in the northern parts of the districts

discussed here, because of the high proportion of desert annuals in the total species list. These ephemerals tend to be poorly correlated with communities and, in transition zones, even with the wider floristic units.

The present author, following a more selective floristic approach, feels that given the persisting lack of detailed floristic analysis of much of the Peninsula, the strategy of Engler (1910) in alloting major weight to the presence of *Acacia* as an indicator of Sudanian conditions (in Zohary's sense) is useful over much of this region. *Acacia,* itself often dominant, is frequently correlated with other tropical derivatives and may be conspicuous even where high aridity has blocked the development of fuller Sudanian communities. This approach was also advocated by Zohary (1973), although his regional terminology differed fundamentally from that of Engler. For Engler, the northern limits of *Acacia* marked the boundary of a sub-tropical 'North African–Indian Desert Region' with his 'Mediterranean Region'; for Zohary (and the present author) they help delimit the northern frontier of the Sudanian Region.

Burtt (1971) questioned the definition of Zohary's Sudanian Region and pointed out that phytogeographers dealing primarily with Africa recognize a more extensive zone referred to as 'Sudano-Zambesian'. Takhtajan (1978) used the latter name while assigning the region's contact with Saharo-Arabian territory generally along Eig's and Zohary's lines. Takhtajan makes this also a major frontier between broader units, his Palaeotropical and Holarctic Kingdoms. Monod (1957) used the term 'Sudano-Angolan'; he, also, saw a more fundamental boundary here, between his 'Mediterranean' and 'Tropico-African' groups.

The Sudanian Region is often subdivided, and it is quite possible that parts of it merit recognition as separate regions in such units as Good's (1974) 'North-east African Highland and Steppe Region', including the Yemen and 'Asir of the south-western Peninsula. We are concerned here, however, only with the northern limits of the super-unit. Whatever the best names and outer boundaries for these regions may be—and such questions will be left for workers with broader experience—it is felt that there is a real floristic frontier in Arabia corresponding to concepts of Sudanian versus Saharo-Arabian (or Mediterranean) elements. Recent field observations do suggest a need for a realignment of Sudanian/Saharo-Arabian boundaries in Arabia—one that substantially increases the Sudanian area beyond that traditionally portrayed. Before discussing this, however, it will be useful to consider some of the geological and other early environmental developments that have conditioned today's plant distribution in the central and eastern Peninsula.

PALAEO-ENVIRONMENTAL FACTORS

The single most important geological factor influencing the distribution of today's Arabian flora is the division of the Peninsula into two clear-cut geological provinces: the Arabian Shield of the Hijaz highlands, and the sedimentary province bounding it to the east along a great arc trending south-east, then south, then south-west (Fig. 2). Each has provided very different conditions for plant growth and migration, and these are clearly reflected in today's vegetation.

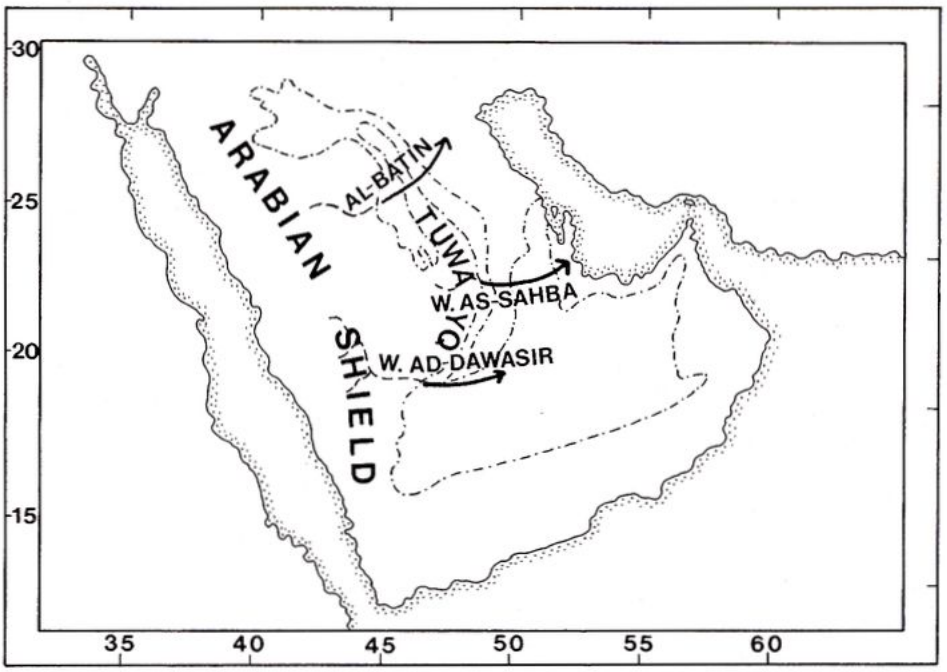

FIG. 2. Late Tertiary—early Quaternary routes for the reintroduction of Sudanian elements into central-eastern Arabia from the west.

The Shield, composed of igneous and metamorphic rocks, is essentially a highland with relatively well-drained soils. More significantly, except along the Red Sea coast it has been continually emergent and unaffected by marine incursions and marine sedimentation throughout the post-Cambrian. It is geologically identifiable with the igneous shield on the African side of the Red Sea, a body of water formed only with the rift separation of the Arabian Plate in relatively recent geological times. Plant life on both the African and Arabian parts of this unit thus developed along very similar lines, with a gradual evolution of Palaeo-African flora into units of today's Sudanian vegetation. The Shield area has thus provided a virtually uninterrupted reservoir of Sudanian species probably dominated, at least since the late Tertiary, by an Acacietum.

The sedimentary province to the east, on the other hand, developed through successive periods of deposition in a long, sometimes interrupted, series of marine transgressions from Palaeozoic times down to the present. Such rocks, rich in evaporites, led to different soil chemistry and different factors affecting soil drainage; most important, it necessarily involved a series of vegetation destructions by submergence and subsequent re-colonizations in harsher edaphic conditions.

In the broadest sense, therefore, one may visualise the long-term history of vegetation in central and eastern Arabia as a series of Sudanian floristic expansions and retreats across widening shores of a western Sudanian 'homeland' into the more hostile basins of the east.

Evidence from fossil spores in drill cores from the earlier sediments

indicates that the central and eastern Arabian flora through Mesozoic times followed generalized regional and world trends in generic composition. It is to later Tertiary and subsequent times that one must look for clues to the history of today's vegetation.

With the withdrawal of the Tethys after the early Eocene, eastern Arabia seems to have experienced mainly continental conditions interrupted by lesser marine incursions in the Miocene-Pliocene. During the middle-late Eocene and Oligocene there was presumably a spread of Palaeo-African vegetation into the east from the yet unrifted Arabian-Nubian Shield and adjacent older sediments, although later erosion left little fossil record of this development.

Fossil pollen from Miocene horizons in eastern Arabia indicate the presence then of many present-day groups such as the Cyperaceae, Gramineae, Compositae, Chenopodiaceae, and Caryophyllaceae, as well as families with tropical distributions such as the Palmae, Meliaceae-Sapotaceae, Combretaceae, Myrtaceae, and Ceratopteridaceae (Aramco, unpublished).

Other direct and indirect evidence of Neogene plant life and environments in eastern Arabia are provided by reports of fossil plants and vertebrate fauna from several sites. Whybrow & McClure (1981) report fossil mangroves in the Dam Formation (early to middle Miocene) associated with a marine incursion inland at Dawmat al-'Awdah (27°16′N 48°11′E) and a similar deposit on the eastern Gulf coast, at Jabal Barakah (24°00′N 52°20′E), probably of upper to late Miocene age. Findings at these and other sites suggest a coastal environment of broad alluvial flood plains with local swamps fed by palm-fringed streams, and with mangroves in the intertidal zone. They show no evidence for high aridity during the Arabian late Tertiary. Conditions were relatively dry, but with open savannah grasslands, shallow fresh water, and vegetation-fringed rivers and streams that flowed at least seasonally.

Hamilton, Whybrow & McClure (1978), describing an early to middle Miocene vertebrate fossil assemblage from ad-Dabtiyah, suggest it represents a contemporary fluviatile coastal plain environment. The fauna, which included turtle, fish, crocodiles, rodents, hyrax, rhinoceros, pig, giraffe and bovids, appears to be consistent with tropical savannah vegetation.

Middle Miocene marine incursions and the following development of highly arid conditions put an end to this vegetation in the zone up to 100 km from the present Gulf coast. Its general absence in most of the other lands east of the Dahna (Fig. 3) that experienced continuous continental conditions during these times is probably due to both climate changes and inhospitable edaphic conditions. *Acacia,* for example, in arid Arabia, is usually associated with alluvial soils with fairly salt-free water at phreatophytic depths. In north-eastern Arabia these conditions are generally limited to a few of the larger wadis and basins.

These wadi systems also provided channels for the migration of Sudanian vegetation, even into present Saharo-Arabian territory, during late Pliocene or early Pleistocene times. Dated lateritic deposits in the Arabian Shield and the mass transport of shield detrius across the Arabian foreland as far east as the lower Qatar Peninsula provide

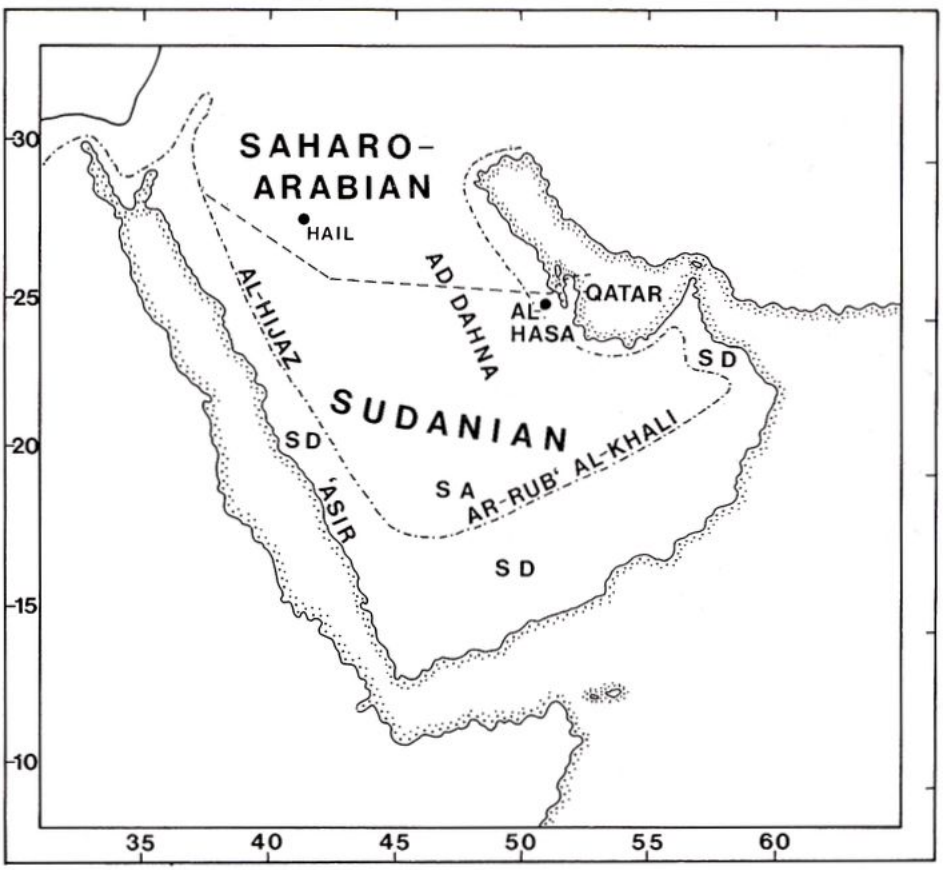

FIG. 3. The Saharo-Arabian and Sudanian floristic regions in Arabia as delimited by Zohary (1973, dash and dot line) and as proposed schematically by the author (dashed line). The symbols SA (Saharo-Arabian) and SD (Sudanian) label Zohary's regional assignments. A few of the more important localities referred to in the text are also indicated.

evidence of a highly humid period in the late Pliocene or early Pleistocene between 3·5 million and 1·2 million years B.P. (Hötzl *et al.*, 1978; Hötzl, Krämer & Maurin, 1978). At this time al-Batin in the north, Wadi as-Sahba in the middle, and Wadi ad-Dawasir in the south were in energetic flow, carrying masses of erosional materials from the western highlands (Fig. 2). The great fan-shaped deposits of cobbles and gravels radiating from the eastern debouchements of these wadis—the Dibdibah gravel plain from al-Batin in the north (Fig. 2), the gravel sheets and trains from Wadi as-Sahba east of the Summan, and the now sand-submerged deposits of Wadi ad-Dawasir—are remnants of these discharges.

These flows cut channels across the coastal lowlands to the east, and in this process the wadis apparently became avenues for migration of the central Arabian Sudanian flora across the former sea bottom. They did so not only by physically transporting seeds and supporting other vectors, but also by flushing out salts and providing favourable soils and moisture conditions. Meanwhile, growing aridity and unsuitable soils apparently prevented re-establishment of tropically-derived plants outside the in-

fluence of these channels. Saharo-Arabian plant communities developed in those broader habitats, abetted by additions of Irano-Turanian derivatives from the north or north-east.

These late Pliocene Sudanian invasions are still marked in the present flora of the al-Batin, Wadi as-Sahba, and Wadi ad-Dawasir channels and their eastern extensions. *Acacia gerrardii* moved down al-Batin, along which at an-Na'ayim (27°57′N 45°28′E) and a few other scattered locations it is still found today. Other Sudanian relicts in the Batin as far down as Hafar al-Batin or beyond include *Blepharis ciliaris, Ziziphus nummularia, Cleome amblyocarpa,* and *Ephedra foliata.*

The Wadi as-Sahba breakthrough in Tuwayq provided a more important channel for Sudanian invasion. Its alluvium accommodated penetrations of *Acacia* and other tropical derivatives not only along its main line to the east-south-east but also along several extensions to the north and south. These avenues are today marked by relict Acacias (Fig. 4), particularly along the main axis, where *A. ehrenbergiana* is found in the Sahba channel along with Sudanian associates such as *Pulicaria incisa* (*P. undulata* auct.) and *Astragalus eremophilus* almost as far east as the Jafurah sands. *Acacia tortilis* is found in the edges of the fringing higher terrain. A diversion from the main channel northward behind the western edge of the Ghawar anticline into Jaww ad-Dukhan may have been responsible for examples found there today of *Acacia raddiana,* rare

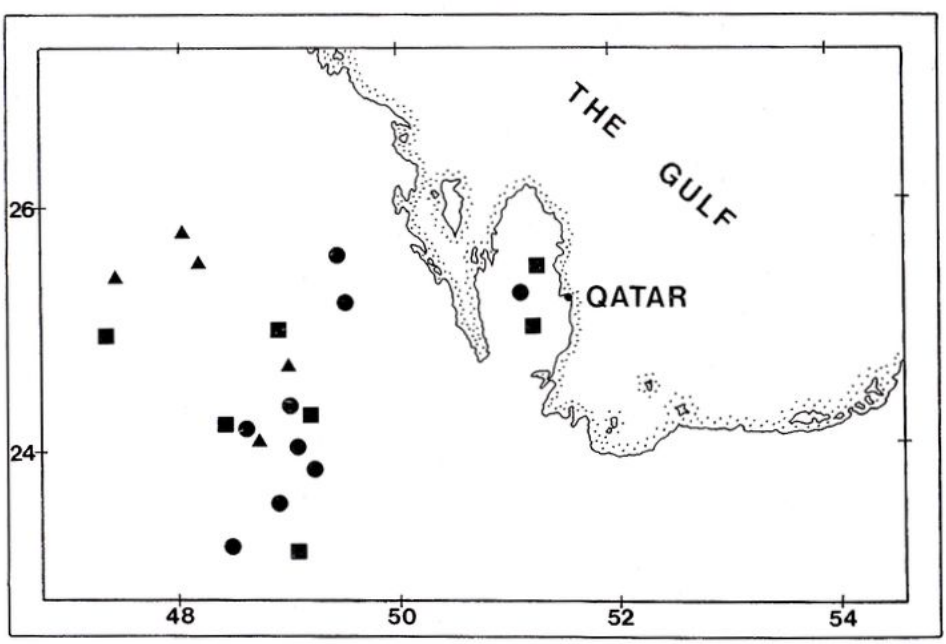

FIG. 4. Distribution of *Acacia* in the central Arabian Gulf coastal lowlands: ●, *A. ehrenbergiana*; ▲, *A. raddiana*; ■, *A. tortilis*. The majority of these occurrences are associated with early primary or secondary flow channels of Wadi as-Sahba. Mapped units range from diffuse stands of several hundred trees to (mainly in the north-west) 1–2 individuals. Data was not available for the mapped territory east of longitude 51°30′E, where *Acacia* may occur rarely. The northern limit of the genus in these parts, as indicated by the symbols, falls slightly below the 26th parallel.

isolated *A. tortilis,* and other Sudanian associates including *Capparis* and *Leptadenia.* A more important extension left the main channel of as-Sahba just east of Harad and flowed north as far as the al-Hasa Oasis depression. As a result, scattered *Acacia ehrenbergiana* at the northern end of the depression near Shadqam today mark the northernmost limit of *Acacia* in the central coastal lowlands. Just south of the city of al-Hufuf this species could be seen in relatively dense stands until recent clearing for farms.

Other Sudanian invaders in the al-Hasa area include *Cassia* and *Pergularia,* while further south toward the turning point from the main Sahba channel one may also see *Blepharis* and *Cleome.* Two other Sudanian genera in the coastal lowlands are noteworthy although their presence today might be ascribed to activities of man: isolated stands of *Salvadora persica* at al-'Uqayr and just west of the ruined Hellenistic caravan station of Thaj; and examples of *Prosopis cineraria* on the fringes of the al-Hasa Oasis and near Thaj. *Ziziphus spina-christi,* an important tree of wadis draining the Oman mountains in clearly Sudanian territory, is widely planted in gardens and oases and is sometimes seen on ruin sites, but it is probably never found truly wild in north-eastern Arabia.

From the main Sahba channel near Harad another extension of flow can be traced southward across the gravel fan, into the Yabrin depression, and also on to the south-east beneath present sand cover where its lag gravels probably merge with those from Wadi ad-Dawasir. *Acacia* is found today around Yabrin; there is a good stand of *A. tortilis* on the slopes of the hill complex, Barqa as-Samur, south of the derelict oasis.

Whether and where the main Sahba channel reached the present Gulf coastline has long been a question of interest. Recent earth satellite images appear for the first time to show the full length of its route through the Jafurah sands and on into the Batn at-Tarfa depression, the lowest point in central-eastern Arabia (−19 m). The same image shows suggestions of secondary channels leading toward the north and the base of the Qatar Peninsula. It is thus quite possible that these extensions of the Sahba system were avenues for the introduction of *Acacia* and other Sudanian species into Qatar. There is some uncertainty, however, about whether Qatar was emergent throughout the later Neogene—allowing persistence of a relict tropical flora—or whether it was intermittently marine and thus requiring restocking. A link with the clearly Sudanian vegetation of the far eastern Arabian Gulf coast is probable, but this must have been interrupted during periods of high sea level.

The third major route for Sudanian vegetation advance to the east was through the Wadi ad-Dawasir system, which cuts through Tuwayq and has left wide alluvial deposits in the Rub' al-Khali around and under the present sands. The direction of this flow was north-easterly, following the topographic trend, and there was probably some overlapping with the Wadi as-Sahba deposits. A unique isolated stand of *Suaeda monoica* south-east of Yabrin around a *sabkhah* depression in 22°55′N 49°59′E can probably be attributed to old drainage extensions along this route. This Sudanian associate is not now known in the Wadi as-Sahba system, but a well developed colony is found west of as-Sulayyil in the mouth of Wadi ad-Dawasir.

The post-Pliocene trend toward increasing aridity in eastern Arabia probably saw the invasion from the north and north-east of other floristic elements, particularly Irano-Turanian ones, and other derivatives important in the Saharo-Arabian flora today. Pleistocene periods of low sea level brought the drying up of most of the Arabian Gulf, allowing freer migration by such elements. Most recently, between 20,000 and 15,000 years ago, the Gulf was virtually dry land during the Würm glacial period and its marine regression that took the sea more than 100 m below present levels (Vita-Finzi, 1978). Vita-Finzi (1978) believes the Gulf floor was then a generally waterless desert depression with dune fields and a few swampy tracts. The following rise in sea level was most rapid between 12000 and 8000 B.P.; by 5000 B.P. it was near its present position. Nützel (1979), who is in general agreement with this chronology, reconstructs the Gulf area during this time as a river basin with 'flow-through' lakes along the deep axis closer to the Iranian side. Such developments would have brought riverine vegetation well down into middle Gulf latitudes as well as some increased siltation and fertility during the subsequent sea rise.

Although the Arabian climate was probably arid to semi-arid during Pleistocene times, intermittent wetter periods led to important changes in local environment. McClure (1976, 1978) describes two radiocarbon-dated series of late Quaternary freshwater lakes in the western Rub' al-Khali. One of these gives dates concentrating between 30000 and 21000 years B.P., the second between 9000 and 6000 B.P. The latter correlates with a probable northerly shift of the monsoon rains postulated by Kutzbach (1981) as a consequence of changes in the earth's orbital parameters. Deposits of the earlier series include freshwater mollusc shells and algae, while mammal fossils including *Bos* and *Hippopotamus* suggest a savannah grassland with lakes. Poorly preserved fossil pollen included some grasses. The Holocene lake series provided both freshwater shells and some bovid bones. Plant remains subsequently noted at these sites include rhizome and culm casts of coarse lakeshore grasses, probably chiefly *Phragmites*.

To summarize: available evidence suggests that most of eastern Arabia after the recession of the Eocene Tethys supported a palaeo-tropical vegetation—probably a savannah-like grassland of Sudanian composition—through continental phases of the Miocene. Later Miocene marine incursions coupled with a following arid trend destroyed or greatly impoverished this vegetation and set the stage for the development of today's desert plant associations in both Sudanian territory and an expanding Saharo-Arabian region. The three trans-Tuwayq wadi systems provided avenues for a limited reintroduction of Sudanian vegetation from its reservoir in western and central Arabia. Eustatic sea level changes of the Pleistocene had a marked effect on the configuration of the Gulf coastline and, consequently, the littoral vegetation. Late Pleistocene and a more recent freshwater lake series in the Rub' al-Khali are evidence for temporarily less arid periods, probably coupled at least in the south with an advance of more typically Sudanian vegetation.

Sudanian—Saharo-Arabian Borderlands in Arabia

As suggested earlier, field observations have left the present author with

the impression that Sudanian territory in Arabia is of significantly greater extent than earlier workers have portrayed. Given our still incomplete knowledge and analysis of the Arabian flora, any attempt to delimit this frontier in detail would be premature. One might venture, however, to suggest by the schematic line in Fig. 3 the regions to be regarded as possible parts of this borderland. This comprises two line segements: the first, starting in the north-west on Zohary's (1973) boundary, trends south-east past the south-western corner of the Great Nafud to around the intersection of the 26th parallel and the 42nd meridian; the second extends from the last point to the Gulf of Salwah, west of Qatar, thence to the north around the Qatar Peninsula.

The author's field experience in the Hijaz does not extend north of Mada'in Salih or, in northern Najd, farther west than Ha'il. Musil's (1928) description of that north-western country, however, refers to *Acacia* there, and it will probably be shown to grade into the more decidedly Sudanian country to the south. Jabal Shammar is a transitional district, and one is tempted to place it in Sudanian territory on the known presence of *Acacia* and associates such as *Trichodesma africana, Senecio flavus,* and *Osteospermum vaillanti* (listed by Zohary, 1957). The hills here are outliers of igneous Shield rocks, probably with Sudanian vegetation relicts. Pending more detailed field study, however, it seems preferable to suggest a frontier somewhat further south.

In these northern parts, Sudanian borderlands appear to be characterized by the northern range of *Acacia gerrardii* (syn. *A. iraqensis* Rech. f., also ?*A. pachyceras* O. Schwartz), an important Arabian tree which extends farther to the north-east than do other *Acacias* such as *A. tortilis* and *A. ehrenbergiana.* Najd is a heartland for this large-boled, gum-bearing species, and it is often dominant there in dense stands in wadi bottoms. It appears to have penetrated north along the Gulf of 'Aqabah rift into the southern Negev. It also has an extension to the north-east through the Wadi ar-Rimah/al-Batin drainage system, and it is found in wadi lines in the Qasim and even deeper in Saharo-Arabian territory along the Batin. Its presence near northern stations on the Darb Zubaydah pilgrim track, however, as at Zubalah, suggests that its feeble extension into Iraq may have been a consequence of early caravan traffic.

South-east of the Qasim one begins to find increasing and more diverse examples of Sudanian elements in the uplands of Najd. *Acacia tortilis* and *A. ehrenbergiana* become frequent. As the latitude of Riyadh is approached the Tuwayq mountain flora as a whole becomes predominantly Sudanian, as evidenced by the following records from the Tuwayq and adjacent scarplands: *Ficus salicifolia, F. pseudosycomorus, Gaillonia calycoptera, Forsskaolea tenacissima, Indigofera oblongifolia, Cucumis prophetarum, Abutilon fruticosum, Hibiscus micranthus, Morettia parviflora, Ochradenus baccatus, Pulicaria somalensis* (*P. adenensis* auct.), and *Kohautia caespitosa.* In Tuwayq south of Riyadh this picture is strengthened further by the addition of such species as *Maerua crassifolia* and *Capparis cartilaginea.* On the east, *Acacia, Ziziphus, Rhazya,* and locally *Capparis decidua* extend down-slope in wadi bottoms towards the edge of the Dahna sands. Traverses by the present author from Wadi ad-Dawasir through Tathlith to 'Asir, and north-west from Wadi ad-Dawasir through

Hadb ad-Dawasir to central Najd, proved the continuity of the southern Tuwayq Sudanian vegetation with that of the west. Between middle Tuwayq and the Hijaz the Acacietum is strongly contracted but still intermittently present, showing again that Tuwayq is not just an outlying relict. *Acacia oerfota* (*A. nubica* auct.) is found at least as far north and east as central west Tuwayq in 23°32′N 46°18′E.

East of the Dahna sand belt, the *Acacia*-dotted basins of southern Ghawar again suggest Sudanian conditions, and our proposed frontier would pass through the Bay of Salwah and then arch northward to leave all but perhaps the northern tip of the Qatar Peninsula in Sudanian territory.

This borderland is indeed ill-defined in its eastern extremity, but the distribution of *Acacia* provides some guidance (Fig. 4). The transition zone is marked by a steep gradient in species diversity of the annual flora, which declines rapidly as one approaches Sudanian territory from the north.

Zohary (1973) treated a narrow strip of the Gulf coast in Arabia, as far north as Kuwait, as an extension of the Sudanian region (Fig. 3). This was presumably based on an evaluation of Vesey-Fitzgerald's (1957) account of the east Arabian vegetation, perhaps specifically his 'coastal white sands association' dominated in part by *Panicum turgidum*, and perhaps on his reports of communities led by *Rhanterium epapposum* and *Ziziphus nummularia*. In the present author's view Zohary's delimitation of Sudanian territory in Arabia, probably largely as a result of the very limited information available, over-emphasized the significance of quasi-Sudanian elements in the far north-east, while giving insufficient weight to the contracted Sudanian vegetation of the central Peninsula.

The assignment of the Rub' al-Khali is a special problem. This is a hyper-arid region analogous to central parts of the Sahara where all vegetation is highly conditioned by climatic and edaphic extremes. One is reduced almost to describing potential rather than actual communities here when seeking broader affiliations for them. Most writers have left the Rub' al-Khali in Saharo-Sindian or Saharo-Arabian territory. Monod (1957) expressed his belief that the flora of the Rub' al-Khali as a whole was 'Saharo-Mediterranean'; he suggested, however, that a Saharo-African zone might separate the core from Sahelian formations in the south, and his map leaves large parts of the southern and eastern sands in his Sudano-Angolan Region.

The flora of the Rub' al-Khali does exhibit increasing Sudanian affinities from north to south. This is particularly evident as the 22nd parallel is approached; about this latitude both *Hammada* and *Haloxylon* lose their importance in the sand communities, while *Limeum arabicum* becomes significant as does the robust *Tribulus arabicus*. The endemic *Cornulaca arabica* is first encountered and becomes an important dominant as does, locally, a *Zygophyllum*. *Cyperus conglomeratus* is a widespread constituent of several communities. In the Dahna, around this latitude, the *Artemisia monosperma* typical of the central red sands reaches its southern limit. A notable feature of the Rub' al-Khali is the almost complete absence, even after good rains, of the annual plants that are relatively abundant in the Saharo-Arabian sands of the north.

Calligonum comosum, which occurs widely as a co-dominant in the Saharo-Arabian sands, is replaced a bit south of the 24th parallel by *C. crinitum* subsp. *arabicum,* which is widespread in the Rub' al-Khali. The latter is derived from a south Iranian species, presumably as the result of early migration across the present Gulf basin near its southern end.

All of these factors, coupled with the largely non-Mediterranean rainfall pattern and the floristic context of surrounding regions, lead toward a treatment of the Rub' al-Khali as a highly modified Sudanian borderland rather than a Saharo-Arabian variant. The flora there was probably much more typically Sudanian between 10000 and 5000 B.P. when monsoon rains apparently reached that far north in a regional climate shift (McClure, 1976; Kutzbach, 1981). Its present hyper-aridity has such a powerful masking effect that on the northern edges of the sands, near the Wadi as-Sahba entrant, one can count more Sudanian species to the north than to the south.

A case could perhaps also be made for assigning the Rub' al-Khali to a sub-Sudanian sub-unit of an extended Saharo-Arabian or Saharo-Sindian region. This, however (but depending on one's definition of 'Saharo-Sindian'), would appear to involve placing physiognomic considerations above floristic ones.

The vegetation of the Qatar Peninsula is also of special plant-geographical interest. This Sudanian enclave along the central Gulf coast has silty flats with relatively rich stands of *Acacia, Ziziphus* and sub-tropical associates such as *Zygophyllum simplex, Cassia italica, Corchorus depressus, Blepharis ciliaris* and even *Indigofera* and *Abutilon.* Qatar also lies at the coastal terminus of a ready path of Sudanian intrusion from the Wadi as-Sahba system. I prefer to place it inside the edge of Sudanian territory rather than treat it as a local relict because of the wide areal extent of its tropically-derived vegetation and because some species, such as *Indigofera intricata* (also found by the present author east of Qatar in 24°10′N 51°29′E) seem to indicate a continuity with Sudanian territory in the eastern Gulf. The present interruption of the Acacietum along the desolate coast between Qatar and Ras al-Khaymah is almost certainly a result of late Tertiary sea level changes and related edaphic effects.

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