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A COMPARATIVE STUDY OF THE STRUCTURE, FUNCTION AND ADAPTATION TO DIFFERENT HABITATS OF BURROWS IN THE SCORPION GENUS *URODACUS* (SCORPIONIDA, SCORPIONIDAE)

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ABSTRACT

Data are presented on the sites and nature of spiralling of *Urodacus* burrows. The dispositions of the burrows of *U. hoplurus* in three areas in Western Australia are statistically analysed in relation to various features of the environment. Burrow parameters of *U. hoplurus* and *U. yaschenkoi* are compared. Members of the genus *Urodacus* have been able to colonize desert areas owing to the evolution of the deep spiral burrowing habit which is an adaptation for the maintenance of suitable levels of moisture and temperature.

INTRODUCTION

Scorpions of the genus *Urodacus* (endemic Australian subfamily Urodacinae, Scorpionidae) construct burrows which range from shallow to about 100 cm deep and which may or may not be under cover. The burrows of a few *Urodacus* species have been mentioned (Kraepelin, 1916; Anon, 1917; Butler, 1930; Glauert, 1946, 1957; Southcott, 1954) and studies have been made of the burrow sites of *U. manicatus* in Canberra, A.C.T. (Smith, 1966) and of the burrows of *U. yaschenkoi* in N.S.W. (Shorthouse, 1971). The taxonomy of the genus *Urodacus* has recently been revised (Koch, 1977).

The present paper on *Urodacus* species includes the results of observations on large numbers of burrows of *U. hoplurus* and *U. yaschenkoi*. Because the burrow sites of one of the *Urodacus* species that has shallow burrows *(U. manicatus)* had been studied in detail (Smith, 1966) it was decided to make observations on a species that makes deep burrows *(U. hoplurus)*. Results of studies of its burrows in relation to various environmental features

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are given below. These studies were at three specially selected localities in Western Australia. The burrow-form in this species is compared and contrasted with that in *U. yaschenkoi* which also has deep burrows. The available information on these and other *Urodacus* species gained by observations made at scattered localities is presented and discussed.

For assistance in the field I thank Mr D.D. Giuliani, Big Pine, California, U.S.A. I am grateful to Mr T. Wachtel, Hawthorn, Victoria, for the statistical analyses. Plant names were provided by the State Herbarium, Western Australia. The present paper is abridged from part of a chapter in a Ph.D. thesis (University of Reading, England).

SPECIMENS AND RECORDING

The tables of raw data pertaining to this study are deposited in the library of the Western Australian Museum.

Specimens. The scorpions collected from the burrows have been coded, registered and lodged in the Western Australian Museum. The burrows are given these code numbers, e.g. A1, in the plan drawings.

Collecting and Burrow Recording. The following digging procedure was adopted for recording burrow characteristics. A cylindrical column of soil (usually of 15 cm radius) was left undisturbed around the entrance of the burrow, and a circular excavation (usually 60 cm wide and 30 cm deep) was made around this column. The path of the burrow was then followed by careful digging of the column and recorded as a plan drawing on squared paper, with the corresponding depths at successive selected points being noted. The scorpion was eventually collected from the terminal chamber.

After rain (e.g. at Marloo, W.A., where a large series of scorpions was collected) the scorpions were in the upper part of the first spiral near the entrance. Each burrow was approached from behind the entrance so as not to disturb the scorpion and cause it to descend. The scorpion was then collected by lifting it out in a spadeful of soil.

Measurements of the study areas and burrow dimensions have been converted to metric: burrow entrance dimensions had been measured to the nearest 1/16 inch, tree-distance to the nearest foot, and other burrow dimensions to the nearest 1/4 inch.

Plan Drawings and Graphs of the Burrows. The caption of each plan drawing of a burrow's path includes the data on burrow depth at the successive points measured from ground level (x) to full depth.

In order to construct the plan drawings, the following parameters were included: the length (sl) and depth (dl) from burrow entrance to completion of the first quarter turn; the length and depth from last quarter turn (i.e. at the penultimate point on the plan drawing) to the middle of the terminal chamber. Also included, in some sections of the work, are the total length (l) and total depth (d) of the burrow, the total number of turns, and the angle in degrees of descent (ϕ) during the first quarter turn ($\tan \phi = dl/sl$).

In an attempt to determine any common characteristics of the burrows, the data in the plan drawings were graphed. In these graphs, the successive points corresponded with those on the plan drawings. The ordinate was the vertical depth of the burrow, the abscissa the horizontal projection of the burrow from its entrance (as measured from the plan drawing). The ordinate and abscissa were drawn to the same scale. The curve of the graph showed the burrow unwound from its spiral-form while keeping the slope unchanged at all points: the actual length of the burrow was the length of the curve (the arc length) as measured with a piece of string. The overall slopes of these graphs, i.e. the lines joining the first and last points (entrance and terminal chamber) are discussed.

BURROW FORMS IN *URODACUS*

General Characteristics

The burrow entrance of *Urodacus* species is elongate, elliptical and slit-like. On the ground nearby there is usually a tumulus of freshly dug soil, produced as a result of the digging and burrow-cleaning activities of the occupant. The scorpion burrow entrances are easily distinguishable from those made by other creatures, e.g. ants, by their shape and by the tumulus being present only on one, the vestibular, side of the entrance.

In species that have burrows under rocks, e.g. *U. manicatus*, *U. planimanus* and in some areas *U. novaehollandiae* (and probably also *U. elongatus* which taxonomically is close to these three species), the burrow entrance leads immediately into an expanded cleared area under the rock. This area is thought to be constructed to give the scorpion room to manoeuvre while eating or mating, and has been termed the "living area" by Smith (1966) for *U. manicatus* (as *U. abruptus*). The burrow proceeds from the living area and is usually shallow (i.e. less than 10 cm deep).

Burrows that occur in "open ground" (i.e. those with their entrances not under cover of rocks or other large objects on the ground) do not have the above type of living area. Instead, the burrows are deep, spiral, and have a horizontal terminal chamber which, unlike the otherwise uniform cross-section, is somewhat larger and of adequate size for the scorpion to turn around. In these burrows, the angle of descent during the first quarter turn ranges from 14° to 49°. These burrows have up to ten turns; they are referred to as tortuously spiral when they have more than two turns. The shape of the burrow entrance of all deep spiralling species is similar; that of *U. hoplurus* has been illustrated (Koch, 1970).

In later sections, the burrows of *U. hoplurus* and *U. yaschenkoi* are analysed. Of the other species, the burrows of *U. novaehollandiae* are the least spiral and usually occur in sheltered sites under rocks or logs, whereas those of *U. giulianii* are the most spiral and occur in open ground. The plan drawings (**Figs 1, 2**) and the ranges and means of the burrow parameters (**Table 1**) indicate that the two species in the taxonomically based *hoplurus* species-group, *U. giulianii* and *U. lowei* (Koch, 1977), have noticeably longer and deeper burrows and greater angles of descent during the first quarter turn than those in the *armatus* species-group, *U. novaehollandiae* and *U. armatus*.

Nature of Burrow Graphs

The overall slopes of the burrow graphs were drawn for all the data and ranged from 18° to 53°. The species have the following ranges (mean, and n).

U. novaehollandiae	22° to 25° (23.5, n = 2)
U. armatus	22° to 29° (25.5, n = 4)
U. hoplurus	18° to 53° (33.5, n = 25)
U. giulianii	19° to 23° (21.0, n = 2)
U. lowei	27° to 39° (34.5, n = 4)
U. yaschenkoi	24° to 46° (32.2, n = 23)

There is obviously no significant difference between the mean values of the slopes of *U. hoplurus* and *U. yaschenkoi*.

For the above six species, the surface distance between entrance and terminal chamber ranged from 2 to 50 cm.

Data for Species

Information on the distribution and habitats of the species has been given (Koch, 1977). Data, including that available from the literature,

TABLE 1

RANGES AND MEANS OF BURROW PARAMETERS IN VARIOUS *URODACUS* SPECIES

(Measurements in cm)

Statistic	Burrow entrance to first quarter turn: Length (sl)	Burrow entrance to first quarter turn: Depth (dl)	Last quarter turn to middle of chamber: Length	Last quarter turn to middle of chamber: Depth	Total length (l)	Total depth (d)	Total no. of turns	Angle of descent (o) during first quarter turn (ϕ) ($\tan \phi$ = dl/sl)	Grade (o) (= sin d/l)
					U. novaehollandiae				
Range	19-23	6-10	13-19	5.6	43-50	18-20	0.5-0.8	19-26	24-25
Mean (N = 2)	21.0	8.0	16.0	5.5	46.5	19.0	0.7	22.5	24.5
					U. armatus				
Range	9-14	3-6	2-18	1-10	29-60	11-29	0.8-1.5	17-35	22-29
Mean (N = 4)	9.5	3.5	14.5	7.0	44.5	20	1.2	19.5	25.5
					U. giulianii				
Range	8-13	5-6	10-18	1-3	63-99	21-48	4.0-10.0	39-42	19-23
Mean (& N)	10.0 (4)	5.5 (2)	13.3 (4)	2.0 (2)	81.0 (2)	35.5 (4)	6.7 (3)	40.5 (2)	21.0 (2)
					U. lowei				
Range	10-26	7-19	11-35	5-13	65-100	26-58	0.3-2.0	39-49	31-36
Mean (& N)	18.0 (4)	12.5 (4)	27.8 (4)	8.8 (4)	84.0 (4)	42.8 (5)	1.3 (5)	44.5 (4)	34.0 (4)

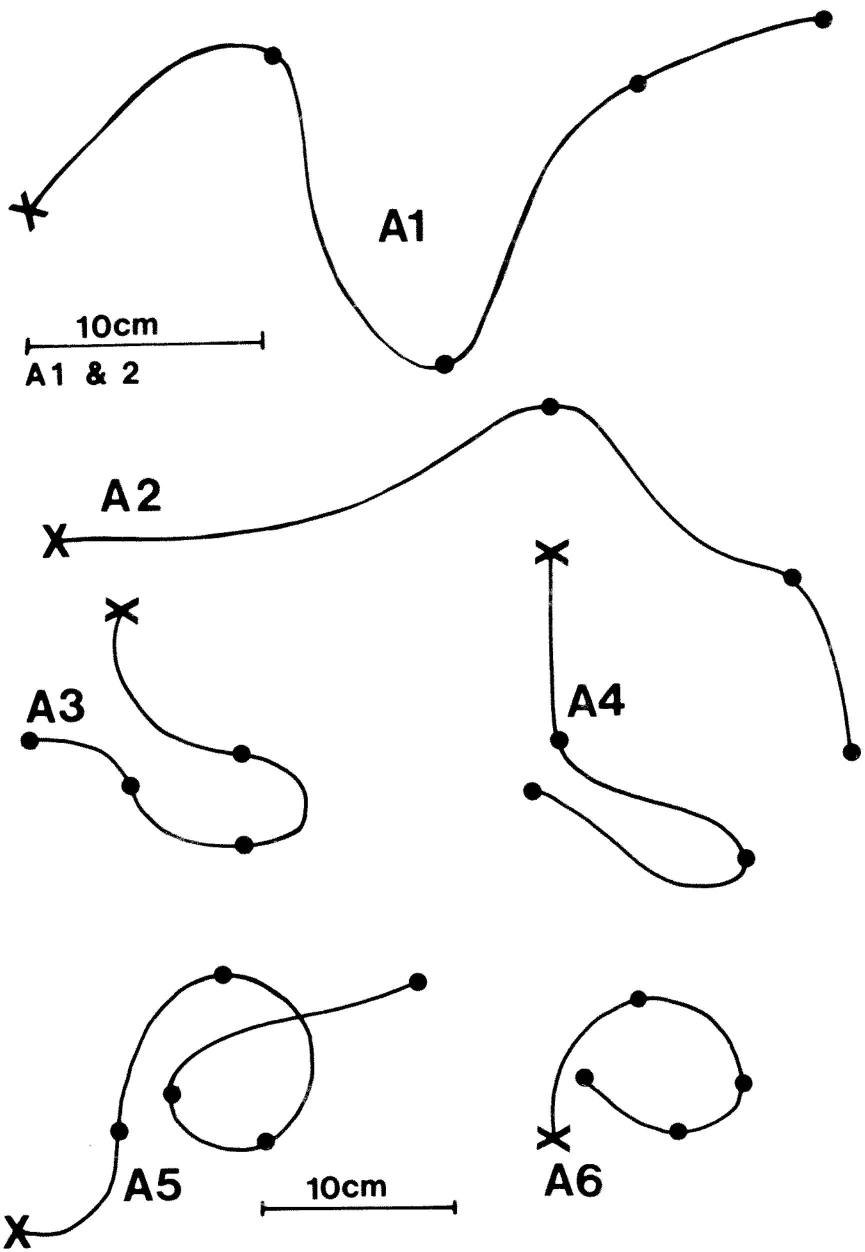

Fig. 1: Plan drawings of the burrows of various *Urodacus* species. A1, A2, *U. novaehollandiae*. A3 to A6, *U. armatus*. Burrow depths (cm) at the successive points from ground level (x = 0) are as follows: A1—0, 4, 11, 18, 20; A2—0, 10, 14, 18; A3—0, 6, 9, 13, 14; A4—0, 6, 15, 20; A5—0, 3, 9, 17, 19, 29; A6—0, 4, 6, 9, 11.

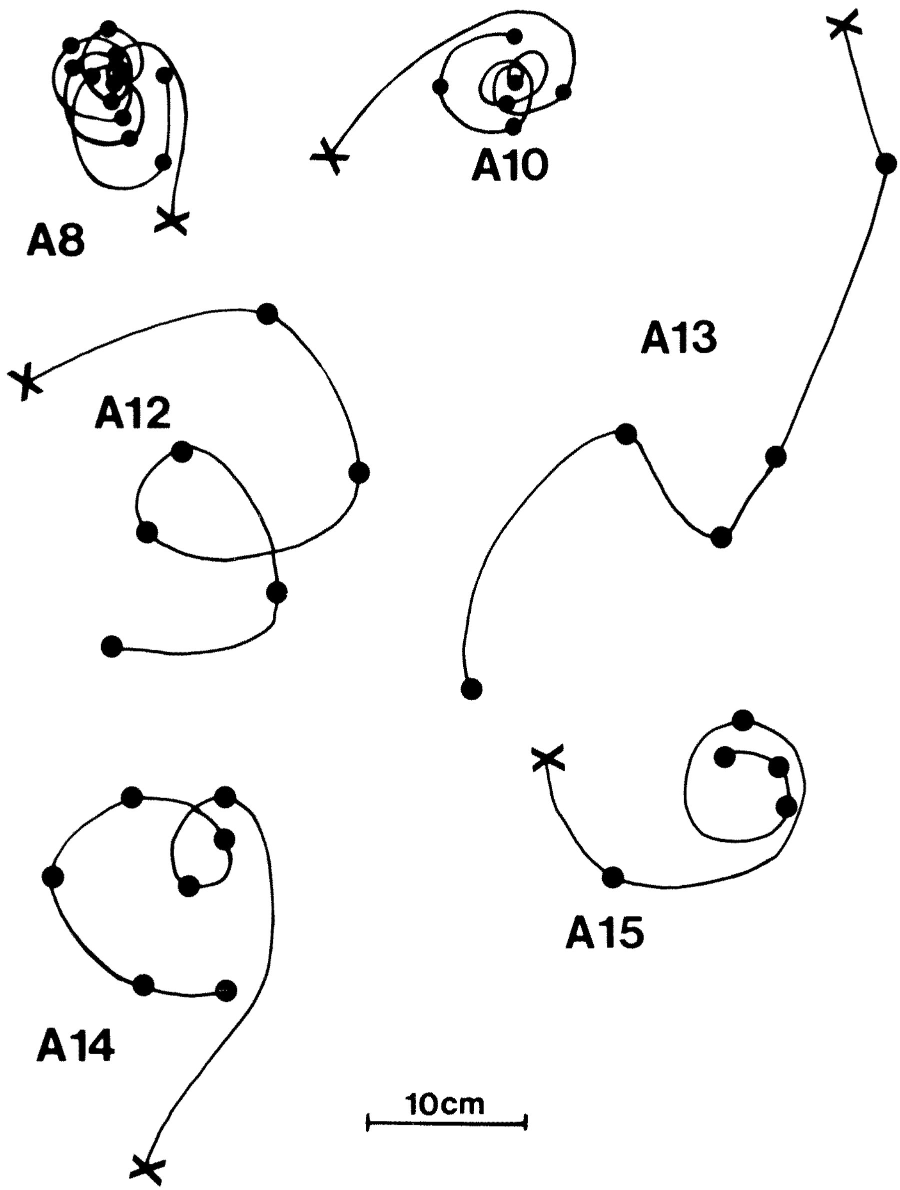

Fig. 2: Plan drawings of the burrows of various *Urodacus* species. A8, A10, *U. giulianii*. A12 to A15, *U. lowei*. Burrow depths (cm) at the successive points from ground level (x = 0) are as follows: A8—0, 6, 9, 10, 13, 17, 20, 22, 25, 32, 33, 38, 38; A10—0, 5, 7, 11, 15, 19, 22; A12—0, 11, 27, 30, 38, 52, 53; A13—0, 19, 28, 30, 36, 39; A14—0, 5, 12, 25, 30, 47, 52, 58; A15—0, 5, 8, 27, 36, 38.

Museum labels, and collectors, regarding the sites and nature of the burrows of *Urodacus* species are as follows.

U. manicatus. Burrows occur almost exclusively under rocks (viz. in an area at Canberra, A.C.T.; Smith, 1966). The rock selected by each scorpion usually covers a ground area of 36-71 sq. cm. Home sites have little or no leaf litter. The burrow is shallow, and horizontal or inclined.

U. novaehollandiae. Burrows may or may not be under rocks. In the hills, near Perth, W.A., e.g. at Boya and Darlington, the species occurs under rocks; each rock usually covers a ground area of about 91-897 sq. cm. Burrow depth is usually 25-30 cm, sometimes as much as 60 cm. There seems to be no fixed pattern of spiralling, the only common features being (1) the living area, (2) the terminal chamber of about 5 cm by 5 cm, and (3) that the burrow spirals slightly and irregularly to a depth of 10-20 cm before descending sharply to 25-60 cm.

Where the species occurs in rock-free ground, e.g. in the sandy coastal country at Bullsbrook, W.A., and Gnangara, W.A., the burrow entrances are found amongst the roots of shrubs and under fallen twigs and branches and also in open ground. The entrance width is 19 mm. These burrows spiral to a depth of about 30 cm ending more or less directly under the entrance. Burrows can be very abundant in these sandy areas, and were found as close together as 64 cm.

U. planimanus. Burrows are under rocks mainly on the foothills and slopes of lateritic hills. Each of these rocks usually covers a ground area of about 30 sq. cm. The burrow is shallow and sometimes scarcely evident.

U. armatus. Burrows are either under rocks (e.g. at Red Hill, W.A., the rock covered a ground area of 124-206 sq. cm) or, more often, in open ground. Burrows proceed downwards at about 45° and spiral loosely, sometimes tortuously. At Mt Remarkable, W.A., (in June 1969) the burrows were 15 cm deep, but at other localities they reached 36 cm. Some burrow plaster-casts made by a University of W.A. biology field-study group in a disturbed area at Dryandra, W.A., have a horizontal side tunnel about 6 cm long at 7 cm from the entrance.

U. megamastigus. Burrows are about 28 cm deep and occur in open ground.

U. hoplurus. Burrows are up to 68 cm deep. They are tortuously spiral, and occur under fallen branches or in open ground. Maximum entrance dimensions are length 41.3 mm, width 22.2 mm.

TABLE 2

CHARACTERISTICS OF THE BURROWS OF *URODACUS* SPECIES

Species	If burrows unknown: Expectation* (= x, y or z)	Cover: (+) Under rocks, logs, fallen twigs (—) In open ground	Depth: (A) Shallow (B) Moderately deep (C) Deep	Spiralling: (+) Yes (—) No	If spiralling, then tortuous: (+) Yes (—) No
1. *manicatus*		+	A	—	
2. *elongatus*	x				
3. *novaehollandiae*		+ and —	A to B	+	—
4. *planimanus*		—	A	—	
5. *centralis*	x				
6. *armatus*		+	B to C	+	—
7. *koolanensis*	y				
8. *megamastigus*		—	B	+	—
9. *varians*	y				
10. *hoplurus*		+ and —	B to C	+	+
11. *giulianii*		—	B to C	+	+
12. *carinatus*	z				
13. *macrurus*	z				
14. *excellens*	z				
15. *spinatus*		—	C	+	+
16. *lowei*		—	C	+	—
17. *similis*	z				
18. *hartmeyeri*		—	B (to C?)	+	—?
19. *yaschenkoi*		—	C	+	+

* x = expected to be similar to *novaehollandiae*
y = expected to be similar to *armatus*
z = expected to be similar to *lowei*

U. giulianii. Burrows are up to 48 cm deep, tortuously spiral, and occur in open ground.

U. spinatus. Burrows are tortuously spiral and mostly about 46 cm deep, but up to 92 cm deep at Cape York, Qld. They have been found in hard sandy soil (Kraepelin 1916), and in a sand and gravel ridge at Blue Mountains (Cape York Peninsula) Qld.

U. lowei. Burrows are loosely spiral, up to 58 cm deep, and occur in open ground.

U. hartmeyeri. Burrows occur in open ground in sandhills, and apparently are of moderate depth (about 15 cm). Entrance size is 25.4 mm by 19.0 mm.

U. yaschenkoi. Burrows are found in sandy soil. They are tortuously spiral, up to 100 cm deep, and occur in open ground. Entrance size reaches 55.0 mm by 25.0 mm.

The available information on entrance location, depth, and form of the burrows of all *Urodacus* species is summarized (**Table 2**). For those *Urodacus* species on which there are no direct observations, the burrow form that is to be expected is indicated. This expectation is based on the taxonomic resemblance of the species to other species in the genus and on the assumption that there is direct correlation between morphological similarity of the species and their burrow characteristics.

THE BURROWS OF *U. HOPLURUS* AND THEIR RELATIONS TO ENVIRONMENTAL FEATURES

The Study Areas

The following three areas were chosen because they had high abundance of *U. hoplurus* burrows and relatively homogeneous substrate.

(1) **Marloo, W.A.** — The observations were made from 31 January to 3 February, 1968, near the Marloo (28° 20′ S, 116° 08′ E) bungalow, 21 km from Gabyon Homestead. The area was of flat-land and the soil was shallow earthy loam with red-brown hardpan, rating Um 5.3 (Northcote, 1965). The vegetation was open mulga. Burrows were studied in a linear transect 3.7 m wide, orientated east to west from the bungalow.

In a nearby area of size 54 m by 91 m, on the afternoon of 2 February, 1968, after a short but heavy shower of rain, 55 *U. hoplurus* (consisting of 18 males 37 females) were dug from their burrows. That night in an adjacent area, three adult *U. hoplurus* were observed roaming on the ground.

(2) **Mt Remarkable, W.A.** — The observations were made from 14 to 17 June, 1969. The study area was near the junction of the road to Kalgoorlie (through Yerilla) and the road to the Mt Remarkable homestead (29° 20′

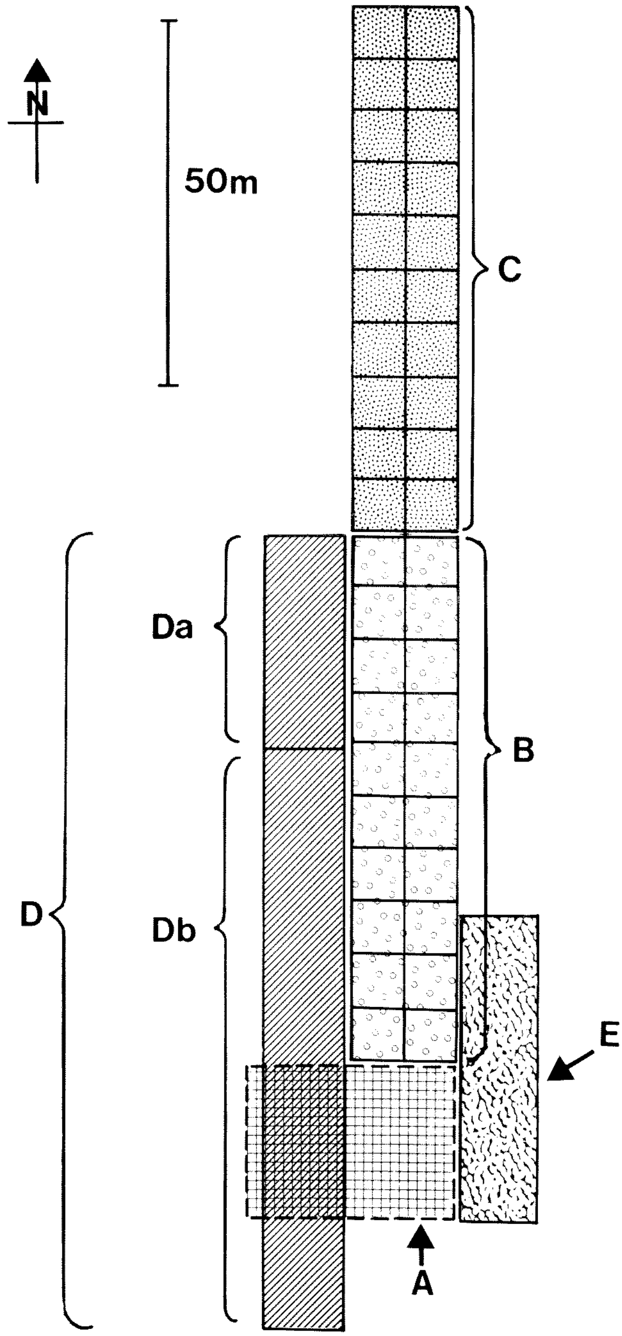

Fig. 3: Sub-areas A to E at Mt Remarkable, Western Australia.

S, 121° 59′ E). The land was flat with soil similar to that at Marloo. Vegetation consisted of four main shrubs and trees: *Acacia aneura* F. Muell., *A. craspedocarpa* F. Muell., *A. tetragonophylla* F. Muell., and *Eremophila compacta* S. Moore. The first two were the most common. There were many dry branches on the ground. There were no recently dead trees or fresh fallen branches. Night searches were conducted during the period, but no roaming scorpions were found.

The area was divided into five sub-areas (**Fig. 3**) by scraping straight lines to form grids on the ground. These sub-areas had the following dimensions.

Sub-area A	21.6 m by 28.8 m
Sub-areas B and C	Each sub-area was 14.4 m by 72.0 m, and was further sub-divided into 20 squares, each of side length 7.2 m
Sub-area D	10.8 m by 108.0 m Da was 10.8 m by 28.8 m; Db was 10.8 m by 79.2 m
Sub-area E	11.8 m by 42.0 m

In sub-area A, plan drawings were made of the burrows and the scorpions were collected; in sub-areas B to E, the disposition of the burrows was recorded in relation to various habitat features.

(3) **8 km ESE of Kookynie, W.A.** — This is 48 km W of the Mt Remarkable sampling area. On 19 June 1969, burrows were investigated in an area 100 m by 100 m.

Nature of the Data Recorded

1. Burrow entrance dimensions.
2. Various burrow parameters (**Table 3**; and **Tables 4-7** for *U. hoplurus* and *U. yaschenkoi*).
3. Direction (to nearest 22° 30′) that burrow entrance faced.
4. Clockwise or anticlockwise spiralling of burrow.
5. Presence or absence of a nearby shrub (30 cm to 3 m in height) or tree (3 m or more in height) within 3.0 m (also within 3.7 m) of burrow entrance.
6. Distance (to nearest 30 cm) from mid-point of burrow opening to middle of base of closest tree. Whether the tree was living or dead was noted.
7. The angle of the burrow (along burrow width) to closest tree. Four categories: facing, backing, right angle, intermediate angle.

8. The turning angle, i.e. the smaller of the two angles required to be turned by a scorpion leaving the burrow in order to face the tree. Four categories: facing, backing, parallel, intermediate angle.
9. The number of burrows that had a fallen branch along the top edge of entrance.
10. Presence or absence of a fallen branch within 3.8 m (also within 60 cm) of burrow entrance.
11. The angle that a branch formed with the burrow entrance. Four categories: parallel, right angle, 45^{o} angle, intermediate angle.
12. The number of isolated fallen branches with no burrow entrance within 75 cm. To be counted a branch had to be of length 107 cm or more, width 60 cm or more, and obviously not part of another fallen branch.
13. Presence or absence of a fresh tumulus of soil.
14. Presence or absence of litter, i.e. leaves and twigs within 15.2 cm of the entrance; twigs were defined as having a diameter of less than 2.0 mm.

Results and Analysis

At Marloo, *U. hoplurus* burrows had entrance widths of 3.2 cm to 3.8 cm (n = 12). Burrows were 20 cm to 25 cm deep and the terminal chamber was 5.0 cm wide, 2.5 cm high and 5.0 cm long (n = 4). The surface distance from entrance to chamber was 10 cm. Compass direction and number of burrows were: N 2, NW 1, S 2, SE 1, ESE 2, NE 2. There was 50% (i.e. n = 6) clockwise spiralling. There were two burrows 50 cm from a 1.2 m to 1.5 m high shrub, and there was one burrow 3.7 m from a large tree with its entrance turned 90^{o} from the tree. Two of the burrows (16.7%) had a fallen branch across the top edge of the entrance. In the area 54 m by 91 m, near Marloo, the closest two burrows were 1 m apart. Since there were 55 burrows, the abundance of burrows was 1 every 8.8 sq. m.

At Mt Remarkable, sub-area B, of size 14.4 m by 72.0 m, had 63 burrows. The frequency of occurrence of the burrows in the 20 squares was 0 burrows (3 squares), 1 (4), 2 (3), 3 (0), 4 (3), 5 (3), 6 (2), 7 (2). Sub-areas B to E with a total area of 3725.6 sq. m had 176 burrows; hence the abundance of burrows was 1 every 21.2 sq. m. (In sub-area A, which partly overlaps part of area D, the abundance of burrows was 1 every 41.5 sq. m). The highest abundance of burrows was 1 every 7.4 sq m; this was in sub-area E, 11.8 m by 42.0 m.

For a total of 166 *U. hoplurus* burrows, 71 were clockwise giving a figure of 42.8% clockwise spiralling. [For a total of 93 *U. yaschenkoi* burrows, 47 were clockwise giving a figure of 50.6% clockwise spiralling. Spiralling direction in terms of burrow dimensions is analysed later (**Table 6**).]

The direction of facing of the burrow entrance appears to bear no relation to any particular compass direction, the values for 154 *U. hoplurus* burrows being: N 12, NNE 3, NE 19, ENE 6, E 9, ESE 8, SE 18, SSE 4, S 14, SSW 4, SW 18, WSW 7, W 1, WNW 6, NW 12, NNW 8. In sub-area E, the turning angle of 56% (total n = 29) of the burrow entrances was parallel in relation to orientation to trees within 3 m.

U. hoplurus is among those species of *Urodacus* that have large burrow entrances. The following ranges and mean values of entrance dimensions (mm) of *U. hoplurus* were obtained for the combined data from one locality, Mt Remarkable: length 15.9-41.3 (29.2) n = 78; width 6.4-22.2 (12.8) n = 78.

The numbers of burrow entrances in relation to orientation to trees at Mt Remarkable were as follows. Entrance facing a tree, 7; entrance backing a tree, 6; entrance at 90° to a tree, 14. Thus about half of burrow entrances were orientated at 90° and the other half were edge on to the trees. About half the trees, having burrow entrances within 3 m, in the total area were living trees. Shrubs having burrow entrances within 3 m, in sub-area E, represented 6% of the total number of trees and shrubs.

The number of burrow entrances in relation to the angles they made with fallen branches were as follows. Entrance parallel to a branch, 18; entrance at 90° to a branch, 4. Thus 81.8% of those burrow entrances that were near fallen branches were oriented parallel to the branches.

TABLE 3

PRESENCE AND ABSENCE OF *URODACUS HOPLURUS* BURROW SITES IN RELATION TO VARIOUS ENVIRONMENTAL FEATURES

Feature	Present	Absent	% Present
Litter	82	50	62.1
Fallen branch	124	52	70.4
Tree	109	67	61.9
Fresh tumulus	94	36	72.3

Totals (**Table 3**) of the presence or absence of litter, a fallen branch, a tree within 3 m, and a fresh tumulus at each burrow site reveal that high percentages (61.9 to 72.3%) of burrows were associated with the presence of each of these environmental features. A Chi-square analysis of these various features against one another shows that the number of burrows associated with any one of these features is not more significantly higher (at 5% probability level) than that with any other of the features: litter *vs* fallen branch χ^2 =

2.006, d.f. = 1, P = 0.16; litter *vs* tree χ^2 = 0.001, d.f. = 1, P = –; fallen branch *vs* tree χ^2 = 2.860, d.f. = 1, P = 0.01.

THE BURROWS OF *U. HOPLURUS* AND *U. YASCHENKOI*

U. hoplurus and *U. yaschenkoi* are both large species which have deep, tortuously spiral burrows. But whereas the burrows of *U. yaschenkoi* occur in open ground, those of *U. hoplurus* occur not only in open ground but also under cover.

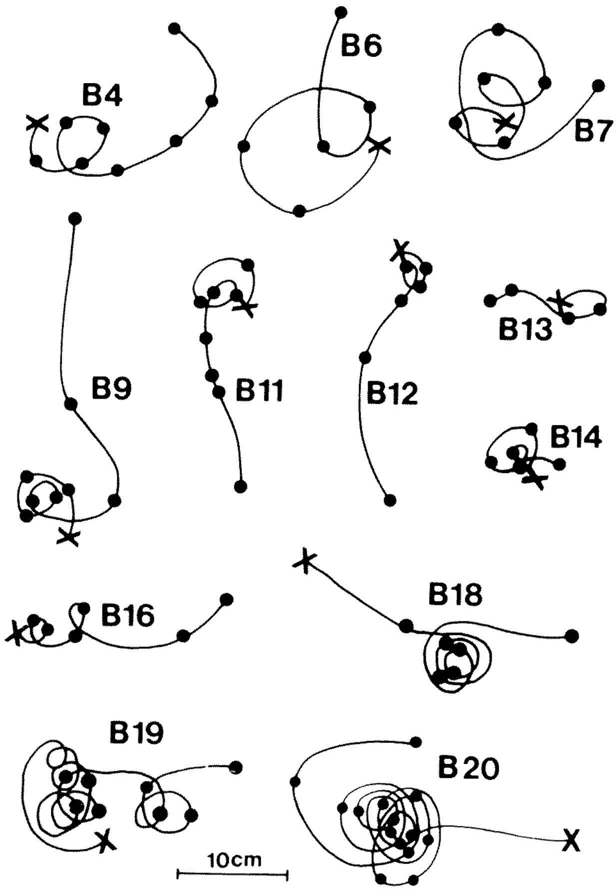

Fig. 4: Plan drawings of the burrows of *Urodacus hoplurus*. Burrow depths (cm) at the successive points from ground level (x = 0) are as follows: B4—0, 4, 6, 8, 9, 15, 22, 24, 25; B6—0, 10, 13, 25, 34, 39; B7—0, 4, 6, 10, 17, 23, 30; B9—0, 4, 6, 7, 8, 10, 22, 25, 30; B11—0, 4, 6, 8, 10, 15, 20, 20, 23; B12—0, 5, 5, 8, 10, 20, 25; B13—0, 5, 11, 18, 20; B14—0, 3, 6, 8, 14, 20; B16—0, 8, 10, 13, 15, 27, 28; B18—0, 9, 11, 18, 22, 26, 27; B19—0, 8, 11, 15, 22, 25, 33, 39, 46; B20—0, 9, 10, 14, 16, 19, 22, 27, 30, 32, 37, 38, 43, 47, 52.

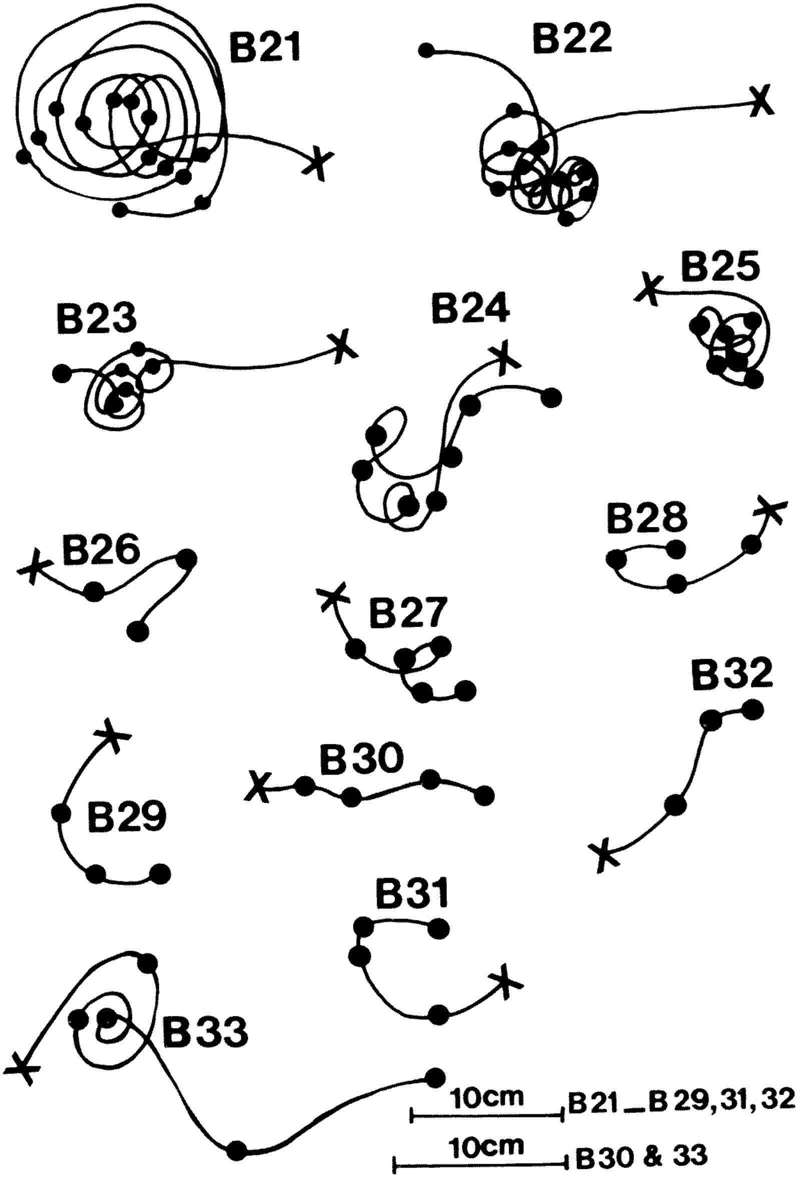

Fig. 5: Plan drawings of the burrows of *Urodacus hoplurus.* Burrow depths (cm) at the successive points from ground level (x = 0) are as follows: B21—0, 4, 9, 13, 18, 22, 29, 34, 45, 50, 57, 60, 64, 68; B22—0, 6, 13, 17, 18, 25, 36, 46, 52, 59, 64; B23—0, 4, 6, 8, 11, 13, 15; B24—0, 5, 6, 8, 13, 15, 18, 19; B25—0, 3, 5, 7, 10, 13, 14; B26—0, 5, 15, 18; B27—0, 1, 1, 2, 10, 12; B28—0, 3, 10, 15, 17; B29—0, 5, 13, 16; B30—0, 3, 11, 14, 15; B31—0, 4, 3, 15, 15; B32—0, 1, 13, 17; B33—0, 8, 14, 18, 21, 25.

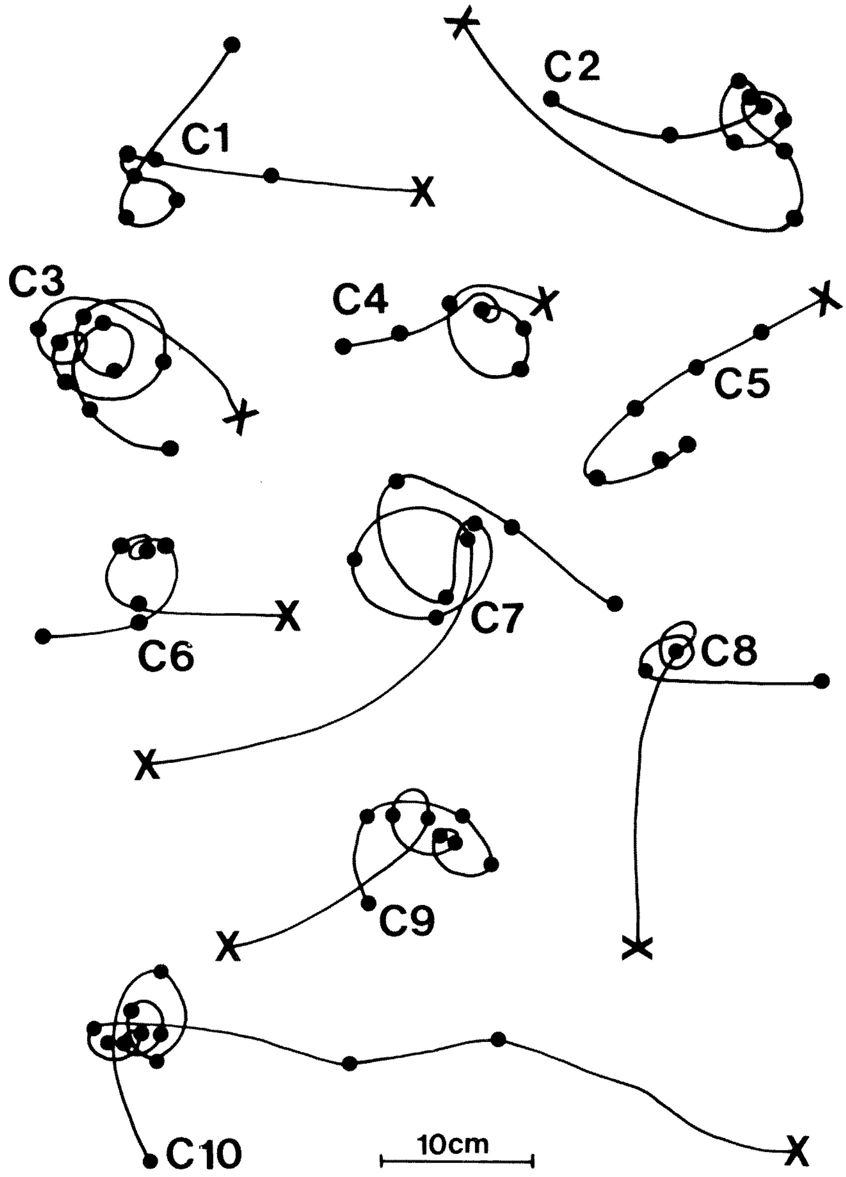

Fig. 6: Plan drawings of the burrows of *Urodacus yaschenkoi*. Burrow depths (cm) at the successive points from ground level (x = 0) are as follows: C1—0, 8, 14, 18, 21, 26, 29, 31; C2—0, 6, 11, 15, 19, 24, 25, 30, 37, 39; C3—0, 6, 9, 11, 15, 17, 19, 24, 28, 30; C4—0, 5, 14, 15, 21, 26, 27; C5—0, 5, 7, 10, 14, 19, 20; C6—0, 6, 9, 11, 17, 23, 25; C7—0, 7, 14, 17, 21, 27, 37, 45, 46; C8—0, 6, 28, 30; C9—0, 4, 10, 15, 18, 24, 30, 35, 38; C10—0, 6, 9, 13, 15, 22, 27, 34, 38, 40, 40, 46.

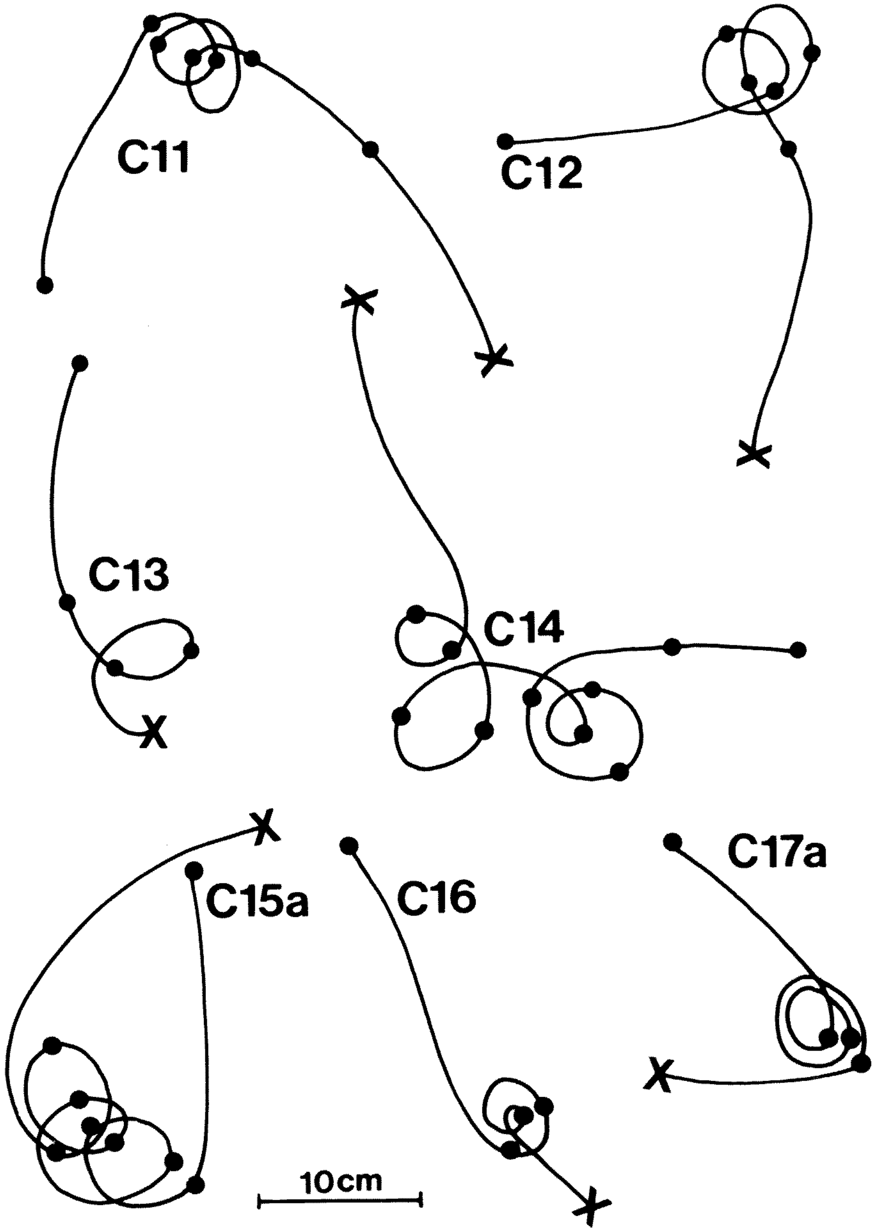

Fig. 7: Plan drawings of the burrows of *Urodacus yaschenkoi*. Burrow depths (cm) at the successive points from ground level (x = 0) are as follows: C11—0, 6, 14, 30, 35, 38, 39, 40; C12—0, 10, 15, 23, 27, 32, 36; C13—0, 8, 10, 17, 23; C14—0, 5, 11, 17, 20, 32, 47, 54, 66, 69, 72; C15a—0, 10, 13, 18, 25, 33, 41, 50, 55; C16—0, 15, 18, 25, 29; C17a—0, 10, 19, 37, 42.

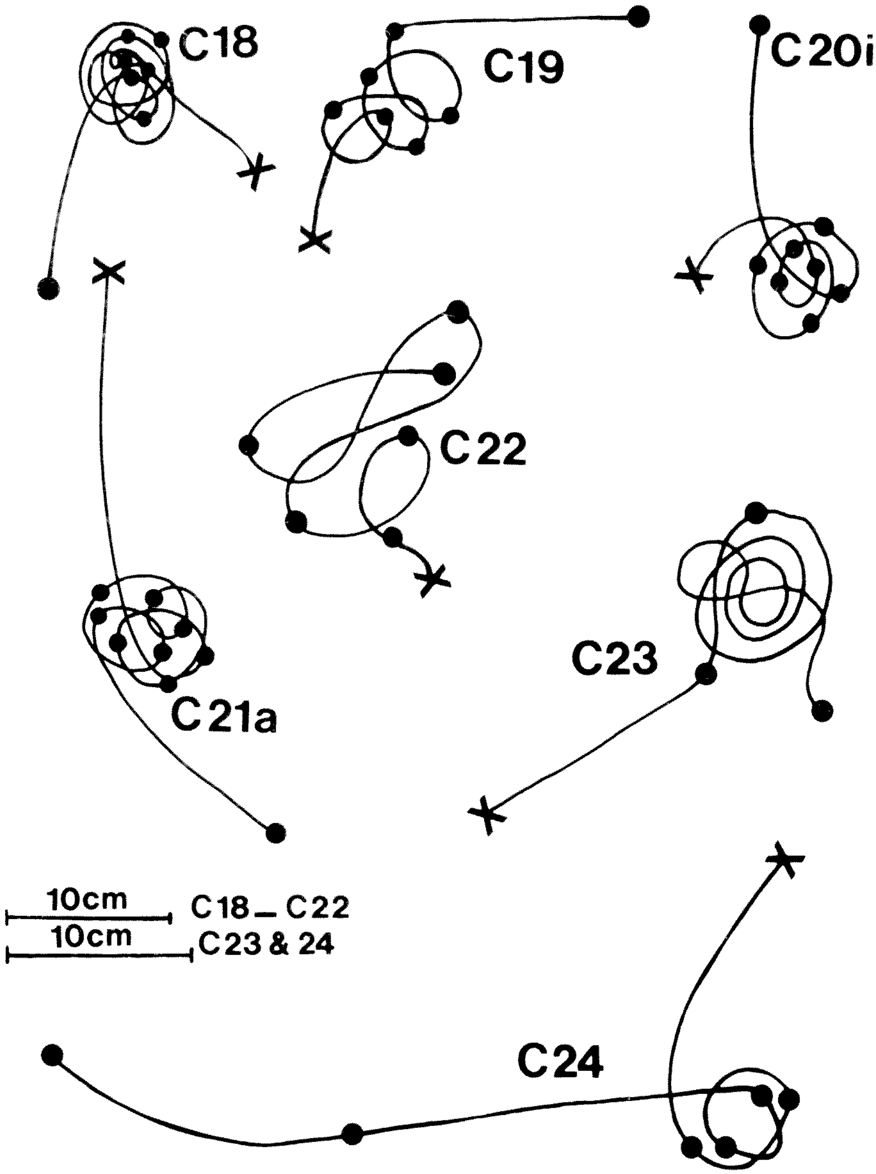

Fig. 8: Plan drawings of the burrows of *Urodacus yaschenkoi*. Burrow depths (cm) at the successive points from ground level (x = 0) are as follows: C18—0, 8, 13, 19, 24, 34, 53, 54, 60; C19—0, 9, 14, 22, 30, 43, 48, 53; C20i—0, 10, 18, 24, 30, 37, 44, 53, 60; C21a—0, 11, 17, 20, 27, 30, 40, 44, 54, 58; C22—0, 8, 14, 29, 41, 47, 50; C23—0, -, -, 71; C24—0, 11, 23, 28, 33, 38, 39.

TABLE 4

VALUES OF BURROW PARAMETERS IN *URODACUS HOPLURUS* AND *URODACUS YASCHENKOI*

(measurements in cm)

Burrow Nos: *U. hoplurus* B4, B6, B7, B9, B11-14, B16, B18-35
U. yaschenkoi C1-4, C6-14, C15a, C17a, C18-20, C21a, C22-24

Statistic	Burrow entrance to first quarter turn		Last quarter turn to middle of chamber		Total length (l)	Total depth (d)	Total no. of turns	Angle of descent (o) during first quarter turn (ϕ) ($\tan \phi = dl/sl$)
	Length (sl)	Depth (dl)	Length	Depth				
				U. hoplurus				
Range	5.08-17.78	1.27-10.16	6.35-35.56	1.27-13.97	20.32-182.88	12.70-67.31	0.3-8.0	14-59
Mean	8.89	5.56	15.66	4.68	61.13	27.78	2.68	37.46
S.D.	3.76	2.39	8.27	3.36	43.31	15.31	2.20	9.12
N	26	24	24	22	23	24	25	24
				U. yaschenkoi				
Range	10.16-27.94	5.08-16.51	7.62-53.34	1.27-10.16	45.72-125.73	25.40-72.39	1.3-5.5	18-42
Mean	19.63	10.04	22.51	5.26	84.18	44.74	2.95	30.76
S.D.	4.60	3.26	10.84	2.06	24.54	13.90	1.00	5.90
N	22	21	22	21	21	22	22	21

Plan drawings are presented of the burrows of *U. hoplurus* (Figs 4, 5) and *U. yaschenkoi* (Figs 6, 7, 8). The ranges, means and standard deviations of the burrow parameters are presented for *U. hoplurus* (Table 4) and *U. yaschenkoi* (Tables 4, 8 and 9). The results of statistical comparisons ('t' tests) of the burrow parameters of these two species are presented in Table 6. The analysis reveals some significant differences between the two species. *U. yaschenkoi* has significantly greater length and depth of burrow from entrance to first quarter turn (P<0.001), length from last quarter turn to middle of terminal chamber (P<0.05), and total length (P<0.05) and total depth (P<0.001) of burrow. *U. hoplurus* has a significantly greater angle of descent from burrow entrance to first quarter turn (P<0.01 and P<0.001).

TABLE 5

STATISTICAL COMPARISONS ('t' TESTS) OF BURROW PARAMETERS OF *URODACUS HOPLURUS* AND *U. YASCHENKOI*

(measurements in cm)

[Data from Raw Data Tables A.4.6 and A.4.7; including all clockwise and anticlockwise spiralling]

Parameter:
- A Burrow entrance to first quarter turn, length
- B Burrow entrance to first quarter turn, depth
- C Last quarter turn to middle of chamber, length
- D Last quarter turn to middle of chamber, depth
- E Total length
- F Total depth
- G Total number of turns
- H Angle of descent to first quarter turn

Parameter	Mean *U. hoplurus*	Mean *U. yaschenkoi*	t	d.f.	P
A	8.89	19.63	30.73	46	***
A (including data from Raw Data Tables A.4.8 and A.4.9)	8.89	18.58	10.83	119	***
B	5.56	10.04	5.30	43	***
B (including data from Raw Data Tables A.4.8 and A.4.9)	5.56	9.23	6.05	81	***
C	15.66	22.51	2.42	44	*
D	4.68	5.26	0.68	41	n.s.
E	61.13	84.18	2.14	42	*
F	27.78	44.74	3.92	44	***
G	2.68	2.95	0.53	45	n.s.
H	37.46	30.76	2.88	43	**
H (including data from Raw Data Table A.4.8)	37.46	30.92	4.02	81	***

* P<0.05 ** P<0.01 *** P<0.001

TABLE 6

STATISTICAL COMPARISONS ('t' TESTS) OF DIRECTION OF SPIRALLING IN RELATION TO BURROW PARAMETERS IN *URODACUS HOPLURUS* AND *U. YASCHENKOI*

(measurements in cm)

Parameter:
- A Burrow entrance to first quarter turn, length
- B Burrow entrance to first quarter turn, depth
- C Last quarter turn to middle of chamber, length
- D Last quarter turn to middle of chamber, depth
- E Total length of burrow
- F Total depth of burrow
- G Total number of turns
- H Angle of descent to first quarter turn

Parameter	Mean		t	d.f.	P
	Clockwise	Anticlockwise			
	U. hoplurus				
A	9.11	9.49	0.21	20	n.s.
B	5.72	5.93	0.18	18	n.s.
C	17.42	16.31	0.27	18	n.s.
D	5.81	4.50	0.74	16	n.s.
E	56.24	76.43	0.91	16	n.s.
F	28.30	32.07	0.48	17	n.s.
G	2.76	4.43	2.14	18	*
H	37.57	37.50	0.01	17	n.s.
	U. yaschenkoi				
A	18.42	21.34	1.41	18	n.s.
A (Raw Data Table A.4.8)	16.87	17.93	0.90	36	n.s.
A (Raw Data Table A.4.9)	20.96	17.85	2.37	33	*
B	8.38	11.94	2.82	18	**
B (Raw Data Table A.4.8)	8.22	9.49	2.05	36	*
C	25.65	21.59	0.84	18	n.s.
D	5.59	4.57	1.19	18	n.s.
E	88.14	82.04	0.54	18	n.s.
F	42.80	43.43	0.11	18	n.s.
G	3.25	2.46	1.97	18	n.s.
H	28.10	33.70	2.31	18	*
H (Raw Data Table A.4.8)	29.57	17.93	9.20	36	***

* $P<0.05$ ** $P<0.01$ *** $P<0.001$

TABLE 7

CORRELATION ANALYSIS OF BURROW PARAMETERS IN *URODACUS HOPLURUS* AND *U. YASCHENKOI*

Parameter:
- A Burrow entrance to first quarter turn, length *vs* depth
- B Last quarter turn to middle of chamber, length *vs* depth
- C Total length *vs* total depth
- D Total length *vs* total number of turns
- E Total depth *vs* total number of turns
- F Total length *vs* angle of descent
- G Total depth *vs* angle of descent
- H Total number of turns *vs* angle of descent
- I Burrow entrance to first quarter turn (Raw Data Table A.4.8), length *vs* depth
- J Burrow entrance to first quarter turn (Raw Data Table A.4.8), length *vs* angle of descent
- K Burrow entrance to first quarter turn (Raw Data Table A.4.8), depth *vs* angle of descent

Parameter	r	d.f.	P
	U. hoplurus		
A	0.88	22	**
B	0.59	20	**
C	0.94	21	**
D	0.86	21	**
E	0.79	22	**
F	—0.24	20	n.s.
G	—0.12	20	n.s.
H	—0.23	20	n.s.
	U. yaschenkoi		
A	0.81	19	**
B	0.14	19	n.s.
C	0.82	19	**
D	0.64	19	**
E	0.76	20	**
F	—0.25	19	n.s.
G	—0.33	19	n.s.
H	—0.39	19	n.s.
I	0.76	36	**
J	—0.30	36	n.s.
K	0.38	36	*

* $P<0.05$ ** $P<0.01$

TABLE 8

VALUES OF BURROW PARAMETERS IN *URODACUS YASCHENKOI*

Burrow Nos: C5, C13, C15b-h, C17b-u, C21b-j

Statistic	Burrow entrance to first quarter turn		Angle (o) of descent during first quarter turn
	Length (cm)	Depth (cm)	
Range	11.43-26.67	6.35-13.97	22-46
Mean	17.35	8.79	31.00
S.D.	3.57	1.97	5.30
N	38	38	38

The significance of clockwise against anticlockwise spiralling has been statistically analysed ('t' tests) in relation to each of the burrow parameters (Table 6). The analysis shows that for most burrow parameters of *U. hoplurus* there is no significant difference between the two directions of spiralling, but that the total number of turns is greater ($P<0.05$) in burrows exhibiting anticlockwise spiralling. This last result, however, is on the borderline of significance.

In the data pertaining to *U. yaschenkoi*, there is no significant difference between the two directions of spiralling. But with respect to the length from burrow entrance to first quarter turn there is a significantly higher number ($P<0.05$) of burrows having clockwise spiralling in one analysis (that of the data referred to in Table 9). With respect to the depth from burrow entrance to first quarter turn there are significantly higher numbers ($P<0.01$ and $P<0.05$) of burrows having anticlockwise spiralling in two analyses (that of the data referred to in Tables 4 and 8). (The angle of descent to the first quarter turn is more highly significant ($P<0.05$) anticlockwise in one analysis and more highly significant ($P<0.001$) clockwise in an analysis using another set of data.)

The results are presented of correlation analyses of the various parameters (Table 7). As would be expected, both length and depth are very strongly correlated. Similarly, there are very strong correlations between total length and total number of turns, as well as total depth and total number of turns. Although the correlation between the angle of descent to the first quarter turn and either length or depth of burrow is not statistically significant, the analysis shows that the relationship is inverse as would be expected on a logical basis.

TABLE 9

VALUES OF A BURROW PARAMETER IN *URODACUS YASCHENKOI*

Burrow Nos: C20ii-xxxvi

Statistic	Burrow entrance to first quarter turn Length (cm)
Range	12.70-27.94
Mean	19.27
S.D.	4.12
N	35

Discussion

Neither *U. hoplurus* nor *U. yaschenkoi* was observed digging during the daytime, but observations made at night showed much evidence of fresh soil having been added to tumuli. In hard soil, *U. hoplurus* ceased digging at about 3 cm; there were five such "false-start burrows" in sub-area B, 14.4 m by 72.0 m, at Mt Remarkable.

The sampling area at Marloo, as well as the Mt Remarkable areas, are low-lying and were damp; they would be under water at frequent intervals during the wet season. In general, it seems that the areas of red-brown soil, in which *U. hoplurus* is abundant, are subject to flooding. Examination of such areas during wet years indicates that places around trees are the least likely to become flooded. There are naturally more fallen branches in places with dead trees and more litter in places with living trees. As shown in the present study, the abundance of *U. hoplurus* burrows is positively correlated with such places. This finding could indicate an adaptation by *U. hoplurus* to maintain a permanent burrow by reducing the chances of excess flooding of its burrows. General observations on *U. yaschenkoi* indicate that it occurs mainly in open country. Its burrows occur in sandy soil which would make them less prone to flooding than *U. hoplurus* burrows.

Burrow entrances of *U. hoplurus* are orientated in the same direction as fallen branches where these contact the ground. The choice by individuals of the actual direction of facing of these burrows would be expected to be influenced by prevailing wind direction, with orientation of the entrances being such as to avoid sand and litter being blown into the burrows. Studies of general wind direction in an area, however, would be difficult because wind direction would alter depending upon many factors and their combinations in the micro-environment around burrows situated amongst rocks, logs, tree bases and branches on the ground. Topography in general has to affect the direction of entrance facing in any burrowing species, but does not apply here because *U. hoplurus* was studied on level ground. The choice of direction of burrow facing would not be influenced by factors such as intense light or shade from trees because burrows are constructed mainly at night.

All the *U. hoplurus* burrows in the study areas were occupied except for a few (less than 1%) that were old. This indicates low mortality because higher percentages of abandoned burrows, estimated as being several weeks old, had been noted at other localities.

Except in a few burrows (less than 4%), the direction of spiralling did not reverse. The choice of burrow spiralling direction seems to be fortuitous. The possibility that abnormalities in features of the hands are responsible for choice of spiralling direction is precluded because these scorpions do not lose their hands in combat and they are bilaterally symmetrical. Advantages of the extensive spiralling would include reducing the effects of wind-blown debris and sheet-flooding, and the avoidance of neighbouring burrows under crowded conditions; also the continual change in direction would make it difficult for predators (e.g. the large lizard, *Varanus gouldi*, as recorded by Koch, 1970) to locate the scorpion. The main function of spiralling, however, is the maintenance of suitable levels of moisture and temperature (as discussed in the next section).

ADAPTATIONAL AND EVOLUTIONARY TRENDS REVEALED BY *URODACUS* BURROWS

The species of *Urodacus* can be classified according to the type of burrow they build.

Type 1: shallow burrows under objects, especially small rocks, on the ground.

Type 2: deep tortuously spiral burrows present in open ground.

Most *Urodacus* species belong to one or other of these types, e.g. *U. manicatus* and *U. planimanus* to Type 1 and *U. spinatus* and *U. yaschenkoi* to Type 2. Two examples of intermediate species are *U. novaehollandiae* and *U. hoplurus*. *U. novaehollandiae* has burrows of Type 1, but in a few areas has moderately deep, loosely spiral burrows in open ground; thus it is an intermediate species which is closer to Type 1 than to Type 2. *U. hoplurus* has moderately deep to deep tortuously spiral burrows which occur either under cover, usually consisting of branches on the ground, or in open ground. Thus *U. hoplurus* also is an intermediate species. The presented study on the distribution and abundance of *U. hoplurus* burrows in relation to various environmental features has been in areas having cover in the form of fallen branches, twigs and litter. The results reveal in particular that *U. hoplurus* shows a preference for making its burrows under cover. Hence in this regard *U. hoplurus* is closer to Type 1 than to Type 2, although in regard to the depth and tortuousness of its burrows it is closer to Type 2.

The burrows of *Urodacus* scorpions, like those of other creatures, reach a depth where conditions are favourable. It is well known (Andrewartha, 1964; Gray, 1968; Ettershank, 1971; Shorthouse, 1971) that, in contrast to the wide range of temperature and the excessive heat and dryness at ground level, the air in soil-burrows remains at moderate temperature and high humidity. For example, at least the air in the bottom chamber of burrows of ctenizid trapdoor spiders remains saturated while hot dry summer conditions prevail at the surface. Saturated air occurs below 8-10 cm in clay soils and 20 cm in sandy soils (Gray, 1968). Spider burrows which have plastered silken linings and often have lids can afford to be considerably shallower than the unlined burrows of carabid beetles and scorpions. Certain other small animals rely upon underground refuges at least during the hottest times of day, e.g. some species of the lizard genus *Amphibolurus* which have penetrated extensively into arid regions (Bradshaw & Main, 1968).

The burrows of *Urodacus* in open ground, in contrast to those under surface objects, are deeper, have more spirals, and occur in the more arid parts of Australia. These observations indicate the important role of the numerous spirals of a scorpion's open burrow in maintaining a suitable micro-environment of moisture and temperature.

These traits in burrowing habits are paralleled by evolutionary trends in the morphology of the scorpions (Koch, 1977). These changes in *Urodacus* species in relation to increasing aridity include larger size, lighter colour, higher trichobothrial numbers, more complex capsule of male paraxial organ, and more exaggerated development of unequal terminal claws on the legs. *U. yaschenkoi*, which is widespread where the annual rainfall is less than 550 mm, displays all these morphological trends and is the extreme example of the Type 2 burrow recognized above.

In conclusion, it is clear that deep spiral burrow construction has evolved as an adaptation for the avoidance of harsh surface conditions, and has enabled species of the genus *Urodacus* to spread to otherwise inhospitable arid environments.

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