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Pedal specialisations in dune-dwelling geckos

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Gekkonid lizards are important components of desert faunas, but are rare in dune habitats. Pedal modifications for dune-dwelling are found in geckos of the subfamilies Diplodactylinae and Gekkoninae. Three types of pedal morphologies are associated with dunes—fringed toes, spinous, swollen plantar surfaces, and webbed feet. The first is associated with the occupation of loose, leeward dune faces, the second with the utilisation of sandy substrates in general, and the third with burrowing in the compacted sand of windward dune faces. Although webs and fringes increase surface area and may aid in surface locomotion on sand, both appear primarily to facilitate movement within the substrate or in burrowing.

Introduction

Dune regions are inhabited by distinctive, and often depauperate herpetofaunas (Mertens, 1955; Lawrence, 1959; Haacke, 1975*a*; Lambert, 1984). Aside from euryoecious species which marginally enter the dunes, these generally consist of two types of animals, sand-swimmers and sand-burrowers. For both, the ability to enter the sand is critical, as daytime temperatures in most desert dune areas are high, cover is sparse, and small vertebrates need a strategy to escape the sun or predators.

Classic sand-swimmers include the lacertid *Aporosaura anchietae* (Louw & Holm, 1972) and the viperid *Bitis peringueyi* (Broadley, 1983) in the Namib Desert, the scincids *Scincus* spp. and *Chalcides sepsoides* in North Africa and the Near East (Mosauer, 1932; Arnold & Leviton, 1977), and the colubrid *Chionactis* (Norris & Kavanau, 1966) and iguanids of the genus *Uma* in the dune regions of the Mojave Desert (Pough, 1969; Luke, 1986). These animals use either low-amplitude, high-frequency, lateral undulations to disappear into the substrate, or dive headfirst into the sand (Sukhanov, 1968). Because they do not construct burrows and are, therefore, buried in the substrate, most have morphological and/or physiological modifications for under-sand breathing (Stebbins, 1943; Pough, 1969; Huey *et al.*, 1974).

Sand-burrowers, on the other hand, often have relatively short bodies, poorly constructed for lateral undulations, and frequently exhibit modifications of the manus and pes for digging. These animals excavate patent tunnels and therefore do not require modifications for undersand breathing. Most of the dune-dwelling geckos fall into the latter category (but see Loveridge, 1947 and Gallagher, 1971 for possible exceptions among *Stenodactylus* spp.).

Much systematic work on gekkonid lizards has been based on foot structure. Indeed the

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root '-dactylus' is the basis for a high proportion of gekkonid generic names. Such phrases as 'digits often modified for climbing' are commonly listed among the attributes of the family as a whole. While expanded digital scansors are typical of many forms, they are not by any means universal. Approximately 40% of recognised genera lack these modifications, either primitively or secondarily (Wermuth, 1965; Russell, 1972). Many of these forms are terrestrial, and most of these, in turn, are inhabitants of the arid or semi-arid regions of the world. Indeed, geckos form one of the most significant components of the reptile fauna of the world's deserts, especially in southern Africa and Australia (Brain, 1962; Pianka & Huey, 1978; Pianka, 1986). While these terrestrial inhabitants of deserts generally lack the scansorial pads of their arboreal relatives, their digits typically display suites of modifications specific to the substrates on which they are active.

The majority of desert-dwelling geckos are inhabitants of rocky outcrops, or more rarely, desert vegetation (Fitzsimons, 1943; Lambert, 1984; but see Haacke, 1984 for comments on Kalahari reptiles). Other species are typical of sand flats or gravel plains. Stenoecious psammophiles (Werner, 1987) which inhabit sandy biotopes exclusively, form another group. The most highly specialised and structurally modified desert geckos are those that are largely or entirely limited in their distribution to sand dunes.

Within dune habitats there is extensive specialisation in lizard microhabitat preference. This has been demonstrated for the lacertids *Meroles cuneirostris* and *Aporosaura anchietae* in the Namib, which prefer sandy interdune valleys and dune slipfaces respectively (Robinson & Cunningham, 1978). Huey & Pianka (1974) and Pianka & Huey (1978) recognised four microgeographical subdivisions of dunes—interdune flats or streets, base, slope, and crest. Smaller interdune valleys and slopes may lie between the crests of adjacent larger dunes (Holm & Scholtz, 1980). Equally important are the divisions of dunes into windward and leeward faces, each of which is typified by its own characteristics (Seely *et al.*, 1988). The compacted windward faces are generally more suitable for sand-burrowers (Werner, 1915), which are typically nocturnal (Steyn & Haacke, 1966), while the slipfaces of the leeward side are more often the habitat of diurnal sand-swimming reptiles (Broadley, 1983). Despite these subdivisions, however, many of the dune microhabitats may be utilised to a greater or lesser extent by most psammophilous reptiles (Holm & Scholtz, 1980).

In this paper we characterise the morphological modifications of the manus and pes of dune-dwelling geckos to the wind-blown sand substrate.

Materials and methods

Comparative material of dune-dwelling geckos was obtained from the reference collections of the authors and the collections of the following museums: American Museum of Natural History, New York (AMNH); Los Angeles County Museum of Natural History (LACM); California Academy of Sciences, San Francisco (CAS); Museum of Vertebrate Zoology, Berkeley (MVZ); British Museum (Natural History), London (BMNH); Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn (ZFMK); and Transvaal Museum, Pretoria (TM). Ethanol-stored material was used for the investigation of external features and dissections of associated musculature. Osteological features were examined on radiographs and cleared and double-stained specimens prepared from formalin-fixed material according to a modification of the method of Wassersug (1976; see Bauer, 1986). Histological sections of the digits of certain specimens were sectioned on a rotary microtome at a thickness of 8–10 μm and stained with haemotoxylin and eosin or Mallory's azan trichrome stain (Humason, 1979). Specimens for scanning electron microscopy were critical-point dried or dehydrated in hexamethyldisilazane, sputter coated with gold, and examined with a Hitachi S 570 scanning electron microscope. Photographs were taken on Polaroid Type 52 and Type 55 films.

Namib dune sand particle size distribution was determined by manual and automatic shaker sieving using U.S.A. standard soil testing sieves (numbers 10, 16, 18, 25, 30, 50, 70, 80, 100, 120, 140, 170, 200, 230 and 270).

Results and discussion

The geographic distribution of dune-dwelling gekkonids

Extensive areas of dunes characterise most of the world's temperate and tropical deserts (McKee, 1979). Each of these areas is inhabited by one or more species of geckos that are obligate or facultative dune-dwellers. Dune sands demarcate the limits of the ranges of certain highly modified forms, acting as islands for stenoecious psammophiles (Werner, 1968, 1987). They also limit the ranges of non-psammophilous species; *Rhoptropus* (Haacke & Odendaal, 1981), *Afroedura* (Onderstall, 1964), and *Pachydactylus bibronii* (Haacke, 1975*a*) are all limited in their distribution by sand encroachment into rocky habitats. The following, by region, are those taxa that have been identified, through reference to the literature or personal observation, as dune specialists.

North America

The deserts of western North America (Mojave, Colorado, Sonoran) are depauperate with respect to geckos, as is the New World as a whole. There are no dune specialists, although a single species, *Coleonyx variegatus,* inhabits dunes in addition to sandplains, stony desert and other habitat types, especially in the Mojave (Mosauer, 1935, 1936; Klauber, 1945).

South America

Desert areas in South America include several arid regions in southern and western Argentina and the Peruvian/Atacama coastal desert in the rain shadow of the Andes. Several species of the genera *Homonota* and *Phyllodactylus* are terrestrial and occur in areas of sandy soils. Of these only *P. microphyllus, P. gerrhopygus,* and *P. kofordi* appear to be directly associated with dunes. *Phyllodactylus microphyllus* occurs in the Sechura portion of the Atacama in areas of barchan and hummock-stabilised dunes (Dixon & Huey, 1970; Huey, 1979). It also occurs in coastal dune regions of the desert. *Phyllodactylus gerrhopygus* is endemic to sand dune regions of the Atacama Desert and has been collected and observed near dune bases along the Pacific coast (Dixon & Huey, 1970). The remaining species, *P. kofordi,* is an inhabitant of beach dune communities only (Dixon & Huey, 1970).

Asia

Dune regions occur in parts of the Gobi Desert, the arid regions of Soviet central Asia, and in Arabia and adjacent regions of the Persian Gulf. At least some members of six genera are known to occur in these dune regions. These include *Stenodactylus arabicus* (Gallagher, 1971; Arnold 1977, 1980*b*), an obligate dune-dweller, *S. doriae* (Werner & Broza, 1969; Arnold, 1977; Werner, 1987), *S. petrii* (Haas, 1956; Werner, 1987, 1988), *S. slevini* (Gallagher, 1971), *S. sthenodactylus* (Werner & Broza, 1969; Werner, 1987, 1988), *Teratoscincus przewalskii* (T. J. Papenfuss, pers. comm.), *T. scincus* (Arnold, 1977; Szcherbak & Golubev, 1986), *Bunopus blanfordii* (Haas & Batersby, 1959; Russell, 1972; Werner, 1987, 1988), *B. tuberculatus* (Arnold, 1977, 1980*a*), *Tropiocolotes steudneri* (Werner, 1987, 1988), *Crossobamon eversmanni* (Nikol'skii, 1963; Szcherbak & Golubev, 1986), *C. maynardi* (Minton, 1966), and *Cyrtodactylus russowi* (Szcherbak & Golubev, 1986).

Australia

Most of Australia to the west of the Great Dividing Range and exclusive of the far north and far south-west falls within the Eyrean zoogeographic subregion (Heatwole, 1987), and can be characterised as arid or semi-arid; sandy soils predominate in many areas. Although most of the desert-dwelling geckos in Australia are restricted to rocky outcrops or *Triodia* plants, at least some are active on sand. *Diplodactylus elderi, D. conspicilatus,* and *D. ornatus* have all been reported from sandy soils (Wilson & Knowles, 1988), and *Diplodactylus rankini* is endemic to the sandy coastal dune areas of Western Australia but none of these species are true dune-dwellers.

Diplodactylus damaeus (Kluge, 1967*a*; Cogger, 1986), *D. stenodactylus* (Pianka, 1972; Pianka & Pianka, 1976), *Nephrurus deleani* (Delean, 1982; Harvey, 1983), *N. laevissimus* (Mertens, 1958; Pianka & Pianka, 1976), *N. levis* (Storr & Harold, 1978; Storr & Hanlon, 1980), and *N. vertebralis* (Delean, 1982; Harvey, 1983) are typically found in microhabitat types that include dunes or sand ridges in the Gibson, Tanami, Great Victoria, Simpson, and Great Sandy Deserts (Bridgewater, 1987). *Rhynchoedura ornata* and *Heteronotia binoei* also occur in Australian sand ridge and sand hill country (Pianka, 1972; Pianka & Pianka, 1976), but are generally only peripherally associated with the dunes themselves. Among *Nephrurus* there appears to be some selectivity within the dune microhabitat, with *N. deleani* and *N. vertebralis* favouring dune crests, while *N. levis* is typically an inhabitant of interdune valleys. This latter species has, however, been reported from both inland and coastal dunes in Western Australia (Storr & Harold, 1978; Storr & Hanlon, 1980).

Africa

The major dune systems of Africa include those of the Sahara (both coastal and inland), Namib and Kalahari. Dune-dwelling geckos and, indeed, all reptiles are scarce in the Saharan dunes (Lambert, 1984). Nonetheless, *Stenodactylus petrii* (Papenfuss, 1969; but see Loveridge, 1947) and *S. sthenodactylus* (Loveridge, 1947), which also occur in south-western Asia, have been reported from Saharan erg regions, and *Geckonia chazaliae* occurs in association with *Euphorbia* and *Salicornia* stabilised dunes in the coastal region of north-west Africa (Rieppel, 1973; Seufer, 1988).

In the Namib, *Palmatogecko rangei* is a dune-specific taxon, preferring the hard-packed sand of windward dune faces (Steyn & Haacke, 1966). *Ptenopus garrulus garrulus* and *P. g. maculatus* may be found marginally in dune fields (Fitzsimons, 1935*a*, 1935*b*; Loveridge, 1947; Stuart, 1980), but generally avoid the dunes themselves (although at Port Nolloth, South Africa *P. g. maculatus* does occur in the dunes—Haacke, 1975*b*). *Ptenopus kochi,* apparently a river-bed soil specialist, may also utilise fine-grained sand dunes (Haacke, 1964, 1975*b*). *Colopus wahlbergii furcifer* is endemic to the dune fields of the southern Kalahari (Fitzsimons, 1935*b*; Pianka, 1971; Pianka & Huey, 1978; Haacke, 1976*b*, 1984), where it prefers dune slopes (Pianka & Huey, 1978). *Chondrodactylus angulifer* is psammophilous (Fitzsimons, 1935*a*), but is only peripherally associated with dune bases in both of the southern African arid regions (Pianka & Huey, 1978; Stuart, 1980), preferring flat interdune valleys and gravel plains to dune slopes (Haacke, 1976*c*). A number of *Pachydactylus* species also occur in dune regions (Pianka, 1971; Pianka & Huey, 1978), but are not strictly inhabitants of sandy dune microhabitats, preferring instead interdune vegetation or interridge sand streets.

The phylogenetic distribution of dune-dwelling gekkonids.

The Gekkonidae is presently regarded as consisting of three major phylogenetic sublineages (Kluge, 1987); the Eublepharinae, Diplodactylinae (including the Pygopodidae), and Gekkoninae. These groupings are sometimes regarded as distinct at the family level (Kluge, 1987; Grismer, 1988). Pedal modifications for dune-dwelling are found in the last two groups. Within the diplodactylines, both recognised tribes—the Carphodactylini and Diplodactylini show tendencies in this regard. Likewise, in the Gekkoninae representatives of both the Gekkoni and the paraphyletic 'Ptyodactylini' display morphological correlates of psammophily.

Within both the Diplodactylinae and Gekkoninae some of the genera exhibiting such features maintain primitive pedal characteristics that have not been secondarily complicated by the addition of a scansorial system (Russell, 1972, 1976, 1979). The only diplodactyline representatives of this type are members of the carphodactyline genus *Nephrurus*. Of the five gekkonine dune genera that are also primitively padless, *Stenodactylus, Crossobamon*, and *Bunopus* belong to the Gekkonini. Although relationships within the gekkonines are not particularly well known (Joger, 1985), *Crossobamon* and *Bunopus* appear to be close to each other whereas the affinities of *Stenodactylus* remain unclear. The latter genus had been associated with the primitively padless 'ptyodactyline' *Teratoscincus* (Kluge, 1967*b*), which has itself more recently been postulated to be the sister taxon of all remaining gekkonines (Kluge, 1987). The last of the primitively padless gekkonines is *Ptenopus*, which is also enigmatic with respect to its genealogy.

The gekkonine genus *Pachydactylus* and its satellite genera *Chondrodactylus, Colopus, Kaokogecko*, and *Palmatogecko*, and the diplodactyline genus *Diplodactylus* and its satellite *Rhynchoedura* are in many ways comparable radiations (Pianka, 1975; Russell, 1979; Haacke, 1982) that have converged on dune-dwelling modifications from primitively pad-bearing ancestries. Both taxa are species-rich and both have their primary radiations in arid regions—the south-western African Arid Zone (Moreau, 1952) in the case of the former, and central and western Australia in the latter. Each assemblage encompasses a wide range of morphological variation but is united by an identifiable digital pattern expressed through a continuum of forms.

Comparable diversity is seen in the polyphyletic gekkonine forms presently assigned to the genus *Phyllodactylus. Diplodactylus* and *Phyllodactylus* are characterised by terminal apical scansors and lack proximal elaboration of the scansorial pad. These lineages are only distantly related and have independently evolved their respective modifications. The distal scansor toe-type appears to have arisen as a modification for saxicolous existence (Russell & Bauer, 1989), and indeed, the majority of taxa exhibiting this general form are rupicolous (Dixon & Huey, 1970).

In *Pachydactylus* the scansors primitively encompass much of the proximal region of each toe (Russell, 1976: figs 8–10) and thus differ greatly from the primitive condition in *Diplodactylus* and *Phyllodactylus*. Within the genus, however, there has been a reduction and shift of the scansorial system to a terminal position, analogous to that found in the other genera under consideration. A similar phenomenon in the *Tarentola* lineage of North Africa, which may or may not be closely related to *Pachydactylus* (Russell, 1972; Joger, 1985), culminates in the terminal scansors of *Geckonia*.

In each of the lineages, at least some species have invaded sandy habitats. Included are forms with little or no modification of the terminal scansors that are active on flat sandy substrates (e.g. *Pachydactylus serval* and *P. oreophilus*, Steyn & Mitchell, 1967; *Diplodactylus conspicillatus*, and *D. ornatus*, Wilson & Knowles, 1988; and several species of South American *Phyllodactylus*, Dixon & Huey, 1970). In most cases, however, the true dune-dwelling forms in these lineages have undergone more extensive reduction of the adhesive apparatus.

In *Diplodactylus* the greatest reduction of the adhesive apparatus is seen in the most psammophilous taxa, *D. stenodactylus* and especially *D. damaeus* (Fig. 1). In the former species the subdigital scales are small and non-lamellar and the apical scansors are greatly reduced. In the latter the scansors have been lost entirely and the autopodium and digits are covered with small, spinous scales.

Phyllodactylus spp. of the Peruvian/Atacama Desert show few adaptations to psammophilous life. *Phyllodactylus gerrhopygus*, which frequents dunes but neither burrows nor sand-swims, shows no digital modification. *P. microphyllus* (Fig. 2), a form more restricted to sand, though not necessarily dunes, does exhibit some reduction of the terminal scansor adhesive apparatus (Dixon & Huey, 1970) and has granular palmar scales tending towards the spinous condition reported above for *Diplodactylus damaeus* [Fig. 1(c)].

The most complete morphocline towards dune specialisation within a primitively pad-

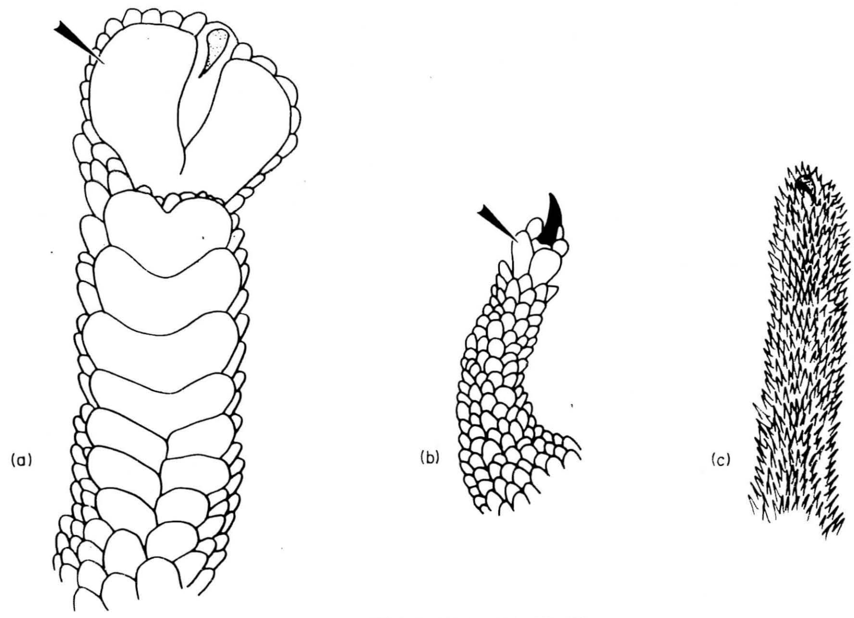

Figure 1. Oblique ventral views of digit IV of the pes of (a) *Diplodactylus strophurus*, a non-psammophilous diplodactyline gecko; (b) *D. stenodactylus*, a euryoecious psammophile; and (c) *D. damaeus*, a stenoecious psammophile that may inhabit dunes. Note the reduction of the apical scansors (arrows) in (b) and their complete absence in (c). Note also the presence of spinous scales in (c). Scale bar = 2 mm.

bearing lineage is that seen in the burrowing gekkonine geckos of southern Africa (Haacke, 1975*b*, 1976*a*, 1976*b*, 1976*c*, 1976*d*). In *Pachydactylus* there is a reduction in the basal scansors in some lineages. Species such as *P. mariquensis* [Russell, 1976; Fig. 10(d)] exhibit an intermediate condition between the large pads of its congeners and the reduced adhesive apparatus of the burrowing geckos (Russell, 1972, 1976, 1979; Haacke, 1975*b*). The monophyly of the burrowing genera, *Colopus*, *Chondrodactylus*, *Kaokogecko*, and *Palmatogecko*, remains uncertain, but the hyperphalangy of digit I (Russell, 1972, 1976, 1979; Haacke, 1976*d*) and other features (Kluge, 1983) strongly support the union of these taxa plus *Pachydactylus*.

Pedal modifications for dune-dwelling

Dune system herpetofaunas consist of both euryoecious species, which lack digital or other modifications for sand-living, and stenoecious psammophiles, some of which are strictly dune-dwelling. Three major types of pedal modifications, fringes, swollen plantar surfaces, and interdigital webs, seem to encompass the diversity of form seen in psammophilous geckos (Mertens, 1955; Russell, 1976, 1979). All three exhibit the primitive or secondary absence of the adhesive apparatus of the digits. The complex subdigital setae present in pad-bearing arboreal and saxicolous forms require a firm substrate to which they can adhere. Loose sand not only lacks this prerequisite, but might serve to clog the setae. This can be seen in non-sand-dwelling, pad-bearing geckos which will hyperextend the toes if placed on sandy substrates in order to avoid this clogging.

Only in the primitively padless gekkonines *Ptenopus*, *Stenodactylus*, *Teratoscincus*, *Bunopus*, and *Crossobamon* are toe fringes present (Brain, 1962; Haacke, 1975*b*; Luke,

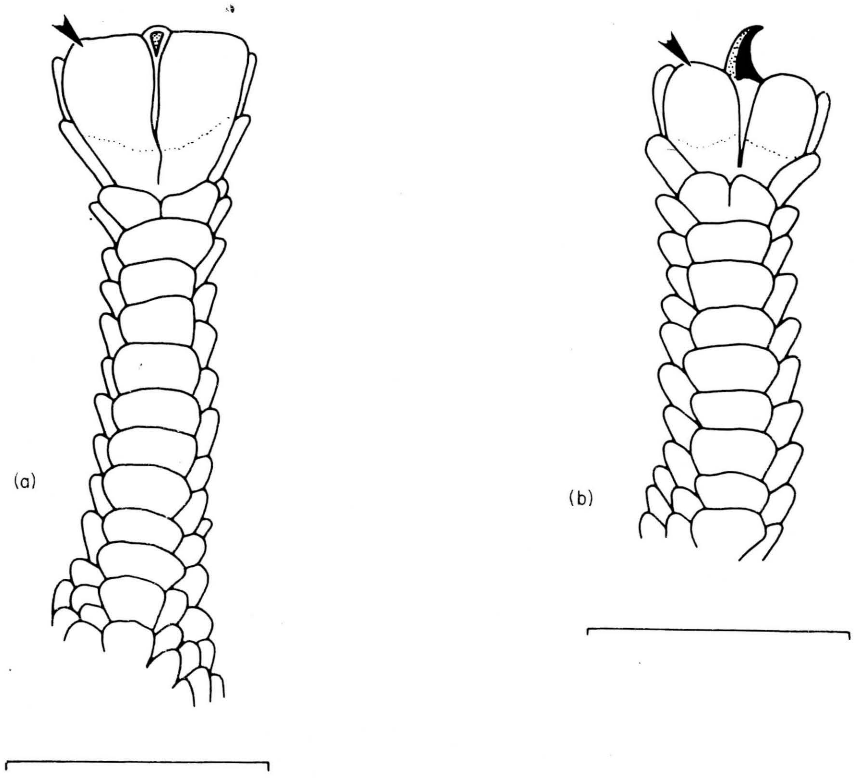

Figure 2. Ventral views of digit IV of the pes of (a) *Phyllodactylus julieni* (BMNH 1923.5.19.1), a non-psammophilous gekkonine gecko; and (b) *P. microphyllus* (BMNH 1926.3.24.4), a dune-dwelling species. Note the relative reduction in the size of the adhesive apical scansors (arrows). Scale bars for both species = 2 mm.

1986). Luke (1986) classified fringes into four morphological types, three of which are found in lizards inhabiting wind-blown sand. Of these, two (triangular and conical) are found in geckos. The former is typical of *Bunopus* (Fig. 3) and *Crossobamon,* while the latter characterises the remaining fringed taxa [Figs 4(a)–(b)].

In the diplodactyline *Nephrurus* [Fig. 4(c)] and the gekkonines *Chondrodactylus* [Figs 4(d)–(e)], *Colopus* [Fig. 4(f)], *Geckonia,* and *Kaokogecko* the digits and/or plantar surfaces of the feet have a puffy appearance and bear spinous scales (Russell, 1972, 1976, 1979). These forms, whether primarily or secondarily padless, also generally show a reduction in the length of the digits. This may be expressed either by diminution in the size of the terminal phalanges (as in *Chondrodactylus*—Haacke, 1976*d*) or in reduced phalangeal formulae (as in *Nephrurus* and *Stenodactylus*—Russell, 1979; Arnold, 1980*b*). The presence of spinous scales on the subdigital surfaces of the toes and palms of *Chondrodactylus* was first noted by Peters (1870) in his description of the sole species, *C. angulifer.* Hewitt (1910) and subsequent authors further remarked on this peculiar morphology. Although Haacke (1976*d*) considered the spinous scales of the burrowing geckos of no particular significance, Russell (1972, 1976, 1979) has argued for the functional importance of both the spinous scales and the swollen aspect of the palms and digits. This topology is not limited to primitively padless forms, as it co-occurs with terminal scansorial plates in *Colopus, Geckonia,* and *Kaokogecko* (Haacke, 1976*a*, 1976*b*). Similarly it may co-occur with the third sand specialisation, interdigital webbing, as in *Kaokogecko* (Fig. 5), *Palmatogecko* (Fig. 6), and several species of *Stenodactylus,* especially *S. arabicus.*

By far the most complex and specialised pedal morphology is exhibited by the web-

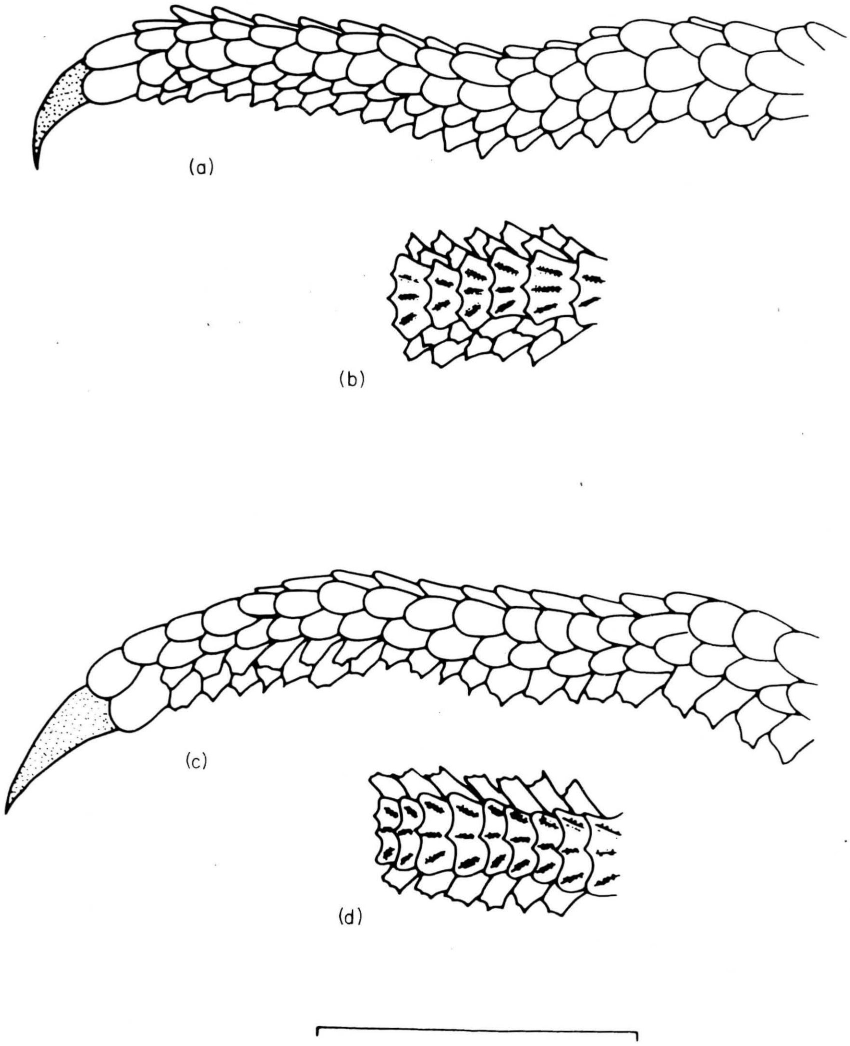

Figure 3. Lateral (a) and (c) and ventral (b) and (d) views of digit IV of the pes of *Bunopus tuberculatus* (BMNH 1971.1370) (a) and (b), and *B. blanfordi* (BMNH 1970.1531) (c) and (d), dune-dwelling species of primitively padless gekkonine geckos with modified triangular lateral fringes. Scale bar = 2 mm.

footed geckos, as exemplified by *Palmatogecko.* The osteology of the manus and pes of *Palmatogecko rangei* and other southern African burrowing geckos was described by Haacke (1976*d*) who demonstrated the presence of cartilaginous paraphalanges at the interphalangeal articulations. Russell & Bauer (1988) investigated these structures in more detail and confirmed the presence of paraphalanges in *Palmatogecko* but not in *Kaokogecko* (*contra* Haacke, 1976*d*), in which broad distal phalangeal heads occur at the same points. In *Palmatogecko* paraphalanges occur in all digits of the manus and pes (Fig. 6), at the metapodial–phalangeal and first interphalangeal joints in all digits, and at the second interphalangeal joint in digit IV (Russell & Bauer, 1988). In digit V of the pes, however, the paraphalanges are present at the first and second interphalangeal joints, but not at the metatarsal–phalangeal junction. This restriction of paraphalanges to the basal regions of the digits is unique among geckos and is indicative of the very different role played by these structures in *Palmatogecko* relative to arboreal or saxicolous geckos. In this species the paraphalanges, which may remain cartilaginous or partially calcify, are horn-shaped (Fig. 6) and extend into the extensive webbing between the toes. The web itself is unique among gekkonids in that it contains complex intrinsic musculature (Fig. 6). In all digits interparaphalangeal muscles run between proximal and distal ipsilateral paraphalanges. In addition, the proximal paraphalanges of digits IV and V of the pes are also connected by musculature. These intrinsic muscles are associated with the short digital flexors and are probably coordinated with these during digging motions. No muscles span between the paraphalanges of adjacent pairs of the first four digits.

Mechanical correlates of pedal morphology

Each of the pedal modifications discussed above is related to the physical or mechanical properties of the loose sand substrate on which dune geckos move. The convergence of several distantly related lineages on these three pedal types is strongly indicative of the functional significance of each morphology in particular situations. Of the morphological suites mentioned above, toe fringing has received the greatest amount of attention, probably because it occurs in a variety of other lizard groups (Luke, 1986).

Haacke (1964, 1975*b*) stressed the relationship between fringe size and soil softness for *Ptenopus*. Since softer sand is generally more finely-grained, fringes may be viewed as being correlated with particle size, and indeed, the longest fringes are found in *P. kochi*, an alluvial soil specialist (which also utilises fine sand), and the shortest in *P. carpi*, a gravel plains-dweller. *Ptenopus garrulus*, which may inhabit dunes, is intermediate in this regard (Haacke, 1975*b*). Werner (1987) also reported inter- and intraspecific positive correlations of increasing fringe length with decreasing soil firmness. Fringes appear to be used both in running on slipface surfaces and in shimmy-burial—a form of sand-swimming (Stebbins, 1944; Norris, 1958; Carothers, 1986; Luke, 1986).

Sand particle size varies widely but may generally be defined by the lower and upper limits of 62 and 1600 μm (Ahlbrandt, 1979). While most naturally occurring desert sands are composed of particles of several size classes, there is typically a predominant diameter which may be as low as 80 μm for very fine sand, but is more typically in the range of 150–300 μm (Bagnold, 1954). Using Bagnold's (1954) method for the calculation of equivalent diameters, the Namib dune sample examined here has a predominant diameter (55·6% of sample by weight) of about 190 μm and, as is typical (Ahlbrandt, 1979), particles are well sorted, trailing off rapidly both above and below this modal value (range 50–400 μm). By comparison, reported particle sizes for a number of other dune regions are generally slightly to considerably larger (Table 1). In some regions, such as white sand dune fields in the Kalahari, no fine sand particles occur (Bagnold, 1954).

A comparison between the dimensions of lateral digital fringes (Table 2) and mean (or modal) sand dimensions (Table 1) indicates that some sand grains may be able to pass through the interdigital spaces, at least distally where the gaps are largest. Proximally, increasingly smaller particles may be excluded by the converging bases of the fringes [Figs 4(a)–(b)]. The distal fringe spaces in *Ptenopus* are roughly comparable to the reported sand grain sizes for southern African sites, whereas in *Teratoscincus* the distances are nearly twice that of the Takla Makan sand sample, the only sample from within the range of this taxon. Although the relative mobility of fringes and the geometry of their expanded bases are clearly significant in determining the true functional particle exclusion limits of the digits, it is apparent that triangular and conical fringes, while increasing surface area for burrowing and locomotion (Carothers, 1986), may be relatively inefficient in areas of small modal sand grain size. A precise evaluation of the correlation of interfringe distances with substrate particle size must await a more detailed analysis of fringe functional morphology and the ultimate sieving of sand samples from specific microhabitats known to harbour the species of concern.

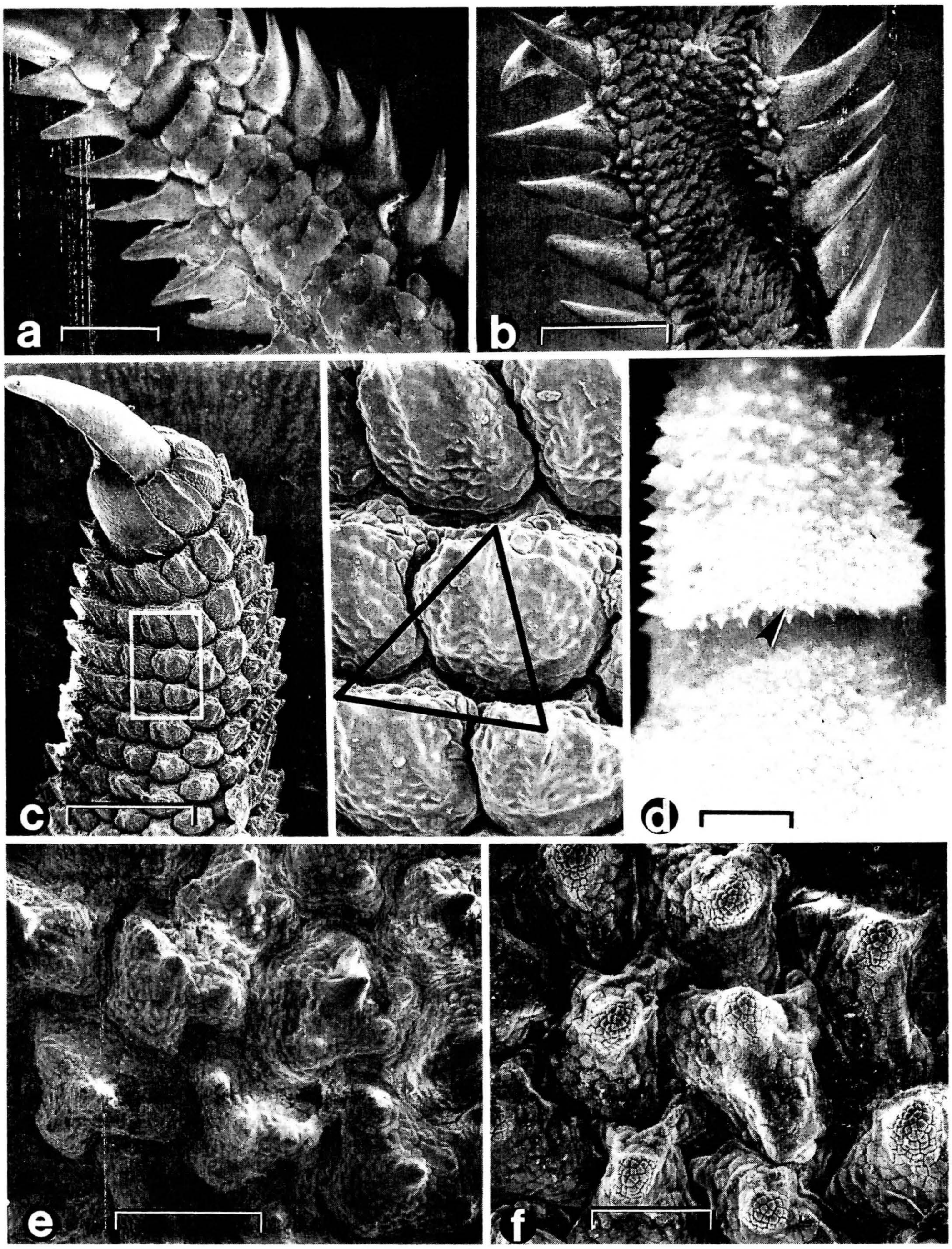

Figure 4. (a) Scanning electron micrograph of the ventral surface of digit IV of the pes of a juvenile *Ptenopus garrulus.* Note the broad fringing scales. Mean minimum particle exclusion size (see Table 2) was determined by measuring the distance between adjacent distal fringe tips. Scale bar = 500 μm. (b) Scanning electron micrograph of the ventral surface of digit IV of the pes of a juvenile *Teratoscincus scincus.* The absolute value of the interfringe gaps is considerably greater than that seen in *Ptenopus.* Scale bar = 500 μm. (c) Scanning electron micrograph of the ventral surface of digit IV of the pes of an adult *Nephrurus levis.* Note the spinous subdigital scales, which continue proximally to the swollen plantar surface. The right side of the figure is a 5× enlargement of the boxed area on

Perhaps significantly, of terrestrial fringe-toed lizards, only two have contacting or overlapping fringes (Luke, 1986). These two lizards, *Angolosaurus skoogi* and *Aporosaura anchietae,* are both obligate Namib dune dwellers (Pietruszka, 1988). Whereas the former species is at the upper weight limit for fringe-toed lizards (120 g, Seely *et al.*,1988) and might be expected to require overlap as a form of mechanical bracing of the fringes, *Aporosaura* weighs approximately 5 g and suggests that particle exclusion may be particularly difficult in the fine Namib sand and/or that sand-swimming places additional restrictions on particle exclusion efficiency.

The spinous scales of those geckos with swollen plantar surfaces may also serve to exclude sand grains. In this case, however, it has been postulated that exclusion serves to avoid clogging of the plantar surfaces with sand (Russell, 1972, 1979). Available experimental evidence (Russell, 1979) indicates that this may be especially important if the surface layers of the sand are moistened. Species that may occupy littoral hibitats, such as *Stenodactylus khobarensis* and *Diplodactylus stenodactylus,* for example, frequently encounter such conditions. The same may be true for desert taxa such as *Geckonia* in coastal Morocco and several of the *Pachydactylus* group geckos in the coastal Namib, where fog may regularly dampen windward dune faces (Nagel, 1962). The significance of this anti-clogging mechanism in inland taxa is less clear. Nonetheless, measurements of interspine distances for several taxa (Table 2) are small enough to exclude sand grains of the local modal size. The role of the swollen tissue of the plantar regions in the function of this foot type remains enigmatic, but probably endows the plantar surfaces with greater compliance.

Sand shoes vs. shovels

Interdigital webbing is the rarest of the dune-dwelling pedal specialisations. It is always associated with the spinous plantar surfaces discussed above. Since webs exclude all sand grains from passing between the digits, sand size correlations are not particularly relevant. There has been considerable speculation about the role of webbing in desert geckos, centring almost exclusively on *Palmatogecko rangei,* as the remaining webbed taxa—*Kaokogecko vanzyli* and *Stenodactylus arabicus* have been described only relatively recently.

Andersson (1908) first assumed that the webbed feet of *Palmatogecko* served as adhesive organs for climbing on stones. As observations of the animal in the wild became available, this view was quickly abandoned. Barbour (1926) hypothesised that *Palmatogecko rangei* used its webbed feet as 'sand shoes' for running across the sand surface, and for 'diving' into the sand. Werner (1910) and Sukhanov (1968) also regarded *Palmatogecko* as a sand-swimmer, although neither apparently observed the living animal. Proctor (1928) believed that the webs served as (burrowing) shovels and sand shoes and these dual functions have been repeated ever since (e.g. Fitzsimons, 1943; Haacke, 1976*a*; Holm & Scholtz, 1980).

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the left. Dark lines on the right indicate interspine distances used as a measure of particle exclusion size in geckos exhibiting spinous foot morphology. Scale bar (for left photo) = 500 μm. (d) Photograph of the ventral surface of digit I of the manus of *Chondrodactylus angulifer,* showing the pattern of spinous scales characteristic of a number of psammophilous and dune-dwelling geckos. The fold in the digit (arrow) is a swollen region containing loose connective tissue and is also characteristic of this pedal design. Scale bar = 1 mm. (e) Scanning electron micrograph of the spinous scales on the ventral surface of digit IV of the pes of *Chondrodactylus angulifer.* Scale bar = 200 μm. (f) Scanning electron micrograph of the ventral surface of the plantar surface of the pes of *Colopus wahlbergi.* The tips of the largest spines bear minute, probably functionless setae, indicative of the primitively pad-bearing origin of this dune-dwelling species. Scale bar = 100 μm.

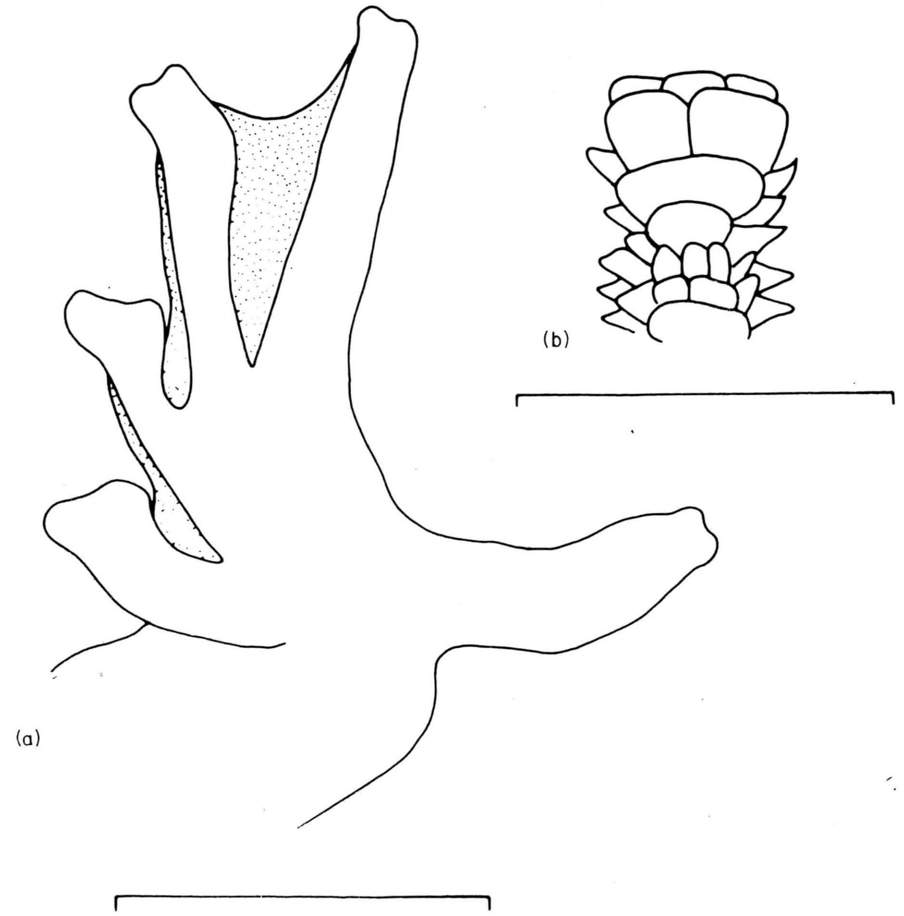

Figure 5. (a) Ventral view of the left pes of *Kaokogecko vanzyli* (TM 39024), showing the extent of webbing (stipple). (b) Ventral view of the distal extremity of digit IV of the manus of *K. vanzyli*, showing the retention of adhesive scansors. *Kaokogecko* is one of several satellite genera of *Pachydactylus* that form a morphotypic series in the shift and reduction of the adhesive apparatus. Scale bar = 5 mm (a); 2 mm (b).

The relative significance of these two functions has yet to be critically assessed. Increased surface area for the distribution of weight over an unstable, friable substrate, such as sand or snow, is indeed important for larger animals—hence human use of snow shoes and the increased foot area of camels (Gauthier-Pilters & Dagg, 1981). However, at very small body size (less than 5 g in most *Palmatogecko* and *Kaokogecko,* and much less in *Stenodactylus arabicus*) surface area-increasing mechanisms are probably of minimal functional importance, and are rather automatic outcomes of any selective regimes that act to increase pedal size. Clearly the occurrence of non-webbed geckos in sandy areas of comparable particle size and presumably consistency suggests that webs, though sufficient, are not necessary for locomotion on wind-blown sands.

Values for the bearing capacity (Goodwin, 1965) of Namib sand have not been reported, but it is clearly sufficient to support the weight of such small lizards. Windward dune faces may even support the weight of a 100 kg human (pers. obs.) or a car (Bagnold, 1954), due in part to aeolian compaction and the effect of moisture. Leeward slipfaces are not as resistant to incident compressive and shear forces. Nonetheless, laboratory tests indicate that a variety of lizards with unmodified digits (weights 4·8–20·0 g) were able to walk easily on horizontal surfaces of dry Namib sand without inducing surface failure or sinking. Likewise, Carothers (1986) found that the fringe-toed iguanid *Uma scoparia* (mean mass 18·5 g) did not sink into the sandy substrate when its fringes were removed. At angles of 30° or more from the horizontal, however, the test animals (*Anolis sagrei*, *Eumeces laticeps*, *Eumeces fasciatus*) did experience difficulty in progressing, as did Carothers' *Uma*, although sinking in the sand was minimal. The addition of even the slightest amount of moisture to the sand surface facilitated walking, even at the steepest angles. As noted for *Palmatogecko* (Fitzsimons, 1935*a*) no tracks were left on surfaces simulating moistened windward dune slopes.

It appears unnecessary to invoke weight-bearing as the primary functional role of *Palmatogecko* interdigital webs, although this may now be one role of these structures. Rather the structure of the feet, with their paraphalanges and associated musculature appears suited to the precise manipulation of the webs as used in digging, as postulated in the sand-shovelling model. This has been demonstrated by a detailed examination of the kinematics of digging in living *P. rangei* (Russell & Bauer, 1990).

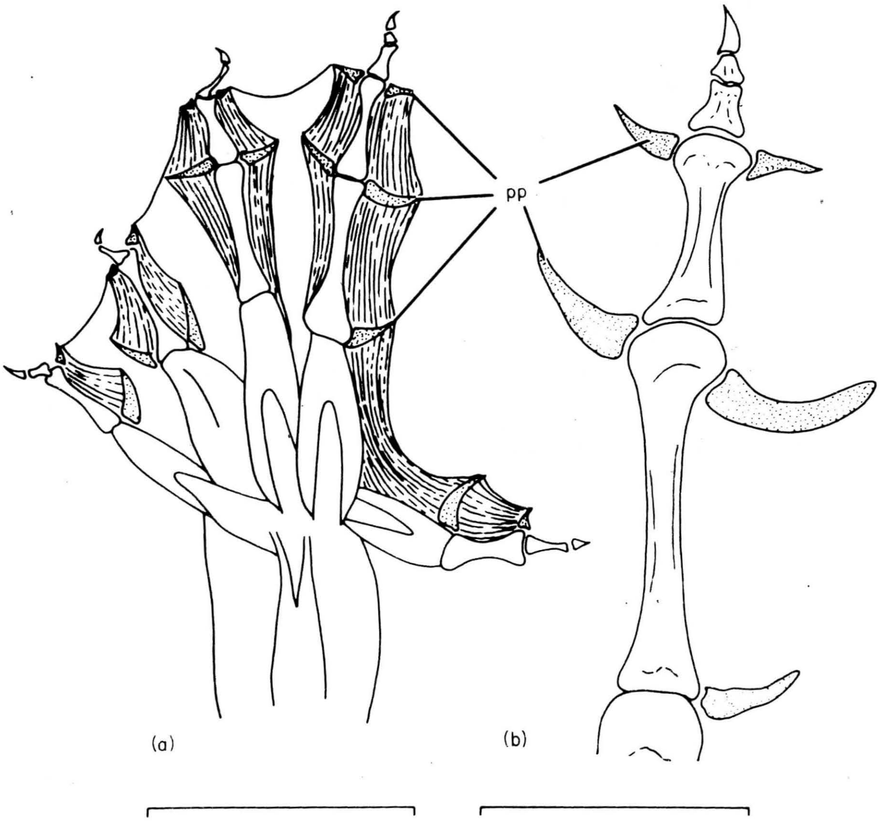

Figure 6. (a) Dorsal view of the dissected right pes of *Palmatogecko rangei* (BMNH 1938.4.7.7). The solid line connecting the tips of the digits indicates the extent of the interdigital web. Paraphalangeal elements (pp) are stippled. Note the extensive intrinsic paraphalangeal musculature (striations) and the linkage of digits IV and V via these muscles. (b) Dorsal view of digit IV of the pes of *P. rangei*. Note the reduction of the terminal phalanges and the asymmetrical disposition of the horn-shaped cartilaginous paraphalanges. Scale bar = 5 mm (a); 2 mm (b).

Table 1. *Predominant sand grain size in selected aeolian dune regions. Sand grain size figures represent means (*), modes (**), or ranges (***) as reported in the literature. Values obtained from Ahlbrandt, 1979 (A), Werner, 1987 (W), and this study (BR). Ahlbrandt (1979) should be consulted for reference to the original sources of sand textural parameter measurements*

Dune area	Sand grain size µm	Source
North America		
1. Algodanes Dunes, California	230*, 280*	A
2. Navajo Indian Res., Arizona	200*	A
Asia		
3. Takla Makan Desert, China	170*	A
4. Rub'al Khali, Saudi Arabia	250*	A
5. Peski Kyzylkum, U.S.S.R.	130–250***	A
6. Northern Negev, Israel	250–500**	W
7. ha-'Arava Valley, Israel	250–500**	W
Australia		
8. Great Sandy Desert, Australia	280*, 530*	A
9. Great Victoria Desert, Australia	260–300***, 500*	A
10. Simpson Desert, Australia	140–190***, 160*	A
Africa		
11. Grand Erg, Algeria	100–300***	A
12. Mauritania, Mali	250–400***	A
13. Libya, Niger, Chad	200*, 340*	A
14. Kalahari Desert, South Africa	210*	A
15. Namib Desert, Namibia	192**, 230*	BR, A

Table 2. *Pedal surface dimensions of dune-dwelling geckos. Minimum particle exclusion size is the size of the smallest sand grain that would be prevented from passing between the tips of fringing scales or from wedging between the plantar scales of spinous, swollen palmed species (determined from photographic measurements)*

Taxon	Pedal type	Dune region (from Table 1)	Mean minimum particle exclusion size (*n*)
Ptenopus garrulus			
(adult)	Fringe	14–16	248 µm (16)
(juvenile)			156 µm (32)
Teratoscincus scincus			
(adult)	Fringe	3	356 µm (16)
(juvenile)			262 µm (11)
Chondrodactylus angulifer	Spinous	14–16	225 µm (15)
Colopus wahlbergi	Spinous	14	133 µm (25)
Nephrurus levis	Spinous	8–10	225 µm (8)

Conclusions

While the majority of work devoted to the study of locomotion in geckos has concentrated on climbing adaptations (for a summary see Russell, 1976, 1979), the terrestrial specialisations of this family are also noteworthy (Haacke, 1976*d*). A branch of such non-climbing specialisations is seen in psammophilous forms, and here several suites of features have been developed convergently by different gekkonid lineages occupying similar sandy habitats. Dune-dwelling represents an extreme commitment to psammophily. Although a wide range of pedal morphologies, from unmodified digits in some *Phyllodactylus* to the spines, fringes, and webs of the taxa discussed above, are represented in geckos occupying dune areas, it is apparent that not all characteristics of these morphologies are directly related to dune habitation itself.

The spinous, swollen plantar surfaces of genera such as *Nephrurus* and *Chondrodactylus* may be generally related to psammophily but are not peculiar to dune regions and are only marginally present in such areas. While some dune-dwelling taxa exhibit these features, they appear to have been co-opted into other suites of modifications that are more strictly associated with dune areas. Thus, *Palmatogecko, Kaokogecko,* and *Stenodactylus arabicus* possess the spinous morphology but have combined this with the presence of interdigital webs. It is the latter that is more strictly associated with dune-dwelling. The spinous structure probably prevents the plantar surface from becoming clogged with sand, particularly if the substrate is damp, but does not offer any additional advantage to movement on dune faces.

Fringes and webs, on the other hand, are more indicative of dune occupancy. The former is found only in geckos that are primitively padless. The biology and microhabitat distribution of those taxa possessing fringes indicates that these structures are specifically correlated with surface locomotion and/or excavation in the loose sand of leeward dune slip-faces. Fringes are frequently associated with sand-swimming but may be used in burrowing, as in *Ptenopus* in interdune streets or marginally in the dunes themselves.

Several major types of fringing scales exist (Luke, 1986) and it is therefore difficult to make a strict association of 'fringes' in the generic sense with any particular microhabitat. The fringes of gekkonid lizards may be regarded as being useful in a variety of situations, although they have been associated specifically with rapid movement on sloping dune faces in other lizards (Carothers, 1986). While the fringes may function to increase surface area, their effect in this regard may be relatively small, but as the animals themselves are quite light, this may not be problematic in terms of locomotion on sandy substrates without slippage. Interfringe spaces are relatively large and allow the passage of at least some particles of sand. Thus, the fringes may not be particularly efficient in digging and burrowing. If the animal sand-swims, however, the movement of the feet in a horizontal plane may be involved in shimmy burial and the fringes may confer a significant advantage in such activities.

Webs between the digits represent a more major pedal modification than that of possessing fringes, since the continuous skin between the digits restricts the freedom of movement and independence of each digit. This may account for the relative rarity of webs as they restrict the versatility of the feet in terms of the variety of activities they can perform and the types of habitats to which they are suited. The webbed feet of *Palmatogecko rangei* appear to be much more efficient excavating devices than the fringes of dune-dwelling geckos as they are able to trap sand in a contained receptacle and move it as a unitary mass. *Palmatogecko* occupies the compacted windward dune faces and the webs allow an unbroken excavating surface to be brought into contact with the more resistant substrate, to loosen it along a continuous line of contact and to shift it away in a more controlled and predictable fashion. This ability is particularly important in the construction of patent burrows in the compact sand of the windward dune face; in the loose sand of the leeward face, where sand is merely displaced rather than excavated, bulk sand transport would be relatively useless. In terms of weight distribution, webs are probably passively of some effect, but given the small mass of the animals this rôle is of relatively minor significance. Although *Kaokogecko* does not strictly occupy dune faces, it does inhabit adjacent gravel plains and is known to move small pebbles by grasping them in the continuous web, lifting them and depositing them to the rear. Thus again the web provides a receptacle for controlled and deliberate excavation in a substrate that requires the movement of less friable material.

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