THE ODORIFEROUS GLANDS OF SOME PALPATORES PHALANGIDA (OPILIONES) (ARACHNIDA)

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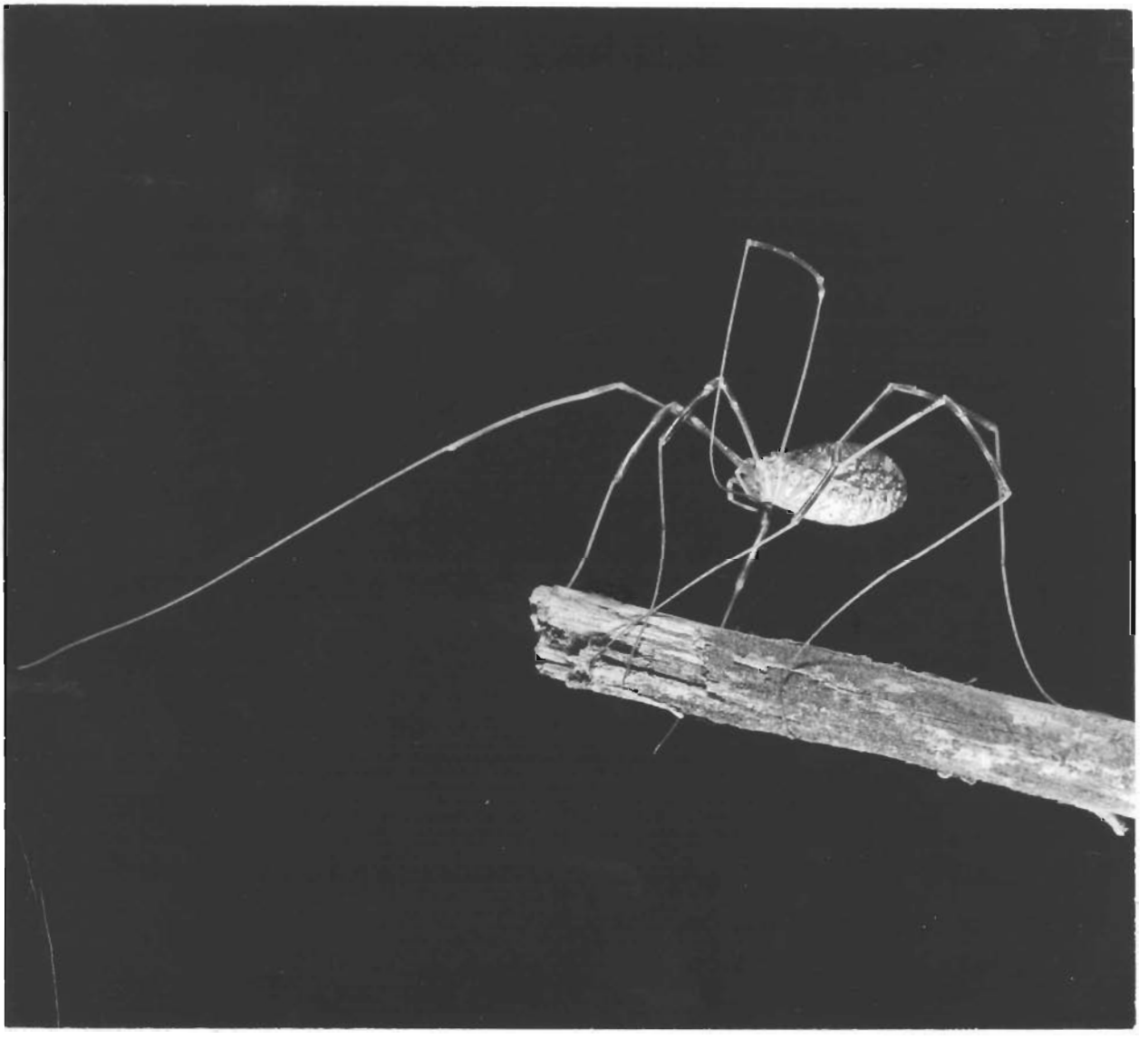

Frontispiece. Female Opilio parietinus cleaning her second leg.

ABSTRACT

The odoriferous glands of especially Phalangium opilio and to a lesser extent Opilio parietinus, Odiellus pictus, Homolophus biceps, Leiobunum calcar and L. vittatum were investigated by: external examination; dissection; light microscopy; predator-phalangid encounter experiments with amphibians, birds, mammals, spiders, centipedes and ants. Amphibian stomach content analysis and a field experiment involving frogs as predators were also performed.

No liquid odoriferous gland secretion was observed externally in P. opilio, O. parietinus or O. pictus. Liquid secretion may have been present in H. biceps. Only P. opilio and H. biceps produced a detectable odor.

Observations on the construction of the glands confirmed previous descriptions. However, it was shown that the phalangids studied have some control over which gland operates and that the secretions probably differ between species.

Vertebrate-phalangid encounter experiments suggest that all vertebrate predators can eat phalangids of the suborder Palpatores without harm.

Although a number of spiders and one species of centipede were not repelled by the odoriferous glands, some spiders and an ant species were repelled.

It is concluded that phalangid odoriferous glands are most likely defensive in function, although limited in effectiveness, and are not used for trail marking, species recognition, sexual recognition, anti-microbial protection or excretion.

ACKNOWLEDGEMENTS

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1. INTRODUCTION

Phalangida or Opiliones, commonly known as harvestmen or daddy-long-legs, constitute a minor order of the class Arachnida of the phylum Arthropoda. Living arthropods are commonly divided into the mandibulates and the chelicerates, based on the form of their mouthparts. The arachnids constitute the largest class of the chelicerate-bearing arthropods.

Phalangids are unique among the arachnids in that they possess a pair of glands which open on the dorso-lateral edge of the prosoma or cephalothorax. These glands are variously called odoriferous, repugnatory, scent or stink glands and have generally been considered to function in defense against predators.

Detailed descriptions of the general biology of phalangids were given by Berland (1949), Edgar (1960), Savory (1962) and Cloudsley-Thompson (1968). Phalangids have been shown to feed mainly on living and dead arthropods as well as on some plant material (Bristowe, 1949; Sankey, 1949a). They capture living prey by means of their legs and palps (Phillipson, 1960a). The chelicerae, palps and the basal projections of the legs and palps are used to masticate the food before it is taken into the mouth. The legs consist of seven segments: coxa, trochanter, femur, patella, tibia, metatarsus and tarsus. The four pairs of legs are born on the prosoma which is broadly joined to a segmented opisthosoma or abdomen. Detailed descriptions of the external structure have been given by Hansen and Sörensen (1904), Roewer (1923), Kästner (1935) and Berland (1949).

The Order Phalangida is divided into three suborders, the Cyphophthalmi, the Laniatores and the Palpatores. A taxonomic classification of the suborders is given in Appendix I. The following three paragraphs describe each suborder and review the literature on phalangid odoriferous glands.

The Cyphophthalmi are secretive, mite-like phalangids which inhabit moist leaf litter. They tend to be less than three mm in length. All the species of this suborder are placed on one family, the Sironidae. Members of the suborder tend to be sporadically distributed in the tropical, subtropical and temperate regions of the world. In North America specimens have only been collected from Florida, Oregon and Washington (Hoffman, 1963). Hansen and Sörensen (1904) were the first to state that the two elevated projections between the coxae of legs II and III were odoriferous glands. Previously the projections were referred to as stalked eyes. Hansen and Sörensen did not section any material but did relate that, when seized, Purecellia illustrans Hansen and Sörensen released a fluid from its odoriferous glands. The odoriferous glands were also examined by Juberthie (1961a and b) who showed that the glands of Siro rubens Latreille and Parasiro coiffaiti Juberthie consisted of chitin lined sacs which opened to the exterior by a short canal. Each gland had one muscle for opening the orifice of the canal, one muscle for closing the orifice of the canal and a sheath of helical muscles for emptying the sac. Juberthie also observed that, in both species, when an

appendage was seized by a pair of forceps, a drop of secretion from the odoriferous glands was usually exuded on the side which was under attack. The drop was then transferred by one of the free appendages to the site of attack. He tested the action of the secretion of S. rubens by rubbing pieces of a fly in the fluid and then presenting them to another species of phalangid (Odiellus sp., Palpatores). The second species of phalangid refused the treated flies but accepted untreated flies a few hours later.

Members of the suborder Laniatores are mainly tropical and subtropical in their distribution but a few specimens have been found as far north as the Queen Charlotte Islands, British Columbia (Kästner, 1935; Berland, 1949; Goodnight and Goodnight, 1960). The palps tend to be heavily spined and are tipped with strong movable claws. Legs III and IV terminate in either a double or single but divided claw. Leg IV is usually the longest. According to Roewer (1923) there are six families. The odoriferous glands open above coxae II. In this suborder, Gervais (1849) was the first to note that these structures were glandular and produced an odor. Sörensen (1879) showed that the odoriferous glands produced a yellow liquid when the animals were irritated. According to Sörensen the secretion had an odor similar to horse-radish and irritated the eyes. He also mentioned that the secretions of the Oncopodidae, Assamiidae, Cosmetidae and some Phalangodidae and Gonyleptidae flowed backwards along lateral or ventral grooves on the carapace. Bristowe (1924) mentioned that some species of Gonyleptidae gave off no smell while others produced "...a strong and rather sweet odour...". However, it is not clear from his text whether the odor produced was the result

of the odoriferous glands or the excretory organs (ie. the coxal glands). Stipperger (1928) collected hundreds of phalangids but only once noticed an odor produced by one specimen of Gyas titanus Simon; the odor was obnoxious and lasted about two minutes. Lawrence (1938) showed that the secretions of Larifuga capensis, Larifugella natalensis, Adaeulum robustum and Cryptobunus silvicolous appear in the form of a drop or fine spray of liquid and in Metabiantes leighi the secretion flowed posteriorly along grooves in the carapace and collected on the posterior part of the body. Usually mechanical squeezing of the specimens was used to stimulate the release of secretion, but in one case an ant walking over the dorsum of an animal, secured by its legs for photography, elicited the reaction. Lawrence described the odoriferous gland liquid of L. capensis as similar to iodoform; L. natalensis as "...acrid and rather unpleasant..." and like the smell "...of freshly-cut horse-radish..."; and M. leighi as "unpleasant". The first detailed chemical analysis of phalangid odoriferous gland secretions was made by Fieser and Ardao (1956) on a member of the Gonyleptidae. The species was identified as Heteropachyloidellus robustus Roewer by Saez and Drets (1956). The chemical mixture, termed gonyleptidine, was found to consist mainly of 2,3-dimethyl-1,4 quinone with small amounts of 2,5-dimethyl-1,4 quinone and 2,3,5-trimethyl-1,4 quinone. Gonyleptidine was shown to possess antibiotic properties effective against at least eighteen genera of bacteria and protozoa (Estable et al., 1955). Juberthie (1961b) briefly described the structure of the odoriferous glands (mainly in Scotolemon lespesi Luc.) and the lateral grooves in the carapace used for the conduction of the glandular secretion along the sides of the body. In comparison with his

work on the odoriferous glands of some Cyphthathalmi, Juberthie found that the Laniatores had a simplified muscular system for closing the orifice of the canal, no muscles associated with opening the canal and a reduced muscular sheath around the base of the canal, not around the whole gland.

In the Palpatores, legs III and IV terminate in a single undivided claw. Leg II tends to be the longest. The odoriferous glands open above coxae I. The palps are slender and may have a reduced claw (Tribe Eupnoi) or no claw at all (Tribe Dyspnoi). Roewer (1923) included four families in the Dyspnoi. The Eupnoi are the most commonly collected phalangids in temperate regions of the world and are all placed in one family, the Phalangiidae. An example of this family is shown in the Frontispiece. The earliest mention of the possession of a peculiar smell by any phalangid was made by Latreille (1804) who stated that several species of "Phalangium" emitted a very strong odor similar to walnut leaves. Latreille however mistook the openings of the glands (possibly responsible for the smell) for a second pair of spiracles and did not postulate any source for the odor. Treviranus (1816), Tulk (1843) and Leydig (1862) referred to the glandular openings as eyes. Krohn (1867) first recognized these structures in the Palpatores as glands and described in some detail the structure of the secretory cells. However he did not relate any odoriferous function to them or postulate a use for them. Thorell (1876) used the openings of the glands as a character for distinguishing some of the genera within the Palpatores. Simon (1879) suggested that the glands were special organs used to secrete an odoriferous liquid peculiar to phalangids. He suggested that the

secretion was a means of defense, and that in Phalangium opilio it smelled, to him, like walnut shells. Loman (1881) was undecided as to the function of these glands in the Family Phalangiidae. Rössler (1882) stated that Opilio albescens (Mitopus morio according to Kästner, 1935) produced an aromatic smell. Kolosvary (1929) showed that when Phalangium cornatum (P. opilio) were placed in a tube containing ammonia, alcohol, iodine or perfume vapors, drops of secretion formed at the openings of the glands. Kolosvary, however, came to the conclusion that the glandular secretions were used to neutralize the irritant effects of the chemicals. He also noted that mechanical stimulation, such as grasping the animals, produced drops of secretion. Kästner (1935) handled hundreds of P. opilio, either in collecting or in observing the animals under a binocular microscope, but was not usually aware of any odor or production of a liquid from the odoriferous glands. Only on one occasion was he able to smell a distinct odor of green walnuts. Lawrence (1938) examined only one species of Palpatores, Rhampsinitus levis, which did not secrete readily. He stated: "The liquid oozed slowly out of the gland openings; it was clear, light violet in colour, and did not possess a distinctive odour. No fine jets of liquid were observed in this species." Bristowe (1949) stated: "Few spiders will sustain an attack on adult harvestmen. Usually they retreat after one bite and wipe their mouths on a leaf as I have recorded in experiments with nine British harvestmen in 1941 to which I could now add Oligolophus tridens C.L.K.". Juberthie (1961b) also briefly described the odoriferous glands of some Palpatores. He noted that the secretion is difficult to obtain in this suborder and that the only muscles associated with the glands are concerned with closing the

entrances of the canals. Blum (personal communication) and his colleagues have examined the glandular secretions of several species of Leiobunum but have identified only one ketone, 4-methyl-3-heptanone.

The above three paragraphs review the most important references to date on phalangid odoriferous glands. From this information it has been generally concluded that phalangid odoriferous glands are, in all species within the three suborders, used as a means of defense against their enemies. However much of the evidence for this information is fragmentary and has usually come from observations incidental to other work. (The papers of Krohn, Lawrence and Juberthie are exceptions to this.) A number of people have also made suggestions, usually from single observations, that have not been thoroughly followed up but have nevertheless become part of the "evidence" proving that phalangid odoriferous glands are defensive in function. Some of these suggestions are quoted below.

Bristowe (1924) stated that "Each species [of Laniatores] probably produces a characteristic odour; in some no smell, could be detected at all, in which case the liquid probably had a disagreeable taste or else its odour is outside our range of smell, for few things will attack these creatures;...". Lawrence (1938) said: "The ejection of the odoriferous substance is almost certainly a defence (sic) reflex, though its use by harvest-spiders against other organisms has not yet been observed under natural conditions." In 1944 Roters observed that "...it is remarkable that other species [of phalangids] do not attempt to assault Liobunum [Leiobunum]. For example, a Phalangium opilio which, when placed with Mitopus morio had continually come into

conflict with it and had finally eaten it, did not make the slightest attempt to capture a Liobunum in whose company I placed it later." Edgar (1960) mentioned "Frogs, for example, have been observed to take opilionids into their mouths only to expel them forcibly, almost immediately. Since phalangids have little or no means of inflicting physical damage the scent gland secretion is probably the cause of such action."

The scope of this work has been to investigate the structure and histology of the odoriferous glands of some phalangids as well as to attempt to find out if these glands are effective as deterrents to predators. Since Phalangium opilio L. was the most readily obtainable, this work deals mainly with this species of the Suborder Palpatores. Five other Palpatores, Opilio parietinus (De Geer), Odiellus pictus (Wood), Homolophus biceps (Thorell), Leiobunum calcar (Wood) and L. vittatum (Say) are dealt with in less detail. The structure and some aspects of histology of the odoriferous glands were determined by light microscopy. A field experiment and laboratory experiments with predaceous arthropods and vertebrates were used to test whether the odoriferous glands were effective as a defense mechanism. Some observations on the presence of phalangids in vertebrate stomachs and in spider webs are also presented and discussed.

2. MATERIALS AND METHODS

2.1. Identification and treatment of the material studied

2.1.1. The phalangids studied

In order to determine which species of phalangids were obtainable in large enough numbers to be useful for experimental purposes, collections were made throughout the southern half of Saskatchewan. Six species, all belonging to the Family Phalangiidae, were collected: Odiellus pictus (Wood), Phalangium opilio Linnaeus, Opilio parietinus (De Geer), Homolophus biceps (Thorell), Leiobunum calcar (Wood) and L. vittatum (Say). Three of these species have been collected in Saskatchewan before: P. opilio, O. parietinus, and L. calcar (Davis, 1934; Edgar, 1960 and personal communication). Although Edgar (personal communication) also noted that Sabacon crassipalpe (C.L. Koch) (Family: Ischyropsalidae) has been collected previously in the province, it has not been collected in this study.

The six species are listed in Appendix II, each with a list of references, a short taxonomical description, a list of North American records and a list of Saskatchewan records. Sample collections of these phalangids have been deposited in the Canadian National Collection, Ottawa, Ontario and in the collection of Dr. A.L. Edgar, Department of Biology, Alma College, Alma, Michigan.

Body and leg lengths were measured to the nearest 0.5 mm; femur lengths (with the aid of an optical micrometer) to the nearest 0.1 mm. Leg lengths exclude the coxae. F_2 stands for the femur of the second leg. It must be remembered when comparing body and leg lengths of specimens collected in different localities that there is a great deal of

variation as well as a clinal gradation (with the longest legs and body in the south and the shortest in the north) in both measurements (Weed, 1892c, 1893c; Suzuki, 1949).

Although Edgar (1960) gave a list of the provinces and states in which eighteen species of phalangids occur, he did not say which records came from published reports and which came from material which he had examined. Thus the North American distributional records listed in Appendix II omit Edgar's 1960 listings when earlier references have been found. Edgar's 1960 and 1966 references are listed only when no previous published records could be found or in the cases of the five states and the single province with which he dealt directly in his 1966 paper.

Unless otherwise stated, the Saskatchewan collections were made by myself.

2.1.2. Procedures used in instar determination of phalangids

Since size of potential prey greatly affects prey-predator relationships, a method of femur length measurement coupled with other characters was used to determine the instars (and thus the size) of the phalangids studied.

Instars were determined for Phalangium opilio by measuring the femur of the second leg (F_2) with an ocular micrometer and plotting the lengths obtained vs. the frequency of occurrence. Not enough material was available to do this for the other species studied. F_2 was used as it is the longest and straightest segment of all the appendages of P. opilio. Phillipson (1960b) used F_2 for determining the instars of Mitopus morio. Edgar (1960) used the length of leg IV

in his work with Leiobunum spp. Body length was not used for the following reason. When a phalangid first moults, the last few segments of the opisthosoma are partly telescoped together but throughout that instar the opisthosoma gradually unfolds. Thus phalangids, unlike most other arthropods, can increase in size within one instar (Roewer, 1923; Edgar, 1960). Also when a starved or thirsty phalangid takes in a large quantity of food or water the opisthosoma unfolds.

Femur lengths were obtained from specimens taken weekly between May and September 1967 by E. Gorin and R. Lein from Kernen's Prairie (about 4 km NE Saskatoon) supplemented by Saskatoon specimens collected or hatched from eggs and raised in the laboratory. The eggs usually hatched within 3-4 weeks at 20°C and high relative humidity. The young were raised on cold-killed, adult Drosophilia melanogaster and a moist, ground mixture of cornmeal, bran and Tenebrio molitor larvae.* Water was supplied by means of wet pieces of paper towel or synthetic sponge. Crowding was avoided because of the danger of cannibalism. Under these conditions, wild immature P. opilio matured, mated and laid eggs which hatched. However, no young were raised to maturity; probably due to deficiencies in the diet or causes of a high failure rate in moulting.** The data from over 350 F_2 measurements best fit the postulate that P. opilio has eight instars. The results are summarized in Table 2.1.

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* Todd (1949) fed her phalangids a mixture of dried egg, whole wheat flour and yeast, supplemented by live psocids (Liposcelis granicola) and Tribolium confusum larvae. Naisse (1959) used vestigial Drosophilia for feeding phalangids; Klee and Butcher (1968) used dried bacon and cornmeal; Edgar and Yuan (1968) used powdered beef and freshly killed Drosophilia.

** G.E. Klee (personal communication) suggested that a daily change in relative humidity may be necessary for many successful moultings.

Table 2.1. Determination of Phalangium opilio instars by measurement of the femur of leg II (F_2).

Instar		F_2 (mm)
I	egg tooth	0.15-0.35
II	young	0.35-0.9
III	young	0.8 -1.3
IV	immature	1.2 -2.7
V	immature	2.6 -4.5
VI	immature	4.0 -5.7
VII	subadult	
	male	5.6 -8.5
	female	5.4 -6.6
VIII	adult	
	male	7.5 -9.5
	mean (male)	8.3
	female	6.0 -7.5
	mean (female)	6.7

In P. opilio, the first instar is characterized by an "egg tooth" and by the fact that the eye tubercle is flat against the carapace. The first instar only lasts a few hours and in some cases the phalangid may even moult into the second instar before becoming entirely free of the egg chorion. The second instar has no egg tooth and the eye tubercle extends above the carapace. Except in size,

the second to fifth instars are similar. During the fifth or sixth instar, the appendages of the male begin to lengthen more than those of the female and the body size of the female tends to become larger than that of the male. Since only some males show the beginnings of cheliceral spurs in the sixth instar, sexual recognition by external observations is not certain and the delineation with respect to F_2 measurements of instars V and VI is not clear cut. In the seventh instar all males have small cheliceral spurs. In the eighth instar the male cheliceral spurs are larger and the anterior margin of the genital plate, in both sexes, is fully opened. The adult female tends to have a distinct central figure or marking on the opisthosoma. In the male, it is more diffuse. Male legs tend to be larger in diameter and more spinose than those of the female.

Similar sexual differences, except for the cheliceral spurs, occur in the subadults and adults of the other phalangid species studied.

The postulate that P. opilio has eight instars is in agreement with Todd (1949) but is in disagreement with Naisse (1959). Todd recorded seven ecdyses (eight instars) for P. opilio, Leiobunum rotundum and Platybunus triangularis. Naisse (1959) estimated only seven instars for P. opilio and L. rotundum. [Sankey (1949a) recorded eight moults (nine instars) for Odiellus spinosus; Edgar (1960), eight instars for four species of Leiobunum; Phillipson (1960b), seven instars for Mitopus morio.] The discrepancies for P. opilio and L. rotundum may be due to the method used for instar determination or due to differences in the number of moults needed

for phalangids of the same species to reach maturity. Naisse used body length for instar determination; Todd's method was not stated. Kaston (1970) gave a number of references to examples of instar differences in spiders. Whatever the reason(s) for the differences, in this study the instars for P. opilio were usually assigned by measuring the F_2 and referring to Table 2.1. However because (a) femur lengths overlapped between consecutive instars and (b) the possibility that some phalangids may not need eight instars to attain maturity, the instars were referred to as egg tooth, young, immature, subadult and adult rather than I, II, III, etc. This terminology was also used for the other phalangid species studied but with less accuracy because other characteristics such as general body and leg size, color and secondary sexual characteristics were used rather than F_2 lengths.

In referring to non-adult phalangids mentioned in the literature, the term "larvae" will be used henceforth.

2.2. Histological and other methods used in the study of the odoriferous glands

Attempts were made to smell the odoriferous secretions of Phalangium opilio, Opilio parietinus, Odiellus pictus and Homolophus biceps by slightly squeezing the animals between the thumb and finger and by mechanically stimulating the animals with a pair of forceps or a dissecting needle. In order to trace the odor of P. opilio to the odoriferous glands, it was found that cooling live specimens for about 10-15 minutes at -15 to -20°C prevented release of the odor prior to or during dissection. Using this method the glands could be completely exposed before the secretion was volatilized. Some

specimens of P. opilio were captured and kept in a refrigerator for 0-3 days in order to determine if cold storage affected odor retention. The same P. opilio were also squeezed and then given water and food. They were tested at different intervals to determine how long it took for the odor to be replenished. Since preservation in alcohol or fixation in modified Brasil's fluid (see Appendix III) tended to discolor the contents of the odoriferous glands or allow them to diffuse out, some observations were made on freshly dissected material of P. opilio, O. parietinus and O. pictus.

The external features of the odoriferous glands were examined under a microscope, measured, described and photographed. All material so examined was preserved in 70% ethanol.

The internal features of the glands were examined by light microscopy. Specimens were fixed in modified Brasil's fluid, dehydrated in a series of ethanol baths and cleared in benzene. Some whole mounts were made with this procedure but the majority were embedded in Paraplast (Fisher Sc. Co. Ltd.; m.p. 56 - 57°C) for sectioning. Other specimens for whole mounts were cleared in KOH.

Six micron sections were made of P. opilio (young to adult, $n > 60$); O. parietinus (immature to adult, $n > 20$); O. pictus (subadult to adult, $n=13$); and H. biceps (immature to adult, $n=6$). No fixed specimens of Leiobunum calcar or L. vittatum were available for sectioning. The sections were stained with Mallory's triple stain by the procedure outlined in Pantin (1962). The whole mounts and sections were examined under a microscope, described and photographed.

2.3. Methods used in the potential predator-phalangid encounters

In order to test whether certain potential predators of phalangids were or were not repelled by the phalangid odoriferous glands, a series of behavioural experiments were performed.

Since Phalangium opilio was the most readily obtainable phalangid, it was tested more extensively than any other species. Since attempting to measure F_2 lengths before the experiments would have caused the odoriferous glands to release prior to the actual testing and since nothing was left of the phalangids when a vertebrate predator ate them, estimates of phalangid size were made by other characteristics (as discussed on pages 12-13) than F_2 measurements for encounter experiments done with amphibians, birds and mammals. In the arthropod experiments, even if the bodies of the phalangid were eaten, the legs usually were sufficiently intact to measure the F_2 lengths. For the encounter experiments, phalangids were collected and either stored in a refrigerator at 7 - 10°C (usually 1-48 hours) or stored in an incubator at 20°C and supplied with food and water. Unless otherwise stated, in the individual results sections, the former procedure was used.

The major predator-phalangid encounters were done with one species of frog, bird, mammal and insect; and with three species of spiders. Usually other species of each group were also tested but less extensively. Since phalangids tend to be nocturnal (Edgar and Yuan, 1968), I chose nocturnal potential predators. The birds were an exception to this. Furthermore the tests were mainly done in the evening between 8 P.M. and 12 midnight. Most of the potential predators were collected from areas where phalangids were or had been collected and, unless otherwise stated, were from around Saskatoon or Lady Lake, the site of the field experiment. All encounter experiments were performed at room temperature.

2.3.1. Methods used with amphibians as potential predators

Newly transformed or metamorphosed Wood Frogs, Rana sylvatica, were the main amphibian predator tested. Twenty 18-24 mm (average 20.5 mm) frogs were collected and kept separately at 20°C when not being tested. The measurements of the Anurans refer to the distance from the tip of the snout to the vent. On a test evening, frogs were removed from their containers and placed in an arena for individual observation. The arena* consisted of a glass crystallization dish 10 cm in diameter with the bottom covered by moist sand. The arena was placed on a short stand and covered with a cardboard structure 40 cm by 40 cm by 35 cm high. The cardboard structure was constructed in a "house" shape with the apex of the "roof" cut off (see Fig. 2.1) so that one could observe the test animals in the arena with minimal disturbance. The room in which observations were made was darkened; a small lamp with a 7.5 watt incandescent bulb within the cardboard structure supplied enough light for observations.

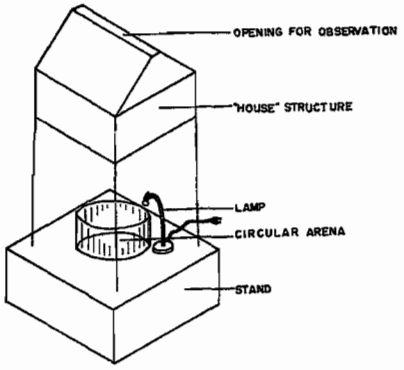


Fig. 2.1. Simplified diagram of equipment used for predator-phalangid encounters. The cardboard "house" structure is drawn lifted up to show the arena and lamp.

* It was found that circular arenas were better than arenas with corners because the phalangids and potential predators tended to be more active in the former. In square or rectangular arenas, the test animals tended to remain in one corner. Thus with a circular arena, more predator-phalangid encounters occurred per unit of time.

A frog was left undisturbed for 2-5 minutes before a phalangid was dropped into the arena. Observations were dictated into a tape recorder and later transferred to standard observation forms. Observations continued until either the frog had eaten the phalangid or until one hour had elapsed from the time the phalangid had been added. If the phalangid tended to remain motionless for over one minute, it was usually prodded into activity with the use of a piece of wire 1 mm in diameter. This also tended to increase the number of predator-phalangid encounters per unit of time.

It was not possible to repeat these kinds of experiments with other amphibian species due to shortages of amphibians in the same size groups. However, phalangid acceptance or rejection was tested in adult Rana sylvatica, adult R. pipiens, juvenile Bufo hemiophrys and Ambystoma tigrinum by moving phalangids, held in forceps, in front of the amphibians and observing whether or not they ate the phalangids.

Amphibian size classes were designated as newly transformed, juvenile or adult based on snout-vent lengths.

Amphibian nomenclature follows Conant (1958).

2.3.2. Methods used with birds as potential predators

Gallus domesticus(leghorn variety) chicks were the main avian predator tested. Twelve 24-84 hour old chicks were kept in the laboratory and supplied, ad libitum, with a mixture of "chick starter" and ground rodent pellets when not being tested. Before testing, the food (but not the water) was removed for 0-40 minutes. Observations were conducted in a similar manner to those with newly transformed Rana sylvatica except that the arena was larger (a plastic "hat box" 32 cm in diameter and

16.5 cm high with no sand) and that two chicks and four Phalangium opilio were tested at one time. It was found that chicks tested separately did not feed but constantly emitted "distress calls". Four phalangids were added at once to increase chick-phalangid encounters per unit of time. Observations were continued until all four phalangids were eaten or 15 minutes had elapsed from the beginning of the test. Each chick was marked with red food coloring or methylene blue dye for easy identification. Three test series were performed. Test Series A was performed when the chicks were 24-36 hours old; Test Series B when 48-60 hours old; and Test Series C when 72-84 hours old. Usually different chicks were paired together in each test series. However chicks B and L and chicks D and I were accidentally paired together in the second and third test series.

Attempts were also made to feed immature Phalangium opilio to three fledgling house sparrows, Passer domesticus.

2.3.3. Methods used with mammals as potential predators

Albino Mus musculus were the main mammalian predator tested. Ten male, adult, laboratory mice were kept individually in the laboratory and supplied ad libitum with water and rodent pellets when not being tested. On a test evening, food (but not water) was removed for 15-60 minutes before the experiment. Observations were conducted in a manner similar to those with chicks. The mice were individually tested with subadult to adult Phalangium opilio. Observations were continued until the phalangid was eaten or 60 minutes had elapsed from the time the phalangid was first added. Three test series were performed on three successive evenings.

A single male field mouse, Microtus pennsylvanicus, was tested with Phalangium opilio in a manner similar to that described above. Attempts to maintain other M. pennsylvanicus in captivity failed and so no further testing was carried out with this species.

On one occasion attempts were made to feed young to immature Phalangium opilio to three captive, 5-6 week old, male skunks, Mephites mephites.

2.3.4. Methods used with spiders as potential predators

Subadult to adult female Pardosa fuscula, P. groenlandica and P. modica were the main spider predators tested. These lycosids were kept individually at 20°C with a piece of wet synthetic sponge. They were periodically fed adult Drosophilia melanogaster; ceasing 2-4 days before they were tested with young to adult Phalangium opilio or Opilio parietinus. On a test evening, spiders were placed in a plastic arena 5 cm in diameter and left undisturbed for 2-5 minutes before a phalangid was introduced. To minimize disturbance to the spider, the arena was placed within a small cardboard box so that the spider could not see any movements outside the arena. The room was darkened except for a 40 watt incandescent lamp placed directly above the arena. Thus few shadows were cast upon the arena. Observations were made with the aid of a dissecting microscope. Detailed observations were continued until either the spider began sustained feeding on the phalangid or 10 minutes had elapsed since the phalangid was added to the arena. Sustained feeding was taken at the time when the spider had full control over the phalangid and had been feeding one minute. If the phalangid was not fed upon in 10 minutes, both arachnids were usually left together in the arena and observed

periodically throughout the rest of the test evening and again the next morning. As in the other encounter experiments, the phalangids were often prodded into activity with a piece of wire if they remained motionless for over one minute.

A similar experimental set-up was used to test adult female Pardosa mackenzieng ~~xerampelina~~ with Phalangium opilio and Odiellus pictus.

Four adult House Spiders, Tegenaria derhami, of the Family Agelenidae were tested with Phalangium opilio using a method similar to the Pardosa experiments.

A few incidental observations were also made on phalangids found in spider webs in the field.

Spider nomenclature follows Kaston (1948); Levi and Levi (1951) and Levi (1957).

2.3.5. Methods used with centipedes as potential predators

Three centipedes of the genus Lithobius (L. forfiatus L.?) were tested with immature Phalangium opilio and young to subadult Odiellus pictus by holding the phalangid in a pair of forceps and moving it near the centipede. If the centipede did not feed, the phalangid and centipede were left together in a petri dish overnight.

2.3.6. Methods used with ants as potential predators

About one hundred major and minor workers of Formica oreas Wheeler were collected and maintained as a colony in the laboratory. They were fed sucrose and adult Drosophilia melanogaster. Young to adult Phalangium opilio were dropped into the colony and observed with the aid of a dissecting microscope for 5-30 minutes.

2.4. Methods used in a field experiment with frogs as potential predators on phalangids

In order to test the natural feeding of vertebrates on phalangids, a field experiment was performed. Amphibians were chosen to be tested because of their lower rate of digestion (as compared to birds and mammals) and their habit of swallowing their prey whole. Amphibian stomach samples and potential prey samples were taken at a parkland slough at the same times during one summer. In this way relative amounts of feeding on certain prey (ie. phalangids) and the availability of that prey in the area could be compared.

2.4.1. A description of the study area

The study area was located about 2.4 km west of the village of Lady Lake, Saskatchewan (52° 02' N; 102° 37' W) on the farm of Mr. Lasco Gogal (Township 35, Range 5, SW quarter of Section 27). The area consisted of a permanent slough and the land immediately surrounding it; a total area of 342.3 ares. The total area and the areas of the different communities sampled were estimated by: surveying the area with a transit; drawing a detailed map; and measuring the map with a planimeter. A map of the study area is given in Fig. 2.2. The study area was divided into five communities in which prey and predator samples were taken. These communities were: (a) woods, (b) grass-willow, (c) sedge, (d) cat-tail and (e) open water. The dry grassland in quadrants A-1, A-2, B-1, B-2, C-1, C-2, D-1, E-1 and F-1; the low wet areas in quadrants A-2, A-3, B-2, B-3, A-7 and A-8; the lake and lake shore area in quadrants G-1, G-2, H-1, H-2, I-1 and I-2; the lumbered area in quadrants E-9, F-8 and F-9; and the road were not sampled. The last five areas were

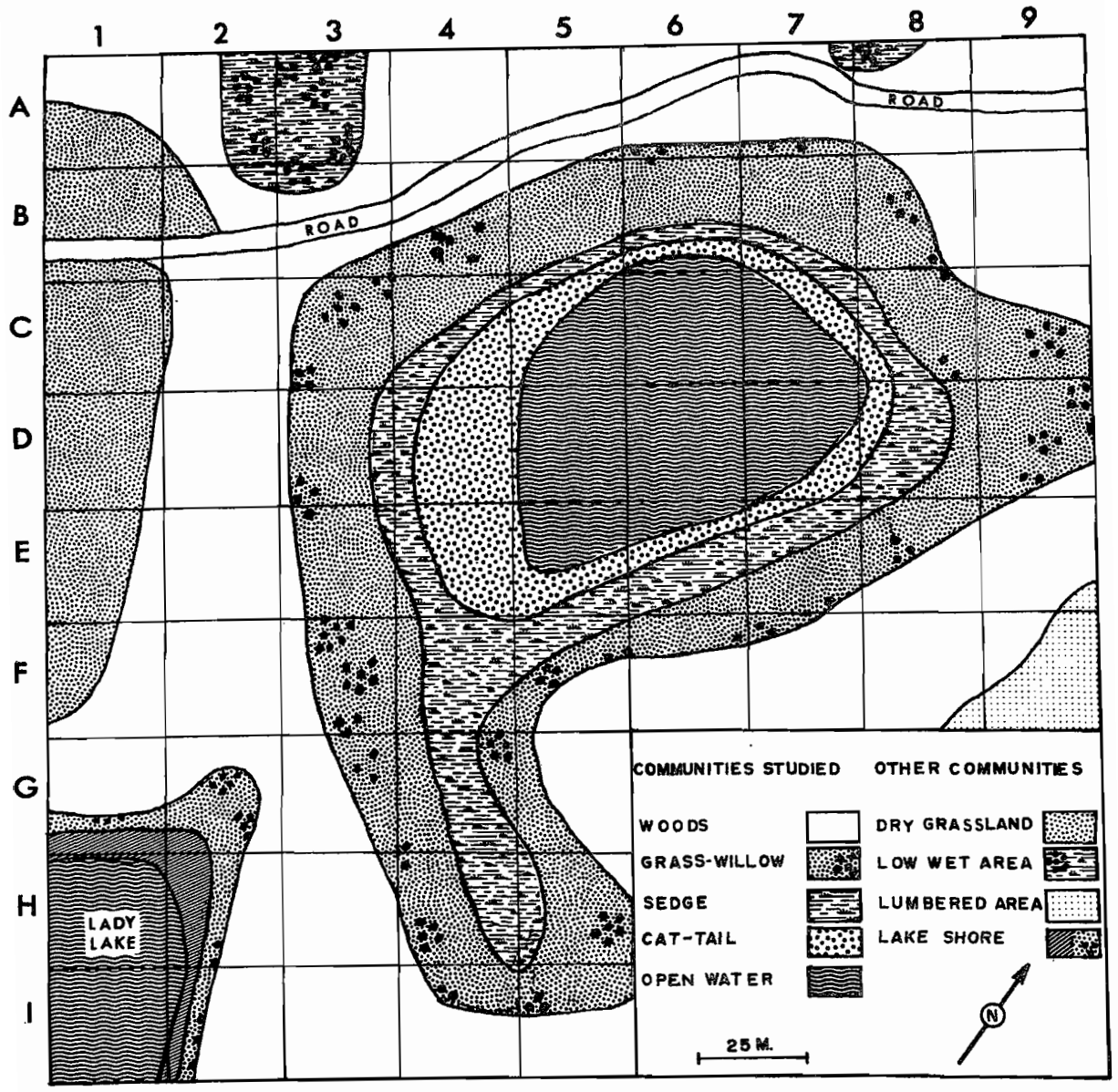


Fig. 2.2. Map of study area.

deemed as separate communities from (a) to (e) and were not sampled due to lack of time and facilities.

The woods community was characterized by Populus balsamifera along with some P. tremuloides and a few Picea glauca. The shrub and ground layer plants were typical of parkland communities (see Bird, 1961). This community consisted of 158.5 ares, the largest portion of the study area.

The grass-willow community consisted of willows, grasses, sedges and numerous low growing herbacious plants. This area occupied 92.4 ares.

The sedge community was mainly comprised of one or two species of Carex. Some small reeds and mosses were also present. It covered 33.2 ares.

The cat-tail community consisted mainly of Typha latifolia. Other emergent plants included the water lily (Nupar variegatum) and Potomogeton spp. Submergent plants included bladder-wort (Utricularia vulgaris), Ceratophyllum demersum, and Myriophyllum exalbescens. This was the smallest community, occupying only 20.0 ares.

The open-water community began beyond the stands of mature Typha. Some floating plants such as Nupar variegatum and Potomogeton spp. were present but the bulk of the vegetation was submergent and consisted of Ceratophyllum demersum. This community occupied 38.2 ares. The maximum depth of the water, in September 1969, was 60 cm.

The above plant nomenclature follows Budd and Best (1964).

Since cattle used the slough and immediate area for drinking and feeding, all the communities were somewhat affected by them. The wood-

had numerous trails through it but showed little signs of grazing. The grass-willow community was nearly completely delineated from the woods by a cattle trail which circled the slough. This community was heavily grazed and the wetter areas were full of holes made by the cattles' hoofs. The sedges were grazed closer and closer to the center of the open-water community as the water level dropped during the summer. This area was also greatly affected by the cattles' hoofs. The cat-tails were only broken down by the cattle in a few locations and only during the drier part of the year. The open-water was relatively unaffected by the physical presence of the cattle.

2.4.2. The amphibians in the study area

The amphibians around Lady Lake and including the study site have been previously studied by Buckle (1965). The most common Anuran in the area was the Wood Frog, Rana sylvatica. R. pipiens was also fairly common. Two other Anurans in the study area were the Boreal Chorus Frog, Pseudacris triseriata maculata, and the Canadian Toad, Bufo hemiophrys, but both were uncommon. A fifth amphibian, the Tiger Salamander, Ambystoma tigrinum, was also present in the study area but in very few numbers.

2.4.3. Amphibian collection and treatment

Frogs and toads were collected by hand or with a net once a month between May and September, 1969. Upon capture the specimens were killed by injecting 4% formaldehyde into the body cavity and, in the case of the larger Rana pipiens, into the brain as well. Later the frogs were measured, placed in age classes and the stomach contents removed and

preserved in 70% ethanol for microscopic examination. The age classes used for R. sylvatica were: 21-35 mm (juvenile) and 36-50 mm (adult); for R. pipiens: 36-50 mm (juvenile) and 51-80 mm (adult). These figures were derived from Conant (1958) and Buckle (1965). The amphibians collected in the study area have been deposited in the Canadian National Museum. Attempts were made to collect amphibians of as many different species as possible, of all age groups, from all five communities and at different times during the day.

2.4.4. Potential prey collection and treatment

The potential prey of the amphibians were sampled by means of "quick traps" and sweep netting. The traps used were a modification of those described by Turnbull and Nicholls (1966). Each quick trap consisted of a tripod with a suspended trap (see Fig. 2.3). The tripod was made of three wooden dowels ca. 2.6 cm in diameter. Two dowels were ca. 120 cm long and one ca. 150 cm long. About 10 cm pieces of copper pipe, slightly smaller in diameter than the dowels, were pounded one-half way onto one end of the shorter dowels and then the free end was flattened. A piece of tin ca. 4 cm by 16 cm was looped around the longer dowel about 2 to 12 cm from the end. Holes were drilled through the free ends of the tin and flattened copper pipe. Thus when bolted together, the three dowels formed a tripod. Eye-screws were fastened to the opposite ends of the dowels. Steel pegs (Coleman Anker Tent Pegs), hooked through the eye-screws, were used to anchor the tripod. The trap consisted of a section (ca. 22 cm high by 56 cm in diameter) of a circular metal barrel with three metal strips riveted to the sides of the barrel and to each other, and with the same end covered with cotton

Fig. 2.3. Quick trap in set position in grass-willow community.

cloth or light canvas. The trap sampled *ca.* ¼ m^2. The cylindrical covering was attached to the metal section by string or light gauge wire and was gathered and tied in the center with string in a conical shape above the three metal strips. The trap was suspended within the tripod by a cord. The cord was tied around the three metal strips and passed upwards through the gathered covering. The cord was knotted and placed into a groove cut into the end of the longer dowel of the tripod. Eight to ten meters of cord were left to release the trap. Three metal door springs (36 cm long unstretched) were attached to the

barrel section and the bases of the tripod. When the quick trap was set the knot in the suspension end of the cord held the trap ca. 30-40 cm off the ground. When the release end of the cord was pulled, the knot slipped out of the groove in the tripod and the springs pulled the trap to the ground. The trap was released at a minimum distance of four meters to lessen the chance of disturbing potential prey.

Immediately after the trap was released, the covering was untied and the area and vegetation under the trap were thoroughly vacuumed with a gasoline portable vacuum (D-Vac, P.O. Box 2095, Riverside, California). The material taken up by the vacuum was then carefully shaken into a plastic bag and temporarily stored in a picnic cooler. Later the collected material was frozen or the bag injected with ether to kill the living organisms. The animals were sorted from the plant material by hand and were placed in 70% ethanol for later examination.

In the woods community samples, all the leaf litter down to bare ground was taken up by hand after a thorough vacuuming. This was also done for some grass-willow community samples which had much dead vegetation. In the cat-tail community some modifications were used. Wooden poles ca. 2.1 m long were used for a tripod because of the soft mud bottom. Springs could not be used and so the trap was released by letting it fall to the surface of the water.

Attempts were made to quick trap sample each of the woods, grass-willow, sedge and cat-tail communities about ten times in a 2-3 day period when the amphibian samples were taken. In order to do this, about one-fourth of the traps were set and released in a minimum of four hours. About one-fourth were left for over 12 hours and the other one-half for varying times between four and 12 hours. Trap set-up and release

occurred between 10:00 A.M. and sunset for each month.

Although quick traps are better than any other known method of sampling invertebrate animals in short vegetation (Turnbull and Nicholls, 1966) the problem of water in the cat-tail and open-water communities and the problem of high vegetation in the grass-willow and woods communities made sampling by this means only incomplete. To help compensate for these inadequacies, sweeping was carried out. Five afternoon and five evening water samples were taken with an aquatic net in the open-water and cat-tail communities. In the sedge, grass-willow and woods communities 100 "standard" sweeps were made in the afternoon with an insect net. The aquatic net was made with nylon window screening (openings 1.5 by 1.5 mm) and was basically pyramidal in shape. The apex of the pyramid opened into a 40 ml receiving vial. The insect net was made of light canvas and was conical in shape (diameter = 37 cm). All material from the sweepings was preserved in 70% ethanol or 4% formaldehyde and then sorted into 70% ethanol for storage.

3. RESULTS

3.1. The odoriferous glands: their secretion, structure and histology

3.1.1. Observations concerning the odoriferous gland secretion and its replenishment

No live Leiobunum specimens were obtained for testing. When live Opilio parietinus, Odiellus pictus, Phalangium opilio and Homolophus biceps were squeezed or prodded, only the latter two species produced an odor. Except for H. biceps, where only three subadults to adults were available for testing, at least 20 attempts were made to smell the secretion of each of the above species. The odor from P. opilio was similar to an antiseptic but not unpleasant. It could be obtained from all life stages. No differences were detected between male and female odors. The odor of H. biceps was much stronger than that of P. opilio and tended to irritate the nose. No liquid secretion was detected externally in P. opilio, O. parietinus or O. pictus that was definitely associated with the odoriferous glands. Squeezing may have produced small drops of liquid near the odoriferous glands of H. biceps (single observation). However, squeezing did produce various liquids that oozed from the buccal region, from between the coxae and from the anus. The liquid from between the coxae often ran down the sides of the coxae and formed a drop of clear liquid near the opening of the mouth. In P. opilio, none of these liquids produced an odor. Dissection showed that the odor came from the odoriferous glands.

The color of freshly dissected odoriferous glands of both sexes and various sizes was reddish brown in Phalangium opilio and Odiellus pictus but dark brown to black in Opilio parietinus. The contents of

the glands were liquid and partially contributed to the color of the whole glands.

When freshly caught immature to adult Phalangium opilio were squeezed, four out of nine specimens produced a definite odor. Two out of ten produced a definite odor after 24 hours at 6-8°C; four out of nine produced a definite odor after 48 hours of refrigeration; and four out of nine produced an odor after 72 hours.

Some observations were made to determine how long Phalangium opilio needed to replenish its odoriferous glands lasted 10 days. Refer to Table 3.1. On Day 1, nine immature to adult phalangids were squeezed to detect the presence or absence of the odoriferous gland odor and were then placed in separate containers at 20°C with a supply of water. This constituted Test Series A. In Test Series B, C and D 10, 9 and 9 immature to adult phalangids, respectively, were placed in separate containers at 6-8°C. On Day 2, Test Series A and B phalangids were squeezed and then stored at 20°C with water. On Day 3, Test Series A, B and C were squeezed and stored at 20°C with water. On Day 4, all surviving phalangids were squeezed and stored at 20°C with water and six adult Drosophilia melanogaster. On Day 6, the phalangids were squeezed again, but not fed with D. melanogaster until Day 7. On Day 10, all surviving phalangids were squeezed for the last time. If odor was definitely present the phalangid was scored "+"; if it was questionable that the odor was present, "?"; and if there was no odor, "-". From the table one can see that, when the phalangids were supplied with water only, the glands were not replenished within 24 hours. When the phalangids were supplied with food and water, about the same amount of replenishment occurred within 2 days as within 2-4 days.

Table 3.1. Results of squeezing Phalangium opilio before and after giving water and food. Odor present "+"; odor questionable "?"; odor absent "-". See text for details of experiment.

Days	Test Series A			Test Series B			Test Series C			Test Series D		
	+	?	-	+	?	-	+	?	-	+	?	-
1	4	2	3	---	---	---	---	---	---	---	---	---
2	1	3	4	2	6	2	---	---	---	---	---	---
3	0	1	6	0	2	8	4	0	5	---	---	---
4	0	1	5	1	2	5	0	2	5	4	1	4
6	4	1	0	1	2	4	0	3	3	1	0	5
10	3	0	0	1	0	3	2	0	1	2	0	1

3.1.2. External appearance of the odoriferous glands

The odoriferous gland openings in Phalangium opilio are visible, in both sexes, from the egg tooth (Fig. 3.1) to the adult stages (Fig. 3.2). The glands open dorsally on the lateral edge of the prosoma above coxa I. The opening proper is in the form of a downwardly curved slit located on the top edge of an elliptical flap-like piece of flexible cuticle. The opening is about 0.2 mm in length in the adult male and female. In some partially cleared specimens (Fig. 3.1B) a dark pigment is visible in the glandular region.

In Opilio parietinus (Fig. 3.3) the glandular openings are slightly less obvious (about 0.2 mm in length in the adults) but in all other respects are similar to those of Phalangium opilio.

The openings of Odiellus pictus (Fig. 3.4A and B) are smaller

Fig. 3.1. Dorsal views of the first two instars of Phalangium opilio. A, egg tooth stage. Central arrow points to egg tooth; lateral arrow to opening of odoriferous gland. B, young stage. Arrow points to opening of odoriferous gland. Note dark pigment in region of the odoriferous gland.

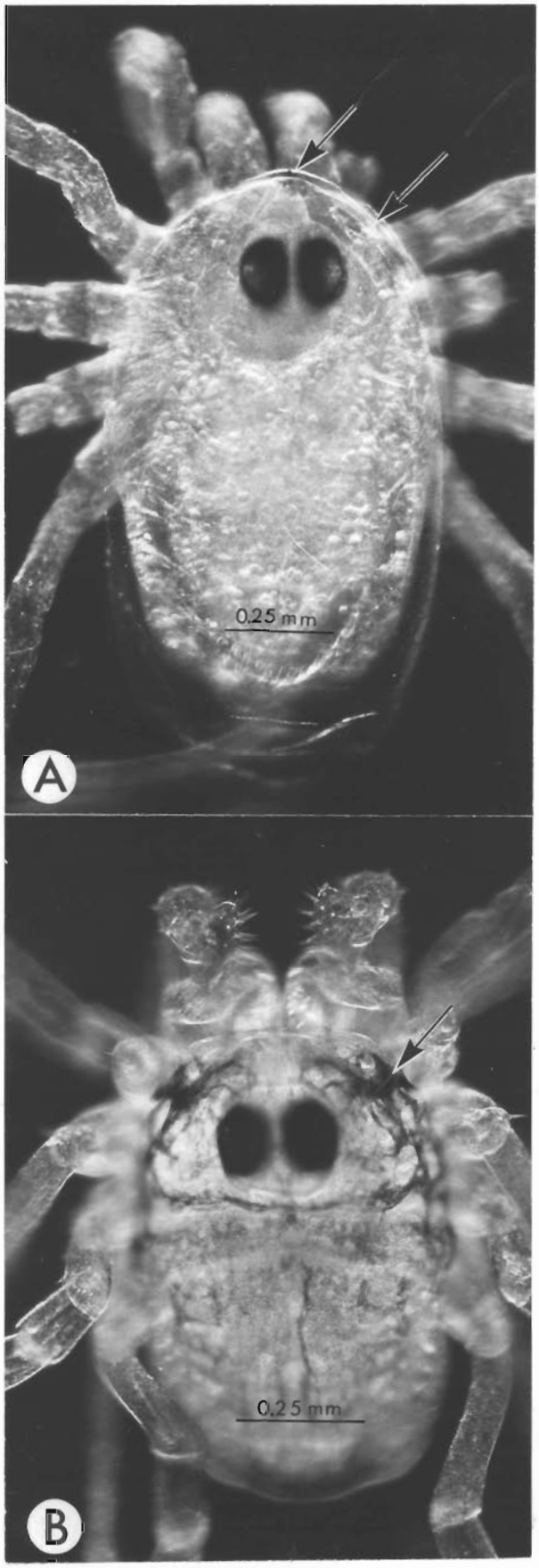

0.25 mm
A
0.25 mm
B

Fig. 3.2. Dorsal and dorso-lateral views of adult Phalangium opilio. Arrows point to the openings of the odoriferous glands. A and B, male; C and D, female.

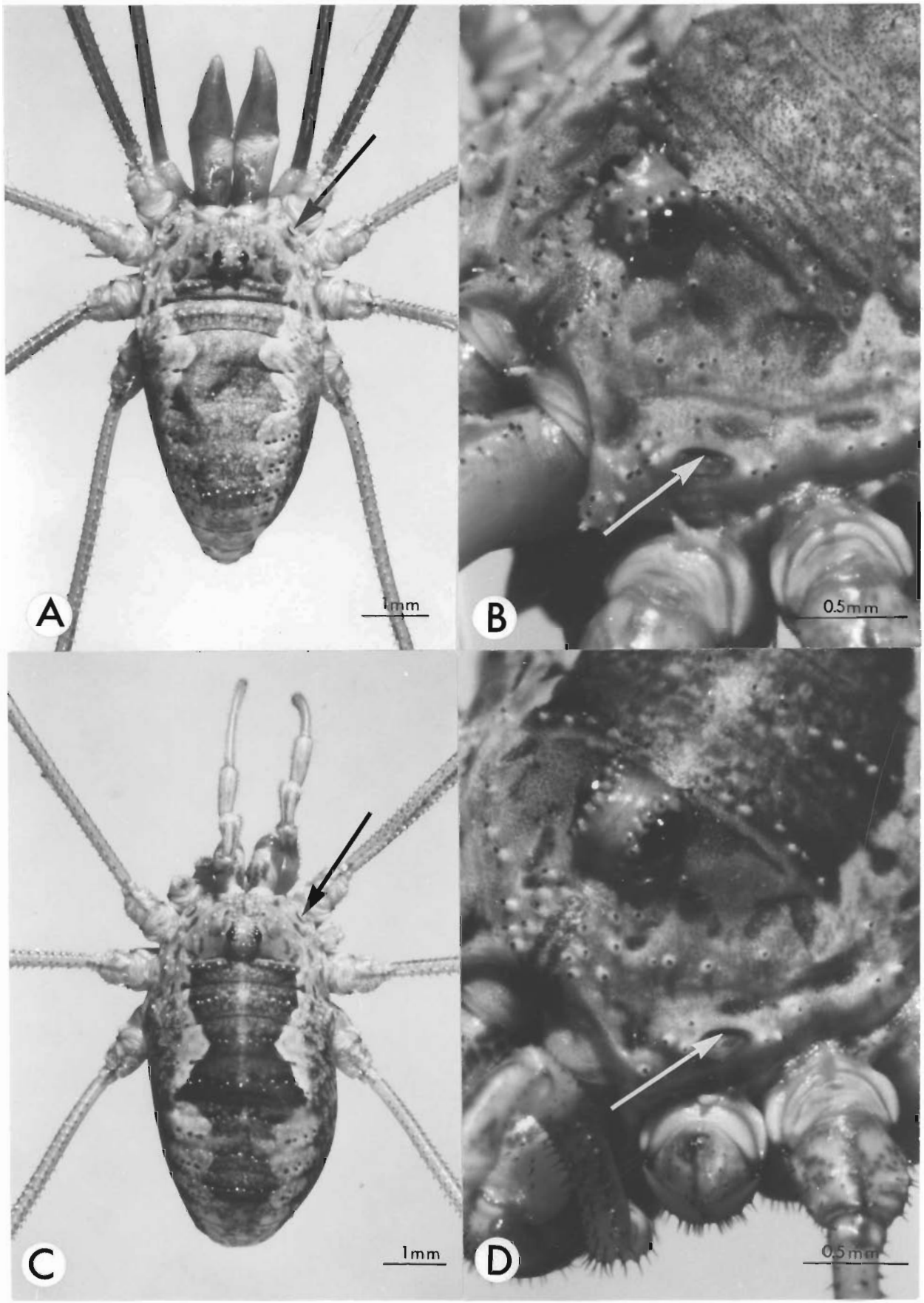

A
1mm
B
0.5mm
C
1mm
D
0.5mm

Fig. 3.3. Dorsal and dorso-lateral views of adult Opilio parietinus. Arrows point to openings of the odoriferous glands. A and B, male; C and D, female.

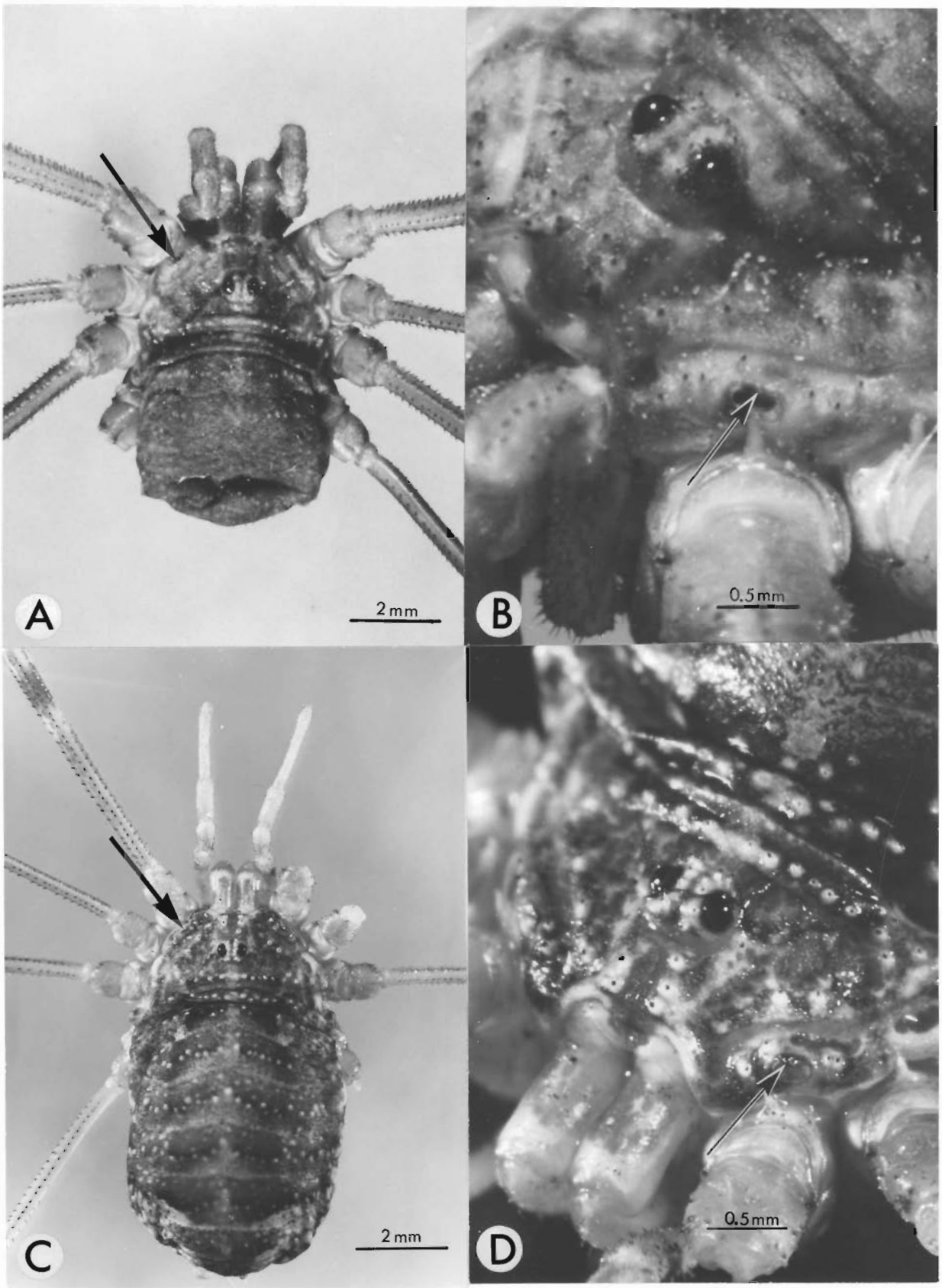

A
2 mm
B
0.5 mm
C
2 mm
D
0.5 mm

Fig. 3.4. Dorsal and dorso-lateral views of adult Odiellus pictus and Homolophus biceps. Arrows point to openings of odoriferous glands. A, male O. pictus; B, female O. pictus; C and D, male H. biceps.

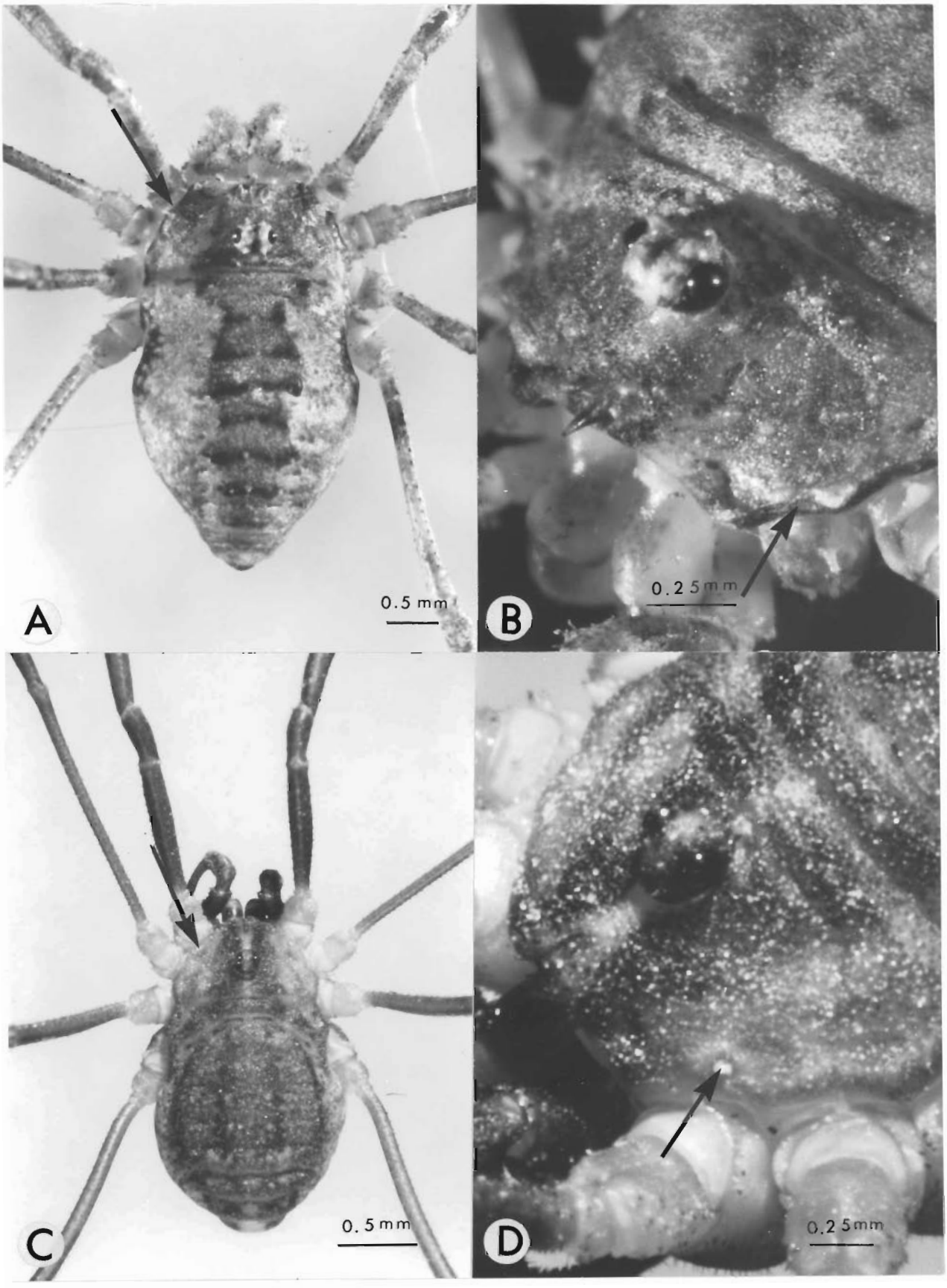
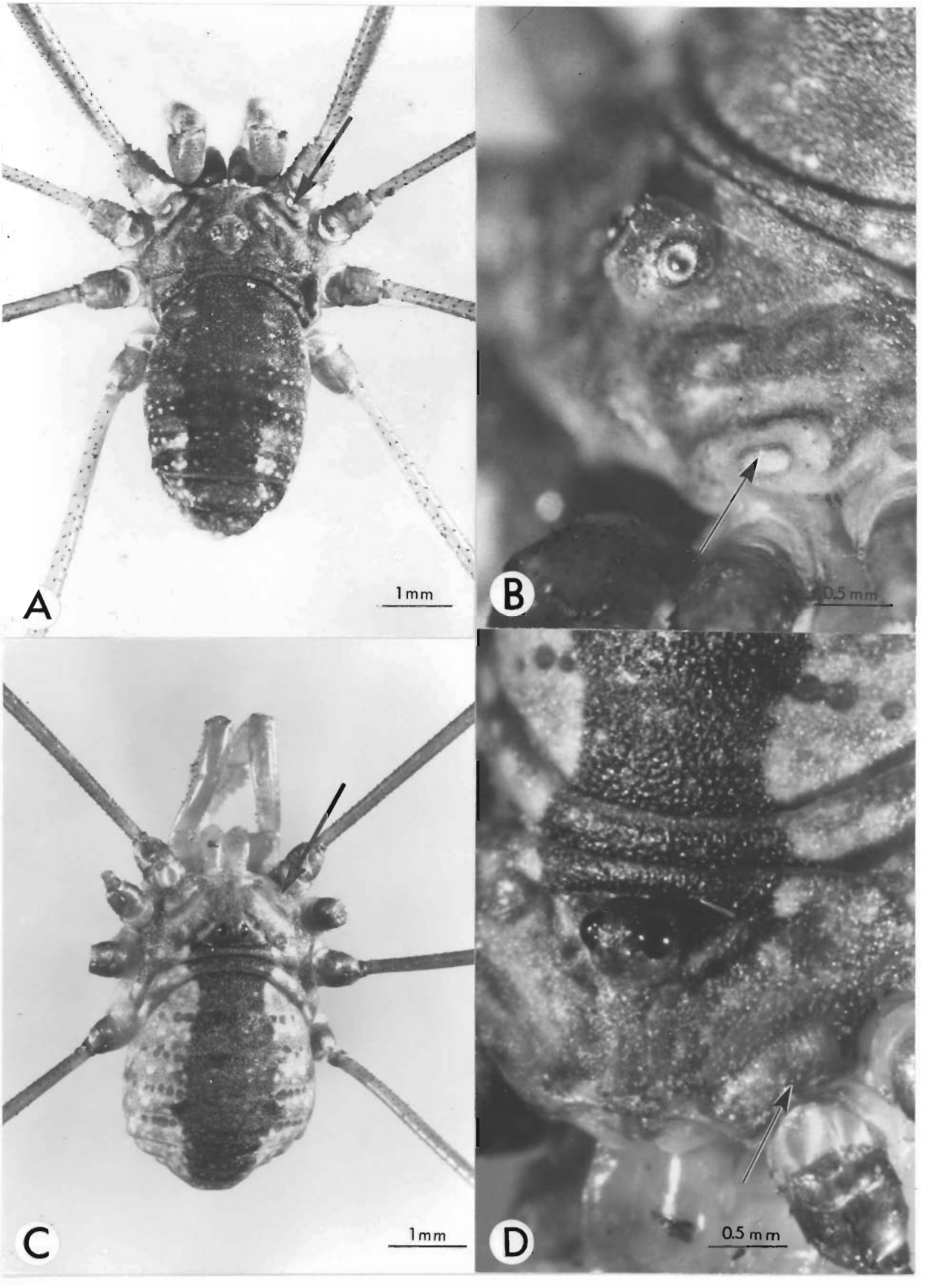

A
0.5 mm
B
0.25mm
C
0.5 mm
D
0.25mm

Fig. 3.5. Dorsal and dorso-lateral views of adult male Leiobunum species. Arrows point to openings of odoriferous glands. A and B, L. calcar; C and D, L. vittatum.


A
1mm
B
0.5 mm
C
1mm
D
0.5 mm

(about 0.05 mm in length in the adults) and less obvious than those of Phalangium opilio and Opilio parietinus. They are situated more laterally and so are not easily seen in a dorsal view.

The openings of Homolophus biceps (Fig. 3.4C and D) are comparatively the smallest of all the species studied. They are about 0.05 mm in length in the adults. The flap of flexible cuticle is circular and directed dorsally rather than laterally.

The openings of the Leiobunum species studied (Fig. 3.5) are similar to those of Phalangium opilio and Opilio parietinus. In L. calcar the openings are about 0.25 mm in length; in L. vittatum, about 0.15 mm in length. No females were observed in the last mentioned species.

3.1.3. Internal structure and histology of the odoriferous glands

In Phalangium opilio the odoriferous glands each consist of a hollow sac located near the dorsal, anterior edge of the prosoma. The shape of the sac varies according to the amount of secretion in it. When the sac is full of secretion, it resembles a squat Erlenmeyer flask with the neck directed upwards, opening above coxa I. The gland, when full, usually extends from slightly anterior of coxa I back to the eye tubercle region (Fig. 3.6A).

When the gland is empty, it becomes folded and occupies much less space. Fig. 3.6G shows a transverse section through empty and full glands in one individual. The gland is surrounded on the top and one side by the integument; on the bottom, other side and back by two or three lobes of digestive diverticula; and on the front by a group of muscles which extend from the tergum to coxa I. Another group of muscles extend from the tergum along the outside of the gland to

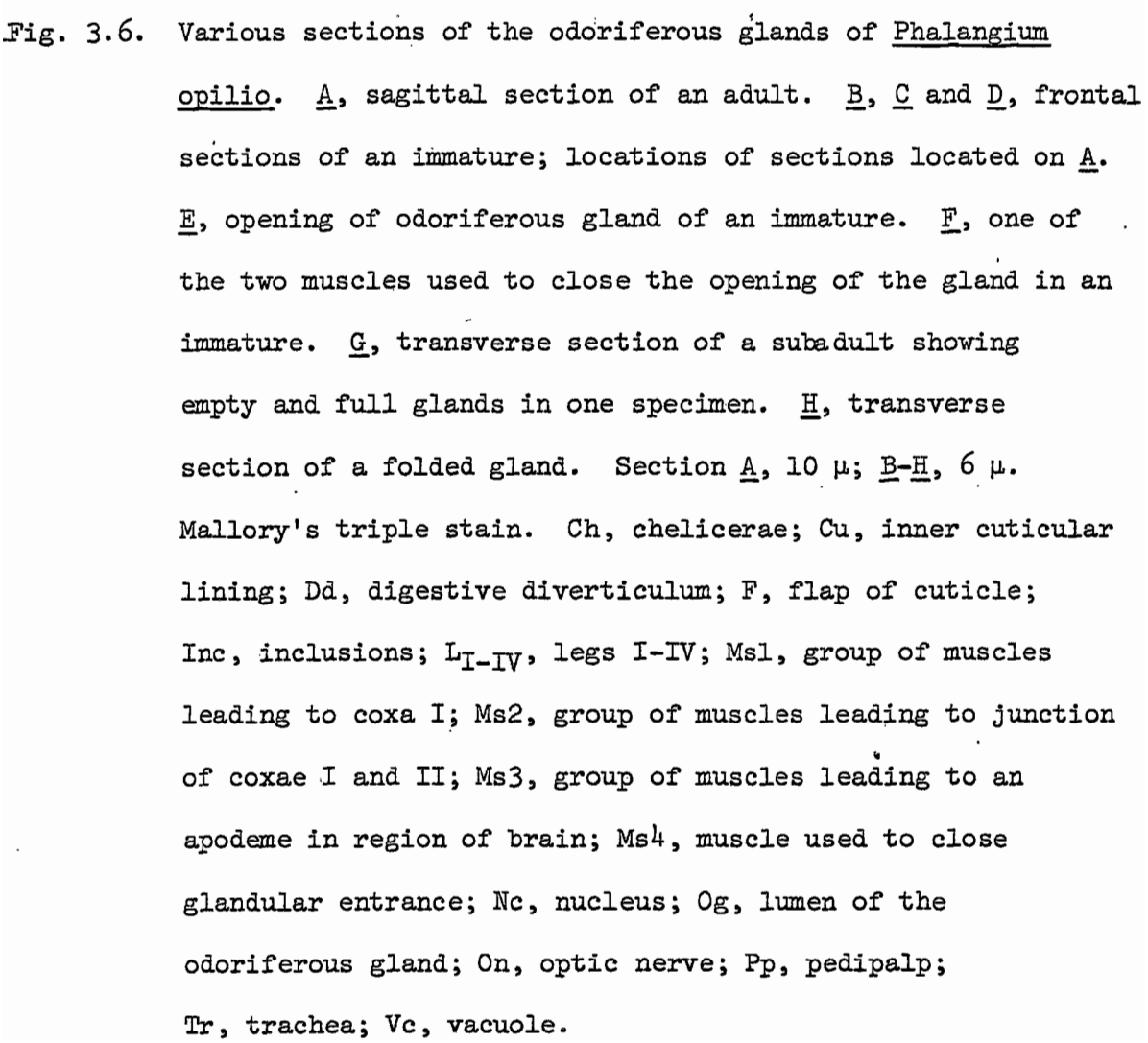
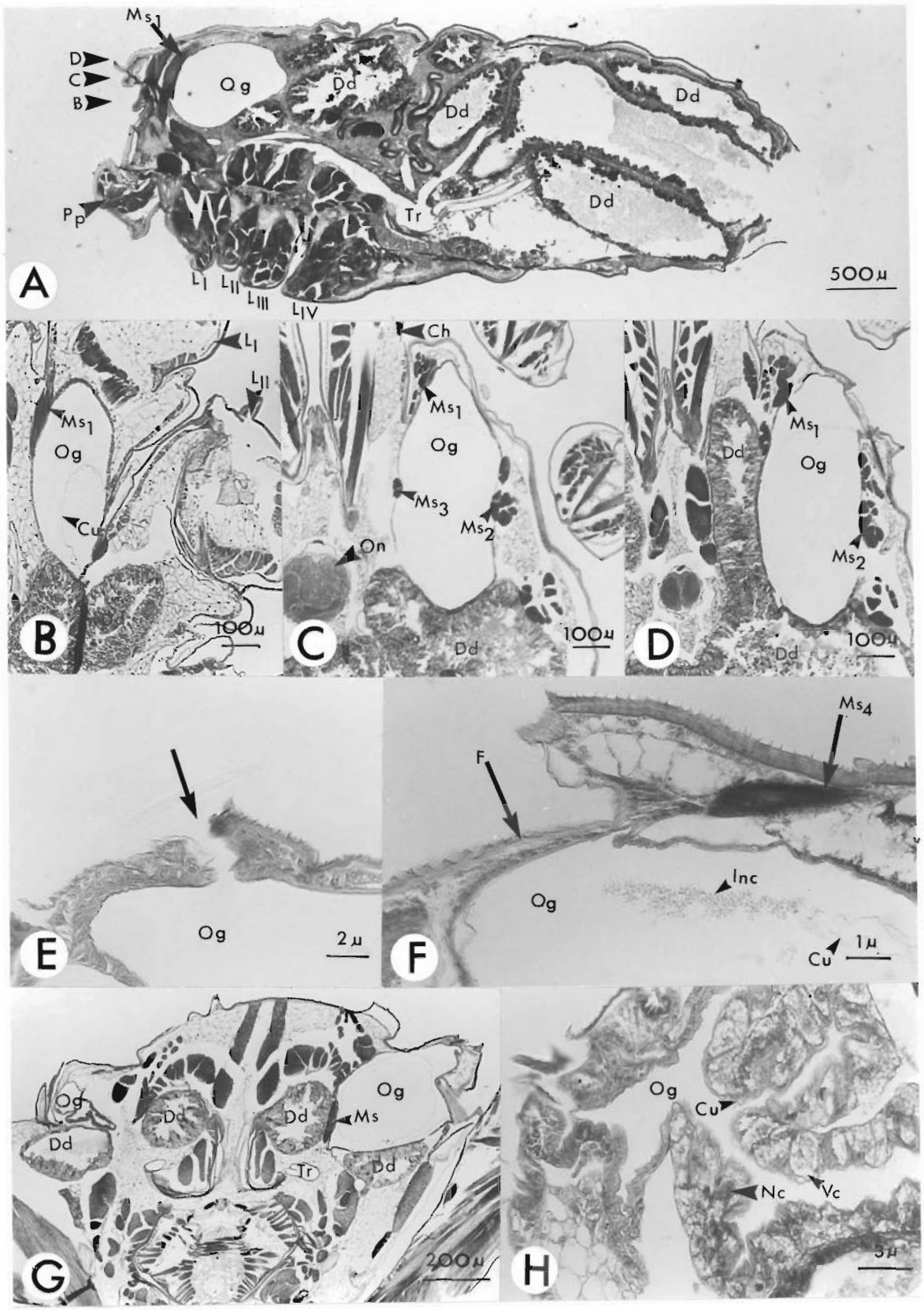


Fig. 3.6. Various sections of the odoriferous glands of Phalangium opilio. A, sagittal section of an adult. B, C and D, frontal sections of an immature; locations of sections located on A. E, opening of odoriferous gland of an immature. F, one of the two muscles used to close the opening of the gland in an immature. G, transverse section of a subadult showing empty and full glands in one specimen. H, transverse section of a folded gland. Section A, 10 μ; B-H, 6 μ. Mallory's triple stain. Ch, chelicerae; Cu, inner cuticular lining; Dd, digestive diverticulum; F, flap of cuticle; Inc, inclusions; L_{I-IV}, legs I-IV; Ms1, group of muscles leading to coxa I; Ms2, group of muscles leading to junction of coxae I and II; Ms3, group of muscles leading to an apodeme in region of brain; Ms4, muscle used to close glandular entrance; Nc, nucleus; Og, lumen of the odoriferous gland; On, optic nerve; Pp, pedipalp; Tr, trachea; Vc, vacuole.


A
Ms1
D
C
B
Og
Dd
Dd
Dd
Dd
Pp
Tr
L I
L II
L III
L IV
500µ
B
L I
L II
Ms1
Og
Cu
100µ
C
Ch
Ms1
Og
Ms3
Ms2
On
Dd
100µ
D
Ms1
Dd
Og
Ms2
Dd
100µ
E
Og
2µ
F
Ms4
F
Inc
Og
Cu
1µ
G
Og
Dd
Dd
Dd
Ms
Tr
Dd
Og
200µ
H
Og
Cu
Nc
Vc
5µ

the junction of coxae I and II. A third group slants posteriorly down from the tergum to an apodeme near the anterior part of the brain. These various structures are shown in Fig. 3.6A-D.

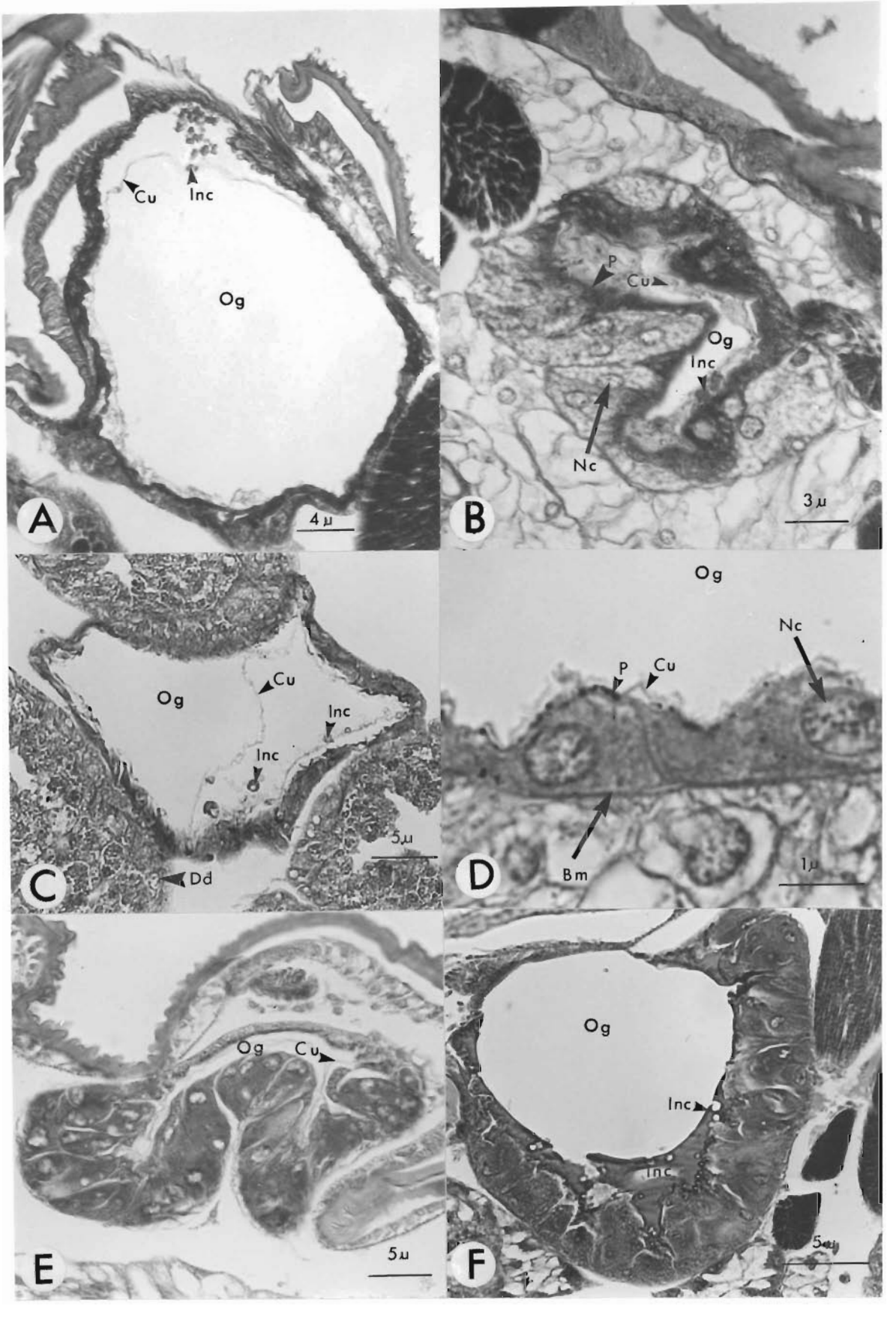
The only muscles directly associated with the gland are two small muscles located on either side of the glandular opening which are used to close the flap of flexible cuticle (Fig. 3.6E and F). Since the flap of cuticle is flexible and stained light blue with Mallory's triple stain, it is probably mainly endocuticle.

The fixation, sectioning and staining techniques employed usually removed the glandular secretion from the sections. In situ it takes the form of small inclusions about 0.05 μ in diameter (Fig. 3.6F).

A gland consists of three layers, an inner cuticular layer, a middle cellular layer and a basement membrane. The inner cuticular layer lines the interior of the sac and is continuous with the outside. The three layers are thrown into numerous wrinkles especially when the gland is depleted of secretion. When the gland is full of secretion, the middle layer of cells tend to become flattened, showing little cellular detail. When the gland is empty and folded, the middle layer of cells in the base of the gland, but not in the neck, become columnar having large nuclei with one or two nucleoli and granular or vacuolar cytoplasm (Fig. 3.6H). Sometimes dark colored grains of pigment occurred in between the cells and the inner cuticular layer.

All the other species of phalangids studied tended to have very similar odoriferous glands to those of Phalangium opilio. The following were the differences noted. In Opilio parietinus, the neck of the sac

Fig. 3.7. Various sections of the odoriferous glands of immature to adult Opilio parietinus (A, B), subadult to adult Odiellus pictus (C, D) and subadult to adult Homolophus biceps (E, F). A and B, transverse sections of full and empty glands with inclusions. C, transverse section of partially empty gland with inclusions. D, secretory cells of partially empty gland. E, sagittal section of an empty gland. F, transverse section of a partially empty gland with inclusions. All are 6 μ sections stained with Mallory's triple stain. Bm, basement membrane; Cu, inner cuticular layer; Dd, digestive diverticulum; Inc, inclusions; Nc, nucleus; Og, lumen of odoriferous gland; P, pigment.


A
Cu
Inc
Og
4 µ
B
P
Cu
Og
Inc
Nc
3 µ
C
Og
Cu
Inc
Inc
5 µ
Dd
D
Og
Nc
P
Cu
Bm
1 µ
E
Og
Cu
5 µ
F
Og
Inc
Inc
5 µ

was slightly longer and, in the folded glands, there was much more pigment. The pigment stained brown and red in color. The inclusions of this species consisted of flattened square or rectangular crystals which stained orange (Fig. 3.7A and B). The odoriferous glands of Odiellus pictus extended more anteriorly and the inclusions appeared in the form of collapsed hollow spheres which stained yellow to orange (Fig. 3.7C). The dark pigment granules are clearly shown in Fig. 3.7D. In Homolophus biceps the inclusions appeared as a mass of red staining material with a few bubbles in it (Fig. 3.7F). More obvious layering of secretory cells existed in this species than in the others studied (Fig. 3.7E).

3.2. Observations on predator-phalangid encounters

3.2.1. Amphibians as potential predators on phalangids

Three sets of experiments were performed with newly transformed Rana sylvatica and young to immature Phalangium opilio. The results are summarized in Table 3.2. Test Series A was performed on the third evening after the frogs were captured. The frogs had not been fed before the experiments. They were tested individually with a single phalangid. The next evening they were tested in the same way (Test Series B). About two hours after Test Series B, 13 of the frogs were tested again (Test Series C). Not enough phalangids were available to test all 20 frogs again. The table shows that many of the young or immature phalangids were eaten within 5 minutes and most were eaten within 60 minutes.

Table 3.2. Newly transformed Rana sylvatica-Phalangium opilio encounters. Test Series A performed three days after capture; B, 24 hours later; C, about 26 hours later.

Test Series	Number of frogs	Number P. opilio eaten (+) or not eaten (-)		
		0-5 min	5-30 min	30-60 min
A	20	12+	---	3+, 5-
B	20	15+	1+	3+, 1-
C	13	9+	1+	2+, 1-

Rothschild (1966) showed that jays can learn to reject certain grasshoppers, which contained cardenolides, not because of noxious stimuli present at the time of ingestion but because of stimuli later associated with digestion. This may also be true for frogs and phalangids. Since each frog was tested individually, changes in its feeding habits (ie. changes from eating phalangids to not eating phalangids or vice versa) could be followed through the three test series. This was done but too few frogs changed their feeding habits to be statistically significant.

On the third evening (Test Series C), five of the frogs were tested with subadult to adult Phalangium opilio. One phalangid was eaten within 30 minutes and four remained after 60 minutes. In the single case of a frog eating a subadult or adult phalangid, the frog lunged at the phalangid, engulfed it and then released it, wiping its mouth with its front legs. The phalangid was picked up and the typical odoriferous gland smell was detected. The phalangid was quickly returned to the arena and the frog made a number of lunges and misses and finally

ate it 25 minutes after the odor was first detected. This was the only time any amphibian was observed to take a phalangid into its mouth and then expel it. At other times it was observed that when a frog lunged at a phalangid but missed, picking up some sand from the arena in its mouth, it would wipe its mouth with its front legs. In the remainder of these observations, the frogs either moved away from the phalangids or made repeated lunges at them but failed to eat them.

About 10 adult Rana sylvatica were fed, with forceps, at least 10 immature and 25 subadult to adult Phalangium opilio (maintained at least one day at 20°C with food and water) with no apparent ill effects. The frogs were deprived of food from 4-7 days before feeding.

Seven adult Rana pipiens (obtained from Carolina Biological Supply Co., North Carolina) each ate a single adult Phalangium opilio (maintained at least one day at 20°C with food and water) without any adverse effects. The frogs were usually fed Tenebrio molitor larvae and had been without food for seven days before the experiment.

About six newly transformed Canadian Toads, Bufo hemiophrys (ca. 18 mm), were observed in the laboratory to feed upon young or immature Phalangium opilio (which had been raised in the laboratory). At least two toads ate more than one phalangid. The size of the phalangids, rather than anything else, seemed to prevent the toads from eating any more than they did.

Two Ambystoma tigrinum (total lengths = 135 and 175 mm) were kept in the laboratory and normally fed Tenebrio molitor larvae and adults. Before attempting to feed Phalangium opilio to them, they were deprived of food from 1-7 days. At least 25 immature to adult

P. opilio were eaten by the salamanders with no ill effects. In one case three P. opilio were squeezed, to release the odoriferous gland secretion, and were presented to each salamander. Both ate the three phalangids plus another two presented immediately after and three more presented 24 hours later. Thus each salamander ate eight P. opilio in two days. The larger salamander was presented with two subadult female Opilio parietinus and ate both without any adverse effects.

3.2.2. Birds as potential predators on phalangids

The results from the Gallus domestica chicks and Phalangium opilio experiments are summarized in Table 3.3. Out of 61 observations of chicks eating phalangids, 60 did not show any signs of the chicks being repelled by the phalangid odoriferous glands. The table shows that the percentage of phalangids eaten by chicks increased from 50% in the first test series to 100% in the third test series. Also, though the food deprival time decreased, the chicks began to feed more quickly from the first to the third test series. Although they had never been exposed to phalangids before the experiments, chicks I, J, K and L did not eat any phalangids. This could not have been due to previous learning that "phalangids taste bad". Two of these four chicks did attempt to eat phalangids, in that one pecked at one phalangid and the other attempted stealing a phalangid from another chick but neither ever got a phalangid into its mouth. Stealing of phalangids by one chick from another was observed at least three times in the three sets of experiments. In the third test series one chick in each experiment tended to eat all four phalangids before the other chick even began to feed. On only one occasion was a chick observed

Table 3.3. Results of Gallus domestica chicks-Phalangium opilio encounters. Chicks were tested in pairs. Food deprival time = feeding time if less than 15 minutes. Imm=immature; subadt=subadult; adt=adult.

	Test Series A. Chicks 24-36 hr old					Test Series B. Chicks 48-60 hr old					Test Series C. Chicks 72-84 hr old					
Chick	Food deprival time (min)	Chick tested with	Number and instar of phalangid eaten	Observation time (min)	Remarks	Food deprival time (min)	Chick tested with	Number and instar of phalangid eaten	Observation time (min)	Remarks	Food deprival time (min)	Chick tested with	Number and instar of phalangid eaten	Observation time (min)	Remarks	Total phalangids eaten
A	30	D	3 imm. 1 adt.♂	7	ate 1 imm. killed by D	15	J	3 imm. 1 subadt.	2	—	10	F	3 imm. 1 adt.♀	1	—	12/12
B	25	G	1 imm. 1 subadt.	7	? repelled by adt.♀	25	L	3 imm. 1 adt.♀	4	—	15	L	3 imm. 1 adt.♂	1	—	10/12
C	40	H	4 imm.	15	—	15	K	3 imm. 1 subadt.	5	—	10	E	2 imm.	1	—	10/12
D	30	A	0	7	pecked at and killed 1 imm.	5	I	3 imm.	15	killed 4th imm. but did not eat it	10	I	3 imm. 1 subadt.	10	—	7/12
E	30	F	0	15	no pecking at P. opilio	25	G	1 imm.	10	stole subadt. from G	10	C	2 imm.	1	—	3/12
F	30	E	0	15	no pecking at P. opilio	10	H	3 imm.	10	pecked at adt. ♀ but stolen by H	10	A	0	1	—	3/12
G	25	B	1 imm. 1 adt. ♀	7	ate adt. ♀ pecked at by B	25	E	3 imm.	10	killed subadt. but stolen by E	10	K	4 imm.	1	—	9/12
H	40	C	0	15	no pecking at P. opilio	10	F	1 adt.♀	10	stole adt.♀ from G	12	J	4 imm.	10	—	5/12
I	0	J	0	15	no pecking at P. opilio	5	D	0	15	no pecking at P. opilio	10	D	0	10	unsuccessful at stealing from D.	0/12
J	0	I	0	15	no pecking at P. opilio	15	A	0	2	no pecking at P. opilio	12	H	0	10	no pecking at P. opilio	0/12
K	10	L	0	15	no pecking at imm. P. opilio	15	C	0	5	some pecking at P. opilio	10	G	0	1	—	0/12
L	10	K	0	15	no pecking at imm. P. opilio	25	B	0	4	no pecking at P. opilio	15	B	0	1	—	0/12
Av.	22	—	1.2/ chick	12	—	14	—	1.9/ chick	8	—	11	—	2/chick	4	—	—
Totals		—	12/24; 50%	—	—	—	—	23/24; 96%	—	—	—	—	24/24; 100%	—	—	59/72; 82%

which may have been repelled by a phalangid. This was chick B in Test Series A. The bird had eaten one immature and one subadult phalangid before it began pecking at an adult female. The chick picked up the phalangid in its bill and then dropped it and began wiping its bill on the floor of the arena. (Bill wiping was also observed in chicks which pecked up pieces of feces in their bills.) The phalangid was removed from the arena and a faint odor was detected. When the phalangid was returned to the arena, within 30 seconds, the same chick again picked up the phalangid in its bill and began to eat it. The second chick stole the phalangid from the first chick and ate it. However, in the second and third test series chick B ate three immatures plus one adult female and three immatures plus one adult male, respectively.

The observations on attempting to feed Phalangium opilio to three Passer domesticus fledglings were as follows: in two cases (birds from the same nest) the fledglings did not eat immature phalangids or Tenebrio molitor larvae; in the third case the bird ate at least four immature P. opilio and numerous T. molitor larvae within five hours.

3.2.3. Mammals as potential predators on phalangids

The results from the Mus musculus - Phalangium opilio encounters are outlined in Table 3.4. The experiments were performed on three successive evenings. No observations were made that indicated that phalangid odoriferous glands were in any way repellent to the mice. Out of 10 mice tested six ate all three phalangids offered; two did not eat any; and two did not eat the first phalangid offered but ate subsequent

Table 3.4. Results of Mus musculus-Phalangium opilio encounters. Subadt=subadult; adt=adult.

Mouse	Evening 1					Evening 2					Evening 3					Total phalangids eaten
	Food deprival time (min)	Size and sex of phalangid tested	Phalangid eaten (+) or not eaten (-)	Observation time (min)	Remarks	Food deprival time (min)	Size and sex of phalangid tested	Phalangid eaten (+) or not eaten (-)	Observation time (min)	Remarks	Food deprival time (min)	Size and sex of phalangid tested	Phalangid eaten (+) or not eaten (-)	Observation time (min)	Remarks	
1	15	adt., ♂	+	22	P. opilio first squeezed producing typical odor	25	adt., ♂	+	25	---	18	subadt., ♀	+	8	---	3/3
2	30	adt., ♂	+	40	---	55	adt., ♀	+	25	---	25	subadt., ♀	+	15	---	3/3
3	20	sub-adt., ♀	-	60	few feeding attempts	25	adt., ♂	-	60	few feeding attempts	47	adt., ♂	-	60	few feeding attempts	0/3
4	50	sub-adt., ♂	-	60	killed P. opilio in 35 min	60	adt., ♀	+	26	---	25	subadt., ♀	+	17	---	2/3
5	45	adt., ♀	-	60	number feeding attempts	Cancelled as phalangid escaped during experiment.					35	adt., ♂	+	40	---	1/2
6	55	adt., ♂	+	5	---	60	adt., ♀	+	29	---	28	subadt., ♀	+	10	---	3/3
7	35	adt., ♀	+	13	---	57	adt., ♂	+	9	---	43	subadt., ♀	+	11	---	3/3
8	25	adt., ♀	+	7	---	28	adt., ♀	+	57	---	32	subadt., ♂	+	9	---	0/3
9	15	adt., ♀	-	60	P. opilio first squeezed, no odor; few feeding attempts	25	adt., ♂	-	60	few feeding attempts	15	adt., ♂	-	60	some feeding attempts	0/3
10	35	adt., ♀	+	17	---	38	adt., ♀	+	10	---	17	adt., ♂	+	13	---	3/3
Total	325	---	6+, 4-	344	---	373	---	7+, 2-	301	---	285	---	8+, 2-	243	---	21/29
Av.	32.5	---	60%	34.4	---	41.4	---	77.7%	33.4	---	28.5	---	80%	24.3	---	72.4%

ones. None accepted a phalangid and then rejected later ones. In these experiments it was often observed that the legs of the phalangids tended to prevent the mice from eating the phalangid, at least on the first attempt. The mice tended to seize, in their mouths or with their fore-feet, one or two legs which were then autotomized, allowing the phalangid to escape.

In the experiments performed with a single Microtus pennsylvanicus, the mouse ate Tenebrio molitor larvae but not Phalangium opilio.

Two out of the three Mephites mephites did not attempt to eat any Phalangium opilio offered to them. The third skunk ate at least six young to immature P. opilio without apparent harm.

3.2.4. Spiders as potential predators on phalangids

Pardosa fuscula were tested nine days after their capture (Test Series A), three days later (Test Series B), seven days later (Test Series C) and 24 days later (Test Series D). The spiders were fed six adult Drosophilia melanogaster two days before Test Series A and D. No food (besides the phalangids) was offered before Test Series B and C. The results are outlined in Table 3.5. Since observations were continuous for only 10 minutes, the "Time to begin sustained feeding" was only approximate after that time. Out of 41 young to adult Phalangium opilio and seven immature Opilio parietinus offered to the spiders, 33 were fed upon within two minutes; five within 10 minutes; one within one hour and three overnight. Only six phalangids were not eaten overnight, all were P. opilio. These were: spider #1 (Test Series A) which did not attack or eat an immature but died overnight; spider #12 (Test Series A) which did not attack or eat an immature but

Table 3.5. Results of Pardosa fuscula vs. Phalangium opilio and Opilio parietinus encounters. Test Series A performed two days after feeding; B, three days after A; C, four days after B; and D, 24 days after A but two days after feeding. Yg=young; imm= immature; subadt=subadult; adt=adult, P.O.=P. opilio; O.p.= O. parietinus.

Test Series A

Spider	Food deprival time (days)	Species and size of phalangid tested	Time (min) to first attack	Time (min) to begin sustained feeding	Time elapsed with no feeding	Remarks
1	2	P.o., imm.	no attacks observed	did not feed	30 min	died overnight
2	2	P.o., imm.	immediate	<1	---	---
3	2	P.o., yg.	4	<5	---	---
4	2	P.o., imm.	10	<13	---	did not finish eating
5	2	P.o., imm.	4	<5	---	---
6	2	P.o., imm.	immediate	<1	---	---
7	2	P.o., imm.	immediate	<1	---	---
8	2	P.o., imm.	immediate	?, fed overnight	>2 hr	may have been repelled once
9	2	P.o., imm.	immediate	<40	---	repeated attacks before feeding
10	2	P.o., imm.	immediate	<1	---	---
11	2	P.o., imm.	<1	<2	---	---
12	2	P.o., imm.	no attacks observed	did not feed	overnight	spider moulted within 3 days
13	2	P.o., imm.	immediate	<1	---	---
14	2	P.o., imm.	<1	<2	---	---

Table 3.5. cont'd

Test Series B

Spider	Food deprival time (days)	Species and size of phalangid tested	Time (min) to first attack	Time (min) to begin sustained feeding	Time elapsed with no feeding	Remarks
2	3	P.o., imm.	immediate	< 1	---	---
3	3	P.o., imm.	< 1	< 3	---	---
4	3	P.o., imm.	< 1	< 2	---	---
5	3	P.o., imm.	< 1	< 2	---	---
6	3	P.o., imm.	< 1	< 2	---	---
7	3	P.o., sub-adt.♂	immediate	< 1	---	spider attacked before P.o. even released
8	3	P.o., adt. ♀	no attacks observed	did not feed	overnight	---
9	3	P.o., imm.	immediate	< 1	---	---
10	3	P.o., imm.	< 1	< 2	---	died within four days
11	3	P.o., imm.	< 1	< 2	---	---
12	5	P.o., imm.	immediate	?, fed overnight	> 30 min	may have been repelled once
13	3	P.o., imm.	no attacks observed	?, fed overnight	> 30 min	---
14	3	P.o., imm.	immediate	< 1	---	---

Table 3.5. cont'd

Test Series C

Spider	Food deprival time (days)	Species and size of phalangid tested	Time (min) to first attack	Time (min) to begin sustained feeding	Time elapsed with no feeding	Remarks
2	4	O.p., imm.	immediate	<1	---	---
3	4	O.p., imm.	immediate	<1	---	---
4	4	O.p., imm.	4	<5	---	---
5	4	O.p., imm.	immediate	<1	---	---
6	4	O.p., imm.	immediate	<1	---	---
7	4	P.o., imm.	immediate	<1	---	died next day
8	7	P.o., imm. (near sub-adt.)	immediate	did not feed	overnight	did not attack after first try
10	4	P.o., adt. ♂	no attacks observed	did not feed	overnight	died over 7 days later
11	4	P.o., imm.	<1	<2	---	---
12	4	P.o., imm.	<1	<2	---	died over 7 days later
13	4	P.o., imm.	immediate	<1	---	---
14	4	P.o., imm.	<1	<2	---	---

Table 3.5. cont'd

Test Series D

Spider	Food deprival time (days)	Species and size of phalangid tested	Time (min) to first attack	Time (min) to begin sustained feeding	Time elapsed with no feeding	Remarks
2	2	O.p., imm.	<1	<2	---	---
3	2	O.p., imm.	immediate	<1	---	---
4	2	P.o., imm.	<1	<2	---	---
5	2	P.o., imm.	immediate	<1	---	---
6	2	P.o., imm.	immediate	<1	---	---
8	2	P.o., imm.	<1	<2	---	---
11	2	P.o., imm.	<1	<2	---	---
13	2	P.o., sub-adt.♂	<1	?, fed overnight	>1 hr	---
14	2	P.o., sub-adt.♂	<2	did not feed	overnight	weak attacks

moulted within three days; spider #8 (Test Series B and C) which did not attack or eat an adult female nor an immature (near subadult); spider #10 (Test Series C) which did not attack or eat an adult male; and spider #14 (Test Series D) which weakly attacked a subadult male but did not eat it. Only twice were observations made which may be interpreted to mean that the odoriferous glands repelled a spider. These occurred in Test Series A with spider #8 and in Test Series B with spider #12. Both spiders, on attacking an immature P. opilio quickly retreated and wiped their chelicerae on the floor of the arena. The smell of odoriferous gland secretion was detected with spider #8 but not with #12. Both spiders ate their respective phalangids overnight. At numerous other times spiders were observed to feed directly over an odoriferous gland and in about 30% of some observations (5-7 out of 19 P. opilio experiments checked) odoriferous gland secretion could be detected while the spider was feeding. In none of these cases did the spiders seem to be adversely affected.

The experiments with Pardosa groenlandica and Pardosa modica vs. Phalangium opilio were performed in the same manner as those with Pardosa fuscula. The results are outlined in Tables 3.6 and 3.7.

Out of 20 young to subadult Phalangium opilio offered to Pardosa groenlandica, 11 were fed upon within two minutes; one within 10 minutes; two within one hour and five overnight. Only one immature phalangid was not eaten (spider #2, Test Series D). In this case the spider died overnight. No observations were made on Pardosa groenlandica being directly repelled by P. opilio odoriferous glands.

Out of 19 young to adult Phalangium opilio offered to Pardosa

Table 3.6. Results of Pardosa groenlandica-Phalangium opilio encounters. Test Series A performed two days after feeding; B, three days after A; C, four days after B; and D, 24 days after A but two days after feeding. Yg=young; subadt=subadult; adt=adult.

	Spider	Food deprival time (days)	Size P. opilio	Time (min) to first attack	Time (min) to begin sustained feeding	Time elapsed with no feeding	Remarks
Test Series A	1	2	imm.	10	< 12	---	---
	2	2	imm.	< 1	< 2	---	---
	3	2	imm. (near subadt.)	no attacks observed	?, fed overnight	>15 min	---
	4	2	imm.	no attacks observed	?, fed overnight	>10 min	---
	5	2	imm.	no attacks observed	?, fed overnight	>10 min	---
Test Series B	1	3	imm.	no attacks observed	?, fed overnight	>15 min	---
	2	3	yg.	immediate	<1	---	---
	3	3	imm.	immediate	<1	---	---
	4	3	imm.	immediate	< 1	---	---
	5	3	imm.	immediate	< 1	---	---

Table 3.6. cont'd

	Spider	Food deprival time (days)	Size P. opilio	Time (min) to first attack	Time (min) to begin sustained feeding	Time elapsed with no feeding	Remarks
Test Series C	1	4	imm.	no attacks observed	< 50	>10 min	died over 7 days later
	2	4	imm.	< 1	< 2	---	---
	3	4	imm.	< 2	< 3	---	died over 7 days later
	4	4	imm.	immediate	< 1	---	---
	5	4	imm.	< 1	< 2	---	---
	6	2+?	imm.	no attacks observed	?, fed overnight	>45 min	captured 2 days before experiment
Test Series D	2	2	imm.	no attacks observed	did not feed	overnight	spider died overnight
	4	2	imm.	immediate	< 1	---	---
	5	2	imm.	immediate	< 1	---	---
	6	2	subadt. ♂	immediate	< 1	---	---

Table 3.7. Results of Pardosa modica-Phalangium opilio encounters. Test Series A performed two days after feeding; B, three days after A; C, four days after B; and D, 24 days after A but two days after feeding. Yg=young; imm=immature, subadt=subadult; adt=adult.

	Spider	Food deprival time (days)	Size P. opilio	Time (min) to first attack	Time (min) to begin sustained feeding	Time elapsed with no feeding	Remarks
Test Series A	1	2	imm.	< 1	< 2	---	died within 3 days
	2	2	imm. (near sub-adt.)	no attacks observed	did not feed	overnight	---
	3	2	imm.	no attacks observed	?, fed overnight	>1 hr	---
	4	2	imm.	immediate	< 1	---	---
	5	2	imm.	< 2	< 3	---	weak attacks
	6	2	imm.	< 2	< 3	---	---
Test Series B	2	3	yg.	< 5	< 6	---	---
	3	3	imm.	no attacks observed	did not feed	overnight	---
	4	3	imm.	< 2	< 3	---	---
	5	3	imm. (near sub-adt.)	no attacks observed	did not feed	overnight	---
	6	3	imm. (near sub-adt.)	no attacks observed	did not feed	overnight	P. opilio swathed in silk

Table 3.7. cont'd

	Spider	Food deprival time (days)	Size P. opilio	Time (min) before first attack	Time (min) to begin sustained feeding	Time elapsed with no feeding	Remarks
Test Series C	2	4	imm.	<10	< 13	---	---
	3	4	adt., ♀	no attacks observed	did not feed	overnight	---
	4	4	imm.	<1	< 27	---	many attacks before feeding
	5	4	imm.	< 2	?, fed overnight	overnight	died 7 days later
	6	4	imm.	< 5	< 6	---	died overnight
Test Series D	2	2	imm.	no attacks observed	did not feed	overnight	spider morbid
	3	2	imm.	no attacks observed	did not feed	overnight	spider died overnight
	4	2	subadt. ♂	no attacks observed	did not feed	overnight	spider morbid

modica, two were fed upon within two minutes; five within 10 minutes; two within one hour; and two overnight. Eight phalangids were not eaten: spider #12 (Test Series A) did not attack or eat an immature (near subadult); spiders #'s 3, 5 and 6 (Test Series B) did not attack or eat three immatures (two near subadult); spider #3 (Test Series C) did not attack or eat an adult female; spiders #'s 2, 3 and 4 (Test Series D) did not attack or eat two immatures or a subadult male. No observations were made on spiders being directly repelled by P. opilio odoriferous glands.

Pardosa mackenziana were tested eight days after capture and were each fed six adult Drosophilia melanogaster twice, the second time three days before the experiments. The experiments were performed in a way similar to the other Pardosa experiments except that if a spider had not fed upon a phalangid overnight, six D. melanogaster adults were dropped into the arena with the spider and observed for five minutes to see if the spider would feed or not. The results are outlined in Tables 3.8 and 3.9. Out of the six immature to subadult Phalangium opilio offered to the spiders, the three immatures were eaten but the three subadults were not. These results are similar to those found with Pardosa fuscula, P. groenlandica and P. modica. Of the eight Odiellus pictus offered to the spiders, only one was eaten. In all four cases where attacks were observed, the spiders tended to attack and then quickly withdraw. In one case a spider wiped its chelicerae on the floor of the arena. Unfortunately since these tests were performed late in the season, not enough phalangids were available to replicate the experiments.

One male and three female adult Tegenaria derhami were tested with young to immature P. opilio. The spiders had been left in separate arenas (5 cm in diameter) for over one week before the experiments. This

Table 3.8. Results of Pardosa mackenziana-Phalangium opilio encounters.

Imm=immature; subadt=subadult.

Spider	Size phalangid	Time (min) to first attack	Time (min) to begin sustained feeding	Time elapsed with no feeding	Ate flies (+); did not eat flies (-)	Remarks
5	imm.	1	2	---	---	---
9	imm.	no attacks observed	?, fed overnight	>1 hr	---	---
12	subadt. ♂	no attacks observed	did not feed	overnight	+	---
14	imm.	immediate	?, fed overnight	>15	---	---
15	subadt. ♂	no attacks observed	did not feed	overnight	-	---
16	subadt. ♂	no attacks observed	did not feed	overnight	-	---

Table 3.9. Results of Pardosa mackenziana-Odiellus pictus encounters.

Subadt=subadult; adt=adult.

Spider	Size phalangid	Time (min) to first attack	Time (min) to begin sustained feeding	Time elapsed with no feeding	Ate flies (+); did not eat flies (-)	Remarks
2	subadt.	< 1	did not feed	overnight	+	number of attacks; may have been repelled
3	subadt. or adt.	< 1	did not feed	overnight	+	as spider #2
4	subadt.	no attacks observed	did not feed	overnight	+	---
6	subadt. or adt.	immediate	?, fed overnight	>75 min	---	after first attack spider cleaned chelicerae
7	subadt.	no attacks observed	did not feed	overnight	-	---
8	subadt. or adt.	no attacks observed	did not feed	overnight	-	---
10	subadt.	no attacks observed	did not feed	overnight	-	---
11	subadt.	< 1	did not feed	overnight	+	withdrew after first attack; may have been repelled

allowed the spiders to spin webs and become adjusted to their new environments. In all other respects, they were treated as the Pardosa spp. The spiders were fed six adult Drosophilia melanogaster three days before Test Series A. Test Series B occurred two days after Test Series A. The results are outlined in Table 3.10. Out of eight P. opilio offered, six were eaten. Two were not eaten, both by the same spider. In one case a spider (#4, Test Series A) attacked and seemingly was repelled by an immature phalangid. The spider was observed wiping its chelicerae on the floor of the arena. The phalangid, however, was eaten within 15 minutes.

3.2.5. Incidental observations on phalangids found in spider webs or retreats

Table 3.11 lists the observations made during 1969-70 on phalangids found in spider webs or retreats. All the spiders listed, except those belonging to the Family Agelenidae, were small, tending to be about the size of immature Phalangium opilio.

3.2.6. Centipedes as potential predators on phalangids

Of the three centipedes tested, one ate 10 young to immature Phalangium opilio (raised in the laboratory) and two subadult or adult Odiellus pictus (maintained in the laboratory) either from a pair of forceps or when the phalangids were left with the centipedes overnight; one ate a single young P. opilio overnight; and one did not eat an O. pictus which was left for four days in the same container. The first mentioned centipede fed directly over the odoriferous glands on at least four occasions; involving two immature P. opilio and two O. pictus. In the case of the two P. opilio, strong odoriferous gland odor was present both

Table 3.10. Results of Tegenaria derhami-Phalangium opilio encounters. Test Series A, spiders fed three days before; Test Series B, two days after first test series. Yg=young; imm=immature.

	Spider	Food deprival time (days)	Size P. opilio	Time (min) to first attack	Time (min) to begin sustained feeding	Time elapsed with no feeding	Remarks
Test Series A	1 ♂	3	yg.	< 1	< 2	---	---
	2 ♀	3	imm.	< 1	< 2	---	---
	3 ♀	3	imm.	no attacks observed	did not feed	overnight	---
	4 ♀	3	imm.	< 1	< 15	---	attacked and withdrew;odor present; spider cleaned chelicerae
Test Series B	1 ♂	2	imm.	< 4	?, fed overnight	> 90 min	---
	2 ♀	2	imm.	< 1	< 50	---	---
	3 ♀	2	imm.	no attacks observed	did not feed	overnight	---
	4 ♀	2	imm.	no attacks observed	?, fed overnight	> 1 hr	---

Table 3.11. Phalangids found in the webs or retreats of spiders

Spider	Phalangid	Remarks
Family: Theridiidae *Steadoda borealis*; female	*Phalangium opilio*; adult males and females	numerous observations but none were eaten
Theridium ornatum; female	*P. opilio*; subadults, adult male and female	numerous observations but seldom were any phalangids eaten
T. frondeum; female	*P. opilio*; immature	one observation of spider feeding
Family: Linyphiidae *Pitychyphantes* sp.; penultimate male	*P. opilio*; immature	phalangid in web but too dried to determine if fed upon
Family: Tetragnathidae *Tetragnatha* sp.; immature	*P. opilio*; immature	phalangid in web but too dried to determine if fed upon
Family: Agelenidae *Tegenaria derhami*; males and females	*P. opilio*; immature and subadult males and females	numerous observations but seldom were phalangids eaten
Agelenopsis sp.; immature	*Homolophus biceps*; immature or subadult	spider in retreat feeding on phalangid

times. All centipedes ate cold-killed Drosophilia melanogaster adults. Food deprival times, before feeding phalangids to the centipedes, varied from 2-7 days.

3.2.7. Ants as potential predators on phalangids

Ten young to adult Phalangium opilio of both sexes were individually added to a colony of ants and observed. The phalangids were maintained in the laboratory for at least two days before testing. When a phalangid was added, the ants went into "alarm behavior", which was usual whenever the cover of the colony was raised, and began to bite the phalangid on the legs and body. When bitten, the phalangid usually produced the typical odoriferous gland odor immediately. The ants were not affected by the glands' secretion unless their mouthparts came into contact with the region directly around the odoriferous gland opening. Unless the glandular secretion was exhausted, the ants immediately released their mandibles, moved away from the phalangids and began wiping their mouthparts on the sand substrate. After 2-20 seconds, the ants stopped this activity and began cleaning their mouthparts, and sometimes their antennae, with their front legs. Adult phalangids could repel ants up to five minutes, about 2-3 minutes after the distinctive odor could not be detected. Young phalangids were able to repel ants just as effectively but for shorter lengths of time. When the glandular secretion seemed to be exhausted, the ants bit the phalangids in the regions of the odoriferous glands with impunity.

The ants' antennae did not seem to be capable of detecting the glandular secretion. The secretion may be able to adhere to regions around the glands' openings for in one case an ant was repelled when its

mouthparts touched a palp in the region adjacent to an active gland.

It was noted that only young and immature phalangids were greatly harmed by the ants' attacks. The hardness of the subadult and adult cuticle prevented the ants mandibles from causing much damage.

3.3. Results of a field experiment at Lady Lake

3.3.1. Amphibian stomach data

During a five month period from May to September 552 Rana sylvatica, 56 R. pipiens, four Pseudacris triseriata maculata and two Bufo hemiophrys were taken for stomach content analysis. The numbers taken per month are shown in Table 3.12. Only one Ambystoma tigrinum was found. It was not killed but retained for behavioral experiments, recorded above in section 3.2.1. Tables 3.13 and 3.14 give the numbers and species of phalangids found in the stomachs of R. sylvatica and R. pipiens, respectively. Table 3.15 gives the percentage of phalangids found in the total diet of these two frogs. No phalangids were found in the stomachs of P. triseriata maculata or B. hemiophrys.

Table 3.12. Numbers of Anurans taken each month in the study area.

Anuran species	26-28 May	19-20 June	18-21 July	25-27 Aug.	18-19 Sept.	Total
Rana sylvatica	59	76	129	145	143	552
Rana pipiens	0	9	7	28	12	56
Pseudacris triseriata maculata	1	0	0	0	3	4
Bufo hemiophrys	1	0	1	0	0	2
Total for year						614

Table 3.13. Phalangids found in the stomachs of 552 Rana sylvatica.

Date	Size Frog	Phalangid	Size Phalangid
26-28 May	---	---	---
19 June	juvenile	1 Phalangium opilio	immature
17 July	juvenile	1 phalangid	immature
18 July	adult	1 P. opilio	immature
19 July	adult	1 P. opilio	young or immature
19 July	juvenile	1 P. opilio	immature
20 July	adult	1 P. opilio	immature
20 July	adult	1 Leiobunum calcar	female subadult or adult
25 August	juvenile	1 P. opilio	male subadult
27 August	adult	1 P. opilio	immature
27 August	adult	1 P. opilio	female adult
27 August	adult	1 P. opilio	immature
		1 Odiellus pictus	immature
18-19 September	---	---	---

Table 3.14. Phalangids found in the stomachs of 56 Rana pipiens.

Date	Size Frog	Phalangid	Size Phalangid
26-28 May	---	---	---
19-20 June	---	---	---
18-21 July	---	---	---
25 August	juvenile	1 Phalangium opilio	immature
27 August	juvenile	1 P. opilio	female adult or subadult
18-19 September	juvenile	1 P. opilio	male adult

Table 3.15. Percentage of phalangids in the diets of Rana sylvatica and R. pipiens. "n" is the number of stomachs examined to calculate "Av. no. organisms per stomach".

Anuran species	No. stomachs examined	Av. no. organisms /stomach	Total no. organisms in all stomachs	No. phalangids found in all stomachs	Percentage of phalangids in diet
Rana sylvatica	552	6.0 (n= 274)	3,312	12	0.4%
Rana pipiens	56	4.9 (n= 56)	274	3	1.1%

3.3.2. Potential prey data

Although the numbers of phalangids found in the frog stomachs were low, the numbers found in the study area with the quick traps and sweep nets were far lower. Only two phalangids were taken in the sampling; one immature Phalangium opilio in June with the sweepings and one immature Odiellus pictus in July with the quick traps. The numbers of organisms taken in the different communities of the study area by the quick traps and by insect net sweepings are given in Table 3.16. The frequency of occurrence of all phalangids was less than 0.01%. Samples taken with the aquatic net are not given as few frogs fed upon organisms which lived below the surface of the water and no frogs were ever seen in the open-water community.

Table 3.16. Number of phalangids and other organisms taken in different communities of the study area by quick traps and 100 standard sweeps with the insect net. No. organisms/m^2 = $\left(\frac{\text{No. of organisms collected}}{\text{No. of samples taken}} \times \text{Factor for converting trap area to one } m^2\right)$.

Date	Community	Sweep netting		Quick traps			
		No. phalangids taken	Total no. organisms taken	No. samples taken	No. phalangids taken	Total no. organisms taken	No. organisms/ m^2
26-28 May	Cat-tail	---	---	6	0	32	21.3
(2 June for	Sedge	0	249	9	0	552	246.7
sweepings)	Grass-willow	0	293	12	0	1430	476.7
	Woods	0	416	13	0	436	134.2
18-19 June	Cat-tail	---	---	10	0	273	109.2
	Sedge	0	598	9	0	819	364.0
	Grass-willow	0	96	10	0	318	127.2
	Woods	1	323	11	0	276	100.4
18-21 July	Cat-tail	---	---	10	0	278	111.2
	Sedge	0	439	9	0	948	421.3
	Grass-willow	0	81	10	0	317	126.8
	Woods	0	84	10	1	480	192.0
25-26	Cat-tail	---	---	10	0	452	180.8
August	Sedge	0	425	10	0	1486	594.4
	Grass-willow	0	109	10	0	358	143.2
	Woods	0	70	7	0	176	100.6
18-19	Cat-tail	---	---	10	0	137	54.8
September	Sedge	0	252	10	0	865	346.0
	Grass-willow	0	70	9	0	157	69.8
	Woods	0	20	10	0	178	71.2
Totals	---	1	3525	195	1	9971	---

3.4. Incidental amphibian stomach data

The results from the analysis of various amphibian stomachs taken in the summers of 1969 and 1970 are given in Table 3.17. The table clearly shows that the numbers of phalangids found in the stomachs varied extremely, in these cases from 25.9% to 0.1%.

Table 3.17. Percentage occurrence of phalangids found in various amphibian stomachs. Yg=young; imm=immature; subadt=subadult; adt=adult; P.o.=*Phalangium opilio*; H.b.=*Homolophus biceps*.

Amphibian	Number of stomachs examined	Average amphibian snout-vent length (mm)	Location and habitat	Estimate of phalangid population	Number and species of phalangids in stomachs	Size of phalangids in stomachs	Total no. organisms eaten	Percentage occurrence of phalangids in
Rana pipiens	1	35	Lady Lake; marsh	Moderate; imm. to subadt. P.o.	7 P.o.	imm. to subadt.	27	25.9%
Pseudacris triseriata maculata	3	17.0	Saskatoon; roadside ditch	Moderate; imm. P.o.	4 P.o.	imm.	17	23.5%
Pseudacris triseriata maculata	16	17.4	Saskatoon; slough	Abundant; imm. and subadt.P.o.	14 P.o.	imm. and subadt.	111	12.6%
Bufo hemiophrys	13	14.7	Kelvington; roadside	Moderate; yg. and imm.	2 P.o.	yg. and imm.	265	0.8%
Rana pipiens	39	Av. ?; Range *ca.* 30-70	Cypress Hills; stream and beaver pond	Few; yg. P.o. and imm. or subadt. H.b.	1 H.b.	imm. or subadt.	*ca.* 250	0.4%
Bufo hemiophrys	34	11.3	Saskatoon; roadside ditch	Few; mainly imm. P.o.	1 P.o.	yg.	853	0.1%

4. DISCUSSION

4.1. The odoriferous glands: their secretion, structure and histology

It is most probable that the odoriferous glands of the species studied produce a liquid secretion which volatilizes rapidly in contact with air. I have not observed any external liquid which was positively derived from the odoriferous glands of Phalangium opilio, Opilio parietinus or Odiellus pictus; but some liquid secretion probably was present in Homolophus biceps. Odor was detected only in P. opilio and H. biceps. In P. opilio the observations that ants were repelled by biting structures in the immediate vicinity of the odoriferous gland openings tend to support the idea that some liquid is produced which spreads over a part of the cuticle before volatilizing. Juberthie (1961b) classified the Palpatores into two groups, based on the method of odoriferous gland secretion. He maintained that one group produces an easily visible drop of secretion and the second group produces an odor without much liquid formation. He gave P. opilio as an example of the first type and for the second type"...Rhampsinitus levis et dans certaines conditions P. opilio (chez des individus enfermés dans une même boîte)." Thus the amount of liquid secretion may vary greatly. Although I did not examine any live Leiobunum species for a liquid secretion, it has been observed to occur in this genus (eg. Bishop, 1949). Bishop (1950) noted that in L. longipes the glandular secretion first appeared as a slightly viscid clear fluid and then after further stimulation, as a milky fluid. He stated further "...the clear fluid had a neutral or slightly alkaline reaction and the milky fluid a decidedly acid one. But when specimens were starved for 48 hours the clear fluid became acid and could only be

restored to its original condition by feeding the specimens for a couple of days. On the other hand, the milky fluid remained acid whether the animals were fed or starved.".

It was observed that Phalangium opilio at 20°C may need less than 2-4 days to replenish their odoriferous gland secretions when food and water were present and that they could not do it in less than 24 hours with only water present. Cold storage did not seem to affect odor production.

Only 14 out of 37, of 39%, of the freshly caught or refrigerated Phalangium opilio produced an odor upon squeezing (section 3.1.1). Although this does not necessarily mean that only 39% of the phalangids had sufficient quantities of odoriferous gland secretion to repel potential predators, providing that the secretions could repel predators, it probably does indicate that less than 100% of the phalangids had full glands. Thus it is possible that the predator-phalangid encounter experiments performed with freshly caught or refrigerated phalangids produced fewer repulsions than if the phalangids were maintained in the laboratory for a few days with food and water before testing. The latter procedure was used only for the experiments performed with P. opilio and adult Rana sylvatica, R. pipiens, Bufo hemiophrys, Lithobius sp. and Formica oreas; and with Odiellus pictus and Pardosa mackenziana and Lithobius sp. The former procedure was followed for all other encounter experiments.

However, even if only 25% of the freshly caught or refrigerated phalangids had sufficient secretion, out of the 165 phalangids which were eaten by the vertebrate predators, 41 should have been able, if possible, to defend themselves with their secretions. In fact only two instances occurred where vertebrates may have been repelled. In the spider experiments, out of the 79 phalangids eaten, 19 should have been capable of defending themselves. In this case only three observations,

where freshly caught phalangids were used, showed any signs of the phalangids being capable of repelling the spiders. Thus even though the phalangids which were freshly caught probably had less odoriferous gland secretion than those maintained in the laboratory, far too few instances of repulsion occurred for this factor to be operating.

The glands of the Palpatores phalangids were first described by Krohn (1867) and later by Kästner (1935) and Juberthie (1961b). My descriptions of the gross appearance of the glands agrees in general with that of Krohn's except that any tracheae I observed were more closely associated with the muscles than with the glands.

Concerning the histology of the glands, Krohn (1867) described small coiled channels in association with the middle layer of cells which were made easily visible by application of a weak KOH solution. Juberthie (1961b) did not record these channels and I have not seen them in my preparations. It is possible that Krohn mistook some folds of the inner cuticular lining for channels. Krohn also mentioned the presence of square or rectangular shaped crystals in some specimens of Leiobunum and "Phalangium", which now includes Phalangium and Opilio. Since the inclusions and in some cases the pigments of the species studied tended to be different, it is most likely that the chemical nature of the odoriferous secretions of all four species is also different. My description of the histology of the glands agrees in general with that of Juberthie (1961b) except that he recognized two cell types within the middle cellular layer, large basal cells and smaller cells located between the large cells and the inner cuticular lining. The only species in which layering of the cellular layer may have occurred was Homolophus biceps.

Since the glands are lined with cuticle, this inner layer is probably lost during moulting. Whether the stored secretion is also lost is questionable because it is located between the inner cuticular lining and the middle cellular layer. Cuticular linings in arthropod glands are also present in other arachnids (Eisner et al., 1961), crustaceans (Gorvett, 1956), millipedes (Woodring and Blum, 1963) and insects (references in Eisner and Meinwald, 1966).

Since the glands have no muscle system, except for closing the opening of the gland, and since the liquid secretions of other Palpatores phalangids slowly ooze out of the glands (Lawrence, 1938; Bishop, 1950) it is most likely that expansion of the digestive diverticulae by muscle contraction further down the alimentary canal and muscle contraction of the three major groups of muscles surrounding the glands indirectly constrict the glands, causing them to void their contents. It is also possible, but unlikely, that chemical means, as occurs in Bombardier beetles (Aneshansley et al., 1969), are used to empty the glands.

Since full and partially empty glands can be found in the same individual, it is most likely that the Palpatores phalangids have some control over which gland is operated. Control of this kind has been demonstrated in the Laniatores (Lawrence, 1938) and in the Cyphophthalmi (Juberthie, 1961a). Once a gland has been emptied, it probably then collapses and becomes much folded. Perhaps this is the stimulus needed to activate the middle layer of cells to begin a secretory phase.

4.2. Defensive function of the odoriferous glands

Although phalangid odoriferous glands have been generally regarded as a means of defense, actual observations of phalangids repelling

potential predators have been rare. Table 4.1 summarizes all reported observations of phalangids repelling potential predators. Juberthie (1961a) reported on the Cyphophthalmi; Forster (1954) on the Laniatores; and Bristowe (1941, 1949) and Edgar (1960) on the Palpatores. It is not clear from Strahnke's (1945) paper which suborder was involved in repelling scorpions.

The reports of phalangids being eaten by different predators far outweighs those of phalangids repelling potential predators. The results of a partial literature search are summarized in Tables 4.2 to 4.7. Unfortunately most of the records are non-specific about the phalangids eaten. Some of the predators listed do not commonly feed upon phalangids. These include snails (Edgar, 1960) and fish (Bristowe, 1949). Man could also be added to this list of infrequent predators since Bristowe (1949) stated "...I have been told that Phalangium opilio has a nutty flavour to which an occasional schoolboy used not to be averse!". Other examples of predators from Tables 4.2 to 4.7 may not be natural predators in that they are ecologically separated from at least certain species of phalangids. For example, not all the species of phalangids listed in Table 4.4 that were eaten by a hedgehog would necessarily be found in the habitat that the hedgehog normally frequents. This applies to all laboratory feeding situations unless it is known that the species of phalangid being tested can be found in the predator's natural habitat. Also just because an animal eats something once, it does not follow that it will eat it again. If the prey is in some way noxious to the predator and if the predator can associate the noxious stimulus with a particular prey, it may learn to avoid that or similar species in the future.

Table 4.1. References to phalangids repelling potential predators.

Predator	Phalangid	Remarks	References
1. Scorpionida (a) *Hadrurus* spp.	"harvestmen"	"Although they do not eat sow bugs or harvestmen, a hungry specimen will frequently grab one of these, only to reject it."	Stahnke, 1945
2. Araneae (a) Various spiders (at least 16 genera)	Palpatores; Phalangiidae: *Mitopus morio*, *Megabunus diadema*, *Platybunus triangularis*, *P. corniger*, *Leiobunum rotundum*, *L. blackwallii*, *Oligolophus agrestis*, *O. hansenii*, *O. tridens*; Nemastomatidae: *Nemastoma lugubre*.	phalangids were either touched and refused or bitten and refused; at least four spiders (*Meta reticulata* and *Agelena labyrinthica* vs. *L. blackwallii*; and *M. reticulata* and *Zygiella* sp. vs. *O. agrestis*) wiped their mouthparts on a leaf after biting a phalangid	Bristowe, 1941, 1949
(b) Spiders	Laniatores	"The group is not attacked by spiders but infestation by nematodes and chalcid wasps has been noted. Specimens are often found heavily infested with mites..."	Forster, 1954
3. Phalangida (a) *Odiellus* sp. (Palpatores)	*Siro rubens* (Cyphophthalmi)	odoriferous secretion from *S. rubens* on pieces of fly caused the second phalangid to reject them	Juberthie, 1961a
4. Amphibia (a) *Rana clamitans*	*Leiobunum vittatum* (Palpatores)	frog rejected phalangid; single observation	Edgar, 1960 and personal communication

Since many authors of feeding study reports tend to lump phalangids together with other arachnids under headings such as "Spiders" and "Arachnids", it is likely that more predators eat phalangids than the literature would suggest.

My amphibian-phalangid encounter experiments (see section 3.2.1) suggest that Rana sylvatica, R. pipiens, Bufo hemiophrys and Ambystoma tigrinum are, in general, unaffected by the odoriferous glands of Phalangium opilio. In the few cases of newly transformed R. sylvatica and B. hemiophrys which either made repeated lunges at the phalangids but failed to eat them or avoided contact with them, both kinds of behavior may be explained by the size of the phalangids. That is, after a critical size a phalangid may be just too large to eat or the frog may treat the phalangid as a potential predator rather than the other way around. This critical size may be subadult or adult Phalangium opilio in the case of newly transformed R. sylvatica and late immature to adult P. opilio in the case of newly transformed B. hemiophrys.

The single case of a newly transformed Rana sylvatica which expelled a subadult Phalangium opilio may be explained by either (a) the phalangid odoriferous glands being effective or (b) the frog taking in sand along with the phalangid and then rejecting the phalangid because of the sand. Since (i) the frog eventually did eat the phalangid; (ii) no other newly transformed R. sylvatica rejected phalangids once in their mouths; (iii) adult R. sylvatica ate numerous subadult to adult P. opilio with no apparent ill affects; and (iv) other R. sylvatica reacted in a similar way to this specific case when they just got sand in their mouths, explanation (b) is probably correct.

Although the percentage of phalangids in the diet of Rana sylvatica

and R. pipiens taken in the study area was only 0.4% and 0.1%, respectively, (see section 3.4.1) the frequency of occurrence of phalangids on the study area (see section 3.4.2) was $<0.01\%$ of the potential prey available.* Thus the frogs tended to take whatever phalangids were available to them. These included Phalangium opilio, Odiellus pictus and Leiobunum calcar.

The incidental stomach data (see section 3.4.3) tend to show that the numbers of phalangids eaten varies directly with the number of phalangids present. The percentage occurrence of phalangids varied from 25.9% to 0.1%.

Thus, in general, the results from the amphibian-phalangid encounter experiments, the field study results, the incidental stomach data and the information from the literature (see Table 4.2) show that salamanders, frogs and toads tend to eat phalangids of the suborder Palpatores without harm. The amounts eaten probably vary only with abundance and size of the phalangids available.

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* The small number of phalangids found in the study area may have resulted from (a) sampling techniques; (b) a poor year for phalangids or (c) the area was a poor habitat for phalangids. Since phalangids were specifically searched for in addition to regular use of sweep netting and quick traps, it is unlikely that the low numbers collected resulted from inadequate sampling. Data from four years of invertebrate collecting in connection with bird feeding studies made on Kernen's Prairie by students and assistants of Dr. W.J. Maher tend to show great fluctuations in the phalangid population from year to year. However 1969 had a high concentration of phalangids on Kernen's Prairie, thus, unless two different localities can have high and low phalangid populations at the same time, explanation (b) is improbable. The third explanation seems to be most likely. Edgar (1960) recorded larger temperature and relative humidity fluctuations in an aspen groove than in a maple forest and suggested that this factor may limit phalangid abundance. He also suggested that cattle movements may adversely affect eggs laid by phalangids.

Table 4.2. References to phalangids eaten by amphibians.

Predator	Phalangid	Remarks	References
1. Urodela			
(a) Plethodon cinereus cinereus	"daddy longlegs spider"	two specimens in one stomach out of 47 examined; no phalangids in five other species studied	Smallwood, 1928
(b) P. cinereus	"phalangids"	field and laboratory observations	Edgar, 1960
(c) P. glutinosus	"phalangids"	two phalangids in 13 stomachs; no phalangids in two other species studied	Brandon, 1965
2. Anura			
(a) Bufo marinus	"phalangids"	---	Leonard, 1933
(b) B. terrestris americanus, B. woodhousii woodhousii, B. cognatus and B. compactilis	"Phalangida"	maximum % of phalangids of diets 0.85% for B.t. americanus	Smith and Bragg, 1949
(c) B. bufo and Rana temporia	Anelasmocephalus cambridgei, Nemastoma lugubre, N. chrysomelas, Leiobunum rotundum, L. blackwallii, Oligolophus agrestis, Lacinius ephippiatus, Platybunus triangularis and Phalangium opilio	N. lugubre and P. opilio were the most common in the frogs and toads examined; out of 292 R. temporia stomachs with 1500 food items, there were 17 phalangids; out of 350 B. bufo and 9799 items, 188 phalangids	Bristowe,(1949
(d) R. clamitans	"Phalangida"	% frequency of phalangids = 2.5 for June, 2.4 for July and 0.2 for year average; % composition of phalangids of ingested material = 0.1 for June, 0.4 for July and "Trace" for year	Jenssen and Klimstra, 1966
(e) R. pipiens sphenocephala	Leiobunum sp., L. aurugineum and Mesosoma nigrum	phalangids constituted 3.2% of diet	Kilby, 1945
(f) R. pipiens	"Phalangida"	10 phalangids out of 20 stomachs (0.02% of food items); no phalangids in stomachs of two other amphibians studied	Moore and Strickland, 1954
(g) Hyla cinerrum	M. nigrum, Libitiodes sayi	phalangids constituted 0.4% of diet	Kilby, 1945

The bird-phalangid encounter experiments suggest that the odoriferous glands of Phalangium opilio were not effective against domestic chicks and fledgling house sparrows. In the single instance of a chick possibly being repelled by the odoriferous glands, it was not demonstrated that the chick learned to avoid other phalangids. Others have shown that young birds will eat phalangids or that the parents feed phalangids to their young. These birds include: golden-winged warblers (Edgar, 1960), Passerculus sandwichensis (Dillery, 1961; D. Karasiuk, unpublished data), Pica pica (Owen, 1956) and Bonasa umbellus (Stewart, 1956). Refer to Table 4.3. Thus it is probable that birds, like amphibians, eat Palpatores phalangids in proportion to their availability and are not affected by their odoriferous glands.

The Mus musculus-Phalangium opilio encounter experiments suggested that the mice were not repelled by the phalangids. The experiments with a single Microtus pennsylvanicus were inconclusive as the mouse did not eat any P. opilio and it was possible that it had learned that phalangids were obnoxious prior to the experiments. The skunk which did eat P. opilio did so without apparent harm. Table 4.4 gives a few more examples of mammals which have been observed to eat phalangids.

Thus as a whole vertebrate predators do not tend to be affected by the odoriferous glands of Palpatores phalangids. The Cyphophthalmi would probably also be eaten without harm because they are very small and so there would be little glandular secretion. The Laniatores may be different. Unlike the cryptically colored Palpatores, some Laniatores are brightly colored with red, yellow and black markings (see Levi and Levi, 1968, for an illustration). These colors may be aposematic, facilitating

Table 4.3. References to phalangids eaten by birds.

Predator	Phalangid	Remarks	References
"birds"	"opilionids"	---	Weed and Dearborn, 1912
"birds", 16 species including: *Colinus virginianus*, *Coccyzus americanus*, *Coccyzus erthrophalmus* and *Seiurnus aurocapillus*	"harvestmen" or "daddy-long-legs"	the listed birds preyed relatively heavily on phalangids; one *C. americanus* had 20 phalangids in its stomach, a *S. aurocapillus* had 77; data compiled from U.S. Biological Survey	McAtee, 1926, 1932; Bristowe, 1949
"house sparrow"	attacked *Leiobunum rotundum*	"the harvest-spider escaped by dropping down amongst grass at base of wall"	Sankey, 1949a
"golden-winged warblers"	"phalangids"	brought phalangids to young as food	Edgar, 1960
"rose-breasted grosbeak"	*L. longipes*, *L. vittatum* and *L. calcar*	laboratory observations	Edgar, 1960
Parus major	*Platybunus triangularis* and *Nemastoma lugubre*	three other tits were also studied but no phalangids were found in their stomachs	Betts, 1955
Passerculus sandwichensis	"Phalangida"	results from stomach samples and laboratory experiments	Dillery, 1961
Dolichonyx oryzivorus and *P. sandwichensis*	"Phalangida"	stomach samples	Wiens, 1969
P. sandwichensis	*Phalangium opilio*	in July 1969 about 5-20% of food brought to nestlings were *P. opilio*; in 1970 $<<$0.1% were *P. opilio*	D. Karasiuk, unpublished data
Pica pica	*P. triangularis*	fed by Magpies to nestlings	Owen, 1956
Bonasa umbellus	"Phalangida"	eaten in small numbers by young ruffed grouse	Stewart, 1956

Table 4.4. References to phalangids eaten by non-amphibian and non-avian vertebrates.

Predator	Phalangid	Remarks	References
1. Teleosts			
(a) "minnows and other fishes"	phalangids	---	Bishop, 1950
(b) *Salmo trutta*	"harvestmen"	"the fish were caught just after a sudden rise in the level of the river"	Bristowe, 1949
(c) *Squalius cephalus*	*Phalangium opilio*	chub stomachs	Bristowe, 1949
2. Reptilia			
(a) *Basiliscus basiliscus*	"Phalangida"	one phalangid in 106 stomachs; % of food items = 0.09%	Barden, 1943
(b) "lizards"	"harvestmen"	---	Bristowe, 1949
(c) "grass-snake"	"possible Opilionid remains"	stomach sample	Sankey, 1949a
3. Mammalia			
(a) "shrews"	"harvestmen"	---	Bristowe, 1949
(b) "badger"	*Odiellus spinosus*, *Oligolophus agrestis* and *P. opilio*	phalangids fed to two captive badgers	Sankey, 1949a
(c) "fox"	*P. opilio*	fed in captivity	Sankey, 1949a
(d) "hedgehog"	*Mitopus morio*, *Leiobunum blackwallii*, *L. rotundum*, *Ol. agrestis*, *Ol. tridens*, *O. spinosus*, *P. opilio* and *Opilio parietinus*	fed in captivity	Sankey, 1949a

learning by vertebrates.

The results of the spider-phalangid encounter experiments are less clear-cut than the others performed. It seems that the phalangids tested may have a limited defense mechanism against some spiders. Spiders may not have fed because they were satiated, about to moult or diseased. Since Pardosa fuscula were deprived of food for at least two days, satiation was unlikely. Moulting or disease may have been the cause of spiders #1 (Table 3.5; Test Series A) and #12 (Test Series A) not feeding. Also spiders may not have fed because the phalangids were too large or they were repelled by the phalangids' odoriferous glands. Size may have had some bearing with spiders #8 (twice) (Test Series B and C), #10 (Test Series C) and perhaps even #14 (Test Series D). Spiders #8 and #10 were the only ones offered adult Phalangium opilio. Subadults were offered to spiders #'s 7, 8 (?), 13 and 14 but only 7 and 13 ate their respective phalangids. This leaves two instances where odoriferous glands may have prevented the spiders from feeding. Although both of these spiders ate their phalangids overnight, depletion of the odoriferous glands may have played some role. However, many spiders fed directly over the odoriferous glands, which often produced a discernable odor, with impunity. Thus with regard to P. fuscula and P. opilio the effectiveness of the odoriferous glands is uncertain.

Since all the immature Opilio parietinus offered were eaten without hesitation, the odoriferous glands were not effective in repelling Pardosa fuscula.

All but one of the Phalangium opilio offered to the Pardosa groenlandica were eaten without ill effects. The spider which did not feed died overnight, making it difficult to interpret the interaction.

All the cases of Pardosa modica not eating Phalangium opilio except #3 (Table 3.6; Test Series B) may be explained by the size of the phalangid or by the morbidity of the spiders (Test Series D). Regarding the encounter involving spider #3, since (i) no attacks on the phalangids were observed; (ii) the phalangid was immature and small enough to eat; (iii) the spider was not satiated as it had not fed in three days; and (iv) the spider did not seem to be diseased at that time; there is no obvious reason why the spider did not feed. Thus, as with Pardosa fuscula, the results of the P. modica-P. opilio encounter experiments tend to show that the spiders are not repelled by the phalangid odoriferous glands, but this conclusion is held with uncertainty.

The results of the Pardosa mackenziana-Phalangium opilio encounters (Table 3.8) did not show that the phalangids could repel the spiders with their odoriferous glands. However the P. mackenziana-Odiellus pictus results (Table 3.9) tend to show that this species of phalangid can repel the spider involved. Out of eight O. pictus offered to the spiders, only one was eaten and three of the spiders cleaned their chelicerae right after an attack. Size may have prevented the spiders from feeding on these phalangids but subadult to adult O. pictus are only about the size of immature P. opilio, which were readily eaten. Satiation probably did not prevent the spiders from feeding as they were deprived of food for three days before the experiment and on the next morning four out of seven ate at least one fly within five minutes.

Interpretation of results of the Tegenaria derhami-Phalangium opilio encounter experiments (Table 3.10) are difficult. Six out of eight phalangids were eaten; two were not eaten by one spider. In one case a spider ma

have been repelled by the odoriferous glands. However, it ate the phalangid within 15 minutes. In the second test series feeding tended to be slower, perhaps because the spiders were partially satiated from the first test series.

The individual observations of phalangids in spider webs tend to show that phalangids are often captured in webs but are not always eaten. The size of the phalangid caught and the strength of its cuticle as well as the properties of its odoriferous glands may determine whether the phalangid is fed upon. Satiation, moulting, disease and senility may also be important.

Table 4.5 lists the published reports of phalangids which have been taken by spiders. The observations of phalangids found in webs tell little about the possible effects of the odoriferous glands and are subject to the same problems of interpretation as those outlined in the paragraph above. The direct observations of spiders eating phalangids (Bristowe, 1941; Edgar, unpublished data) at least tell us that of the spiders and phalangids observed being eaten, the odoriferous glands were not effective as a deterrent mechanism. However if the reports were based on a single or a few observations, the conclusion that the odoriferous glands can not repel these spiders is not valid as the glands may have been empty. The observations of Bristowe (1941; 1949; outlined in Table 4.1) suggest that certain phalangids can repel spiders. The phalangids may not repel them on all occasions because the glandular secretion may be exhausted or the phalangid is too small in comparison to the spider.

The problems outlined in the two paragraphs above also apply in

Table 4.5. References to phalangids eaten by spiders.

Predator	Phalangid	Remarks	References
"spiders"	"phalangids"	---	Savory, 1928
"spider-webs"	"phalangids"	---	Sankey, 1949a
"web-making spiders"	Phalangium cinereum (Opilio parietinus)	phalangids became entangled in webs	Weed, 1892a
Tegenaria sp.	Oligolophus tridens	in web	Sankey, 1949a
Theridion pictum	"Opiliones"	out of 202 prey from 103 webs, one phalangid (0.5% of prey)	Luczak and Dabrowski-Prot, 1970
Agelenidae naevia	"harvestmen"	of "several hundred webs examined... 2% contained Harvestmen and spiders"	Bilsing, 1920
Agelena sp. and Aranea diadina	O. agrestis	"accepted" by spiders	Bristowe, 1941
A. diadema	Leiobunum rotundum	"sometimes accepted with hesitation"	Bristowe, 1941
Lycosa gulosa	L. vittatum, L. longipes and L. politum	larval phalangids	A.L. Edgar, unpublished data
Xysticus viaticus	L. rotundum	"accepted" by spider	Bristowe, 1941
Pisaura sp. Xysticus bifasciatus, T. atrica, Pholcus phalangiodes, Meta merianae and A. cucuribitum	L. blackwallii	"accepted" by spiders	Bristowe, 1941

interpretation of the observations on phalangids being eaten by non-spider and non-arachnid invertebrates (Tables 4.6 and 4.7).

Certain centipedes do not seem to be affected by the odoriferous glands of many phalangids. From the observations outlined in section 3.2.6 and from the centipede references listed in Table 4.7, members of the genus Lithobius are probably capable of eating small phalangids, without harm from the odoriferous glands, of the genera Phalangium, Opilio, Oligolophus and Leiobunum.

The results of the Formica oreas experiments strongly suggest that the odoriferous gland secretion of Phalangium opilio can repel this species of ant. The long legs of the larger phalangids also protected them in two ways: (a) the phalangids could easily out-run the ants; and (b) the more vulnerable bodies of the phalangids were carried off the ground, surrounded by the less vulnerable legs. Thus subadult and adult phalangids with their relatively thick cuticle and their long legs would have little trouble escaping ants in the field. However Bishop (1950) (see Table 4.7) did see an ant capture a phalangid. Young and immature phalangids probably would be very susceptible to attacks by ants.

Besides predators, a number of parasitic mites have been observed attacking phalangids. The most commonly reported ones belong to the family Erythraeidae. Sankey (1949a) listed mites occurring on Phalangium opilio, Leiobunum blackwallii, L. rotundum, Mitopus morio, Oligolophus agrestis, O. tridens, Platybunus triangularis and Opilis parietinus. Edgar (1960) added L. politum to the list. I have observed mites on P. opilio and Homolophus biceps. Thus the odoriferous glands do not seem to be effective in preventing attacks by mites.

In general then, at least some arthropod predators are repelled

Table 4.6. References to phalangids eaten by non-spider arachnids.

Predator	Phalangid	Remarks	References
1. Scorpionida (a) "scorpions"	"harvestmen"	---	Cloudsley-Thompson, 1958
2. Phalangida (Palpatores; Phalangiidae) (a) *Lacinius ephippiatus*	*Nemastoma lugubre*	female ate female	Todd, 1950
(b) *Oligolophus tridens*	*Mitopus morio*	field observation	Bristowe, 1949
(c) *Mitopus morio*	*Oligolophus agrestis* and *O. tridens*	field observations	Bristowe, 1949
(d) *Phalangium opilio*	*O. tridens*	field observations	Bristowe, 1949
(e) *P. opilio*	*M. morio*	laboratory observation	Roters, 1944
(f) *Leiobunum rotundum*	*O. tridens*	field observation	Bristowe, 1949
(g) *L. blackwallii*	*O. tridens*	field observation	Bristowe, 1949

Table 4.7. References to phalangids eaten by non-arachnid invertebrates.

Predator	Phalangid	Remarks	References
1. Gastropoda			
(a) *Polygyra albolabris*	*Leiobunum longipes*	forest snail entangled legs of two phalangids and consumed all but parts of the legs	Edgar, 1960
2. Diplopoda			
(a) Order: Nematophora	"phalangids"	"prey includes phalangids, insects, centipedes, and earthworms"	Barnes, 1968
3. Chilipoda			
(a) *Lithobius forficatus*	*Oligolophus agrestis* and *Oligolophus agrestis*	larval phalangids taken in the field	Sankey, 1949a
(b) *L. vulgaris*	*L. vittatum*, *L. longipes* and *L. politum*	larvae taken in laboratory under conditions of hunger	Edgar, 1960 and personal communication
4. Insecta			
(a) Hemiptera			
(i) *Zelus* sp.	"phalangids"	in the laboratory	Edgar, 1960
(ii) *Reduvius personatus*	"various young harvest-spiders"	in captivity	Sankey, 1949a
(iii) *Pentatoma prasina*	*Phalangium opilio*	"almost certainly feeding" on a phalangid; field observation	Sankey, 1949a
(b) Coleoptera			
(i) *Carabus violaceus*	"young Oligolophid" and "young harvest-spider"	field observations	Sankey, 1949a
(c) Hymenoptera			
(i) ant	phalangid	"in one instance, a ...'long-legs' was observed being dragged along the ground by a large black ant"	Bishop, 1950

by the odoriferous glands of some Palpatores phalangids. Whether the repulsion of Formica oreas is indicative of Palpatores phalangids being capable of repelling ants in general or is similar to some Palpatores being able to repel some spiders, can only be decided by further experiments with different species of phalangids and ants. One point in favor of the first suggestion is that Blum (personal communication) and his colleagues have discovered 4-methyl-3-heptanone in some Leiobunum species. This compound has also been found in the mandibular glands of Pogonomyrmex and Atta ants and seems to function as an alarm pheromone (McGurk et al., 1966; Blum et al. 1968). If the Palpatores are generally capable of repelling most ant species, it might be postulated that the odoriferous glands primarily evolved to combat ants or that more recently the phalangids have been selected for glandular characteristics which tended to be especially useful against ants but only incidentally repugnant to some spiders and other predators.

4.3. Other possible functions of the odoriferous glands of phalangids

Although phalangid odoriferous glands have been shown to be used defensively against at least some potential predators, they may also serve other functions. These other functions might include trail marking, sexual recognition, species recognition, anti-microbial protection and excretion.

Bishop (1950) suggested that the glandular secretion may not serve in a defensive role but as a "means of communication". He stated: "I have observed many times that this [odoriferous gland] secretion... drains almost immediately to the lower side of the body, where it may come in contact with the surface over which the harvestman is moving. In fact, many individuals in the course of their wanderings, bob up and

down at frequent intervals, the body tapping the surface beneath them in such a rhythmic fashion as to suggest a definite purpose. This assumption receives some support from the fact that different individuals sometimes follow the same route to a particular spot...". The above behavior may have resulted in three different ways: (a) the phalangids may have laid down a chemical trail (similar to those made by ants) for others to follow to find food; (b) females may have made a trail and males may have followed it, stopping along the way in order to detect the chemical; (c) a certain topography and microclimate may have tended to channel the phalangids along a similar route to a location optimal in respect to temperature, humidity and light. Since high densities of phalangids are probably best explained by habitat preferences, they are not likely colonial. Furthermore, in Phalangium opilio, Opilio parietinus and Odiellus pictus the glandular products tend to be highly volatile, therefore explanation (a) seems unlikely. Arguments against explanation (b) include the following: the construction of the odoriferous glands is identical in males and females; the glands seem to be just as active in non-adults and adults; the secretions tend to be similar in all life stages; and according to Bishop (1949) males often make mistakes and try to mate with other males. Explanation (c) therefore appears most probable.

Cannibalism under laboratory conditions has been reported in Oligolophus agrestis (Sankey, 1949a), Platybunus triangularis (Sankey, 1949a), Phalangium opilio (Roters, 1944; personal observations), Opilio parietinus (Roters, 1944), and Leiobunum longipes, L. politum and L. vittatum (Edgar, 1960). Fewer field observations of cannibalism have been reported. However, Bristowe (1949) observed Mitopus morio eating

another M. morio and Todd (1950) observed a female L. rotundum eating another female - both observations were made out-of-doors. In contradiction to Todd, Roters (1944) stated: "How much of this cannibalism is due to captivity is difficult to determine, but the fact that some species are given to it while others are not is evident from my failure ever to induce Liobunum [Leiobunum] rotundum to adopt the habit in any circumstances." Savory (1938, 1962) also maintained that phalangids are not particularly cannibalistic, if enough other food is present. It is therefore possible that the odoriferous glands provide an individual with some immunity from cannibalism, until food becomes scarce.

Estable et al. (1955) found that the odoriferous secretion of Heteropachyloidellus robustus was an effective antibiotic against numerous bacteria and protozoa and suggested that the secretion may function as an anti-microbial agent to keep the phalangid free from disease. In the Palpatores, at least, the glandular products tend to vaporize immediately. Thus its effectiveness against microbial disease is doubtful. It is most likely that the anti-microbial properties of the phalangid odoriferous gland secretions are incidental to their function as a defensive mechanism against non-microbial organisms.

A fifth possible function of the odoriferous glands is excretion, analogous to the green glands of malacostracan crustaceans. However, the construction of the glands, especially their probable mechanism of emptying, and the presence of other excretory systems or organs, including nephrocytes, circum-neural organs and coxal glands (Kästner, 1935; Moritz, 1957) make

this unlikely.

Thus even though the evidence is meager, the best postulate still is that phalangid odoriferous glands are mainly defensive in function. Any other function is most probably secondary.

5. SUMMARY

(a) A review of the literature has shown that the odoriferous glands of phalangids are generally considered to serve in a defensive function but the evidence for this idea is fragmentary.

(b) The odoriferous glands have been investigated by: external examination; dissection; light microscopy and behavioral experiments with amphibians, birds, mammals, spiders, centipedes and ants.

(c) No external liquid secretion has been found associated with the odoriferous glands of Phalangium opilio, Opilio parietinus or Odiellus pictus. In Homolophus biceps liquid secretion may have been present. Only P. opilio and H. biceps produced a detectable odor. In P. opilio it was present in all life stages and in both sexes.

(d) It has been observed that P. opilio may need less than 2-4 days to replenish their glandular secretions when provided with food and water.

(e) Externally the openings of the glands appear as downwardly curved slits located on the top edge of an elliptically shaped piece of flexible cuticle. The size of the openings and the direction in which they point varies with different species but not within adults of one species.

(f) A gland consists of a sac-like structure almost entirely surrounded by digestive diverticula, various groups of muscles and the cuticular covering of the animal. Since the only muscles directly attached to the gland are concerned with closing its entrance, emptying of the gland is probably accomplished indirectly by expansion of the

digestive diverticula and contraction of the groups of muscles around the gland.

(g) Histologically a gland consists of an inner cuticular layer, a middle cellular layer and an outer basement membrane. When the glands are full of secretion, the cells are stretched out, showing little cellular detail. When the glands are empty of secretion, they become folded. In the folded state the cells show their greatest activity. Since the glandular inclusions and pigments of the different species studied showed a number of differences, the secretions of the glands are probably different. The animals tend to have some control over which of the two glands is operated.

(h) From the behavioral or predator-phalangid encounter experiments, it has been shown that Rana sylvatica, R. pipiens, Bufo hemiophrys and Ambystoma tigrinum fed upon P. opilio or O. parietinus, as long as they were small enough to eat, without apparent harm. Along with these experiments, data from the field experiment, incidental amphibian stomach analysis and from the literature tend to suggest that all amphibians probably eat Palpatores phalangids with impunity.

(i) Encounter experiments with Gallus domesticus chicks and P. opilio have shown that chicks eat phalangids without apparent harm. Similar conclusions followed experiments performed with fledgling house sparrows, white mice and young skunks. This information together with previous data suggests that all vertebrate predators eat Palpatores phalangids without harm.

(j) The encounter experiments involving Pardosa fuscula and O. parietinus and Pardosa groenlandica and Pardosa mackenziana with P. opilio

have shown no repulsion of the spiders by the phalangid odoriferous glands. The experiments involving Pardosa modica, P. fuscula and Tegenaria derhami with P. opilio tended to show that these spiders may eat P. opilio with impunity, but the results are not completely convincing. The experiments involving P. mackenziana with O. pictus suggest that O. pictus can repel these spiders.

(k) From the few experiments performed and information from the literature it is concluded that centipedes of the genus Lithobius are not affected by the odoriferous glands of a number of Palpatores phalangids.

(l) Ants of the species Formica oreas have been shown to be repelled by young to adult P. opilio. It is postulated that other phalangids probably repel other species of ants just as effectively.

(m) Experiments performed in this and other studies suggest that it is unlikely that phalangid odoriferous glands are used for trail marking, sexual recognition, species recognition, anti-microbial protection or excretion.

(n) The odoriferous glands are most likely defensive in function but are probably not used against as large a variety of potential predators as is generally supposed.

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* Denotes references quoted from Hansen and Sorensen, 1904.

APPENDIX I

The following is a shortened form of Roewer's (1923) classification of the phalangids. Although Sörensen (1932) presented a slightly different scheme for the Laniatores no one since Roewer has made a major revision of the whole order.

Order: Opiliones or Phalangida

1. Suborder: Cyphophthalmi
    1. Family: Sironidae
2. Suborder: Laniatores
    1. Family: Oncopodidae
    2. Family: Phalangodidae
    3. Family: Assamiidae
    4. Family: Cosmetidae
    5. Family: Gonyleptidae
    6. Family: Triaenonychidae
3. Suborder: Palpatores
    1. Tribe: Dyspnoi
        1. Family: Trogulidae
        2. Family: Nemastomatidae
        3. Family: Acropsopilionidae
        4. Family: Ischropsalidae
    2. Tribe: Eupnoi
        1. Family: Phalangiidae
            1. Subfamily: Sclerosmatinae
            2. Subfamily: Oligophinae
            3. Subfamily: Phalangiinae

4. Subfamily: Leptobuninae

5. Subfamily: Leiobuninae

6. Subfamily: Gagrellinae

APPENDIX II

The following is a list of references, a short taxonomic description, a list of North American records and a list of Saskatchewan records of the six species of phalangids collected in connection with this study. All belong to the family Phalangiidae. The references were derived mainly from Roewer (1912, 1923); Bishop (1949) and Edgar (1966).

1. Subfamily: Oligophinae, Odiellus pictus (Wood)

Phalangium pictum Wood, 1886, Commun. Essex Instit. 6:30-31, 1 fig.

Oligolophus pictus Weed, 1887, Amer. Natur. 21:935.

Oligolophus ohioensis Weed, 1889, Amer. Natur. 23:1102-1104, pl. 42, fig. 1-2.

Mitopus pictus Weed, 1893, Proc. U.S. Nat. Mus. 16:557-558, pl. 62, fig. 2.

Mitopus ohioensis Weed, ibid., p. 558-559, pl. 68, fig. 1-2.

Lacinius ohioensis Banks, 1893, Can. Ent. 25:207.

Oligolophus pictus Banks, ibid., p. 207.

Odius pictus Roewer, 1912, Abhandl. Gebiete Naturwiss. 20:70-71.

Lacinius ohioensis Roewer, ibid., p. 80-81.

Odiellus pictus Roewer, 1923, Die Weberknechte der Erde, p. 734-735, fig. 910.

Lacinius ohioensis Roewer, ibid., p. 743.

Odiellus pictus Comstock, 1940, The Spider Book, revised ed., p. 70-71.

Lacinius ohioensis Comstock, ibid,, p. 70.

Odiellus pictus + Lacinius ohioensis Bishop, 1949, Proc. Rochester Acad. Sc. 9:179-182, pl. 2, fig. 23-28.

Odiellus pictus Edgar, 1966, Amer. Mid. Natur. 75:357-358, 1 fig.

Male, 4 mm long; legs I-IV 8, 16, 8.5, 13 mm long; F_2 3.7 mm (n=20).

Female, 5 mm long; legs I-IV 6.5, 15, 7, 11 mm long; F_2 3.3 mm (n=6).

This species can most easily be distinguished from other Saskatchewan phalangids by the presence of three large spines on the carapace edge anterior to the eye tubercle and by the 6-10 spines on the ventro-lateral side of the femur (ie. the third segment) of the palp. See Fig. 314A and B. Edgar (1960, 1966) divided this species into two subspecies, Odiellus pictus pictus and O. pictus argentus, based mainly on the general coloration and the shape of the central figure or marking on the opisthosoma. The specimens taken in Saskatchewan most closely resemble the description for O. pictus pictus.

Odiellus pictus prefers a moist habitat. Edgar (1966) gave the typical habitat of this species as "...the grassy edges of forests on sparsely wooded, grassy ridges and on unflooded river flats. The young are found in moist litter while adults are frequently seen on tree trunks and low vegetation." The Saskatchewan collections were made in the wet grass-sedge regions of a slough, in the bases of sedges along a river and in a Tamarack-Black Spruce bog.

Distribution: The known range of Odiellus pictus was restricted, until now, to eastern North America. United States records include: Georgia (Weed, 1889a; Bishop, 1949); Illinois (Weed, 1890b; Edgar, 1960, 1966); Indiana (Edgar, 1960, 1966); Maine (Banks, 1902; Bishop, 1949); Massachusetts (Wood, 1868); Michigan (Edgar, 1960, 1966); New Hampshire (Weed, 1892b); New York

(Crosby et al., 1926; Bishop, 1949); North Carolina (Banks, 1911; Bishop, 1949; Roewer, 1952); Ohio (Weed, 1889; Edgar, 1960, 1966); Pennsylvania (Bishop, 1949); Tennessee (Bishop, 1949); Virginia (Bishop, 1949); and Wisconsin (Levi and Levi, 1952; Edgar, 1960, 1966). Canadian records include: Newfoundland (Hackman, 1956); Labrador (Roewer, 1957); Ontario (Bishop, 1949; Edgar, 1960, 1966) and Quebec (Crosby and Zorsch, 1935; Bishop, 1949).

Saskatchewan collections were all made within a 2 kilometer radius of Lady Lake by D.J. Buckle and myself. See Fig. A.1 for the Saskatchewan collection sites.

2. Subfamily: Phalangiinae, Phalangium opilio Linnaeus

Phalangium opilio Linnaeus, 1758, Systema Naturae, 10th ed., 1:618

Phalangium longipalpis Weed, 1890, Amer. Natur. 24:783-785, pl. 27, fig. 1-3.

Phalangium cornutum Roewer, 1912, Abhandl. Gebiete Naturw. 20: 91-94, pl 2, fig. 28.

Phalangium opilio Roewer, 1923, Die Weberknechte der Erde, pp. 751-752, fig. 927. Gives detailed European synonyms between 1761 and 1918.

Phalangium opilio Comstock, 1940, The Spider Book, revised ed., p. 69.

Phalangium opilio Bishop, 1949, Proc. Rochester Acad. Sc. 9:183-185, pl. 2, fig. 29-33.

?Opilio angulatichelis Roewer, 1952, Zool. Anz. 149:267-268, fig. 1. See Levi and Levi, 1955, for discussion.

Phalangium opilio Edgar, 1966, Amer. Midl. Natur. 75:358-359, 1 fig.

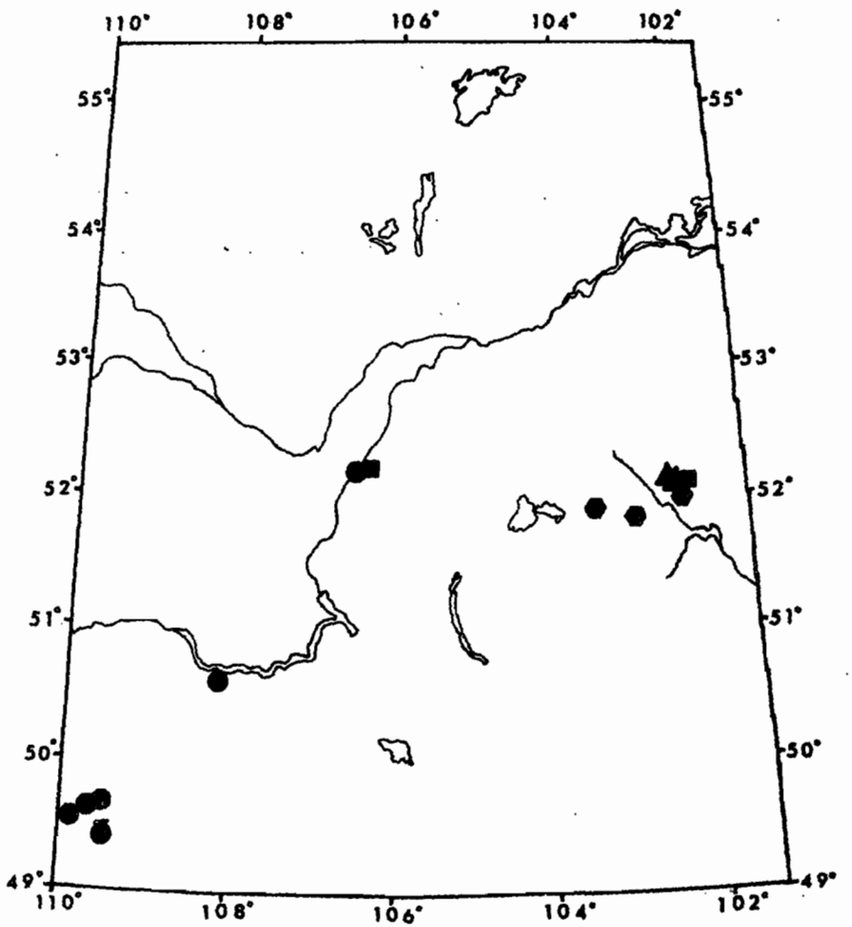

Fig. A.1. Saskatchewan collection sites of Odiellus pictus (triangles), Homolophus biceps (circles), Leiobunum calcar (hexagons) and L. vittatum (squares).

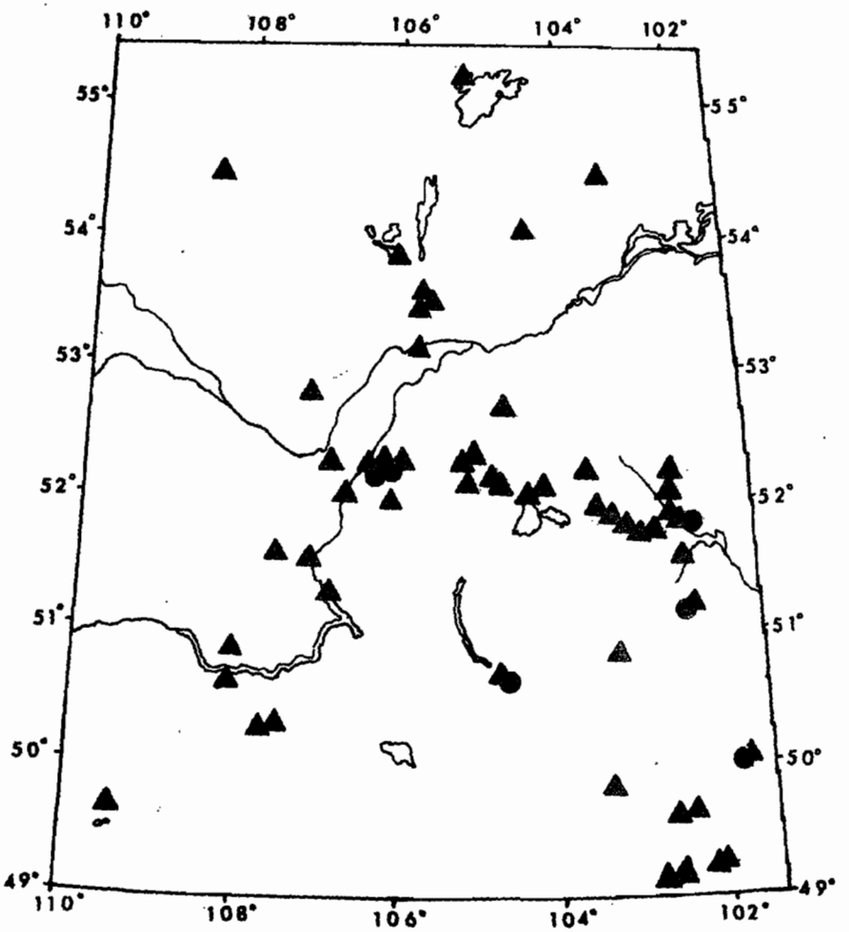

Fig. A.2. Saskatchewan collection sites of Phalangium opilio (triangles) and Opilio parietinus (circles).

Male, 5 mm long; legs I-IV 22.5, 38, 24, 33 mm long; F_2 8.3 mm (n=16-21).

Female, 6.5 mm long; legs I-IV 16.5, 31, 18.5, 27 mm long; F_2 6.7 mm (n=21-25).

The above measurements were taken from Saskatchewan material. Mature males can be readily separated from other phalangids by the presence of a long spur on the femur of their chelicerae and by their very long palps. The length of the femoral spur varies according to the degree of maturity and perhaps with local differences within the species or the environment. A short cheliceral spur is illustrated in Bishop (1949) pl. 2, fig. 29. A long cheliceral spur is illustrated in Roewer (1923) fig. 927 and in Edgar (1966) fig. 13. Both extremes can be found in Saskatchewan specimens. Immatures and females can be identified by the following characteristics. The eyes are separated by more than the diameter of one eye and are situated more laterally than dorsally. There is a row of 6-7 sharp spines on each carnia of the eye tubercle. Tibia IV is distinctly angular in cross section with obvious rows of spines. See Fig. 3.2A-D. This species is most often confused with Opilio parietinus.

Phalangium opilio is most commonly found in disturbed areas. In Saskatchewan it has been collected around the foundations of buildings, along road-side ditches, in culverts, in gardens and in grain fields. It is also found in regions relatively undisturbed by man such as in prairie grassland and along slough margins.

Distribution: The range of Phalangium opilio is holarctic. It has been collected in Europe, Siberia, central Asia, Asia Minor, North Africa

and temperate North America (Roewer, 1923). It is present in Great Britain (Todd, 1948) but not in Greenland (Jackson, 1930) or Iceland (Sherriffs, 1934). The United States records include: Alaska (Malkin, 1953); Arkansas (Weed, 1890a); Illinois (Edgar, 1960, 1966); Massachusetts (Bishop, 1949); Michigan (Bishop, 1949; Edgar, 1960, 1966); Montana (Roewer, 1952; Levi and Levi, 1955); New York (Crosby, 1907, 1910; Crosby et al., 1926; Bishop, 1949); Ohio (Walker, 1928; Edgar, 1960, 1966) and Wisconsin (Levi and Levi, 1952; Edgar, 1960, 1966). The published Canadian records include Alberta (Schenkel, 1951); Newfoundland (Hackman, 1956) and Ontario (Edgar, 1966). Dr. C.D. Dondale, Research Institute, Canada Department of Agriculture, Belleville, Ontario has identified some P. opilio taken near Saskatoon, Saskatchewan. Some of these are in the arthropod collection of Canada Agriculture Research Station, Saskatoon. Dr. Dondale also has a number of other Canadian phalangids in his personal collection.

Records from Saskatchewan include the following: Between 49° lat. and 50° lat.: Bienfait, Carlyle, 3.2 km E Creelman, Cypress Hills Provincial Park (Central Block), Estevan, 6.4 km E Kisbey, 6.4 km W and 14.4 km NW Oxbow; Between 50° lat. and 51° lat.: Fort Qu'Appelle, Lumsden (N. Earl), Matador (E. Kardash), 11.2 km S Moosomin (P. Botkin), Saskatchewan Landing, Swift Current,Waldeck; Between 51° lat. and 52° lat.: Blackstrap Lake (8 km S Dundurn) (B.J. Duguid), 4.8 km NW Canora, Cut Bank (Gardiner Dam Site) (E. Kardash), Crystal Lake (near Tadmore), Delisle (Mrs. R. Kilgore), 4.8 km E Kuroki, 3.2 km E Margo, Milden (E. Czarnecki), Outlook, Pike Lake (about 25 km S Saskatoon), 8 km S Preeceville (B.J. Duguid), 6.4 km E Rama, 3.2 km W Rama, Sturgis, Yorkton (R.O. Holmberg); Between 52° lat. and 53° lat.: Blaine Lake (E. Kardash), Burke Lake (23 km E

Saskatoon) (D.J. Buckle), Burton Lake (9.6 km N Humboldt) (D. Waite), Englefield (D.J. Buckle), 4.8 km W Humboldt, 15 km W Kelvington, Kutawagon Marsh (just N of Quill Lake) (D. McKiel), Lady Lake (D.J. Buckle), Melfort, 4 km E Quill Lake (town), Saskatoon (numerous collections within and without the city by a number of collectors), 32 km W Saskatoon (D.J. Buckle), Stoney Lake (Humboldt Lake), Usherville (D.J. Buckle), Watson; Between 53° lat. and 54° lat.: Anglin Lake (E. Kardash), Emma Lake, Northside (D.W.A. Whitfield), Prince Albert (G. Harrison), Waskesieu Lake (D.J. Buckle); Between 54° lat. and 55° lat.: Mustus Lake (Meadow Lake Provincial Park) (W.W. Sawchyn), Paskwakakau River (48 km S town of Deschambault Lake) (W.W. Sawchyn), Sealy Lake (on Hanson Lake Road) (W.W. Sawchyn); Between 55° lat. and 56° lat.: Lac La Ronge (Waden Bay) (P. Kozak). See Fig. A.2 for the Saskatchewan collection sites.

3. Subfamily Phalangiinae. Opilio parietinus (De Geer)

Phalangium parietinum De Geer, 1778, Mem. Hist. Ins. 7:166-172, pl. 10, fig. 1-11.

Phalangium cinereum Wood, 1868, Commun. Essex Instit. 6:25-26, fig. 5.

Opilio parietinus Roewer, 1912, Abhandl. Gebiete Naturw. 20:124-127.

Phalangium parietinus Comstock, 1940, The Spider Book, revised ed., p. 69.

Opilio parietinus Bishop, 1949, Proc. Rochester Acad. Sc. 9:185-187, pl. 3, fig. 34-37.

Opilio parietinus Edgar, 1966, Amer. Midl. Natur. 75:359, 1 fig.

Male, 5 mm long; legs I-IV 27.5, 48, 28, 37.5 mm long; F_2 11.0 mm (n=11-19).

Female, 6.5 mm long; legs I-IV 23, 45, 23.5, 34 mm long; F_2 9.8 mm (n=8-17).

The above measurements were taken from Saskatchewan material. Specimens of Opilio parietinus are separated from Phalangium opilio by their more dorsal than lateral eye orientation (the eyes are separated by the diameter or less of one eye) and by having tibia IV round in cross section without obvious rows of spines. The eye carniae are devoid of large sharp spines. Unlike P. opilio, there are no cheliceral spurs and the palps are relatively short in mature males of O. parietinus. See Fig. 3.3A-D.

Weed (1892a) stated that "This species is pre-eminently what may be called an in-door species. It abounds especially in sheds, out-houses and neglected board piles, being rarely found, so far as my experience goes, in the open field." Edgar (1966) collected specimens "...mostly from shaded, cool, cement walls late in summer and fall." These two descriptions aptly describe the habitats in which Opilio parietinus has been collected in Saskatchewan.

Distribution: This species is also holarctic in distribution and has been extensively collected in Europe, Asia and North America (Roewer, 1923). It occurs in Great Britain (Todd, 1948) but not in Greenland (Jackson, 1930) or Iceland (Sherriffs, 1934). The records from the United States include: Illinois (Weed, 1889a; Edgar, 1960, 1966); Idaho (Bishop, 1949); Michigan (Bishop, 1949; Edgar, 1960, 1966); Montana (Bishop, 1949); Nebraska (Weed, 1890b); New Hampshire (Weed, 1892b); New York (Wood, 1868; Crosby et al., 1926; Bishop, 1949); Ohio (Weed, 1893a; Walker, 1928; Edgar, 1960, 1966); South Dakota (Weed, 1893d) and Wisconsin (Levi and Levi, 1952;

Edgar, 1960, 1966). Published Canadian records only are limited to Quebec (Bishop, 1949).

Saskatchewan collections have been made from Lumsden (N. Earl), 11.2 km S Moosomin (P. Botkin), numerous sites within and without Saskatoon, Sturgis and Yorkton (R.O. Holmberg). See Fig. A.2 for the Saskatchewan collection sites. Opilio parietinus probably occurs throughout the southern half of Saskatchewan, as does Phalangium opilio, but is restricted to moister places than P. opilio. (Usually P. opilio was collected, but in larger numbers, at the same time and from the same sites as O. parietinus.)

4. Subfamily Leptobuninae, Homolophus biceps (Thorell)

Mitopus biceps Thorell, 1877, Bull. U.S. Geol. Surv. 3:525.

Mitopus biceps Banks, 1893, Can. Ent. 25:207.

Homolophus biceps Banks, 1894, Can. Ent. 26:163-164.

Homolophus punctatis Banks, ibid., p. 164.

Homolophus biceps + Homolophus punctatis Banks, 1901, Amer. Natur. 35:674.

Homolophus biceps Roewer, 1923, Die Weberknecte der Erde, p. 880.

Homolophus punctatis Roewer, ibid., p. 880-881.

Homolophus biceps Comstock, 1940, The Spider Book, revised ed., p. 71.

Togwoteeus granipalpus Roewer, 1952, Zool. Anz. 149:268-269, fig.2.

Homolophus biceps + Togwoteeus granipalpus Levi and Levi, 1955, Can. Field-Natur. 69:32, fig. 1.

Male, 5 mm long; legs I-IV 12.5, 2.15, 13, 18.5 mm long; F_2 4.3 mm (n=9-12).

Female, 5.5 mm long; legs I-IV 11, 19.5, 12, 18 mm long; F_2 3.9 mm (n=8-9).

The above measurements were taken from Saskatchewan material. This species is readily distinguished from other Saskatchewan phalangids by the presence of a white bifid stripe that extends from the eye tubercle to the anterior margin of the carapace. See Fig. 3.4C and D. There are also two prominent supracheliceral teeth. In mature or nearly mature specimens there is a single, anterior row of marginal denticles along coxae I-III but coxae IV has a single, anterior marginal row as well as a posterior marginal row of denticles.

Most of the Saskatchewan collections came from mixed stands of Lodgepole Pine, White Spruce and poplar; under rocks near a stand of Lodgepole Pine; under boards and from the bases of grasses and sedges along the margin of a lake and slough. One collection was made from an outhouse in a small field of grass and near some poplar trees. Another was found under a board near a coulee. Most of these habitats roughly agree with the Wyoming collection sites mentioned by Levi and Levi (1951) except that the elevations were from 4,000 ft (1,219 m) to under 1,800 ft (548 m)(Levi and Levi collected between 10,000 ft and 7,000 ft; or 3,048 m and 2,134 m). Also some of the collection areas were far removed from mountainous or foot-hill habitat types.

Distribution: This species is restricted to western North America. United States records include: Colorado (Thorell, 1877; Roewer, 1957); Idaho (Banks, 1894; Levi and Levi, 1955); New Mexico (Roewer, 1923); Washington (Banks, 1894) and Wyoming (Roewer, 1952; Levi and Levi, 1951, 1955).

The Saskatchewan records include: 1.6 km S Fort Walsh (Western Block of Cypress Hills Provincial Park), Cypress Hills Provincial Park (Central Block), Cypress Lake, Saskatchewan Landing and Saskatoon. See Fig. A.1 for the Saskatchewan collection sites.

5. Subfamily Leiobuninae, Leiobunum calcar (Wood)

Phalangium calcar Wood, 1868, Commun. Essex Instit. 6:26-27, fig. 6.

Liobunum calcar Weed, 1887, Amer. Natur. 21:935.

Liobunum calcar Roewer, 1923, Die Weberknecte der Erde, p. 899, fig. 1054.

Liobunum calcar Walker, 1928, Ohio Biol. Surv. Bull. 19, 4:163, pl. 1, fig. 9.

Liobunum brunnea Walker, ibid., p. 167, pl. 2, fig. 12.

Leiobunum calcar Davis, 1934, Amer. Midl. Natur. 15:670-672, pl. 32, fig. 16-17, pl. 33, fig. 31.

Leiobunum calcar Bishop, 1949, Proc. Rochester Acad. Sc. 9:189-191, pl. 3, fig. 43-50.

Leiobunum calcar Edgar, 1966, Amer. Midl. Natur. 75:360, fig. 5.

Male, 6 mm long; legs I-IV 17.5, 34, 18.5, 28 mm long; F_2 6.8 mm (n=11).

Female, 7 mm long; legs I-IV 17, 34.5, 18, 26 mm long; F_2 7.1 mm (n=2-5).

The above measurements were taken from specimens from Saskatchewan and Manitoba. The males can be easily recognized by the presence of a large ventrolateral spur on the femur of the palps. The femur of the female palps possess several black-tipped tubercles in the region of the spur of the male and a few proximo-lateral tubercles. The femur of the palp extends less than the height of the eye tubercle above the

carapace. The central figure in the male is distinct but stops short of the eye tubercle. The central figure of the female is similar to that of the male but is less distinct. See Fig. 3.5A and B. The coxae of legs I-III have a single marginal row of anterior denticles. There are no anterior marginal denticles on coxae IV.

Bishop (1949) stated that Leiobunum calcar "...could be collected in large numbers from the trunks of trees and from the ground in a beech-hemlock forest bordering Lincoln Pond [New York state]." The Saskatchewan collections were taken in a wet sedge and willow area, at the edge of a stand of poplar and spruce and under rocks along roadsides. At all collection sites, Phalangium opilio were collected at the same time or had been collected previously.

Distribution: Leiobunum calcar is restricted to eastern and central North America. It has been collected in the following states: Arkansas (Davis, 1934); Connecticut (Bishop, 1949); Illinois (Weed, 1889a; Edgar, 1960, 1966); Indiana (Davis, 1934; Edgar, 1960, 1966); Maine (Davis, 1934); Michigan (Davis, 1934; Edgar, 1960, 1966); New Hampshire (Davis, 1934); New York (Crosby et al., 1926; Davis, 1934; Bishop, 1949); North Carolina (Davis, 1934; Bishop, 1949); South Dakota (Weed, 1893d); Ohio (Weed, 1893a; Walker, 1928; Edgar, 1960, 1966); Pennsylvania (Davis, 1934); Virginia (Wood, 1868); West Virginia (Davis, 1934) and Wisconsin (Levi and Levi, 1952; Edgar, 1960, 1966). Published Canadian records include: Newfoundland (Hackman, 1956); Nova Scotia (Davis, 1934); Ontario (Davis, 1934; Edgar, 1960, 1966) and Saskatchewan, "1, 2 (Scudder)" (Davis, 1934).

Unpublished Saskatchewan records include: Lady Lake (D.J. Buckle), 3.2 km E Margo and 6.4 km E Rama. See Fig. A.1 for the collection sites.

6. Subfamily Leiobuninae, Leiobunum vittatum (Say)

Phalangium vittatum Say, 1821, J. Acad. Natur. Sc. Phila. 2:65-66.

Phalangium dorsatum Say, ibid., p. 66.

Liobunum vittatum-dorsatum Weed, 1892, Amer. Natur. 26:999-1008, pl. 27-28.

Leiobunum vittatum Davis, 1934, Amer. Midl. Natur. 15:696-699, pl. 31, fig. 5; pl. 33, fig. 34.

Leiobunum vittatum Comstock, 1940, The Spider Book, revised ed., p. 74.

Leiobunum vittatum Bishop, 1949, Proc. Rochester Acad. Sc. 9:211-214, pl. 7, fig. 101-104.

Leiobunum vittatum Edgar, 1966, Amer. Midl. Natur. 75:364.

Male, 5-7 mm long; legs I-IV 31, 57 (range = 50-88), 31, 43 mm long.

Female, 7-9 mm long; legs I-IV 34, 65, 34, 48 mm long.

The above measurements were taken from Edgar (1966). Both sexes have a distinct dark central figure extending to include the eye tubercle. In the male, the femur of the palp extends above the surface of the carapace a distance 3 to 8 times the height of the eye tubercle. In the female, the femur of the palp extends above the carapace 1 to 2 times the height of the eye tubercle. See Fig. 3.5C and D. The coxae of legs I-IV have similar denticle arrangements as in Leiobunum calcar.

Although Leiobunum vittatum has often been collected in the United States, little has been published about the habitat it occupies. However, Clingenpeel and Edgar (1965) believe that it prefers less disturbed and moister areas than Phalangium opilio.

Distribution: Leiobunum vittatum is distributed throughout much of North America. The United States records include: Alabama (Bishop, 1949); Arkansas (Davis, 1934; Bishop, 1949); Connecticut (Davis, 1934); Georgia (Davis, 1934; Bishop, 1949); Illinois (Weed, 1889a; Davis, 1934; Bishop, 1949; Edgar, 1960, 1966); Indiana (Davis, 1934; Edgar, 1960, 1966); Iowa (Davis, 1934; Bishop, 1949); Kansas (Davis, 1934); Kentucky (Davis, 1934; Bishop, 1949); Louisiana (Davis, 1934; Bishop, 1949); Maine (Weed, 1892c); Maryland (Roewer, 1957); Michigan (Weed, 1892c; Davis, 1934; Edgar, 1960, 1966); Mississippi (Davis, 1934); Missouri (Davis, 1934); Montana (Bishop, 1949); Nebraska (Weed, 1892c); New Hampshire (Weed, 1893c); New Jersey (Davis, 1934; Bishop, 1949); New York (Weed, 1892c; Crosby et al., 1926; Davis, 1934; Bishop, 1949); North Carolina (Davis, 1934; Bishop, 1949); Ohio (Davis, 1934; Bishop, 1949; Edgar, 1960, 1966); Oklahoma (Davis, 1934; Bishop, 1949); Pennsylvania (Weed, 1892c; Davis, 1934); South Carolina (Davis, 1934); South Dakota (Weed, 1892c; 1893d); Tennessee (Davis, 1934); Texas (Wood, 1868); Vermont (Davis, 1934); Virginia (Davis, 1934; Bishop, 1949) and Wisconsin (Davis, 1934; Levi and Levi, 1952; Edgar, 1960, 1966). Canadian records include: Manitoba (Davis, 1934) and Ontario (Davis, 1934; Bishop, 1949; Edgar, 1960, 1966).

The Saskatchewan specimens were taken at Lady Lake (D.J. Buckle) and at Kernen's Prairie (4 km NE Saskatoon) (E. Gorin and R. Lein). See Fig. A.1 for the collection sites.

7. Other possible Saskatchewan Phalangida

Since the genera Odiellus, Phalangium, Opilio and most likely Homolophus are monospecific to North America, no further species of these

genera are likely to be discovered in Saskatchewan. However, other species of Leiobunum are almost certain to be collected. For example, L. exilipes (Wood) has been reported from Montana and British Columbia (Davis, 1934). Mitopus morio (Fabricius) is holarctic in distribution and has been collected in North America from Newfoundland (Hackman, 1956); Nova Scotia (Bishop, 1949) and New York (Bishop, 1949). It may also occur in northern Saskatchewan.

APPENDIX III

The formula for modified Brasil's fluid is as follows:

95% ethanol	50.0 ml
40% formaldehyde	30.0 ml
glacial acetic acid	7.5 ml
picric acid (sat. aqueous)	12.5 ml
distilled water	12.0 ml
total	112.0 ml

This fixative is also called Dubosq-Brasil or alcoholic Bouin by some authors. Various variations of the formula of this fixative are given by Gatenby and Beams (1950), Pantin (1962) and Humason (1962).