

An introduction to the Lepismatidae (Thysanura: Insecta) of the Namib Desert Sand Dunes

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1 INTRODUCTION

The insect order Thysanura (known as fishmoths or silverfish) is commonly found in most terrestrial environments (Richards and Davies 1977). The family Lepismatidae is, in general, widely distributed in arid regions (Crawford 1979), where their ability to maintain a water balance in atmospheres below saturation level for short periods, without free water or food, has been considered a preadaptation to life in arid conditions (Edney 1971, Wallwork 1982). Apart from those species that live commensally with man, there is little information on the ecology of any free living Lepismatidae species worldwide. Kaplin and Martynova (1976) and Kaplin (1978) described the ecology of five Lepismatidae species from a central Asian sandy desert, but most other work refers to commensal species.

At least 40 species of Lepismatidae have been recorded from the Namib Desert between the Orange and Kunene Rivers, of which nine dune-living species occur in the main southern dune sea, between the Koichab and Kuiseb Rivers. Eight of the latter are treated here. The ninth is exceedingly rare and has not yet been recorded from Gobabeb. It belongs to an as yet undescribed genus, resembles a small *Ctenolepisma* species, and may be distinguished from the other species treated here by its colour pattern: two dark dorsal longitudinal lines running the whole length of the body. Another species which is not treated here is *Ctenolepisma spinipes* Irish. It occurs only on mixed sand and gravel substrates on interdune valleys of the main southern dune sea, and is not considered to be a dune-living species. It was recorded in small numbers only in the interdune

ABSTRACT

Eight Lepismatidae commonly co-exist on the Namib dunes south of the Kuiseb River. Their field identification, spatial distribution and temporal activity patterns are described. Each species occupies distinct habitats on the dune, and is active at times of day characteristic of the species. The relationships between morphological adaptations and life in a sandy substrate, as well as other adaptations to the Namib Desert environment are discussed.

valley traps during this survey. Virtually nothing is known of the ecology or biology of any of these species. Some work has been done on the adaptations of the Namib Lepismatidae to the desert environment (Edney 1971, Holm and Edney 1973, Holm and Scholtz 1980), but the identification of the species involved has subsequently been questioned (Irish 1986, 1987), and without voucher specimens they remain equivocal.

Seven of the eight lepismatid species considered here are endemic to the Namib. Only *Ctenolepisma terebrans* is known to occur outside of the Namib. It was first described by Silvestri (1908) from specimens collected in the Kalahari and occurs in sandy habitats throughout the western half of southern Africa. *Ctenolepisma pauliani* and *Hyperlepisma australis* were described by Wygodzinsky (1959). Irish (1986) described three *Mormisma* species, but has since transferred two of these species to *Namibmormisma* as follows, *Mormisma wygodzinskyi*, *N. muricaudata* and *N. setosa* (Irish & Mendes, in press). The latter two species are so similar that it is impossible to reliably distinguish them in the field and therefore, for the purposes of this preliminary paper, they are dealt with collectively under the name of *Namibmormisma muricaudata* s.l. The remaining two species, *Sabulepisma multififormis* and *Swalepisma mirabilis*, are readily distinguished in the field and are described by Irish and Mendes (in press).

The purpose of this paper is to provide an introduction to the Lepismatidae of the Namib dunes. First, we present a key based on gross morphology, and a photographic guide to assist the field identification of the eight dune-living species. Secondly, we present observations on two basic aspects of their ecology, that is, their spatial distribution in relation to the dune habitat, and their temporal activity patterns. In addition, adaptations of the Namib dune Lepismatidae to a desert environment and their role in the sand dune ecosystem are discussed.

2 METHODS

2.1 Key and Photographic Guide

Specimens used in the photographic guide were collected from the Namib dunes in the vicinity of Gobabeb (23°34'S, 15°03'E), and are now kept in the D.E.R.U. reference collection. Voucher specimens of each species are also housed in the State Museum, Windhoek.

The morphological features used in the key are the body breadth/length ratio (i.e. squat vs. slender), the relative lengths of the antennae, cerci, terminal filament, and the shape of the pronotum and frons (Fig. 1). Colour patterns are not used as a definitive part of

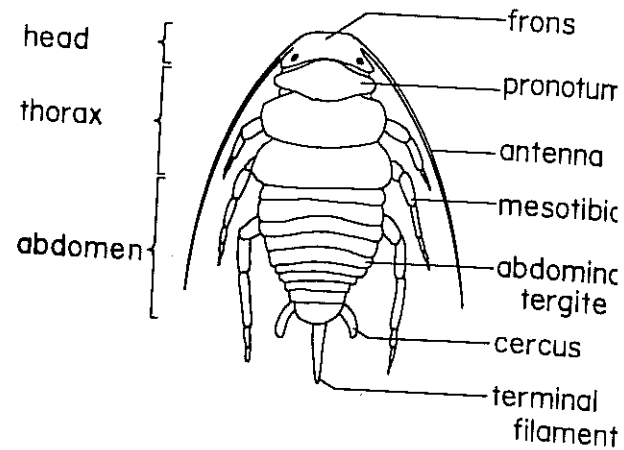


FIGURE 1: Diagram of a lepismatid (*M. wygodzinskyi*) to illustrate the terminology used in the field identification key.

the key, but are provided in the general description of each species, as they can be useful for the identification of undamaged specimens. For example, scales impart a colour pattern to the *Ctenolepisma* and *Hyperlepisma* species. However, because scales fall off with abrasion the colour of a newly moulted individual may be quite different to one that is about to moult. In addition, although the *Namibmormisma* species have colourless scales, their cuticle has orange pigments arranged in distinctive patterns. These colour patterns are useful for identification in the field only, as the pigments are usually lost when specimens are placed in alcohol.

2.2 Spatial and Temporal Activity Patterns

Pit-fall trapping was used to study the temporal activity patterns, and the distribution in relation to habitat, of the Lepismatidae. Robinson and Seely (1980) identified four distinct habitat related biotic communities on the Namib dunes, referred to as interdune, dune base, plinth, and slipface. These habitats were characterised by differences in abiotic factors such as sand grain size, soil moisture, and sand stability. For the purpose of this study six habitats were delineated on the basis that the micro-environments in each may be different. These were the interdune and slipface, as in Robinson and Seely (1980), plus upper, middle and lower slopes (the latter is equivalent to plinth and dune base combined), as well as "within vegetation" on the dune slopes. The only vegetation sampled was a common perennial grass species, *Stipagrostis sabulicola* (Pilger) de Winter (Poaceae). Data were obtained during September 1981 to April 1982, and July 1982 to October 1982.

Traps were set up in four 2x5-trap grids with 40m between traps, and 120m between grids on the leeward interdune and dune slope (Fig. 2). An additional 50 traps were set at 1m intervals into the base of the slipface, regardless of their distance from the slope traps. During the July to October trapping period, ten traps

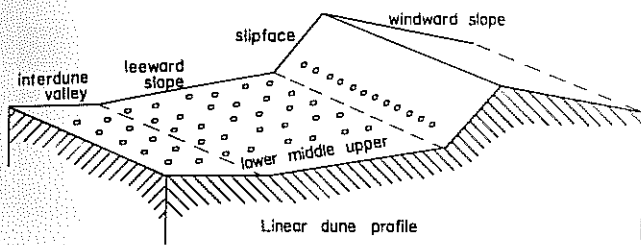


FIGURE 2: Illustration of the trap grid system on a typical linear dune.

were set in the centre of selected vegetation clumps situated on the dune slope. During the September to April trapping period, grids were placed at each of seven different dunes along a 120km east-west transect spanning the southern Namib dune field and trapping was carried out at each dune consecutively for three days. During the second trapping period, only one site was used near Gobabeb and trapping was conducted for fourteen consecutive days at monthly intervals. Traps were checked hourly, resulting in a total of 19 963 trap-hours.

During the first trapping period every capture was preserved in alcohol for identification. The time of day and trap location in relation to the habitat were also noted. Lepismatidae caught during the second trapping period were identified in the field where possible and released near the trap. Individuals not identifiable in the field were preserved for later identification.

The analysis of distribution in relation to habitat was complicated because the different habitats on the dune were sampled with unequal effort (trap-hours). To compensate for this bias, capture data from each of the six habitats were corrected using the equation, $C_{ij} = (H/z)/h_i \times n_{ij}$, where C_{ij} is the corrected number caught, and i refers to each habitat and j refers to each species. H is the total number of trap-hours, h_i is the number of trap-hours in each habitat and z is the number of habitats (6). The corrected sample size (C_{ij}) method was used rather than calculating trapping rate (n_{ij}/h_i) to facilitate comparison with the uncorrected sample size (n) and to avoid dealing with the very low trapping rate values (10^{-3}).

Similarly, trapping was not consistent with time of day (nocturnal hours being under-represented). Therefore, for the analysis of daily activity patterns, the capture data was corrected for trapping effort in each hour of the day by substituting $z = 6$ with $z = 24$ in the equation above. In this case i refers to each hour of the day.

The total sample size for each species, derived from the sum of the corrected number caught in each habitat ($\sum C_{ij}$), was used as a single index incorporating both the abundance of the species and its degree of surface activity.

3 RESULTS

3.1 Key and Photographic Guide

TABLE 1: Key to the field identification of seven Lepismatidae found in the southern Namib sand dunes. Further descriptive information is given with each plate.

1. Antennae short, about as long as width of head (plate 4 & 5)2
Antennae long, at least half body length (Plates 1,2,3,6&7)3
2. Cerci swollen (width: length=0,44:1) (Plate 5)*N. muricaudata s.l.*
Cerci slender (width: length=0,15:1) (Plate 6)*H. australis*
3. Body slender (width: length=0,25:1), elongate (plates 1,2&3)4
Body squat (width: length=0,3 to 0,4:1) (Plates 6 & 7)6
4. Frons bulging; body spindle-shaped, widest on the abdomen (Plate 3) ...*S. mirabilis*
Frons not bulging; body parallel-sided, and widest at thorax (Plates 1&2)5
5. Terminal filament shorter by half than cerci; body usually lighter coloured and larger than *C. terebrans* (Plate 1)*C. pauliani*
Terminal filament as long as or longer than cerci; body usually darker coloured and smaller than *C. pauliani* (Plate 2)*C. terebrans*
6. Pronotum subrectangular (Plate 7) .*S. multiformis* (7)
Pronotum subelliptical (Plate 6) ...*M. wygodzinskyi*
7. Cerci shorter than terminal filament, slender juveniles & mature females
Cerci as long as terminal filament, swollen mature males

3.2 Spatial Distribution on the Dunes

Lepismatidae were found in all six dune habitats sampled (Fig. 3), but there was considerable habitat specificity amongst the species. *C. terebrans* were limited mainly to the interdune valley, with a few individuals captured on the middle to lower slopes, and none in the *S. sabulicola* clumps (Fig. 3). Although no *C. terebrans* were trapped in the vegetation clumps during this survey, they have been collected manually from this habitat (*pers. obs.* RTW & JI). In contrast, most *C. pauliani* were found associated with vegetation, a few on the middle to lower slopes and none on the interdune valley (Fig. 3). A few individuals of both *C. terebrans* and *C. pauliani* were located on the slipface. The single abundance and activity index (Fig. 3) shows that *C. pauliani* were high in the range of indices for all species, while *C. terebrans* were in the middle of the range.

M. wygodzinskyi were the most habitat specific of the more abundant/active species, located only on the dune slipface (Fig. 3). *S. multiformis*, also an abundant/active species, had a distribution which overlapped that of *M. wygodzinskyi*, but were also found on the upper and middle slopes and within *S. sabulicola*.

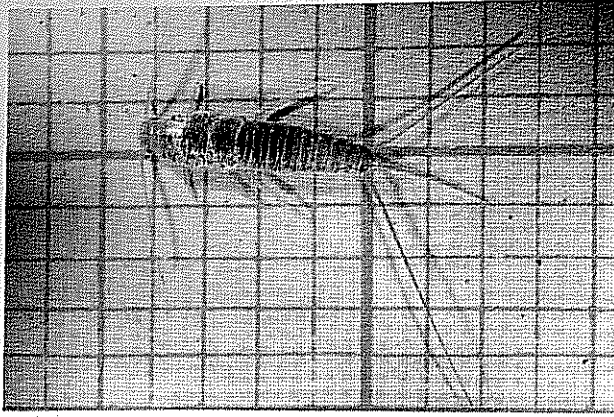


PLATE 1: *C. pauliani*: slender body, long antennae, cerci longer than terminal filament (upto 2,5X body length), frons flattened with macrosetae plumose, well developed setal comb on mesotibia, posterior edge of some abdominal tergites with 3+3 bristlecombs.

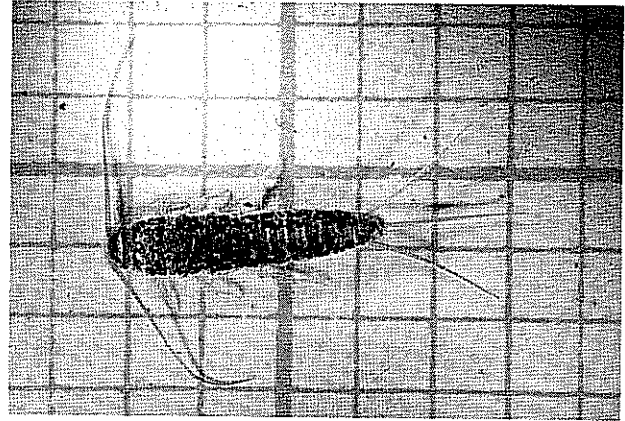


PLATE 2: *C. terebrans*: slender body, long antennae, cerci about the same length or slightly shorter than terminal filament (about 0,5-1,0X body length), frons flattened with macrosetae plumose, well developed mesotibial setation but not forming a setal comb, posterior edge of some abdominal tergites with 3+3 bristlecombs.

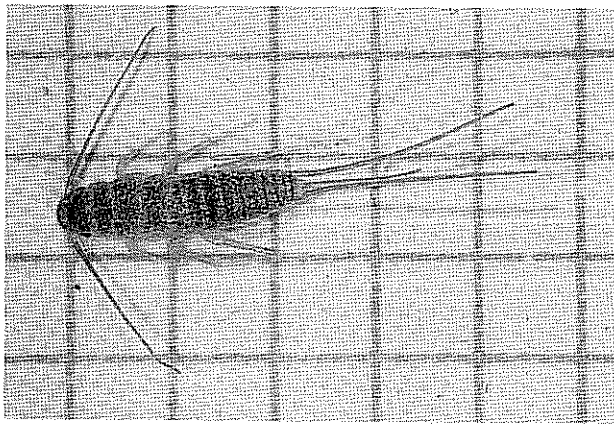


PLATE 3: *S. mirabilis*: body intermediate between slender and squat, more spindle shaped, antennae long, cerci about equal in length to terminal filament (about 0,5X body length) in males but less than half terminal filament length in females and juveniles, frons "bulged" and macrosetae finely plumose, 3+3 bristlecombs on posterior edge of most abdominal tergites.

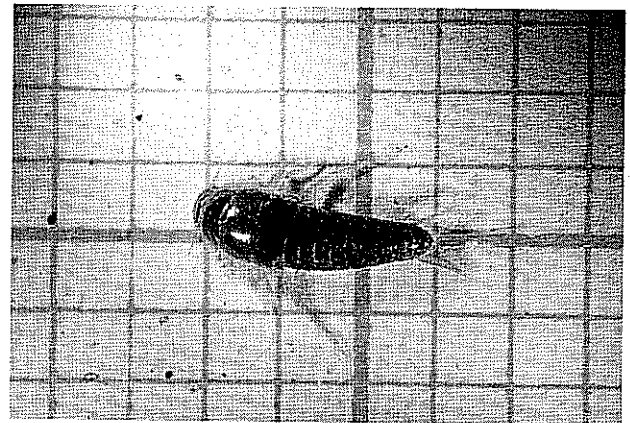


PLATE 4: *H. australis*: squat body, very short antennae, short slender cerci and short terminal filament, frons flattened with macrosetae plumose, 3+3 bristlecombs on posterior edge of most abdominal tergites.

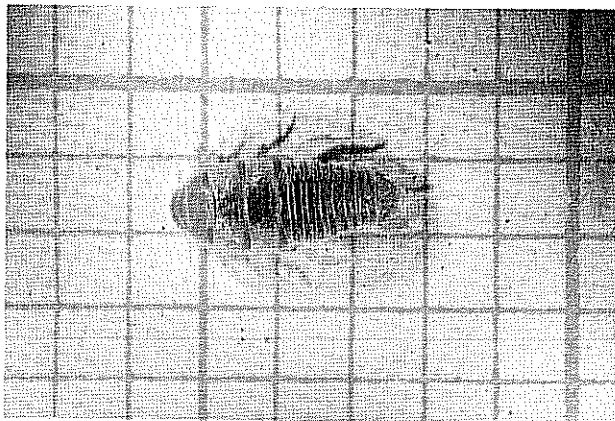


PLATE 5: *N. muricaudata*: squat body, short antennae, cerci very short and swollen, short terminal filament, frons flattened with macrosetae smooth, posterior edges of abdominal tergites with 1+1 setal fringes.

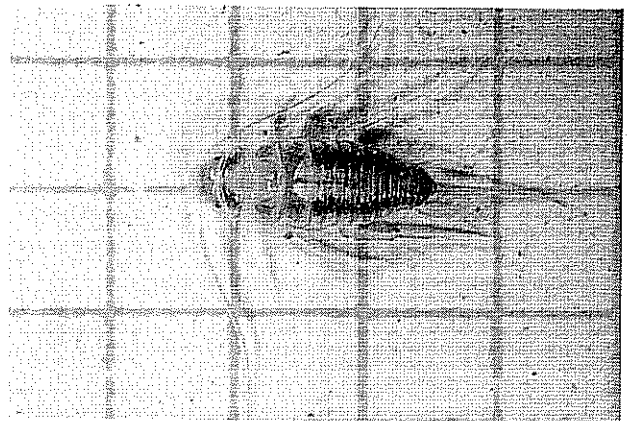


PLATE 6: *M. wygodzinskyi*: squat body, long antennae, cerci short (female and immature) or relatively longer cerci (male) but not swollen, terminal filament about 0,5X body length, frons bulging with macrosetae smooth, posterior edges of abdominal tergites with 1+1 setal fringes, pronotum subeliptical.

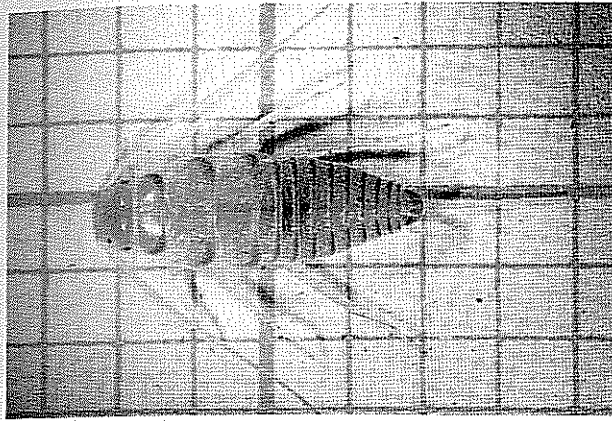


PLATE 7: *S. multiformis*: squat body, long antennae, cerci short and not swollen (female and immature) or long and swollen (male), terminal filament about 0.5X body length, frons bulging with some macrosetae finely plumose, posterior edges of abdominal tergites with 1+1 setal fringes, pronotum subrectangular.

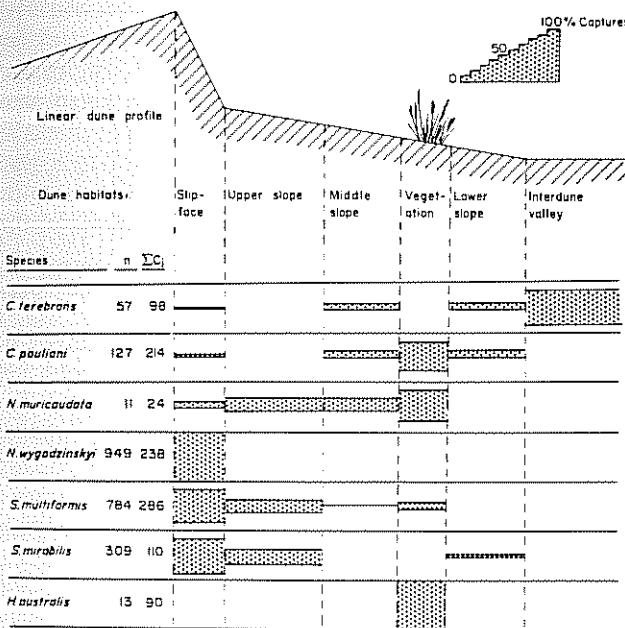


FIGURE 3: Distribution of Lepismatidae on a sand dune, shown as the percentage of weighted captures (ΣC_i) in each of six habitats. ΣC_i = abundance/activity index (see text for derivation). n = uncorrected sample size of each species.

la clumps (Fig. 3). Like the previous two species, *S. mirabilis* were mainly found on the slipface and upper slope with a few individuals on the lower slope (Fig. 3). *S. mirabilis* were in the middle of the range of abundance/activity indices.

The distribution patterns of *N. muricaudata s.l.* and *H. australis* were difficult to interpret because of low sample sizes (Fig. 3). It appeared that *N. muricaudata s.l.* were the most ubiquitous but least abundant/active of the eight species. They were found in similar abundance from the slipface to mid-slope, but with the greatest number of individuals associated with vegetation. All specimens of *H. australis* were found in *S.*

subulicola clumps, so they appear to be as habitat specific as the exclusively slipface dwelling *M. wygodzinskyi*. Although the sample size for this species was low (n = 13), subsequent sampling has confirmed that this species is only found associated with vegetation clumps. This observation is contrary to that of Holm (1970) who described *H. australis* as strictly a plains dweller. It is probable that Holm (1970) misidentified *C. spinipes* which is an interdune plains dwelling species (Irish 1987) that resembles *H. australis*. Correcting for sampling effort indicates that *H. australis* were in the middle of the range of abundance/activity indices for all species (Fig. 3).

3.3 Temporal Activity Pattern

The temporal activity pattern is presented for each species separately, as the percentage of the total number of each species caught in each hour of the day (Fig. 4). Despite the fact that trap results are summed for several months spanning both summer and winter, and that they represent population trends rather than individual behaviours, certain patterns are evident.

Most of the species show a distinctly bimodal activity pattern (Fig. 4) which is similar to other dune dwelling arthropods (Holm and Edney 1973, Holm and Scholtz 1980). Both *Ctenolepisma* species were most active in the period just after sunrise, and for an extended period from just after sunset to midnight and early morning (Fig. 4a & b).

The activity of *M. wygodzinskyi* and *S. multiformis* was predominantly bimodal but continued at lower levels throughout the day (Fig. 4e & f). In contrast, the activity pattern of *S. mirabilis*, which is also a slipface and upper slope dwelling species, reached a peak in the few hours after sunrise but with negligible activity throughout the rest of the day (Fig. 4g). Activity of *S. mirabilis* started again after sunset, reached a peak about midnight but, also contrary to *M. wygodzinskyi* and *S. multiformis*, continued through the coldest part of the night to sunrise (Fig. 4g).

The interpretation of graphs for *N. muricaudata s.l.* and *H. australis* was difficult because of the low sample sizes involved. The few *H. australis* that were trapped were only caught at night (Fig. 4c), while *N. muricaudata s.l.* was caught during both day and night (Fig. 4d).

4 DISCUSSION

4.1 Morphological Adaptations and their Relationship to Spatial Distribution

In general, desert environments are relatively harsh because of extremes of temperature, lack of water and the effect of wind on unstable substrates (Louw and Seely 1982). In the Namib, as in other deserts, the abi-

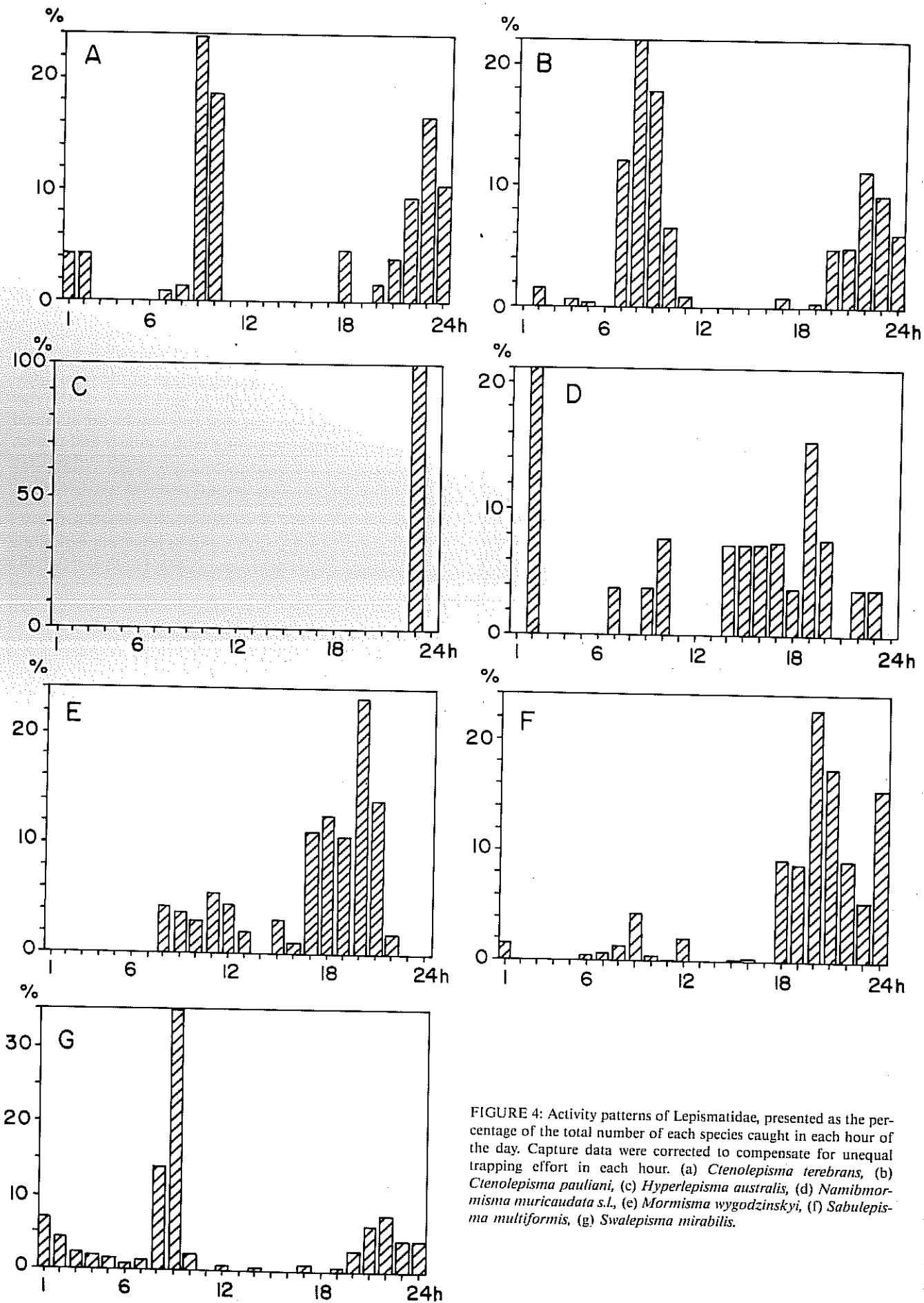


FIGURE 4: Activity patterns of Lepismatidae, presented as the percentage of the total number of each species caught in each hour of the day. Capture data were corrected to compensate for unequal trapping effort in each hour. (a) *Ctenolepisma terebrans*, (b) *Ctenolepisma pauliani*, (c) *Hyperlepisma australis*, (d) *Namibmormisma muricaudata s.l.*, (e) *Mormisma wygodzinskyi*, (f) *Sabulepisma multiformis*, (g) *Swalepisma mirabilis*.

otic environment is likely to be the major factor affecting both plant and animal populations (Noy-Meir 1979/80). Insects, because of their small size, are able to make use of micro-environments that exist on an otherwise homogeneous looking sand dune, thereby avoiding the harsh desert conditions (Seely 1983). The existence of many micro-environments that can be exploited in different ways using a diverse array of adaptations may have contributed to the diversification of much of the Namib arthropod fauna (Seely 1978, Robinson and Seely 1980), though this is probably neither the main nor the only reason for the observed diversity. The distinct morphologies, and spatial and temporal distributions of the Lepismatidae living in the Namib dunes may exemplify this phenomenon of diversification in response to abiotic conditions.

A number of examples of morphological adaptations that relate to the distribution of the Lepismatidae are apparent. In most cases an adaptive gradient can be discerned for any particular adaptation. The unmodified form is the one commonly found in most non-psammophilous *Ctenolepisma* species, particularly those belonging to the nominal (mainly Palaearctic) subgenus. Moderate adaptations are found in the many psammophilous southern African species of the sub-genus *Ctenolepisma* (*Sceletolepisma*) (which includes *C. terebrans* and *C. pauliani*), while the most extreme psammophilous adaptations are found in *Namibmormisma* and *Hyperlepisma*.

All the species considered here have robustly setated legs. Most non-psammophilous *Ctenolepisma* species have very few and very short spines on the legs. Psammophilous species in the Namib and elsewhere in southern Africa generally have longer and more numerous spines on the legs (Irish 1987). Robust leg setation probably aids locomotion on and digging in sand by increasing the surface area of the leg. In the case of *C. terebrans* the leg spination is fairly well developed, and the species occurs in moderately sandy habitats (Fig. 3). *C. pauliani*, which occurs in much sandier habitats, probably has the best developed leg setation of any species in the genus, sporting a setal comb on the mesotibia. Leg spination in the other species here considered, all of which live exclusively in the sand dune habitat, resembles that of *C. pauliani*.

The unmodified thysanuran has all three pairs of legs of similar length. The psammophilous species have the first pair of legs much shorter, and the third pair much longer than the intermediate pair. The relative difference in the lengths of the different pairs of legs increases with an increase in the degree of sandiness of the habitat occupied. This is probably an adaptation to digging in soft sand; the shorter, stronger legs do the actual digging, while the longer hind legs shove the accumulated sand out of the way behind the body.

Body shape in psammophilous lepismatids also changes from the usual elongate shape which is still

found in the Namib *Ctenolepisma* species, to the compact, streamlined shape of the *Namibmormisma* and *Hyperlepisma* species. Kaplin (1978) observed a similar trend when comparing psammophilous and non-psammophilous Lepismatidae in the eastern Karakum. The trend to become more streamlined with sand living suggests that, for animals of this size range, sand presents a fluid medium through which they move in a manner similar to other animals that live in fluids, such as fish or birds. A compact body shape may also assist surface activity in those species which are active under windy conditions.

Furthermore, all non-locomotory appendages (antennae, caudal filaments, labial and maxillary palpi, styli and ovipositors) are to a greater or lesser degree reduced in length (or number, in the case of styli) in most psammophilous Lepismatidae. This reduction apparently serves to streamline the body. There are two obvious exceptions to this rule. *C. pauliani* has very long antennae and caudal filaments. *C. pauliani* and *S. multififormis* also have widely dilated distal segments of the labial palp. These apparent anomalies cannot be explained at present.

4.2 Temporal Activity Patterns

In many desert arthropods, distinct patterns of diurnal activity have been attributed to adaptations for the maximisation of thermal conditions (Hamilton 1971), minimisation of heat and water stress (Holm and Edney 1973, Holm and Scholtz 1980, but see Seely & Mitchell, 1987), or facilitation of moisture gain (Hamilton and Seely 1976, Seely and Hamilton 1976, Seely 1979, Seely *et al.* 1983), as well as exploitation of other abiotic and biotic resources (Seely 1983, Curtis *et al.* 1984). Lepismatidae in the Namib dunes show activity patterns distinct to each species. Some are active throughout most of the diel cycle, and one may suppose that these species have evolved specific behavioural and/or physiological adaptations to cope with hostile environmental conditions. In contrast, other species, which show distinct activity patterns, may have less well developed adaptations and may simply avoid extreme conditions and/or limit activity to less extreme conditions. For example, the activity of the *Ctenolepisma* species during daylight is contrary to the negative phototactic responses exhibited by the majority of lepismatids, e.g. *C. longicaudata* (Heeg 1967). Rather, observed activity was probably a response to the equitable temperatures experienced at those times of day (see Robinson and Seely 1980). This response has also been observed in other Namib Desert arthropods (Holm and Edney 1973).

In contrast to the *Ctenolepisma* species, *M. wygodzinskyi* and *S. multififormis* continued activity throughout the day, albeit at a reduced level, when temperatures and water vapour deficits may be high. It is possible that these species, like the tenebrionid beetles *Zopho-*

sis (Cardiosis) fairmairei (Péringuey) and *Z. (C.) hamiltonuli* (Koch), become active at times when their temperature can be maintained at an optimum level, regardless of other environmental factors pertaining at the time (Hamilton 1971). In addition, Holm and Scholtz (1980) noted that *Mormisma* species (probably *S. multiformis*) were facultatively wind active. This phenomenon has been described for other slipface dwelling arthropods, such as the tenebrionid beetles *Cardiosis* spp., *Lepidochora* spp., and *Onymacris* spp. (Holm and Scholtz 1980, Seely 1983, Curtis *et al.* 1984), so one might also expect adaptations within these species to cope with wind and the resultant sand movement and desiccation.

The activity pattern of *S. mirabilis* was unusual compared to all the other species because activity continued through the coldest part of the night. Observation of behaviour suggests that this species responds to the presence of early morning fog in the manner of some other dune arthropods (Seely 1979, Seely *et al.* 1983), possibly becoming active on the surface in order to take up moisture as it condenses on the sand. Therefore, this species may maintain a water balance in this arid environment in a manner different to other Namib dune Lepismatidae. In addition, *S. mirabilis* seems to be more abundant on the dunes closer to the coast, which receive a higher proportion of fog precipitation than inland dunes.

In summary, the Lepismatidae of the Namib dunes have spatial distributions and temporal activity patterns distinct to each species. Spatial distribution appears to relate to the degree of morphological adaptation to sand living, while temporal activity patterns may relate to different physiological adaptations and/or behavioural responses to desertic conditions. In addition, the Lepismatidae of the Namib dunes, like the more conspicuous Tenebrionidae, are detritivores. In a desert environment, arthropod detritivores may have an important direct or indirect rate limiting role in the breakdown and release of nutrients and energy into the ecosystem (Crawford 1979, Crawford and Taylor 1984). Therefore, as one of the most numerically abundant detritivorous arthropods of the Namib dunes (pers. obs. RTW), the Lepismatidae may be an important animal component of this ecosystem.

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