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BURROWING HABITS AND SUBSTRATE SELECTION IN ULTRAPSAMMOPHILOUS TENEBRIONID BEETLES OF THE NAMIB DESERT

Y. COINEAU (1), *N. LANCASTER* (2), *R. PRODON* (3), *and M.K. SEELY* (2)

(1) *Laboratoire de Zoologie des Arthropodes,*
Muséum National d'Histoire Naturelle,
61, rue de Buffon, F-75231 Paris Cedex 05
(2) *Desert Ecological Research Unit.,*
P.O. Box 953, Walwis Bay 9190, SWA-Namibia
(3) *Laboratoire Arago, F-66650 Banyuls-sur-Mer*

TÉNÉBRIONIDES
CHOIX D'UN SUBSTRAT
COMPORTEMENT FOUISSEUR
DÉSERT DU NAMIB

RÉSUMÉ. – Les Ténébrionides du genre *Lepidochora* sont des fouisseurs hyperpsammophiles des dunes de sable du désert du Namib. *L. discoidalis* est surtout confiné sur les pentes sous le vent (avalancheuses) des dunes, où s'accumulent les débris végétaux transportés par le vent, et où se trouve le sable le plus fin (0,125 à 0,180 mm), le mieux trié et le plus meuble. Toutefois, dans les expériences de choix effectuées au laboratoire avec des sables tamisés, *L. discoidalis* s'enfouit de préférence dans du sable de 0,045 à 0,090 mm. Il y a donc un désaccord entre ce preferendum mesuré expérimentalement et la granulométrie du sable naturel. Le choix d'un substrat pour l'enfouissement se fait vraisemblablement sur critère mécanique.

TENEBRIONIDS
SUBSTRATE SELECTION
BURROWING HABITS
NAMIB DESERT

ABSTRACT. – The Tenebrionids of the genus *Lepidochora* are ultrapsammophilous diggers living in the sand dune of the Namib Desert. *L. discoidalis* is mainly confined to the leeward slopes (slip-faces) of the dunes. Here wind-blown vegetable detritus accumulates, and the finest (0.125 to 0.180 mm), the best sorted and the least compact sand is to be found. However, in multichoice experiments carried out in the laboratory with artificially sorted sands, *L. discoidalis* is found to prefer digging in 0.045 to 0.090 mm sand. Thus there is a discrepancy between this experimental grain-size preferendum, and the sand naturally available in the dune environment. The substrate selection is very likely to be based mainly on mechanical criteria.

INTRODUCTION

The Namib is a cool, coastal desert on the south-western coast of Africa. A long, narrow dune field extends south from the vicinity of the Curoca River in Angola to the southern border of SWA/Namibia at the Orange River.

Tenebrionid beetles form a conspicuous part of an unusually diverse endemic fauna occupying this desert. They are dependant on fog as a major source of moisture (Seely, 1978, 1979) and use wind-blown plant detritus as their main energy source (Koch, 1961, Seely, 1978). Species of *Lepidochora* are found throughout the dune field of the Namib (Koch, 1962 and pers. obs.) and form an important component of its crepuscular to nocturnal fauna.

Lepidochora discoidalis Gebien (Syn. *L. argentogrisea* Koch) is the most common species of this genus in the southern dune ecosystem and consequently aspects of its biology have received considerable attention. Kuhnelt (1969) and Louw and Hamilton (1972) considered activity rhythms and their relation to temperature, Louw and Hamilton (1972) also considered metabolic rate, nutrition and digestion. Its unique fog-water uptake behaviour has been investigated (Seely and Hamilton, 1976; Seely, 1979; Seely *et al.*, in press), while recently the cuticular lipids of *L. discoidalis* have been described and their effect on water loss discussed. In this paper we discuss aspects of the digging behaviour of *L. discoidalis* and *L. Kahani* Koch and relate these to the ecology of the dunes of the Namib desert.

DUNE TRANSECT AND LOCALIZATION OF THE *LEPIDOCHORA* IN THE FIELD

The slope of a typical dune is about 5° on the plinth, increasing to 15-20° in the windward side of the crest (Fig. 1*a*). The angle of repose at about 32° is reached in the slip-face, where "the avalanching of sand takes place in a series of overlapping lobes" (Lancaster, 1981). On each dune, there is a decrease in mean and modal grain size from the base to the crest, with the finer sand on the slip face (Fig. 1*b*). In accordance with Lancaster's observations, several populations of sand grains can be observed : a coarser population at the base of the dunes has a prominent mode of about 0,355 mm. A finer population prevails in the upper part of the dune with a mode between 0,125 and 0,180 mm. The samples taken near the interdune corridor show a secondary mode near 0,090 mm which perhaps corresponds to a third sand grain population.

The variations of the sorting index show clearly that the best sorted sand is to be found on the slip-face and the least sorted on the interdune (Fig. 1*c*). The substrate compactness, measured with a penetrometer, is minimal on the unstable slip-face and maximal on the plinth and above all on the windward side of the crest (wind compaction) (Fig. 1*d*). Due to a decrease of wind speed behind the dune, dry wind-blown plant detritus accumulate in the form of cushions on the lee slope at the base of the uncompacted slip-face (Fig. 1*f*). This wind blown plant detritus also accumulates, however, at the base of the perennial vegetation which occurs patchily on the dune slope, where sand is gently sloping and relatively stable.

Lepidochora discoidalis and *L. kahani* are species primarily of the slip-face and avalanche base habitat. They are considered psammophyllic diggers "swimming" through the uncompacted sand medium. These species are entirely substrate dependant and show extensive adaptations for occupation of this uncompacted substrate. *L. discoidalis* are somewhat more crepuscular than *L. kahani* but may be active in strong winds before sunset or long after sunrise on slip-faces which are in shadow. They occupy the active slip-face often apparently foraging on detritus as it is being distributed by wind. *L. kahani* are somewhat larger and almost entirely nocturnal during periods of slip-face activity. They forage on the more compact sand in the vicinity of the avalanche base or at the mats of detritus which accumulate there (Fig. 1*g* and *h*).

MORPHOLOGICAL FEATURES OF *LEPIDOCHORA* TENEBRIONIDS

The Tenebrionids of the genus *Lepidochora* typically have a discoidal shape, while the body becomes progressively thinner at its periphery. This shape facilitates penetration into the sand as well as change of direction within the substrate. The body surface is entirely covered with flattened recumbent setae. This covering is very dense in *L. discoidalis* providing its typical grey colour (Fig. 2*a*). It is suggested that these scales protect the tegument from sand abrasion, while the longer setae protect the articulation between the pro- and mesothorax against the intrusion of sand grains (Fig. 2*b*). The long bristles found under the outer margin of the elytra seem to keep the sand from the ventral side of the animal when it burrows, without hampering the movements of the tibiae and tarsi. In this way, the margins of the pronotum and of the elytra shelter the movements of the legs, as the sand is moved backwards during burrowing.

The fore-legs are relatively short; the broad extremities of their tibiae bear short but strong spurs (Fig. 3*c*). The middle and specially the hind-legs are longer; the tibial spurs are very long, digitated and spatula-shaped; the tarsal claws are long and slightly curved (Fig. 3*d*).

All these characters clearly represent adaptations for digging; the division of labour between the fore-legs scraping the substrate, and the middle- and hind-legs sweeping the sand backward and pushing the body foreward is typical. The general shape of the body is, according to Medvedev (1965), characteristic of beetles "swimming" in the sand (i.e. digging without constructing burrows) : a streamlined and "drop-shaped" body, the pronotum merging smoothly with the elytra, a small head withdrawn into the thorax so that the eyes are protected by the anterior pronotal angles, prothorax and mesothorax broadly and tightly joined...

DIGGING HABITS

When the animal begins to burrow, the fore-legs, which are stretched sideways when walking, are brought back under the body, and excavate the sand under the head and the prothorax (Fig. 3*a*). The articulation between the pro- and mesothorax bends as the head is brought into the depression excavated by the fore-legs and, as a result of the action of the middle and hind-legs, the head then penetrates the sand. The antennae are drawn back under the lateral expansions of the prothorax. As is also observed during walking, the legs of a same pair move synchronously in the opposite direction, one foreward, the other backward (occasionally, the fore-legs act simlultaneously to pull the body forward). There is no strict synchronism between the fore-and hind-legs of one side and the middle leg of the opposite side, although the fore-leg of one side usually reaches its hindmost position just after the middle leg of

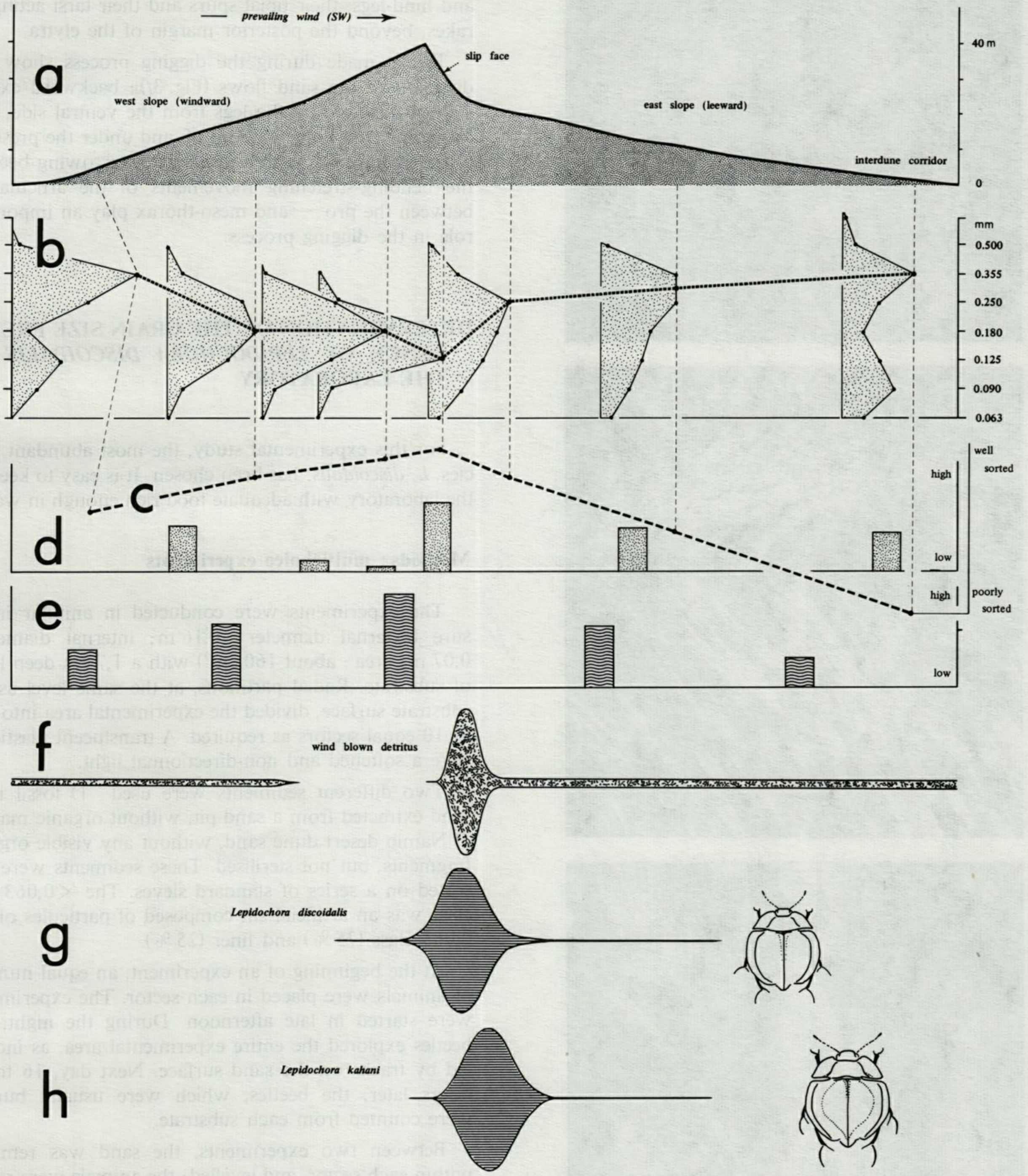

Fig. 1. – Diagram showing schematically the variations of some ecological parameters along a dune profile. a, Dune profile; b, Grain – size frequency distributions; c, Variation of TRASK's sorting index; d, Relative penetrability of the dune surface; e, fog water precipitations; f, Distribution of wind-blown detritus; g, Distribution of *Lepidochora discoidalis*; h, Distribution of *L. Kahani*.

the same side has reached its foremost position. The rhythm of the hind-legs is somewhat slower. The fore-legs dig the sand and pull it within reach of the middle legs. The sand is then moved backwards by the middle and hind-legs, their tibial spurs and their tarsi acting as rakes, beyond the posterior margin of the elytra.

Tracks made during the digging process show the direction of the sand flows (Fig. 3*f*) : backward expulsion of the sand by the legs from the ventral side, and formation of a bulge in front of, and under the pressure of the prothorax. As in a number of burrowing beetles, the bending-stretching movements of the articulation between the pro – and meso-thorax play an important role in the digging process.

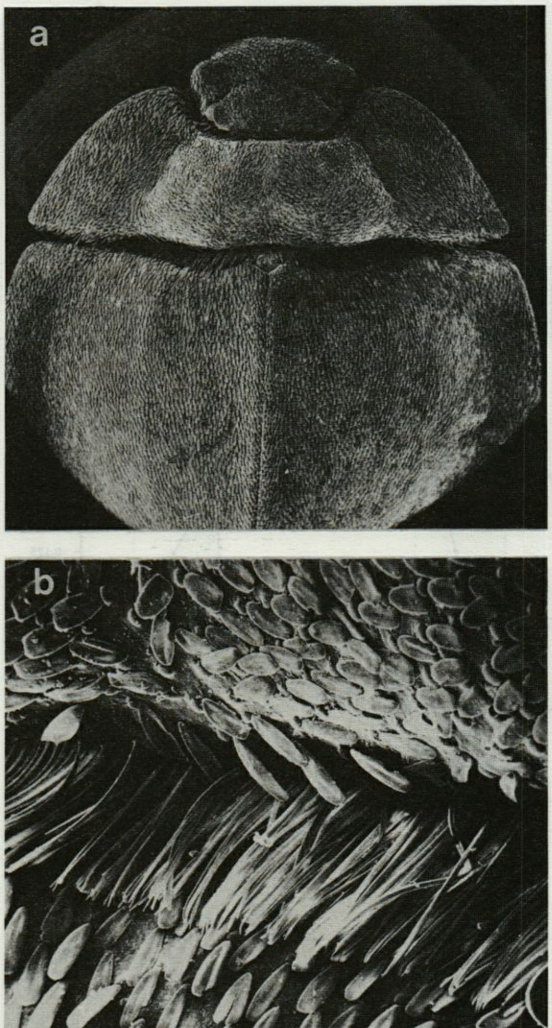

Fig. 2. – a, Dorsal view of the anterior half of the body (scanning electron microscope photo); b, Setae protecting the articulation between pro – and mesothorax (× 85); c, Detail of setae on the elytra (× 628).

DETERMINATION OF THE GRAIN SIZE PREFERENCE OF *LEPIDOCHORA DISCOIDALIS* IN THE LABORATORY

For this experimental study, the most abundant species, *L. discoidalis,* has been chosen. It is easy to keep in the laboratory with adequate food rich enough in water.

Methods : multichoice experiments

The experiments were conducted in annular inclosure (external diameter : 0,16 m; internal diameter : 0,07 m; area : about 160 cm^2) with a 1,7 cm deep layer of substrate. Radial partitions, at the same level as the substrate surface, divided the experimental area into 3, 4 or 10 equal sectors as required. A translucent plastic lid gave a softened and non-directionnal light.

Two different sediments were used : 1) fossil river sand extracted from a sand pit, without organic matter; 2) Namib desert dune sand, without any visible organic fragments, but not sterilised. These sediments were dry sorted on a series of standard sieves. The $<0,063$ mm class was an artificial silt composed of particules of the 0,063 class (75 %) and finer (25 %).

At the beginning of an experiment, an equal number of animals were placed in each sector. The experiments were started in late afternoon. During the night, the beetles explored the entire experimental area, as indicated by tracks on the sand surface. Next day, 16 to 24 hours later, the beetles, which were usually buried, were counted from each substrate.

Between two experiments, the sand was remixed within each sector, and levelled; the animals were returned to a terrarium with fresh food and a new group

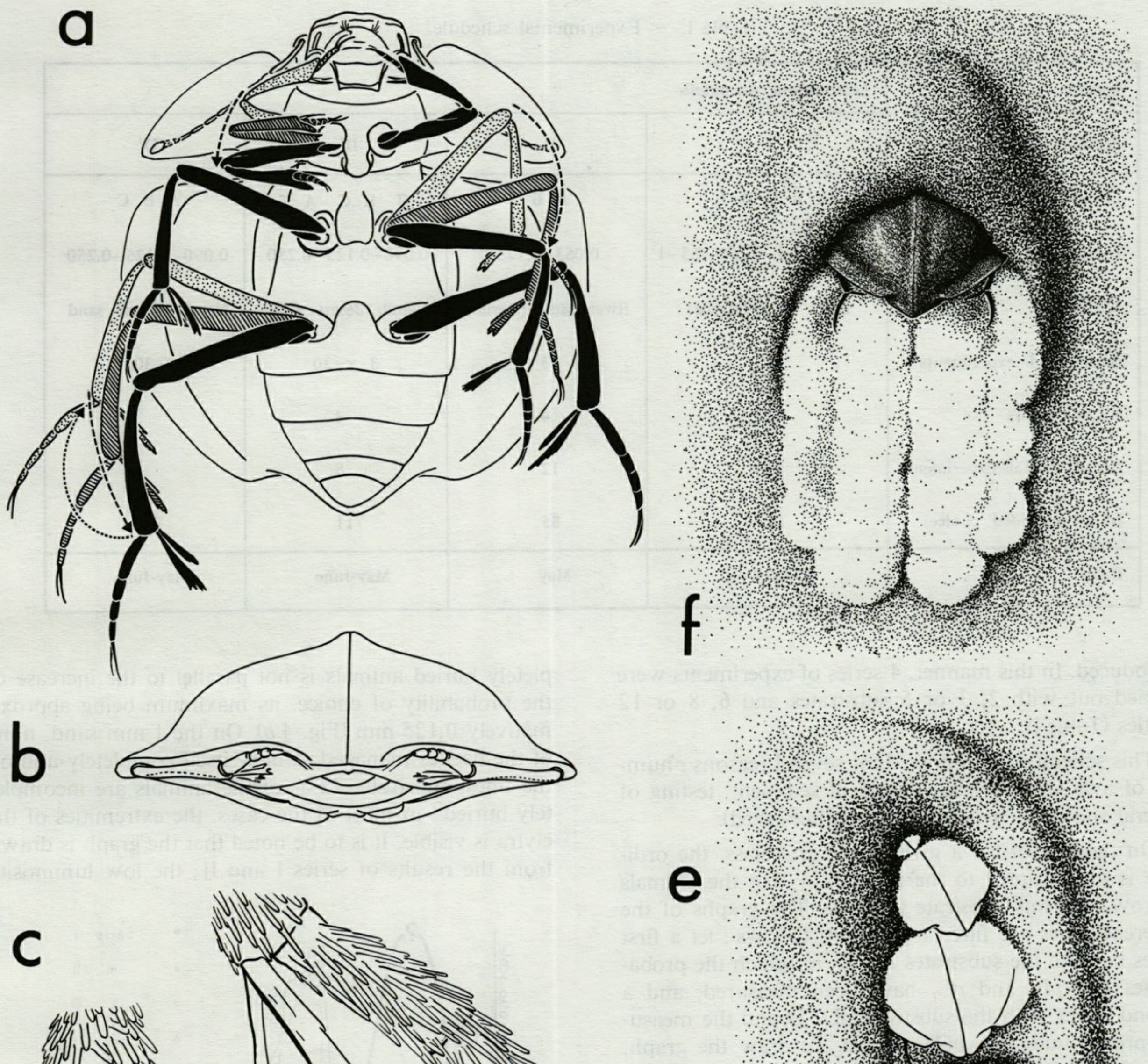

Fig. 3. – a, Positions of the legs of *Lepidochora kahani* during digging, drawn from film and from life (× 5,8). b, Posterior view of *L. discoidalis*; the following figures refer to this species (× 7,8). c, d, Tarsi and tibial extremities of the fore (c) and middle (d) legs (× 40). e, Successives stages of digging. f, Tracks after digging (illustrated by using white sand covered by a thin layer of dark sand).

Table I. – Experimental schedule.

Species	*Lepidochora discoidalis*			
Series	I	II	III	IV
Choice combination	A B C D E	A B	A B B C A C	A B C
Grain size classes (mm)	<0.063–0.125–0.250–0.5–1	0.063–0.125	0.090–0.125–0.250	0.090–0.125–0.250
Substrate	River sand (sterile)	River sand (sterile)	Namib desert sand	Namib desert sand
Number of experiments	16	13	3 x 30	30
N. of sectors	10	4	4	3
N. of animals/experiment	10	12	8	6
N. of recorded choices	141	85	711	180
Date	April	May	May-June	May-June

introduced. In this manner, 4 series of experiments were carried out with 2, 3 or 5 substrates and 6, 8 or 12 beetles (Table I).

This schedule was adopted for several reasons : number of available beetles, volume of sediment, testing of several statistical hypothesis (to be published).

On the graph, for a given grain size class, the ordinate is proportional to the probability that the animals burrow into this substrate (Fig. 4*a*). The graphs of the different series are fitted together as follows : let a first series be with the substrates A B C, in which the probabilities pA, pB_1 and pC_1 have been measured, and a second series with the substrates B C D and the measured probabilities pB_2, pC_2 and pD. To draw the graph, the values $p\,B_2$, $p\,C_2$ and $p\,D$ are multiplied by a coefficient x such as :

$$x = \frac{p\,B_1 + p\,C_1}{p\,B_2 + p\,C_2}$$

Results

The low variability of the counts, and the remarkable concordance between the different series make the statistical examination of the data useless as a first approximation.

L. discoidalis were found not to burrow into substrates with a grain size over 0,5 mm. Between 0,500 and 0,090 mm, the graph increases logarithmically (Fig. 4*a*). Because of the heterogeneous nature of the <0.063 mm substrate (cf. above), the abscissa of the apex of the graph is not known, but estimated to be about 45 μm. The fact remains that the probability of choice decreases with the finest substrates.

Unexpectedly, the increase of the ratio : number of completely buried animals/n. of completely and incompletely buried animals is not parallel to the increase of the probability of choice, its maximum being approximatively 0,125 mm (Fig. 4 *b*). On the 1 mm sand, none of the beetles managed to bury itself completely and on the finest substrate, 72 % of the animals are incompletely buried : in most of the cases, the extremities of the elytra is visible. It is to be noted that the graph is drawn from the results of series I and II; the low luminosity

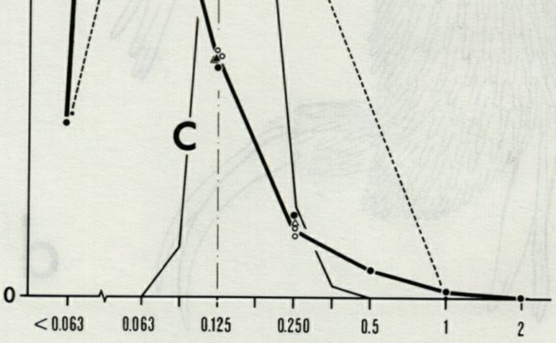

Fig. 4. – a, Grain size-preference graph calculated from the results of 4 series of choice experiments with *L. discoidalis* (ordinate : probability of occurrence in a given substrate). b, Percentage of completely buried beetles (86 % on ø = 0.125 mm). c, Grain size-frequency distribution of the slip-face sand (*cf.* also Fig. 1*b*).

and the relatively low temperature may have resulted in the high number of incompletely buried animals. In series III and IV, in which the luminosity and temperature were higher, the percentage of beetles which were not completely buried was negligible.

A small number of eggs were laid during series III and IV. They were distributed as follows : 0 % on the 0.250 mm sand, 80 % on the 0.125 mm sand, and 20 % on the 0.090 mm sand.

DISCUSSION

On the dune transect (Fig. 1), the *Lepidochora* are located on the slip-face, i.e. the area where the finest and least compact sand is, and where the wind blown organic detritus accumulate. The fact that it is the most suitable area both for burrowing and for feeding is a remarkable coincidence.

But, if we look more closely at the particle-size distribution graphs of the dune sand of the slipe-face (Fig. 1*b* and Fig. 4*c*), it appears that the mode is between 0.125 and 0.180 mm. Thus there seems to be a difference between the preference of *L. discoidalis* in the laboratory, and the primiling grain size of the natural substrate. The beetles occupy a habitat where the sand particules are about three time as large as those selected in the laboratory. Thus, the adaptation of *L. discoidalis* to his natural substrate could, for digging, be considered only sub-optimal.

However, we must note that :

– the natural dune sands have some sand finer than 0.125 mm; this very fine sand, although not important quantitatively, may make the sediment easier to burrow.

– in the experiments of series I and II, the greater number of completely buried animals was not in the 0.063 mm class, but in the 0.125 mm class. The sands finer than 0,090 may pose a problem of respiration to the beetles because of slower diffusion of the gas between the grains.

– in the 0.090 – 0.125 – 0.250 experiments, the greater number of eggs could be expected in the finest sand; but actually it is to be found in the 0.125 mm; this may be the result of a tactile selection by the ovipositor.

These considerations may help to explain the observed difference between the grain size preferendum in the laboratory and the measurements in the field. The adaptation of *L. discoidalis* to its substrate is a compromise between several selective pressures, some of which are contradictory (Prodon, 1976) : the least effort, i.e. the least energy invested in burrowing, the necessities of respiration, the search for food, requirements of egg-laying, etc. The preferendum, which is the result of these various requirements, corresponds to substrates which are to be found in strictly limited areas, i.e. the slip-faces of sand dunes.

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