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CONTRIBUTIONS
TO THE
BIOLOGY, ANATOMY AND PHYSIOLOGY
OF
OPISTHOPHTHALMUS LATIMANUS & OTHER SCORPIONS

by

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TABLE OF CONTENTS.

I. RESUMÉ

1. The work described in this thesis falls into three distinct sections, namely:
   - (i) observations on the biology and behaviour of the scorpion, *Opisthophthalmus latimanus* and other species;
   - (ii) an account of the muscular and nervous anatomy of the pedipalp and tail of *O. latimanus*;
   - (iii) a preliminary account of certain facets of neuro-muscular transmission in *O. latimanus*.
2. For subsequent consideration of the behaviour patterns of these animals, two basic activities, namely burrowing and feeding, are first considered.
3. The mechanism of burrowing is described; some observations on the forms of burrows are presented, while field and laboratory observations on the location of burrows are discussed.
4. The patterns displayed in washing are described and their close relation to feeding patterns emphasised.
5. The feeding behaviour of *O. latimanus* is discussed; it is found that the animals have definite food preferences and the factors involved in the recognition of prey are considered. It is concluded that when dead animals are accepted as food, this is because of their water content and not their nutritional value.
6. The patterns concerned in drinking are described.
7. An account of the process and of the frequency of defaecation is given: evidence for the presence of a peritrophic membrane is presented.
8. The methods of stridulation in *O. latimanus* are studied and compared with those in other species. The biological significance of noise making is considered and evidence presented that this, at least in *O. latimanus*, is a threat display.
9. The origins of stridulatory movements in scorpions are analysed in ethological terms and it is shown that sound stimuli have much in common with visual sign stimuli, as far as their genesis is concerned.

10. It is shown that there are marked anatomical preadaptations for stridulation and that these have probably determined the physical basis of the stridulatory mechanism in different scorpions.

11. The physiological significance of a pattern called "stilting" is considered. It is shown that this has a thermoregulatory rôle and depends for its effectiveness upon local air currents. Extreme heat-stress causes a change in behaviour towards light which is considered to be an adaptation which will remove the scorpion from positions where death from overheating might occur.

12. A brief synopsis of embryonic development is presented, and some experiments concerned with the function of various specialised structures of the embryo described. It is concluded that the labral lobes, first observed by Laurie, are stores of nutriment for first instar nymphs in particular. The reasons for the development of these structures in Opisthophthalmus are considered.

13. The process of parturition in Parabuthus planicauda is described and compared with that of O. latimanus.

14. Certain specialised structures in first instar nymphs are briefly described and a preliminary analysis of the behavioural relation between parent and offspring presented.

15. The process of moulting and its mechanism are briefly considered. It is concluded that, after the first instar, the animals moult only once a year. From a biometrical analysis, it is deduced that there are seven nymphal instars, while some evidence is found that moulting may occur, at least in females, after sexual maturity has been reached.

16. The adult sex ratios shows a marked preponderance of females. At birth the sex ratio is unity, but there is some evidence, from an analysis of the sex ratios in individual broods, that abnormal ratios can occur.

17. The courtship and mating of O. latimanus is described and the ethology of different facets of courtship behaviour considered. A comparative account is given of spermatophore structure in the scorpions and of the courtship patterns found in different species. The evolution of these is considered.

18. The sensory bases of the various patterns associated with mating are studied, including experiments upon the sense of smell in scorpions and a demonstration of the rôle of the pectines in the choice of a suitable site for spermatophore deposition.

19. An hypothesis is developed to account for the evolution of the mating of Arachnids in general + the peculiar events associated with insemination in spiders.

20. The thesis now turns to a consideration of the anatomy of the pedipalp and tail as a prelude to investigations upon the myo-neural physiology of <u>Opisthophthalmus</u>.

21. An account is given of the myology and nervous anatomy of the pedipalp and tail of <u>O. latimanus</u>. Certain joints of the pedipalp lack any muscular extension mechanism and experimental evidence is offered of the mechanism of extension of these joints. The study of the myology of the pedipalp reveals the presence of certain other unusual muscular arrangements and the mechanical significance of these is considered.

22. On the foundation of these observations the morphological relations of the pedipalp to a walking leg are considered. Further, the lack of muscular extension at certain joints is a common characteristic of the walking legs of many arachnids. The implication of this in terms both of the evolution and the homologies of arachnid walking legs is considered.

23. Using the anatomical information described, various possible preparations for experimental study of the myo-neural physiology of the animal are considered. It is shown that, in practical terms, none of the preparations of muscles of the pedipalp considered is suitable for experimental work, but that a satisfactory preparation can be obtained by the use of the muscles operating the bulb of the sting.

24. Preliminary experiments with this preparation are described. Evidence is presented which suggests that the control of these muscles depends upon myo-neural facilitation as in other arthropods, and some indications are found of the presence of a nerve supply inhibiting the muscles' mechanical responses, as in the Crustacea. The implications of these observations are briefly considered.

II. INTRODUCTION.

For many years the problem of interrelationships within the Arthropoda and, indeed, the origin of the Phylum itself have been of interest to many zoologists. It was felt, for reasons which will be given later, that one of the studies which might throw some light on this matter is that of the neuromuscular physiology of arachnid appendages. Consequently it was proposed that the work which is reported here should be primarily concerned with this problem.

As in so many cases involving live animals, both the experimental subjects and the experimenter gradually managed to change the direction in which work was proceeding and the result is that only a preliminary attack has been made on the original problem, while most of the material submitted here deals either with functional anatomy or with biological-cum-behavioural characteristics of the experimental animal.

Thus it was found that to develop experimental preparations for neuro-muscular studies, it was necessary to work out the anatomy of the muscles and nerves of the appendages used; but this is not enough. For these nerves and muscles are part of a functional complex which operates as a unit and have therefore to be studied in relation to the structures that they move. Considerations at this level, in fact, carried the study to the plane of functional anatomy.

Furthermore it was recognised that even the comprehension of a limb as a functional complex cannot be acquired in isolation. All structures have an evolution~~al~~ary history and in any consideration of functional anatomy this history must be taken into account - even if the consideration requires extension to the problem of the origin of the group immediately under study.

Such a line of thought can be taken further in explaining how functional anatomy leads the study legitimately to that of behaviour; how knowledge of the various habits of the animals themselves may throw further light upon the peculiarities of structure and function. Whether such an argument is conceded or not, considerations of this kind were not the cause of behavioural work reported here. It merely happened that the experimental animals were available for behavioural observation and experiment, and that, during intervals between anatomical and neuro-muscular work, they exhibited many of their behaviour patterns.

No matter what consideration lay behind the behavioural observations, they inevitably do contribute towards a complete understanding of both the whole and its parts, although in submitting them, it is freely admitted that they were not made directly in relation to the original subject of study.

Thus it is that the thesis covers three distinct facets of the biology of the animal studied. Firstly observations upon its behaviour are recorded, though as indicated above, they do not generally cast light directly upon the physiology of the appendages. Secondly the anatomy of certain appendages is considered in both descriptive and comparative terms. And lastly a preliminary account is given of the actual methods of neural control of the muscular machinery.

III. MATERIAL

Once it was clear that the animal to be studied should be an arachnid, it was also clear that it should be a scorpion. Firstly, a scorpion should yield a suitable neuromuscular preparation much more easily than any of the other arachnids. Amongst the reasons for this are the following. The scorpion has an exoskeleton which is relatively hard when compared with those of other arachnids, so that the scorpion can be used more easily in mechanically recording muscular activity. Buffon remarks (1821) that "the scorpion is one of the largest of the insect tribe and is no less terrible from its size than its malignity." The size is conveniently large for neuromuscular studies while of the malignity we will speak later. Lastly the scorpion has a claw terminating its pedipalp and this appeared ideal for the work planned here. Firstly it meant that direct recording could be made of its musuclar movements without recourse to lever systems. Secondly, it operates strictly in one plane and this also should facilitate recording. Finally, the claw possesses no muscles antagonistic to its closing.

The animal used throughout the study was the dark-brown scorpion, Opisthophthalmus latimanus typicus Koch (Plate I). It can be caught fairly easily in the district around Grahamstown as it is a simple matter in some parts to find a scorpion burrow and to dig out the animal. A high percentage of the animals collected are females: the ratio is about 7 : 4. Males are moreover less tractable in general so that the females were preferred for experiments. The animals brought into the laboratory varied in size from 45 - 85 mm. measuring their length from the chelicera to tail tip. The large animals are easier to handle experimentally, but smaller ones were occasionally used as a check that there were no young : adult differences that were being missed.

Returning to the disparaging Buffon: "were it worth the trouble, these animals (scorpions) might be kept living as long as

Plate I. *Opisthophthalmus* *latimanus* *typicus* Koch.
Adult Female

curiosity should think proper." This is quite true of O. latimanus. The animals are hardy as far as disease and bad treatment are concerned, and appear healthy and active at normal laboratory temperatures. Because of slight cannibalistic tendencies, the scorpions, when they were kept in small dishes, were kept singly: this was the case with most experimental animals. Each was provided with water and about once a week all were fed. Most animals would eat small pieces of raw beef, sometimes needing a little persuasion. Live macopterous termites, diplopods and small chopped-up earthworms were readily taken.

With due regard for the warnings of literature and legend, it was thought wise, at the beginning of the study, to take precautions against being stung by the scorpions; the sharp lance of each sting was therefore removed as soon as the animal was brought into the laboratory. A drop of collodin stopped the bleeding and the animal appeared to suffer no ill-effects from this treatment. Later, it was found that, if animals are handled gently and quickly enough, there is no danger of the experimenter being stung. Not only can the scorpions be handled with impunity, but if in a misguided moment the experimenter jabs some part of his anatomy on to the scorpion sting before the animal can move it out of the way, the effect is far less painful than is a bee sting: the pain lasts for about 3 - 8 minutes and the slight swelling and inflammation has disappeared within half an hour.

IV. BEHAVIOURAL OBSERVATIONS.

1. INTRODUCTION.

As has just been mentioned, the scorpions were dug out of their burrows in the field and were kept in the laboratory in small plastic dishes. Animals that were not being used immediately for either anatomical or physiological work were often liberated into large earth-filled terraria. Some of the terraria were made from normal aquarium tanks and the insides of burrows constructed against the glass walls were therefore visible to the observer. One of these terraria was placed out of doors so that conditions in it were more nearly those of the field. Behavioural observations were made under all four conditions mentioned above; when the animals were being captured from the field, in the small dishes, in the indoor terraria and outside in their tank. The scorpions' behaviour did not appear to differ strikingly with the different environments, and unless the investigator deliberately disturbed them or by mistake breathed on them, they appeared to pay no attention to human observers. Laboratory disturbances, such as heavy footsteps or slamming doors usually interrupted their activity for only a short time and unless the disturbance was of the nature of a vibration, they paid no heed.

The activities were never watched under a binocular microscope though Baerg (1954b) suggests that this is desirable. The interruption caused by moving the scorpions, together with the fact that such large animals provided no great difficulty in observation, prevented any such action from giving a distinct advantage. Occasionally, behaviour was watched from beneath a glass plate, but this was seldom satisfactory as the scorpions tended to slip on the glass as they tried to move and this normally ended their undisturbed activity.

2. BURROWING

In the districts in which it is found, O. latimanus has never been caught hiding anywhere but in a burrow, while within a short time (15 minutes or so) after a freshly captured animal is brought into the laboratory it has usually begun to burrow, or at least to try to dig, in the soil in its dish. Thus it is clear that there is no difficulty in starting an investigation into the burrowing behaviour of this scorpion.

The Mechanism of Burrowing

The question of how a scorpion digs has been dealt with by many observers in the past. Becker (1880) and Lankester (1883) report that the shallow scrapes of the Buthidae are excavated by the animal with its chelae and legs, while Pocock (1893) states that the scorpion Parabuthus capensis (H & E) kicks soil out backwards from its burrow using its second and third legs, the others serving as support. More recently Glauert (1946) and Thornton (1956) agree that Urodacus sp. and Leiurus quinquestriatus (H & E) respectively burrow by digging with the front pair of legs while the back ones push the loosened soil out behind the scorpion.

Though the pedipalps of O. latimanus are similar to those of Scorpio maurus L., being large and spade-like, they are not used in digging as is reported in this latter species (Cloudsley-Thompson, 1955b). In O. latimanus only the chelicerae and the first pair of legs loosen the soil: the pedipalps are closed, closely folded and held out of the way of the chelicerae as much as possible. In carrying the loose soil out of the burrow the pedipalps are used to some extent for the scorpion backs outwards pulling itself by its third and fourth pairs of legs and pushing itself backwards with its pedipalps. The tail, which is held far forward over the head, assists in this. The loose soil is pushed backwards and beneath the scorpion's belly by alternate movements of the first and second pairs of legs.

As the burrow gets deeper, the soil is dragged further from the opening before it is deposited, the distance being sometimes as much as 50 cm. The path along which it is dragged may be twisted and tortuous. In some cases the soil is just dropped but the scorpion~~s~~ may spread it fairly widely with its two pairs of hind legs.

A different method of spreading has been noted about a dozen times. Instead of the two hind legs being used, the tail makes two or three wide sweeps and this flattens the pile of soil most effectively. The movement is no mere chance one. The scorpion stands with her tail towards the pile of soil, she then lays the whole length of the tail to one side of the soil pile and swings the back part of her body in a wide arc. This method of soil smoothing was also noticed by Pocock (1893) in *P. capensis*, by Fabre (1907) in Buthus occitanus (Am) ~~Buthotus alticola (Poc.)~~, and by Glauert (1946) in a "sand scorpion". In the two former cases it was interpreted as a measure taken to prevent the soil pile blocking the view from the mouth of the burrow. This interpretation can certainly not be used in the case of *O. latimanus* since the pile is usually at a fair distance from the burrow opening and has never been found directly in front of its mouth. There are three obvious teleological explanations of this soil smoothing: none of them rests on any evidence. Firstly the action may reduce the danger of the burrow being recognised by the soil pile outside it. Certainly when these piles are not properly smoothed the human collector can easily recognise them as landmarks of the burrows and it may well be that baboons and possibly other enemies search in a similar manner. Secondly the behaviour may be concerned with keeping the path leading to the burrow clear, either for the use of the scorpion itself or so that wandering insects may be tempted to use it and thus end as scorpion prey, a possibility which has been suggested by Schultze (1927) regarding the prey catching habits of *Heterometrus longimanus* (Hrbst.) Lastly it may be concerned simply with making the construction work easier. There seems no easy way of distinguishing experimentally between these or any other explanations.

The Form of the Burrows.

Highly characteristic of scorpion diggings is the oval cross section of the entrance and burrow (Plate II). There is a strong local belief that the inhabitant of a burrow may be sexed by its shape, the burrow of the male being a narrower ellipse than that of the female. This prejudice was tested by blocking the mouths of a number of burrows with lumps of soft plasticine; the soil around the plasticine was then dug out carefully so that the mould of the burrow entrance was not disturbed; the burrow was then completely excavated and the sex of the occupant determined. The mould was taken to the laboratory and chilled until it was hard enough to section: a section was then cut ~~out~~ at a depth of 1 cm. from the surface of the mould corresponding to the mouth of the burrow and plaster of Paris built on to the section to provide a permanent record of its shape. When a number of such moulds had been made an attempt was made to sort them into two groups which would correspond to the sex of the inhabitants according to tradition. This attempt was in the main unsuccessful, no clear-cut difference in burrow shape being observable. There are however slight indications of two tendencies. Firstly the female burrow is in section very often a broader ellipse than that of the male: secondly the male burrow has a more marked dorso-ventral differentiation, the cross-section being slightly crescent shaped. The dimorphism in the form of the burrow entrance correlates possibly with the greater girth of the female when she is pregnant or carrying new born young.

It may be noted here that in some cases a scorpion will orient to the shape of the burrow entrance. To explain more clearly - a clod of earth including the entrance and part of the burrow of a male was cut out and replanted in a terrarium upside down. This was done on three occasions and on each of these males have been found to live upside down in the burrow when allowed to enter it. Females however lived the correct way up. It has been pounted out above that the burrows of males are frequently dorso-ventrally differentiated and it might be that the limited space always obliges the animal to enter with the same orientation to the bore. This however seems unlikely as observations show that the animals can turn freely in

Plate II Female O. latimanus at the entrance to her burrow in the field; the elliptical shape of the entrance can just be distinguished.

their burrows, a feat they could hardly perform were conditions really cramped.

The burrow of *O. latimanus* is never longer than 35 cm. Small animals may, of course, have much shorter burrows but there does not seem to be any simple correlation between the weight of a small animal and the size of its burrow. From this almost any conclusion may be drawn: that young scorpions sometimes take over disused burrows; that there is no regularity in the amount of digging that a young scorpion will do, or merely that these animals are orphans, having been left alone in their mother's burrows after their mothers had been killed outside.

Rubbish Piles

In the field the site of a scorpion burrow is often recognised by the skeletons of various arthropods in a pile within a few inches of the entrance. Both the fact that these remains are normally on a partially smoothed soil heap and that carrying activities of the scorpions have been witnessed in the laboratory would suggest that the remnants of past meals have been dragged out of the burrow during further digging operations. Of course in some instances the meal may have been eaten on the soil pile. On a few occasions it was clear from the size of the remains, generally beetle skeletons, that they could not have fitted into the burrow and that the scorpion could only have eaten them at or near the mouth of its dwelling.

Near the inner end of the burrow, in a side chamber or more usually blocking its end, is a further deposit of rubbish consisting of the exo-skeletons of diplopods, beetles, crickets and other arthropods (~~Plate III~~). In the terraria an animal would usually drag food down into its burrow but would sometimes eat it in the open. Certain observations suggest that food may also be stored at the bottom of the burrows. On one occasion a female had half finished digging a burrow; since this was against the glass wall of a terrarium her behaviour was easily observed. She caught a large spider and started eating this in the open, then she pushed and pulled it into the hole. Next morning it was rammed down solidly and the scorpion was sitting outside, a foot or so away from the burrow, beneath a clump of grass. During the following night she went back to the spider and resumed her meal. Again another female had been fed a large number of locusts within a few days. When she caught yet another she wandered about for ten minutes or so with the corpse in her claws. She had not dug a burrow and therefore had nowhere to retreat. She was then given a small cardboard box into which she immediately retired with the food. Here she dropped the locust and turned her back to it, but later she ate it. While these observations suggest that food may be stored in the burrows, definite evidence of this habit has not been obtained in the field; mayhap such behaviour would only be shown when food is very abundant.

Nests.

At the bottom of the burrows there are not only the remains of former meals but also a small quantity of dried grass, roots and pieces of stick. The significance of these 'nests' is not clear. It seems improbable that they are just incidental to the digging operations or that the material is collected unintentionally while passing in and out of the burrow, for the material is found at the bottom of the deepest burrows; none is found in the passage ways. The nests consist of grass leaves and not only the roots of plants, so that they would appear to have been deliberately cut and not just casually carried off by the legs or claws; the occasional presence of pieces of stick supports this. Nests are found in the burrows of females during the non-reproductive season, in those of males and also to some extent in those of immature adults. This suggests that the nests are in no way concerned with the production or care of the young.

It is possible that O. latimanus prefers sitting on a grass bed to hard soil. This suggestion is however unsatisfying in so far as the scorpions in the terraria have never been found to sit on any patches of grass provided, but normally rest on the cleared soil.

The retrieving habit is well illustrated by one incident. In excavating burrows the normal practice was to search an area and place a mark near the burrows' entrances before commencing any digging. On one occasion tissue handkerchiefs were used as markers. Three such marks were set out and digging commenced. After two burrows had been excavated, no sign of the third marker could be found. A few days later the same area was visited and, in excavating a burrow, the shredded remains of the tissue were found at the bottom of the burrow.

The habit of building nests is, of course, found in other arachnids, most notably the spiders. In most cases it would appear to have some very definite significance such as reproduction (spiders and pseudoscorpions), protection (male spiders), feeding (spiders) or moulting (spiders and pseudoscorpions). Such nests may often consist of debris as well as silk, but so far there appears to be no record of a nest of grass or debris only.

Distribution and Orientation of Burrows.

The next problem to be considered is where, within an area whose topography is generally acceptable to C. latimanus, its burrows are to be found. Preliminary observations in the laboratory on animals kept in small plastic dishes half filled with soil showed that the scorpions invariably burrowed in the better-lit half of the containers. If the diggings were erased and the dishes reversed the scorpions again burrowed in the lightest half of the dish. There is, however, a strong local belief that the scorpion has a knowledge of the magnetic poles and will dig in such a position that the entrance of the burrow faces either due east or due west. The question therefore arose as to whether the light orientation shown by the scorpions was not really a magnetic orientation. The experiment was repeated so that the light source, originally roughly from the east, now came from the north. The same pattern of light orientation was found in both cases.

It should be noticed however that a photo-reaction by the scorpions might still produce an east-west orientation of the burrow mouths, for, if digging is initiated in either early morning or towards sunset, then, if the scorpion faces the light, some burrows will face east, others west. To check this point observations were made in the field. Quadrants were marked out and the ground worked over carefully so that no burrow openings should be missed. As has been explained above, the opening of a scorpion burrow is oval so that, as each burrow was found, a line was taken along the major axis of the oval and the angle between this and the north-south line noted. As can be seen from fig. 1, no striking orientation is apparent in a sample of over 50 burrows examined. A χ^2 test shows that the chance~~s~~ of the distribution being ~~differing are~~ random is ~~to~~ > 0.1.

It has been assumed that burrowing occurs during the hours of daylight. No observations of the initiation of digging have been made in the field, but it has been ascertained, by sprinkling powdered chalk at the entrances to scorpion burrows, that excavation mainly occurs at night, though it may commence at sunset. If this is true also for the initiation of a new burrow, then clearly the observations in the laboratory merit further interpretation.

Behaviour in small containers showed two possible aspects of the choice of a digging site: the animals not only dig on the lighter side, but also in corners. However, care must be taken in interpreting the digging in these small containers as simply burrow construction: it may rather be in the nature of an escape reaction. Certainly newly caught scorpions when placed in small dishes or large terraria move towards the light. In large terraria if the animals are left undisturbed, the response presently ceases and when burrowing commences it is not invariably in the best lit area.

But in large terraria the burrows nevertheless are dug in a corner, in the curve of an earth clod or in a grassy niche: never out in the open. This distribution of burrows is found also in the field where they are always at the edge of a clump of grass or under an overhanging piece of bush. This is illustrated in fig. 2, where

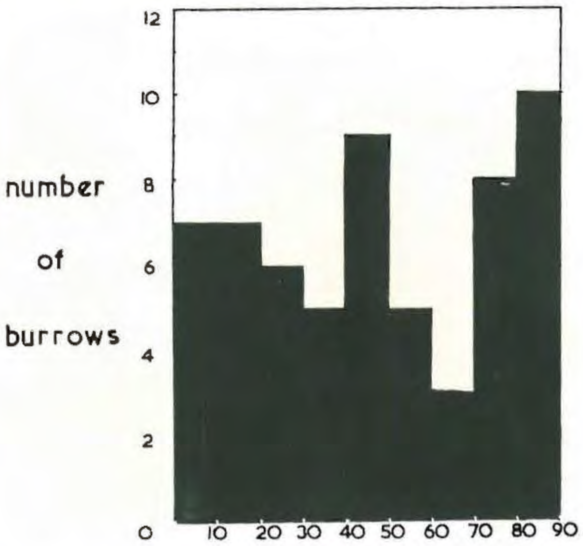

Fig. 1. Orientation of burrow mouths with respect to magnetic north. The convention adopted in measuring the inclination is that a burrow facing north or south is at 0°, one facing east or west is at 90°. Abscissa therefore is degrees.

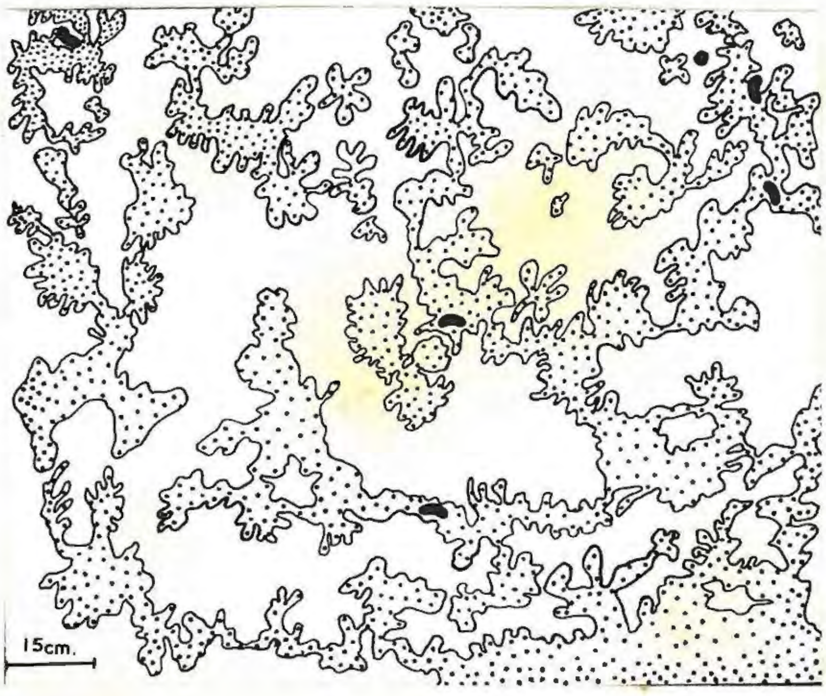

Fig. 2. Diagrammatic representation of a piece of veld in which five burrows of O. latimanus were situated; the stippled areas indicate plant cover and the black oval shapes the scorpion burrows. It is clear that these latter are, in the main, under cover, thus contrasting with the entrance to a burrow of some lizard, which is indicated as a round shape in the top right-hand corner.

the distribution of five burrows in an area of veld 1.5 x 1.2 sq.m. is shown. The adaptive significance of this distribution, based perhaps on thigomopausic behaviour, is clear in so far as it assists in concealing the entrances of the burrows from both predators and prey.

Soil Preference.

A number of preliminary experiments were run to see whether evidence for a preference for a particular type of soil could be found. Long rectangular troughs were filled, half with clean builders'-sand, half with loam from the habitat of the scorpions. All experiments were conducted in the dark, the soil emptied from the dishes after each observation and the dishes themselves washed. Each scorpion was allowed two hours in such a choice chamber and the position in which it had commenced to burrow, if at all, was then noted. The results obtained showed no clear indication of a preference for one type of soil rather than the other, but there were some indications that individuals showed personal preferences, some digging more frequently in the sand, others more frequently in the loam. In the absence of a clear-cut effect, the matter was taken no further although clearly the subject is worthy of detailed study.

Washing

Finally there must be mentioned a pattern which appears to have arisen in association with burrowing. This is the washing pattern. Baerg (1954a) refers to a very similar habit in the Jamaican scorpion, Centruroides insulans Thor. and records, apparently for the first time, that scorpions will clean themselves with an oral secretion. In O. latimanus the cleaning has often been watched, occurring most frequently at night but also during the day and more specifically either when the animal has covered itself with mud during its burrowing activity or the experimenter has painted it with mud or other mush.

Firstly the two fingers of one pedipalp are cleaned; they are taken between the two chelicerae which move alternately in and out, the claws opening and closing all the while. On the median and ventral surface of each chelicera, on its second segment (fig. 3) a large mass

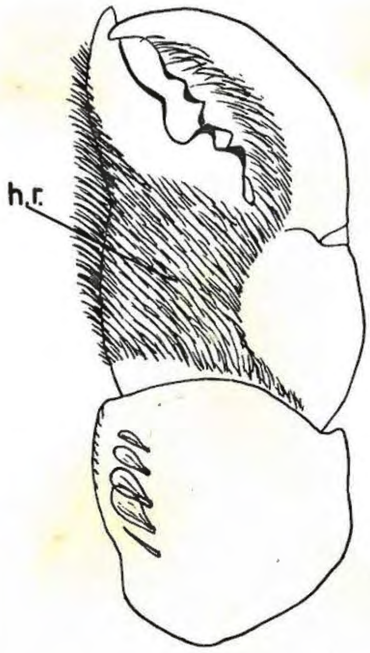

Fig. 3. Ventral view of the left chelicera of O. latimanus showing the hair-covered region, h.r., used in washing.

of fairly long, soft hair can be seen. It is this hair that is used to scrub the pedipalp claws. The cheliceral jaws will remove large or hard pieces of soil with their claws. As the chelicerae move in and out, a clear to whiteish secretion appears at the opening of the preoral cavity and is pushed on to the parts that are to be washed by the action of the chelicerae. This secretion is very like that which appears during feeding and in fact Baerg implies that it is the same. Whether this is true or not the cheliceral movements of washing and feeding are very similar. Moreover in feeding rhythmic movements are made by the first and second pairs of legs. These same movements, albeit only on one side, are also to be seen in washing which may reflect a genuine relation between the two patterns.

The base of the first leg as well as those of the second and third get covered with the liquid, but it is not clear whether this is just incidental to the main oral washing operations or whether the legs are actually being washed or being used to wash any other parts. The foot of the first leg has been seen rhythmically stroking the anterior edge of the coxae of the first and second legs, but exactly what part this plays in cleaning is unclear. Pavlovsky and Zarin (1926) state that in many scorpions these two pairs of lobes contain glands that are associated in some way with feeding, but they give no indication at all where they open. It is possible that, if such glands are present in <u>O. latimanus</u>, it is their secretion that is used in washing and the movement of the foot in stroking the coxae of the first and second legs is either spreading the fluid or stimulating its production or release.

The inner surface of the hand is normally washed thoroughly, though the outer part is often left partially dirty. Each of the fingers, however, is normally polished so that even in the tiny second instar animals it is quite clear when they have washed off the dried mud that has been painted on by the experimenter. During the washing of the ventral part of the hand the scorpion often gets into the most ludicrous poses (fig. 4a) and the ventral part of the hand sweeps across the anterior part of the dorsal carapace, thus washing the region of the eyes (fig. 4b). This operation does not, however, always occur, even

Fig. 4. (a) A female O. latimanus washing her pedipalp by brushing it between her chelicerae. The first three legs of the left side are bent beneath the animal and assist in some way with the operation.

(b) The anterior end of a female O. latimanus as she uses her recently wetted pedipalp for cleaning the front of her carapace.

when the dorsal carapace has been especially dirtied, so that this washing may well be purely incidental to the cleaning of the claws.

Besides the hands, the more distal segments of the legs and the anterior region of the carapace, no other parts have been observed to be cleaned by the scorpion in the laboratory. In C. insulans Baerg reports that the tail may be brought down to the mouth, covered with fluid and then used for 'sponge-bathing' the back. Though individuals of O. latimanus have been carefully watched and their tails stained so that any use of them as sponges would be apparent, no such behaviour has ever been observed. In Uroplectes triangulifer Thor., however, the washing behaviour has been found to be almost identical with that described for C. insulans. The chelicerae move very actively, the three legs of the one side are all bent so that the feet are close to the mouth region and are moved rhythmically, while the tail touches on to their bases, on to the chelicerae and then wipes clear the region of the carapace.

When O. latimanus has finished washing itself, it will continue the alternate cheliceral movements for some time, occasionally moving its legs as well. It is presumed that this is concerned with cleaning the chelicerae themselves of dirt, either dropping or swallowing it. When a scorpion cleans her pedipalps of Gestetner Correcting Fluid, particles of it are clearly seen below her chelicerae after the operation, so that it would appear that at least some of the dirt is let fall from the cheliceral bristles. Unfortunately the faeces have not been examined, so that it is not clear whether any is swallowed as well.

It may be noted at this point that the anatomy of the stings of O. latimanus and Uroplectes fits in well with the different washing technique used by the two animals, especially that surface which is morphologically ventral and topographically ventral during washing (fig. 5). In O. latimanus the sting is rounded and covered with fairly long sensory hairs, while in Uroplectes it is flattened by the protuberance h and almost entirely without sensory hairs. It is interesting to note that the form of the sting of Uroplectes is a systematic character used to

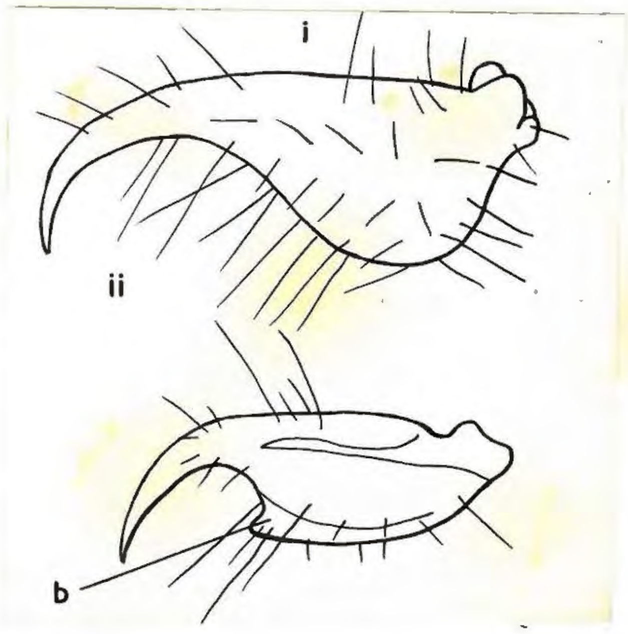

Fig. 5. The sting of (i) O. latimanus and (ii), below, that of Uroplectes triangulifer showing how the tubercule, b. on the latter appears to increase the surface on the sting which can be used for washing.

separate ~~it from other genera of the Buthidae~~ species of the genus Uroplectes and to recognise how an apparently meaningless systematic character has in fact significance in the life of the animal.*

Beside the record of Baerg quoted above, there are several references to cases of washing among arachnids. Bristowe (1954) states that spiders clean themselves, using their chelicerae and presumably some oral secretion. Lawrence (personal communication) says the same is true of solfugids, while my own observations show that the pedipalp, *Damon variagatus* Perty, certainly cleans its pedipalps between its chelicerae.

It is clear that there is some measure of similarity between all these cases of arachnid washing and this might be ascribed to a common phylogenetic origin. It seems more probable however that it is correlated with direct functional considerations. The parts that have been reported to be cleaned - in the scorpions, the fingers of the pedipalps, that part of the dorsal carapace on which the eyes are situate~~d~~, the sensory legs, and in the spiders the tips of the feet and pedipalps - are all sensory areas which, if left covered with dirt, might well be useless. The fact that the chelicerae are the structures used for the cleaning operations may well be due merely to their nearness to the mouth and source of a 'cleaning fluid', or alternatively, as has been adumbrated above, to the adaptibility of the feeding pattern, in which these structures are concerned, to the purposes of cleaning the animal.

* The character is a specific rather than a generic one; many genera of Buthidae have a large triangular tooth beneath the aculeus.
It is also more of a sex character used for systematic purposes. The flattening of the ~~sting~~ ventral surface of the sting is much more strongly developed in the males of *Uroplectes triangulifer marshalli* than in females.

3. FEEDING, DRINKING AND DEFAECATION OF THE SCORPION.

The process of capture of prey in the scorpion involves the use of the sting and venom: scorpions are "well-known" to be cannibalistic, eating their mates and even their young ones: for long periods, sometimes as long as a year, these animals may go without feeding, still running about and "exhibiting all signs of life." These three aspects of scorpion biology are those traditionally of interest in any consideration of the feeding habits of the scorpion. They are treated at some length by Fabre (1923) and have been referred to fairly constantly by scorpion observers before and since. In the case of *O. latimanus* not one of the three can be embroidered to any extent. The sting is seldom used in the capture of prey; animals eat one another only in exceptional and rather unnatural conditions; there seemed little profit to be gained from experiments of leaving the animals in the laboratory without food for any time longer than a week or two. However, various less spectacular behavioural characteristics concerned with feeding were noticed, and they appear important and interesting, if only in that they are "natural" and may lead to further analysis of the behaviour concerned.

Type of Prey Taken.

Numbers of records of the animals caught and eaten by various types of scorpion make it fairly clear that, in general, scorpions tend to feed on other arthropods almost exclusively. Another point that comes out fairly markedly in these records is that different species of scorpion have different arthropods as their staple diet and prefer these to others (see Lankester, 1883). Pocock (1893) comments on this fact, saying "this difference of instinct in the choice of food is remarkable, seeing how similar these two scorpions (*Euscorpius carpathicus* (L) and *Androctonus australis* (L.)) are in other particulars, both of habit and structure." Schultze (1927) remarks how the difference of food preference tallies with the difference of availability of potential prey in the different habitats of the scorpions concerned.

Such differences of food preference were quite clear among the various species of scorpion that were kept in the laboratory at one time or another. Uroplectes triangulifer Thor., for instance, would not usually catch any of the normal prey of O. latimanus, living entirely on one particular species of termite. Though O. latimanus would sometimes catch and eat this termite, or others refused by U. triangulifer, it was by no means keen on such fare.

The preferences shown by O. latimanus itself are of some interest. A list of the arthropods taken in order of their apparent preference has been determined mainly by two factors: the "avidity" with which an animal is caught and eaten, and the number of cases in which a high-listed animal is caught after a scorpion has just previously refused a lower-listed one. Due regard was, of course, paid to the state of hunger of the scorpion being used, but with a large number of observations spread over two years, discrepancies arising from the physiological state of the animals tended to be evened out.

A list of the prey in order of their apparent acceptability to O. latimanus runs thus:- crickets, locust nymphs, winged termites, cockroaches, spiders, larvae of some sub-terranean beetle, a local tenebrionid adult, various diplopoda, moths and pieces of small terrestrial annelid. Animals which were never taken were wood-lice, small crabs, diptera and their maggots, snails, and hairy lepidopterous larvae. All of the prey tested were of roughly the same order of size, so that should not have influenced the selection. It would seem initially that the degree of movement might well have some influence, the animals at the top of the "selected" group being on the whole more active than those lower down. It is however clear that this would not explain the manner in which the very active diptera and also the crustacea were ignored. It is possible that it is not the amount of movement but the type of movement that is selected: either the erratic jumping of the cricket and locust or the fairly fast but smooth running of the cockroach, beetle, etc. being preferred, while the jerkiness of the fly without wings or the crab's scuttling is ignored. On the other hand it is possible that the form or scent of the arthropod allows it to be recognised. Further discussion of these points must await the closer observation of how the scorpion appears to perceive its prey.

Perception of Prey

There have been many suggestions regarding this subject. As is mentioned in the section on digging, Schultze (1927) believes that insects that are the prey of scorpions wander into their burrows to hide and are captured: that there is really no "perceiving" in as far as it means "recognising a prey", but that the scorpion eats what falls into its claws. Such a suggestion in regard to O. latimanus is clearly in conflict with the fact of prey selection described above. However, it is not wholly at variance with the opinion of Cloudsley-Thompson (1955b), who states that "scorpions do not usually go to seek their prey, but the insects which serve for this purpose come to the scorpion's lair to hide." Lankester (1883) holds that Androctonus australis comes upon its prey "by stealth". Probably due to the disturbance of my footsteps, no capture of prey by O. latimanus was ever witnessed in the field. Only observations in the laboratory can therefore be quoted here.

Normally the scorpions were fed on the insects which were reported earlier to be at the top of the list of preference: small locusts, crickets, termites, beetles and diplopoda. In the field, either beside or inside the burrow, the remnants of some of their normal prey indicate that the insects preferred in the laboratory are not very different from the normal (skeletons of mole crickets, beetles, diplopoda and locusts were found), and that the laboratory behaviour may therefore not be abnormal.

The food was dropped into the scorpion dishes or terraria and the scorpion usually took it within the first five minutes, or at least the first hour of its being put there. Occasionally, however, the intended prey would remain with a scorpion for as long as a month, apparently perfectly immune from attack. The same sort of behaviour has been observed in snakes, and the subject may prove of interest in regard to problems of habituation.

The scorpion was usually walking about or washing when prey was put in at night, though often during the day it was merely sitting or standing with "stilted pose" (p. 57). If the prey stayed still where it was dropped it was frequently ignored, but sometimes the scorpion would come forward, pick it up with its claws and after crunching it several times, bring it up to the alternately grasping chelicerae. These would then start to tear the animal to pieces before the food was passed into the preoral cavity.

If the prey is moving, it is almost certain to be caught after a short time. If, however, the scorpion has fed fairly recently, the prey may be partially crushed and then released. The movement of the prey may, moreover, be entirely ignored by a fully fed scorpion, so that it is not true that in all cases the movement of an animal the size of normal scorpion-prey evokes a capture response.

Often when the prey runs or jumps away from the clutching pedipalps of the scorpion the latter will give chase, rushing this way and that in short spurts without apparently any clear knowledge of the whereabouts of the prey. It is in such circumstances that behaviour that has been called "seeking" is seen. The scorpion moves forward with widespread pedipalps, the claws of which are open. It stops, then lifts and lowers both pedipalps in a slightly jerky movement. Sometimes this may be done several times in fairly quick succession and the whole body may become involved. If the prey makes any slight movement at this point the scorpion will immediately dash forward or turn and run in the direction of the movement. This behaviour gives the impression that the scorpion was searching for its prey with its pedipalps which were being used as antennae.

Support for this comes from the fact that the reaction and also the actual capture of escaping prey is carried on quite efficiently by a scorpion that has had both the median and lateral eyes completely blacked out. (As evidence for the fact that this blacking-out had been done properly, is the fact that the scorpion's reaction towards light had disappeared altogether).

As will be shown later, O. latimanus shows no reaction to noise, so that there was no reason to suspect that it was catching the prey by the sounds being made. It is clear (p. 38) however, that the scorpion is able to react to vibration on the ground, while from the violent stridulation evoked when an animal is blown at, it is also clear that it can sense air currents. It was suspected that the former stimuli, those through the ground, were perceived by way of the pectines (see Cloudsley Thompson 1955a), while the form of the trichobothria on the pedipalps and the manner in which they could be seen to move when any vibration of the air was produced near them, indicated that the pedipalps might well be responsible for the latter reaction.

At first removal of the pectines was not very successful, the animals usually dying within a week or two of the operation. If, however, the base of the pectine is ligatured with fine hair before amputation, practically no blood is lost and the scorpion suffers no apparent ill-effects. Such an animal, however, is quite capable of catching and beginning to eat a cricket within 30 minutes of its being offered.

Testing the trichobothria is more difficult. It is necessary to scrape these out carefully, one by one, for if the whole pedipalp be covered with a thick layer of vaseline, or painted with Duco, Gestetner Correcting Fluid, etc. the scorpion will pay no attention to potential prey, but merely sit and wash its claws. An animal without visible trace of pedipalpar hairs appeared to catch its prey with no more difficulty than did the control. From these experiments it is clear that neither the pectines nor the trichobothria alone are essential for prey catching, but the possibility has not been excluded that if both are eliminated the prey-catching ability may be lost.

A second behavioural trait must also be taken into account.

So far, all the evidence that has been considered relates to the scorpion obtaining its food by perceiving its movement and then capturing the animal. Accounts of the scorpion feeding, such as those of Lankester (1883), Pocock (1893), Snodgrass (1948) and Vachon (1953), take it for granted that the prey is alive, while Glauert (1946) and Rayment (1955) state positively that scorpions (of Australia anyway) will not accept dead animals as food. However, *O. latimanus*, as *Centruroides vittatus* Say., reported by Smith (19~~48~~27), feeds fairly willingly on raw lean beef. It is true that this is taken more readily if it is moved so as to simulate the movement of live prey, but it will certainly be taken on some occasions when just left lying in the scorpion dish. It seemed that the scorpion might be reacting either to the smell of the meat or to its water content. Both of these, but more particularly the latter, were supported by the fact that a scorpion would not normally react to an insect lying still upon the ground, walking over it without ever stopping to try and eat it. The same scorpion would, however, stop, "investigate" and then begin to eat the insect as soon as it was cut open and the body contents exposed.

To test these two possibilities, the scorpions were given little blobs of cotton wool soaked in various liquids. As a preliminary test, blood-soaked wool was tried: the scorpion picked this up as readily as ever it did the piece of meat so that there is no question of the good beefy appearance of a little piece of steak being the releaser. There is no reaction to the colour of blood, since this was disguised by dirt. Given a piece of wool soaked in pure water, the scorpion took it as readily as it had the blood-soaked wool, and the behaviour elicited by this was virtually indistinguishable from that with the blood. It was clear that the scorpion would react to the water content only and that the reaction could not be distinguished in any way from that which might be evoked by some smell.

A scorpion was then allowed to drink from a pot of water and when the animal had "finished", it started to walk away. When put back beside the water, it left once more without drinking further; when presented with blobs of cotton wool soaked in water or red ink, it ignored them. A piece of raw beef was then placed before the animal; it ignored this as well. The observation was repeated a number of times and in no case did the scorpion ever treat the meat in a manner at all different from that shown towards the water- or ink-soaked cotton wool. From this, it appears that the eating of raw meat is, in *O. latimanus*, possibly a way of drinking water.

Support for this view was obtained when a group of 20 scorpions was starved of both food and water for three weeks. One lot of ten were then given water to drink and both lots had pieces of raw beef put in each animal's dish. Where the scorpions had just taken their fill of water, not one piece of beef was eaten, whereas in the "thirsty" group seven out of the ten had eaten their meat within an hour and a half. In *O. latimanus* it appears that the feeding reaction, when directed towards food other than living and moving prey, is possibly in all cases merely a "drinking" response.

It is, however, true that *O. latimanus* does react to smell, and this apparently be way of its pedipalps and legs (pp. 167-170) and indeed Pocock (1893) reports what he suspects is evidence for such a sense in the pectines of a scorpion. He reports that an adult *Parabuthus capensis* was walking over a fragment of dead cockroach, when half-way across the scorpion backed and began to feed, an event that Pocock attributes to the sensory information from the pectines. Though no such behaviour has ever been witnessed in the adult *O. latimanus*, the young, second instars particularly, often walk on to a piece of meat, stop when the first pair of legs is over the food, put down their chelicerae and begin to eat. There has been no evidence, however, that this behaviour involves the use of the pectines and in fact it seems that these structures were still too far back to have been affected by the food. The possibility of a pectinal sense of smell has, however, still to be disproved before Pocock's observations can be explained as being due merely to a coincidence.

Killing the Prey

O. latimanus uses its sting very infrequently when dealing with prey. Normally it will catch at the animal with one claw, then grip further along the body with the other. Holding the prey still with one, it will move the other claw along the animal's body, crunching here and there, frequently concentrating on the head ~~or other half portion~~. At this point the prey is very often turned round in the pedipalp so that the head is nearest the mouth of the scorpion. Waterman (1950) mentions that Tityus trinitatis (Poc.) also appears to prefer eating its prey head first, so that the trait may be more general than the lack of reference to it would suggest.

If there is to be any stinging at all by O. latimanus, it is usually only when the pedipalps have a grip on prey which nevertheless continues to struggle. The scorpion brings its sting fairly slowly over its head and inserts it carefully in some relatively soft point, moving the whole organ about until a suitable area is found. A sharp upward thrust of the lance of the sting occurs, and this is occasionally repeated. The sting is then returned to its normal position behind and over the body. The effect of the sting is not very obvious on the prey, but it does seem, to some extent, to reduce its struggles. Usually, however, when the chelicerae have already begun to tear the head of the animal to pieces, the hind part is still moving violently. This reluctance to use its sting in killing or paralysing prey contrasts strongly with the classical picture as presented by Fabre (1923): Buthus occitanus (Am.) plunges its sting into prey immediately it is caught. Schultze (1927) however reports that Heterometrus longimanus (Herbst.) behaves in a manner very like that of O. latimanus: in fact he says that he has never known this scorpion "use its poisonous stinger at any time in procuring or subduing the insects serving as its food." It would seem that the majority of Scorpionids, with their thin tails and relatively large and strong pedipalps, resort more to crushing their prey to death; the Buthidae with minute, weak pedipalps and thick, strong tails, use their stings to a far greater extent in obtaining their food. It would appear, in addition, that the toxicity of the scorpions which are not prone to sting is less than of those which are. Baerg (1925), comparing the toxicity of Centruroides margaritatus Gerv. and Opisthacanthus lepturus Pal de B., remarks how the latter, with almost no poisonous effect in contrast to the former, will only use its sting if the pedipalps are immobilised, while C. margaritatus needs no encouragement to sting.

Eating

The superficial behaviour shown in this pattern of activity has been described by Pocock (1893) for Parabuthus capensis and Euscorpius carpathicus, while earlier, 1883, Lankester had written of the feeding behaviour of E. italicus (Herbst) and Androctonus australis. Various workers have since repeated the observations and a paper by Snodgrass (1948) summarises well what is known of the process.

In O. latimanus, as in other scorpions that have been observed, the pedipalps hold the food, sometimes both limbs being used, sometimes only one. These put it within reach of the chelicerae which make alternate grasping movements towards it, opening and closing the claws at the end of the appendages so that, when they come in contact with the food, they effectively tear pieces off it. These pieces are pulled in towards the preoral cavity and at about each tenth cheliceral grasp a large burst of whitish to transparent fluid is poured over the food particles torn free by the chelicerae. This fluid appears to come from the mouth and Snodgrass (1948) suggests that it is from the salivary glands, while Kastner (1931) thinks, with apparently as little supporting evidence, that it arises in the mid-gut caeca. Whatever its origin, the observations on O. latimanus agree with those on other scorpions that it and the particles are drawn back into the preoral cavity. According to Snodgrass this suction is due to the muscular pharynx. In O. latimanus however, it would appear that, whether or not the pharynx is sucking (and there would seem to be no reason why it should not be) there is an additional mechanism coming into play. When the scorpion is being watched from above, conspicuous and rhythmical movements of both pedipalps can be seen. These move slightly outward and then in again in unison. If, as sometimes happens, the scorpion continues to hold the prey in one pedipalp, its claw can be seen to move rhythmically up and down as the scorpion "chews" the food already in the preoral cavity. Sometimes it can be seen that the first legs are also moving rhythmically and in unison. When the procedure is watched through a glass plate on which the scorpion is sitting, it is quite clear that there is a definite association of the movements of the pedipalp base and of the first leg with that of the fluid. Very often the movements do not affect the distal part of the leg, since this is fixed to the ground and only the pedipalpar movement could be seen from a dorsal view of the scorpion.

Since the base of the first leg partly overlaps that of the pedipalp, the details of the movements are not very easily observed. Fig. 6 is an attempt to represent the movement: that of the leg base, swinging on ~~the~~ a pivot, moves anteriorly and medially and then back again. The pedipalp coxa, moves medially and then out laterally again.

To see these movements in respect to the process of feeding, where they clearly play some part, it is instructive to look at a cross-section of the preoral cavity of the scorpion, fig. 7. The dorsal wall is provided by the soft but muscular labrum (rostrum of Pavlovsky and Zarin, 1926), the lateral walls by the medial portion of the pedipalp coxae, and the ventral walls by the medial processes of the first and second legs, those of the latter lying below those of the former. The surfaces of the labrum, pedipalp coxae and coxae of the first leg, which go towards forming this cavity are covered with long fine hairs, all directed in towards the mouth at the ventral and most posterior point of the preoral cavity. It is clear that movement of the walls of this cavity, with its directed hairs, could well be used either in sucking

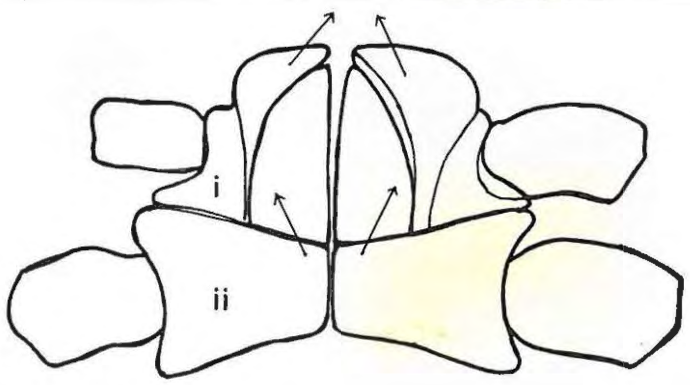

Fig. 6. Diagrammatic representation of the anterior, ventral region of O. latimanus, indicating by arrows the approximate movements of the limb bases during feeding. i., coxa of the first leg; ii., coxa of the second leg.

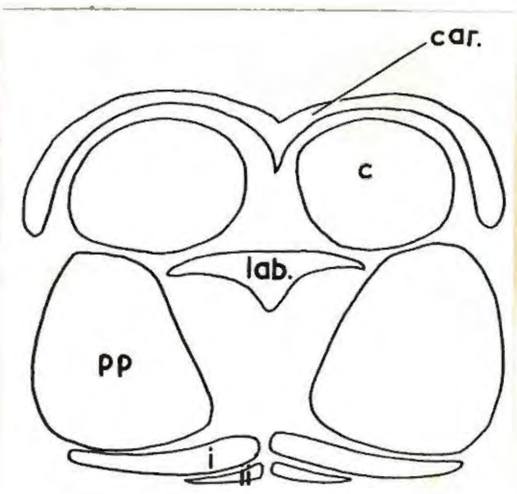

Fig. 7. Diagrammatic representation of a cross-section through the preoral cavity of O. latimanus, indicating how its volume changes by lateral movements of the coxae of the pedipalps. car., dorsal carapace; c., chelicera; lab., labrum; pp., pedipalp coxa; i,ii., coxa of the first and second legs respectively.

food particles and digestive juices back towards the mouth by the expansion of the cavity or in the expulsion of both digestive juices and pieces of waste food from the cavity by reducing its volume. The sideways or medial movement of the pedipalp coxae is evidently associated with enlarging the cavity or reducing it. The exact result of the movement of the base of the first leg has, however, not been deduced. It may not directly alter the volume of the preoral cavity but may dislodge solid particles which have dropped down on to its hair-covered surface.

This cheliceral chewing, fluid expulsion and then retraction with its associated pedipalpar and pedal movements may continue for as long as three hours, but is interrupted at intervals for the rejection of some particles.

Rejection of Waste Particles

After the scorpion has torn a certain amount of material from the animal that it is eating, it will stop further tearing cheliceral-movements but will continue sucking fluid in and out of the preoral cavity. A small pellet of chitinised remnants is eventually partially extruded from the mouth. The scorpion may move slightly to free itself from this, but usually hooks it with both of the front legs and pushes it away with these limbs. Very often O. latimanus will only eat enough of an insect to form a single pellet but may occasionally go back and chew again at the prey after the first pellet has been ejected. In one case six pellets were left from a single cricket.

These pellets are very firmly stuck together and it is difficult to get them undone without adding further to the disintegration of the remnants. Being shaken up in warm alcohol usually frees many of the fragments and the rest of the pellet can be pulled to pieces with a little care and a needle. Almost no entire structures are ever present, except the mandibles of beetles; even the segments of legs and antennae are crushed or split open. Much of the general exoskeleton that covered the body of the prey is shredded very finely, and, out of context, quite unrecognisable. Looking at the pieces freed from one of these pellets it is very clear how mistaken one could be if one believed that all scorpions habitually suck the body fluids of their prey, as Rayment (1955) asserts.

Immediately after ejection, a pellet containing remnants of a cricket may weigh as much as 15% of the insect before its death. Pellets containing winged termites appear to contain a slightly lower percentage of the whole insect, i.e. 7 - 11%. Lafon (1943) reports that in the case of Tenebrio larvae the cuticle contributes 14% of the total weight of the insect. The type of cricket fed to the scorpions appears to be sclerotised to roughly the same degree as is a Tenebrio larva, and it would seem reasonable to expect about the same percentage of the body weight of the cricket to be made up of cuticle. The chewed pellet, which appears on microscopical examination to consist almost entirely of the exoskeleton, tallies very roughly with the weight that might be expected for it, if it consisted of the cricket cuticle alone. In the alate termite, where the degree of sclerotisation appears superficially to be less, and where there is certainly a large store of oily material, the weight of the pellet as a percentage of the total termite is much lower; again this is what would be expected if the scorpion had cleaned the exoskeleton and thrown it out as a pellet.

Irrelevant, but perhaps of some interest in a comparison of feeding methods of arthropods, is the fact that the onychophoran, Opisthopatus cintipes ~~Wood-Mason~~ Purcell, leaves approximately the same amount of reject from an alate termite or cricket as does O. latimanus, though the method used, that of injecting digestive juices into the insect body and sucking up the resultant "broth", is very different from the thorough chewing that the scorpion gives its prey.

Drinking.

Baerg (1954) reports that the scorpions under his observation frequently drank from wet cotton wool or drops of water which he placed for them. He writes of this as a rather rare observation, saying that until 1933 it was not realised that scorpions drank at all. True, Pocock (1893) says P. capensis and Euscorpius carpathicus do not drink. In 1927, however, Schultze stated that his scorpion, Heterometrus "had to be given a certain amount of water every day", and now most workers on scorpions recognise that these animals must have water available if they are to live healthily for some time. O. latimanus is no exception, and can readily be seen to drink, especially if left for a few days without access to moisture.

Perception of Water.

When water is put into the dish of a desiccated scorpion, the animal will usually go towards it within a few minutes and start drinking. If the water is spilt on to the ground the scorpion will go towards the spot and will try to pick up the dampened soil. Occasionally, the water has been put to one side of the scorpion and it has been noticed that, as the animal passes and its pedipalp moves across the area in which the water was spilt, it will react to the water, turning and trying to drink. This aroused the suspicion that some organ on the pedipalp is sensitive to the presence of water.

Such an hypothesis was supported by the behaviour of a scorpion that had been found in the field and had only one pedipalp, the stump of the left one being well healed. After she had been without water for a few days, this was then put on her right side. She quickly turned to it, whereas if it were placed on the left side, she often did not find it for a long time, sometimes walking directly away from it, though if one of her legs came in contact with the water, the scorpion would stop and drink.

Support for the thesis that the hygroreceptors are situated on the pedipalp claws and the legs may be obtained by touching a wetted paint brush tip on to various parts of the body of a desiccated scorpion. On the body, on the tail, or on the first four segments of the pedipalp, this touch caused no reaction different from that of the control, to the touch of a dry brush. On the hand or claws of the pedipalp, or on any one of the legs, the wet brush elicited part or all of the drinking reaction, depending on whether the wetted area was accessible to the chelicerae or not. Sometimes, though no water (or in other cases almost none) was taken up, the animal would chew its chelicerae alternately for a minute or two. Very often the scorpion would act as if it were trying to reach water that was just slightly *above* its head, but as yet no explanation can be offered for this. Certainly, however, water on the pedipalps and legs will elicit a drinking reaction.

Attempts to place water on certain of the pedipalpar hairs only, gave no clear-cut results, as the animal's movements dislodged the drops. A couple of scorpions had as much as possible of their pedipalpar hair removed by cautery, but they both reacted as did the control to water on their hands. It is, of course, possible that hygroreceptors in the form of hairs were in each case missed, though this seems unlikely. It is also possible that they were missed not as an oversight, but because they were too short for the cautery to burn without burning the scorpion's hand; certainly there are a number of minute, fine hairs on the claws as well as in other places. However, it is well to remember that Blumenthal (1935) has described minute pit-sense organs on the tarsi of spiders and that in twenty-two species he has experimental evidence that they function as hygroreceptors. No serious effort has yet been made to investigate the possibility of such organs occurring in the scorpion, but it should cause no great surprise if they are discovered on the claw and legs of *O. latimanus*.

Drinking Behaviour

Schultze (1927) describes how *Heterometrus longimanus* drinks by taking up water in her mandibles from grooves in pieces of the bark of trees or "reachable parts of its legs." He says further that a scorpion would sometimes sip water from between the fingers of its pedipalps, holding the latter close to the chelicerae "in the way a man holds a glass in his hand and brings it towards his mouth."

O. latimanus will often dip her *claws* into the water, pedipalp claws apparently deliberately and will chew with alternate chelicerae at the water held between the fingers. However, this normally stops after a few seconds and the chelicerae themselves are dipped into the water and continue their chewing movements. Soon this also stops and the scorpion sits in the attitude shown by that of the animal of fig. 8 There are occasional movements of the whole pedipalp, and it would seem that the sucking pump and possibly that of the preoral cavity (see page 26) are drawing the water into the scorpion.

It seems possible that the pedipalps of the scorpion are used in drinking in cases where it is impossible for the chelicerae to get anywhere near the source of water, and that, where a free water surface is provided, the pedipalpar drinking occurs only in the preliminary stages of the behaviour. To test this the scorpions were given glass tubes of 3 mm. diameter in which a little water was placed. It was impossible for the chelicerae to touch this water but by using the pedipalp fingers, the scorpion would have managed to get some of the liquid. Under such conditions the scorpions juggled with the tubes for ten minutes or so: trying to push their chelicerae into the narrow aperture. Not one made the slightest attempt to insert its fingers and then to drink from them. If the explanation of the pedipalpar movements in drinking is correct, no evidence to support it appears from this observation. It seemed possible that the test might be considered a little unfair in that the scorpion could obviously sense the water but could not push its chelicerae through the glass, i.e. the test was too "unnatural". A small empty snail-shell was therefore used, a wadge of wet weed being pushed fairly far into it, so that the scorpion could not see it. The desiccated scorpion was certainly aware of the dampness within the snail shell but no attempt was made to pull the weed out, so that the water could be sucked up from it.

It seems more probable that the pattern of drinking behaviour is derived from the feeding pattern wherein the pedipalps play an initial role. This has been retained in the drinking behaviour, albeit it seems to have no especial value in obtaining water unavailable to the chelicerae. That the two patterns are closely similar or almost identical is not surprising in view of the fact that both largely involve the sucking up of fluid.

Fig. 8. *O. latimanus* seen drinking from a water dish. The chelicerae are being inserted into the water and drinking from the claws of the pedipalps has already occurred.

Defaecation.

I have found only two references to this behaviour in the scorpion, one by Lankester (1883), the other by Pavlovsky and Zarin (1926). The former states that he has not witnessed the actual event but describes the faeces: the latter describe the mechanism of the event but do not say how the details of their report were acquired, nor do they mention the overt behaviour of the animal during the process of defaecation. In O. latimanus the behaviour has only been witnessed on two occasions and the mechanism has been ignored altogether, posing too complicated a technical problem for so small a reward.

Both occasions on which the behaviour was watched were during the afternoon, though this is in fact merely coincidence, indirect observations showing that it may occur at any time of the day or night. The scorpion held its tail down on to the ground, so that the anus was in contact with the soil. The faeces consist of a long greyish-white thread, about 1 mm. in diameter, soft, and about 20 mm. long on the average. As the thread came out of the anus, the scorpion walked forward, moving its tail slightly from side to side, though this walking forward during defaecation does not invariably occur, as in many cases the thread is not spread out in a long line. A trail of clear brownish liquid followed at the end of the thread and, for some distance after this had ended (about 70 mm.), the scorpion still held its anus down on to the ground as it walked. An examination of numerous fresh faecal threads showed that a fair amount of liquid is invariably extruded with the thread.

As described by Pavlovsky and Zarin (1926), the faecal matter of the various animals they studied consists of "bright-white irregularly cylindrical lumps" while Lankester states that in Androctonus australis it is "white and opaque", consisting of a "fine moist powder." From the manner in which the observations were made by the workers concerned, it seems probable that the former are speaking of the appearance of the faeces within the intestine and the latter of their appearance some hours after they had been shed. If this is so, the two descriptions would fit very well the superficial appearance of the faeces of O. latimanus. If the faecal thread is more closely examined shortly after it is evacuated, it is quite clear that there is a membrane-like covering around the actual faecal material. If this membrane is broken with a needle, the fine whitish contents of the thread are freed; these contents dry to a fine powder in an hour or two. Within the intestine the faeces do appear as lumps, but this is dependent merely on the fact that the thread is folded upon itself in the gut; if trouble is taken to dissect it free of the gut wall, the whole is seen as a long faecal thread covered by a thin membrane.

The nature of this membrane has not yet been established in as far as we have no knowledge where it is formed or what are its functions. It is approximately 12 μ thick and stains blue with Mallory. Both of these characteristics are similar to those of the peritrophic membranes reported for other arthropods, e.g. that of Onychophora (Manton and Heatley, 1937). As yet I have found no record of such a structure in the arachnida. However it certainly does occur in most insects, the Onychophora and some Crustacea, so that there appears to be no obvious reason why it should not also occur in the scorpion.

Symphyla! Scutigerella have a peri. membrane & other orders? and mentioned by Manton

An attempt was made to discover how often the scorpions defaecate, although this was with some misgivings as Lankester (1893) reports that, in the four months that he kept some specimens of Androctonus australis, these did not defaecate at all. From Table I it is clear that such is not the case in O. latimanus or Opisthacanthus validus Thor. The maximum number of days between the scorpion's having a meal and defaecating is eight, while on two occasions an animal defaecated twice within twenty-four hours. The normal pattern appears to be the following: the scorpion feeds, waits a couple of days, defaecates, and may repeat this after another two days. In many cases, however, there is a defaecation a few days after a meal, and then, on the following day, a second evacuation. This might be explained as a case of incomplete elimination of the peritrophic membrane and its contents at one attempt. Certainly there is no daily elimination of a peritropic membrane, as is recorded for the Onychophora (Manton, 1937).

TABLE I.

Frequencies of Feeding and Defaecation in Individual Scorpions.

	Opisthophthalmus latimanus						*Opisthacanthus validus*
Specimen No. -	1	2	3	4	5	6	1
Date:							
26.ix.56	f	f	f	f	f	f	f
27.ix.	d	f			dd		
28.ix.	d					d	
29.ix.							
30.ix.		d		d			
1. x.	d			d	d		d
2. x.	f		f	d			fd
3. x.							
4. x.	d		d	d	d		d
5. x.							
6. x.							
7. x.	fd		fd	d	dd		d
8. x.	fd		f				
9. x.							
10. x.							
11. x.		d	d	d			
12. x.			d				d.

Key. f - fed; d - defaecated; dd - defaecated twice within 24 hours.

4. STRIDULATION

During the course of these experimental studies upon *O. latimanus* the animals were often hurt, frightened or annoyed. This normally resulted in their producing a hissing sound rather like that made by rubbing the flat part of a comb across a stiff brush. The stridulatory reaction was also easily elicited by blowing gently at the animal.

Pocock (1896) records the observation of Mr. G.A.K. Marshall that the "hissing" of the scorpion, *O. glabrifrons* Pet. "appears to be caused by the movement of the mandibles alternately backwards and forwards." This is also true of *O. latimanus*. A study of the structure of the chelicerae of *O. glabrifrons* led Pocock to suggest that the noise was made by the movement of a row of chitinous platelets on the mesial surface of the basal segment, rubbing against a similar row on the opposite side (Fig. 9a:*pl*) He recorded the presence of such structures in a number of other species of *Opisthophthalmus* - *O. carinatus* (Pet.); *O. nitidiceps* Poc.; *O. pugnax* Thor.; *O. breviceps* Poc. and also *O. latimanus*. He further stated that in two species, *O. wahlbergi* (Thor.) and *O. pallidimanus* (= *O. pallidepes* Koch?) this apparatus is absent, but there is present a patch of bristles on the dorsal surface of the basal joint of the chelicerae. Pocock had noted the presence of a similar patch of bristles in *Heterometrus*, had concluded that they were stridulatory, and therefore assigned the same function to the similar bristles in *Opisthophthalmus*. The bristles, he says, could be "thrown into a state of vibration by scraping against the front edge of the carapace, as the mandible is forcibly withdrawn beneath it." In *O. capensis* Koch, Pocock mentions that both of these two possible stridulatory mechanisms are present together. It appears that since 1896 no further studies have been made on sound production in these animals, except for the addition of other species in which anatomical observations have suggested the possibility that stridulation occurs in the same manner as proposed for the animals mentioned above.

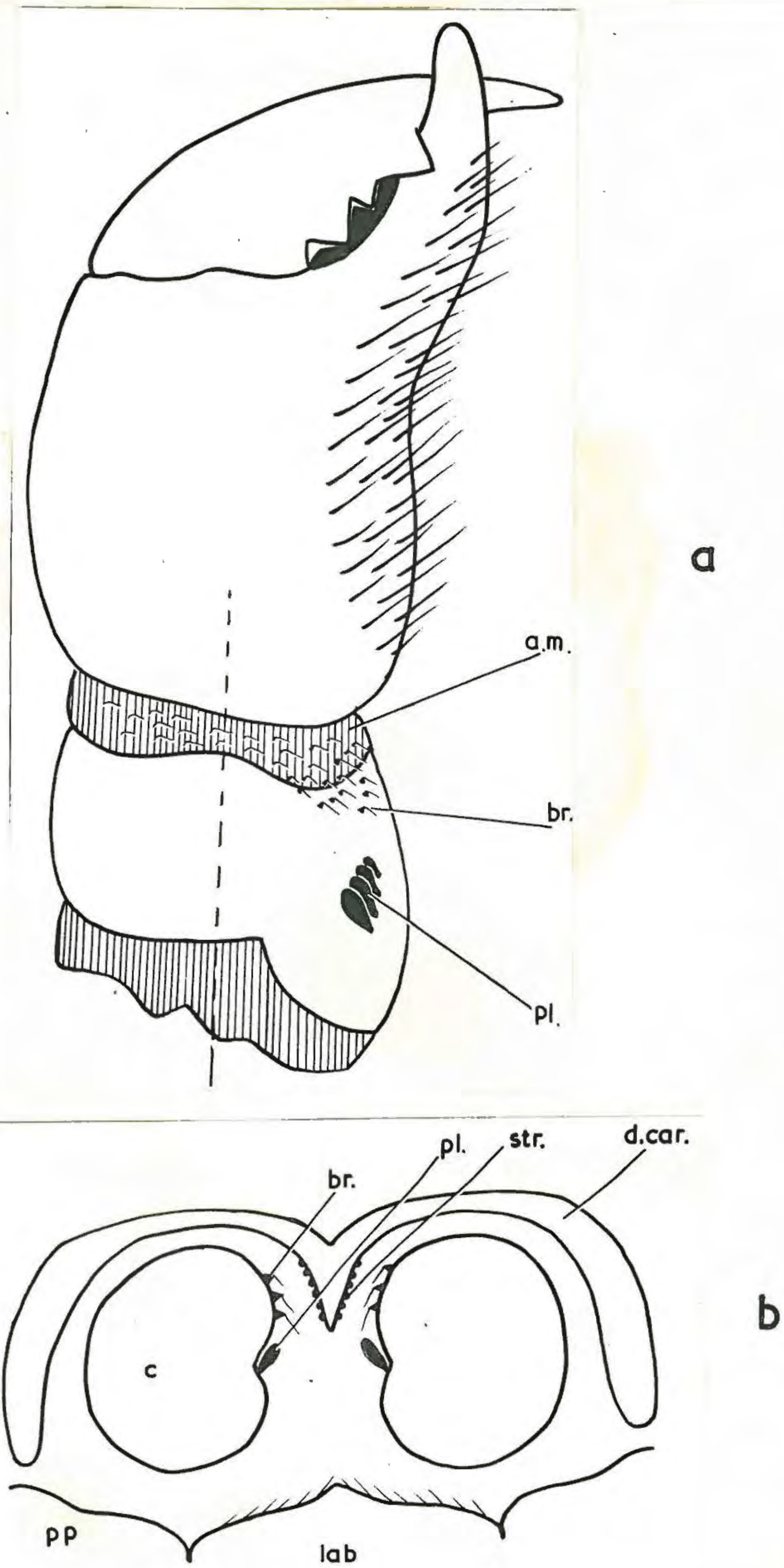

Fig. 9. (a) Dorsal view of the left chelicera of *O. latimanus* showing stridulatory apparatus a.m., arthrodial membrane between the first and second segment; br., specialised stridulatory bristles; pl., median platelets.

(b) Representation to show the relationship of parts of the stridulatory apparatus to each other. br., bristles; c., chelicerae; d.car., dorsal carapace; lab., labrum; pl., median platelets; pp., coxa of pedipalp; str., striated area on the undersurface of the carapace.

The Stridulatory Mechanism of O. latimanus

As reported by Pocock, there is a row of small chitinous platelets on the mesial surface of the first segment of the chelicera of O. latimanus. There were three to seven of these platelets in the animals examined, though the mode was clearly four (see Fig.10). The shape and size varies quite considerably within the species. There is also a conspicuous patch of specialised bristles on the dorso-mesial surface of the first cheliceral segment (Fig.9a,br), clearly similar to that described for O. wahlbergi and O. pallidimanus. In addition there are, on the inner surface of the carapace, on either side of the deep median furrow, two patches of striated chitin (Fig. 9b. str). These striations are at right angles to the long axis of the body, and when the chelicerae make their alternate movements, they move the bristles across these striations. The bristles are never moved forward beyond the edge of the carapace as Pocock had supposed. In species in which there is little or no specialisation of the bristles, namely O. carinatus, O. capensis and O. nitidiceps, no such striations are seen on the under surface of the carapace. Thus O. latimanus would appear to have two possible mechanisms of stridulation; clearly either or both could be used.

why two? it seems to me more like two stridulatory surfaces, but only one mechanism

It is easy to demonstrate that during stridulation both structures could be involved in sound production. If the mesial platelets of one side are painted with a thin layer of molten lipstick and the animals stimulated to stridulate, it is found that the lipstick has been transferred to the platelets of the opposite side, but nowhere else. Similarly, if the dorsal bristles are painted, the lipstick is transferred to the striated area, showing that they are rubbed against this during stridulation. These observations show clearly that the relevant parts are rubbed against each other while the noise is being produced; they prove nothing about whether these parts are concerned with noise production.

If the chelicera of one side is held with a pair of forceps so that both movement and contact with the opposite appendage are

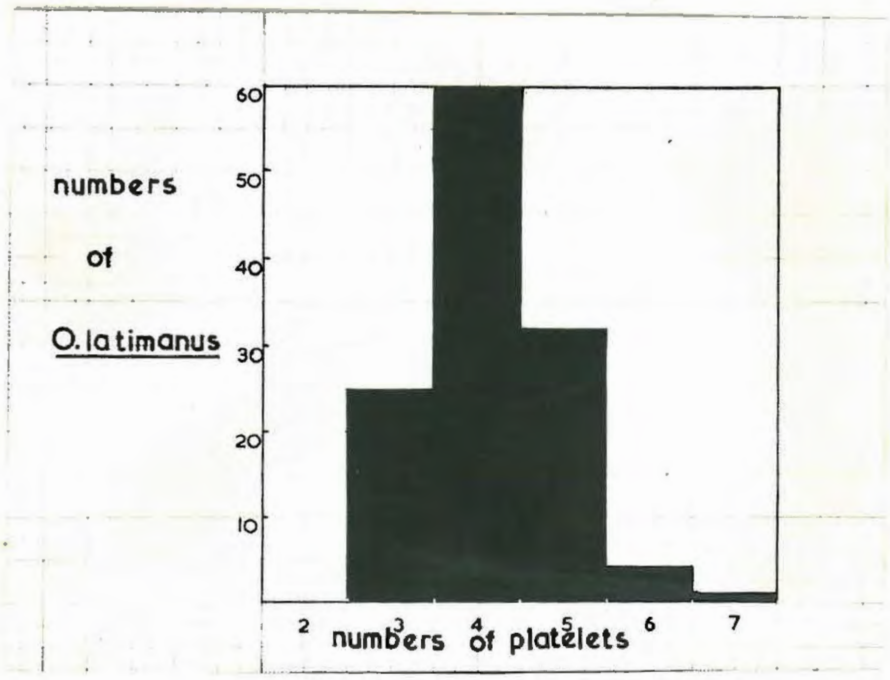

Fig. 10. Distribution of the number of cheliceral platelets in *O. latimanus*.

prevented and the animal is then stimulated by blowing upon it lightly, the free chelicera is moved in and out with an accompanying hiss. Again if the mesial platelets are completely cut away, the scorpion will still stridulate and the noise sounds no different from that of the normal animal. It is clear that the dorsal bristles and striated areas on the carapace are capable of acting together to form an effective stridulatory mechanism.

It is less easy to obtain positive information about the mesial platelets. The specialised bristles cannot be removed without damaging the chelicerae, but it is possible, without upsetting the animal, to remove almost completely that part of the carapace against which the bristles normally rub. After such an operation the experimental animals, when stimulated, were found to move their chelicerae as vigorously as normal ones, but the only result of these movements was a number of rather irregular and barely audible clicks. It is impossible to remove the whole of the carapace area against which the specialised bristles rub without destroying the insertions of certain of the cheliceral muscles and it seemed possible that the clicking noise might originate from the small remaining stridulatory area. If however the mesial platelets are cut off an animal from which the dorsal striated area has already been removed, only the very faintest sound is produced. It would therefore appear that the mesial platelets do contribute to the general stridulatory noise, but that their contribution is relatively small.

These conclusions may be checked on a dead scorpion. If the chelicerae are moved so that only the bristles rub against the striated area, a hissing noise is produced. If the chelicerae are held so that only the platelets rub together, a clicking noise is heard. Once the two sounds are learned, it is possible to recognise the clicking sound in the stridulation of a normal animal. It is only definitely distinguishable at the end of a bout of striduation, presumably as the animal lowers its chelicerae. It has not been possible to determine whether this clicking is a normal component of of the entire stridulation, drowned in the far louder hiss, or whether it is normally made only at the end of stridulation.

Stridulation in O. nitidiceps.

In this species, as already stated, the dorsal bristles of the chelicerae are not basally flattened and lie only on the arthrodial membrane between the first and second cheliceral joints (cf. Fig. 9a of O. latimanus, where the bristles are also on the first podomere). The carapace is not deeply keeled between the chelicerae and there are no transverse striations on its ventral surface. The median platelets are however more abundant than in O. latimanus, with a modal value of six. This animal may, with difficulty, be prevailed upon to stridulate. The movement is similar to that in O. latimanus, but the noise is very much weaker. Like that of O. latimanus it is not markedly reduced if the median platelets are removed, while it is very faint if the carapace is cut away. It therefore seems that in this species also the major noise of the stridulation, albeit of little volume, arises from the dorsal cheliceral bristles, though these show none of the stridulatory specialisations seen in O. latimanus.

The Biological Significance of Stridulation in O. latimanus.

As stated earlier, animals in the laboratory may be stimulated to stridulate by various noxious stimuli, but this casts no light upon the normal role of this behaviour. Lankester (1883), working with Androctonus australis and Euscorpius italicus; Pocock (1893) with Parabuthus capensis and E. carpathicus, and more recently Cloudsley-Thompson (1955a) with A. australis, all state that there is no reaction from a scorpion to air-borne sounds. Since there are two reports (Becker, 1880; Gaubert, 1889) that scorpions have a well-developed auditory sense, it seemed desirable to test the response to sounds of the animals under study. Tested with tuning forks and a toy pistol, O. latimanus showed no behavioural responses. There is, however, sometimes an orientation response to vibrations of the soil and this may be accompanied by stridulation. However, when two scorpions are on the same substrate only a centimeter or two apart, but separated by a strip of black paper to obviate visual responses, the one gives no response at all to the stridulation of the other.

It therefore seems unlikely that stridulation has any intra-specific significance in O. latimanus: certainly it has not been observed as a normal element in courtship or mating, in the relationship of the mother to her brood or when one animal invades the burrow occupied by another. It is true that when two scorpions meet in the open either or both may stridulate and retreat. This however is probably the same reaction as is shown in response to a large grasshopper, a spider, a human hand or a snake, and the stimulus probably has the general valency "unknown movement, perhaps hostile." In scorpion to scorpion encounters, once the animals actually come into contact, whether in a fight or a skirmish of threatening, no further stridulation occurs.

It seems probable then that the stridulation is a warning or a threat. Its value in this connection was tested upon such mammals as were available in the laboratory. The tests were performed both with normal scorpions and with scorpions from which both the striated area of the carapace and the platelets had been removed so as to reduce stridulation to a minimum.

The mammals tested appeared to fall into four categories. The first is that in which the stridulation produced no apparent reaction from the mammal, both control and experimental scorpions being eaten. In this class came the white rats of the laboratory. Normally these were so quick to kill a scorpion that it did not have time to stridulate at all. Whether this would be true of wild rats is not known, though it is possible that, had the tame ones not been so used to receiving only "good" food at the hands of the experimenter, they would have been a little more circumspect in their approach and the scorpion would have been given a chance to frighten them off. In this category also fell a tame mongoose, Suricata suricatta (Schr.) and a wild shrew (Suncus varillus (Thomas)). Both these animals killed scorpions with great skill, the shrew being able to deal with an individual almost as big as itself.

In the second group, a rather heterogeneous collection, are those animals on whom the stridulation had no effect, but which did not eat the scorpions. Here belongs a porcupine, *Hystrix africaeaustralis* Pet., which was tested. This animal was very tame and had been kept for some months in the laboratory. When a scorpion came near him he would usually stamp on it, crunch it up in his mouth and then spit it out; but he paid no apparent attention to the noise it was making. The domestic dog also belongs here for it showed no difference in approach to normal and silent scorpions and ate neither. Though falling in the same class, the behaviour of a vervet monkey, *Cercopithecus aethiops* (L.) and the bush baby, *Galago senegalensis* E. Geoff., is rather different. While no difference in their reaction to a stridulating individual and a control could be seen, both mammals crouched away as far as possible from the scorpions, though the monkeys would readily take locusts of the same size as the scorpions.

In the third class come those animals on whom stridulation clearly had an "intimidating" effect, although the silent controls were eaten. Only one animal tested, the hedgehog *Erinaceus frontalis* A. Smith, belongs to this category. The beast had been feeding on beetles, locusts and diplopods when an entire scorpion was put into his run. He trotted towards it and it stridulated. He immediately shuffled backwards and turned away. Two further encounters produced the same result. This response was not due to the animal being satiated as it readily accepted beetles as food immediately after these observations were made. The experimental scorpion was then replaced by a silent control. At the first encounter the hedgehog sniffed towards the scorpion and then, in spite of the waving of claws and sting, and the stridulatory movements of the chelicerae, he crunched up the scorpion, finishing the whole meal in a minute or two. After an interval of half an hour, the hedgehog was fed a few more beetles and then another normal scorpion. There was a noticeable hestiation as he sniffed at the stridulating animal, but he attacked it despite the noise. Though there was a week's interval before the next scorpion was offered, he took it also regardless of the hissing. After a few scorpion meals, the hedgehog dealt with scorpions almost as quickly as did the rats; it was quite clear that, although the stridulation might be an effective protection initially against hedgehogs, these animals quickly learn to disregard the stridulation once they have sampled scorpions as food. These events recall the behaviour of Hale Carpenter's (1921) monkeys towards the threat display of mantids. Crane (1952) states that the effectiveness of mantid display seems to be due not to a "true intimidation" but "simply to the momentary respite gained when the attacking predator pauses at the sudden apparition - startled, at most, but scarcely truly warned off or "afraid"." This was undoubtedly true in the case of the hedgehog and O. latimanus. The fifth scorpion offered to the insectivore was placed at the entrance of a burrow brought into the laboratory for the purpose. The back end of the burrow was open so that the scorpion could be prevented from disappearing down it before the hedgehog had a chance to investigate. The hedgehog came sniffing towards the burrow and as the scorpion stridulated he hesitated and then dashed forward: just too late to catch the scorpion which had shot down the burrow. As Crane says, the threat display "gives the insect an opportunity to slip out of the way or fly to safety."

In the last group come animals which obviously react to the stridulation although they make no attempt to eat either normal or silent controls. Falling into this category is the domestic cat and a small striped polecat, Poecilogale albinuca (Gray). Neither of these were ever seen to eat either the silent controls or the corpses of recently killed scorpions, though both would sniff at them and the polecats would turn dead scorpions over with their noses. On several occasions both members of a pair of the polecats were observed to be "frightened off" by the stridulation of O. latimanus, sniffing towards the animal, then starting back and finally running off, usually after about the third outburst of stridulation. With domestic cats the outcome of the experiment was clearly affected by the individuals used. In one case the animals tested were in their own home with an experimenter from whom they had never had any physically painful experience. They failed to show any shock reaction to the stridulation; such a result is not unexpected as the animals would not be "on their guard" or expecting to be offered dangerous food. In another instance, however, a cat strayed into the laboratory. Both territory and experimenter were unknown, but the cat readily accepted meat. Towards a scorpion however its behaviour was different. When the creature stridulated, the cat gave a violent start back and later, when he backed up on the arachnid, leapt into the air in a typical shock reaction at the sudden hisses. In neither case did the cat make any further attempt to investigate the scorpion, although he sniffed at and then ignored a scorpion corpse.

With the ten different types of mammal tested, the stridulation unquestionably was of protective value to the scorpion in three cases. When the different reactions of domestic cats are considered, it may well be that the figure in nature would be higher. It certainly seems legitimate to conclude that the stridulation is an interspecific threat display.

Stridulation in *Parabuthus planicauda* Poc.

Despite the statement of Hewitt (1918), this species does stridulate, but it can only be induced to do so with some difficulty, and, indeed, many specimens will not stridulate at all. When stridulation does occur it is effected by a movement of the tip of the tail which is scraped forwards about four to eight times across the first caudal segment and the tergite of the last segment of the mesosoma, sometimes catching the second caudal segment as well. This produces a shrill grating sound. In 1927 Lawrence observed such behaviour in living specimens of *P. flavidus* Poc., *P. granulatus* (H. & E.) and *P. brachystylus* Lawrence. In these species the tip of the sting is scraped against the first two segments of the tail which are characterised by the presence of well marked transverse ridges. Such ridging is however absent both on the tail and the last mesosomal tergite of P. planicauda, though these areas are clearly more granulated than is the rest of the tail and mesosoma (Fig.14). The form of the sting is Parabuthus differs from that in Opisthophthalmus in what is probably an adaptive modification to this method of stridulation. The sting of P. planicauda has a stouter curve, which tapers less towards the tip and the openings of the two poison ducts are slightly further from the tip than those of O. latimanus. Both of these features may well be modifications which allow vigorous scraping to be done without damage to the lance of the sting or the openings of the poison ducts.

The Biological Significance of Stridulation in Parabuthus

It would seem reasonable to assume that, as in Opisthophthalmus, stridulation in Parabuthus, is part of a threat pattern . Lawrence (1927) described how, in P. brachystylus, the sting drips venom as the scraping action is performed. He suggests that the function of the tail scraping is not to produce a noise, but rather a "purely mechanical method of stimulating rapid and continuous contraction of the muscle surrounding the poison sac and so ensuring a liberal secretion of poison." There is no evidence against this hypothesis any more than there is evidence that the scraping is a threat behaviour pattern. There are, however, several considerations that speak against Lawrence's theory. Firstly, the poison sacs, of P. ~~capensis~~ planicauda anyway, are supplied in no lesser degree with muscles and nerves, than are those of O. latimanus and, though the sting of O. latimanus is used conspicuously less, there appears no difficulty in producing a poison flow when it is used, without recourse to such peculiar stimulation. Secondly, there seems no physiological reason why scraping the sting tip should cause either the poison sac muscles to contract or their nerves to be excited: such stimulation of a sting recently amputated from P. ~~capensis~~ planicauda shows no poison production. Finally, in teleological terms there is no obvious advantage in such a pattern;

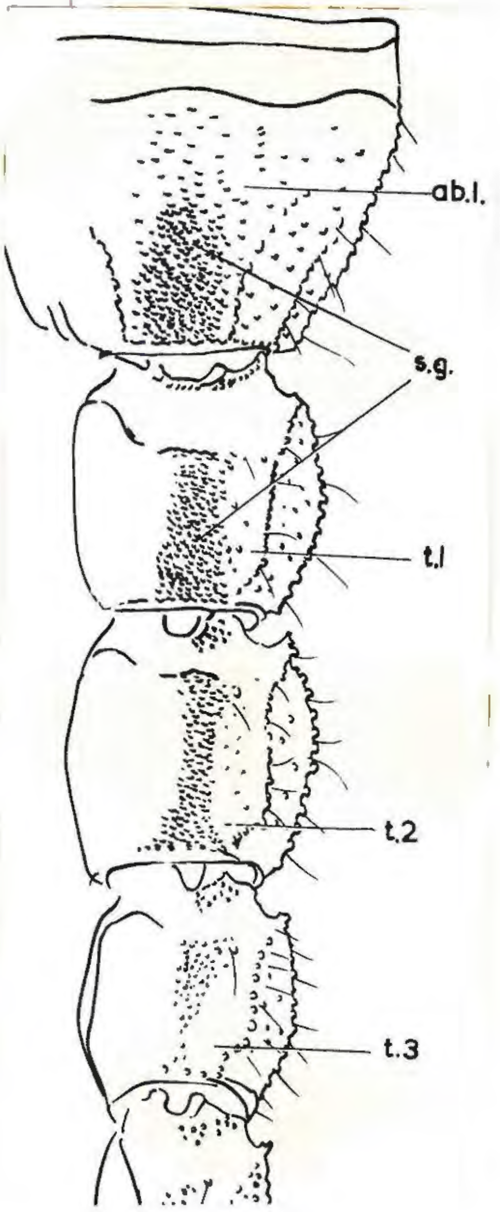

Fig. 14. Dorsal view of the last abdominal segment, ab.l. and first four metasomatic segments, t.1-3., of P. planicauda, showing how the tergal granulations are concentrated in the formation of stridulatory areas, s.g.

indeed such wastage of venom would seem to be positively disadvantageous. On the other hand, it would appear more likely that the venom flow is an incidental consequence of the general excitement of the animal in a situation which has led it to stridulate, a thesis which receives support from the fact that, without any scraping, a similar dripping of venom occurs in O. latimanus and O. nitidiceps when these animals are highly excited. For these reasons, it is suggested, albeit in the absence of direct evidence, that the tail scraping in Parabuthus is a true stridulation whose significance is that of a threat.

A Comparison of the Behaviour of Opisthophthalmus and Parabuthus

As has been shown above, these two animals stridulate in very different ways. It is clear, however, from observations upon their general behaviour that the difference can be regarded as but one constituent of a complex of structural and behavioural differences associated with attack and defence.

Parabuthus is the more poisonous of the two animals (Grasset et al, 1945). Its tail is thick and conspicuous by being a slightly lighter colour than the body; the pedipalpar hands and claws are small and weak. In Opisthophthalmus, on the other hand, the hands and claws are powerfully developed while the tail is of the same colour as the body and not always not conspicuously thickened.

not always reliable

Not a [illegible] character separating genera

Behavioural differences are just as marked, as may be shown by two examples. The first, illustrative of offensive behaviour, is their respective methods of feeding upon a cricket. As has already been described, O. latimanus catches the animal in one claw as it moves past. The cricket is then pulled in front of the scorpion's mouth and the other claw is moved along the body of the prey until the head is between the fingers of the claw; the head is then crushed once or twice and the corpse moved to the chelicerae which have already started making chewing movements. The sting is not normally brought into play at all. In P. planicauda the picture is very different. The cricket is again caught by the pedipalps but almost immediately the tail is swung over the head to sting the prey. At the same time the chelicerae are extended towards the cricket and, far sooner than in <u>O. latimanus</u>, are chewing the body. Further, contrary to the behaviour of <u>O. latimanus</u>, the claws tend to relinquish the cricket, leaving all the manipulative part of the feeding to the chelicerae and the first pair of legs.

The second example, illustrative of defence, is when the third leg of the animal is touched. In this case <u>O. latimanus</u> immediately swings round and presents the source of irritation with a pair of snapping claws. <u>P. planicauda</u>, however, does not change position at all but, with remarkable agility, whips the sting towards the area stimulated.

Thus in <u>O. latimanus</u> the claws are the main weapons of attack and defence, in <u>Parabuthus</u> the sting. Moreover, the two species, in their stridulation, are emphasising their two different quarters of offence, the posterior one in <u>Parabuthus</u>, the anterior one in <u>Opisthophthalmus</u>.

suggestive idea

As has been mentioned earlier, stridulation is not easily elicited from <u>P. planicauda</u>, though this difficulty does not seem to arise in the other species with caudal stridulation. In the laboratory, stimulation of <u>P. planicauda</u> often produces repeated strokes of the tail without stridulation. If these are watched, it is seen that they are entirely similar to the stroke of the tail that ends in stinging. That is, they may be regarded as intention-stinging movements. In stridulation the stroke is very similar to this movement, but there the tip of the sting is lowered slightly so that it touches on to the tail and last mesosomal tergite. It seems therefore highly probable that the stridulatory movements of <u>P. planicauda</u> may be thought of as ritualised intention-stinging movements: indeed on one occasion, when the instrument being used to stimulate the scorpion was in a suitable position, the stridulatory stroke did end in a stinging stroke.

It thus seems reasonable to suggest that in <u>Pafabuthus</u>

generally the stridulatory strokes are derived from stinging-intention movements which have been elaborated as a stridulatory sign stimulus. The stridulation may thus be regarded as an example, at the intra-specific level, of a phenomenon already well attested at the inter-specific level, the evolution of a sign stimulus from an intention movement.

Stridulation in Other Scorpions.

With the idea in mind, suggested by the beavhiour of Parabuthus, that a stridulatory movement has been built upon an intention movement, it appeared worth examining the known cases of stridulation in other genera. Consideration will be given to Opisthophthalmus later.

There are three other species wherein some details of stridulatory behaviour are known, namely Heterometrus swammerdami (Simon), Pandinus imperator Koch, described by Pocock (1896), and the Brazilian Rhopalurus borelli Poc. described by Pocock (1904)[1]

In both Heterometrus and Pandinus the stridulatory areas are on the coxa of the pedipalp and of the first leg. In both cases the apparatus consists, to use Pocock's terms, of a "key-board" of basally-flattened bristles, recalling the specialised cheliceral bristles of O. latimanus, and a "rasp", analogous to the striated area on the ventral surface of its carapace. There is however a striking difference between the two genera. In Heterometrus the key-board is on the pedipalp and the rasp on the first leg, while in Pandinus the position is reversed. Clearly, although the two genera are fairly closely related, the stridulatory apparatus has been evolved independently.

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[1] Vachon (1949) records that caudal stridulation occurs in Androctonus. No details of the behaviour are given, however.

Heterometrus unquestionably uses the stridulation as part of a threat display with the pedipalps. When the animals are "goaded into fury" they "beat the air with their great pincers", stridulating at the same time. There appears to be no information on the behaviour of *Pandinus*, but Pocock assumes that it stridulates in similar circumstances to *Heterometrus*. It would seem reasonable to suggest that the basic threat display of these animals is a clutching movement directed at the potential enemy. This behaviour can be seen clearly in *O. latimanus* and more particularly in *O. nitidiceps* where the pedipalp claws grab fiercely at the source of stimulation but, in point of fact, let go should they actually catch hold. It would seem that the stridulatory movement of *Pandinus* and *Heterometrus* has been elaborated upon the pedipalp action of intention clutching.

In *Rhopalurus* the key-board is formed from striations upon the pectinal teeth, while the mesosomal sternites overlying the pectines have a granulated area which acts as a rasp. The stridulation appears to be effected by the movement of the pectines over this area. Sound production in *Rhopalurus* was recorded by Burchell in his diary (Pocock, 1904) and it seems likely that once again it is part of a threat display, but new observations on the animal are clearly needed.

Before considering the possible origin of this type of stridulation, it is necessary to digress to consider the functions and movements of the pectines. These structures are concerned, in some way, with sensory information either about the character of the substrate or with the detection of ground vibrations; possibly with both. Their activity in *O. latimanus* has been observed by allowing the scorpions to walk on smoked paper. In normal walking the pectines are held down onto the surface, though the pressure they exert varies rhythmically (Fig. 11a). If, however, the animal is disturbed, the pectines are immediately lifted and, if the animal runs away, they are held close to the body, leaving no trace upon the paper (Fig. 11b). Moreover in *P. planicauda* where the pectines are long and fairly easily

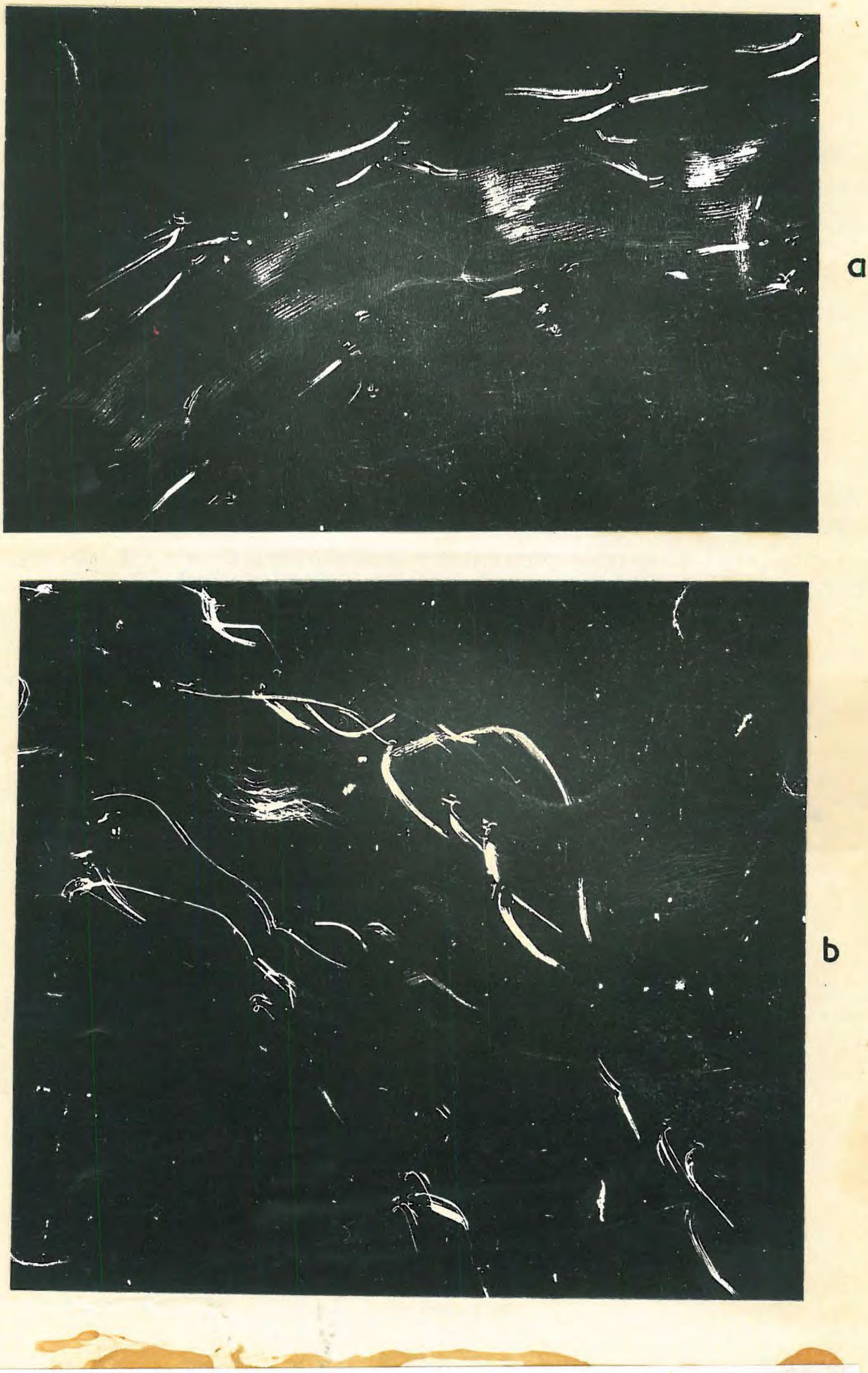

Fig. 11. Records made by *O. latimanus* walking across smoked paper.

(a) Record from an undisturbed individual showing the rhythmic strokes of the pectines on the substratum.

(b) Record left by a frightened animal that was running away leaving almost no pectinal track.

visible, they may occasionally be raised, partly lowered and then raised again before retreat. This movement of the pectines precedes flight and may be regarded as a movement made when there is a conflict situation between the drives of fight and flight. It seems possible that the threat stridulation of *Rhopalurus* has been developed from such a movement of the pectines. A partial parallel may be seen in the intimidation display of certain mantids such as *Stagmatoptera*, which Crane (1952) has interpreted as arising from a conflict of opposing elements of escape pattern - namely those of flight and of remaining motionless.

General Considerations.

Pocock (1896) says "sound producing organs in the vast majority of the Arthropods are developed exclusively where friction occurs between two adjacent surfaces." Among the scorpions we have considered, the adjacent surfaces used for stridulation are very different and the problem, once the possibility of stridulation between relatively moving surfaces is accepted, is one of determining as far as possible the factors which may have led to the selection of particular regions for the development of stridulatory organs, both in behavioural and anatomical terms.

To turn first to behaviour: in all four cases which have been examined, stridulation appears to be associated with threat and from an analysis of the characteristics of threat we may learn more. In presenting this analysis, I would like to express my gratitude to Dr. R.F. Ewer, with whom the general theoretical ideas outlined below were developed.

Threat consists essentially of an attack which is not pressed home, ritualised to a greater or lesser extent. Threat, rather than full attack, might result from the failure of the threatened object to provide the stimuli adequate to elicit the full pattern, but is much more likely to be caused by the simultaneous presence of stimuli tending to evoke flight. If this is the case, there are then three possible origins for movements which may become ritualised into a threat display.

(i) The intention movements of attack itself. These are autochthonous, and by virtue of their origin, will involve the organs normally used in attack. Ritualisation of such an intention attack movement will therefore normally serve to display, or call attention to, the normal offensive weapons.

(ii) The intention movements of flight. If a conflict of flight and fight is considered to be an essential part of the threat-evoking situation, then movements based on intention flight will be autochthonous to the threat situation, but they will not be specifically related to the weapons of offence.

(iii) Allochthonous displacement activities, arising from the fight-flight conflict, but not directly related to either of its components. Movements elaborated from such displacement activities will not necessarily involve the offensive weapons, but may do so if the displaced activity is one in which the weapons are used for some purpose other than attack.

An analysis in these terms serves to throw some light on the possible origins of the various stridulatory movements in scorpions. In P. planicauda the stridulation appears to be based on a stinging intention movement, and belongs therefore to the first category - ritualisation of an autochthonous intention attack movement. The same appears to be the case in Pandinus and Heterometrus where an attacking movement of the pedipalps had been exploited to develop a stridulatory movement, which is again autochthonous. As a result, in all these three genera there is a close anatomical association between the offensive weapons and the source of the noise, the noise directly drawing attention to the organ of offense.

Rhopalurus belongs to the second category. We have no information about its offensive behaviour, but the stridulatory movement seems to have been elaborated from an intention movement of flight in the conflict situation typical of threat. As is to be expected, the movement involves structures which can hardly be visualised in the rôle of offensive weapons.

Finally there is the case of *Opisthophthalmus*. Pocock believed that in some species of this genus two distinct stridulatory areas were present, but the present observations on living specimens make it very unlikely that the mesial platelets have any real stridulatory function. They have a remarkable resemblance to the "modified leaf-like hairs" found on the first leg of the pedipalp *Damon variagatus*, and it will be shown below that they are chemo-receptors (p. 55) My observations on *O. nitidiceps* show that the dorsal bristles of the chelicerae, even in the absence of any obvious anatomical specialisation , do produce a sound and it is likely that, upon this potential, selection has worked to produce the striking stridulation of *O. latimanus*.

The stridulatory movement of *Opisthophthalmus* is an alternate extrusion of the chelicerae. In *O. latimanus*, at least, alternating cheliceral movements occur in other patterns of behaviour such as feeding, washing, burrowing and courting. But these movements are not accompanied by stridulation. It follows that the stridulatory movement is specialised, the chelicerae being held dorsally against the keyboard of the carapace. Nevertheless, there is good reason to believe that the stridulatory movement is derived, since it is invariably accompanied by a functionally useless opening and closing of the cheliceral claws. One characteristic of the movement is that it has a slight transverse component, reflected in the fact that the mesial platelets do strike against each other. Such a transverse movement of the chelicerae is made in tearing food apart, and it seems probable that the stridulation has been elaborated from this tearing movement. It is not possible, as yet, to decide whether this should be regarded as belonging to the third category - an allochthonous displacement movement resulting from the fight-flight conflict - or as an integral autochthonous part of the attack component of threat. It is true that, in this species, the pedipalps are used in attack, but the chelicerae perform the stridulatory movement, which would seem to indicate that in this case we are dealing with an allochthonous displacement movement. It must, however, be borne in mind that in attacking prey the chelicerae begin to make chewing movements before the prey is brought within their reach. It is therefore possible that the stridulatory movement should be regarded as derived from an intention movement of attack.

Stridulatory movements in scorpions may thus be regarded as derived, with varying degrees of ritualisation, from intention movements, or in some cases, possibly from displacement activities; though it is freely admitted that these suggestions involve much that is speculative, for our knowledge of the habits of the living animals is still very fragmentary.

The general idea outlined above, namely that the intention movements of attack may become ritualised in such a manner as to call attention to the offensive weapons, can be applied more generally than to scorpions alone, and two cases of threatening sounds produced by mammals kept in the laboratory show clearly how this idea may have general validity.

The first example is that of the porcupine, whose threat behaviour can be interpreted by this hypothesis. The shaking of the hind end and particularly the rattling of the special noise-producing quills of the tail, may have been derived from the intention movement of porcupine attack, the animal thrusting itself tail first at an assailant and moving its hind-quarters this way and that, so that the foe has little chance of being missed.

Threat may also be accompanied by a grunting noise made by moving the jaws. In this, all three stages in the development of a ritual threatening sound may be seen. When the animal is thoroughly startled, it will bite while at the same time making this grunting noise; when less disturbed, the beast may snap viciously with its mouth while making the same noise, but will deliberately miss a hand held out for it to bite; finally the porcupine may just make the grunting noise which, while retaining its value as a threat, has become reduced to jaw movements, themselves incapable of harming an enemy.

The second example of how this hypothesis can be applied is taken from personal observation of the threat display of the white rat. This consists of a loud chattering of the teeth as the rat turns to face and in some cases attack the enemy. That this is a threat is shown by its effect on the enemy, in this case the pole cat *P. albinuca*. These small carnivores are very eager to attack until they have been subjected for some time to this gnashing of teeth and feint attack. It seems clear from the sharp quick bites with which the rat attacks the skunk that the teeth-chattering could well be an in-tention movement for this type of biting. The sound is certainly the part of a behaviour pattern that calls attention to the presence and intention of the rat.

These ideas concerning the ethology of sound production in animals are in close agreement with present concepts of the rôle of intention movements, in visual communication between animals, and have also been developed by Jacobs (1953) in his extensive study of noise production in grasshoppers. In this latter group the ritualisation of the stridulatory movements is extreme, frequently making recognition of the original movement a matter of great difficulty. The interest of scorpion stridulation lies in the relatively simple analysis which can be made of the behavioural origin of the stridulatory movements; a simplicity which enhances one's faith in the validity of the general thesis that stridulatory movements are derived movements and broadly comparable in origin with the movements of visual communication.

Anatomical Preadaptations for Stridulation

It has been pointed out above that, in considering the origin of a stridulatory mechanism, it is necessary to elucidate not only the behavioural basis of such an event, but enquire into the origin of the precise anatomical structures involved; that is whether there are any preadaptations for such a function.

The first case to be considered is that of the scorpionids *Pandinus* and *Heterometrus* where noise production occurs by the relative movements of the coxae of the pedipalps and first pair of legs, but where the key-board is on the pedipalp in Heterometrus and on the leg in Pandinus. A study of the detailed structure of this region in O. latimanus, another scorpionid which shows no specialisation in this direction, appears to throw light upon the way in which these two distinct mechanisms, phylogenetically unquestionably of separate origin, may have arisen.

Consider the interface of the pedipalp coxa and that of the first leg in the three scorpions under discussion. They can be represented diagrammatically as in fig. 12 in which the material is shown as if the pedipalp had been pushed up and backwards, so that the mid-point of the diagram is that at which the base of the pedipalp coxa and that of the first leg meet. Fig. 12a shows the distribution in O. latimanus of hairs on the pedipalp and coxal surfaces which come in contact, while Fig. 12b and 12c show the arrangement of the stridulatory hairs and striations in Heterometrus and Pandinus respectively. It can easily be seen that in O. latimanus there are two areas of hair (i.e. potential material for the evolution of stridulatory bristles) on the pedipalp-first leg interface, the more mesial one on the pedipalp coxa, the lateral one on the coxa of the first leg. Thus in an animal which shows no structural adaptations for pedipalpar stridulation, there is the potentiality for evolution of stridulation either along the direction taken by Pandinus or Heterometrus.

Furthermore it can be seen that the distribution of bristles in Heterometrus and Pandinus support such a theory; the bristles in Heterometrus are on the coxa of the first leg and the whole stridulatory apparatus is markedly more lateral than that in Pandinus where the bristles are on the pedipalp coxa.

The second case to be considered is that of Rhopalurus. We know very little about the behaviour associated with the stridulation of this animal or of the anatomy of closely related species. However, a casual but relevant observation has been made on the anatomy of P. planicauda, another buthid but one which certainly has never been heard to make any stridulatory sound with its pectines. The first abdominal sternite has a small granulated patch of chitin just beside

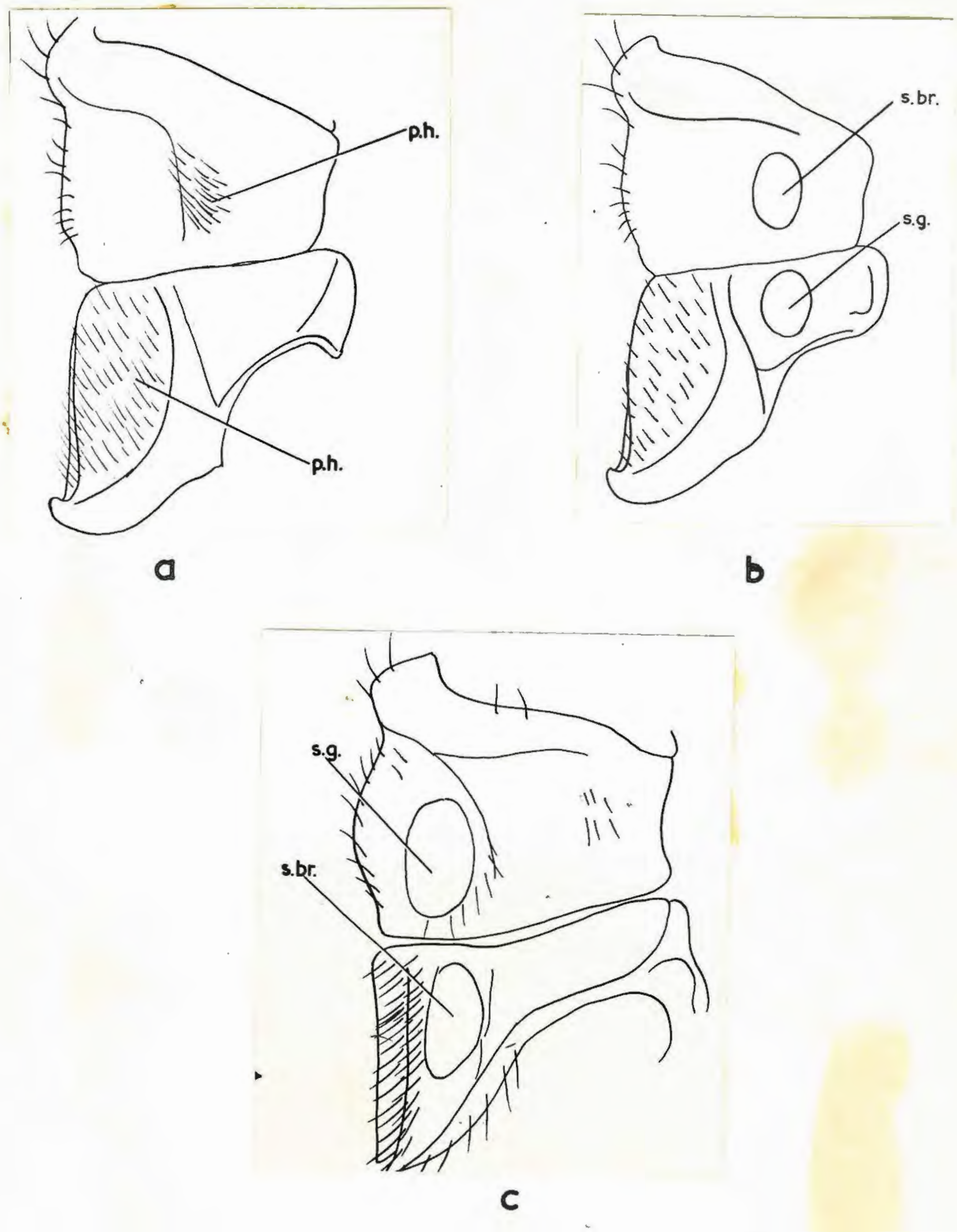

Fig. 12. Basal segments of scorpion pedipalp and first leg, showing the position of unspecialised and stridulatory hairs.

(a) *O. latimanus*

(b) *Heterometrus maurus* (L.) (modified to illustrate Pocock's account of the condition in *H. swammerdami*)

(c) *Pandinus imperator*

p.h., patch of unspecialised bristles; *s.br.*, stridulatory bristles; *s.g.*, stridulatory granulations.

the opening to the book-lung (Fig. 13a). In such a position it is clear that the main body of the pectine must sweep across it as the appendage is lifted and lowered and, though the area is less extensive than that shown for R. borelli by Pocock (1904) (Fig. 13b), yet it seems very similar. Furthermore an examination of the back of the pectine, that is the morphologically dorsal or posterior face, shows the presence of a row of about 15 small lumps (Fig. 13c). They are only on that part of the pectine which would come in contact with the sternal granulations as they are swung past the belly, so that, although P. planicauda shows no sign of the longitudinal striations on the pectinal teeth comparable with those of R. borelli, yet there would appear to be an analogous arrangement relating to the contact between pectine and sternum.

tubercles

(seen in 6th [illegible])

As yet nothing definite is known of the function of this anatomical arrangement on P. planicauda. It was remarked earlier that the animal may often lift and lower its pectines rapidly just before flight, behaviour which was described in an attempt to derive an explanation of the stridulatory movements of R. borelli. There is however a further piece of pectinal behaviour which almost invariably occurs and which appears to be relevant. P. planicauda normally walks in short jerks of activity and, at the end of each, it will lift its pectines from the substratum ~~(Fig. 14)~~. With each occasion that the pectines are lifted there is a slight though unmistakable forward jerk, as if the animal were ridding its pectines of dirt collected over the last bout of ground-sweeping. It is virtually impossible to get direct evidence on this point, but it seems very probable that this stroke of the pectines involves their being brushed across the granulations and that the significance of the "pseudo-stridulatory" area is that of jerking the pectinal surface free of adhering dust particles. Support for the thesis is the fact that the behaviour is very much more marked after the scorpions have been made to walk on smoked paper on which they invariably collect a large amount of material on their pectines.

It would be interesting to examine the pectines of Parabuthus spp. which are known to stridulate Parabuthus brachystylus etc

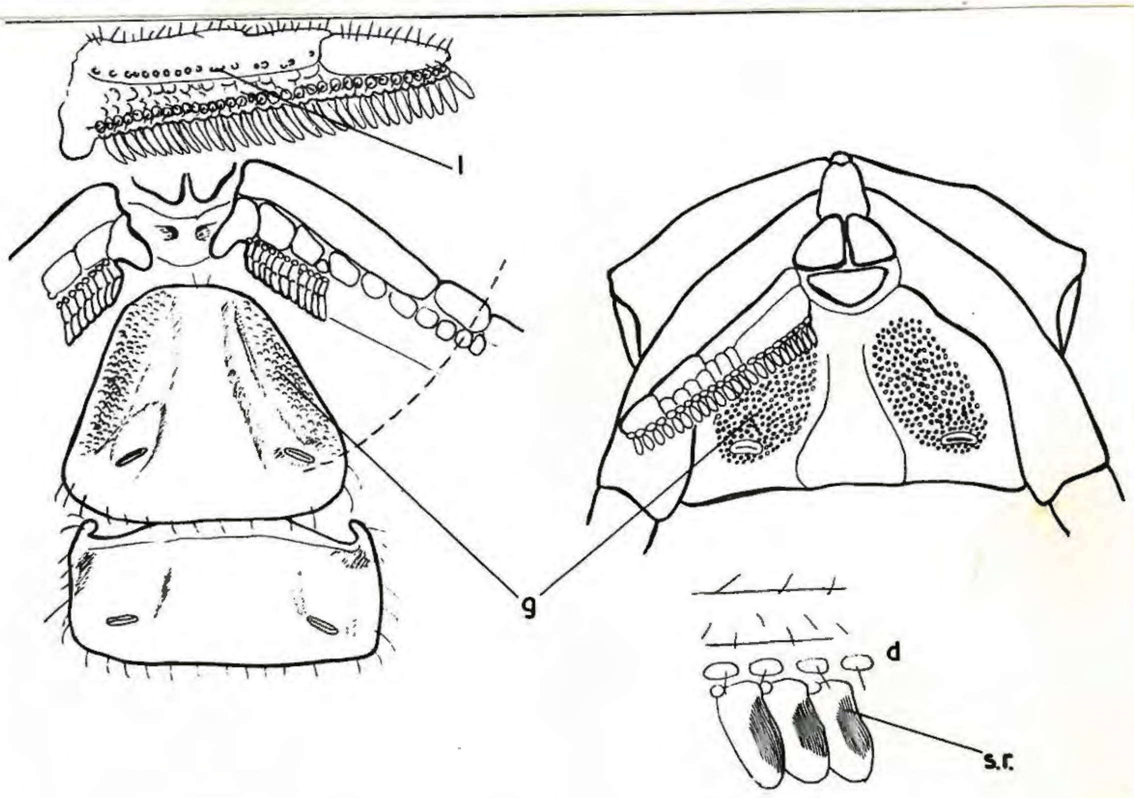

Fig. 13. (a) Lower left - First abdominal sternite of *P.planicauda* showing the "pseudostridulatory" area, g., in a position in which it will be covered by the sweep of the pectines, as indicated by the dotted line.

(b) Upper right - first abdominal sternite of *Rhopalurus borelli* showing the stridulatory areas, g., (after Pocock, 1904)

(c) Upper left - dorsal surface of the pectine of *P. planicauda* showing the row of little lumps, l., which contact the pseudostridulatory areas on the abdominal sternite. The dotted line in Fig.13a shows how this row of lumps is limited to that part of the pectine which contacts the sternal granulations, g., as the pectine swings past the belly.

(d) Lower right - dorsal view of three pectinal teeth of *R. borelli* showing the longitudinal stridulatory surface (after Pocock).

Lastly there is the case of Opisthophthalmus where, as has already been pointed out, unspecialised bristles occur on the chelicerae of O. nitidiceps. In this animal the noise production is weak compared with O. latimanus where not only are the bristles specialised for stridulation, but a granulated area is developed upon the carapace. It is therefore highly probable that in this case also the anatomical foundations of the stridulatory mechanism exist in forms which do not actually stridulate.

The Cheliceral Platelets as Chemo-receptors.

The superficial similarity of the cheliceral platelets to the leaf-like organs on the first leg of the pedipalp Damon has already been mentioned and suggests that the platelets have some sensory function. Their close anatomical association with the mouth and all the organs concerned with mastication of food points to their being used to taste the food before it is taken into the mouth. This possibility has therefore been tested upon O. latimanus.

The tests undertaken were very simple. Live prey, treated with a bitter solution, was offered to normal animals and to experimental ones from which the platelets had been removed. The behaviour of the two series of animals was observed. Preliminary trials showed that tincture of quinine was unsuitable as a test solution owing to its smell, but Tinctura Quassiae (B.P.),which is almost odourless, proved to be satisfactory.

The tincture of quassia invariably killed the prey - locust nymphs and crickets - and, since it is difficult to prevail upon a scorpion to accept dead insects, the following procedure was adopted. The scorpion was offered a live insect; shortly after feeding commenced a few drops of the tincture were dropped on to the food being torn off by the chelicerae. It is necessary to be careful in this, for chemo-receptors also occur on the pedipalps and legs and, should these be wetted with the tincture, it is not only the platelets that are being tested.

Normal entire scorpions treated in this way immediately released their grip on the insect and pushed it as far as possible from them. They rejected the pellets of food which they had already in their oral cavities and, extending the chelicerae fully, rubbed them together and into the sand at their feet. This behaviour often went on for as long as a minute and the scorpion could not be persuaded to take up the treated corpse. If, after ten minutes or so, a clean, freshly killed insect was offered, the scorpion would accept this, showing clearly that it was still hungry.

Nine animals lacking the rows of platelets were tested. In six cases the animals paid almost no attention to the addition of the quassia, merely moving the food about a little with their chelicerae, behaviour which was also observed when insect Ringer solution was dropped on to the food as it was being eaten. Clearly there was no unpleasant sensation here as there had been in the case of the controls. Two of the remaining experimental animals rejected the food but took it up again later. This was probably the result of direct stimulation of the pedipalps by the fluid, for there was none of the cheliceral rubbing characteristic of the controls under similar conditions. The last of the experimental animals rejected the treated food just as did the controls, pushing away the insect and trying to clean its chelicerae.

On being killed, this animal was found still to possess one of the cheliceral platelets, overlooked in the operation. This rejection was indeed what should have been expected in the circumstances, and the case only adds support to the thesis that the cheliceral platelets are chemo-receptors and can serve to inform the scorpion that the food it is chewing is "unpleasant."

5. THERMOREGULATORY BEHAVIOUR.

In discussing the possible functions of the pectines of the scorpion, von Ubisch (1922) suggests that they serve "um den Stigmen frische Luft zuzufuhren" by their fanning movements or, alternatively, they prop up the mesosoma so that fresh air can reach the stigmata. Both of these suggestions imply that under conditions of respiratory stress a scorpion will lift its mesosoma clear of the ground so that the bock-lungs have free access to air. Although von Ubisch did not apparently observe such behaviour, the recent report of "abdominal elevation" in the Australian scorpion, *Urodacus abruptus* Poc. (Southcott, 1955) lends colour to such an hypothesis, although work on the functions of the pectines makes it seem very improbable that they actually serve as "respiratory fans". Southcott gives an illustration (Fig 15a)/of a female of *U. abruptus* in the attitude typical of "abdominal elevating behaviour" and from a comparison of this with some of the stances observed in various local scorpions it becomes clear that such behaviour occurs also in the latter. *Opisthophthalmus latimanus*, *O. nitidiceps*, *O. austerus Karsch.*, *Parabuthus planicauda* and *Uroplectes triangulifer* all show the pattern to varying extents and it was felt that with so many species available for study, it would be profitable to follow up Southcott's observations. Preliminary tests indicated that the biological significance of this phenomenon appeared to be the same in all these species and the results described below refer particularly to *O. latimanus* which has been most intensively studied.

In this animal the pattern generally does not consist of a simple elevation of the abdomen but more usually of a raising up of the entire body of the scorpion by a straightening of all the legs. Fig. 15 illustrates semi-diagrammatically the differences between (a) the normal resting stance of *O. latimanus*, (b) the stance in which the whole body is lifted clear of the ground, and (c) the more extreme "abdominal elevation". There is indeed no sharp distinction between these last two, and other rather rarer variations occur, e.g. that in which the abdomen, lifted clear of the ground, is supported by the tail

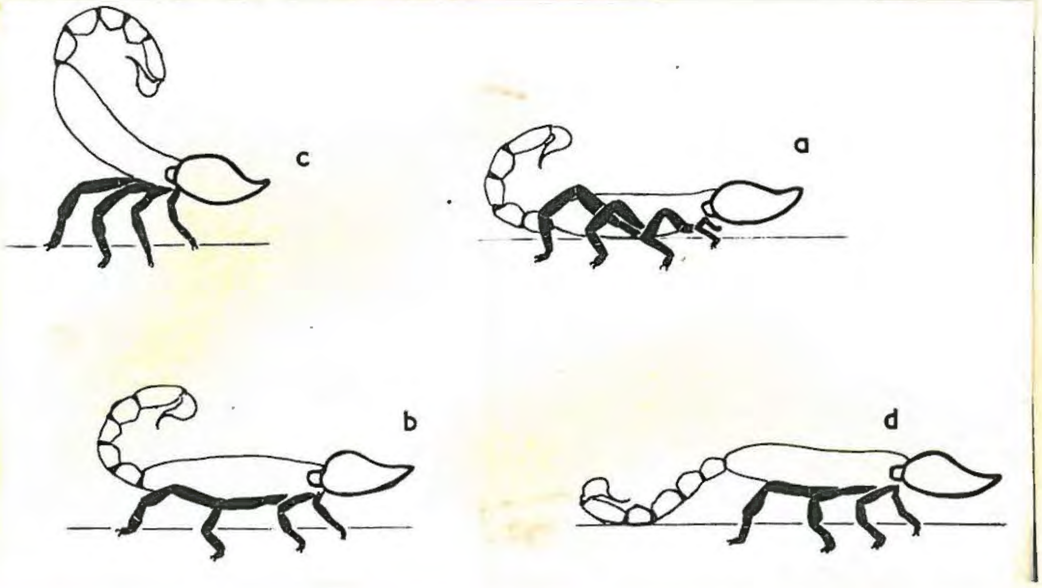

Fig. 15. Semi-diagrammatic representation of postures adopted in thermoregulation by O. latimanus
(a) Resting stance, venter to the substratum and legs folded.
(b) Stilted pose in which the whole body is lifted away from the substratum by straightening the legs.
(c) Stilted pose in which the mesosoma is sharply elevated.
(d) Rather rare stilted pose in which the tail appears to help in propping the body away from the substratum.

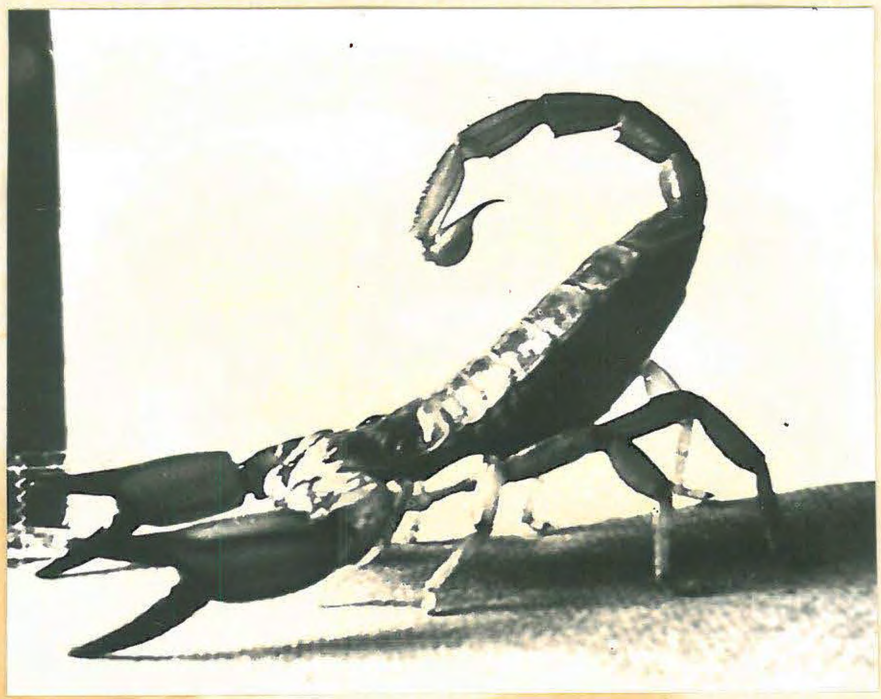

Fig. 15a. Urodacus abruptus in a "stilted" pose.
Photograph by Dr. Southcott.

(Fig.15d). All of these different stances have in common a straightening of the legs; they will collectively be referred to here as "stilted poses" and the behaviour itself as "stilting". In none of the species studied here, nor in *Androctonus australis* (Cloudsley-Thompson, 1955a) is there any indication that the pectines might be used to prop up the abdomen, as von Ubisch has suggested. As in *U. abruptus*, stilting occurs in both sexes of *O. latimanus* and it has been observed in all instars except the first, where it might well not be recognisable.

Function of the Stilting

Working along the same lines as von Ubisch, Southcott (1955) states that stilting occurs in hot and humid conditions, and concludes that "it would appear most likely that the stance .... is an effort to lift the stigmata free from the humid layer of the air and soil, when the scorpion's metabolism is increased by a hot environment." Cloudsley-Thompson (1955a) has pointed out, with reference to the postulate of von Ubisch, that a scorpion has normally a very considerable respiratory margin of safety. For this reason it seems improbable that respiratory adaptive behaviour as such would be of importance in the life of a scorpion.

However the effect of respiratory stress appeared to be worthy of further experimental investigation. The problem had already been studied in *A. australis* by Cloudsley-Thompson (1955a), using streams of gas composed of nitrogen and carbon dioxide. Observation of *O. latimanus* has, however, shown that if a stilting animal is disturbed by a sudden draught of air, it drops its stilted pose and will often not resume it for some time. It was therefore considered desirable for observations to be made in still air. Furthermore, since extreme respiratory stress, such as that used by Cloudsley-Thompson, might itself inhibit an adaptive response, a series of gas mixtures was used: namely, mixtures of air with approximately 20 or 75% carbon dioxide, and air with 60 or 90% nitrogen. In none of these mixtures were there the slightest signs of stilting. This was not due to the inability of the animals to stilt, for, if other suitable stimuli were applied, the scorpions would stilt in these gas mixtures. Moreover stilting was more easily elicited by these means in those gas mixtures containing the lower concentrations of carbon dioxide or nitrogen, a fact speaking against the importance of stilting in respiratory stress.

As a check, observations were made on scorpions which had had the openings of the book-lungs blocked. This was done in one of two ways: either the mesosternites were smeared with vaseline, or the openings of the lungs were painted over with Gestetner Correcting Fluid or Samsonite. Observations lasting over 12 hours showed no stilting by any of the animals, though the fact that two of the animals died shortly after indicates that their respiratory system had probably been affected by the treatment. Controls with their backs painted all survived.

These experiments, together with the observations of Cloudsley-Thompson (1955a) on A. australis, make it unlikely that stilting has an adaptive significance in respiratory stress. To comprehend the phenomenon, it is therefore necessary to turn once more to observations of the conditions in which this pattern is shown.

Southcott (personal communication) states that in summer he need only pour a little water into his scorpion culture dishes to elicit stilting behaviour. Unlike U. abruptus, O. latimanus shows no such direct relationship between the humidity and stilting; it may occur when the scorpion is standing in a pool of water or, conversely, in a desiccator. The character of the substratum, whether it be smooth or rough, whether or not it be covered with chemicals distasteful to the scorpions, does not determine whether the animals will stilt.

However, although the pattern may occur at any time during the day or night, it is most frequently seen during the afternoon.

This suggested that temperature might be a factor of importance in determining the onset of stilting. Confirmation of this can be obtained by observing the behaviour of animals in a dish of soil, the dish being warmed or cooled as desired. Below 18°C stilting in not normally observed and if the soil on which a stilting scorpion is standing be cooled below this temperature, the animal's pose gradually reverts to the normal resting stance. Between 18°C and 25°C animals may or may not be found to be stilting, but at a higher temperature any animal that is standing still will usually be stilting to some degree, or may be reared up against the side of the dish, a condition amounting in effect to a stilted stance.

As mentioned earlier, <u>O. latimanus</u> does not stilt in direct response to the presence of water. Unlike the condition in <u>U. abruptus</u> there is no indication here that, with a higher humidity, the stilting behaviour is elicited at a lower temperature. This point was studied by trials on pairs of animals, one animal being kept in a dish at 40-60% RH; the other at 85-90% RH. If anything, there was a slight indication that the animals reacted a little more quickly and at a slightly lower temperature when at the lower humidity.

Once it is clear that stilting is not concerned with respiratory adaptation but is elicited merely by a high temperature, it is reasonable to ask whether the stilted pose may not have some thermoregulatory rôle. Drawing on the techniques used by Colbert, Cowles and Bogert (1946) in their experiments on temperature adaptations in alligators, the following arrangement was used. Two live animals were fixed so that one, the experimental animal, could be held in a stilted pose, while the other, the control, could be restrained in the normal resting position. In the absence of more complicated apparatus, abdominal temperatures were determined by clinical thermometers whose bulbs were inserted through a small lateral incision. In these experiments the scorpions were placed upon a copper plate lying on the ground. The plate was initially left in the sun to equilibrate. A small shade was then placed so as to screen the area of plate upon which the two animals would be placed and the scorpions were then quickly put in position and their abdominal temperatures recorded. After ten minutes their temperatures had not changed; the shade was then removed so that the sunlight fell on the animals and the observations on their temperatures were continued. Preliminary experiments showed that the orientation of the animals towards the sun was not critical and in all those reported below the scorpions were oriented with their longitudinal axes at right angles to the sun's rays.[1]

A typical result of such an experiment is shown in Fig. 16. Both animals were initially in the shade, their abdominal temperatures were recorded: the screen was then removed and the temperatures of their bodies noted at intervals. As can be seen, the temperature of the control animal rose rapidly, while that of the scorpion held in a stilted position hardly rose above the minimal temperature calibration of the thermometer.

The question now arises as to how the stilted pose prevents the large increase in abdominal temperature found in animals held in the resting position. Three possibilities have been considered. The first is that the space provided between the body and substratum by the stilting allows evaporation to occur from the openings of the book-lungs and that this cools the scorpion's body. The second is that the stilting merely lifts the body away from the substratum so that absorption of heat from this source is curtailed. Thirdly it is possible that, by raising the abdomen, air currents are permitted to pass beneath and around the scorpion's body, thus cooling it to air temperature. These explanations are not, of course, mutually exclusive.

The first suggestion, namely that stilting keeps the body temperature low by facilitating evaporation from the book-lungs has

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[1] It must be noted here that the initial temperature of each of the scorpions, 91-93°F (33-34°C) reflects, in the main, only the minimal reading on the thermometers used.

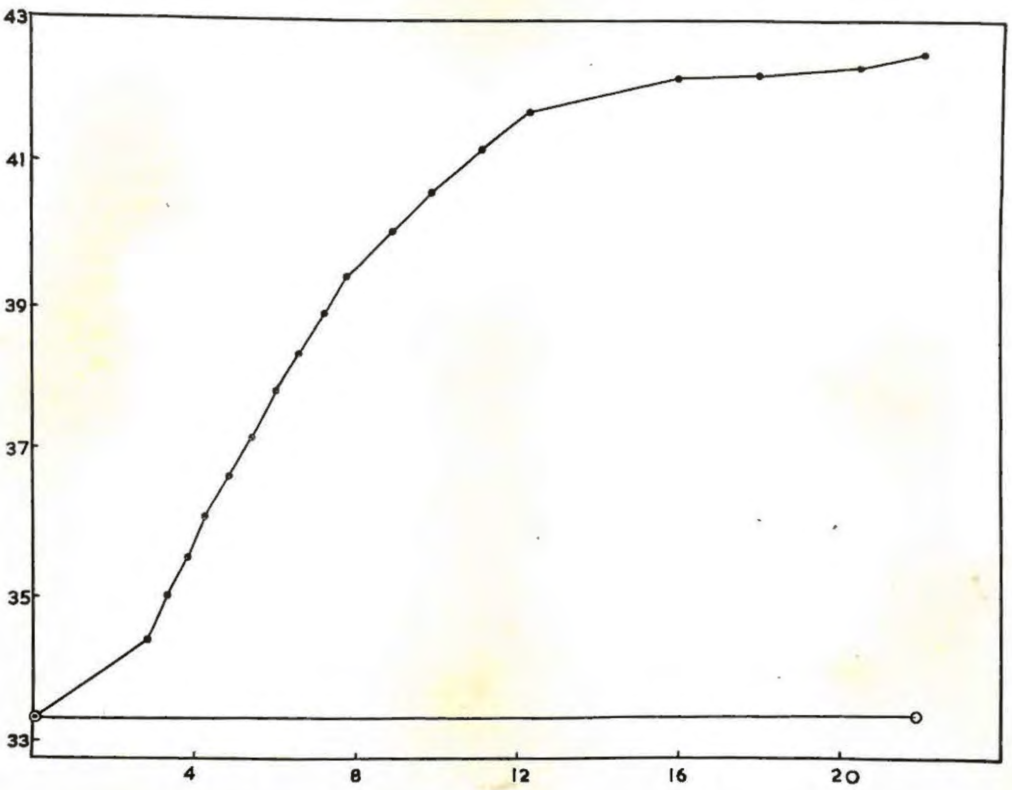


Fig. 16. Effect of stilted posture on the internal temperature of O. latimanus. Abscissa - time in minutes: ordinate - body temperature in °C. Open circles - experimental animal; closed circles - control in resting position.

some measure of support in the fact that in insects a high percentage of the cooling which is effected occurs by way of the respiratory openings (Wigglesworth, 1950). The point is, however, easily investigated in the scorpion and Fig. 17a shows the result of such an observation on O. latimanus.

The book-lungs of the experimental animal were painted over with Samsonite to prevent evaporation, initially both experimental and control animals were shaded from direct sunlight and it can be seen that, when the shade was removed, the body temperature of the experimental, stilting animal hardly altered, although that of the control rose rapidly. Certainly any evaporation from the book-lungs contributes only slightly, if at all, to the cooling effect of the stance.

Such a conclusion, though not in keeping with that expected from an insect, is supported by the findings of Parry (1951) with model discs and locusts, namely that cooling by evaporation is likely to be less important than heat loss by radiation and convection in determining the body temperature of terrestrial arthropods placed in direct sunlight.

The second suggestion, that stilting decreases heat conduction and radiation from the ground surface, is not so easily investigated. Parry (1951) reports that the temperature of a small black disc exposed to direct sunlight will fall by as much as 12°C if it is moved to a height of one inch above the substratum. He considers that at such small distances from the ground the steepness of the "temperature profile" is probably due to a rapid fall off of radiation effects from the substratum, and that convectional losses are likely to be low. To test the importance of convectional loss it is necessary to eliminate as far as possible all "forced convection" (Digby, 1955), that is, all air currents caused by factors other than the presence of the scorpion itself. On the suggestion of Professor D.W. Ewer, this was done by covering the animal, its stand and the thermometer with a bell-jar; both experimental and control scorpions were then exposed to direct sunlight.

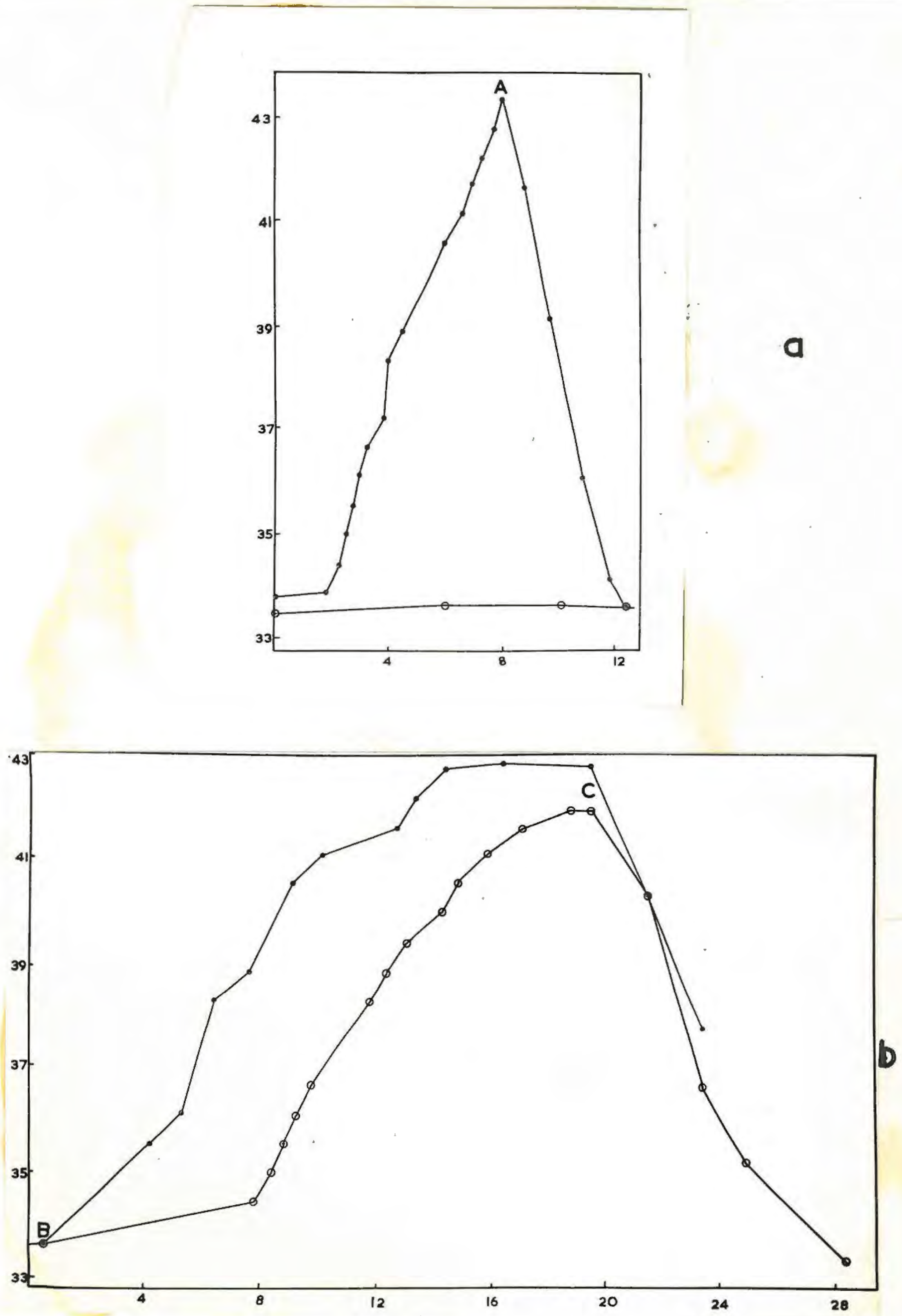


Fig. 17. Effect of stilted posture on the internal temperature of O. latimanus. Abscissae and ordinates as in Fig. 16.

(a) Comparison of animal in normal resting stance, closed circles, and experimental scorpion with book lungs sealed and in stilting stance, open circles. Initially both animals were shaded, but exposed to sunlight at time 0. At time A, both animals were again shaded.

(b) A continuation of the above experiment. Both animals shaded initially. At time B, a glass bell-jar was placed over the experimental animal and both exposed to sunlight. At time C. the cover was removed from the experimental animal, the control only was shaded from direct sunlight.

As can be seen from Fig. 17b, the temperature of the control animal again rose rapidly, but on this occasion, after a short lag, so also did that of the experimental animal. The glass cover was then removed from the latter while the control was shaded from the sun. The body temperature of both animals then fell quickly.

To check that the effect of the glass cover over the scorpion was not that of concentrating the sun's rays but was indeed decreasing the cooling of the animal, the simple test of lifting the cover an inch from the substratum was made. Under such conditions the temperature of the stilting scorpion altered as little as if no cover were over the animal at all.

These results indicate strongly that the temperature controlling effect of the stilting behaviour is due mainly to an enhanced circulation of air around the scorpion. Since the above effects may all be imitated using recently killed animals held in suitable positions, there is no suggestion that the cooling phenomenon is due to any "vital" activity of the animal. This incidentally supports Parry's assertion that in dealing with arthropods of a fair size, it is legitimate to work with models of reasonable size and shape.

These results with O. latimanus, while not eliminating the possibility that stilting may lower heat uptake by radiation from the substratum and by natural convection, suggest that the exposure of the whole body surface to local air currents is a more effective mechanism of temperature control. It seems likely that this may be of general importance in the temperature regulation of other arthropods such as ants and certain tenebrionid beetles where patterns akin to stilting are known to occur. The precise importance of local air currents was not directly studied by Parry in his work with models. Digby (1955) who investigated the point with controlled conditions and live animals, reports that, with wind speeds of 20-30 cm./sec. the animal's temperature excess (i.e. the difference between that of the animal and the surrounding air) varies inversely with the square root of the wind speed. Below this wind-speed the natural convection of the animal itself became of more importance. As Digby points out, it is unfortunate that we know so little of wind speed and other microclimatic factors close to the ground.

Once it is clear that the adaptive significance of the stilting behaviour pattern is one of thermo-regulation, two further questions arise: firstly, where are the thermo-receptors situated? and secondly, what are the circumstances in which the pattern is evoked in natural conditions?

<u>Thermo-receptors</u>.

Nothing appears to be known of the location of thermo-receptors in scorpions, nor in fact in other arachnids. It appears desirable to point out initially that stilting is not simply a direct response to the temperature of the substratum, that is, the animal does not lift its belly away from the "burning" ground. This can be shown by placing the scorpion on a copper plate with running cold water beneath and then directing a heating radiator on to the animal's body from above. Although the substratum on which the animal stands is very much cooler than the air above it, the scorpion will raise its abdomen into the warmer layer of air.

It can readily be shown that the stilting reponse to high temperature persists after the pectines have been removed: similarly removal of the pectines does not alter the preferred temperature when the animals are studied in a gradient. Further operative procedures are impossible and the point was therefore examined by observing the response of scorpions to a red-hot cauterising needle held near different parts of the body. These experiments showed that the poison bulb of the sting is very sensitive to a local heat source; the pedipalps are also sensitive though seemingly less so than the sting; the sensitivity of the legs is still less marked, while no evidence was found for any thermo-receptors upon the back.

It would thus appear that thermal exteroceptors are widely scattered over the scorpion's appendages and therefore any attempt to eliminate them experimentally is effectively precluded; thus it cannot be determined whether the stilting response is mediated by way of these thermal receptors. Moreover it seems possible that a postural thermoregulatory reaction, such as this, may well be controlled by central thermoreceptors, responding to general body temperature, rather than by thermal exteroceptors.

Some measure of support for this suggestion comes from a consideration of observations on a number of O. latimanus which were heated until they adopted extreme stilting poses. Then, with as little disturbance as possible, they were moved to cool dishes in conditions where controls showed no sign of stilting. Here four, of seven animals used, reverted to the stilting pose for at least three minutes and only later relapsed to the normal resting posture. This indicates that when scorpions have been well heated they may sometimes stilt in a cool dish where exteroceptors would not be receiving stimulation from the environment.

Stilting in Relation to Life in Natural Conditions.

In attempting to answer the question "When does O. latimanus stilt under natural conditions?" it is desirable to consider first some other aspects of the biology of this scorpion.

The animals in laboratory terraria spend many hours of daylight at the entrance of their burrows or two or three cm. down them. A limited number of observations were made in the field and these confirm the fact that O. latimanus is not confined to the depths of its burrow during the day. It seems probable that this "door-keeping" which occurs during the daylight hours is connected with feeding. Certainly a study of food fragments in and around their burrows shows that O. latimanus feeds upon insects which are active during the day. Further, a scorpion at the entrance to its burrow will grab viciously at a stick which is moved carefully and "temptingly" towards it, while a partially immobilised grasshopper placed near the entrance of the burrow will be hastily dragged down by the tenant.

Using a temperature "orgel" it has been established that the temperature preference of *O. latimanus* lies within the range 32-38°C. The soil temperature at the mouth of the burrows may rise as high as 70°C. So that it would seem that *O. latimanus* must be able to tolerate temperatures considerably higher than its preferred one if it is to sit in its burrow mouth and catch prey which comes within grabbing distance. Theoretically the stilting pattern would be of considerable use in such circumstances; in practice it has very frequently been observed to occur in the laboratory terraria where the scorpions are door-keeping during the warm part of the day. Observations in the field are not possible as only the pedipalps of a door-keeping scorpion can be seen clearly.

Behaviour Resorted to when Stilting become Inadequate.

It has been found that the lethal temperature of *O. latimanus* lies roughly in the range 40-45°C. It appeared of interest to find out whether, if the temperature of its body approaches the lethal temperature, a scorpion will merely continue to stilt or whether some other pattern is evoked. The answer to this question involves a consideration of responses to directional light.

Many scorpions show a marked photonegative response to directional light. This is true of *Androctonus australis*, *Scorpio maurus* and *Buthus occitanus* (Sergent, 1947). Of the species studied here it is also true of *Parabuthus planicauda*, but *O. latimanus* and *O. nitidiceps* show a very striking photopositive reaction. Further, in agreement with the observations of Sergent upon the various European species mentioned above, *O. latimanus* shows well-marked thigmopausic behaviour. A combination of these two elementary behaviour patterns would serve to direct *O. latimanus* to the entrance of its burrow: so long as no other pattern interferes the scorpion could be expected to remain at the mouth of its burrow, facing the light but not leaving the contact provided by the walls. As has been emphasised above, should a scorpion maintain this position upon a hot day the environmental temperature might well exceed the lethal temperature for several hours and the immediate problem is whether a rising temperature releases an escape reaction.

The problem was studied by placing idividuals in long glass troughs whose floors were covered with soil. All the sides of the trough were blackened except one, through which there shone a light. The temperature of the trough could be changed as required. In such a piece of apparatus at room temperature, the scorpions showed a marked preference for the end of the trough nearer the light source. As the temperature is raised, the scorpions will stilt, but they remain oriented towards the light. Then with a further increase in temperature there is a sudden reversal of the sign of the light response, the scorpion turns away from the light and moves rapidly to the other end of the trough. If the temperature is then allowed to fall, the scorpion presently reorients itself towards the light.

Often just before the reversal of photopositive to photonegative behaviour occurs, there are signs of a general activity: frequently these movements belong to no obvious pattern, sometimes the animal will abruptly if ineffectively begin to burrow. The exact interpretation of this latter is not at the moment clear: it might be regarded as an attempt to construct a burrow for protection, a mere effort to get away from an unpleasant stimulus or a displacement activity arising from a conflict between opposing photopositive and photonegative drives.

Interpreted in terms of its normal life, these observations imply that as temperatures rise and general activity of the animal increases, the light reaction will not direct the animal in such a way as to cause it to leave the safety of its burrow, but rather its reversal of sign will result in the scorpion retreating into the deeper parts which, as rough measurements in the field have shown, may be more than 20°C below the soil temperature outside. It would seem that this reversal of light behaviour is the basis of an escape from a potentially lethal position.

It is interesting to note that the protective behaviour pattern of this scorpion in relation to high temperature has two facets - a static postural behaviour pattern which permits a certain degree of regulation, followed by a dynamic locomotory pattern which allows the animal to evade the difficulty by leaving the potentially lethal environment.

6. DEVELOPMENTAL BIOLOGY

Scorpion eggs can be separated into two kinds: apoikogenic are those which, having yolk, are more or less self-sufficient as far as material for development is concerned, while katoikogenic eggs, lacking appreciable amounts of yolk, are characterised by various interactions of maternal and foetal tissues elaborated so that the developing scorpions can be "fed" during the time spent inside the mother.

The embryology of the scorpions with yolked eggs appears to have been well covered by the works of Brauer (1894, 1895), Percyaslazewa (1907), Pavlovsky (1924, 1925) and Abd-el-Waheb (1952) so that although I have made observations upon parturition in two species of scorpion with such eggs, namely *Parabuthus planicauda* and *Uroplectes triangulifer*, no study has been made here of the pre-parturitional stages.

In the case of the katoikogenic type, three genera of scorpion occurring locally have this kind of development, *Hadogenes*, *Opisthacanthus* and *Opisthophthalmus*. In spite of the work of Pavlovsky (1924, 1925), Mathew (1948, 1956) and Vachon (1950), there are still several problems which appear of interest. Certain questions relating to the function of accessory maternal and foetal structures are considered here. These structures are the "biberon" which is maternal in origin, the "dorsal flaps" which are foetal, and the "labral lobes" which are a complex developed from both mother and embryo. The first two are common to all scorpionids; the last is found only in *Opisthophthalmus* and, since all three structures are thus represented in *O. latimanus*, the investigations described below will relate to this species. It seems desirable, for clarity, to start with a brief survey of the development of this species.

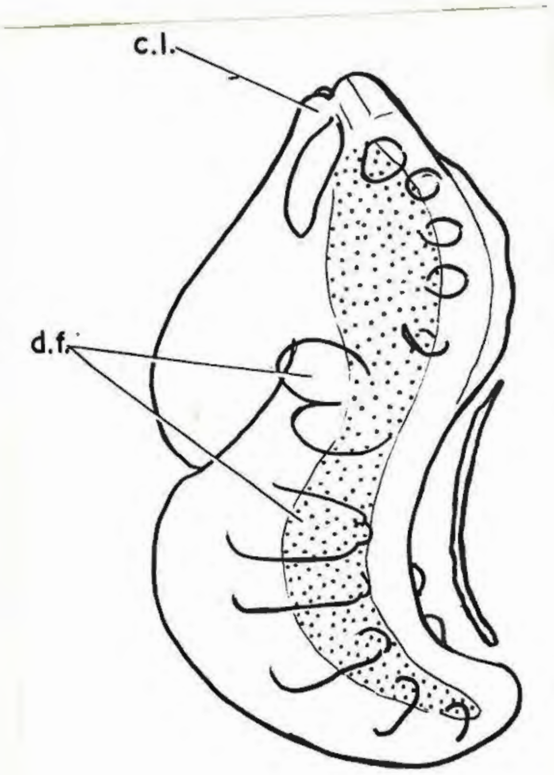
Outline of the Embryology of *O. latimanus*

The initial stages, that is fertilisation and cleavage, have not been followed in *O. latimanus*. There seems little agreement about the time of fertilisation in scorpions, in fact Piza (1950) reports that one female scorpion in his laboratory produced two separate broods without any possibility of mating between parturitions. I have made a similar observation on an unidentified species of Opisthacanthus. Piza makes various suggestions as to how this could have occurred, but has overlooked the possibility of simple parthenogenesis. Campbell (1883) and Damin (1893) both report parthenogenesis in spiders and there is no obvious reason why it should not occur among scorpions. Further a male scorpion will court and mate with a female that is already pregnant. If, in such conditions, the female is successfully impregnated, and there seems no reason to believe that this would not occur, it raises the possibility of either delayed fertilisation, as in the Onychophora, or delayed implantation.

Whatever the time of fertilisation, it is generally agreed that the union of egg and sperm occurs in the tip of a small outpocketing on the tubular ovary of the female, this outpocketing being called the embryonic diverticulum. Very shortly after the egg starts cleavage a long process begins to extend from the tip of the diverticulum. This process, the appendix (Laurie, 1891) or more aptly, the biberon (Vachon, 1950) comes to lie freely amongst the liver lobes of the mother and is considered to function as a channel for nutriment from the mother to the foetus.

In O. latimanus, by May, the shape of the transparent embryo is fairly distinct: it is attached by its anterior end to the top of the diverticulum at the point where the biberon begins and there is no sign of external body segmentation.

By July the embryos have increased in size from the 3 mm. of May to 5 mm. and, though still transparent, show signs of a developing gut, recognisable as shiny translucent globules and stretching from the point of attachment of the embryo back into the tail. A globular portion in front of the "mouth" presumably represents the pharynx (Fig. 18a). Incipient segmentation can be seen in the hind part of the prosoma and in the tail region, while there are two



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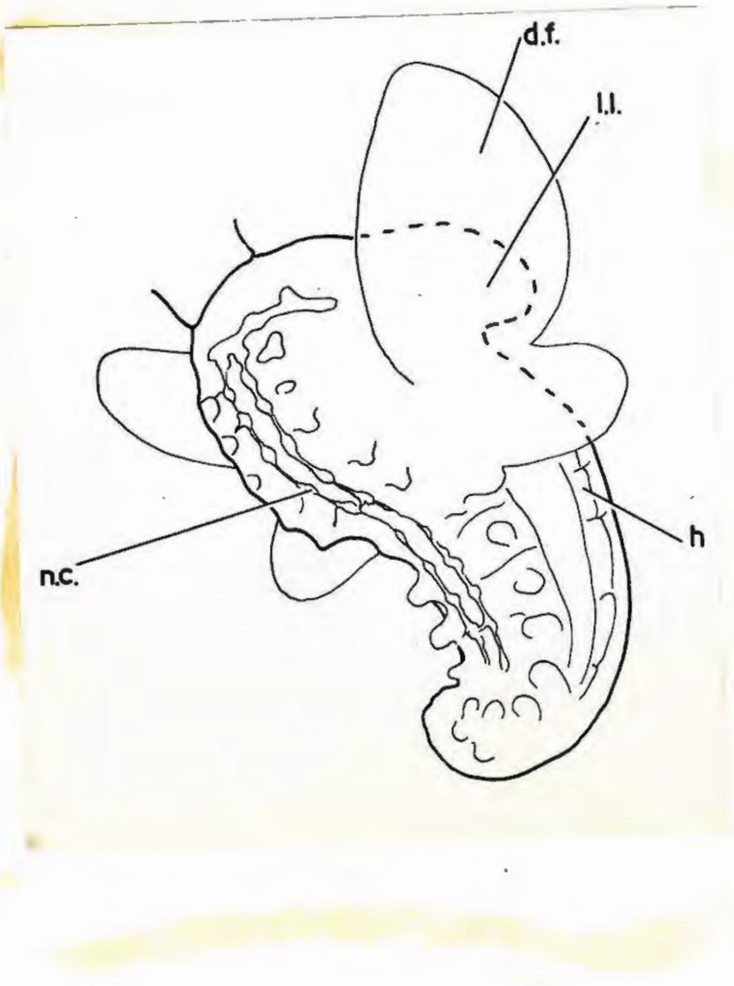

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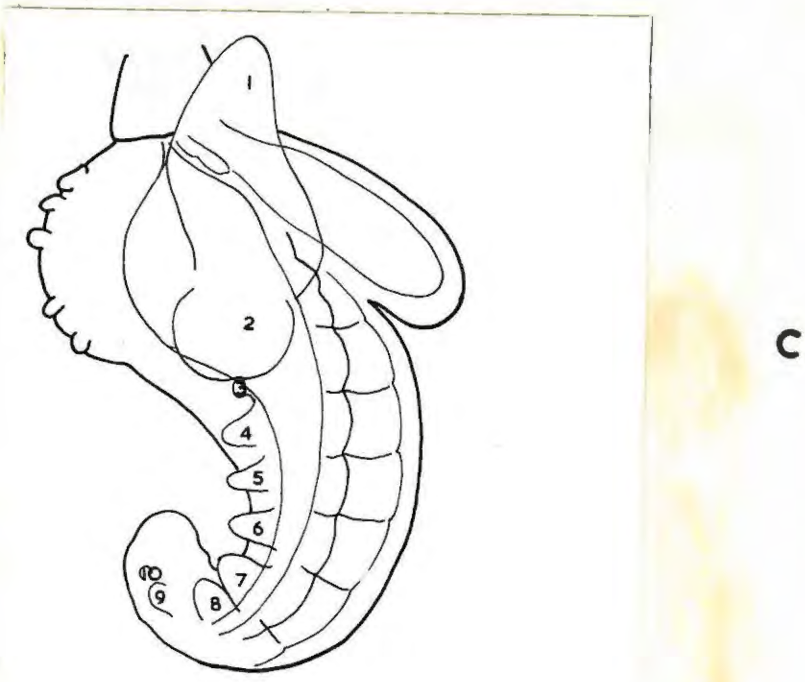


Fig. 18. O. latimanus embryos dissected out of their embryonic diverticula.

(a) Lateral view of an embryo in July. The gut and perhaps the pharynx can be made out, stippled. Anteriorly a slight projection on either side, c.lx., is concerned with holding the biberon in position. Lumps, d.f., along the side of the animal are presumptive dorsal flaps.

(b) Dorso-lateral view on a later embryo. The ganglionated nerve cord, n.c., and the heart, h., both show the segmentation. The dorsal flaps, d.f., are well developed, the first two pairs being especially large and turgid. The limb buds are apparent and the beginnings of the labral lobe, l.l., can be seen through the dorsal flaps.

(c) Ventro-lateral view of an embryo at the same stage. The dorsal flaps are numbered and the gut shows clearly enough to establish that there is no connection between it and the dorsal flaps or labral lobe.

prominent lumps on either side of the prosoma. These mark the first two pairs of what will be called the "dorsal flaps" and which later develop, a pair to each segment, all along the length of the mesosoma and almost all the way along the tail. At this stage the first indications of another structure can be made out as a hump forming on the presumptive dorsal surface of the prosoma. This grows out as a process which will be called the "labral lobe" because in the young nymphs its vestige can still be seen as a protrusion of the labrum.

By October the segmentation of the body is fairly clear and can be readily recognised by reference to the dorsal flaps, which have become fairly large, though the first two pairs are still very much more marked (Fig. 18b). The tip of the labral lobe projection is just beginning to make contact with the wall of the diverticulum.

During November the limb buds begin to show clearly and by December the segmentation of the legs and the claws of the pedipalps is obvious. At this time the dorsal flaps have enlarged even further, the first two pairs spreading forward and around the front part of the embryo, while the whole embryo has grown so as to occupy almost the whole diverticulum.

There are two layers of tissue forming the wall of the anterior part of the diverticulum and by early January the tip of the labral lobe has broken through the inner one and the outer is slowly being extended by the growth of the lobe (Fig. 19). Later root-like processes appear at the end of the labral lobe, formed of maternal tissue only (Fig. 20).

It is at this time that the body of the embryo begins to darken in colour and is conspicuously different from the white of the maternal uterine structures.

The dorsal lobes begin to shrink early in January and as the details of the embryonic body become clear, they show up merely as

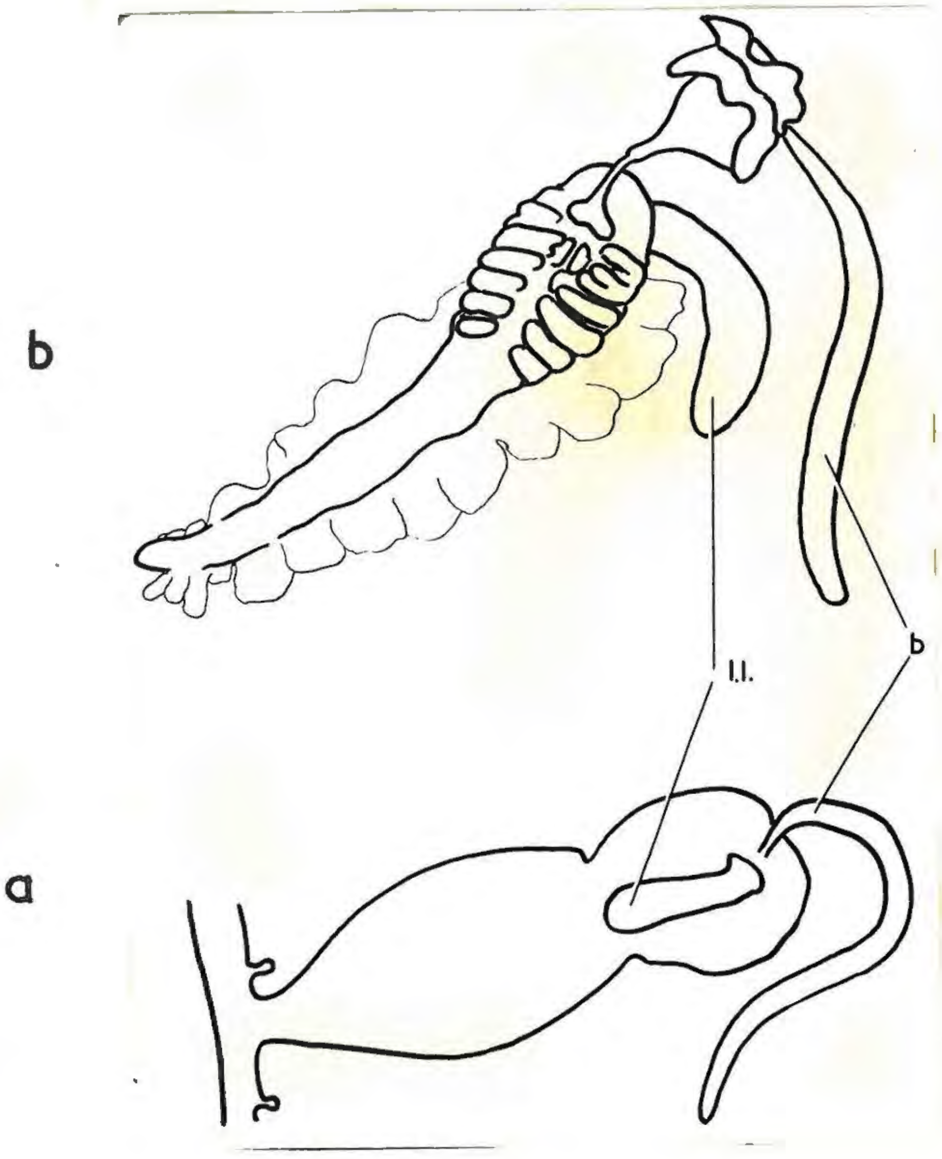


Fig. 19. *O. latimanus* embryos in early January.
(a) Entire diverticulum
(b) Ventral view of the embryo dissected free of the diverticulum and showing the labral lobe, *l.l.*, soon after it has extended beyond the diverticulum. No root-like processes are yet visible on it. Some retraction of the dorsal flaps, especially the more anterior ones, is evident. *b.*, the biberon.

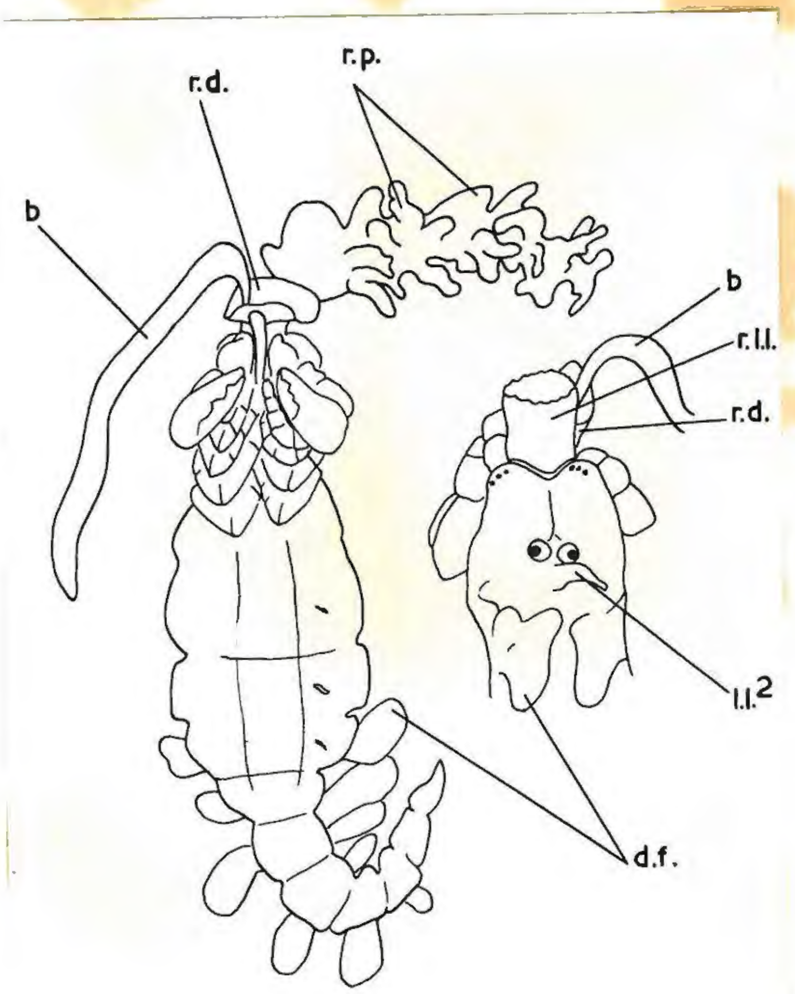


Fig. 20. (a) Left hand figure. Ventral view of O.latimanus embryo shortly before birth, i.e. late January or early February.

(b) Right hand figure. Dorsal view of the prosomal region of the same embryo.

b., biberon; d.f., dorsal flaps which are dwindling rapidly; l.l^2, second lobe of the "labral lobe complex", lying immediately behind the pair of median eyes; r.d., remnant of the diverticulum which has been dissected away; r.l.l., remnant of the labral lobe which has been cut away in Fig.20b; r.p., root-like processes developed on the labral lobe.

small flaps on the back of the foetus. The size of the embryo is now such that it stretches out of the diverticulum and into the ovari-uterus itself, sometimes the tails of a number of animals may be seen lying side by side in one tubule.

By mid-February most of the young scorpions are ready to be born and when this occurs each slips completely out of its embryonic diverticulum, leaving the entire biberon attached to the tip of the diverticulum, while the inner core of the labral lobe, that is the foetal contribution, is pulled free, the knobbled maternal covering being left attached to the diverticulum.

Organisation and Form of the Embryonic Diverticula.

In a pregnant O. latimanus there are normally 16 to 20 embryonic diverticula with developing young inside, though along the ovarian tubules there may be diverticula in various other stages of development (Fig. 22a), as has also been reported for Hormarus australasiae Fab. by Pflugfelder (1930) and Heterometrus scaber (Thor.) by Mathew (1956). Both of these workers report that very small diverticula, without any sign of biberons, occur among the series of developing embryos. In O. latimanus these fall into three size groups, a condition which is reported also for Heterometrus by Mathew. In small females there is no differentiation of the diverticula into size groups; in later instars there are more diverticula and they appear to be of two sizes, while by the pre-adult instar all three sizes have appeared.

Contrary to the apparent randomness in Ischnurus ochropus (Vachon, 1950), there is a definite arrangement of both diverticula and liver lobes in O. latimanus. This symmetrical organisation (Fig. 21) presumably ensures that each of the embryos and its associated structures is adequately covered by the lobes of the mother's liver, from which the embryonic nourishment appears to be derived.

The embryonic diverticula themselves are always either

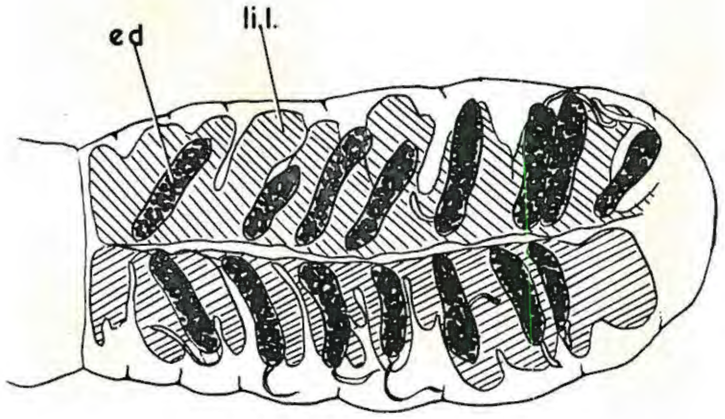


Fig. 21. Dissection of a pregnant O. latimanus from the dorsal surface, the layer of liver lobes, li.l., which covered the embryos, has been removed to expose the embryonic diverticula, ed.

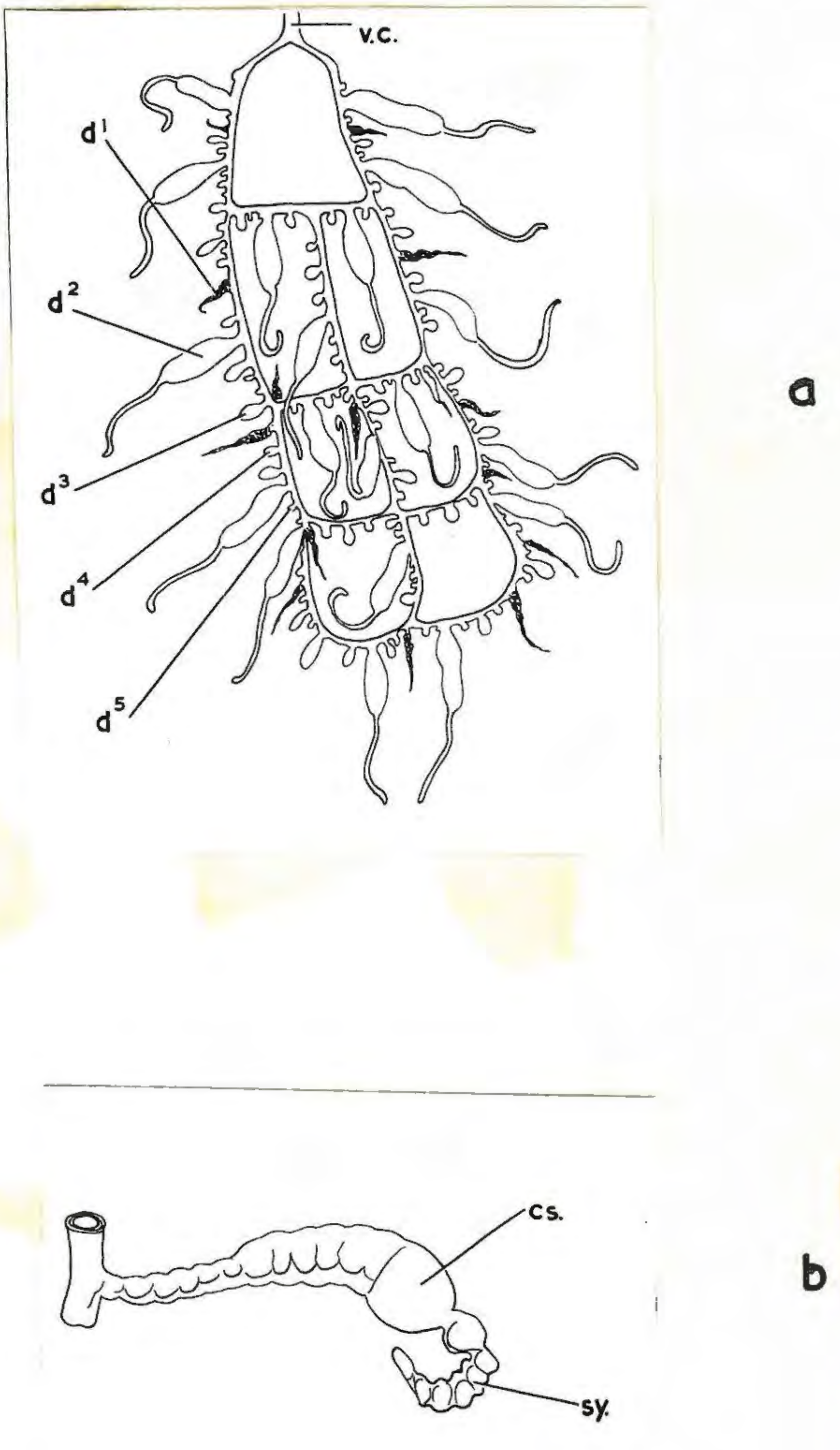


Fig.22. (a) Ovariuterus and diverticula of a pregnant O. latimanus. d^1., degenerating diverticulum; d^2., diverticulum with developing young inside; d^{3-5}., small diverticula at different stages of development; v.c., common vagina
(b) Single embryonic diverticulum of Ischnurus ochropus showing the differentiation of a "casque", cs., a feature which is not marked in O. latimanus. A coiling effect, sy., is apparent within the biberon, a further difference from O. latir
(after Vachon, 1950).

white, or, as they are stretched by the developing embryo, slightly transparent. In shape there is less differentiation here than appears in the other scorpions which have been studied. There is no definite "casque" about the prosomal region (Vachon, 1950) and the tail of the embryo is not marked externally by a narrowing of the diverticulum as is that of I. ochropus (compare Figs. 19a and 22b).

Internally the diverticulum is lined with a thick layer of what would appear to be glandular tissue. It is marked with deep longitudinal furrows and, though no histological studies have yet been made upon them, they would appear to be of some importance in relation to the functioning of the dorsal flaps mentioned above.

In addition, degenerating diverticula of previous pregnancies may be observed. Mathew, in fact, states that from these latter he is able to estimate the number of past pregnancies. In O. latimanus the matter is more complicated, since there are two distinct kinds of degenerating diverticula: those which are like the diverticula illustrated by Pflugfelder and Mathew, and which stay attached to the tubule of the uterus until they are almost too disintegrated to identify, and those which appear to come free of the tubule at an early stage after development ceases in them. These latter may be observed lying freely in the ventral part of the body cavity and sometimes show very little sign of disintegration, as if they had just recently been liberated from the tubule. The significance of this is not clear at the moment. The regularity of the positions of those diverticula which disintegrate while still attached to the uterus suggests that they are the remnants of successful past parturitions. This is supported by the fact that no remnants of embryos have yet been discovered in a set of them and that the "teat" of the biberon is left clear and unencumbered by embryonic material: Mathew (1956) gives the same interpretation to similar structures in H. scaber. It seems possible that the second condition could arise as a result of abortion but the fact that there are normally a large number of these freed diverticula, about 15 or so, makes this seem slightly less probable.

However, in a number of post-partum females of O. latimanus which were dissected, single, apparently fully-formed young were found still in their embryonic diverticula which lay freely within the liver lobes of the parent. This observation seems to support the view that the formation of free diverticula is associated in some way with some type of abortive event.

The Biberon.

Anatomically this appears very similar to that found by Mathew in H. scaber and shows none of the differentiation into Endknopfchen, Korper and Stiel described for Hormurus australasiae (Pflugfelder, 1930). The diameter, 0.3 mm. in a late embryo, is almost uniform along the length, but, towards the diverticulum, the biberon narrows while it ends distally as a slightly rounded point. From various published accounts of the histology of this structure (Pflugfelder, 1930; Mathew, 1948; Vachon, 1950) it is known to contain a number of canals which form its core and which anastomose to different extents at different points along the structure; the outer covering appears slightly more porous nearer the distal end.

The manner of attachment of the embryo to the "teat" of the biberon cannot be made out during the early stages, but it is broken fairly easily; sometimes when a diverticulum is opened and dropped into formol or saline solution the embryo becomes free: occasionally when a diverticulum is opened, the embryo is found to be already free. Mathew's view that the embryo merely holds the tip of the biberon in its mouth and is capable of letting it go, would seem to apply to O. latimanus even before the structures responsible for holding the teat have become significantly differentiated. Later on (Fig.18a) two oval lumps can be seen on either side of the attachment to the biberon and, when the other appendages develop, it is clear that these are the chelicerae. It would appear that here, as in I. ochropus and H. scaber, the chelicerae hold the biberon in place; a remnant of the precise structure concerned in *O. latimanus* is recognisable in the first instar nymph as a hard pad on the second segment of the chelicerae. (Fig. 23a). It is clear from its position that the chelicerae must have rotated through a right angle at the end of the embryonic period; a similar rotation has been found to occur in *U. ochropus*.

Ever since the biberon was first observed, in 1828 by Müller, it has been recognised as the means by which the scorpion embryo obtains nourishment from its mother. Laurie was of the opinion that the young took the end of the biberon and "masticated" it, while Vachon (1953) believes that nourishment is drawn down the biberon by "osmosis" and Mathew (1947) by the suction of the embryo at the end of the tube. The latter reports that in *Hormurus* he has observed the sucking movements of the embryo and says that vital dyes are taken up into the biberon. In *O. latimanus* no movements which were unquestionably "sucking movements" were observed. It is true that pulsating movements are made by the embryo, but in most instances they were clearly related to the beating of the heart.

With a view to repeating the staining observations of Mathew, the following techniques were tried. A tergite of the mesosoma of a pregnant living scorpion was cut so that it could be flapped open and the liver lobes pushed aside to expose the embryonic diverticula. One of two courses was then followed: the diverticulum was freed from the liver lobes and then slipped into a very small tube of vital stain that was introduced amongst the liver lobes, or alternatively the whole diverticulum was cut free of the maternal ovariuterus and placed in a watch-glass with the stain. There was no observable difference resulting from the two different methods used so that, after the first few trials, the latter procedure was adopted.

Putting the diverticulum and enclosed embryo into a vital dye in Ringer solution certainly does show an uptake of the dye in the biberon, starting at the tip and creeping along. Very little dye is taken up by the diverticulum, but here again it is a differential take-up, that part enclosing the tiny embryo, or later the prosoma,

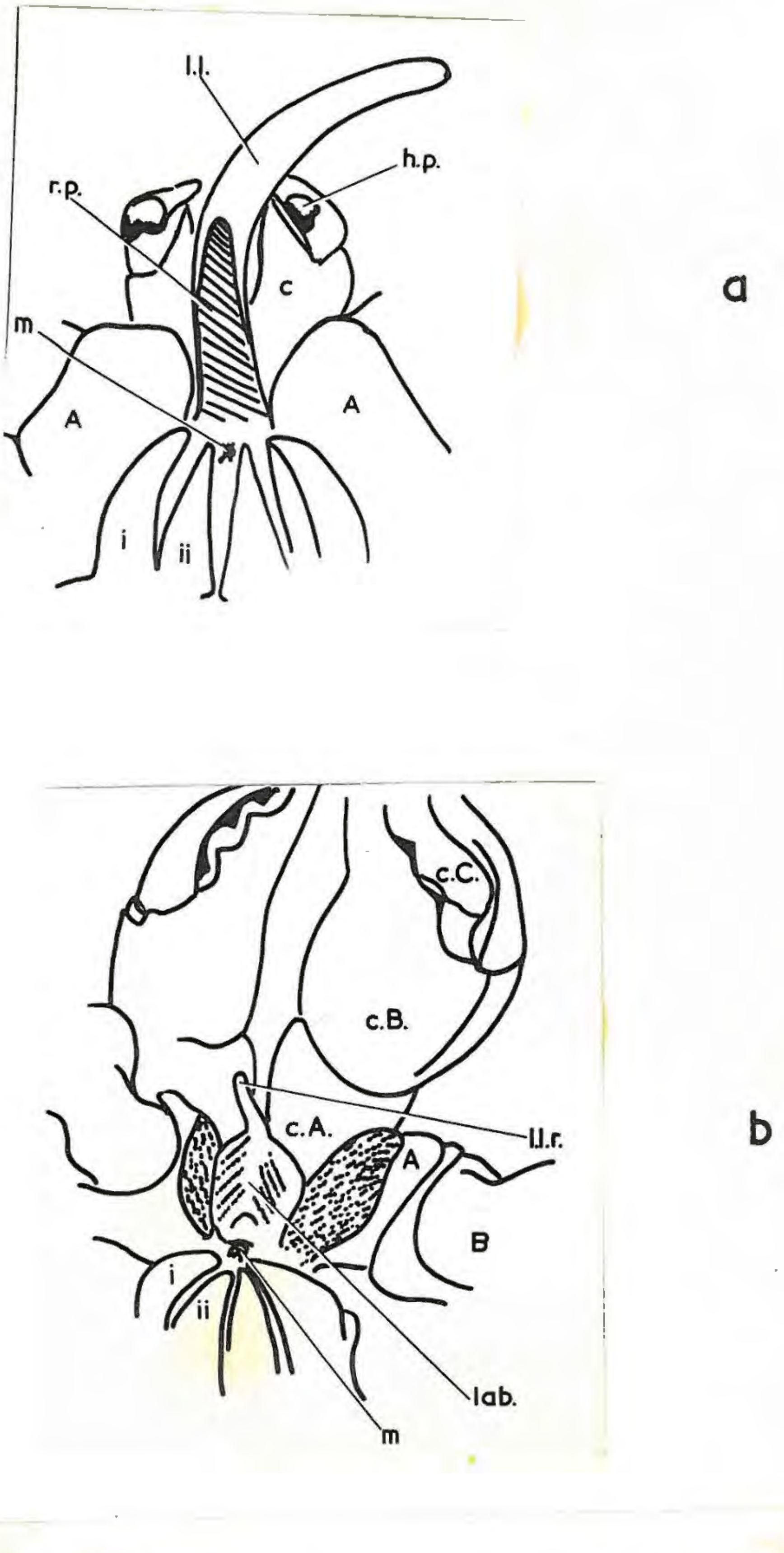


Fig. 23. (a) Ventral view of the anterior region of a first instar nymph of O. latimanus to show the labral lobe, l.l., in relation to the chelicerae, c.; the coxae of the pedipalps, A.; the first and second legs, i and ii respectively; and the mouth, m. The hard plates on the chelicerae, h.p., are shown and the contents of the labral lobe, which are retracted as the nymph grows, can be seen, r.p.

(b) Ventral view of the anterior region of a second instar nymph to show the vestige of the labral lobe, l.l.r., attached to labrum. c.A., c.B. and c.C. are respectively the first, second and third segments of the chelicera: A. and B. are the first and second segments of the pedipalp.

absorbing dye far less readily: a state of affairs recalling the differentiation of a "casque" at the end of the diverticulum of I. ochropus (Vachon, 1950).

When a diverticulum from which the embryo has been removed, or just the cut biberon, is put into the dye, the same differential staining takes place, so that it is not dependent entirely on the presence or activity of the embryo. To be certain that the phenomenon was associated only with living tissue, the diverticulum with or without its contents was either heated to 85° for 10 minutes or placed in concentrated formol for the same time. Both the control, which had been left for 10 minutes in Ringer, and the experimental diverticulum were placed in the vital stain. After a few minutes it was clear that the shade of staining in the experimental case was very different from that in the live one, but that differential uptake of the stain still occurred in both cases. It was found, in fact, that biberons left for five months in alcohol still showed the typical selective staining reaction of the fresh biberon. It is therefore clear that, aside from any possibility of an active uptake of the stain at the end of the biberon, there is a mere anatomical basis for this, as indeed is indicated by its histology. The present observations suggest that Mathew's conclusions are not based upon critical evidence. If the embryo plays an active rôle in food uptake, some technique other than that of simple immersion in solutions of vital stains is necessary to demonstrate the effect.

It has been shown above that the differential staining of the biberon is independent of the presence of the embryo in the diverticulum. There is, however, the possibility that activity by the embryo in ingesting material from the biberon could still be demonstrated by the use of vital dyes if attention was concentrated upon the movement of dye out of the biberon in the direction of the embryo. To study this problem the following simple technique was used.

The bottom of a shallow watch glass was lined with coloured plasticine, the colour contrasting with that of the dye to be used. A cylinder of glass, about 5mm. long with diameter 4mm. and the edges smoothed over, was stuck well into the plasticine, forming the dye chamber. Dye was pipetted into the chamber so that it lay just short of the top of the cylinder and a little Ringer solution was poured carefully into the watch glass. The animal was then placed in position; either the biberon or the body lying in the vital stain and the remaining part hanging over the outer edge of the cylinder. More Ringer was pipetted into the watch glass until that part of the embryo in the outer chamber was almost covered and the Ringer level was just short of the top of the glass tube. A binocular microscope was then mounted over the preparation and any stain passing into that part of the embryo lying in Ringer could easily be seen against the contrasting plasticine colour. Any stray trickles of stain which came over into the Ringer could easily be pipetted up and more Ringer added.

Using this technique it has been found that, when the biberon lies in the dye, while the rest of the diverticulum, including the live embryo, is surrounded by clean Ringer solution, not only does the dye enter the biberon but it passes down this structure and can be seen within the diverticulum in the region of the head of the embryo. If, however, the embryo has been removed, ~~the~~ no dye makes its way into the diverticulum.

These results strongly suggest that the passage of dye, and by extrapolation of other material in solution, down the biberon to the embryo depends in some way upon the activity of the embryo itself, but the precise manner in which the embryo draws material along the biberon has still to be elucidated: clearly such a technique as that described above could assist in further studies of the problem.

The Labral Lobe.

As was mentioned earlier, this structure was observed by Laurie (1896) in museum specimens of Opisthophthalmus. In one animal, *O. capensis*, he obtained both the late embryo and a brood of newly hatched nymphs, while in the other, an undetermined species, only the brood of young themselves was available. In neither case is any detail of the maternal contribution to the foetal structure mentioned, but Laurie states that there is variation in the foetal structures of the nymphs of the two species. In *O. capensis* there are two structures, one arising from the carapace and the other from the region which will produce the labrum. It would seem very likely that this latter part of the *O. capensis* "labral lobe" should be homologised with the entire labral lobe of *O. latimanus*, since it is clear both from its position in the embryo as well as the subsequent history in the nymphs, that here the lobe is produced from the region of the labrum. Even in the second instar nymphs of *O. latimanus* it is still present as a slightly pointed structure which only becomes visible when the bases of the pedipalps are parted (Fig. 23b).

In the undetermined species the "labral lobe complex" corresponds more closely to that of *O. latimanus* in that there is only one lobe, which arises from the area of the presumptive labrum. The second lobe of *O. capensis* is represented by a small and backwardly pointing projection just behind the median eyes. In *O. latimanus* embryos this can be seen as a small stub (Fig. 20); even in the first instar nymphs the remnants can be made out quite clearly (Fig. 24).

A second difference between the labral lobe complex of *O. capensis* and *O. latimanus* is that the two lobes in the embryo of the former penetrate the thick walls of the diverticulum and lie free among the tissues of the mother, that is without any sign of a maternal covering or of the knob-like processes associated with this tissue in *O. latimanus* (cf. Fig. 25, reproduced from that of Laurie (1896)). It seems possible, however, that this might be a fixation artifact.

Laurie reports that internally the labral lobe complex is filled with trabecular tissue, probably also containing blood vessels. He states that there is no connection between either of the labral lobes and the gut of the embryo or nymph. In *O. latimanus* exactly

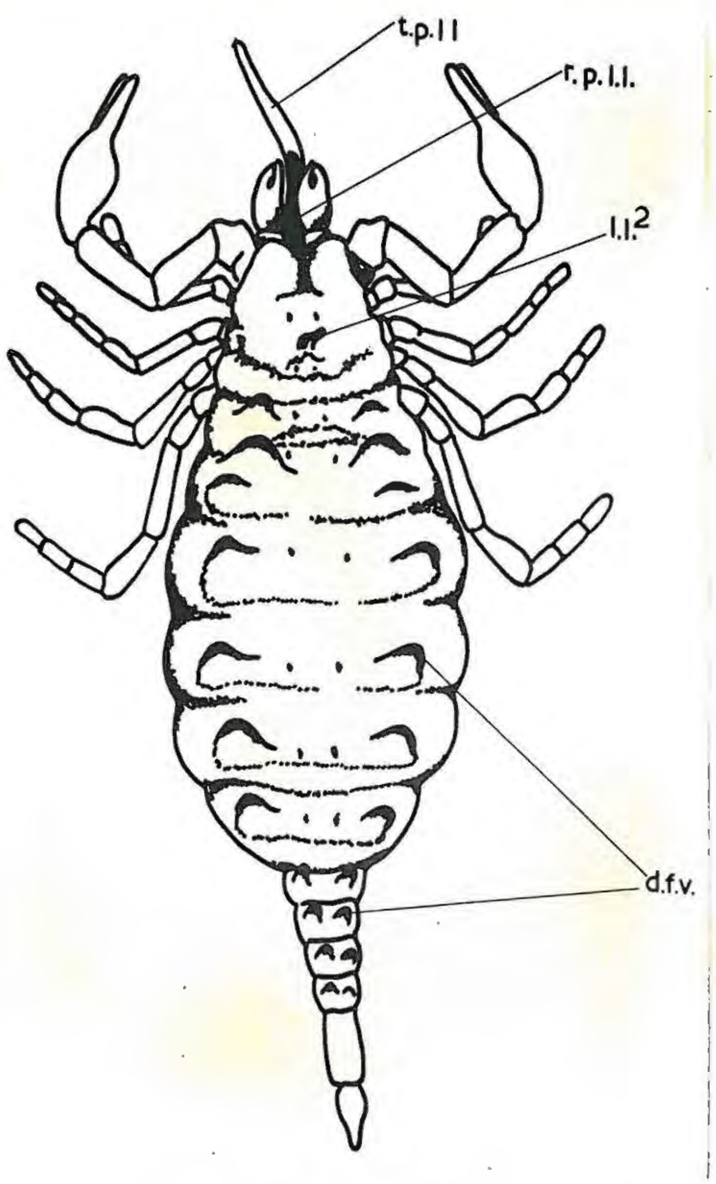


Fig. 24. First instar nymph of O. latimanus showing the labral lobe with contents partly retracted, r.p.l.l., and the transparent covering left, t.p.l.l. Behind the eyes, the small lobe constituting the second part of the labral lobe complex is still visible, l.l.^{2}., as are vestiges of the dorsal flaps, d.f.v.

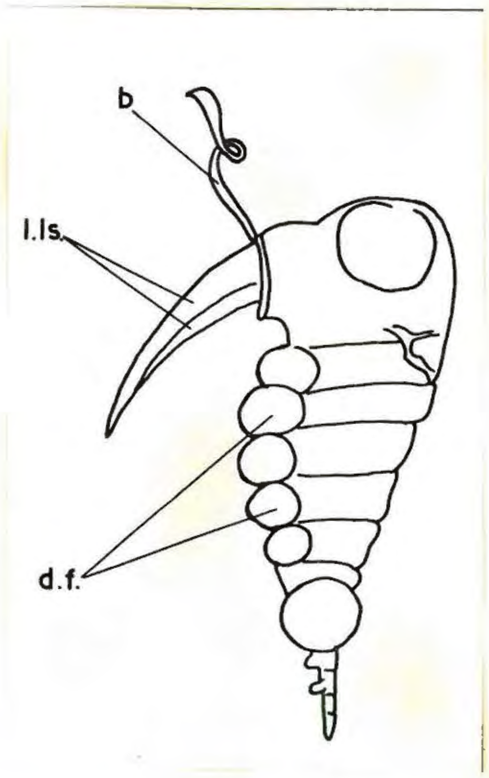


Fig. 25. Lateral view of an embryo of O. capensis showing two lobes, l.l.s., constituting the labral lobe complex. The biberon, b., and dorsal flaps, d.f., are recognisable (after Laurie, 1896)

the same is true: the tissue filling the chitinous covering of both labral lobe proper and the projection from behind the eyes appears to be in contact with the muscle blocks of the prosoma and with nothing else.

With regard to the function of the labral lobe complex, Laurie proposes that it is the same as that suggested for the biberon, namely the absorption of nutriment for the embryo from the surrounding tissues of the mother. This is an entirely reasonable assumption with regard to the labral lobe of O. latimanus, and it seemed worthwhile looking at the behaviour of the structure in solutions of vital dyes.

The maternal covering, with its root-like processes, shows a marked uptake of stain relative to the rest of the embryo or diverticulum, the biberon of course excepted. There is no sign of differntial staining of the labral lobe as there is in the case of the biberon, so that, presumably, the covering of the whole structure is equally permeable to or active in absorbing dyes. If the maternal covering is removed and only the foetal core left, there is no absorption of the dye, the labral lobe behaving just like the rest of the body covering of the embryo. However, the interpretation of this observation is unclear: either it could mean that the embryo was so "upset" by the removal of the maternal covering that the mechanism of absorption was put out of action, or it could mean that only the maternal tissues are capable of absorption of the vital dye and that it is by their activity that it is transmitted into the labral lobe of the foetus.

In the case of the nymphs there seems little doubt that the labral lobe is acting as a store of food. In the new-born young the whole of the structure is a deep, purplish black and gradually, as the animal gets older, the coloured portion is retracted, leaving an anterior transparent protrusion which is only lost with the first moult, (Fig. 24). During this time the baby scorpion remains on the back of the mother and makes no attempt to feed; in fact this would be impossible because of the position of the labral lobe itself.

If it is agreed that the labral lobe probably functions as an organ of absorption or storage of food, the significance of the fact that the structure is peculiar to the genus *Opisthophthalmus* is not immediately clear. Laurie points out that the biberon of *O. capensis* is relatively smaller than that of *Heterometrus* while the young are larger at birth. He suggests that the labral lobe constitutes an auxiliary method of feeding the foetus to compensate for the inadequacy of the biberon.

The large size of *Opisthophthalmus* embryos relative to those of *Heterometrus* may well be compensated for by the smaller number produced. In *Heterometrus*, as Laurie (1892) himself has shown, there are approximately 35 young, while in *Opisthophthalmus* the maximum number seems to be about 20. Nevertheless another interpretation of the occurrence of the labral lobe complex is possible. The argument must, however, relate to *O. latimanus*, since it is only here that the details of development are known at the moment.

Two points affect the argument: firstly the fact that the labral lobe survives into the second nymphal instar as a food store, and secondly the fact that the labral lobes only appear a very short time before the young are due to be born. It is only during January that the labral lobe breaks through the inner wall of the diverticulum and extends the outer one, while the first births observed have occurred in early February - though there are indications that others had occurred earlier in the field. Both of these points support the thesis that the main function of the labral lobe in *Opisthophthalmus* is that of providing a food store for the first and early second instar nymph. It is quite possible that a significant amount of material, absorbed by way of the labral lobe, is utilised by the foetus before parturition but that the main significance of this absorptive structure lies not here, but in the nourishment of the young scorpions.

The question then arises, why should O. latimanus need a more adequate food store for the newly born young than do other scorpions? It seems possible that the answer lies in the amount of time spent on the back of the mother before the young start catching prey for themselves. The duration of this period is not accurately known, but scorpions do not appear to leave the mother until after the first moult. The duration of the first intermoult period in different species is very variable, from less than a week after birth in Centruroides vittatus to at least three weeks in O. latimanus (see Table II for summary). The second instar nymphs are generally reported as staying with their parent for "a few days" after the moult, the maximal period quoted being 8-14 days in Centruroides insulans (Baerg, 1954a). In O. latimanus however the young remain with the mother for a further month. Thus the young of O. latimanus stay with the parent for at least seven weeks, while the absolute maximum period for other scorpions does not exceed four weeks - taking maximal time before moult as a fortnight (e.g. Euscorpius) and maximal time after as a further fortnight (e.g. C. insulans).

Whether the association of the labral lobe with the longer period spent on the mother is valid or no, the question still remains what is the selective advantage to O. latimanus of this longer association with the parent? At the moment there appears to be no definite answer. There is no observation of the mother scorpion leaving the young in the burrow or the shelter and going out to forage, nor is there any indication that the young are taught anything by association with the adult scorpion. The only possibility which need be considered here is one which has no evidence to support it. It may be that the young scorpions need a certain time after parturition for their exoskeletons to harden sufficiently to allow vigorous digging and that where scorpions live in deep burrows, in fairly hard ground, as does O. latimanus, a longer time must be spent between emerging from the mother and leaving her to start life

TABLE II.

Duration of the First Intermoult in Different Scorpions.

Animal	Duration of First Intermoult (days)	Authority.
Centruroides vittatus Say.	3-6	Smith (1927)
Buthus occitanus (Am.)	7	Fabre (1923)
Scorpio europaeus Linn.	7	" "
Tityus trinitatis (Poc.)	7	Waterman (1950)
C. insulans Thorell	7-9	Baerg (1954a)
Mesobuthus eupeus (Koch)	8-10	Kobakhidze (1950)
Heterometrus longimanus (Hbst.)	10	Schultze (1927)
Euscorpius italicus (Hbst)	10-12	Cloudsley-Thompson (1951)
Heterometrus scaber (Thor)	10-12	Mathew (1956)
E. Carpathicus (L.)	14	Berland (1932)
E. germanus (C.L.K.)	16	Cloudsley-Thompson (1955b)
O. latimanus Koch	22 or more	Personal observation.

alone. It seems almost impossible to test this thesis since the abilities of the adult scorpions of different species to burrow may, and very probably are, very different and depend on whether they normally are strong burrowers or not. Thus, for instance, it would mean nothing to report that a nymph of O. latimanus which had just left its mother could excavate a 14 cm. burrow while a comparable Parabuthus planicauda nymph could not dig more than a hole 1 cm. deep, for it must be taken into account that adult P. planicauda never do construct a burrow of more than about 14 cm. even in the softest soil.

Dorsal Flaps.

The dorsal flaps of O. latimanus appear to be homologous with structures first described by Thorell (quoted by Laurie, 1896). These are paired bladder-like structures on certain of the tail segments of the young of Heterometrus. Laurie himself reports that such structures are also present in young O. capensis, but that here they occur in the mesosomatic as well as certain tail segments. It is clear that within the genus Opisthophthalmus there is some variation in the occurrence and form of these outgrowths, for structures in O. nitidiceps (Fig.26) which are clearly homologous with those in O. latimanus, are much larger on the ~~first~~ last two segments on which they occur. It seems possible that foetal differences such as this and the organisation of the labral lobe complex may well be of systematic importance and could give clues to the true relationships of species within the genus as well as with other genera.

Laurie simply states that the wall of the diverticulum covering the dorsal flaps is very thin while over other parts of the body it is thickened. Vachon (1949) however says that the "diverticul~~um~~es abdominale" in Heterometrus and Lychas, which are presumably the dorsal flaps, are connected with the embryonic gut. Neither in embryos of O. latimanus where all internal structures can be clearly seen through the skin, nor in the first instar nymphs as seen in dissection, was there any sign of an association of the

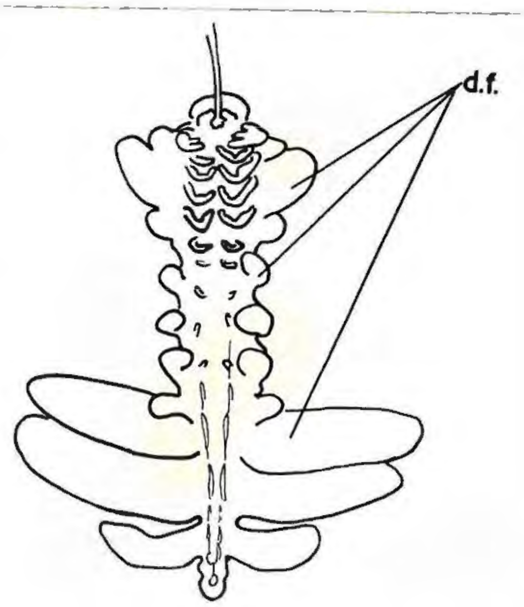


Fig. 26. Ventral view of an embryo of O. nitidiceps dissected free of the diverticulum. The dorsal flaps of the segments near the hind end are very much larger than those in the middle or anterior end.

gut with the dorsal flaps. This is supported by the observation of Mathew (1956) on H. scaber that these structures are filled only with haemolymph spaces.

Laurie suggests, as does Vachon by implication, that the function of the dorsal flaps is that of absorbing nutriment for the embryo. Both Thorell and Mathew maintain that the function is more probably that of respiration, the latter arguing that the dorsal flaps could not be for the uptake of nourishment since it has already been shown that this is the function of the biberon. Although such an argument is clearly of doubtful validity, it seemed worthwhile attempting to investigate the possibility of both functions, i.e. nutritive and respiratory.

In first instar nymphs the dorsal flaps could not of course be cut off without the animal's bleeding to death. If they were covered with grease, so as to prevent their being used for respiration or uptake of water, the nymphs appeared to live just as well as did the controls. Light green dye in Ringer solution was placed on the dorsal flaps but no absorption of stain occurred.

The embryos, stripped of their diverticula and placed in various vital dyes, took up the stains markedly less over the region of the dorsal flaps, so that there is no suggestion from this and the anatomical observations reported above that the structures are concerned with the absorption of nutrient material from the walls of the diverticula,and it seemed worthwhile considering whether they may not, in the embryo, have a respiratory function. A few preliminary trials using methylene blue as an oxidation-reduction indicator were made. The results of these, indeed, suggested that the "dorsal flaps" might be sites of respiratory exchange, but it was considered that the technique was unsatisfactory and the matter taken no further.

To sum up, the evidence here presented suggests that the biberon is an organ of uptake of nutriment from the mother, that the labral lobes may be, at least in O. latimanus, sites of nymphal food reserves, while there is a probability that the dorsal flaps are organs of respiratory exchange in the embryo, but possibly not in the nymph.

Parturition

There are few reports of the birth of scorpions and those which do exist are not detailed to any extent. The difficulties, very like those which arise in trying to observe the mating of scorpions, stem from the fact that the events occur beneath the animal. Moreover it is clearly undesirable to disturb the animals by moving them to a more convenient observation site. Lastly the event can not yet be triggered off by the investigator - a possibility which certainly exists in the case of the mating behaviour.

An attempt was made to overcome this difficulty of observation by keeping the pregnant scorpions on almost flat surfaces with covers which could be removed without disturbing the animals much. The events could then be watched at eye-level. In a number of cases this proved partially successful and some details of the parturitions of various scorpions have been observed in this laboratory.

Table III shows the time of year at which the births of different scorpions are said to occur and also the geographical position of the species on which the observations were made. In spite of the limited number of records available, it seems clear from the table that in the temperate regions the births of scorpions tend to occur during either mid- or late summer, while those in the tropics occur either over a great number of months or the whole year.

The tendency to give birth or breed in summer is common amongst the birds and here also it has been pointed out (Baker, 1938) that tropical species tend to lack a definite breeding season. In some birds at least it has been shown that day-length plays a considerable part in the determination of the onset of the breeding season, but so far the point has not been investigated at all in the scorpions.

As regards the time of day at which scorpion births occur, opinion seems divided. Earlier workers (e.g. Fabre, 1923 and Schultze 1927) supposed birth to occur only at night. In fact, Schultze implies that if the parturition cannot be completed during a single night, no further births will occur until it is once more night time. In the different scorpions which I have observed births appeared to begin at almost any hour of the day or night. It seems improbable that the event is triggered off by a light change since some parturitions began during pitch dark while several started shortly after noon. No information is available about the possible effects of temperature variations, as this factor was uncontrollable.

Parturition has been observed in five species of scorpion; in some cases only one birth was seen, in others several. The animals concerned are *Parabuthus planicauda*, *Uroplectes triangulifer*, *Opisthophthalmus latimanus*, *Opisthacanthus validus*, and a second unidentified species of *Opisthacanthus*. Since a description of the course of events in *P. planicauda* covers almost all points relevant to the other scorpions, this will be discussed first.

Parabuthus planicauda parturition.

The birth of the first baby of a brood was never seen, in *P. planicauda* and in the case of the parturition to be recorded here, about a dozen young were already free of their embryonic membranes before it was realised what was happening. The mother had raised her body slightly in front, but there was no suggestion of a "stilted" posture (see p.57). The pectines were touching the ground but were certainly not acting as "braces" as suggested for *Heterometrus longimanus* by Schultze (1927).

The young, about 1 cm. long in their transparent membranes, came out either tail-end or head-end first, the former seeming to take less time for emergence - 3 to 7 minutes as compared with 15 to 25 minutes. The young were born singly and though in the main all of the progeny are forced forward from the genital opening, alternate babies are pushed out to left and right. They lie inert for a short time, generally about five minutes; then pulsations begin in the anterior part of each embryo and shortly afterwards the chelicerae

TABLE III.

Times of Parturition in Different Species of Scorpion.

Season	Time of parturition			Authority
	Animal	Place	Time	
Mid-summer	*Mesobuthus eupeus* (Koch)	Tbilissi, U.S.S.R.	15th July - 15th August	Kobakhidze (1950)
Summer	*B. occitanus*	Provence, France	15th July -	Fabre (1923)
Later summer	"Spanish scorpion"	Spain	September	Dufour (1856)
Late summer	*Euscorpius italicus*	Italy	Late August	Cloudsley-Thompson (1951)
Summer	*Centruroides vittatus*	Arkansas, U.S.A.	September	Smith (1927)
All summer	*C. insulans*	Jamaica, B.W.I.	December-June	Baerg (1954a)
All summer or year	*Leiurus quinquestriatus*	Khartoum, Egypt	April, September, October	Thornton (1956)
Summer seasons	*Palamnaeus Longimanus*	Philippines	July	Schultze (1927)
All seasons	*Heterometrus scaber*	Trivandrum, S.W.India	All year	Mathew (1956)
All seasons	*Tityus trinitatus*	W. Indies	All year	Waterman (1950)
Summer	*Opisthophthalmus latimanus*	Grahamstown, S.Africa	February - March	Personal observation
Summer	*Parabuthus planicauda*	"	January - February	"
Summer	*Opisthophthalmus nitidiceps*	"	January - early February	"
Summer	*Uroplectes triangulifer*	"	Late December	"
Summer	*Opisthacanthus validus*	"	February - March	"
Summer	*Opisthacanthus* sp.	"	March	"
Late Summer	*Urodacus abruptus*	S.Australia	March	Southcott. Private communication

begin alternate movements. Almost imperceptibly the embryonic membrane is pushed back, with little apparent movement on the part of the nymph and certainly no help from the mother.

It may be noted at this point that Fabre (1923) states that, in Buthus occitanus, the mother tears open the embryonic membranes herself; Waterman (1950) reports the same thing in Tityus trinitatis. Cloudsley-Thompson (1955) regards this as an "unlikely hypothesis" and quotes several accounts in "refutation" of it, i.e. Mingaud (1905) Serfatty & Vachon (1950) and a Mr. E.A. Robins. In spite of this it seems that different behaviour may well occur in different species: maternal help when the young emerge from the chorion may occur only where the number of young per brood is small. In T. trinitatis, Waterman says that there are 28 young while Fabre records that in B. occitanus there are 30 - 40 embryos - though it must be remembered that the number which are born are often fewer than the number of embryos present earlier. Where an animal may have as many as 105 young, as had a specimen of Centruroides insulans reported by Baerg (1954a), elaborate development of maternal care at birth would certainly be surprising.

It is unclear what acts as the stimulus to start the young Parabuthus breaking out of the membranes. There appears to be no maternal action which could have this function, though it is possible that they may be activated by being slowly pushed along the ground by embryos emerging later. By the time the last few are coming out, there is general movement both from the young trying to climb up on to the mother and the mother herself as the nymphs become entangled in her legs. No attempt was made to isolate any newly emerged babies from all movement, for feat of disturbing the mother.

As was mentioned earlier, the young P. planicauda are pushed slightly forward by the subsequent births and at the stage when only the nymph's tail remains enveloped in the embryonic membrane, the little animal is usually just in front of the mother's mouth (Fig. 27). Here a pile of shed membranes accumulates and as each fresh baby passes the pile, its membrane sticks to that of the others; thus the young scorpion tears itself free of the last attachments. In two parturitions that were observed an object resembling an unfertilised egg lay at the bottom of the pile and may well have served as the initial attachment to the ground.

All the newly freed scorpions move slowly forward; if they attempt to go too far, the mother herds them back gently with her pedipalps. Those babies which were initially pushed out to the right usually pass round under the right pedipalp and clamber up the first and second legs of the mother's right side while the others go up the left side. Sometimes however a muddle has occurred at the "chorion-pile" and a whole group will go one way. This path of ascent of the mother appears to be very stereotyped and young which start out on the wrong path soon turn round and join the others. It may well be that the "wrong" paths are in fact more difficult than the "correct" one, but it should be noted in passing that there can be an adaptive significance in the distinction. The shorter, and to our eyes the more obvious, course is that up the anterior end of the mother, either by clinging on to the hairs of the pedipalp bases or directly up the chelicerae. Normally if the adult animal is stimulated lightly in these regions a feeding reaction is elicited; when the scorpions are being "persuaded" to eat dead food, the material is normally touched gently against these areas. It seems possible that this shorter path, which the young <u>P. planicauda</u> avoid, would often prove fatal if used. Support for this hypothesis comes from the fact that on two occasions when a young scorpion was held up against the mother in such a position, it <u>was</u> eaten.

Within half an hour after the last baby had emerged from the mother, the whole brood of 50-60 young is up on her back (Plate III).

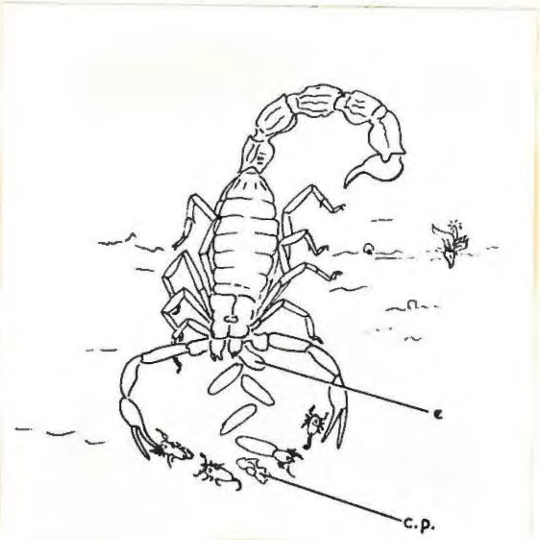


Fig. 27. Representation of *P. planicauda* during parturition. Young, still within their chorions, are immediately in front of the mother's chelicerae, *e.*, while those which have passed the chorion pile, *c.p.* are beginning to circle round to mount on to the mother's back.

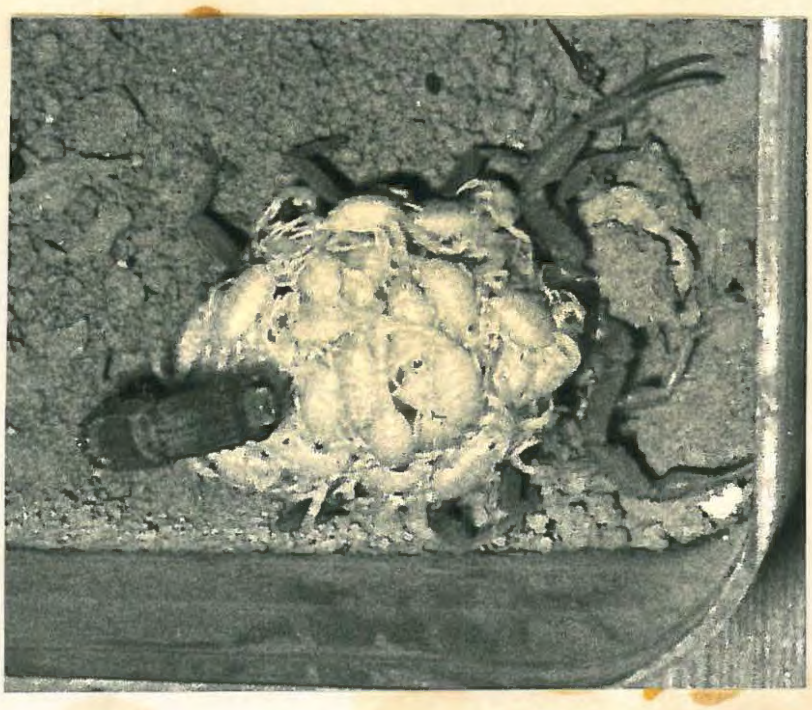


Plate III. Female P. planicauda with her 57 newly born young on her back. There is no indication of an orientation of the nymphs. (cf. Plates IV, IVa and IVb).

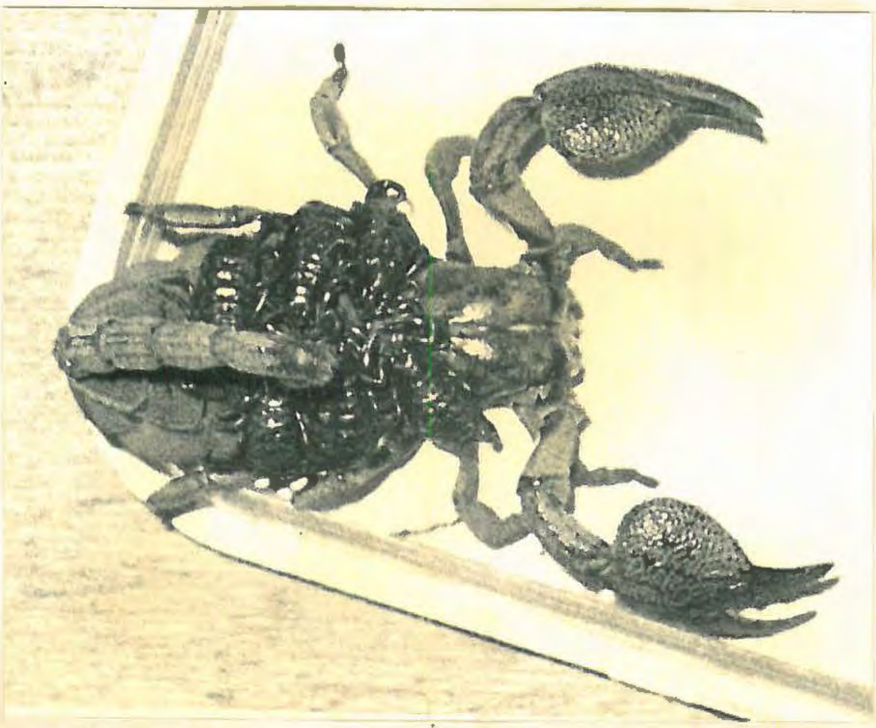


Plate IV. Female O. latimanus with her young upon her back. The nymphs are orientated with their bodies at right angles to that of their mother's and their heads are towards her midline.

Plate IVa. Orientation of young of Cheloctonus anthracinus Poc. on their mother's back. Here the bodies of the young are parallel with that of parent. (From a photograph lent by Dr. R.F. Lawrence).

Plate IVb. Female of Opisthacanthus validus and newly born young. Here the orientation is very like that in C. anthracinus, possibly associated with the fact that the two genera are closely related, possibly with the shallow shelters under which they live.

Parturition in O. latimanus

About a dozen O. latimanus females have given birth to their young in the laboratory and a number of these parturitions have been watched, in part at least. The stance adopted during the event, like that in P. planicauda, is characteristic of scorpion birth.

The young take even longer to emerge than do those of P. planicauda and the whole process, the birth of 10-20 young, may extend over a period of four days. In all the cases observed here, the young emerged tail first and in fact it is difficult to see from an examination of almost fully developed foetuses how it could be otherwise (see Fig. 28). They are not enveloped in a chorion.

There is no elaborate organisation of the behaviour of the emerging young as there is in P. planicauda; in O. latimanus the nymphs may crawl between the mother's front legs and mount on to her back; they may come out on to her side between the legs or they may remain clinging on to the ventral surface of the prosoma for some hours. It may be noted here that in Opisthacanthus validus and in a larger and undertermined species of the same genus, the young remain attached to the undersurface of the mother and only a few come on to her back after several days.

The fact that in one species the young climb quickly on to the mother's back, while in another they do not, deserves some attempt at analysis and it seems possible that it may be dependent on the behaviour of the mother scorpion after parturition.

In the case of the apoikogenic-type scorpion the mother may eat unfertilised eggs which may be voided before or after parturition and may also eat the coverings shed by the young (Fabre, 1923 and personal observation of Uroplectes triangulifer and P. planicauda). This seems biologically reasonable as this material would have been wasted otherwise. In the case of katoikogenic-type scorpions there is no reason why eating patterns should be associated with parturition since there are neither unfertilised eggs nor chorions to be disposed

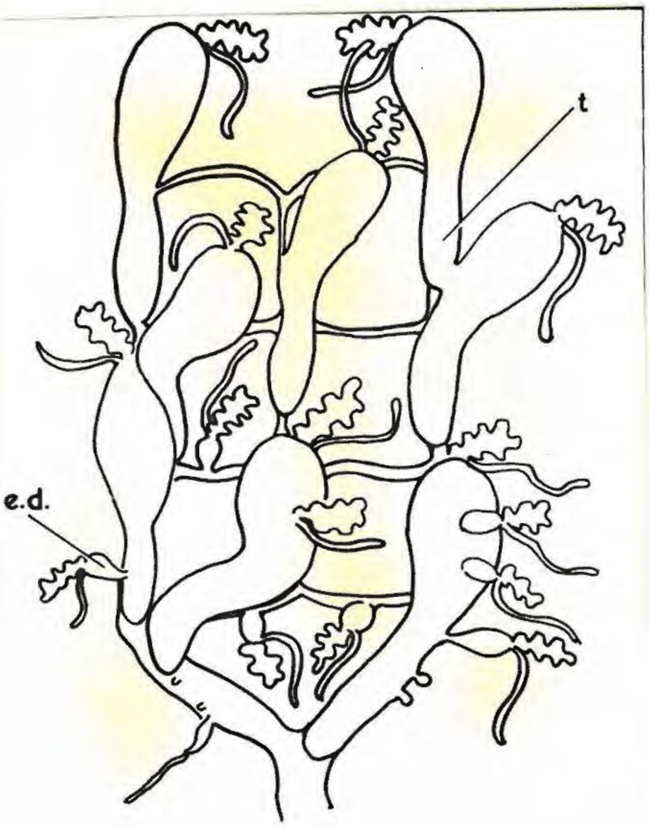


Fig. 28. Representation of the ovariuterus of O. latimanus after the birth of six of her young. The biberons and labral lobes can be seen left on the empty diverticula, e.d. From this figure it is evident how the young extend into the tubules of the ovariuterus so that their tails, t., may lie side by side before parturition.

of. It is true that kat~~io~~oikogenic-type scorpions have also been known to eat young which fail to reach the mother's back but this seems rare and may well be associated with food deprivation of the mother, as suggested by Baerg (1954).

The second point is that in apoikogenic-type scorpions the eating of unfertilised eggs may often be followed by an attack on those young which have not fully emerged from their chorions and even nymphs which were entirely free but had not yet reached their mother's back. Such a case of infanticide did in fact occur with the female Uroplectes triangulifer mentioned above.

It may thus be assumed that in dealing with normal scorpion parturitions there is more danger of the apoikogenic-type young being eaten by the mother than the katoikogenic-type young. If this is true it gives some adaptive significance to the difference in behaviour of the young O. latimanus and P. planicauda, for in the former case it is less important that the young should reach the mother's back and be away from her chelicerae than in the latter.

How the difference is actually achieved is unclear. Scorpionid young, perhaps due to their more elaborate foetal nutritional system, are very fat and rather inactive, whilst buthid nymphs are smaller and, though almost as fat, appear to be much more active.

The Nymphs.

The nymphs, when they are born, are, as Schultze (1927) described the new-born young of Heterometrus longimanus, "extremely sluggish, plump and fat looking" and those of O. latimanus are of a purplish-black colour, very different from the brown of the adult. The body is very large relative to the limbs and tail (Fig. 24). As mentioned earlier a prominent labral lobe protrudes between the chelicerae, which still bear the hardened yellowish patch concerned with holding the biberon.

A further characteristic of the early nymphs was noticed in this way. A mother scorpion with the second instar nymphs (SIBs) on her back was picked up by the tail, the normal way of holding adults. Not one of the babies fell off. A mother with her first instar nymphs (FIBs) was treated in the same manner and none of the offspring remained on her back. When the feet of the FIBs and SIBs are compared, the reason for this difference is apparent. Those of the SIBs have a pair of claws ending each foot, as has the adult. In the first instar, however, a tough membrane is stretched over the tip of the foot and no claws are visible (Fig. 24). The body of a FIB lacks the hairiness of that of an older animal, but the membrane covering the tips of the feet has many small bristles instead of being naked. Vachon (1949) writes of the "absence de griffes aux pattes ambulatoires et, en lieu et en place, l'existence d'un organe adhesif rappelant les ventouses pedieuses des pulli de Thelyphonides." He gives a diagram of the end of the foot of Parabuthus capensis, from which it appears that the structure could function as an adhesive organ. However, in O. latimanus it does not appear to play such a rôle.

Relations with the Parent.

It has so far been assumed that the nymphs should be on the back of their mother. This behavioural trait has been observed and recorded many times for many different species of scorpion (Vachon, 1949). O. latimanus does, however, show three features which are not generally recognised.

Firstly the extreme flatness of the mother's back may be noticed during this time. Drawings tend to minimise the difference between the thickness of the mesosoma of a female that is carrying babies and that of a non-reproductive female, and this difference is difficult to measure. Nevertheless it is very obvious. Teleologically this flatness provides the young with a better chance of security on their mother's back. In practice this may be true, but it seems probable that it is due merely to the uterus having been recently emptied of its load. Even before the young start their first moult, this shape, characteristic of a mother with FIBs, has begun to change. By the time the SIBs are a month or two old, the female is almost back to her normal proportions.

Secondly, when an O. latimanus has FIBs on her back, the spacial regularity with which they are arranged may easily be seen (Plate IV). The babies all lie with their long axis at right angles to that of their mother, their heads to her midline, and their tails nearest the base of her legs. A baby may climb into the wrong position but will soon orient so that it lies as do the others. The older animals do not adhere so strictly to this orientation. Whether the arrangement is of some particular significance where the FIBs are concerned is unclear. It is however possible that the ordering might have some value to the mother in terms of "feed-back stimuli" (Hinde, 1954) or protective value to the young as the mother moves about. Again it is unclear whether the subsequent loss of orientation is purely mechanical, due to the increased size of the older animals and increased slope of the mother's back making such a simple arrangement impossible, or due to a direct behavioural change, independent of change in form. Certainly if a single SIB is allowed to climb on to the back of a mother that already has FIBs on her, this SIB is conspicuously without orientation relative to the other babies.

The last point of interest about O. latimanus carrying her babies concerns the way in which they reach her back. In the main, reports, if they give any indication at all of how the young get on to the mother's back, state simply that the babies climb up, (Mingaud 1905; Schultze 1927; Vachon 1949; Waterman 1950; Cloudsley-Thompson 1951). In O. latimanus it is true that the babies will climb up on their own, usually quite effectively. They do this by way of the mother's legs, pedipalps or chelicerae. There are, however, three records of scorpion mothers that are more solicitous for the welfare of their young. Fabre (1923) describes how a mother Buthus occitanus rakes the sand

and young scorpions towards her with her claws, while earlier she holds her claw flat on the ground to facilitate the babies' first ascent. Smith (1927) speaking of the young of Centruroides vittatus, says "they were assisted by the mother in getting on her back." Lastly Glauert (1924) writes of the babies on the back of Urodacus novae-hollandiae that "should one fall off it is replaced by the mother who lifts it carefully with her claws if it is unable to find its way back unaided." Whether the young O. latimanus can climb up alone or not, the mother makes violent efforts to assist each one of her babies on to her back. She will turn round to a baby moving about on the ground behind her, take it in her claws and pull it towards her mouth as if she were about to eat it (Plate V). She then drops it and encloses it in her pedipalps, diminishing the circle so that the baby is pushed on to the chelicerae or pedipalps. Occasionally a mother will lift her baby further so that she almost puts it on her own back. Normally the baby will climb up from the circle of the mother's "arms" on the chelicerae or pedipalps and thence on to her back. Although the initial movements of this "picking-up-the-baby" are the same as those of feeding, namely clasping with the claws and drawing in towards the mouth, they should not be confused with the feeding movements. In feeding, as the prey is caught, the chelicerae begin their alternate clutching movements and these characterise all preliminaries to the actual eating. Even when the claws are actively rejecting the food, the chelicerae may still be reaching for it. In picking up the young there is, however, no sign whatever of any movement on the part of the chelicerae. The claws appear to close gently and never as fully as they might, considering the softness of the tissue of the young.

Not only do the feeding and picking-up-the-baby responses seem very alike in their initial stages, but the stimulus field to which the scorpion responds appears very similar. An initial part

Plate V. *O. latimanus* female gathering her young to her with her pedipalps.

of both responses is towards a moving object. The baby may keep still after the first movement which has attracted the mother's attention and started her picking-up response. If this immobility lasts for a long time, more than 90-120 seconds, the mother may begin to walk away. If the baby starts to move at this point, the mother will immediately turn round and pick it up. Otherwise she will leave it until, when she comes across it later, it moves.

Usually the young SIBs climb up unaided. The mother may make several rather disorganised clasping movements which seem to indicate her intention of picking-up the baby. The young, more active by this time, evade their parent and it would appear that the SIBs are too quick for her. In addition to this factor, her "decreased interest" in them prevents her picking them up. This hypothesis is partly borne out by the following observations:

If a young SIB is given to a FIB mother she will catch, it, pull it to her and it will mount upon her back. This whole event takes less time than with one of her own FIBs. Give the FIBs to a SIB mother and she will pick them up with only slightly less efficiency than does their own mother. This information can be tabulated thus:-

	FIB	SIB
<u>FIB mother</u>	Pick-up very quick, baby clumsy	Pick-up very quick baby agile.
<u>SIB mother</u>	Pick-up fairly quick, baby clumsy	No real pick-up, baby climbs up.

From this table two ideas emerge. Firstly, the younger baby offers more "pick-up releaser" to the female. Secondly, as her babies grow older, the pick-up response of the mother scorpion develops a higher threshold. If young scorpions, even FIBs, are given to a mother whose babies have already deserted her, no effective response can be elicited from her at all. She will wave her claws in a way rather suggestive of picking-up but does not even take hold of a baby.

Relations between Parents and Young of Different Species.

O. nitidiceps is a scorpion which is superficially very similar to O. latimanus. The former animal has never been captured with FIBs, but interchange of babies was tried nevertheless. FIBs of O. latimanus were put before an O. nitidiceps whose SIBs had just begun to leave her. She did not eat the strange babies but lifted and dropped her claws several times, stretching towards a baby but never opening the claws and taking it. The baby appear to have no doubt that this O. nitidiceps was "mother". It walked straight to her, between her hesitating claws, climbed on to the base of her pedipalps and thence on to her back. Repeated trials gave the same result. From this a number of further conclusions may be drawn. Firstly the baby, though it was of a different species, was giving some sort of "I-am-not-food" sign stimulus to the female and from the fact that her own young had already begun to leave her, it might be suspected that O. nitidiceps does pick-up her young but that, in this particular case, the threshold of the response was just too high for the releasing stimuli. This female showed no signs whatever of picking-up her own brood but the threshold was not sufficiently high to allow her to ignore completely a very young baby. Secondly it is clear from the babies' behaviour that neither the strange colour - O. nitidiceps is yellow and brown compared with the dark brown to black of O. latimanus - nor the rather different shape resulted in a lack of parental sign stimuli for the baby O. latimanus. This yellow scorpion was "home" and once on the back, the baby would not leave though the surface was more curved than that of its own mother.

Since the only O. nitidiceps babies that were obtained were ones which had already begun to leave their mother, it is hardly surprising that they should not react favourably to the "mother" situation presented by an *O. latimanus* female grasping towards them. When the *O. latimanus* FIB mother managed to grab one of the *O. nitidiceps* SIBs, it tried to sting her. The *O. latimanus* SIB mother did not even succeed in catching one of the *O. nitidiceps* young, another indication that her response threshold was higher than that of the mother with younger babies.

Unfortunately the behaviour of a male *O. latimanus* towards the young of his own species was observed on one occasion only. Males have not been found in the same burrows as the females when there are young present, so that there appears to be no necessity for the male to have behaviour patterns which would prevent his catching and eating one of his own young. This, together with the numerous reports of scorpion cannibalism, make the baby : male encounter rather surprising. The male did not eat the baby scorpion that was put with him, though the two animals were left together for two hours in a small dish. It is true that the male was once seen to catch the baby in his claws, his chelicerae working in the normal way preparatory to eating. Suddenly he discarded the little animal and walked off. No apparent reason could be seen for this behaviour, but the violence of the discarding movements suggested that they did not merely betoken that the male had decided that he was not hungry after all. This observation hints of some behavioural avoidance of cannibalism, a phenomenon which will arise again in connection with female : female encounters (p.163). At the moment, however, this is merely an indication that there may be something of interest in this line and that the observation is worth checking.

Analysis of Behavioural Relations between Parents and Young.

It is profitable at this point to return to a consideration of the mother's pick-up-the-baby response. The striking characteristic is that while the baby may be taken in the claws, it is not eaten. Various explanations of this phenomenon can be offered. On the one hand, the young scorpion may have certain characteristics in form, smell or behaviour which act as specific "releasers" of the maternal behaviour. On the other, the behavioural responses of the mother following parturition may be modified so that no object will "release" a feeding response - i.e. the "pick-up-the-baby" pattern has temporarily replaced the feeding pattern. It may be noticed that these two explanations are by no means mutually exclusive.

The second possibility will be considered first. Two observations have been made which might appear to support this thesis. Firstly, during the time that the mother scorpion has FIBs she is rather inactive and, though she eats pieces of cricket when these are given to her, she will not catch prey for herself. This is considered as inconclusive for two reasons: it is an observation on a single animal and, even when they are in a non-reproductive condition scorpions may allow a cricket or beetle to roam around for weeks without attacking or eating it.

The second observation which might be taken to support the inhibition of feeding pattern concerns an observation of what appeared to be "displacement activity" on the part of a mother scorpion. This animal had a single SIB on her back and another that was beginning to desert her. She had already stopped actually picking-up the SIBs, but at times still made vague clutching movements in their direction. This mother caught and began to eat a fairly large cricket. Continually throughout her meal the one baby wandered about her and, with her claws and chelicerae occupied, the mother made no attempt to pick-up or hurt it. Three times, however, she began what was clearly the behavioural pattern for digging. She scraped with her first legs, then moved backwards, hauling the loosened substrate with her first and second legs. Then she walked forward into the place that she had cleared. It may well be considered that there was a conflict of two drives in the mother scorpion. The maternal drive had not quite disappeared and the feeding drive was being actively stimulated. It is under such conditions that displacement activity might be expected to occur. Tinbergen (1950) quotes various cases following along these lines amongst the vertebrates, while Gordon (1955) has reported displacement eating in the crab, Uca. Whether this interpretation of the behaviour is correct further observation alone can tell. It could be postulated that digging is a normal functional activity at this stage, concerned with recalling to the nest those young which have already begun to excavate independent burrows from the walls of their mother's home. (p. 104). This particular scorpion was on saw-dust instead of soil and, though other scorpions have fed on this without showing digging patterns, the strange substrate might have affected her feeding in some way. Even if the observed behaviour can be interpreted as nothing but displacement activity, its occurrence cannot fully support the hypothesis of an inhibition of a maternal feeding pattern. Displacement activity could be explained quite as easily in terms of the specific releaser hypothesis. Clearly neither of the above arguments carry much conviction in their support of the idea of an inhibition of the feeding pattern.

In considering the first possibility it is necessary to recognise that maternal behaviour may have two expressions, possibly only quantitatively different. The first is the response where the young scorpion is picked up and gathered in towards the mouth so that it may climb upon the back. This is the full maternal response. The second is a simpler response which speaks strongly in favour of some specific sign stimuli associated with the young. If a female scorpion has caught a cricket and this subsequently escapes, she will start to hunt, with outstretched claws for the escaped prey. She may catch up a passing SIB in her claws but will quickly release it, apparently "recognising" it as "non-food". When she is feeding and the young ones scramble around trying to get at the food, she may slowly and gently push them away from the area around her mouth. This behaviour is quite distinct from the quick clutch at an interfering insect or withdrawal from some larger intruder; this behaviour supports strongly the first thesis suggested above. Additional evidence also weighs in its favour. Schultze

(1927) remarks of Heterometrus longimanus that the mother "invariably noticed the difference between an insect or other strange object touching her and the contact of her own young." In O. latimanus I have frequently noticed that a mother will pay no attention as the older SIBs climb amongst her legs, up on to her back and across her. A strange insect, even if it be as small as a soldier termite, will be interfered with immediately. The scorpion will kick violently if it tries to climb on to her from behind, and, if it is put on her back amongst the babies, she will try to scrape it off with a leg. So it would appear that the mother is both able to distinguish young scorpions from other arthropods when they are directly ahead of her and might be taken as food; and also small arthropods from her young when they move among her appendages.

The second piece of additional evidence for the presence of a specific releaser has already been mentioned on page 93 . When FIBs and SIBs are offered to the same female, the FIBs are the more effective in eliciting the complete "pick-up-the-baby" response than are the SIBs, i.e. some of the effect, at least, lies in the baby and not in the mother. The exact nature of the sign stimuli provided by the young scorpions to the mother is not known. From the observations on Palamnaeus and Opisthophthalmus on the mother's back, it is possible that there are general non-visual sign stimuli which indicate "I am a baby and not to be eaten." There may be a specific sign which says "The disturbance on your back or legs is only a baby" but it seems probable that there is one signal serving for both messages under different conditions. It may be that the specific nature of the signal which says "I am a baby, pick me up" can be gathered from the morphological or behavioural differences between FIBs and SIBs. However there are obviously a number of behavioural problems here and a separate investigation, exploiting models, etc. is necessary to make any really satisfactory contribution in this field.

Baerg (1954a) reports a case in Centruroides insulans and Southcott (private communication) mentions another in Urodacus abruptus, where the mother scorpion ate her young. It seems possible that here some aspect of the releaser stimuli given out to the mother went wrong. Baerg suggests that cases of such infanticide occur when the mother is starving and it may well be that such circumstances might aggravate any already abnormal condition. However it seems possible that the root of the trouble might well have been that the babies did not give the correct releasers to their mothers. Perhaps the temperature was too high and the young therefore moved too fast or the relative humidity was abnormally low and that their colour and smell was therefore too faint or too strong.

Finally there is the opposite question of recognition of the mother by the young scorpion. Cloudsley-Thompson (1951) suggested, from some observations on Euscorpius italicus, that a thigmokinetic sense might be employed in the reaction of clinging to the parent's back. Such an unspecific response could easily be adequate if either one or both of two things occurred: either the mother scorpion could stay in the burrow or shelter until the babies had left her back, or she could develop a specific "picking-up" response as has been done in O. latimanus and the animals of Fabre, Smith and Glauert.

Moulting.

Moulting seems to be a general arthropod characteristic and presumably occurs in all the arachnids. Certainly it has been recorded in scorpions, pseudoscorpions, spiders, pedipalpi, opilionids, solifugids, limulids and acarines. It is uncertain whether these animals, the arachnids, continue to moult after they have reached maturity, as do the Crustacea and the Onychophora, or whether, as inthe majority of Insecta, moulting ceases. Shuster (1953) maintains that in Limulus the latter case holds, and says that here the animal stops moulting when it reaches adulthood. From the great variation in size of the adults of *O.latimanus* (i.e. females with developing embryos) it would certainly seem surprising if they were to grow no further once they became mature. As yet, however, there is no observation that a freshly moulted female had previously produced young.

Time of moulting.

The first instar nymphs are certainly found only during a couple of months in the middle of summer and by the end of February all have moulted once. At any time during the rest of the year any one of the nymphal stages (except the first) may be collected from the field. This means that there is no possibility of the state of affairs that Schultze (1927) describes for *Heterometrus longimanus* occurring here. In this scorpion Schultze raised the animals from first instar to adult within thirteen or fourteen months so that there was an interval of about two months between moults. From the observations of the variety of nymphal instars available in the field at any one time, only two conclusions can be drawn: either the nymphs are being born throughout the year or *O. latimanus* moults but once a year. As has been said earlier, there is evidence against the first of these, so that the second must be accepted for the present.

Support for this conclusion comes from the fact that fresh exuvia are found in the field only during December, January and February. Furthermore, second instar nymphs, that had their first moult in the laboratory at the beginning of 1956, had shown no signs of moulting by December of that year. Similarly a nymph of a later instar has been kept for at least six months without undergoing any moult. It is just possible that the conditions in the laboratory might in some way inhibit the normal moulting of the scorpions. This however seems highly unlikely as *Uroplectes triangulifer* has been observed to moult twice within a month during its stay in the laboratory.

The length of time between birth and the first moult in various scorpions has already been discussed (p. 81). As Cloudsley-Thompson (1955b) and many earlier workers suggest, the duration of any intermoult may depend very much upon the season and certainly upon the temperature at which the animals are living. Since the FIBs do not feed at all, they seem to be ideal material for the observation of the relationship of intermoult length, temperature and light. No study has been made of this owing to lack of facilities in the present laboratory.

First Moult.

Fabre (1923) says that the first moult is different from all subsequent ones in that it is "sans ordre" and that "en lambeaux, la cuticle eclatant de toutes parts". Schultze (1927) refutes this assertion of Fabre's. In the case of O. latimanus the manner of the first moult is similar to that described by Schultze and the skin splits at one place only - around the anterior edge of the carapace - coming off in a single piece. Only the skin of the pedipalps is turned inside out to any degree, the animal slowly expanding out of the rest. The casts are very light and transparent and can easily be mounted on a slide by gently expanding them on a water surface and slipping the slide under them. Before this is done they do indeed look as if they might be ragged and it is doubtless this appearance that led Fabre to his conclusion. Once on the slide, the labral lobe, the dorsal flaps and the rounded coverings of the feet can be easily seen.

The shedding of the first skin takes about two hours, and in O. latimanus is certainly achieved without the aid of the mother. At this stage the FIBs do seem to be firmly stuck on to their mother's back by their feet. Once the event is over the whole cast is easily freed from the mother's back. From this it would seem possible that, in O. latimanus anyway, the main and perhaps only real use of the "adhesive" organ on each foot of a FIB is during the actual moult. One FIB was wrenched free in midmoult and this animal did not complete its moult. It may thus be that adhesion to the mother is necessary during the first moult and that the form of the feet in the first instar is therefore of vital importance. However it must be remembered that there is no evidence on this point and that the FIB mentioned above may merely have died coincidentally or due to injury through being pulled off its mother. Nevertheless it is during this first moult, that is the only moult when a number of young are together with a larger animal, that the scorpions are in most danger of being trodden on by siblings or parent. Whether it is mechanically possible to moult without being firmly attached to some surface or not, it is certainly true that it would be safer for the moulting young to remain out of the mother's way, and on her back. Without especially considering the dangers of being trodden on by a parent, Heegard (1945) says "the ecdysis in itself is a most critical period in the life of the arthropods, in which the continued life of the animal is at risk".

The Mechanism of Moulting in Scorpions.

Since a whole brood of FIBs always moulted within a few hours, it seemed reasonable to try and find out something of the mechanism of scorpion moulting, using this material. It is known that many insects swallow air shortly before moulting and that this in some way facilitates the actual splitting of the skin. ~~(see review by Wigglesworth, 1954)~~. It was decided to check whether the same sort of thing occurred in the scorpions.

Animals at different stages of the moult sequence were dissected under a light machine oil and a rough estimation made of the amount of gas found in the gut. Recently born FIBs were found to have almost no gas at all and the same held for FIBs in broods which were not anywhere near moulting. FIBs dissected in the middle of moulting or taken from broods in which some animals had already begun to moult, invariably had a large amount of gas in the gut. This supports the idea that scorpions use air in some way to assist in splitting the old cuticle.

Immediately after the moult the body of a new SIB seems "blown up"; so much so that the claws of the pedipalps remain wide open and for some time cannot be closed effectively to a stimulus. Animals in this state still have considerable amounts of gas in their guts. About 25 minutes after the final liberation from the exuvium the appearance of a SIB starts to change in so far as the swollen appearance begins to disappear and the claws gradually close, remaining so except when stimulated. The gas content of SIBs whose claws have closed is very markedly less than when the claws were open or during the moult itself. From this it appears possible that the gas contained in the gut is also used in increasing the internal pressure to stretch the new exoskeleton and that the muscles closing the pedipalp claw are unable to overcome this resistance.

Attempts were made to discover exactly how and when this gas is lost after a moult. SIBs were placed under oil, either immediately after they had freed themselves from their skins or ten minutes later; the air bubbles were cleared away from mouth and anus and the animals were observed over a period of one hour, during which the controls lost their swollen appearance. Except in one case there was no sign of either air bubbles appearing or of the swollen appearance disappearing. In the single case a few bubbles of gas appeared at the mouth opening, while one also emerged from the anus. The widely open claws did not close significantly during this apparent liberation of gas. Thus, although it seems possible that the air is lost by way of the scorpion's mouth, there is no proof of this; nor have we any idea about how the gas is taken into the gut of the FIB in the first instance.

Although the above observations do not by any means show that gas in the scorpion gut is used in splitting the old skin and expanding the new soft one, they do to some extent support the hypothesis.

Second Intermoult and Maturation.

For the first few weeks after the initial moult, O. latimanus SIBs stay firmly on the back of the mother, who is still not extremely active in trying to capture prey, although she will accept food when it is offered to her. For a few days further they remain on her back or wander about her feet. This apparently corresponds to a stage found in the field where some of the young scorpions are still upon the mother's back while the others are in little side passages around the end of the maternal burrow.

Neither FIBs nor SIBs that are still living on the back of their mother have been observed to catch prey, nor, in fact, could the former be expected to feed since the labral lobe still blocks free passage to the mouth. Once the babies have begun to leave their mother's back, however, even if they may still climb up again for short periods, they will catch and eat food for themselves. In this connection there is what may be seen as a striking example of how a behaviour pattern will emerge at the age at which it is to be used approaches. If termites are offered to the FIBs or those animals that have just moulted for the first time, the scorpions show no reaction. They just ignore the insects completely. In the case of the SIB, about 20 days after the first moult and while still firmly attached to the mother's back, the result is different. The SIB will advance on the termite and stretch out a claw towards the insect. Sometimes it may open and then partly close this claw, sometimes the claw remains closed. The baby then suddenly retreats, turns away and shows no further interest in the "prey". A fortnight later the SIBs will clutch at a moving termite and stuff it into their mouths with almost no hesitation whatever. They have not been seen to try and sting prey but termites do not really warrant stinging in that they struggle very little.

A further point about recognition of food by a SIB is this: if a termite is lying dead or immobile on the ground a SIB will pass it by without turning aside to investigate, but if the termite is held in the claws or mouth of another SIB it is immediately recognised as food though it is apparently just as still as the insect on the ground. It would not seem that it is merely the movement of the other SIB which has attracted the attention of the first, because one SIB will never catch at the waving tip of another's sting or empty claw.

A second behavioural feature which can be seen to develop between the end of the first moult and the second is the intraspecific antagonism between scorpions. Fabre (1923) says that when two scorpions are found beneath the same stone they are either mating or the one is eating the other. This appears rather exaggerated when applied to <u>O. latimanus</u>, although antagonism is still clearly shown. Nevertheless when the young scorpions lie together on the back of their mother, there is no sign of mutual animosity. Once the first SIB has managed to catch prey however, all this is changed. In attempting to wrest the body of a termite from another, a SIB will try vigorously to sting the holder of the booty. Soon, within half an hour, there are signs that it does not even need a sclerite of contention to start a stinging match between SIBs. The SIBs begin burrowing individual holes fairly soon after the first feed and here again the "anti-social" tendency is seen. One particular shelter was the refuge of a number of small scorpions until the first feed. A single SIB returned to this shelter and now held it against all comers. With quivering tail and clutching claws the animal would rush forward and attack any of its erstwhile companions that came within an inch of the shelter.

The smallest animals that have been found in the field in short burrows of their own are slightly heavier than the animals in the laboratory that start to feed and dig, so that it cannot be long before these would, in natural conditions, be ready to live independently of their mother and her burrow.

The Number of Moults.

In scorpions the number of nymphal instars or of moults before a scorpion reaches maturity has as yet only been recorded in one case: Schultze (1927) kept a female Heterometrus longimanus and her brood in the laboratory until part, at least, of the latter had reached maturity. In this case there were seven nymphal instars.

In O. latimanus the subject has been investigated, using only material taken from the field: that is, it was considered impossible to gain the information by watching a complete series of moults in the laboratory for, as was pointed out earlier, the animals moult only once a year. Although only adults were required for most of the studies reported here, numbers of the nymphal stages were collected from the field: these were sexed and their approximate sizes gauged by subjective estimation of the length of the pedipalps. It was found that, except in the preadult instar, there was no significant difference between the two sexes as far as size goes and male and female were considered together.

Laying these animals out in a series of increasing pedipalp length, they could be divided roughly into seven groups, a finding which agreed with seven instars found in H. longimanus. When, however, the pedipalp length was measured objectively with calipers and the results plotted graphically (Fig. 29) it can be seen that the age groups do not in fact stand out as might have been expected from the subjective sorting of the animals. It is true that the instars labelled 3 and 4 in the graph are fairly well defined as clear-cut size groups, but the graph as a whole does not show such a series of marked discontinuities as might have been expected. Thus it is impossible to tell the number of instars merely from an examination of the measurements summarised in Fig. 29. The results could be interpreted as implying that there are either seven or eight preadult instars.

It is therefore necessary to turn from measurements of the population to individual measurements. In a limited number of cases it has proved possible to collect an individual together with the

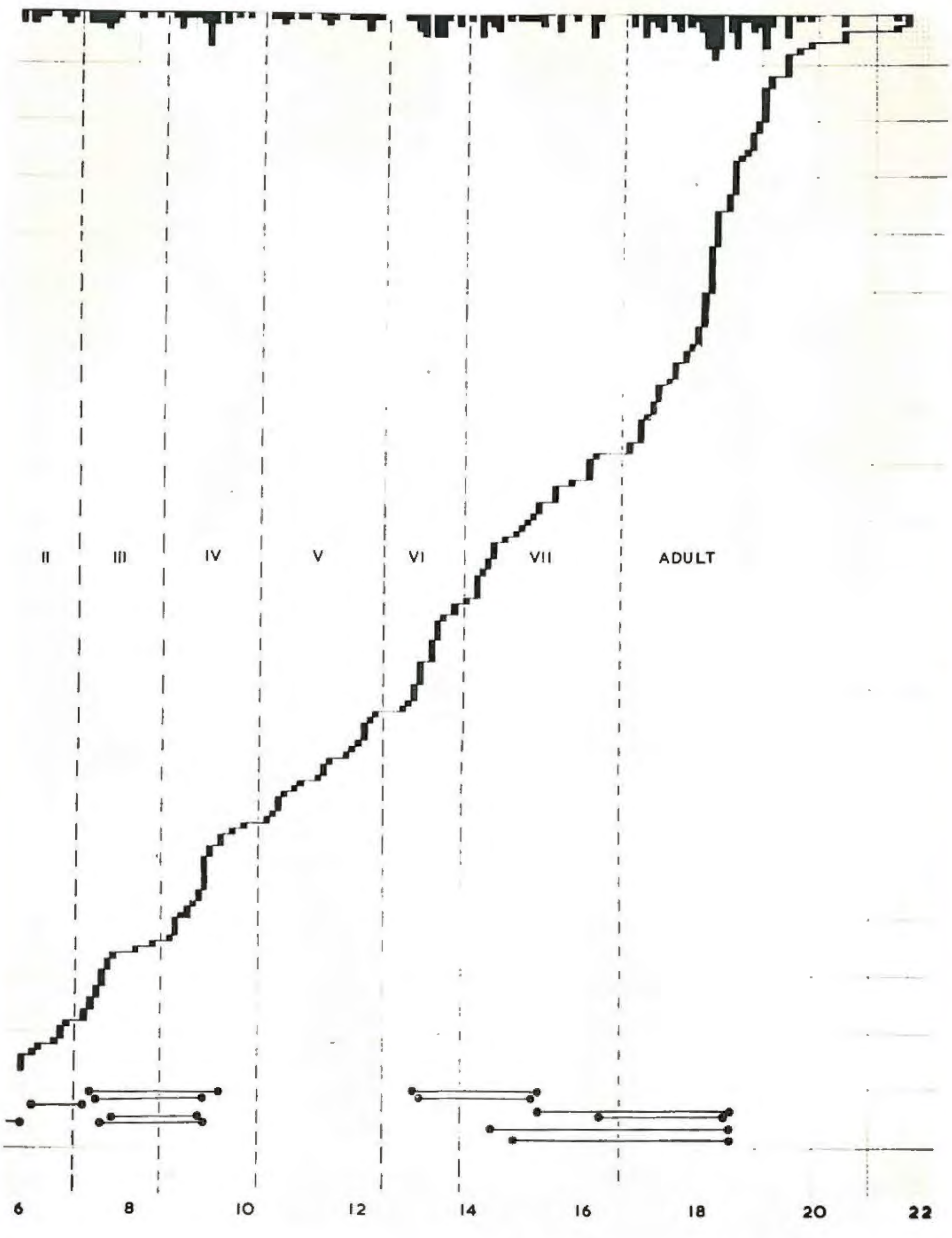


Fig. 29. Range of pedipalp lengths of nymphs and adults of a sample of O. latimanus. Abscissa-pedipalp length in mm. The histogram at the top of the figure shows the distribution of pedipalp lengths, each square denoting one animal, while the curve running diagonally across the figure represents the same information plotted progressively with respect to pedipalp length, so as to emphasise modal lengths. The horizontal lines at the base of the figure join points representing pedipalpar lengths of two successive instars in particular animals. This information has been interpreted to mean that, excluding the FIBs and adults whose status is easily established, there are probably six nymphal instars, II - VII. The divisions between these, in terms of pedipalpar length, are shown by the broken lines which run vertically down the figure.

exuvium of its last moult. Measurements of these give direct information upon the change in size from instar to instar. These data are also shown in Fig. 29. It will be seen that direct measurements are lacking for a period after the fourth instar and that over this period there may, judging by the distribution of pedipalp sizes, be either two or three moults. From the general tendency for the increase in size at each moult to become greater with successive instars, it seems most probable that, as indicated in the figure, there are normally seven instars before maturity.

Two further points warrant comment. It has been pointed out above that clear-cut size groups are limited to the third and fourth instars, but that later the measurements suggest that the variation in size of individuals of the same instar becomes greater. This is indeed what might be expected for increase in size at a moult is likely to be affected by many variables, of which possibly the most important is nutrition. What is striking is that this variation is not eliminated by selection, at least until maturity is reached. This is possibly a reflexion of the great protection which the deep burrows of <u>O. latimanus</u> offer to the individuals, though clearly such an idea requires further study, by the collection of more information on <u>O. latimanus</u> and also on other species which live in more exposed stations.

The second point is that the measurements upon the adults show two small groups of individuals whose pedipalp length is markedly greater than the mode. It is known from dissection of individual females that adults can produce more than one brood of young: this implies that they can survive for more than one year after reaching maturity. It seems possible that the exceptionally large individuals may belong to this category and that their greater size is a reflexion of the fact that moults may occur after the animals are mature. Three of these abnormally large specimens were dissected and in each case evidence of at least two pregnancies were found. However, it is clear that for a definite conclusion upon this point an examination of both the size and reproductive status of a large series of adult females must be made.

The Final Moult.

From the nymphs collected in the field it is quite clear that the sexual dimorphism of the pedipalp, body and tail of O. latimanus arises only during the last moult. In the adult however the sex of an animal is also reflected in the number of pectinal teeth, the shape of the genital operculum and the presence or absence of crochets (Fig. 30a). The shape of the genital operculum appears to become dimorphic during the last moult and though the crochets are sometimes distinguishable on a nymphal male, they are usually well held in by the genital operculum which is not yet freed of the belly. The number of pectinal teeth does, however, seem to be a primary sexual character (Fig. 30b). At the final moult, therefore, only the shape of pedipalps, body, tail and genital operculum change to give the external features of the adult.

Sex Ratios.

It may be remembered that very early in the study it was stated that, amongst adult O. latimanus, females outnumbered males to the extent of 4 : 1. From the dramatic "reports" of a female killing a male immediately after copulation (Fabre, 1923; Thornton, 1956) such a disparity might be easily explained. However, as will be described later, this phenomenon has never been seen in any of the matings observed in the laboratory; if anything, it is usually the male who is somewhat more aggressive. Waterman (1950) remarks of Tityus trinitatis that there is no question of females eating only males, but that any scorpion is likely to eat any other, particularly one smaller or weaker than itself. A last and minor point against the theory of mating with subsequent murder of the male is the fact that Fabre was unable to recognise any external difference between male and female Buthus occitanus and he never witnessed mating.

Montgomery (1903), writing of the predominance of female spiders over males, suggested that this is due to no uxoricide on

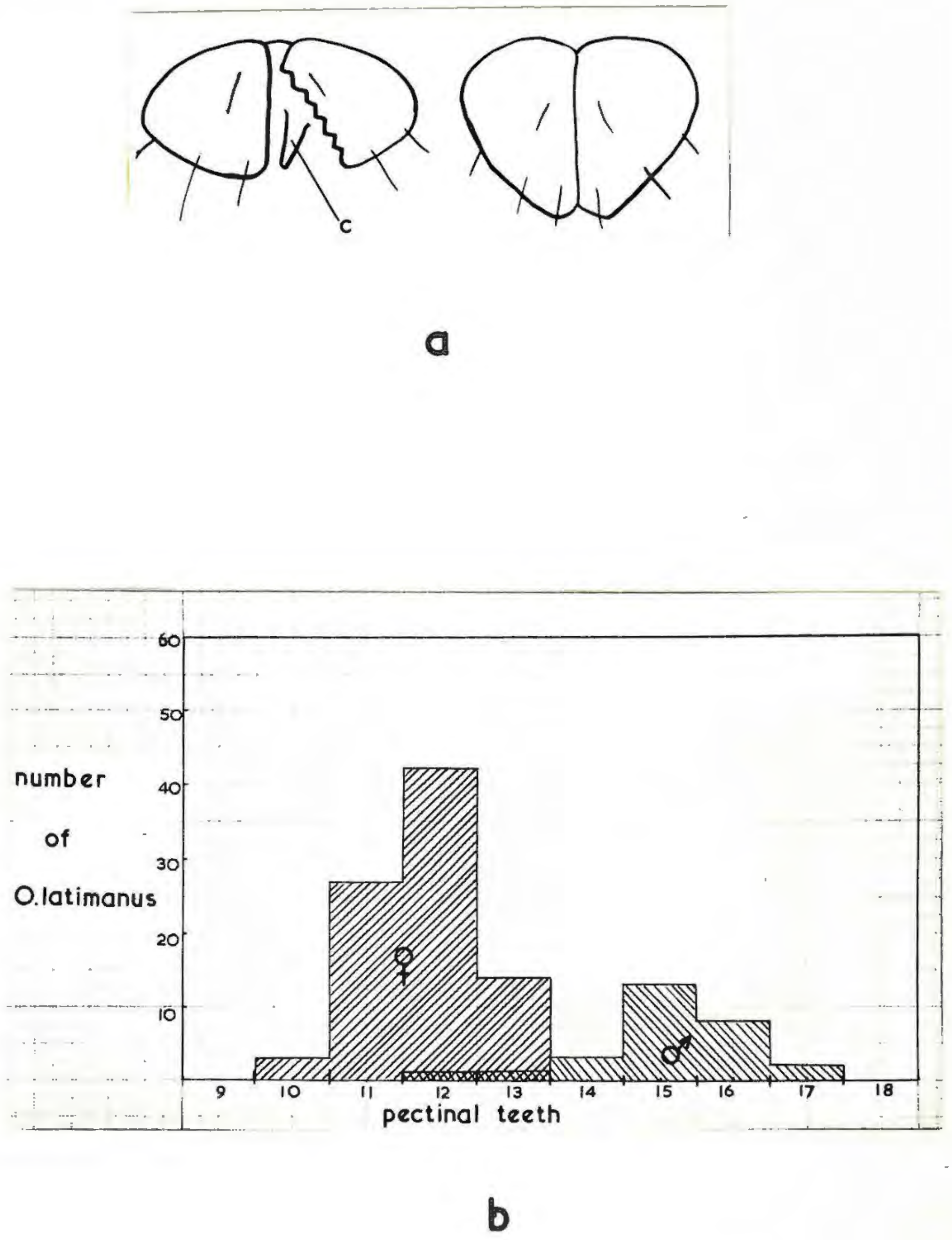


Fig. 30. (a) Genital operculum of *O. latimanus*, showing the sexual dimorphism: left, that of a male with part of one half of the operculum removed to expose the crochet, *c.*: right, that of a female with the halves, which are separated in the male, united to form a single genital plate.
(b) Sexual dimorphism in *O. latimanus* as shown by the number of pectinal teeth.

the part of the female spider but to a weaker male constitution. Montgomery claims that the males are far more prone to die of treatment which would not kill a normal female, while Broekhuysen (1948) remarks on how well the female Thomisius spider stands up to starvation in contrast to the male. The same is certainly true of the scorpion, O. latimanus, as far as neuro-muscular preparations are concerned; the male normally dies after a much shorter time than the female. His claw grip is not as strong as that of a female and as this would be of importance not only in protection of himself against other scorpions and enemies but also in holding large strong prey, it may well contribute towards his overall physical inferiority relative to the female.

The sex ratio in the pre-adult instar is a final indication that the mating-murder theory is probably incorrect for O. latimanus anyway: of 10 nymphs only 2 were male. So that the numbers of the sexes are already highly unequal before sexual contests start. Of four nymphs of the fifth instar, two were male, two female, so that what meagre information is available suggests that from initially equal numbers of both sexes, the females begin gradually to predominate.

The next O. latimanus age class for which adequate material is available is the second instar. Here there are 10 males to four females. Two possible explanations are immediately clear: either the initial sex ratio is not 1 : 1, but some "allowance" is made for a mass slaughter of males before and during maturity, or that it is not a random sample, as the nymphs may have all come from one mother. Doumerc (1840) reported that in the spider Theridion the egg-cocoons give rise individually either to all male or all female spiderlings; the same phenomenon was found by Cambridge (1868) in various epeirids and some non-random control of the sex of the young therefore appears to exist. Vandel (1941) states that some terrestrial isopods (e.g. Armadellidium vulgare) have 50% females which produce only male progeny (androgenic individuals) and 50% females which produce only females (gynogenic individuals). It seems possible therefore that this collection of O. latimanus second instar nymphs could reflect, not a general tendency in O. latimanus to produce a majority of young males, but that when young are collected from a single mother, they are all of the same sex. A few of these animals were not those of a brood collection, but were dug up singly, and it is possible that these were the few females among the males. Vandel goes further with his description of the sex ratios of the terrestrial isopods: he says that in Trichoriscus provisorius the females may produce all female young, all male or a mixture of both (amphogenic). It therefore seems necessary to collect and sex not one whole O. latimanus brood but a number of them.

The data collected from eleven broods are summarised in Table IV, and the results have been analysed statistically. I would like to express my gratitude to Dr. R.F. Ewer for her assistance in this analysis. Firstly it will be seen that of the 158 individuals sexed, 87 are males and 71 are females giving a sex ratio (Males/total sample) of 0.550±0.040, which is not significantly different from 0.50.

However, if the individual broods are examined, it will be seen that in three cases out of the eleven, the sex ratio does differ significantly from expectation, while on the basis of chance this should not occur in more than one brood out of twenty. This suggests that the individual broods do not represent a sample of a uniform population in which males and females occur with equal probability.

The matter may be expressed in another way. If the proportion of males in each litter is calculated, the mean proportion of males in a litter, together with its standard error may be determined. The values thus obtained are 0.543±0.068. Now if the true proportion of males is 0.543, the expected standard error of this proportion for a sample of 158 individuals may be determined. This result is ± 0.040, a value considerably smaller than that obtained when the individual litters are treated separately and again suggesting that the sex-ratios in the individual litters is not what would be expected by chance.

These results indicate that there is no gross disproportion in the two sexes at birth provided the sample is sufficiently large, but that the sexual composition of individual broods is such, at least, as to raise the question whether they may not be a "little cheating somewhere with these accidental variation"s in the processes of sex determination of *O. latimanus*.

TABLE IV.

Sexual Composition of Individual Broods of O. Latimanus.

Number of Males	Number of Females	Unknown	χ^2	P
13	4	1	3.778	0.05*
3	12	1	4.286	<0.05 >0.02*
8	7	0	0.000	1.00
10	6	0	1.000	>0.10
9	5	0	1.143	>0.10
5	9	1	1.143	>0.10
3	9	1	3.000	<0.10 >0.05
8	2	3	3.600	<0.10 >0.05
14	4	0	5.555	0.02*
10	4	0	2.571	>0.10
4	9	0	1.238	>0.10
87	71	7	-	-

7. Sexual Behaviour

Maccary (1810) published a report on the courtship of the scorpion and in 1907 Fabre included a description of this elaborate phenomenon in his "Souvenirs entomologiques", a description which supports the observations of Maccary. Since then there has been little of further detail; for instance Smith (1927) states that the courtship of Centruroides vittatus is "similar" to that described by Fabre for Buthus occitanus, though he neither describes it nor the slight differences which evidently occur. Vachon (1953) does describe the courtship of the scorpion Buthotus alticola (Poc.); in fact, he confirms the picture given by Maccary and Fabre. Within the last three years there have been three papers published on the courtship of three other scorpions: in 1954 that of Baerg (1954a) describing the behaviour of Centruroides insulans; in 1955 that of Southcott on Urodacus abruptus and in 1956 that of Thornton on Leiurus quinquestriatus. A paper by Serfatty and Vachon (1950), though not primarily dealing with courtship in scorpions, does contain an attempt at an analysis of courtship behaviour, so that functions are tentatively seen in different stages. This was, of course, a very difficult task when the consummatory act had not been witnessed in a single case. This consummatory act has been watched successfully in O. latimanus and, in the account below, the behaviour of the animals in courtship is described and analysed. The steps which led to an understanding of the mechanism of insemination are related and the courtship behaviour reinterpreted in the light of this knowledge.

In such an analysis it is useful to start, as background information, with a statement of the anatomical dimorphism of the sexes of O. latimanus.

Anatomical Dimorphism.

As was mentioned earlier, it is normal to find about four adult female O. latimanus to any one male in the field. There is no observable size difference, the largest male found being only 2 mm. shorter from sting to cheliceral tips than the largest female. There are, however, a number of differences in the proportions of different parts of the two sexes. These are not strikingly obvious and no series of measurements has been made to emphasise their existence, but once attention has been called to them they are clear enough. Though the total body length is roughly the same in male and female, the former has a larger proportion of this taken up by the tail segments than has the latter. Each segment of the tail in the male is longer and also slightly thicker than the corresponding one in the female, so that no single tail segment may be expected to have some special significance in sexual behaviour. The mesosoma of the female is invariably wider than that of the male. Here, however, the difference does not seem to lie in the segments themselves but in the amount of stretch which is being put on to the intersegmental membranes and pleura, and may well depend on the presence of a large "uterus" with developing young. The legs are not obviously longer in the male, but the pedipalps are strikingly so. Here the difference seems to lie in the last four segments, the third and fourth being especially extended relative to those in the female. In addition to the difference in overall length in the hand of the claw, the fifth segment is conspicuously narrower in the male. All these differences in proportions of the two sexes may be epitomised in the fact that the tip of the male claw will touch the base of the third tail segment when the pedipalp is held backwards; the female claw will reach only to the proximal part of the last mesosomal segment.

In considering these differences a distinction must be made between those features which are likely to have been present as an initial sex difference and those which may well be the result of sexual activity. It may be that the narrower claws of the male may play some part in courtship, while the characteristic enlargment of the mesosoma of the female is without importance in scorpion behaviour.

To a human there appears no difference in the colour or colour pattern of the two sexes of O. latimanus. Under ultra-violet light these animals do fluoresce as stated by Lawrence (1954) - a pretty violet in the case of O. latimanus - but there is no suggestion of a different pattern in male and female.

pedipalps? The claws and tail, besides being different in shape and size, are considerably more hairy in the male than the female. The pattern and length of the trichobothria are the same in both animals. In the first three claw segments, as well as the four proximal tail segments, both the position and size of individual hairs appear to be the same for both animals. However, the three distal segments of the claw, and the pedipalps two most distal segments of the tail have not only more hairs in the male than the female, but these are appreciably longer in the male. This hairiness of the male, especially on the outer part of the hand and, to a lesser extent, the bulbous part of the sting, is the easiest way of distinguishing the male from the female in the field. Since these hairs are sensory, this sexual dimorphism might lead to the expectation that these areas are used in a sensory action during courtship and mating and also that the male should take the more active part in this procedure.

Other sensory structures in which a sexual difference can be seen are the pectines (see ~~[illegible] discussion [illegible]~~ ~~and~~ Fig. 30b). The female O. latimanus has 11 - 13 combs on her pectines while the teeth male has at least 14, sometimes as many as 18. Since the organs are situated very close to the genital operculum, it would seem possible that this sexual difference in their structure might betoken a different or additional sensory use of the pectines by the male, possibly during mating, a suggestion put forward by numerous workers since Lankester (1883).

Lastly the external sexual organs themselves may be considered. The operculum in the male O. latimanus consists of two flaps which are fairly easily separated (Fig. 30a). In the female these are joined together completely and the operculum must be used as a single unit.

If the operculum is lifted, a pair of "crochets" or stylets (Purcell, 1899) is found in the male. Normally soft and insignificant, these become stiff and protruding when the genital area of the male is stimulated with a needle.

From this lack of any anatomical features that are strikingly different in male and female, it would not be surprising if there were behavioural traits which would distinguish the two sexes.

Behavioural Differences.

The male scorpions are vastly more excitable in general than are the females. When a male is picked up, he is more prone than is a female to try to sting. Because of this excitability a male is rather more difficult to feed. When males catch prey for themselves, however, they do not show any greater facility in the operation, so that the longer claws and more profuse sensory hairs do not seem to give an additional advantage here.

From the tracks made by the animals on smoked paper, there is some slight indication that the male normally has his pectines pressed harder on to the substrate than does the female. This may be due to the one animal holding its pectines in a slightly different way to the other, and may indeed reflect a different or additional function. It would seem reasonable to suppose that the animal that appears more excitable is receiving greater amounts of sensory stimulation. However, further work must be done along the lines indicated by Cloudsley-Thompson (1955a) before anything definite can be said regarding this possibility.

The responses to smells do not seem markedly stronger in the one than the other sex. When testing this latter point, great care had to be taken for, as has already been said, the males are rather more excitable than the females, and would react more to both smells and controls. Indeed Bristowe (1929) points out that in some spiders where sexual difference in response to smell has been reported (McIndoo 1911 and Hewitt 1917) this may be explicable in terms of the "male's extra alertness."

Kept in captivity, the males are not as prone to burrow as are the females. They do, however, appear to dig just as well, and have constructed long burrows in the laboratory. In the field there is no observable difference in length of the male and female burrow. It would seem reasonable to assume that the disinclination of the males to burrow extensively in captivity may be just a reflection of a more intense reaction to a strange environment.

So far there seem to be as few striking behavioural as anatomical differences between the sexes. In relation to their personal encounters, however, this is not true. Firstly, the behaviour which may occur between the two sexes of O. latimanus will be dealt with; then the female to female responses and lastly the male to male behaviour will be described.

Male to Female Encounter.

In an encounter of a male and female O. latimanus the behaviour is not always the same and it would seem that the internal condition of each animal plays just as important a part in determining what pattern or complex will ensue between the scorpions as in other animals. It seems very probable that seasonal factors enter into this; the animals will more frequently court and mate when put together from the beginning of March to the end of August - autumn and winter approximately - while outside this time a male will usually take no notice of a female other than to run away from her if she tries to walk over him. Whether this is merely a temperature effect or an inherent seasonal rhythm has not yet been ascertained.

The male is, in the main, the active agent in courtship. He may, however, approach a female, touch her, then turn round and hurry off so that nothing further develops from the encounter. What determines that a male should be thus unresponsive to the possibilities of mating is unclear. In one case in the laboratory, a male who frequently showed this behaviour was small and it may well be that he was rather young. In other cases a male that has been unsuccessfully courting one female may then actually refuse a second and more responsive animal.

Alternatively it may be the female who will have nothing to do with courtship. Her refusal to participate may take one of two forms. She may run away, as did the male, or she may turn to face and attack the male (Plate VI). This attack is quite different from that used when a scorpion catches prey or tries to defend itself against an enemy other than another scorpion. The claws clutch at the male and then, whether they are holding him or not, the pedipalps are spread apart widely, thus allowing the attacker to close in on the attacked. Usually the pair come together so closely that their chelicerae almost touch. In normal prey-catching, the pedipalps are bent to bring the prize within the reach of the chelicerae and sting, and in no case has there ever been evidence of this "spread pedipalp attack". The sting of the female is not normally brought over her body, though, from the moment that the female begins to clutch at him, the male tries to sting her. Occasionally the female may try to sting the male, but usually he has begun to retreat before this happens. He appears to give in very suddenly, turns around, and runs off rapidly.

Sometimes, however, the female has only to turn towards the male and he will rush away. No scorpion has ever been seen actually to sting one of the opposite sex in any encounter. This may be due to the great excitement of the male and the fact that he runs off before the female has a chance to sting him. It is true, however, that she appears as a rule to make little attempt.

When, instead of attacking the "unwanted" male, the female starts escaping him, he will give chase. He will run a short distance and then stand and exhibit a pattern which will be called "juddering". Standing in one place, claws lifted, the scorpion jerks forwards and backwards about 3 or 4 times very rapidly: waits 10 - 15 seconds, and then repeats the performance. He may then take a few steps forward and start juddering again. So far, I have seen this only in O. latimanus and found it recorded for no other scorpions. Baerg (1954a), however, mentions a "quivering of the front legs" in Centruroides insulans. This has not been described in more detail, but Baerg says (private

Plate VI. Encounter between male and female O. latimanus. The female, left, has attacked the male with her pedipalps and almost overturned him.

communication) that it occurs only when the male has hold of the female. Vachon (1938) reports something which may possibly be related in the pseudo-scorpions.

Initially this piece of behaviour was thought to have only a sexual significance. Later, however, it was seen to occur in second instar nymphs and after this its elements were recognised in the behaviour of a scorpion "seeking" its prey which had just eluded it. (p. 20). In this case it is not normally the whole body that is jerked forwards and backwards, but only the claws. If, however, the scorpion becomes greatly excited, e.g. by a cricket which continually jumps past the hungry predator without the scorpion being able to catch it, the latter may include the whole of its body in the jerk. Usually only a single jerk is given at a time, but again, if excitement runs high, a greater number may be given. Part of what is possibly the same pattern is seen when a scorpion is walking along undisturbed. The claws are not held continuously up or down but are lifted and dropped at intervals. When the animal stands still, "reconnoitering", the claws may be picked up and dropped several times and with each upstroke they are carried slightly forward and outward as described earlier ([redacted]).

If the suggested relationship between these movements described above is correct, juddering may be considered as a highly ritualised "seeking" movement. On the other hand, it might be tied up with the clutching movements which would probably ensue when the seeking response had been rewarded. In the latter case the "seeking" movement would be looked upon as "intention" clutching. Since the juddering does not involve actual opening and closing of the claws, the former would seem the more probable explanation, and juddering may be looked upon as ritualised seeking.

To return to the escaping female: she fairly often evades the male altogether because he loses time in stopping to judder. He may overtake her, turn to face her and treat her as though she had been responsive from the start.

The behavioural complex up to this point ~~is~~ in the description may well bear further analysis. The two patterns shown by an unresponsive female might possibly ensure that a non-receptive female can escape the attentions of a male without being forced to adopt offensive behaviour. The escaping female may sometimes be caught and may then respond favourably to the male while the female who attacks the male has never yet been observed to change her attitude with further attempts on the part of the male. This suggests that there may be some fundamental difference between the behaviour of the two females concerned. It seems possible that, if the female has just been fertilised (that is, she has just passed through the receptive phase) she will behave offensively towards the male. If, on the other hand, she is not yet quite ready for fertilisation, the escape reaction might be shown at the approach of a male. Two possible advantages may be seen in this sort of behaviour in contrast to that of attack. Firstly it means that a male who may soon be needed is not chased off, or, more serious, damaged by the thrust of a sting. Secondly there is the possibility that the sexual state of the female could be stimulated favourably by some aspect of the chase, e.g. by the juddering of the male. Professor Ewer (personal communication) reports the same type of behaviour in a female cat. Before she has been fertilised, she will parade in front of the tom cats, but if they approach, she will run off inside the house. After fertilisation, she will begin vicious attacks on any tom cat who continues his attentions to her.

During neither the chase nor the attack has there ever been any sign of reciprocal juddering on the part of the female. In fact, what appears to be the maximally responive female behaviour is that of lying almost motionless before a juddering male. If the couple achieve this condition the male will come forward and grasp the claws of the female in his own. Sometimes there may be considerable delay while he gets the "correct grasp"; sometimes he will catch hold of her tail and one pedipalp, or a leg and tail. Gradually he works his grip round to that shown in Fig. 31.

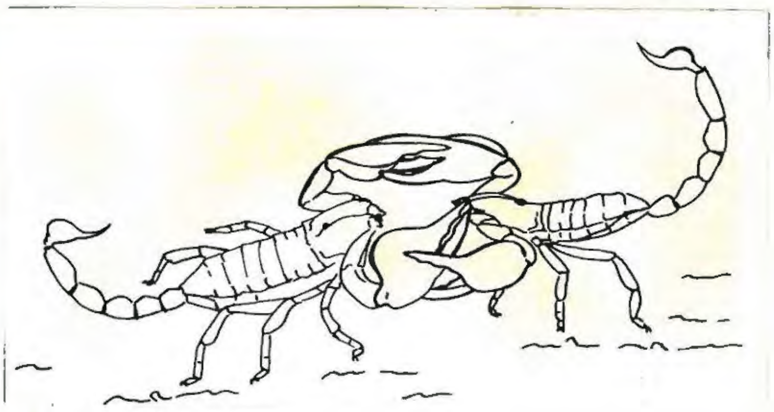


Fig. 31. Pedipalp grasp in O. latimanus courtship. The male, on the right, has hold of the pedipalps of the female with his own.

Arbre droit and Promenade à deux.

At this point one of two pieces of behaviour may be shown in O. latimanus, depending apparently on quite how submissive the female is. If she tries to pull away, the male raises his sting almost straight above his claws (as in the attack pose of Fig. 32). She does likewise, and the classical "arbre droit" is achieved. In O. latimanus this movement happens very rarely and when it does occur is of a few seconds duration. There is none of the appearance of "caressing" or stroking mentioned by Fabre (1923) and Baerg (1954a).

It is not clear exactly what manoeuvres the two stings are involved in: at times they appear to be pricking at each other, at others one sting will just brush past the other. The pattern ends suddenly, both scorpions bring their tails down and the female may break away and a chase starts. More normally, the male begins walking backwards, dragging the female with him. Almost immediately he starts pulling her closer to him by bending his pedipalps. His chelicerae begin alternate grasping movements as in feeding, and, when the two animals are close enough together to allow it, the male takes the chelicerae of the female in his own (Plate VII). For him to be able to do this she must open the claws of her chelicerae so that he can grip them. What induces her to do this is not clear but in some cases it may take some time before his grasping cheliceral claws are finally holding hers.

This dropping of the clawhold of the pedipalps in favour of that of the chelicerae has not apparently been mentioned before in scorpions. The attractive illustrations of the paper in Endeavour by Vachon (1953) do, in fact, show B. occitanus in the arbre droit pose with claw holds relaxed and in such a position that the chelicerae must certainly have been very close together, if not clasping. This grip would undoubtedly give the male better control of the body of the female so that it might not be surprising to find it in all cases where the form and position of the chelicerae allow it.

Fig. ~~1~~ 31.—The wide-spread pedipalp attack of *Opisthophthalmus latimanus.* Both animals have their pedipalps spread apart sideways and are drawing together so that their chelicerae will be in contact. The male (left) has his sting raised vertically prior to an attack on the female's body.

Plate VII. The "promenade à deux" of an O. latimanus pair
(a) A lateral view showing the greater elevation of the tail of the male and the lack of any grasp with the pedipalps. The male is on the right.

(b) A dorsal view indicating the cheliceral grip. Here the male is on the left. Behind the female and on her right side can be seen the ground which has been partially cleared by the sand scraping of the male.

The outlines of the pedipalps have been retouched.

Once the cheliceral hold is established, that of the pedipalps is, of course, immediately released, and the "promenade à deux" begins; the male, walking backwards for short distances, drags the female, and then, walking forwards again, pushes her in front of him. From watching the legs of the two animals, it seems probable that both of these movements are entirely due to the male and the latter not due to the female. It is clear that he pushes her in front of him - her feet can be seen skidding along the ground. This would appear to be the case in B. alticola for Serfatty and Vachon (1950) remark that "le mâle dirigeait les mouvements."

This stage has been known to last for almost an hour but has never been prolonged to the extent of 48 hours, as reported by Serfatty and Vachon. Sometimes, within a few minutes the male has gone into the next phase of the promenade.

Sand Scraping

In O. latimanus this consists of a scraping together of a pile of soil by the male. He uses his first pair of legs for this, and then drags the soil backwards with first and second legs while he pulls the female with his chelicerae. He will then push her back across the newly cleared space and repeat the procedure, never spreading the soil very well at the end of the piling manoeuvre, but creating an area distinctly clearer of large soil particles than the surrounding parts. The behaviour seems very similar to the soil carting shown during burrow construction and the path left by the courting couple looks very like that seen outside a freshly dug burrow. Sometimes the soil carrying pattern may revert to the pure female-dragging action, but it may lead rapidly into what are apparently the final stages of the courtship.

The time spent in dragging the female backward and forward, and in sand scraping varies considerably. Once the cheliceral hold has been established, it may be that the state of the scorpion pair may to some extent determine how long the actual courtship will last, though it is quite clear that, if the animals are really not ready for mating, this will be apparent much earlier, and the promenade à deux will not proceed. What is quite obvious in O. latimanus is that the surface on which the pair are promenading has a strong influence on the length of promenade. On the fairly loose sand or loam of most of the laboratory vivaria the pair may still be walking about after an hour. Transferred either on to a smooth matt table top or a hard clay or loam surface, the next and final stages of courtship will be reached within a minute or two as a rule.

Rearing.

After some measure of back and forth pulling and usually some effort at sand digging has occurred, the first indications of what appears to be "rearing" occur.

The male seems to be pulling the female towards him, as judged by her resisting footholds, but he himself appears to be braced on his hind legs. The first legs of the female may even be lifted off the ground and laid across those of the male. Her claws are still held over his prosoma and his are around her, partly across her back. Both scorpions may be seen to have their genital opercula pushed back at this stage, though this may have occurred much earlier in the courtship.

Up to this stage the proceedings have often been watched in the laboratory. Apparently noise, vibration and changes in light intensity do not disturb the pairs. The behaviour subsequent to this consists mainly of events at ground level and is consequently far more difficult to observe. But for the fact that both animals have reared up slightly, these events would be invisible except from below. In addition, the animals appear to become more sensitive to disturbance subsequent to this stage in the courtship.

Up to this time the events which have been described add little new to our knowledge of the sexual patterns in these animals. Two observations of mating which are described below served as a key for an understanding of the subsequent events. These cases are now described and analysed.

Case A.

Here the animals had reached the stage mentioned above, in which the male gave slight indications of rearing. It was at this point that the spermatophore was seen to be partly protruding from the male genital aperture. A long, creamy-white object, it was gradually pushed out, pointing forward towards the front legs of the male. No details could be made out of any part played by the crochets stylets in the extrusion of the spermatophore. It is possible, however, that these structures were responsible for guiding the organ between the two lobes of the opened operculum. After carrying the spermatophore for about 30 seconds, during which slight backward pulling of the female was continued, the male appeared to jerk in some way so that the spermatophore lay free beneath him. He started moving backwards, pulling the female over the spermatophore. It was at this point that some person in the laboratory slammed a door. The male immediately released his partner's chelicerae and ran away. She stood still for about 20 seconds then, pressing her genital aperture flat against the ground, proceeded to walk about slowly and within a limited area. This behaviour gave the impression that she was searching for something, presumably the spermatophore. She did not actually walk over this structure, though she touched it several times with her pedipalps. It was entirely ignored. She was picked up and put down again, when she immediately continued her "search". Quite suddenly she stopped, raised her genital region from the ground, and ran off to cover. The spermatophore (Fig. 33a), as shed by the male and without having ever entered the female was left lying on the ground.

The Spermatophore

At this stage, a brief description of the spermatophore may be helpful. It is about 1.7 mm. long, is creamy-white in colour except where it is transparent or marked with brown at the sclerotisations. Since there appeared to be no report at all of scorpion spermatophores, and there seems to be no acknowledged terminology for those of arachnids (see Kew, 1912 and 1930 and Vachon, 1938) names have been invented for the parts of the scorpion spermatophore. The "stalk", *st* of Fig. 33a, is a stiffened hollow column, the hollow running into the "capsule", *c*. This stalk was the last part to be extruded from the male. The capsule appears as a swelling in the middle of the spermatophore. A number of knobs are arranged symmetrically on the "dorsal" surface, while towards the stalk and projecting in that direction, is a pair of hooks, *h*. A mass of denser material can be seen within the capsule. Pressure with a needle on some part of the capsule caused the knobs to shoot out and "open" the spermatophore (Fig. 33b). At this stage the capsule has a slightly larger dorsal mound and from this project a pair of large valves, *v*. It is the tips of these valves that are visible as one of the pairs of "knobs" in the closed spermatophore. Pressure on the sides of the capsule caused the dense material within the capsule to rise and spill over between the valves. This material was then seen to consist of numerous sperm, fine and threadlike.

Anterior to the everted valves a pair of small discoidal structures can be seen, the "sacculi", *sc* of Fig. 33b. These are represented in the closed spermatophore by another of the pairs of knobs. Lying anteriorly between the valves is what has been called the "stopper" (*sp*). A slightly amorphic structure, this appears to have lain more posteriorly between the valves in the closed spermatophore, and to have kept the sperm in place. Further, it was suspected that this stopper might act as the "post-nuptial plug" or spermatocleutrum, mentioned by Vachon (1952). In some female *O. latimanus* that were dissected earlier, a mass of tissue that could possibly have been the stoppers of the spermatophores were found in the vaginae. The only difficulty in visualising this structure remaining behind after the spermatophore is removed from the vagina is the fact that it might be expected to be swept out as the more

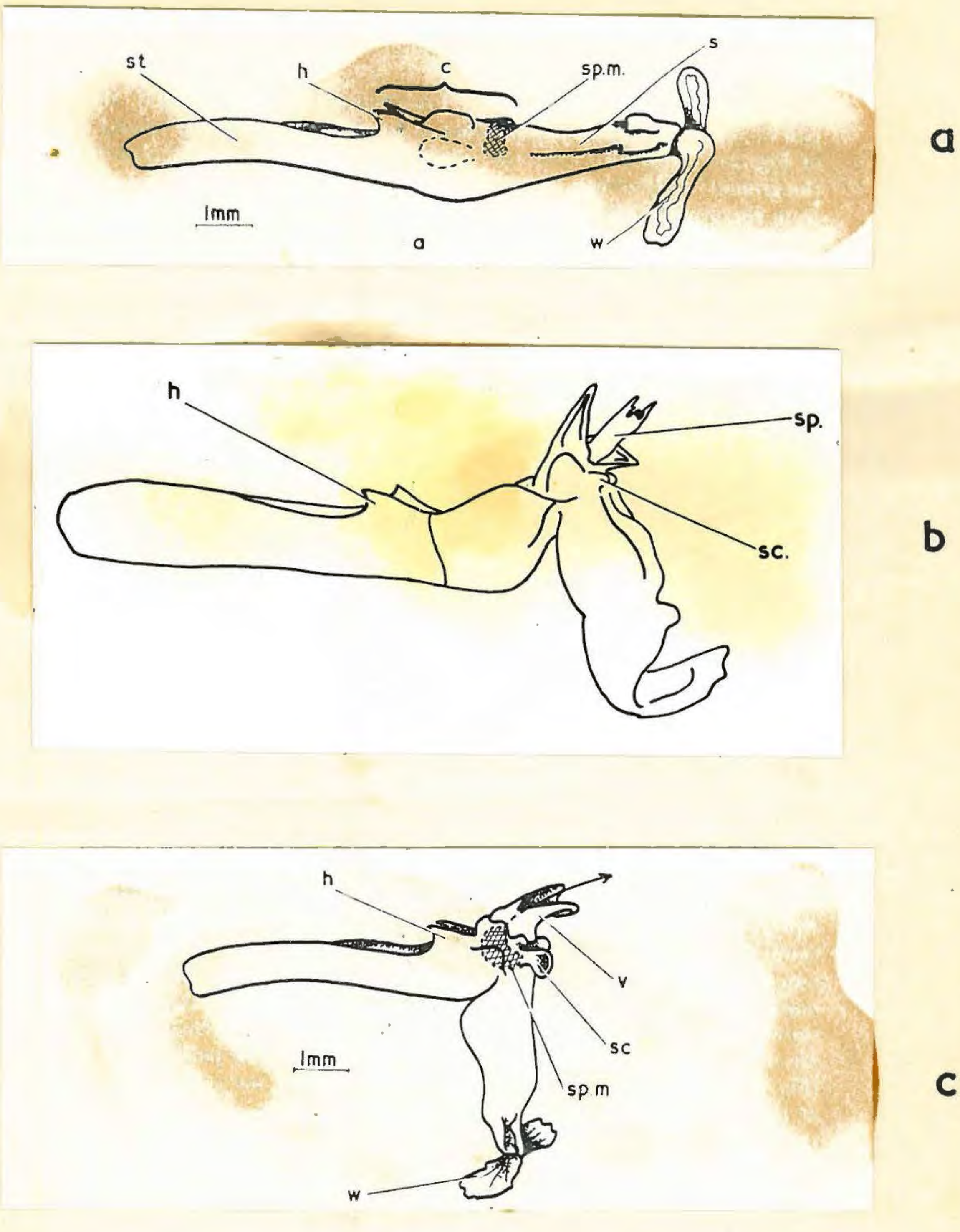


Fig. 33. The spermatophore of O. latimanus
(a) Diagrammatic representation of an unopened spermatophore. The position of the valves and sperm-mass have been indicated.
(b) Spermatophore of case A, valves everted by the experimenter.
(c) Spermatophore bent by the animals during the eversion of the valves. The passage way for the sperm mass formed by the two valves is indicated by an arrow.

c., Capsule portion; h., chitinous hooks; s., stem; sc., sacculus; sp., stopper; st., stalk; sp.m., sperm mass; v., valve; w., pedal wings.

deeply embedded parts of the spermatophore were withdrawn. For such a "plug" to be left in the vagina it would need either to be placed in position after fertilisation, as indeed Vachon (1953) suggests, or the plug must be on that part of the spermatophore which penetrates the female first. With the stopper in the central part of the spermatophore the possibility of its functioning as the plug appeared faint (but see p. 143).

The end of the capsule opposite the stalk continues solidly as the "stem", s of Fig. 38a, to end as the soft bifid "wings", w. There was the possibility that these anteriorly situated structures might act as the vaginal plug, though their lack of any sclerotisation lines did not correspond with that of the plugs found in the females.

Analysis

Whether the scorpions were or were not disturbed by the noise and vibration, the male had already dropped the spermatophore. What remained unclear was whether this represented the end of his rôle in mating, or whether he further assisted in effecting the introduction of the spermatophore into the female. Her searching behaviour might well have been part of a pattern in which she actively picked up the spermatophore and, had she not been disturbed, she might have achieved this end quite effectively.

If the spermatophore were inserted in either of these two ways, it might be opened to release the sperm by a pressure on the capsule from either the male's legs or pedipalps (as in the case of some pseudoscorpions, Vachon, 1938), the female opercular plate, or the actual walls of the vagina. Such a procedure would seem very difficult as the capsule lies in the middle of the spermatophore and the idea seemed to imply that either the wings or the stalk had to be driven deep into the vagina to make insemination mechanically possible.

The pair of stiff chitinous hooks were considered to form a mechanism which prevented the spermatophore slipping easily from the vagina once it was in position.

Case B.

In this instance, not only were the animals "disturbed", so that the end of the pattern was not seen, but a minute or two of observation was missed shortly before the couple broke apart. The animals were observed until they had reached the rearing stage of the promenade, the female with her genital operculum open. When next seen, the female had a bilobed white structure protruding from her genital aperture. It was then that the male rushed off, "disturbed." The female dropped her genital region to the ground and appeared to be either pressing the white structure into her genital aperture or trying to wipe it free. In the latter objective, she was successful, and after a further 20 seconds of wiping her genital region over the substratum in the manner of the "searching" of Case A female, she arose and went her way, leaving the white object, now clearly a spermatophore, on the ground.

The wings of the spermatophore were in this case stuck firmly on to the ground, and were in fact torn off in trying to free it. The two "lobes" of the structure were then seen to be the stalk and stem, these two parts being bent almost at right angles to each other. That part which had been last to leave the genital aperture of the female was the capsule with its valves everted.

Analysis

Two explanations of the phenomenon seem possible. Either the female had just picked up, emptied and had been watched voiding the spermatophore of the male that had run away, or she had been extruding a spermatophore left by an earlier mating, the course of action necessary before she could proceed to mate with the male that had recently been courting her. If the former were true the whole mating would take only a few minutes; if the latter were true, the promenade might be concerned with stimulating the female to deposit the old spermatophore, as well as possibly with a mating. No more support was indicated here for one or other interpretation.

Facts which could, however, be gleaned from the consideration of case B are clear. The spermatophore itself, in part anyway, does enter the female genital operculum, unlike that in the pseudoscorpions where apparently the sperm mass alone is picked up by the female (e.g. Chelifer cancroides L. Vachon, 1938). The problem of how the valves can be everted and the spermatophore introduced into the vagina is solved by the observation that this latter is bent so that the capsule has become "anterior". This fact would also remove the difficulty seen in postulating that the stopper functions as the vaginal plug; in the bent spermatophore the stopper would actually lie deepest in the vagina as the spermatophore is being withdrawn. Lastly the "searching" behaviour of the female is not, or need not be, concerned with actually picking up the spermatophore. It appeared to be either part of a definite behaviour pattern of some unknown function or the behaviour elicited from the female when the male runs off for one reason or another.

Mating Hypothesis.

Consider now the whole question of copulation in the scorpions. Since 1810 when Maccary published the first account of scorpion courtship, workers on the biology of these animals have been anxious to record the actual mating ~~the~~ of scorpions. Some circumstantial evidence has been brought forward at times to suggest that this could be witnessed; for instance, Brongiart and Gaubert (1891) reported that Marés had surprised scorpions "accouplés, ventre à ventre, les peignes enchevêtrés." Lankester (1883) concludes, because he found scorpions clinging to the undersurfaces of wood, that they mate, ventral surface to ventral surface, while Fabre (1923) builds up a dramatic picture of the copulation on finding a male upside down as he lifted the stone above a courting couple. Vachon (1953) writes "the conclusion of the nuptial dances I have not observed, but anatomical investigation bears out the statements of early writers; the male fertilises the female directly in true copulation......In the course of this act, the male protrudes certain special organs to form a temporary penis, with which he inserts the sperm and finally places in position a vaginal plug - a kind of post-nuptial hymen." It seems strange that copulation should not have been seen if in fact it does occur in the scorpions, and it seemed worthwhile considering the possibility that copulation does not occur at all and that this is, in fact, the explanation of why it has not been seen as a consummatory act to the courtship.

Four main points could be urged as supporting this hypothesis. None of them would alone be very convincing, but together they served as a basis guiding further observation.

Firstly the reproductive procedure of the group which appears in many ways closely related to the scorpions, namely the pseudoscorpions, may be taken into account. Vachon (1938) reports that pseudoscorpions go through a complicated courtship during which the male deposits a sperm packet on the ground and the female picks it up. True copulation is "rather rare in other arachnids" (Vachon 1953) and it seems more reasonable to assume that what occurs will be the "normal" than to believe that what has not yet been witnessed will be one of the "rare" occurrences.

Secondly the structure of the spermatophore, genital organs and courtship of the scorpions and pseudoscorpions may be compared. There are no detailed accounts of the structure of the spermatophore in the pseudoscorpion but the general similarity to that occurring in *O. latimanus* can be seen by comparing Figs. 33a and c ~~e~~ with Figs. 39a and b. According to Vachon (1938) that of the pseudoscorpion is produced in a rather peculiar manner: the part which separates the sperm mass from the ground is deposited as a viscous drop, being pulled out gradually to its definitive shape. A possible relationship is immediately seen between this drop which sticks the spermatophore to the ground and the "glandular" wings which are first to touch the ground as the scorpion spermatophore is extruded by the male.

The genital organs are not very fully described in the pseudoscorpion, but the only difference which appears of possible significance is the more complicated nature of the glands in the male and the lack of crochets. Since these latter have seldom been mentioned for any of the Buthidae, though they most certainly do occur in at least *Uroplectes* and *Parabuthus*, one is inclined to consider that in animals as small as the pseudoscorpions, their presence may be even easier to overlook. The courtship is similar in so far as the male takes the female pedipalps in his and then leads her about. In *C. cancroides* (Vachon 1938, Levi 1953) the male releases the female and she comes forward and picks up the sperm mass, but in *C. cyrneus* L. Koch (Kew 1912) the male keeps hold of of the female by at least one hand all through the mating sequence. Vibratory behaviour is common to both *C. cancroides* and *O. latimanus* and has already been mentioned. This similarity of the structure of the genital organs and of courtship behaviour may, of course, stem merely from the close relationship of the two animals, but it seems hardly likely that structures which appear so much alike should be put to different uses, while within the same subphylum there are animals in which the genital organs may differ widely and yet be used in almost the same way, e.g. the palpal organ of the spiders.

Thirdly there is the male's behaviour with regard to the soil on which the courtship proceeds (see page 121). Fabre (1923) records that, towards the end of the promenade à deux, the male begins to dig a shallow shelter with his feet and tail and then pulls the female into this. Glauert (1946) states that a male sand scorpion was once seen trying to drag a female of the same species under a stone. There seems no reason to doubt these observations but they would clearly be more convincing if copulation had been seen to occur after the pair had taken cover. As it is, the writers merely presume that, in the privacy of the shelter, a copulation does occur. In the case of *O. latimanus* the carting of soil appears to have no connection with an effort to take cover. Frequently the terrain in which the animals are performing contains the burrows of both the male and the female and no use has ever been made of the shelter offered by these. Pieces of bark under which the animals could have crawled and low masonite shelters have also been ignored throughout courtship. As indicated, this behaviour has here been interpreted more in the light of a clearing of the soil surface than as an actual digging. This is supported by the fact that, when the animals go through the courtship on a table where there are no soil particles to clear away, none of the "sand-scraping" movements have been seen at all. It is true that the hardness of the table top may have upset the male to such an extent that he would not attempt to "dig" but where there is soil, there is little digging, mainly scraping. Clearly the matter could be settled by allowing a couple to court on a soil surface swept clear of all large and obtrusive particles: under such conditions, no scraping occurred at all.

Lastly in O. latimanus the male does not return to the exact spot where he first scraped together soil particles, but on the return trip will start clearing from an area quite a way removed from the original clearing site. This is hardly in keeping with the digging of a hole, though the pattern is such as to result in a clear space being provided under the feet of the scorpion couple.

There is no record of any soil clearing activity in the pseudoscorpions, but it is obvious that the difficulty of picking up the spermatophore would be vastly increased where the soil is uneven. However, Chelifar, worked on by Vachon, is so small that such considerations may play a minor rôle, in that all soil particles are relatively enormous to them, though in the scorpions it may well be of importance. The soil clearing in scorpions would therefore appear as a reasonable and necessary preliminary to the deposition and uptake of a spermatophore.

It seems extremely probable that previous workers who watched hopefully when a pair of scorpions started the courtship dance had no idea that the substratum on which the animals were performing could be of any importance and that this was normally the loose soil found in prepared vivaria. Failure to observe the consummatory act may well have been due to this factor. This simple assumption that the substratum on which the animals are to perform is of vital importance to the performance provided the basis for further observations in which a fairly hard surface was provided for the pair of courting scorpions.

Lastly, though my own observations recorded above are rather scrappy, they do in fact support ~~a~~ the hypothesis. In the first case, A, quoted, there was no sign of the spermatophore being introduced directly into the female by the male, though the rearing action previously seen might have suggested that such a course was not impossible. If the spermatophore were introduced directly by the male, the subsequent behaviour of the female with her genital aperture pressed to the ground would appear inexplicable; while lastly, the whole significance of the back and forward pattern of the promenade à deux becomes clear as an elaboration of a movement in which the male drags the female back and forth over the spermatophore which she then picks up. The promenade à deux may be looked upon as a ritualised intention movement of the "picking-up" pattern. If on the other hand the true copulation visualised by Vachon does in fact occur, there is no obvious origin of this "prenuptial dance."

A point which may be mentioned here, but which is not seen as either supporting or refuting the hypothesis, is this: frequently the vagina of a female scorpion is found to be filled with dust and grit; at a distance of about 3 mm. from the external genital opening, soil particles are present while there is no sign of dirt at all under the male operculum. This might possibly get into the vagina in one of three ways, though there is no evidence that it occurs in any of them.

Firstly, the birth of the young might in some way cause the extended vagina to come in contact with the soil. However, Schultze (1927) reported that during parturition in *Heterometrus longimanus*, the pectines "act as braces", so that it seemed possible that in *O. latimanus* also the genital aperture does not come anywhere near the soil, an hypothesis whose confirmation has already been described (p. 88).

The second possibility was that the particles are introduced into the female during the extrusion of an empty spermatophore or the "postnuptial plug" described by Vachon. It seemed possible that in Case B, the female could have collected dirt between the lips of her vagina while wiping the spermatophore free. Such an event might well have occurred in natural conditions if the behaviour of this female in ridding herself of a spermatophore is normal.

The third possibility was, of course, that the soil is picked up off the ground with the spermatophore. Without further evidence this latter explanation seems the most acceptable, in that the soil might be expected to penetrate fairly deeply if introduced with the sperm which are carried well into the animal. If, on the other hand, the explanation involving the extrusion of the spermatophore is accepted, there seems no reason why the sand should get further than just around the actual genital aperture; it would seem much easier to travel in with the movement of the spermatophore or sperm than to travel in against the outward force of the extruded spermatophore. However, none of the three explanations rested then on any evidence.

The two cases A and B, the form of the courtship of the scorpion, as well as what is known of arachnids in general, all pointed to the lack of true copulation in scorpions or in *O. latimanus* anyway. Copulation might occur in other scorpions, but, on the deductions recorded above, the most reasonable assumption for this particular animal ~~is~~ was that the male drops a spermatophore towards the end of the promenade à deux, and this is picked up by the female.

After all this elaborate deduction was made on casual observations, a deliberate attempt was made to watch the mating of *O. latimanus*. During an afternoon in mid-May, this was successful, and the whole performance was observed. Since then the observation has been repeated at least a dozen times.

The Mating.

The pair were two animals which had been caught on the previous morning and the fact that they had just been brought into the warm laboratory may have been partly responsible for the successful mating. The courtship started on a table top where the events at "ground level" were observable, but, because the male slipped continuously on this, the pair were put on to a large sheet of blotting paper on which both animals could grip quite easily.

The courtship was very rapid, there was no indication at all of the arbre droit and no soil scraping. The male only just caught hold of the female pedipalps in the "correct" grip before he grasped her chelicerae and entirely released the claws. Within a minute or two, the back and forward movements of the promenade became extremely limited spatially, and the genital operculum of the female could be seen to be open. That of the male opened as the extrusion of the spermatophore began. This slid out gradually, pointing forward as it had done in Case A. Within about two minutes from the beginning of the extrusion the male appeared to pull back slightly more forcibly and the spermatophore lay free on the ground beneath him. He began jerking the female violently towards the spermatophore, moving backwards himself with each millimetre that he drew her forward. This pattern contained the "back and forward" movement characteristic of the promenade though the female was gradually drawn forwards towards the spermatophore. The male half-lifted her with each jerk so that she was actually pulled into a position above the spermatophore. It was therefore not clear whether he dropped her on to it, or she herself plunged down. Whichever was the case the action was very sudden and quick, and the female was almost immediately back in the normal standing position; the spermatophore was bent under her, the stalk projecting outwards but not touching the male, the capsule almost hidden in her genital aperture and the stem passing vertically to the ground where it was held by the "gladdular" wings.

The two scorpions stood immobile for about six minutes in this attitude: both animals slightly reared up anteriorly, the male holding the female who had the valves of the spermatophore inside her genital aperture.

The male then began to make slight retreating movements which the female appeared to resist. Suddenly the male released the chelicerae of his partner and clutched at her with his claws, spreading his pedipalps widely. He brought his tail over and thrust his sting at her back, though he did not actually insert it into her body. She responded by moving off backwards so that she was torn free of the empty spermatophore which was left stuck to the ground. The male drove her about 25 cm. from the spermatophore; she made no attempt to sting him but clutched rather feebly at him with spread pedipalps. The male then turned round, rushed away and hid under some cover.

The female moved about slowly for 30 seconds or so, with her genital aperture pressed to the ground, exhibiting the "searching" behaviour mentioned earlier. When she passed over the spermatophore she ignored it and, as was suggested, it is evident that the searching is not directed towards this. She made chewing movements with alternate chelicerae, then suddenly she seemed to lose interest in her "search" and she also hurried off to cover.

Within an hour the male was observed to judder at another female but when placed with the female that he had just fertilised, the pair fought violently until he retreated. This adds some measure of support to the hypothesis put forward earlier, namely that the offensive behaviour of a female towards a male may indicate that she has already been fertilised and has no need of a male.

Analysis.

This observation of the mating entirely supported the hypothesis which had been erected earlier. Not only does the male deposit a spermatophore on the ground during the promenade, but the movements of this dance persist as he pulls the female into the position above the spermatophore. The exact details of how this is picked up or the valves everted were not clear.

Subsequent observations show that the wings have become cemented to the ground fairly soon after they are deposited, and in most cases have become almost invisible. In consequence of the manner in which this provides a point of attachment, the spermatophore cannot be picked up freely by the female, but bends at the capsular portion. It is possible that this bending is instrumental in everting the valves and pressing the sperm out.

Further detailed study indicated the actual mechanism of spermatophore pick-up and the eversion of the valves. The male pulls the female up and forward very sharply, and then he releases his pull on her, or actively pushes her back, so that the opened genital operculum catches on the pairs of hooks as it passes by the spermatophore (Fig. 34c): this anchorage on the spermatophore would cause it to slide under her belly if it were not that the attachment at the wings prevents this and allows only the buckling which has already been described. The position of the inverted valves indicates that bending may cause their expulsion. It is certainly true that in all the jerks in which the female genital operculum did not catch the spermatophore hooks no bending and eversion of the valves resulted. Support for this hypothesis was obtained in the following way. A couple were allowed to proceed with the mating sequence up to the point where the male just began to pull the female over the spermatophore which he had stuck down. Both animals were then suddenly lifted up by their tails and put down some distance away, leaving the spermatophore unopened on the ground. A loop of fine thread was caught around the pair of hooks and they were pulled, the tension being applied in approximately the same direction as would have been used by the operculum of the female scorpion. A light pull caused the spermatophore to bend a little and the valves to evert immediately. The spermatophore could then be straightened but in no way could the valves be tucked back inside the capsule.

It may be noted in passing that here a functional significance of the difference in shape and form of the male and female genital operculum can be seen. If the male operculum did not consist of two flaps which could be separated from each other, the spermatophore could not pass forward between them. It is true that the male could move further back as the spermatophore is extruded, so as to leave it lying in approximately the same position, but this would require accurately oriented movements by the male. If the female had separated flaps as has the male, the operculum could not be used to effect eversion of the valves. Of course there may well be other functional reasons for this male:female dimorphism of genital opercula, but the presence of such dimorphism and its explanation in O. latimanus points to the possibility of a different mode of eversion of the spermatophore valves and "pick up" in scorpions such as some of the Buthidae where the genital operculum is divided in both species (Pocock, 1893a).

The question arises: how does the male know when to stop jerking the female up and towards him? What indicates to him that the female has picked up the spermatophore? At first the problem seemed insoluble, for it was supposed that only the female of the pair could be aware of the spermatophore within her vagina and that any sign stimulus to the male to terminate the pulling behaviour must be supplied by the female: there was never evidence of any sign stimulus. If, however, the position of the spermatophore under the male is remembered, another possibility can be seen. As shown in Fig. 34b, the stalk, s, is up in the air at an angle of about 50° to the horizontal, so that it is touching the male ventrally in the region of the coxae of the first and second legs. When the female has the capsule part of the spermatophore within her (Fig. 34d) the stalk is not in contact with the male body at all and it was suspected that it is this lack of any contact which serves to let him know that the spermatophore is in the female.

Support for this view comes from five unsuccessful matings which have been observed. In four of these the valves of the

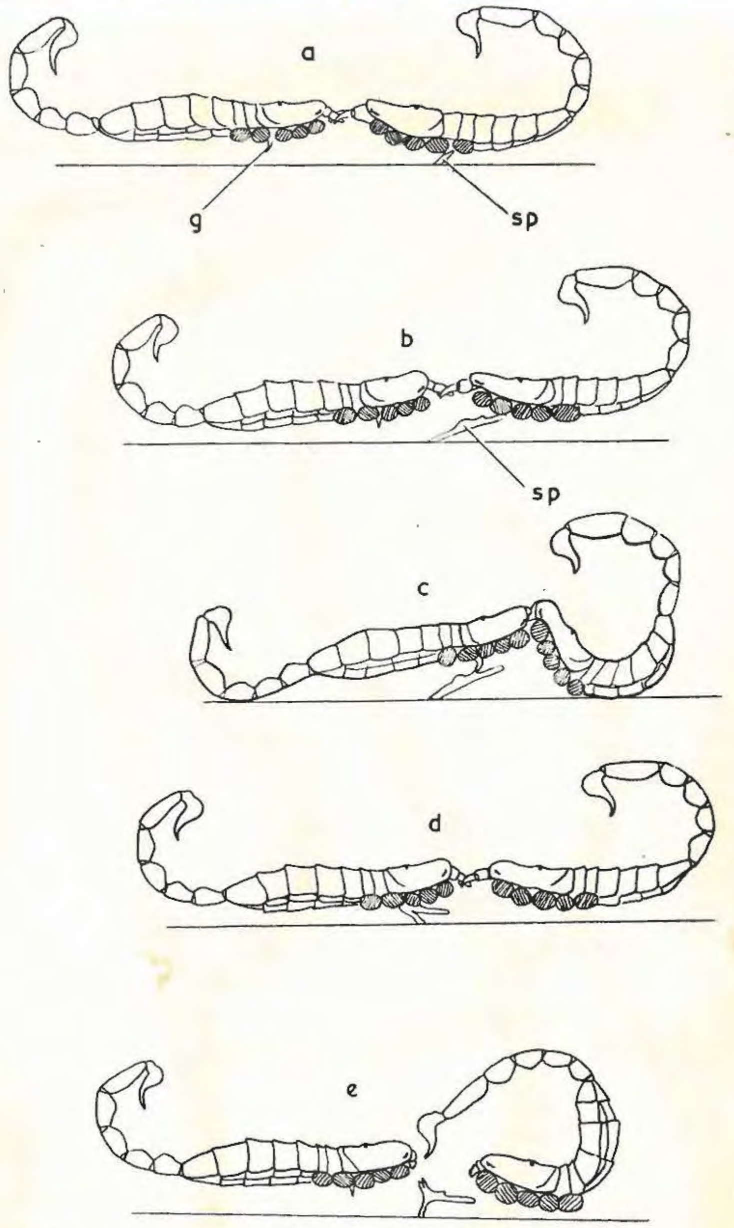


Fig34.—Diagrammatic representation of the deposition of the spermatophore by a male *O. latimanus* and the insemination of the female. The animals are drawn as though their legs were amputated at the coxal level and the stumps are shown by the cross-hatchings. The male is on the right throughout the sequence.

a. The male holds the chelicerae of the female and has begun to extrude the spermatophore (sp) onto the ground. b. The male moves backwards slightly, pulling the female: the whole of the spermatophore is exposed beneath him, the stalk touching him in the ventral region of the prosoma. c. The male jerks the female upwards and towards him, rearing up himself. As he releases his pull on her, her genital operculum (g) catches on the hooks of the spermatophore. d. In pulling the hooks of the spermatophore the female has bent it and the valves have been everted into her genital aperture. In this posture the pair stand for about five minutes. e. The male, with his sting erected, chases the female off the spermatophore.

spermatophore were everted but for some reason they did not enter into the genital ducts of the female. In three of these cases the spermatophore has nevertheless been pulled free of the male's body, and he stood for some time without making any further attempts at jerking the female. The pair then broke up. In the fourth case, the bent spermatophore still remained below the body of the male and he continued his efforts to pull the female into the correct position although there was in fact little hope of inserting the everted spermatophore into the female. Eventually the spermatophore was kicked clear of the pair and they then stood for about five minutes before the male chased the female away.

In the final case, the spermatophore was pulled sideways without ever being opened. It remained, however, touching the male's body and he continued his jerking movements for about a quarter of an hour. The female then suddenly attacked the male and he broke away and retreated. It will be seen that in these cases when the male is no longer stimulated by the spermatophore he moves to the next facet of the normal behaviour pattern, namely that of standing still.

The interval during which both animals remain immobile is presumed to be that in which the sperm are evacuated from the capsule, possibly aided by pressure from the genital operculum. Certainly there is no sign of assistance from the male.

It is clear that the behaviour of the male breaks up the pair; since he has hold of her he can also release the hold. However, on two occasions it was the female who was seen to make the first move. Although the male has frequently been seen to chase the female off the spermatophore this does not always occur, for she will sometimes push the male away before he has made any attack on her. From the facts of case B, it was already known that the female is capable of getting rid of the spermatophore without his assistance. The manner in which the male rushes away after mating may possibly be a general scorpion tendency as suggested by Fabre (1923). It certainly occurs in <u>Parabuthus</u> and <u>Opisthacanthus</u> (p. 145).

The supposition made in considering case B, that the "searching" performed by the female is not directed towards the spermatophore is supported here. Teleologically there is no further use for this unless it is to be eaten by the female, an occurrence reported in certain Thysanura (Lawrence, 1953). This latter possibility might involve the cheliceral chewing which was reported, but the fact that the spermatophore was ignored in two instances when the "searching" brought it within the reach of the female does not support the view. There is some possibility that this "searching" might be concerned in some way with ensuring that the sperm mass travels well into the vagina - it may also be the behaviour by which the sand is picked up into the vagina. If the former is true, i.e. that the "searching" is concerned with sperm travel, it would appear to be a behaviour pattern released when the courting/mating male has made a retreat, since the female in case A "searched" although she had picked up none of the sperm from the spermatophore that the male had deposited.

A point arising from this fact is that, if the male is chased off before the female O. latimanus has picked up the spermatophore, she is unable to do this alone. If she starts "searching" once the male leaves, her genital aperture is pressed flat on to the substrate. In this position she would not be able to stand with it directly over the capsule, the condition which would seem necessary for the entrance of the valves into the vagina.

Lastly, it is possible that the cheliceral chewing in O. latimanus female subsequent to mating might indicate a tendency which Fabre (1923) stressed strongly in B. occitanus, namely that after courtship or mating the female may catch and kill the male if she can. If this were so, there would be good teleological reason why the male should hurry away as soon as the female is free of the spermatophore. However, alternate cheliceral movements are used in so many different behavioural patterns in O. latimanus, e.g. stridulating, digging, washing and feeding, that no definite conclusion can be reached.

One observation remains rather inexplicable in the light of this knowledge of the mating of *O. latimanus*. This is that the males may be found sharing burrows with the females during the summer.

An observation made by Serfatty and Vachon (1950) might offer a possible explanation of this. A male *Buthotus alticola* was seen to promenade with a female and then, without releasing his hold, to assist at the birth of her young. In the case of *O. latimanus* the males and females found cohabiting a burrow in the field were never accompanied by young ~~and~~ but in at least three cases the female was certainly not pregnant. Moreover observations made upon parturition in *O. latimanus* indicate that there is certainly no need for the male to play the rôle of midwife.

Another possible explanation relates to the assumption of Fabre that the scorpion pair seek some shelter, preferably their own burrow, in which to mate. Consideration of this idea involves two distinct problems - namely when, and where, does mating normally occur?

The Time of Mating.

It was in early January that O. *latimanus* males were first found living together with the females. In most cases the females were adult but in two they were preadult, while in a single case an adult male was sharing a burrow with a younger nymph. One of the adult females had only very recently moulted, for when found she was still soft and her moult was yet moist. Brought into the laboratory and kept for a few days, this female then allowed the male who had been sharing her burrow to mate with her. She then attacked him violently and certainly, had they been in the burrow, she would have driven him forth. The idea that a preadult scorpion moults to adulthood, mates with the male who has been waiting for her, and then chases him off, is supported by the following observation. One female, not quite so recently moulted, was found to refuse the advances of a male scorpion and then, when she was killed, her ovariuterus was found to contain numerous active sperm, while the embryonic biberons had begun to develop in the diverticula.

Males waiting for the females to moult to maturity has been reported in the spider, *Philagus militaris* (= *Paraphidippus marginatus*) (The Peckhams, 1889) and there seems no reason why it should not be applicable here. What does seem strange however is that an adult male should be sharing a burrow with a younger nymph, an animal which would not moult to maturity until at least a year later. There would seem to be three fairly obvious explanations to this problem. Either the reasoning which leads us to expect the young nymph to be immature or to need a year to reach maturity is incorrect, the observation was that of a "chance" mistake on the part of the male scorpion, or that the characteristics of a female by which a male scorpion recognises a mate also occur in the nymphs, namely absence of the typical male anatomy and behavioural responses. Suffice it to say here that no actual mating has ever been seen to occur between a preadult female and a male though the latter will often go as far in the courtship as the promenade. The sign stimuli concerned in the recognition of a mate will be discussed later.

The Place of Mating.

Though it would appear probable that the male scorpion sometimes waits in the burrow with the female in order to mate with her when she is ready, it is not clear whether the actual mating occurs in the burrows or not. Braun (1956) reports that spiders in the field will normally mate under cover of some sort, usually in the nest or burrow, while in the laboratory they may be observed to mate out in the open. It seems possible that in the case of *O. latimanus* the same state of affairs obtains: the scorpions have been watched as they go through the entire mating sequence in the open in the laboratory though in the field this would normally occur in the privacy of the burrow. Three arguments can however be raised against this view. Firstly, as was mentioned earlier, courting couples of *O. latimanus* in the laboratory pay no attention either to naturally or artificially made burrows or shelters. In another animal, *O. austerus*, I have found that this is not so, and it is partly the fact that the cover-seeking behaviour is so clear here that leaves little doubt that it has not been overlooked in *O. latimanus*. The second argument is a purely theoretical one: it is difficult to see how the complicated movements and elaborate behaviour patterns could occur in the cramped quarters of a burrow without becoming un-coördinated. Lastly there is a single observation of a male *O. latimanus* meeting a female in her burrow in one of the glass-sided terraria where the events in the burrow could be observed. Here the male came to the mouth of the burrow, juddered and walked in towards the female. Taking her pedipalps he tried to drag her out and after a short time succeeded. The loose soil surface was apparently not suitable as a mating ground and the pair broke apart after a further amount of courtship. Nevertheless the male had definitely removed a female from her burrow with the apparent purpose of mating with her. As it stands, the evidence points towards the conclusion that in *O. latimanus* the mating actually occurs outside the burrow as a rule, though further observations are clearly necessary to settle the matter finally.

Lastly, there is at the moment ~~on~~ no information as to the time of day that the scorpions normally mate. Observations of the event have been made in the laboratory from 9 a.m. until as late as 12 midnight, but this does not mean that mating should be expected to occur at any time over this period in the field. Conjecture, from the fact that the animals are out of the burrows then and the temperature is not too low, makes it probable that courtship and mating in *O. latimanus* probable begin shortly after dusk and last till the early hours of the morning. Seasonal variations in the sexual activity have already been dealt with in the section on development.

The Formation of the Spermatophore.

This structure, formed in two separate sacs within the mesosoma of the male, is clearly the paired "penes" or ejaculatory canals described for *Buthus occitanus* by Dufour (1856) and since referred to either in the terminology of Pavlovsky (1917) as the "chitinous skeleton of the Paraxial organs" or, more recently (Abd-el-Wahab, 1957) as the shaft of the ejaculatory organs. Both the spermatophore sacs and the spermatophores within them have been discussed as systematic characters in various scorpions (Vachon, 1940) but certainly whenever their probable function was mentioned it was that of hemipenes which unite temporarily, that is at the time of mating, and effect fertilisation (e.g. Vachon, 1949, 1953). The fact that the two half-spermatophores do unite as a true spermatophore, which is extruded entirely from the male, is indicated, not only by the manner in which it has been observed to function, but also by its absence in the spermatophore sacs of adult males that were killed immediately after mating.

Thus, to reiterate, there are two quite separate spermatophore sacs in O. latimanus and possibly in all other scorpions as well. So that the spermatophore, in the same manner as the inner layer of that in the cockroach (Gupta, 1947),is formed in two parts and these two must join before the structure can be used. Unlike the cockroach, however, these two parts remain distinct until immediately before the actual ejection; in a dissection of O. latimanus each half-spermatophore can be entirely separated both from the sac in which it is formed and from the spermatophore half of the other sac (Fig. 35a). Each half-spermatophore has its own vas deferens and sperm receptacle. From such a dissection it is clear that the parts of the half-spermatophore which lie mesially contribute to the parts of the entire spermatophore which are dorsal - the single valve, chitinous hook and sacculus. Further, from dissection, it can be seen how the sacculus probably serves to hold part of the sperm mass (sp.m. of Fig. 35b) in position; also how the succulus, and therefore the sperm mass, will move if the valve is shifted to the "everted" position, that is the move that brings the sperm mass to lie in the "correct" position in the complete spermatophore to pass through the funnel made by the pair of valves. (See arrow of Fig. 33c). Lastly from dissection of the spermatophore sacs of

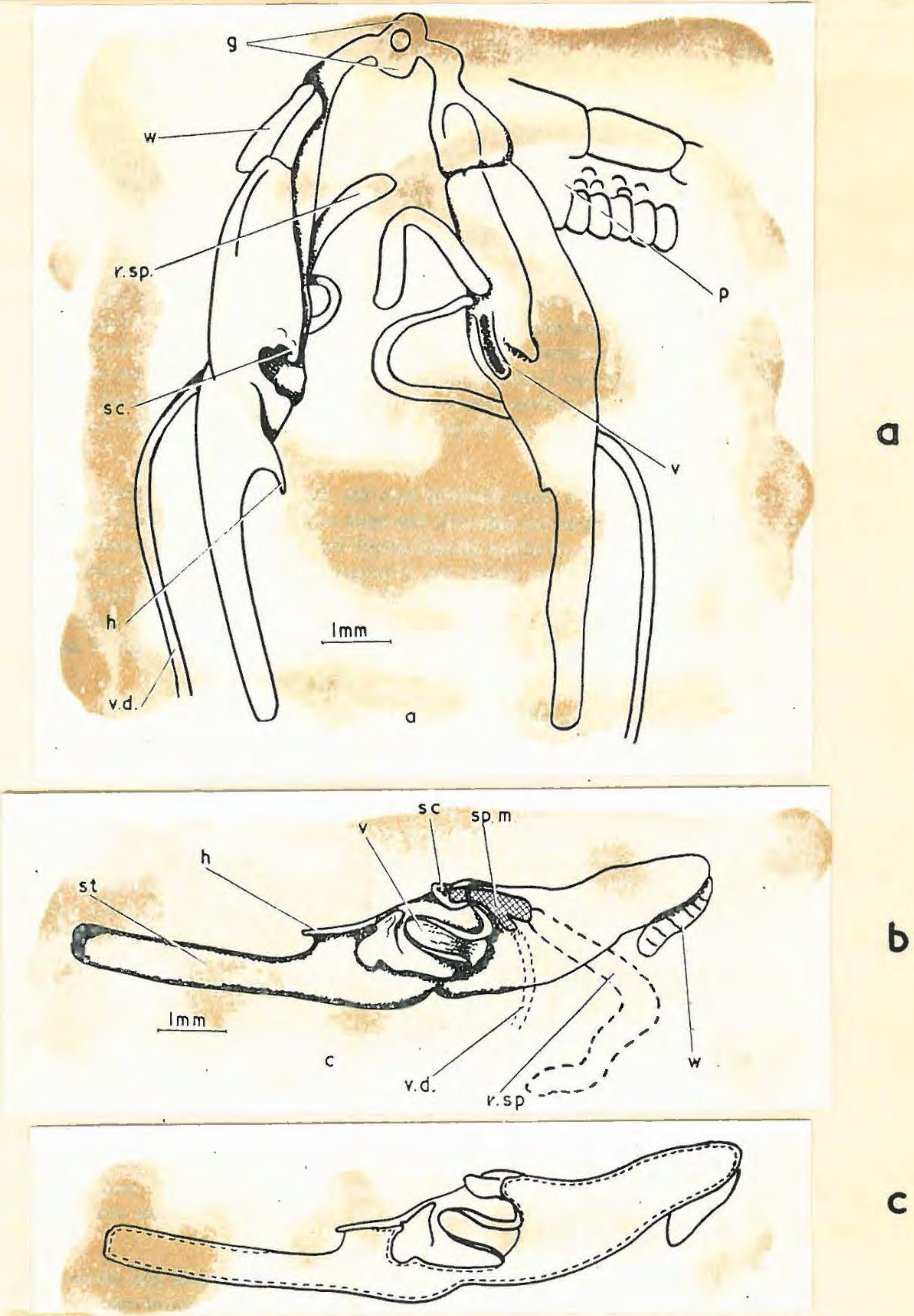


Fig. 35. O. latimanus: the spermatophore sacs.

(a) A dorso-lateral view of the two spermatophore sacs. That on the right is entire and the outlines of the half spermatophore within are indicate. On the left the wall has been partially dissected away to reveal the half spermatophore.

(b) A view of the right side of an half-spermatophore dissected free of the spermatophore sac. The relative position of the vas deferens and sperm receptacle within the spermatophore sac is indicated. For display purposes the wing has been displaced to the right.

(c) Outline of the half-spermatophore shown in Fig. 35b. The edges along which the two spermatophore-halves join are indicated by dotted lines.

g., glands on the common ejaculatory duct; h., hook, p., portion of pectine showing beneath dissection; r.sp., sperm receptacle; sc., sacculus; sp.m., sperm mass; st., stalk; v., valve; v.d., vas deferens; w., pedal wing.

O. latimanus, it is clear that one of the pedal wings is already attached to each of the half-spermatophores. This structure looks superficially like a gland on the spermatophore sac until the whole sac is opened and the real morphology of the parts recognised. It is doubtless the pedal wings within the spermatophore sacs which Vachon (1949) calls the "Glandes anterieures."

At the time of fertilisation, the two half-spermatophores are finally attached over the greater part of their edges, except for a short region of the stalk where they remain separate (Fig. 35c). After ejection of the spermatophore both the sperm receptacles of the male are found to be empty.

It is not known at exactly what time, prior to deposition, the two halves of the structure are joined together. Because of the very short common ejaculatory duct, it is probable that fusion occurs as the spermatophore is actually being extruded; if this is true, it may account for the slowness of the extrusion which may take up to five minutes. Certainly a male that was killed after he had already taken up the cheliceral grip but had not got any further than a few jerks of the "promenade à deux" was found to have the two parts of his spermatophore still quite separate. Two "glands" open into the common ejaculatory duct and may well be concerned with joining the two spermatophore halves together (Fig. 35a). (These are perhaps the "dorsal annex glands" of Abd-el-Wahab, 1957).

The Spermatocleutrum

A structure called the spermatocleutrum was mentioned earlier (p. 124) in connection with the original observations on mating. A piece of tissue, labelled "stopper" in Fig. 33b, was initially thought to constitute the "post-nuptial plug" of O. latimanus and this idea did in fact influence the development of the hypothesis of how mating takes place in these animals.

Subsequent observation showed that the "stopper" in that particular instance, Case A, was not the spermatocleutrum but, in fact, part of the tissue lining the inner surface of the valves. However, as Vachon (1952) affirms, very few adult female scorpions are without a spermatocleutrum in their genital tracts. These structures are fairly small in the scorpions that I have examined, that in O. latimanus being approximately 1.5 mm. wide by 0.6 mm. long (Fig. 36a). In those parts where the spermatocleutrum is sclerotised it is very hard and dark-coloured, but the structure as a whole is very delicate and brittle, and is frequently found in the form of very small remnants within the female. In P. planicauda it has a very much more definite form than that of O. latimanus (Fig. 36b), while within the genus Opisthophthalmus there are certainly differences which are constant between one species and another (cf. Fig. 36 a and c). This fact might well be one which will help in deciding on the exact relationships of the species within the genus.

In 1952 Vachon admitted that there was no evidence on which to decide how the spermatocleutrum arises within the female; yet in 1953 he was prepared, without any apparent further reason, to state that it is the male who places it in position. Evidence from O. latimanus is not conclusive on this point but it strongly indicates that the spermatocleutrum is formed within the female after fertilisation, or at least mating. In three cases where females were killed within fifteen minutes of mating, there was no sign of the normal spermatocleutrum, but one of these animals had a structure lying at the base of the common vagina and this was almost certainly a newly formed spermatocleutrum with the normal lines of sclerotisation very indistinct. This observation, together with the fact that no structure resembling a normal spermatocleutrum has ever been found in an opened spermatophore, leads to a strong suspicion that the spermatocleutrum is the solidifcation of some secretion within the ducts of the female; whether that of a female or male gland is not clear.

The function of the structure is also obscure. Vachon (1952) suggests that it may be concerned with preventing further mating. Certainly the spermatocleutrum is lost at parturition, as examination

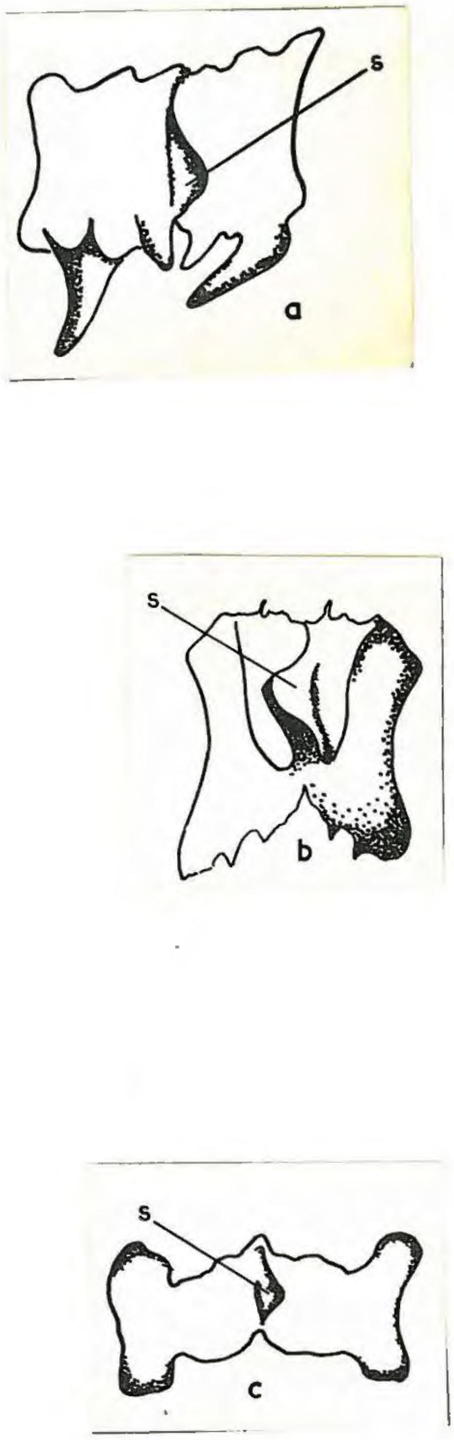


Fig. 36. Spermatocleutra of scorpions. Stippling indicates sclerotisation and in all cases the part of that structure nearest the top of the figure is deeper within the female's duct. *s.*, "sail", a median protrusion, which lies anteriorly within the female.
(a) *O. latimanus*
(b) *P. planicauda*
(c) *O. austerus*.

of recently parturient females has shown, but the spermatocleutrum of *O. latimanus* would certainly seem inadequate as a mechanical impedance to the explosion of the valves of a spermatophore. It might act as a "behavioural impedance" in that a female who still has a spermatocleutrum within her would refuse a courting male, but, as it has already been established that a pregnant female will allow a male to mate with her, the idea lacks support, unless it could have been shown that that particular female had lost her spermatocleutrum in some way other than at parturition.

The other possibility is that is serves to prevent the newly introduced sperm from escaping from the female duct as has sometimes been suggested as a function of the vaginal plug of rodents and chiroptera. It must however be remembered that the characteristic sclerotisations probably only develop after some time, and thus its function may well be one which does not arise immediately after the actual insemination.

Mating in Other Scorpions.

Since the first part of this account was written, and indeed published (Alexander, 1956) my attention has been drawn to a note by Angermann (1955) on the mating of the scorpion *Euscorpius italicus*, while a report on the mating of *Bothriurus bonariensis* (Koch) has also been published (Zolessi 1956). In addition I have been able to watch the insemination of the scorpion *Parabuthus planicauda*. All these three animals use the method of "indirect transference of spermatophore" already described here for *O. latimanus* and it would appear that there are only slight differences in behaviour and in the structure and functioning of the spermatophore. This means that we now have information on the mating habits of scorpions in four of the six families: Scorpionidae (*Ophisthophthalmus*), Chactidae (*Euscorpius*), Bothriuridae (*Bothriurus*) and Buthidae (*Parabuthus*) and it therefore seems likely that the same mechanism for insemination occurs throughout the whole order Scorpiones.

This is satisfactory in a number of ways, the first being that it allows the question of the mechanism of mating in the arachnids to be seen from a wider view, the result of which is presented late (p. 171A). Secondly it permits the testing of certain hypotheses put forward in the case of *O. latimanus*. Furthermore I have now observed scorpionids other than *O. latimanus* both in courtship and mating and these observations, together with those mentioned above, suggest possible explanations for features which had to pass by earlier without analysis. It is proposed therefore that no straight description be given of any of the courtship or mating patterns of other scorpions, but that only those aspects which appear to throw light on the events and their interpretation in *O. latimanus* will be considered.

The Spermatophore

The major features of the structure of the known spermatophores of different scorpions are shown summarily in Fig. 37. From this it can be seen that amongst the three species of *Opisthophthalmus* there is almost no variation in the form of the spermatophore. The length and orientation of the valves after mating, as well as the shape of the end of the stalk appear to be consistent differences between the species and may prove to be of systematic importance.

In *Opisthacanthus* the process, which I will term "capsular explosion", that brings the enclosed sperm masses to the surface of the spermatophore, and the means by which this is brought about, are both apparently identical to those in *O. latimanus*. The valves which are everted are clearly homologous with those found in the three species of *Opisthophthalmus*, but the aperture through which the sperm mass emerges is not at the apex of the valves but nearer the "proximal" end of the capsule, that is nearer the hooks. In addition the aperture is different in shape and appears superficially like two separate sperm-openings though, in point of fact, these are united by a narrow channel.

The differences between *Opisthacanthus* and *Opisthophthalmus* show how the spermatophore of the latter is related to that of *Parabuthus* and, by extension, to the rest of the Buthidae. In

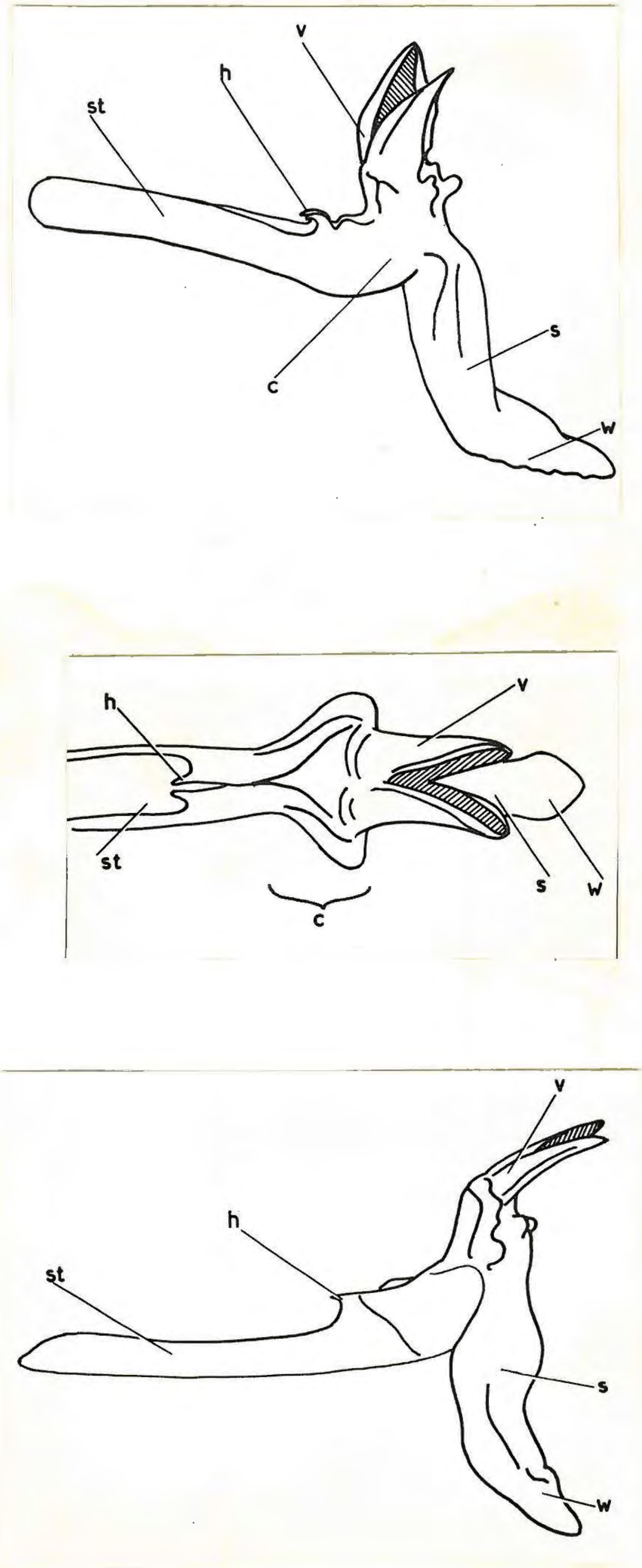
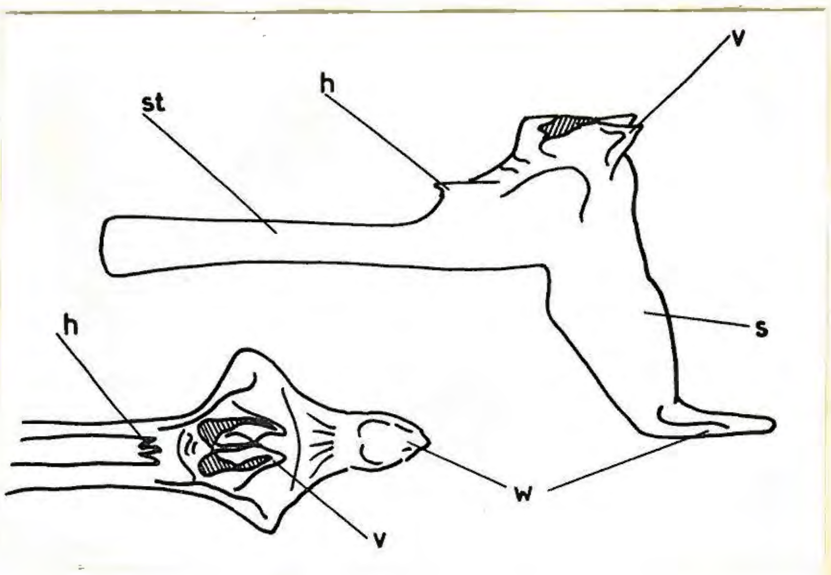


Fig. 37a. For legend, see two sheets on.



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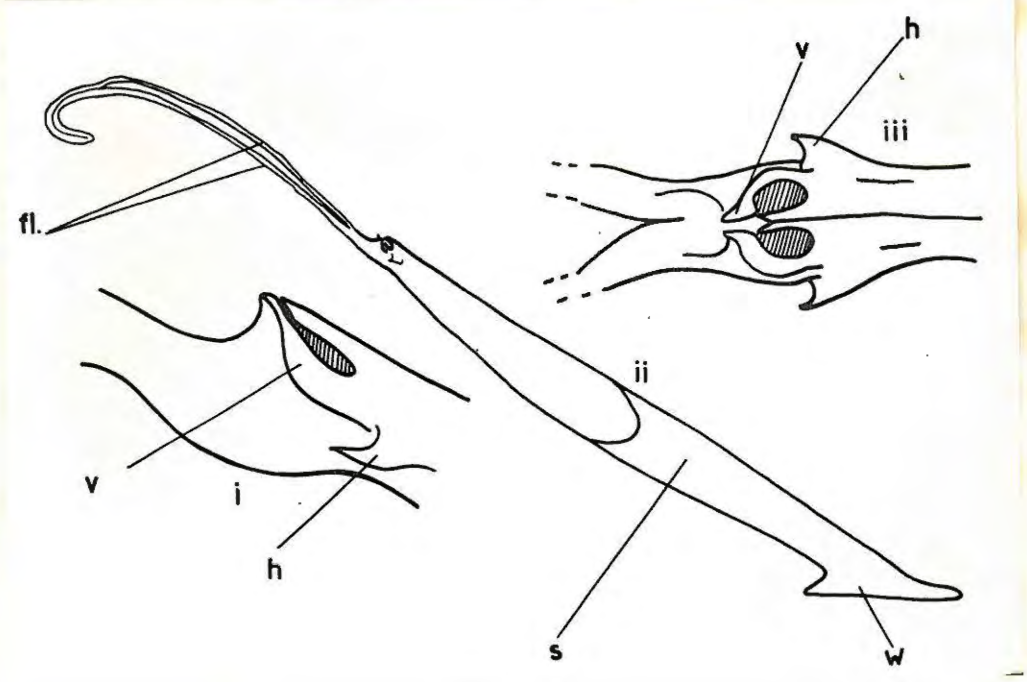

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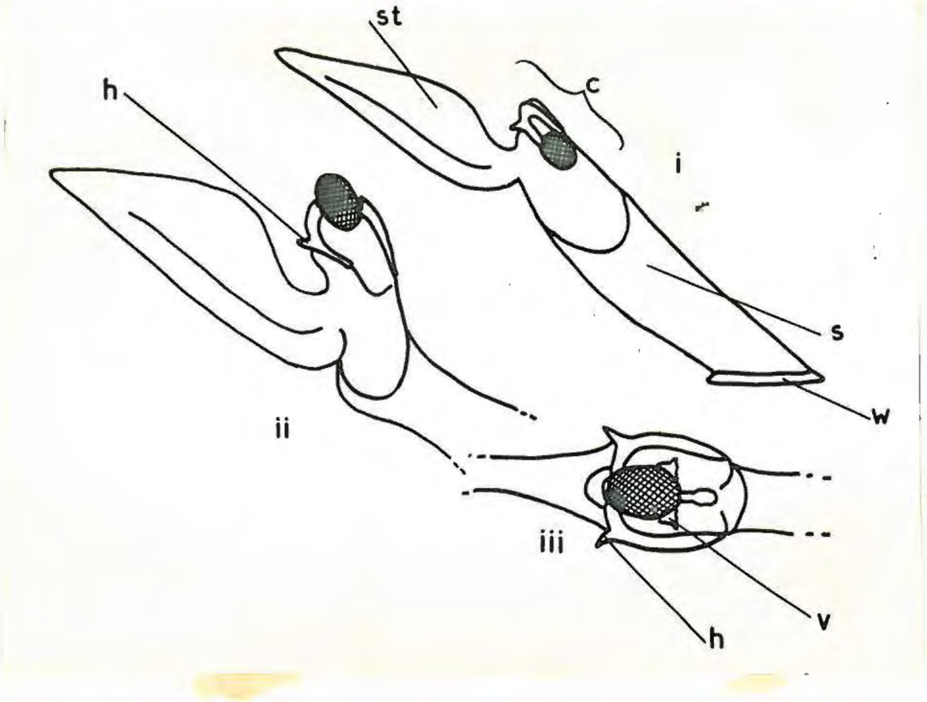

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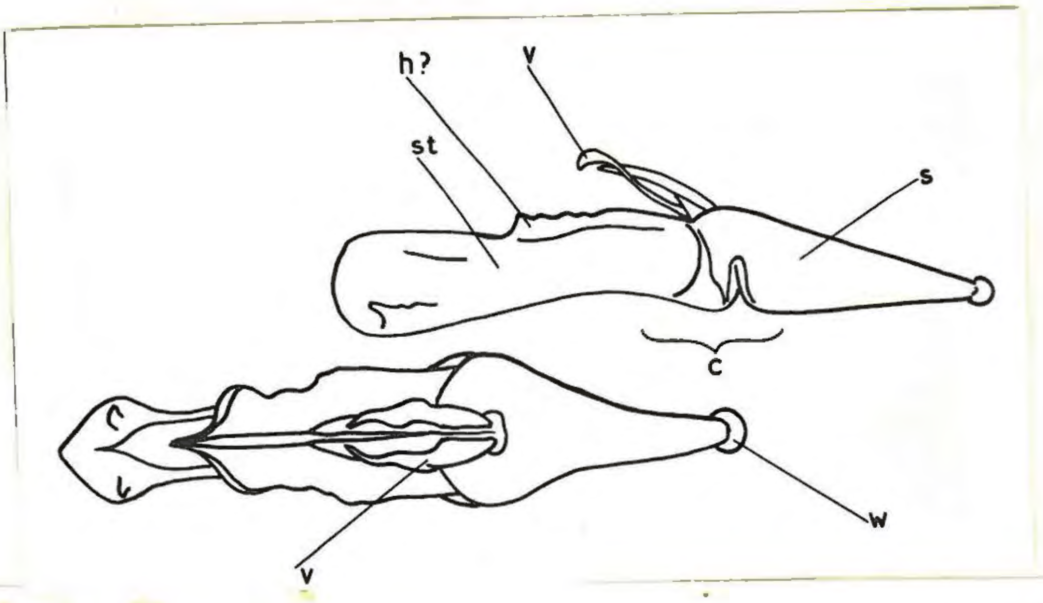


Fig. 37. Spermatophores of different scorpions.
(a) Opisthophthalmus spp. Top, lateral view of that of O. nitidiceps; Middle, dorsal view of that of O. latimanus; Bottom, lateral view of that of O. austerus.
(b) Opisthacanthus validus. Above, lateral view; below, dorsal view.
(c) Parabuthus planicauda. i, lateral view of capsular region; ii, lateral view of entire spermatophore; iii, dorsal view of capsular region.
(d) Euscorpius italicus. i, lateral view of complete unexploded structure; ii, lateral view of the capsule and stalk portion of exploded spermatophore; iii, dorsal view of exploded (?) capsule region.
(i after Angermann, 1955; ii and iii after Angermann and Schaller, 1955)
(e) B. bonariensis. Above, lateral view of entire spermatophore; below, dorsal view of entire spermatophore (after Zolessi, 1956).

Cross-hatched area, aperture through which sperm mass escapes; double cross hatched area, sperm mass.

c., capsule region; fl., flagellum; h., hooks; s., stem portion; st., stalk portion; v., valve; w., pedal wings.

Parabuthus the valves, stippled in Fig. 37, do not stand up as phalanges at all and the partial partition between the sperm openings in *Opisthacanthus* is, in *Parabuthus*, replaced by a substantial pair of struts which separate the sperm-openings. The sperm-openings and the hooks are even closer to each other than in *Opisthacanthus*, the two parts lying at the same level along the spermatophore. In addition the hooks are situated more laterally so that, instead of being medio-dorsal, they are almost lateral. It is clear that there are also some gross differences in form of the spermatophore relative to *Op. validus*; the stem region is much longer and narrower while the two stout halves of the stalk found in *Opisthacanthus* are represented by the long and and separate flagella (Fig. 37, *fl*) in *Parabuthus*.

The differences in the spermatophores of the scorpionids and buthids are explicable in terms of differences in gross anatomy and behaviour which have already been mentioned. Correlated with the large development of the pedipalpar claws, the scorpionids have neither the toxicity nor those behaviour patterns of the buthids in which stinging attack is strongly emphasised; features which appear to be reflected in the generally intractable and antisocial nature of this latter group. Certainly the scorpionids are not prone to kill and eat each other and a claw fight will usually end with the "weaker" scorpion retreating without fatal injury. This difference in general level of sociability would lead us to expect that in the buthids close contact during courtship and mating would be as limited as possible, the whole event would be short and, maybe, the method of sperm uptake would be rapid, perhaps by way of a superficially placed sperm mass which could be taken up by contact, in contrast to the prolonged insemination process in *Opisthophthalmus* where deep union between spermatophore and female ducts is achieved by way of the strongly developed spermatophore valves. In the main these expectations are fulfilled; the buthids use the "safer" pedipalpar grasp which therefore demands a much longer stem to the spermatophore, the valves are almost flat and certainly never held within the female's body and it appears almost certain that the sperm is taken up as two sperm balls almost simultaneously as the spermatophore hooks are jerked by the female. These hooks lie, relative to their position in *Opisthophthalmus* both more laterally and more distally; further the bases of the pectines are specialised in the females of *Parabuthus*. These facts, taken together, suggest that it is the pectines rather than the genital plates which catch the hooks. This idea finds support in the fact that the genital operculum of the female of *Parabuthus*, like that of the male, is paired and unsuitable for pulling the hooks: this may be contrasted with the marked sexual dimorphism in the form of the genital operculum found in *Opisthophthalmus*.

It is very much more difficult to recognise in the spermatophores of *E. italicus* and *B. bonariensis* the parts homologous with those of the scorpions which have already been discussed. The differentiation into stem, stalk and central capsular region is clear enough: further tentative suggestions are implied in the labelling of Fig. 37.

The last point to be mentioned concerns the reaction of the male to the spermatophore beneath him. It was suggested (p. 136) that in *O. latimanus* the male continued to try to pull the female across the spermatophore as long as the stalk continued to stimulate his ventral region. Because the cheliceral grasp of *O. latimanus* allows the couple to be very close together, the stalk of the spermatophore can, in these circumstances, be used effectively as a sign stimulus to the male. Where, however, the couple use the pedipalpar grasp and are consequently always much further apart, it would seem impossible for the same type of signal to be employed. The distance over which the male would be required to pull a female and yet return to his previous position with the stalk of the spermatophore still beneath him, would appear to be too great. In *P. planicauda*, where such a pedipalpar grasp is used, it is clear that the flagella of the spermatophore (Fig. 37c) act as elongated stalks and it is by way of these that the male discovers when his pulling of the female has been successful. As soon as the female has made the "correct contact" with the spermatophore, it is pulled back with her and the flagella, until that moment still partly within the genital operculum of the male, are pulled free, presumably serving as a sign stimulus to him as they leave his body. Certainly his whole behaviour changes once the flagella are freed from him.

In E. italicus and B. bonariensis where apparently the pedipalpar grasp is also used, the problem as such does not arise, for it appears to be the female who plays the active rôle in insemination once the spermatophore has been deposited on the substratum. The male merely draws or "invites" the female forward, presumably until his body is free of the spermatophore stalk. Then, in E. italicus the female, apparently by the use of her pectines, orients her body over the spermatophore, probably in such a manner that her genital operculum will catch the hooks of the spermatophore; she then pulls back, bends the spermatophore and thus effects insemination. In B. bonariensis there are no details of the actual insemination, but certainly it does not appear from the description to depend upon the activity of the male.

The Evolution of the Spermatophore.

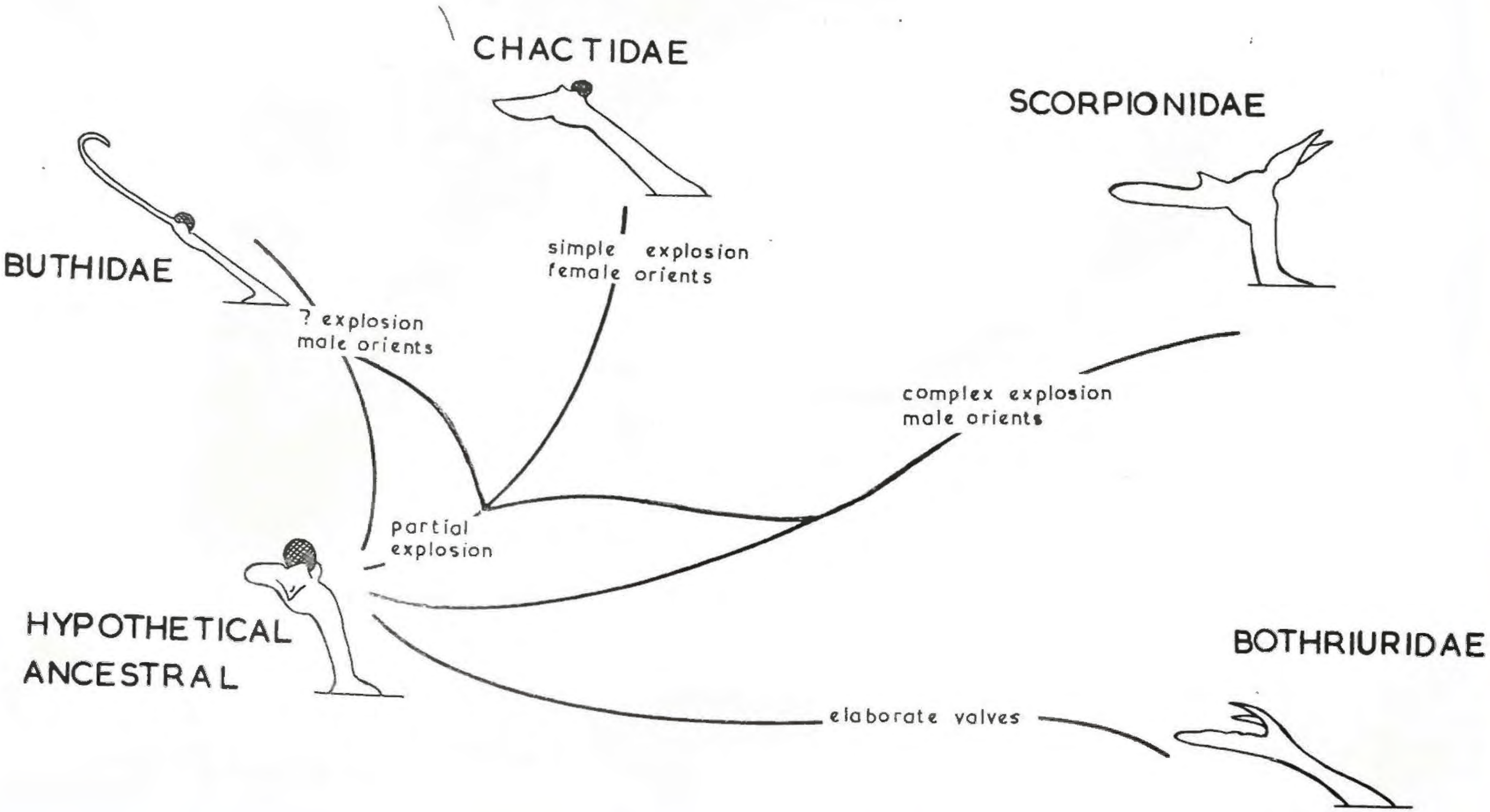
The difficulties which attach to the recognition of the detailed homologies of structures within and adjacent to the capsule of the Chactidae and Bothriuridae with those of the Scorpionidae and Buthidae have been hinted at above and they will certainly remain until the exact function of each structure is known. Moreover we have as yet no information upon the structure of the spermatophores of either the Vejovidae or Diplocentridae, both of which have primitive characteristics. It may therefore seem foolish to speculate upon the original form of the scorpion spermatophore and its subsequent evolution. Nevertheless such an attempt serves to display clearly the major features which have been discussed above and, provided it is treated as only a provisional hypothesis, can focus attention upon certain aspects of the mating of scorpions which, in future studies, seem to deserve particular attention.

It is easiest simply to present the picture as it appears to me rather than to defend the interpretation with arguments which can, in the nature of the case, carry little weight. The ideas which I wish to put forward are summarised diagrammatically in Fig. 38a.

In the primitive scorpions I consider that both partners were active in the process of insemination; the male deposited the spermatophore and perhaps pulled the female across it, but she then orientated to the exposed sperm mass held in position by rudimentary valves. The orientation of the female to the spermatophore was effected by a short stalk and assisted by lateral projections which are later developed into the hooks. Today this pattern persists almost unchanged in the Chactidae, but the hooks have migrated somewhat proximally and become integrated into the structure of the capsule, so that, when they are pulled by the genital operculum of the female, the enclosed sperm mass is brought to the surface by an explosion of the capsule.

From the primitive arrangement three further lines can be recognised. In the Buthidae the sperm mass remains exposed, as I have postulated in the ancestral form, but the active part is played by the male: the function of the long flagella in this process has already been described. In Parabuthus, the hooks are retained in their primitive position close to the capsule, but, lying more laterally, are caught by the specialised regions of the pectines as the female is drawn across the spermatophore. As they engage with the pectines, they bring the exposed sperm mass into contact with the genital opening and thus insemination is effected.

In the Scorpionidae the sperm mass is initially enclosed within the spermatophore as in the Chactidae, but the male is the active agent in the insemination as in the Buthidae. He draws the female across the spermatophore, the stalk acting as a sign stimulus in the same manner as the flagella of the Buthids. The hooks are here far more proximal than in the Buthidae or Chactidae but, as in the latter, integrated in the functioning of the capsule. They are caught by the genital operculum of the female which results in the explosion of the capsule: in the genus Opisthophthalmus, at least,


CHACTIDAE
SCORPIONIDAE
BUTHIDAE
simple explosion
female orients
? explosion
male orients
complex explosion
male orients
partial
explosion
HYPOTHETICAL
ANCESTRAL
BOTHRIURIDAE
elaborate valves

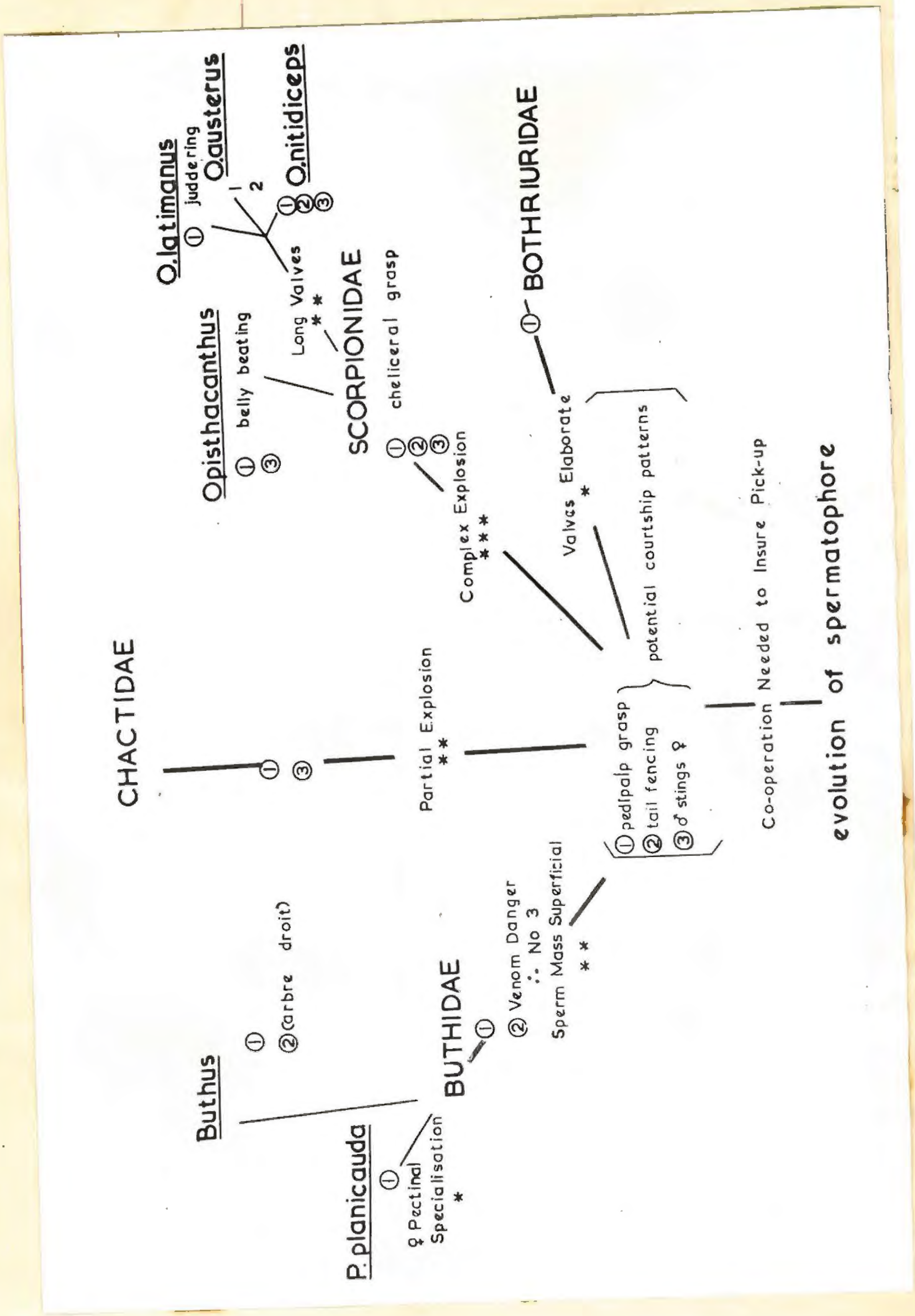


Fig. 38. (a) Representation of the possible evolution of spermatophore form and function in the scorpions
(b) Representation of the possible lines along which courtship might have evolved in the scorpions. Single asterisk denotes that little co-operation between the pair (and, by implication, courtship) is required. Two asterisks denote that some co-operation is necessary, while three asterisks indicate that considerable co-operation should be expected.

the valves, originally simply retaining the sperm mass, have become greatly elaborated to form a funnel which enters deeply into the female genital ducts.

In the Bothriuridae there has been an independent elaboration of the valves to guide the sperm mass into the female duct, but here, as in the Buthidae, there appears to be no capsular explosion: further, in the Buthidae the hooks serve to guide the sperm mass towards the genital opening, while here it seems likely that the elongated valves act both as guides and as a funnel to convey the sperm into the body of the female.

In three of the families the pedipalpar grip is found and it seems probable that this, found also in the pseudoscorpions, is primitive. It has been suggested above that this is a reflection of the unsociable character of these animals. This determined that in the ancestors the process of insemination was hazardous and therefore perforce rapid. In these three families three distinct paths seem to have been taken to ensure a greater likelihood of successful impregnation : In the Chactidae by the development of capsular explosion, in the Buthidae by the elaboration of the hooks into guides, and in the Bothriuridae by a comparable elaboration of the valves. Only in the Scorpionidae is it known for certain that a cheliceral grip is used and here, where the dangers involved in mating are far less, the principle of the capsular explosion has been developed together with enlargement of the valves so as to provide a certain entry of the sperm into the genital ducts of the female.

A Comparison of the Spermatophore of the Scorpion and Pseudoscorpion.

It seems possible that a similar attempt might be made to produce a comparable picture of the evolution of the spermatophore within the pseudoscorpions. Vachon (1938) describes and figures the spermatophore of Chelifer cancroides and here the structure (Fig. 39b) and its mode of deposition and pick-up appear, at least superficially, very like that postulated for the primitive scorpion. The

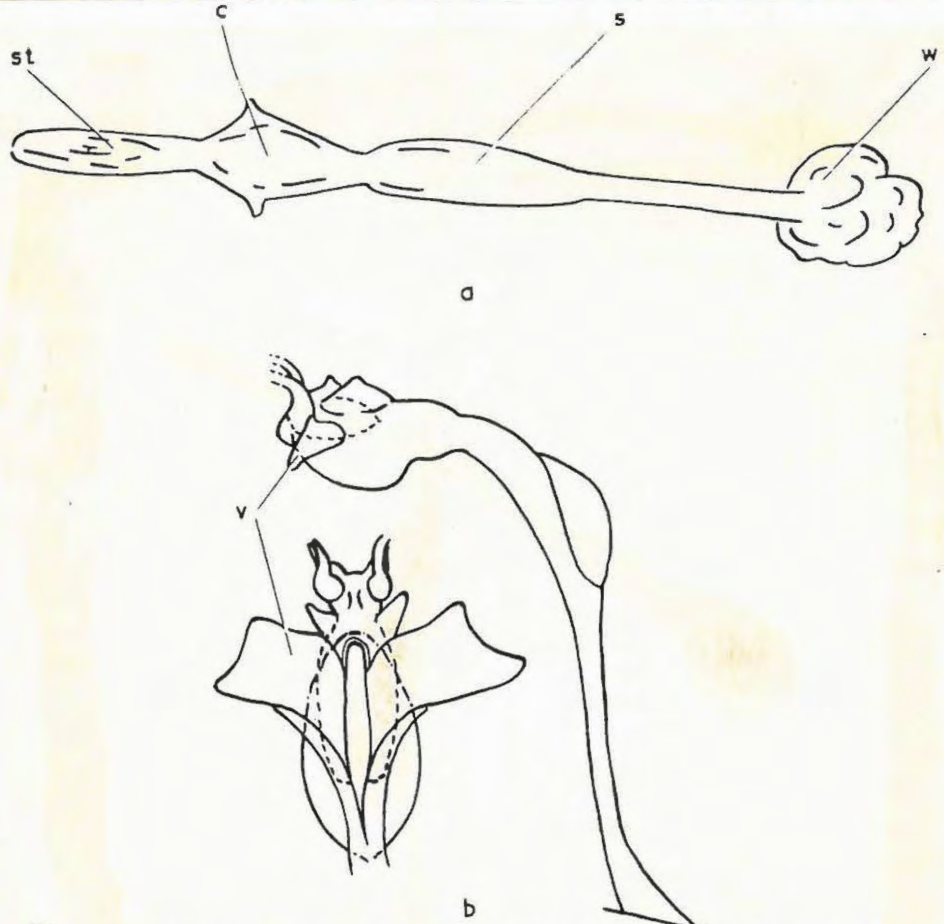


Fig. 39.—Spermatophores of two pseudoscorpions showing a general superficial similarity to that of *O. latimanus*.

a. *Chelifer latreilii* Leach after Kew (1912). The division into stalk (st.) capsule portion (c) and stem (s) with pedal wings (w) is clearly indicated though no details of structure are available.

b. *Chelifer cancroides* L. after Vachon (1938). The lack of pedal wings and a substantial stem contrasts with the form of the *O. latimanus* but superficially the "valves" (v) appear very similar.

spermatophore is ejected forward from the genital opening of the male, the region of the pedal wings, the stem and the capsule being clearly analogous, if not directly homologous, with those of the scorpions. The sperm mass is apparently freely exposed, being merely held by the "valves". There is no significant stem which could be used by the male when he orients the female on to the deposited spermatophore and indeed it is the female herself who is responsible for coming forward and guiding the sperm mass into her genital opening.

In the case of C.latreilii, Fig. 39a, as described by Kew (1912) there are no details of the capsular region available but clearly the presence of the "stalk" here suggests that this may have evolved, as has been postulated for the Scorpionidae and Buthidae, to aid the male in orienting the female relative to the spermatophore. Sure enough, we find that in this animal the male does guide the female aperture on to the capsule region of the spermatophore.

Even if similar explanations of the adaptive modification of spermatophore structure and "pick-up behaviour" can be worked out in detail for the pseudoscorpions, they would not constitute evidence supporting the basic homologies of the spermatophores within the two groups. Indeed Vachon (1938) describes the formation of the spermatophore in C. cancroides and this appears so different from that of O. latimanus as to suggest that no phylogenetic conclusions should be drawn from any comparisons between the two groups. In C. cancroides, according to Vachon, there are not two separate half-spermatophores and the structure is formed as an entirety. On the other hand this difference in mode of formation may reflect only the fact that in the pseudoscorpions the sperm mass is merely deposited on top of the spermatophore, sometimes no even being held in position by the valves, while in the scorpions the sperm mass is, in most cases, within the spermatophore itself. This may necessitate the spermatophore being formed in two distinct halves. Moreover, in Parabuthus the two half spermatophores are not entirely separate in that the tips of the stems are always joined together. It may be significant that it is in this animal there is some possibility that the sperm masses are exposed to begin with.

Courtship - Preliminaries to the Promenade.

It has been tentatively suggested earlier that the promenade à deux is itself concerned with the male's finding or preparing a suitable area for the deposition of the spermatophore and that earlier parts of the courtship behaviour are therefore concerned with the more normal functions of courtship, namely recognition of a member of the other sex as a possible mate and attainment of the necessary degree of co-operation with the partner by "stimulation" to the required state of passiveness or the eliciting of other more active responses at the appropriate times.

A scorpion behaviour pattern which has been generally recognised to fulfil this latter rôle, that is mutual stimulation, is the classical arbre droit, described for E. occitanus by Fabre. In this each scorpion raises its tail above its prosoma and fences with or caresses that of the other animal. Serfatty and Vachon (1950) suggest, from their observations on B. alticola, that this arbre droit may well be concerned with mutual recognition so that both courtship functions have in point of fact been ascribed to this pattern.

It has already been said that only a slight indication of the arbre droit ever occurs in O. latimanus: on very infrequent occasions there may be a brief raising of the tails of the two animals during the time when the male is trying to grasp the pedipalps of the female. Whatever the function of the "classical arbre droit" this is either absent or fulfilled by some other behaviour pattern in O. latimanus. It will be suggested below that this alternative pattern might well be the juddering.

Support for this comes from the fact that in the other two species of Opisthophthalmus whose courtship and mating I have watched, namely O. austerus and O. nitidiceps, there is no sign of any juddering but the arbre droit is considerably more marked. In O. austerus, whose general behaviour is closer to O. latimanus than is that of O.nitidiceps, the male tries to take the pedipalps of the female, both animals raise their stings and push at each other with them, though, as in O. latimanus, there is no sign that either animal ever inserts its sting tip into the tail or body of the other. This modified arbre droit invariably occurs here.

In O. nitidiceps the events are always very much more marked and the encounters of the stings much fiercer. In all cases that I have watched the male has always actually stung the female, sometimes in the pedipalps, sometimes the mesosoma. It may be mentioned in passing that it is O. nitidiceps which shows a fairly marked sexual dimorphism of the tail, a feature which is less noticable in O. austerus and even less so in O. latimanus. This is in keeping with the fact that, of the three species, it is O. nitidiceps whose tail is most used in sexual encounters. Since the tail is covered with hairs which are undoubtedly sensory organs, there is no reason why the arbre droit should not function in mutual stimulation, nor why, both from the sexual dimorphism and the fact that only the male appears actually to sting, it should not also be concerned in mutual recognition.

In the same way, the juddering of O. latimanus could serve for both purposes. The responses of the "other" animal to the juddering would depend on whether it was a female or another male; if it gave no reciprocal juddering it was therefore probably a female, and further juddering might then serve to stimulate her to adopt her responsive pose. The effects in the female could well be mediated by way of vibrations passing through the ground and picked up by the female's pectines, (Cloudsley-Thompson, 1955a). That such vibrational effects might be expected to occur in scorpion courtship is supported by the fact that in the laboratory Op. validus does certainly use a beating on the substratum as a preliminary to the promenade, the male striking his mesosoma about ten times very rapidly on the ground. No serious suggestion can be made here for the evolutionary origin of the behaviour shown by Op. validus. The only possibility envisaged is one which might also apply to the "belly-beatings" and abdominal stridulations of certain male spiders, namely the ritualisation of the initial movements made during the ejection of the spermatophore or those of deposition of the seminal fluid. If this were true, in the cases of *Op. validus* anyway, it would tend to support, however vaguely, the idea that the behaviour is concerned more with stimulation of the female than mutual recognition. This is on the grounds that a piece of behaviour intimately concerned with the actual mating might readily become a "stimulatory sign stimulus" concerned with eliciting the correct responses from the female.

In summary, it would seem possible that the juddering of the male *O. latimanus* is comparable in function with the modified arbre droit which occurs in the other *Opisthophthalmus* species observed, but that the exact function of either piece of behaviour has not been determined. It could be the means of mutual recognition or of stimulation; it would appear very difficult to design experimental techniques which distinguish between these two, since interference with one will invariably affect the other.

The Evolution of Courtship

In discussing the arbre droit, the variations in the expression of this pattern which occur amongst the scorpionids have been described. Similar variations occur among other scorpions. Thus in *E. italicus* the male stings the female; in *Buthotus alticola* and *Buthus occitanus*, the two animals fence with their tails while in *Parabuthus* and *Bothriurus* there is no arbre droit at all. A tentative reconstruction of the evolution of the actual process of insemination has been attempted above. A similar speculative reconstruction can be made of the events of courtship on the assumption that the forerunner of the arbre droit is a simple stinging whose aim was to reduce the female to a condition of sufficient tranquillity to permit her to fulfil her rôle in the process of insemination. This condition persists in *E. italicus*, where the male brings his sting over and stings the female several times, normally in one of the joints of the pedipalp.

In the scorpionids it would seen that the co-operation between the two animals needs to be more firmly established in that the mechanism for "exploding" the spermatophore is complex. This additional co-operation seems to be gained in various ways; in Op. validus the stinging is retained as in E. italicus, but belly-beating is added; in O. nitidiceps stinging together with tail fencing occurs; only the tail fencing occurs in O. austerus, while in O. latimanus these have been replaced by the juddering.

In the case of the last two mentioned scorpions it is possible to see the replacement of a humoral "tranquiliser" by a direct behavioural response; in the case of O. austerus, the mutual movements of the stings directly release passive behaviour in the female. A similar condition would seem to hold in the case of Buthotus and Buthus, as well as Centruroides (Baerg, 1954a), where only the caressing of the two stings occurs. It seems possible that of the steps leading to stinging in the primitve courtship only the early ones are retained in the buthids, since their evolution towards a really toxic venom might endanger the life of the female if the male were required to sting her as part of the courtship pattern. It would be possible to describe this as the ritualisation of an intention movement, but it is clear that it is not the simple replacement of one behaviour pattern by another.

In Parabuthus and Bothriurus, however, there is no arbre droit, nor is it replaced by juddering or other recognisable courtship pattern. It is tentatively suggested here that this may be due to a decrease in the need for co-operation between the two partners. In Parabuthus the specialised pectines of the female, together with superficially situated sperm masses, may well ensure that the behaviour of the male in pulling the female over the spermatophore is comparatively simple: simple in comparison with that in Buthus, Buthotus and Centruroides, where there are no specialised pectines, or in comparison with that in the scorpionids where there is a capsular explosion which must be accurately oriented and in which timing is important. In Bothriurus it is possible that again a modification of structure reduces the difficulty of effecting insemination. Here it seems that the strongly pointed valves may be easily inserted into the female opening so that she need not be especially passive or otherwise co-operative.

To sum up, it is suggested that in the primitive courtship there were three facets - the pedipalpar grasp, tail movements derived probably from threat display, and the actual stinging itself. In Fig. 38b the lines of adaptive radiation arising from such an hypothetical system have been represented. As is shown, new behaviour patterns may be added where further co-operation is required, e.g. the belly-beating in Op. validus or the cheliceral grasp in all the scorpionids so far observed. One of the hypothetical three features may be modified, as for instance in the evolution of the classical arbre droit in Buthus, Buthotus and Centruroides. Where, on the other hand, any reduction in degree of co-operation occurs between the partners, features of the hypothetical courtship may be cut out altogether.

This view of the evolution of courtship in the scorpions is almost certainly grossly oversimplified - the question of sex recognition, and with this sexual dimorphism, as well as the possible stimulatory effect of the promenade, should surely modify the picture presented here. In O. latimanus these points have yet to be discussed, but since no comparative information is available, the facts for this scorpion can not add anything to the scheme proposed here. So although the deficiencies inherent in the representation put forward in Fig. 38b are freely admitted, nothing can yet be done to remove them.

The Promenade à deux.

It has already been suggested that this behaviour in O. latimanus is primarily concerned with finding a suitable surface on which to deposit the spermatophore. Observations on other scorpions has merely confirmed this and the only point which emerges is that a substratum which is the correct releaser for spermatophore deposition in one scorpion will not suit another; for instance, neither the table top, nor a sheet of blotting paper nor a hard earth surface, all of which were releasers for O. latimanus, would release spermatophore deposition in O. austerus, and the only suitable surface appeared to be that of a wooden sheet. As will be mentioned later, the specificity with which P. planicauda reacts to the surface provided as an arena for mating, is very striking, only a particular rough cardboard being effective. It seems very probable that this difference in the releasing effect of different surfaces in various scorpions may well be linked with differences in the types of soil on which the animals are found but so far no work has been done on this problem.

A second possible function of the promenade was that of bringing the female to a suitable degree of co-operation before any attempt is made to mate with her, a point which was briefly mentioned earlier. There is no record for the lengths of different promenades on standard surfaces in the cases of any of the animals observed. However it is very noticeable that, in O. nitidiceps, the female that is resisting strongly at the beginning of the promenade is entirely passive by the time the male stops his pulling of her and begins to mate. This may, however, be a reflection of the time which the venom takes to act.

It seems improbable that any simple relationship can be shown between the presence of courtship before the beginning of the promenade and the length of the promenade itself. Table V confirms this. Indeed, even if we knew that all of the promenades recorded above had been performed on a standard surface, this would be no

TABLE V.

The relationship between the presence of courtship before the beginning of the promenade and the length of the promenade itself.

Animal	Introduction to Promenade	Record of duration of Promenade.
O. latimanus	juddering	1 min.-1 hour (personal obs.)
O. austerus	tail fencing	15 minutes " "
O. nitidiceps	tail fencing + stinging	less than 20 mins. " "
Op. validus	belly-beatiug + "	10-24 mins. " "
B. occitanus	arbre droit	1-24 hours (Fabre, 1923)
E. italicus	stinging	30-60 mins. (Angermann, 1955)
C. insulans	arbre droit	? - 40 hours (Baerg, 1954)
L. quinquestriatus	# - #	3 hours minimum (Thornton,1954)
P. planicauda	# - #	5-30 mins. (personal obs.)
B. bonariensis	# — #	several - 12 hrs. (Zolessi, 1956)

guarantee that the information could be used comparatively, because we have already recognised the fact that one type of surface need not be as good a releaser for deposition of the spermatophore in one species of scorpion as in another.

Whatever the functional significance of the promenade, it certainly appears more and more clearly that the interpretation of its evolutionary origin in O. latimanus, that is the explanation that it has arisen from intention movements of picking up the spermatophore, can be taken for other scorpions as well. This comes out most strongly in the case of Op. validus. Here the promenade is very slow and with none of the violent jerkings which are apparent in the promenade of O. latimanus and more especially P. planicauda. Likewise, when the male draws the female on to the spermatophore the pull is slow and stolid without any of the strong back and forth action that has been described for O. latimanus.

Sensory Physiology of Courtship and Mating.

So far we have, in the main, considered only the behavioural aspects of courtship and mating. Clearly a number of interesting problems relating to the sensory physiology of these events can be formulated. Some of these are discussed below and the results of preliminary studies on this aspect of the biology of O. latimanus presented.

Soil Scraping.

The first matter to be considered is how the male scorpion obtains the information about the nature of the surface on which he is courting: how does he "know" whether it is smooth enough to hold the spermatophore safely or whether he must continue with his scraping activities? Earlier, in discussing burrowing, it was pointed out that O. latimanus appears to show some individual preference in relation to the soil type where it starts a burrow. No satisfactory evidence was obtained during the experiments to support the idea that information on the nature of the soil surface was obtained by way of the pectines. Once again the pectines may be suspected of being concerned with obtaining the necessary information.

The suspicion rests on two points. The first is that throughout courtship the pectines of the male can be seen to be especially active, sweeping very thoroughly over the ground on which the scorpions are courting. It is true that the pectines are almost always active as the scorpions walk but here their activity seems to be far more marked. In addition there is a single observation which must be quoted here: a male was pulling his female along a piece of blotting paper half covered with fine sand, and as soon as his pectinal region had crossed the boundary between the sand and clean paper he stopped his scraping and pulling and presently everted a spermatophore although the whole of the female as well as his anterior part was still in the region of sand. Although this is but a single observation and the event could have been due merely to a coincidence, it does support the hypothesis.

There is also circumstantial evidence from anatomy: the pectines are sexually dimorphic structures, those of the males having the greater number of teeth. Because of this dimorphism and the fact that the pectines are clearly sensory, earlier workers suggested that the male used them in courtship and mating, either to stimulate himself by way of perceiving the female or to find out the orientation of the female genital opening for the actual "copulation". Fabre (1923) goes so far as to suggest that they are also used to hold the pair close together, an idea that he may well have got from suggestions of Brongniart and Gaubert (1891). Even if these suggestions were to hold good for other scorpions, they certainly cannot be applied in the case of O. latimanus. Here it would seem that the only sexually distinct behaviour in which the pectines could be used during courtship and mating is that of site selection. However, as will be explained later, the female O. latimanus does appear to elicit a reaction from the male by way of a smell, so that it seems just as reasonable to assume that the greater development of the pectines in the male may be concerned with allowing him to "track" down the female by her scent-trail.

From these points no clear conclusion can be drawn. Experimental removal or inactivation of the pectines of the male certainly prevent the animal from mating, but as such experimental animals make little attempt at courtship at all, we must conclude that the operation on this species is too drastic to allow any conclusions to be drawn here.

In the buthid, Parabuthus planicauda, however, the body is normally carried much farther from the ground than it is in Opisthophthalmus and this, it would appear, prevents the operation having the unsettling effect that it does on O. latimanus. Amputation of the pectines in both animals can only be done successfully if the appendages are ligatured first and it seems that the stump and its ligature upset O. latimanus as they drag along the ground.

Thus P. planicauda is a much better subject for this particular experiment. Another advantage is that in this scorpion there is very clear selection of material on which the male will deposit his spermatophore. It was found that a particular rough matt carboard acts as a very efficient releaser for this behaviour and that the pair will continue their promenade over smooth paper, soil or plastic material until they reach the cardboard placed for them when they will immediately begin the actual mating behaviour. The distinctness of this "preference" makes P. planicauda an ideal subject for the experiment. In a typical experiment a male was first tested for his readiness to mate. If he proved sexually active his pectines were then amputated. He was then presented with a female in an arena offering a choice of cardboard and either loose soil or smooth plastic. In these conditions he would continue his promenading for so long, regardless of the suitability or otherwise of the substratum, that the female would eventually chase him off. It seemed that she was able to appreciate the difference in the surfaces across which she was pulled because she would go readily across the loose soil or clear plastic but once on the cardboard she would try to remain there. Part of her behaviour might, however, have been due to the fact that it is easier to find a firm foothold on the cardboard than the other two surfaces. Her pectines were nevertheless actively sweeping the surfaces.

From the above experiment there is no doubt that without their pectines, male *P. planicauda* do not recognise the cardboard as a suitable surface on which to deposit a spermatophore, but there is no evidence that the amputation has not merely destroyed their ability to deposit a spermatophore. Admittedly there is clearly no attempt to do anything except continue the promenade but it seemed desirable to make certain that such animals will still be capable of mating.

To meet this requirement the pectines were inactivated, at least as receptors sensing the character of the substratum, by sticking them to the immovable coxae of the legs by bands of a cellulose acetate glue such as Samsonite. These bands in no way incommoded *P. planicauda*, but the technique could not be used with *O. latimanus*. Once it was established that an experimental male would not deposit a spermatophore on the cardboard though he had been ready to do so before, the Samsonite was carefully removed from his pectines and, after a wait of a few minutes, he was replaced with the same female. In all three cases in which this procedure was tried, the male mated with the female after his pectines had been freed.

This result, while open to the general objection that a negative answer in such an experiment can never be conclusive, would appear to make it very highly probable that the pectines do indeed allow the animal to determine whether a surface is suitable or not for mating.

Inter- and Intra-sexual Responses.

Before any discussion of what is involved in releasing the intersexual behaviour, it may be profitable to look at the intrasexual responses.

Female to Female Behaviour.

If the cage is sufficiently large, that is at least more than 20 cm. square, a female O. latimanus will usually ignore or avoid another female. However, they do sometimes fight even when the cage is large, though they invariably do so if it is smaller. Before the animals go into a "clinch", the more aggressive animal or both will perform in a manner slightly reminiscent of the juddering of the male. With movements less jerky than the judder, she will take small steps back and forward, moving her body from side to side at the same time, and quivering the whole of her tail. This behaviour will be referred to as "waltzing". The emphasis lies entirely on the body and tail, while the widespread pedipalps are hardly noticeable.
If the other animal is smaller or less "offensive" she may take up a semi-threatening, semi-defensive posture (Fig. 40a). Her tail is erected in a way which would allow her to sting, but her pedipalps are folded in close to her chelicerae - slightly open but not as in the true "threat" pose (Fig. 40b) at least not the threat used at an "unknown disturbance", a human hand, a rat or a crab. Occasionally these stinging encounters have been seen to end in one scorpion killing and eating the other, but this has only happened after they have separated and re-encountered each other several times.
Usually, one female will break away from the fight after a few seconds, and then turn and rush away. It seems probable that, in the field, any animal that runs off after the attack of another female, could make good her escape (as, in point of fact, has been observed on one occasion). Sometimes the female from which the other is escaping will drop her aggressiveness once she has caused a retreat. More often, however, she will attempt to pursue the vanquished. In

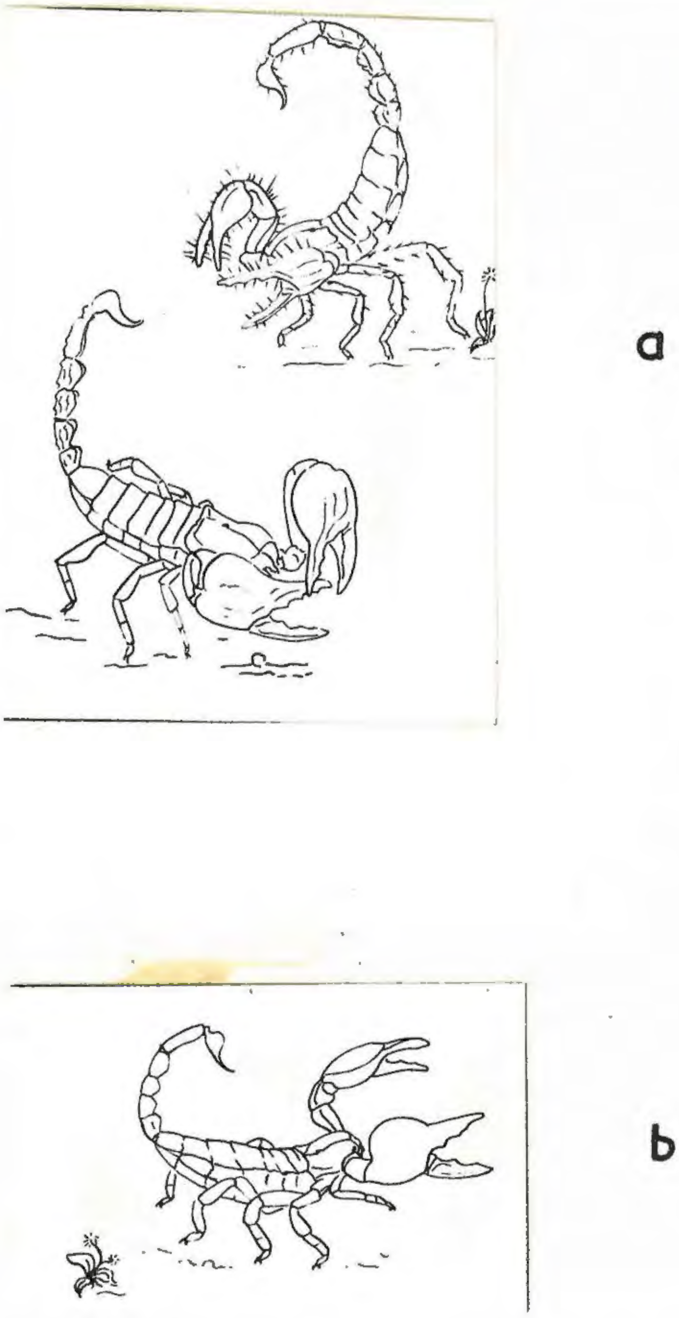


Fig. 40. (a) Representation of the semi-threat--semi-defense posture in a male O. latimanus, above, and in a female, below.
(b) True threat in a female O. latimanus

this the "seeking" behaviour from which it is thought that the judder takes origin can be seen clearly. Here there is no sideways movement of the body or tail, only a slight back and forth action of the pedipalps. The same behaviour is seen in a female who is chasing a male that she has just fought.

Female O. latimanus to female O. nitidiceps.

When the one female is O. latimanus and the other O. nitidiceps the encounters are far more fierce and there is less avoiding behaviour. The same waltzing movement and tail jerking are shown, as well as the same semi-threat, semi-defence pose. In two cases the O. latimanus has killed the female of the other species.

Male to Male Behaviour.

The male to male encounters have been fewer owing to the greater scarcity of males. In those that have been observed, the behaviour appears to depend on the conditions of the meeting. If the one male is almost motionless, an approaching male may judder at him and try to take his claws, the gesture prior to courtship, but then run away. Bristowe (1929) states that in some spiders, notedly the Attids and Lycosids, a male will take up his typical courting attitude in front of another male of the same species (Tarantula barbipes, observation by Locket), while the Peckhams (1889) say that the male of some Attids, (Astia vittata and Aelurillus v-insignitus) will display to their own reflections in a mirror. It is therefore not uncommon among arachnids for the initial sexual releaser stimuli in an animal to appear in both sexes, only the subsequent response of the courted animal indicating to the male whether he should continue with mating behaviour.

When one male approaches, judders at, and tries to take the pedipalps of another, the second male may either start to fight or get free and run away. The fighting, which is without the waltzing or semi-threat, semi-defence posturings of the female to female fights, usually consists almost entirely of wide-spread pedipalp attacks. That which has been observed has always been fairly mild and it is unusual for one male to raise his sting against the other, let alone get it inserted in the other's body. Occasionally a juddering movement will actually be seen in the wide-spread pedipalp attacks themselves, but, though the chelicerae are almost in contact at this stage, there is no indication of the one animal trying to take up the cheliceral grip with the other. (It seems possible that, prior to this step, the female normally gives a characteristic response, which may consist of orientation of chelicerae so that the male can take them). Usually the encounter breaks up after about 30 seconds and both may retreat or one runs off with the other following, juddering, behind, as if chasing a female.

Male O. latimanus to O. nitidiceps.

In addition to the juddering at another animal of the same sex, a male O. latimanus will judder at, and try to promenade with, a female O. nitidiceps. This behaviour has not proceeded further than these preliminaries, but since the female concerned had only just started being deserted by her babies, it is possible that the failure to proceed with the courtship was due to her internal state and not to the anatomical incompatibility of the two animals. Since the areas where the two animals are found are quite distinct and different, it may be that they never do meet in the field so that, while the mating response can still be compatible, the species remain distinct and the progeny fertile.

O. latimanus to P. planicauda.

Encounters with the smaller, lighter-coloured and more fast-moving scorpion, Parabuthus planicauda were interesting in that the scorpions would have nothing to do with each other; the O. latimanus rushed off in one direction, the P. planicauda in the other. Once a female O. latimanus chased but lost an escaping P. planicauda. Since an O. latimanus may sometimes retreat from a beetle the size of

P. planicauda, there is no telling whether *O. latimanus* recognised the other animal as a scorpion or not. The response, however, was clearly different from that directed towards *O. nitidiceps*, who is larger than the normal type of prey but was attacked nevertheless. *Hadogenes sp.* on the other hand, was attacked immediately, without hesitation, waltzing, widespread pedipalps or juddering. Seeking behaviour, however, occurred after its retreat.

Analysis

The conclusions to be drawn from these observations are not at all clear. Firstly there is the possibility that *O. latimanus* is capable of a "scorpion recognition." It must be made clear initially that if any scorpion is absolutely motionless, another animal will ignore it completely, walk over it, in fact. "Scorpion" would apparently include both sexes of *O. latimanus* and at least the female *O. nitidiceps*. The recognition is suggested by the reactions given specially to scorpions, namely the juddering, the waltzing, the semi-threat/semi-defence and the charactersitics widespread pedipalp attack. It may well be that distinctions are made between other kinds of scorpion and prey but as yet there can be no analysis here. What serve as the sign stimuli for "another scorpion" has not yet been ascertained. The fact that *Parabuthus* and *Hadogenes* are not recognised while *O. nitidiceps* is, suggests that there may be some connection with the claws and recognition; since, apart from these, there are no obvious features which link *O. latimanus* and *O. nitidiceps* but separate them from *Parabuthus* and *Hadogenes*. *Hadogenes* is more or less the same size as the two *Opisthophthalmus* spp., is roughly the same dark colour as *O. latimanus*, while both *Parabuthus* and *O. nitidiceps* are almost yellow. *Hadogenes* and the two species of *Opisthophthalmus* move slowly, whereas *Parabuthus* moves fast. A female specimen of *O. latimanus* was found in the field with one of her claws amputated and the stump freshly healed. Males of *O. latimanus* would have nothing to do with her and the females only paid attention after quite some time. Then, however, a threatening animal would orient her threat not at the whole of the mutilated female but at her single claw, behaviour which appears to support the hypothesis,proposed above, that recognition of "scorpion" may be concerned with the size and form of the claws. Removal of both claws has not yet been tried with any success, as the wounds have never healed properly. Immediately after the operation, though the wounds are plugged with plasticine or colloidin, the animal is in such a state of upset that it is pointless to quote any reaction that she elicits in another.

Once the other animal is "recognised" as a scorpion there is the question which of the scorpion specific patterns will be released. As was implied earlier, this seems to depend both on the internal state of the animal concerned as well as the behaviour of the other. The responses of one O. latimanus to another can be most easily summarised in a table (Table VI).

This suggestion of behavioural and internal releasers can in most cases be applied successfully to the interscorpion encounters that have been witnessed in this laboratory. There is, however, another possibility that has been observed here. On one occasion a male and two females were put in one of the terraria at the same time. Both the females in turn attempted to attack the male but he retreated and would have nothin/g to do with them, not even showing any signs of juddering. Another female was taken out of her dish, the male was put into the dish from which she had just been removed, and she was put with the other females. No further attention was paid to the male until he was heard as he battered the sides of the dish noisily in his violent juddering. He was then put with the third female and immediately he returned to his juddering behaviour, later taking her pedipalps in the promenade à deux. Now it is possible that he had been excited up to juddering point by the actual presence of the two females, but had been prevented from exhibiting this by their attacks, and that when he was alone the juddering was shown: that is, there is a possibility that the third female had nothing to do with the fit of juddering

Table VI. Reactions to members of the same or the opposite sex by *O. latimanus* adults.

The responses shown are those of the types of individual shown at the top of each column to those in the left hand column.

	Responsive male	Unresponsive male	Responsive female	Unresponsive female
Responsive female	Juddering + promenade	Retreat	No reaction	No reaction
Attacking female	Fight, then retreat	Immediate retreat	? fight then retreat	Instant retreat
Retreating male or female	Following and juddering	No reaction	Either no reaction or following and seeking.	

in the dish. It is possible that her demeanour at their meeting elicited both juddering and courtship. On the other hand, a more obvious explanation would be that this third female, her responsive state indicated later by her acceptance of her part in the courtship, had left some sign of this state in her dish, presumably ~~a scent~~ an odour. In the terrarium initially, the females had not continued to chase the male so that there appeared ample opportunity for him to judder without interference. In addition the reaction within the dish was given so quickly after the male was put into it that some definite connection was obvious. Another observation which can be seen as possibly supporting this odour hypothesis is the behaviour of one male towards a short length of string over which the female had been climbing. He caught this in his claws after juddering at it and tried to draw it off. Again it is possible that he was just excited to such an extent by the presence of the female that any object of a suitable size would have been enough for him to court.

Furthermore there are indications from a single test case that a male scorpion is capable of following the "trail" of a responsive female scorpion. The test was easy to devise because of the thigmotactic behaviour of <u>O. latimanus</u> mentioned earlier (p. 13). If a male is put into a fairly large dish he will immediately go to the edge of this and will walk round and round the perimeter: thus any behaviour in which a male does other than walk round the edge of a dish is very probably directed by some drive other than that of normal escape. If the "abnormal" path that he takes coincides with that which has been made by a receptive female some short time before, there is a high probability that the male is by some means following the track of the female. A large dish was lined with clean blotting paper, a receptive and attractive female was put in the centre of this and a smaller dish inverted over her. She immediately went to the edge of the inverted dish and began walking round and round inside it, thus leaving an easily defined "track". After some circling, the female and the smaller dish were removed and a responsive male was introduced into the large dish. His initial path can be seen in Fig. 41 and would certainly suggest strongly that he was following the track of the female. His behaviour especially supported this, for he went slowly and "feelingly" and several times when he would have gone beyond the limit of the track, he turned back, apparently deliberately. Although on further trials no such positive result was obtained (see trials, b, c, & d of Fig. 41) this "female tracking" experiment certainly suggested that it was worth testing the olfactory sense of O. latimanus.

To test this, O. latimanus individuals were placed singly on large sheets of blotting paper, within a ring of clove oil, camphorated oil or terpineol. Walking about within this circle a scorpion would occasionally put its pedipalp across the border of chemical substance and then rapidly withdraw and try walking in another direction, Fig. 42. It would therefore seem that the smell of these three substances is offensive to O. latimanus and is possibly detected by sense organs on the pedipalps. In most cases where the scorpion had been trying to cross the smell border for some time, it appeared to accommodate to the smell and would pay no attention to it, though after an hour or so away from it, would react as before when placed within the circle.

Painting the entire pedipalps with Gestetner Correcting Fluid caused the scorpions to ignore the smell boundary in the majority of cases, but occasionally they would react as did the controls. Either the painting upset the animal to such an extent that it could not pay attention to the stimuli coming off the oil, or the sense organs are, to a large extent anyway, situated on the pedipalps. Painting the backs of the controls with the Correcting Fluid did not cause them to ignore the chemicals, so that it appeared probable that the latter explanation is correct.

Dipping just the end of a needle in the chemicals and holding the instrument close to various parts of the scorpion body supported the hypothesis. The animal gave a marked avoiding reaction when the needle was held near the pedipalps, though it was never touching any

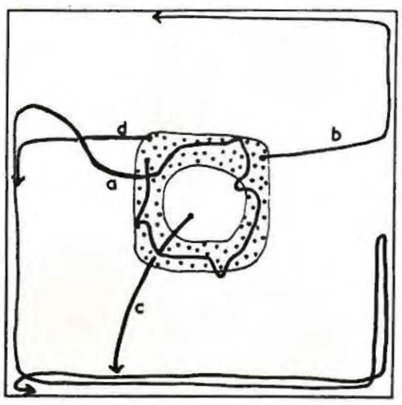


Fig. 41. Result of an experiment for testing whether or not a male scorpion will follow a scent track of a female. Stippled area - track of a sexually responsive female scorpion; a to d successive trails left by a responsive male. Trail a alone gives support for the male's ability to follow the female's scent track.

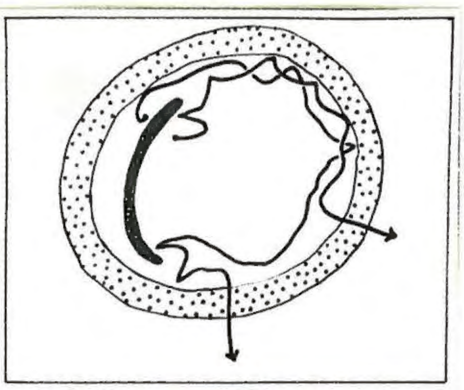


Fig. 42. Result of an experiment for testing the sense of smell in a scorpion. Stippled area - stain of terpineol; double stippled area - stain of clove oil. Two successive tracks of a scorpion put on to the test paper are shown. The initial avoidances, indicated by the zig-zagging of the track, were seen clearly in the behaviour of the animal.

of the sensory hairs, and though there was never any such response to the control (clean) needle. Near the back or the tail, the smell elicited no reaction but held near any of the walking legs it caused the scorpion either to walk away from the site of stimulation or occasionally to lift only the leg being stimulated. Efforts at cauterising away all of the sensory hairs and thus removing the ability to respond to smell met with no success, although an animal that had had its pedipalps and legs covered with vaseline gave almost no response. As it was felt that the negative evidence of "no reaction" would not be of any great conviction if the animal were seriously upset, no attempt was made to remove various parts of the limbs concerned.

It seems clear that in some spiders anyway there is a sense of smell - Pritchett (1904), McIndoo (1911) and Hewitt (1917) - and that in some cases it plays a rôle in the male to female relationship (Bristowe and Locket, 1926, Berland, 1932). The first two mentioned workers relate how a female in two species of tarantula, _Tarantula pulverulenta_ Clerik. and _T. barbipes_ Walck. will begin courtship display if placed in a dish in which a mature female of the same species has been sitting. In the case of _Trochosa ruricola_ DeGeer the male even displayed on one occasion when the female concerned had been only an immature, half-grown spider. Kaston (1936) has, in fact, found that the agent that causes the male _Pardosa milvina_ to initiate display before a female of the same species can be dissolved off by washing the female in ether, and that such an animal is no longer attractive to the male spiders. If, however, the washings are evaporated on to a plate, and the female placed on this, the male will once again display before her. There is no indication as yet that pseudoscorpions use a sense of smell in sex recognition, but in arachnids, terrestrial animals with weak visual responses and in many cases a necessity for some display before it is safe for the male to touch the female, it would not be surprising to find that, in many cases, one of the initial sign stimuli for sexual behaviour is one of smell.

Conclusions.

The elaborate courtship of the scorpion would appear to be related to two difficulties which arise during scorpion fertilisation. Firstly there is the anatomical difficulty. In opisthogoneate animals, internal fertilisation is fairly simple as far as mounting the female and holding on during coition is concerned. A completely receptive female may not be as necessary as she appears to be in the terrestrial progoneate arthropods where the genital apertures are not easily accessible. Unless some elaborate anatomical peculiarity is involved, an intricate courtship, procuring unison in the intersexual responses, seems the most adequate solution to the problem. Whether it would be true to say that, in a comparison of any opisthogoneate and progoneate arthropod, the former would have the simpler courtship is a question which may only be answered when further observations and analysis have been done on more of these animals. If true, it does appear also to be logical; if, however, some opisthogoneate animals have a complicated courtship, they may do so in spite of their opisthogoneate condition.

The second difficulty of fertilisation in the scorpion is the similarity of the two sexes and the generally recognised "antisocial" tendencies of the animal. As has been emphasised already, my observations on O. latimanus in regard to generalised statements of scorpion cannibalism indicate that this may be overemphasised. Be this as it may, the similarity of the sexes and the animal's carnivorous nature may prevent fertilisation from taking place, in that the possible partner may be mistaken for another male or meal.

V. A DIGRESSION ON SPIDER MATING.

"It is difficult .... to give a plausible explanation of the origin of the type of mating characteristic of spiders."

Petrunkevitch (1952).

We have seen above that in the mating of scorpions, the male deposits a fairly substantial spermatophore on the ground and the female receives the sperm from that part of the structure which enters her genital opening. This knowledge, which has been recently ~~re~~acquired, allows arachnid mating habits to be seen as a whole, for there are now only a few groups in which these are totally unknown, and thus permits an approach to the question of the origins of such behaviour. The present consideration of spider mating does not offer any new information on the details of sexual behaviour in spiders but is a re-appraisal of the known fadts in the light of the recent observations on other arachnids.

A male spider, shortly after he reaches maturity, deposits a drop of semen on the web on which he lives, on that of his mate or on one especially constructed for the purpose. Dipping his palps alternately into this drop, he draws the sperm into the swollen tips of these appendages. This is the process of sperm induction, first described by Menge in 1843. In some cases this sperm induction occurs only in the presence of the female (Bristowe & Locket, 1926) while in others (e.g. the tarantulas of Baerg, 1928) the female need not necessarily be there. Later the male advances towards the female with the courtship characteristic of the species or the female may make the advances, as in the cases reported by Montgomery (1903) and Locket (1926). He mounts her, again in a manner characteristic of the species, and inserts first one, then the other palpal tip into her genital opening, although, in certain rare cases, both palps are inserted together. During these insertions the sperm are transferred into the female. In most spiders sperm induction and actual mating occur only once during the life of the male (Petrunkevitch, 1952) but in some, e.g. the tarantulas, they may occur as many as four times, each mating being preceded by the process of sperm induction.

Most workers on the subject would agree with Montgomery (1903) that there is "neither anatomical nor embryological reason for supposing that the ~~aplpi~~ palpi ever had been appendages of the genital aperture." He comments on the peculiarity of the "double process" of spider mating - the sperm induction and then the actual transference of the sperm to the female - and makes two suggestions as to how the phenomenon could have arisen.

If the pedipalps were originally used as clasping organs during a copulation in which the genital apertures of the pairing animals were apposed, the depression in the epigynum of the female might have evolved to correspond to projections upon the palpal organs of the male and thus led to the elaboration of a tube within each of the palpal organs; thus the sperm induction and the actual mating could be dissociated.

Alternatively, he suggests, the palps might have been used originally to carry drops of semen from the male to the female genital opening and later, when the appropriate apparatus for the storage of sperm had been evolved, the male would discharge semen onto the web, take it into his palps and later pass it into the female with these organs.

Both of these hypotheses do in fact allow the possible selective advantages of the behaviour to be recognised: it permits the male to prepare for the mating beforehand, and, when in the proximity of the female, to be as quick as possible with the actual insemination. Where the female is very often bigger than the male, where the animals are carnivorous, preying on arthropods more or less their own size, and where there is no development of social instincts which would check cannibalistic tendencies, it would certainly be safer for the male to remain with the female for as short a time as possible when mating.

The difficulty is that neither of the hypotheses makes any attempt to explain the "double process" which is the basis of the problem. The former shows only how the pedipalps might have been elaborated to form a "sperm-gun"; the latter assumes that the pedipalps played this rôle from the beginning. Neither of them offers any explanation of the origin of a sperm induction where the sperm are first shed externally before being introduced into the female. Indeed both explanations would lead one to expect that the male would take the sperm directly from his genital opening into his pedipalps. In point of fact, Petrunkevitch (1952) states that the male spider cannot reach his genital orifice with his palps.

The only other solution offered is that of Bristowe (1929) and this is, in the main, merely an elaboration of the second hypothesis of Montgomery. Bristowe says: "In the primitive arachnid the chelicerae were chelate, and used by the male to hold the sperm after it had been ejaculated and to place it in the female vulva. Then at a later stage, the sperm was picked up by one of the longer pairs of appendages and transmitted to the female by them. In course of time the appendages used for this purpose became specially modified and small cavities appeared at the tip of the palpi to hold the sperm." Here too the origin of the sperm-induction has merely been side-stepped.

In the hypothesis put forward here some attempt is made to explain this very point. Since the explanation offered arises from a comparative survey of all known arachnid mating behaviour, it is intended to start by considering a hypothetical protoarachnid and its possible manner of fertilisation.

The relationship of the Xiphosura to the true arachnids is still unclear but from the time of the early anatomical work of Lankester (1881) to the serology and heart physiology of recent times (Leone, 1954 and Sawaya & Soares, 1949) it has been apparent that the relationship is fairly close. It is well therefore to consider the mating behaviour of the king-crab. It is very simple: the male clings to the back of the female and when she lays her eggs he covers them with sperm (Shuster, 1950). Quite apart from the possible relationship of the Xiphosura to the true arachnids, this is the sort of mating behaviour which might well be expected in a protoarachnid, in that it is behaviour normal amongst aquatic animals and it is commonly agreed that the arachnids must have arisen from some such beast.

Once the arachnids became truly terrestrial, internal fertilisation became highly desirable because of dangers of desiccation of the genital products. Furthermore, internal development of the embryo, which probably evolved in many forms as a protection against desiccation, clearly demands internal fertilisation. Certainly some form of internal insemination is one of the prerequisites for terrestrial life in general. In the scorpions, pseudoscorpions, solifuges and certainly in some ticks and mites, [redacted] the difficulty was overcome in the following manner: the male still simply extrudes the sperm but a spermatophore is elaborated about it so that a variety of methods become available for its transfer into the female. The problem of the origin of this behaviour will not be considered here, but clearly studies on the evolution of similar habits in newts, where transfer of a spermatophore has evolved from a simple amplexus, may be relevant (see Noble, 1931).

However, where the male is the same size as the female throughout the group, where there is some social instinct developed (e.g. in harvestmen which tend to be gregarious: Savory, private communication and personal observation), where the animals are parasitic (e.g. ticks and some mites) or where they are phytophagous (e.g. some mites) direct insemination could be evolved. The genital opening of one animal could be applied to that of the other and, as has occurred in the phalangids, intromittent organs associated with the genital segment could have evolved. It is not clear whether such a line of evolution could have allowed within it the development of intromittent organs from structures merely associated closely with the genital region, e.g. the mouthparts of the ticks. It seems, however, more probable that, at least in the case of both the ticks and the mites, the rather diverse mating habits reflect an origin from behaviour akin to that of the scorpions. The report of Lipovsky *et al* (1957) of indirect transference of a spermatophore in trombiculid mites, and that of Nuttall and Merriman (1911) on *Ornithodorus* support this strongly.

In the case of the spiders, two interpretations of the behaviour may be postulated: either the animals have retained the Limulus-like habit of depositing sperm on the substratum but have further evolved the elaborate palpal "pick-up" system or they have gone through a stage of mating like that of the modern scorpions and pseudoscorpions but have lost completely the spermatophore covering of the sperm mass. These two possible lines of evolution are shown diagrammatically in Fig. 43.

The first suggestion does not seem very probable if we are considering the evolutionary path of the actual behaviour. Clearly internal fertilisation could not be achieved until the pedipalpar mechanism was developed; at the same time there does not seem any obvious reason why the male should pick up the sperm while fertilisation is still external. The shortcomings of the hypothesis arise from the fact that it requires the simultaneous development of the palpal appendages, or more important, the male behaviour pattern, and the female habit of retaining the eggs inside her.

Consider the second possibility, namely that the spiders have passed through a stage in which they deposited a spermatophore on the ground, this being picked up by the female. That is, the sperm deposition of modern spiders is a phylogenetic vestige of the spermatophore-depositing behaviour of the proto-spiders. It is desirable at this point to look briefly at the various methods by which the spermatophore of an arachnid may be transferred to the female from the ground where the male has deposited it. This is achieved in a number of different ways.

In the scorpions and some of the pseudoscorpions (Kew,1912 and Vachon, 1938) it is done without the direct use of any of the appendages of the male or the female, so that either the co-operation between the two animals or the structure of the spermatophore or both have been greatly elaborated to ensure an efficient mating. In other arachnids various limbs of the male are used in moving the sperm into the female. In the pseudoscorpion, <u>Chelifer latreilli</u>

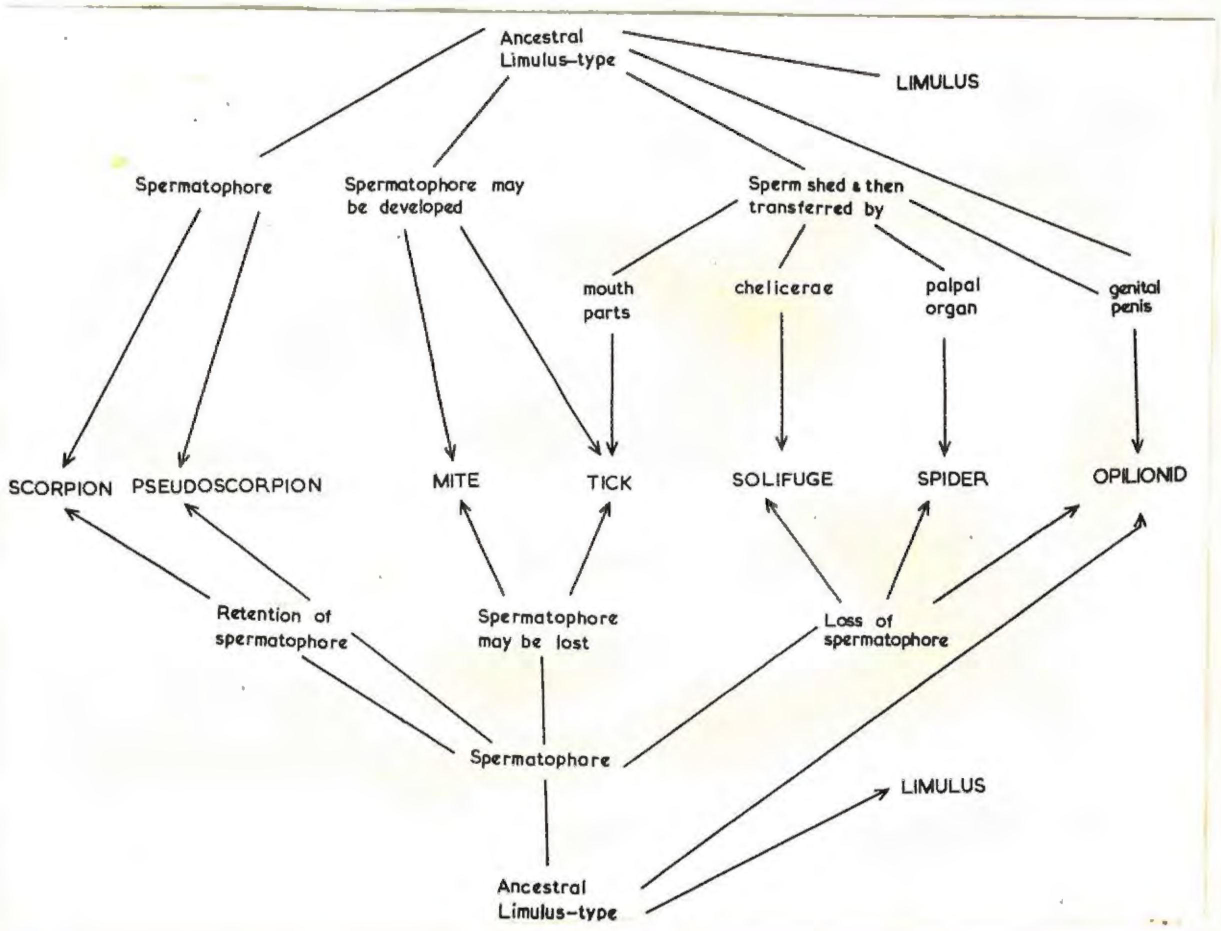


Fig. 43. Representation of two possible lines of evolution of arachnid mating. Two schemes are shown, both starting with a Limulus-type pattern and giving rise to the mating habits of modern arachnids, shown in the centre of the figure. The lower of the two schemes is that for which more evidence seems available.

Very variable methods for the transference of sperm in mites. All the Mesostigmata carry the spermatophore over in a special slit or cavity of the Cheliceral lower jaw.

Leach, Kew (1912) describes how the male holds open the female genital orifice with the modified claws of his first legs while he eases her on to the naked sperm mass on top of the spermatophore. In the ricinulids, Comstock (1940) considers that the third leg is involved in the transference of the spermatophore to the female. In the solfugids the chelicerae are used for moving the "Spermaballen" from the ground, where the males deposit them, to the genital openings of the females (Heymons, 1901).

It is thus clear that the spermatophores or "Spermaballen" may be transferred to the female by the chelicerae, first legs and third legs. There thus seems no obvious objection to the postulate that the primitive spiders used their pedipalps in transferring the sperm from the deposited spermatophore into the female, or, alternatively, that the palps were used for holding open the genital aperture, as are the legs of the pseudoscorpion mentioned above. It is possible that initially there was a tendency to use the chelicerae as well as, or instead of, the pedipalps and thus Bristowe's suggestion may be included within the limits of the present hypothesis.

The question of the loss of the spermatophore can be considered quite separately, beginning once more with the primitive arachnid. A mass of sperm merely deposited on the ground is likely to be absorbed immediately between the soil particles, a factor which may well have influenced the evolution of the spermatophore in the scorpions and pseudoscorpions.[1] The pseudoscorpion, C. cancroides

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[1] Even when the problem of the protection of the sperm from being absorbed into the soil has been solved by the elaboration of a spermatophore, the avilability of a surface suitable for mating remains of great importance. In the scorpions, as has been shown above, mating cannot take place if the surface on which the animals are placed is not hard enough to support the spermatophore. The fact that spiders will normally either meet on a web or can spin one when it is needed, must give them a significant advantage as far as mating is concerned. This may well be one of the reasons for the success of this arachnid group relative to the others.

has a spermatophore which is an almost naked stalk and on this a large sperm mass is perched. Compared with the spermatophore of most other pseudoscorpions and of the scorpions, this is extremely simple and probably reduced: clearly, however, it could not become less substantial without danger of the semen just sinking into the soil on which it is deposited. Once the spiders had begun the habit of spinning webs, such dangers were overcome for them because a drop of semen will not be absorbed by a strand of spider silk. Since there is evidence (Petrunkevitch, 1952) that the spiders had already developed the web-spinning habit in the Oligocene, there would appear to have been adequate time for the spermatophore to be reduced to nothing because, once there was no further need for it, there would almost certainly be selection against any covering for the sperm mass. It would however be of interest to look carefully at the mating habits of the primitive spiders and especially to see whether amongst the Liphistiomorpha there are animals in which some trace of a membrane persists around the sperm mass and whether this is picked up into the shallow palpal cup as a semi-solid mass rather than as a seminal fluid.

While it is possible that such direct evidence will appear, the hypothesis seems fairly sound on its own merits. It is clear the "double process" is very hard to understand on the basis of an evolution stemming either directly from a Limulus-type external fertilisation or indirectly through a stage of ordinary internal fertilisation. The present postulate - that of an intercalated stage of spermatophore deposition and transfer to the female with the aid of the male palps - not only provides a plausible explanation of the origin of this double process, but is in keeping with what we now know of the mating habits of the other arachnid groups.