BULLETIN
OF THE
FLORIDA STATE MUSEUM

BIOLOGICAL SCIENCES

Volume I Number 5

LIFE HISTORY STUDIES ON SOME FLORIDA INSECTS OF THE GENUS *ARCHIPSOCUS* (PSOCOPTERA)

Edward L. Mockford

1853

UNIVERSITY OF FLORIDA
Gainesville
February, 1957

The numbers of THE BULLETIN OF THE FLORIDA STATE MUSEUM, BIOLOGICAL SCIENCES, will be published at irregular intervals. Volumes will contain about 250 to 300 pages, and will not necessarily be completed in any one calendar year.

William J. Riemer, Editor
John C. Briggs, Associate Editor

All communications concerning purchase or exchange of the publication should be addressed to the Curator of Biological Sciences, Florida State Museum, Seagle Building, Gainesville, Florida. Manuscripts should be sent to The Editor, Department of Biology, University of Florida, Gainesville, Florida.

Published February 5, 1957 *Price for this issue $.35*

LIFE HISTORY STUDIES ON SOME FLORIDA INSECTS OF THE GENUS *ARCHIPSOCUS* (PSOCOPTERA)

EDWARD L. MOCKFORD[1]

The genus *Archipsocus* is a natural assemblage of species with a wide distribution in tropical and subtropical regions of the world. It was first found in North America in 1934 (Gurney, 1939) when a species, which proved to be new, became so abundant in the vicinity of New Orleans as to be considered a pest. The heavy webs spun by these insects were regarded as unsightly, and steps were taken to control the spinners. Subsequently this species, *A. nomas* Gurney, has been reported to occur in the Gulf states from Texas to Florida.

From February 1952 to April 1954, I collected *Archipsocus* in Florida. Six species were found in the region most intensively collected, Alachua County. Four of these were new and have been described (Mockford, 1953 and 1956); the other two have been described by Gurney (1939).

Little has been published on the life histories of these insects, and their taxonomy is based entirely on adult morphology. In most other psocid genera adult morphology furnishes adequate means for distinguishing species, and each species becomes characterized primarily by a fixed genitalic type and secondarily by certain other morphological details either more difficult to see or slightly more variable. In *Archipsocus,* genitalic differences between species are frequently difficult to find. Although other differences exist, they are seldom great and are subject to variation, the extent of which is unknown in almost every instance. Taxonomy in this genus is further complicated by the relative scarcity of males and by a considerable amount of polymorphism in adults. In view of these facts, the value of life history information as an aid in the taxonomy of the group is obvious.

SPECIES STUDIED

As pointed out previously by Badonnel (1948b) and Mockford (1953), the genus *Archipsocus* is divisible into two natural groups, considered subgenera, on the basis of mode of reproduction—ovipary or vivipary—and certain morphological characters. The six species

---

[1] The author is at present a doctoral student in the Department of Entomology, University of Illinois, Urbana. The work reported on here was performed while he was a graduate student in the Department of Biology, University of Florida. Manuscript submitted 15 March 1956.

discussed here are arranged in the two subgenera according to the following synopsis:

Subgenus *Archipsocus* (oviparous species)
  A. floridanus Mockford
  A. gurneyi Mockford
  A. nomas Gurney
  A. panama Gurney

Subgenus *Archipsocopsis* (viviparous species)
  A. parvulus Mockford
  A. frater Mockford

METHODS

The size of the subjects restricted the possibility of gaining much life history information in the field. Therefore, colonies were collected by cutting the web-bearing bark or twigs with as little disturbance to the web as possible and removed to the laboratory. The colonies were placed in fingerbowls which were set in a large, shallow pan of water. A cotton wick was placed with one end in the fingerbowl and the other in the water so that water would evaporate from it into the fingerbowl, and the bowl was covered with a pair of glass plates. Relative humidity in the bowls was thus kept at 80-90 percent most of the time.

These cultures were fed on their natural food, which consists of small crustose lichens. Since they showed some food specificity, care had to be taken to give them the same type of lichen each time.

Isolated individuals were kept in large shell vials (25 mm. by 80 mm.) on small pieces of bark or leaf on which their natural food was growing. The shell vials were placed in pint mason jars, and relative humidity was maintained at the proper level by placing a small amount of water in the bottom of the jars and covering the top with a glass plate, leaving a small opening.

EGG STAGE

Eggs are oblong, widest near one end, and tapering somewhat toward the other end. The chorion is smooth and is partially covered with fine granular debris which is usually absent from the small end of the egg where the hatching orifice appears. This debris is probably a product of the parent since it sometimes differs from the substrate in color. Eggs differ interspecifically in color, pattern of oviposition, and to a lesser extent in size. Egg measurements are presented in table 1. The colors of *Archipsocus* eggs are imparted by their contents, the chorion being colorless. No special egg webbing is apparent, but eggs are always laid within the dwelling web.

Eggs of *A. floridanus* are orange; they are deposited singly, often in the webbing, but usually on the substrate. They are covered with pale brown debris distributed as described above.

TABLE I

MEASUREMENTS OF FERTILE EGGS

Species of *Archipsocus*	Number of Eggs	Length (millimeters)			Width (millimeters)		
		Mean	Range	Standard Deviation	Mean	Range	Standard Deviation
floridanus	6	0.48	0.45-0.50	0.02	0.25	0.24-0.26	0.01
gurneyi	6	.44	.37- .46	.03	.25	.22- .28	.02
nomas	10	.39	.33- .42	.03	.21	.15- .24	.03
panama	5	0.40	0.37-0.41	0.02	0.19	0.19-0.20	0.01

Eggs of *A. gurneyi* are pale yellow and are deposited in large compact groups on the substrate. The following numbers of eggs per group have been recorded: 25, 28, 33, 49, 70, 80, 171, 200 (three groups). The larger groups are probably the products of more than one female since isolated females have not laid more than 70 eggs. The eggs are covered with fine debris distributed in the manner described and containing black particles, sometimes in great abundance. Adults of this species "guard" the eggs; both sexes stand over the egg mass and return to it after being forced from it.

Eggs of *A. nomas* are pale gray to white, deposited singly or in loose groups on the substrate, and are partially covered with brown debris. They are somewhat less tapering toward the small end than in other species studied. Loose groups of these eggs sometimes become hidden by an accumulation of excrement.

Eggs of *A. panama* are similar in color to those of *A. nomas*. They are deposited singly, usually on the substrate, but one was found in the webbing. They are partially covered with brown particles of debris.

Duration of the egg stage was determined for *A. floridanus* and *A. gurneyi* at room temperature (approximately 80°F) and relative humidity of about 80%. For the former, the range is from 5 to 12 days with a mean of 7.5; the latter has a range of 3 to 7 days with a mean of 5.5 (table 2).

TABLE 2

FREQUENCY DISTRIBUTION OF DURATION OF EGG STAGE IN *Archipsocus*

Duration in Days	Number of Eggs	
	floridanus	*gurneyi*
3-4	---	1
4-5	---	5
5-6	1	34
6-7	6	9
11-12	2	---
	9	49

HATCHING AND BIRTH

Hatching follows a pattern which appears to be fairly uniform for all psocids. The hatching slit is on the upper surface at the small end of the egg. It parallels the long axis and is about one-fourth the length of the egg. The pronymph pushes through this slit, and when nearly free from the egg it undergoes a molt to become a first nymphal instar. Observations of hatching must be made at normal relative humidity for rearing as nymphs die in hatching at lower relative humidity.

I have not observed the inception of the process of hatching in sufficient detail to resolve a controversy as to whether the egg burster ruptures the chorion or only the pronymphal membrane (Sommerman, 1943a and b, 1944a and b). The form of the hatching orifice, a narrow slit, suggests either the presence of a line of dehiscence or the use of the egg burster to cut it. A dehiscence line has not been demonstrable by application of pressure to nearly mature eggs, hence the alternative hypothesis seems plausible.

Birth of nymphs in *Archipsocus parvulus* apparently involves no action on the part of the mother who merely sits quietly while the nymph wriggles its way, maggotlike, out of the genital duct, posterior end first. It is not covered with a pronymphal membrane, but its appendages are stuck to its sides until it is nearly free from the mother, whereupon it pulls them loose, moves them vigorously, and brings them to aid in pulling itself away from its parent. I have not observed the beginning of birth, hence I cannot state the total time required, but a nymph halfway out required 20 minutes to free itself completely.

NYMPHAL STAGE

DESCRIPTION OF NYMPHS—Early first-instar nymphs are readily recognizable by the fact that the head is the widest part of the body. Before the first nymphal molt the abdomen grows and becomes wider than the head. In later instars, the abdomen becomes increasingly wider and longer in proportion to the head. Nymphs possess little cuticular pigment, hence are much paler than adults. Their body colors are various shades of cream, orange, and pale brown, depending on the age and species. Their compound eyes are black, and their appendages are nearly colorless. The midgut is plainly visible as a dark loop in the abdomen of a well-fed nymph.

Nymphs of *Archipsocus floridanus* are uniformly orange over the body; young nymphs are bright orange and older ones somewhat darker. Nymphs of *A. gurneyi* are pale orange on the abdomen and red orange on the head; they also become darker with age. Early first-instar nymphs of *A. nomas* are creamy white on the thorax and abdomen, pale brown on the head; later they become pale orange brown throughout. First-instar nymphs of *A. panama* are creamy white on the thorax and abdomen, red orange on the head; older nymphs retain the same head color and are light orange on the abdomen. Early nymphs of *A. parvulus* are uniformly orange, but become redder and darker with age. Late instar nymphs of *A. frater* are uniformly orange.

NUMBER AND DURATION OF NYMPHAL INSTARS—The number and duration of nymphal instars has been determined for *Archipsocus floridanus, A. gurneyi,* and *A. parvulus* by rearing them in isolation from birth or hatching to adulthood. Since nymphs were found to eat their exuviae, a marking technique was used to determine the number of nymphal instars. A spot of methylene blue in aqueous solution was placed on the back of each nymph after each molt using a fine cotton point as an applicator. It was found convenient to anesthetize the nymphs with ether before marking. When the mark disappeared, the nymph was assumed to have molted; usually the exuviae, or parts of them, were found close at hand bearing the blue spot. The number of nymphal instars was determined for 57 individuals (table 3). The 48 females all underwent six nymphal instars, while the nine males underwent from four to six, but usually five. The significance of these

TABLE 3

FREQUENCY DISTRIBUTION OF NUMBER OF NYMPHAL INSTARS

Species of *Archipsocus*	Sex	Number of Nymphal Instars 4	5	6
floridanus	♀	----	----	7
gurneyi	♀	----	----	20
parvulus	♀	----	----	21
floridanus	♂	1	1	----
gurneyi	♂	----	2	1
parvulus	♂	----	4	----

data in relation to polymorphism will be discussed in a later section.

Durations of nymphal instars (table 4) are similar for the three species. Generally, the first is from three to five days; the second is from two to five days; the third, fourth, and fifth are from two to four days, and the sixth is from two to six days. These data are for room temperature of about 80°F and relative humidity of about 80 percent.

MOLTING—The entire molting process has not been observed, but it seems to follow a pattern which is fairly uniform for most exopterygotic insects. The nymph stands with its forelegs supported in the web and the posterior end of its abdomen resting on the substrate. The cuticle splits along the back of the thorax, and the nymph arches out. It pulls out its head, most of the abdomen, the thoracic appendages, and finally the tip of the abdomen. Again, as in hatching, relative humidity must be kept high while molting is being observed.

GROWTH RATE AND MORPHOLOGICAL CHANGES—In order to determine the growth rate, measurements of the head capsule between the eyes were made on living nymphs of *A. parvulus* in known instars (table 5). The rate of increase from instars one to five is about 1.13 times, decreasing very slightly with each instar. Between the fifth and sixth instars, the head width increases only 1.04 times, but from the sixth instar to the adult (female) stage, the rate of increase is 1.09 times. These data show a slight departure from Dyar's Rule. The single in-

TABLE 4

FREQUENCY DISTRIBUTION OF DURATION OF NYMPHAL INSTARS

Species of *Archipsocus*	Number of Days	Instar Number					
		1	2	3	4	5	6
floridanus	1	—	—	1	—	—	—
	2	—	5	5	4	4	—
	3	1	1	2	3	2	4
	4	2	1	—	—	1	2
	5	—	—	—	—	—	1
gurneyi	2	—	8	11	12	7	3
	3	3	12	10	8	10	10
	4	12	2	2	2	4	4
	5	6	—	—	—	—	—
	10	—	—	—	—	—	1
parvulus	1	—	—	—	2	—	—
	2	—	5	5	7	7	—
	3	3	5	11	5	8	10
	4	10	4	2	6	4	3
	5	—	5	—	1	—	3
	6	3	—	—	—	1	2
	8	1	—	—	—	1	—
	9	1	—	—	—	—	—

TABLE 5

MEASUREMENTS (IN MILLIMETERS) OF SMALLEST WIDTH BETWEEN EYES FOR NYMPHS OF *Archipsocus parvulus*

Instar	Mean	Range	Standard Deviation	Number of Specimens
1	0.14	------	----	6
2	.16	------	----	4
3	.18	------	----	3
4	.20	0.19-0.21	0.009	5
5	.22	.21- .22	.005	5
6	.23	.22- .23	.006	10
Adult ♀♀	0.25	0.24-0.26	0.006	7

dividual among these nymphs known to be a male showed no increase in head width between the fifth instar and the adult stage.

First-instar nymphs of *A. parvulus* and *A. nomas* have eight antennal segments; the full complement of 13 is attained at the first molt. Wing pads are first visible on female nymphs in the third instar.

ADULT STAGE

DURATION OF ADULT LIFE—Data on duration of adult life are scanty, and all are from individuals reared in the laboratory. One female of *Archipsocus floridanus* lived 24 days, another between 65 and 67 days, and two others between 82 and 86 days. One female of *A. gurneyi* lived three days, another four, another 13, another 27, and another 43 days. Six females of *A. parvulus* lived 28 to 126 days with a mean of 78. One male of *A. parvulus* lived 50 days. Laboratory temperature was about 80°F and relative humidity was about 80 percent. In the field, *A. floridanus* and *A. nomas* have been observed overwintering as adults; this would require a longevity of at least 80 days.

SEX RATIO—The sex ratios of the Florida species of *Archipsocus*, like those of several Belgian Congo species (Badonnel, 1948b, 1949b), show a significant departure from a 1:1 ratio in favor of females. For all of the species in table 6 except *A. floridanus,* the marked divergence of the sex ratio is obvious, but for *A. floridanus* a chi-square (X^2) test was employed to determine this. The low "P" value indicates that there was less than one chance in 100 that the data were randomly derived from a population with a 1:1 sex ratio. Data in table 6 are from two sources: (1) collections in the field representing the total population under the web, and (2) all individuals reared in isolation. The laboratory stock colonies were not subjected to the rather rigorous treatment necessary for sexing. No sex ratio data are available for *A. panama* and *A. frater,* but females predominate in both of these species.

TABLE 6

SEX RATIOS OF *Archipsocus* SPECIES

Species	Number of ♂♂	Number of ♀♀	Ratio (♀/♂)	X^2 for fit to 1:1 ratio	P
A. floridanus	20	43	2.2	8.4	<0.01
A. gurneyi	12	61	5.1	----	------
A. nomas	14	76	5.4	----	------
A. parvulus	7	54	7.7	----	------

TESTS FOR PARTHENOGENESIS—Although males of all of the Florida species are known, and copulation was observed in all but *Archipsocus panama,* the unbalanced sex ratios suggest the possibility of "sporadic parthenogenesis" (Wigglesworth, 1950:486). Badonnel (1943) states that this is of common occurrence in psocids, but I know of no published accounts in which it is adequately demonstrated. Three of the Old World *Archipsocus* species are known from females only.

To test for parthenogenesis, late instar nymphs were reared to adulthood in isolation. The virgin females obtained from these nymphs were observed from time to time for indications of reproduction. The numbers of females used in this study were as follows: *A. floridanus* 5, *A. gurneyi* 17, *A. nomas* 1, *A. parvulus* 11. Only negative results were obtained, hence it is known that not all females of these species resort to parthenogenetic reproduction.

INFERTILE EGGS—An interesting facet of the investigation of parthenogenesis concerns the laying and disposal of infertile eggs. The isolated virgin females of the three oviparous species laid infertile eggs which, when isolated from the female, dried up and collapsed in a few days. Infertile eggs were invariably eaten within a few days after deposition when left with the females; fertile eggs were never eaten, even when the food supply was exhausted. Infertile eggs occasionally differ from fertile eggs in size and shape, being usually smaller and more spherical. They are similar to fertile eggs in color and are always partially covered with debris.

All of five females of *Archipsocus floridanus* laid from one to eight eggs; these were all of normal size and shape. Three of seventeen virgin females of *A. gurneyi* laid eggs: one laid one, the other two laid four each. Five of these eggs were of normal size, while the other four were about one-quarter normal size and more spherical in shape. A virgin female of *A. nomas* laid six eggs, all of normal size.

COURTSHIP AND COPULATION—Courtship is considered any behavior which is obviously preliminary to copulation or which has rarely or never been observed at any time other than immediately prior to copulation. Usually all activity of a potentially copulating pair from the time of first contact to the time of copulation could be considered courtship, and in making observations I attempted to record all activity during this period.

For convenience, the male was usually anesthetized with ether and placed in the female's web. Since ether acts on the nervous system and might change the courtship pattern, several observations were made without the use of anesthesia. No striking differences were noted.

Females copulate only once in their lifetimes, while males are capable of several copulations. In every instance observed, females played an active role in contacting the males with their antennae or fore and middle legs in a stimulatory manner. In copulation the female rests directly above the male, and both face in the same direction. The positions of the parts of the genitalia have not been determined.

Courtship and copulation have been observed for all of the species studied except *Archipsocus panama*. The following are summaries—abbreviated to avoid repetition—of all observations on each species.

A. floridanus (two observations): The two psocids first make contact when one, by chance, brushes against the other. Both cease movement for a few seconds, and then the female crawls around the male, mounting him from time to time and, during mounting, stroking him on the back with, and also supporting herself on, her fore and middle legs. The male responds by making irregular anteroposterior jerking motions of the whole body and crawling about. During this activity there may be a few pauses lasting several seconds which are utilized by the male to preen his tarsi by pulling them between his mandibles. After a short time—17 and 27 minutes in the two cases observed—the female begins to maintain a position above the male's back with her fore and middle legs continuing the stroking motion while her hind legs rest on the substrate. The male wriggles well underneath her, rears the tip of his abdomen, ceases the jerking motion, and they copulate for several seconds—20 and 24 seconds in the two cases observed. Then the male crawls out from under the female.

A. gurneyi (four observations): After initial contact, the female crawls around the male, first touching him with her antennae and the front of her head. The male starts a violent, rapid, anteroposterior jerking motion and turns about following the movement of the female with his head. The female strokes the male's back a few times with her fore and middle legs while circling him. There may be pauses during which both sexes may preen their tarsi. The amount of time required for courtship is similar to that for *A. floridanus.* Copulation is identical to that of *A. floridanus,* except that in most cases the female rests her hind legs—hence all of her legs—on the male. Copulation lasts from 20 to 30 seconds, at the end of which the male usually crawls out from under the female. In one case the female turned to the side and crawled off the male's back.

A. nomas (two observations): After initial contact, the female starts pushing on the male at various places with the front of her head. Then they separate and come back together at least once, meeting head on, tapping antennae together, and pushing clypei together. There may be pauses during which the male preens his tarsi. After one or several head-on meetings, the male starts a rapid anteroposterior jerking motion and wriggles the tip of his abdomen under the foreparts of the female. Then the female strokes the male's back with her fore and middle legs, while her hind legs rest on the substrate. The male wriggles into copulatory position, and they copulate. Copulation lasted for 10 seconds in one case and 27 in the other. In both cases it was ended by the female's turning to the side and dismounting.

A. parvulus (four observations): After initial contact, the male starts crawling around the female and pushing under her at various places with the front of his head. Then the female starts vibrating her antennae rapidly and keeping the male in contact with them by moving when he does. The male pushes under her, head first, at her anterior end, and turns around so that both are facing in the same direction—the small size of the male allows him to turn around readily under the female. The female's antennae stop vibrating as soon as copulation starts. They copulate for 3 to 30 seconds. The male usually terminates copulation by crawling out from under the female, but in one case the female crawled off the male.

A. frater (three observations, one not including copulation): After initial contact, the male starts preening his antennae, one at a time, by holding them down with either fore tarsus and pulling them until their tips are freed. The male also preens his tarsi in the usual manner; preening may also be engaged in by the female. Then the female approaches the male, touches him with her antennae, and places her fore and middle legs on his back. The male responds with antero-posterior jerking motions in a slower rhythm than in other species. The female crawls the rest of the way onto the male's back to assume the usual copulatory position. The male ceases jerking during copulation. In one case copulation lasted for 16 seconds and in the other for 20; it was terminated by the female's turning to the side and dismounting.

One courtship observed for this species did not result in copulation, but is of interest because it shows the extent to which the usual pattern may be modified under special conditions. In this case, the female was very teneral, probably too teneral to copulate. The normal series of events occurred until the female first placed her forelegs on the male's back. Then she promptly removed them and did not participate actively in the courtship thereafter. For the next 15 minutes, the male behaved in a way markedly different from the other two cases. He crawled around the female and four times forced the tip of his abdomen under her head, giving the usual jerking motions—which had followed the female's placing her forelegs on his back—and acting as if he were trying to assume the copulatory position. But the female gave no response except to move aside.

Summary—Three major patterns of courtship and copulation can be distinguished among these species. In the first pattern, the female takes the more active part in courtship, the male responds to her stroking his back by giving a jerking motion of the body, and the female actively mounts the male. This pattern is shown by *A. floridanus, A. gurneyi,* and *A. frater.* In the second pattern, the male and female take nearly equally active parts in courtship; at least one head-on meeting occurs during courtship followed by tapping together of antennae. The male starts the jerking motion following antennal contact with the female and wriggles into copulatory position under the female. This pattern is exhibited by *A. nomas.* In the third pattern, the male takes a more active part in courtship than the female; the female vibrates her antennae rapidly in response to contact of the male, and the male pushes into copulatory position under her with no jerking motion. This pattern is shown by *A. parvulus.*

The first pattern is probably the most primitive of the three since it occurs in both subgenera. The other two must be regarded as separate derivations from a pattern similar to the first.

One purpose in studying courtship and copulation, in addition to the recording of this interesting phase of the life cycle, was to determine whether any ethological isolating mechanisms could be found here, especially among the species of the subgenus *Archipsocus.* There is no geographical isolation, and insufficient ecological isolation among these species—I have found all four species on a single tree—and their morphological and physiological isolating mechanisms appear to be poorly developed. As described above, potential ethological mechanisms for isolating *A. floridanus* from *A. gurneyi* could not be shown, but the differences distinguishing these two species from *A. nomas* in sexual behavior appear to be sufficient, and of the right types, to constitute isolating factors.

Relationships of these five species derived from degree of difference of sexual behavior patterns would not be wholly similar to those derived from morphology. *A. floridanus* and *A. gurneyi* are very similar morphologically and in sexual behavior. *A. nomas* is more readily distinguishable morphologically from these than they are from each other, and it differs markedly from them in sexual habits. *A. parvulus* and *A. frater* are placed in the subgenus *Archipsocopsis* on mostly a morphological basis, but *A. frater* is closer in sexual behavior to *A. floridanus* and *A. gurneyi* than to *A. parvulus.* Apparently then, sexual behavior patterns in *Archipsocus* have evolved in a way more conservative than morphological characters and should be viewed accordingly when used to aid in determining phylogenetic relationships within the group.

POLYMORPHISM—Trends toward nymphalization are frequent among adult psocids. Such trends have produced species, genera, and families which are completely nymphoid, others which show nymphoid-adultoid dimorphism, and others, including *Archipsocus,* which are polymorphic in this respect. The peculiarly adult structures which tend to be poorly developed or absent are the wings, thoracic tergal lobes, and ocelli. The presence or absence, and the degree of development of these structures shows a close positive correlation. Apterous species, and apterous forms of polymorphic species, lack ocelli and possess relatively simple pterothoracic tergites (Badonnel, 1943:7-8), while long-winged individuals possess these structures in a well-developed state. The term polymorphism, as used here, refers only to the correlated variation in these characters in adults.

Polymorphism may be related to sex in three ways: (1) All males are nymphoid while females may be nymphoid or adultoid. (2) All males are adultoid while all females are nymphoid. (3) All males are adultoid while females are either nymphoid or adultoid. *Archipsocus* is in the first of these categories.

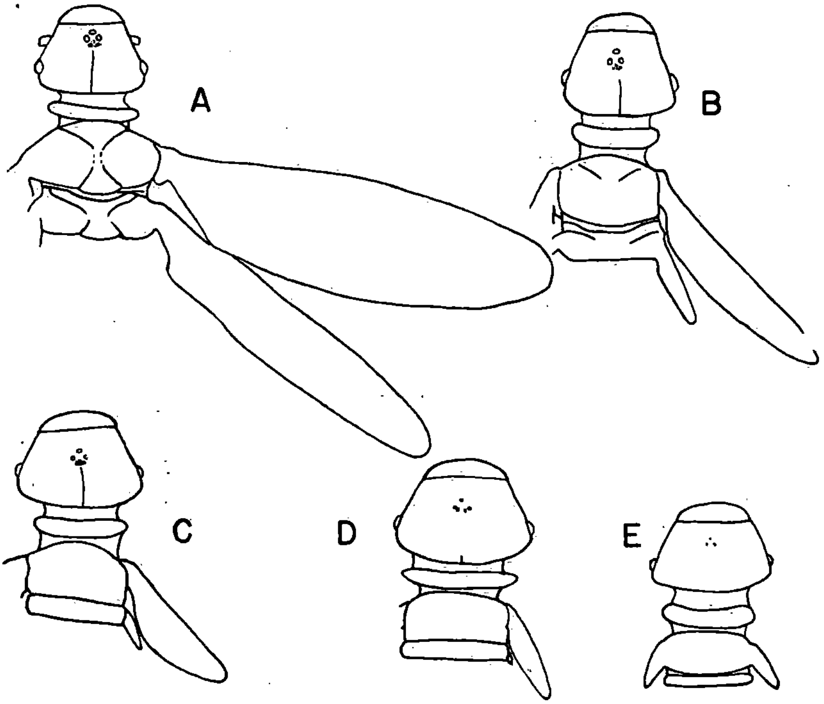

Fig. 1. Outlines of heads and thoraces of adult forms of *Archipsocus nomas*. A. Macropterous female. B-C. Brachypterous females. D. Micropterous female. E. Male.

Figure 1 illustrates variations in the development of the wings, pterothoracic tergites, and ocelli in the known adult forms of *Archipsocus nomas*. It will be noted that the epicranial suture shows variation with these structures. The other Floridian species differ little from

A. nomas in their polymorphism. Micropterous females of *A. floridanus* have shorter wing pads than in *A. nomas,* and they lack ocelli. Only macropterous females of the scarce species *A. frater* have been found. Males of *A. parvulus* lack all trace of wings and ocelli.

The different forms of females occur in different frequencies. The extreme forms constitute the most abundant classes, while intermediate forms are considerably scarcer.

Frequently, nymphalization in psocids is accompanied by reduction in the number of nymphal instars. The primitive number may be established from the works of several authors. Sommerman (1943a,b; 1944a,b) has shown for four species, in which no nymphoid adults are known, that the number of nymphal instars is six. Badonnel (1951), summarizing the work of other authors, reported six nymphal instars for five other species showing little or no nymphalization of adults. Badonnel (1938, 1948a, 1951) reported six nymphal instars for macropterous, brachypterous, and some micropterous females of *Psyllipsocus ramburi.* My own observations show six nymphal instars for micropterous females of *Archipsocus,* while the instar numbers of brachypterous and macropterous females were not determined. Hence, the primitive number of nymphal instars for psocids is evidently six.

Only nymphoid forms have shown reduction of this number. Badonnel (1938, 1948a, 1951) reported five nymphal instars for some micropterous females of *Psyllipsocus ramburi.* The same author (1951), reporting on a study by Jentsch, indicated five nymphal instars for *Cerobasis guestfalica,* an apterous psocid with no ocelli. Broadhead and Hobby (1944) found four nymphal instars for *Liposcelis granicola,* which is also an apterous form lacking ocelli. Broadhead (1947) found four nymphal instars for apterous females and three for apterous males of *Embidopsocus enderleini,* a dimorphic species with apterous adults of both sexes lacking ocelli, and macropterous females possessing well-developed ocelli. My observations (table 3) show that adult males of *Archipsocus,* all of which are micropterous or apterous and lack ocelli, undergo four to six, but usually five, nymphal instars.

The term neoteny can properly be applied to all cases of nymphalization of adult psocids. Wigglesworth (1950:485) defines neoteny as ". . . the retention of youthful characters beyond the usual period in ontogeny." The adult stage, despite the instar in which it is reached, must be regarded as the usual period in ontogeny for loss of youthful characters. As seen from the discussion on number of nymphal instars, some psocids have achieved neoteny by reduction in the number, while others, including females of *Archipsocus,* have retained the primitive number yet fail to lose some nymphal characters as adults.

The retention of macropterous forms in a neotenic insect is probably an adaptation to insure distribution and to relieve local population pressure. In north-central Florida, macropterous females of *Archipsocus* appear in midsummer, when living conditions for these insects—temperature, relative humidity, and food supply—are at their best, and when local populations have become rather large.

The causes of polymorphism in *Archipsocus* are not known. In other psocids, polymorphism has been shown to be due to both genetic factors (Badonnel, 1951) and environmental factors. The available evidence on *Archipsocus* suggests that environmental factors play the major role. The nature of the polymorphism is similar to that in *Psyllipsocus ramburi* studied by Badonnel (1948a, 1949a), in that not only the wings are affected but also the ocelli and tergal lobes, and in that there are intermediates between micropterous and macropterous forms. I have reared 92 females in isolation from first instar to adult stage (7 *A. floridanus,* 20 *A. gurneyi,* 21 *A. parvulus,* and 44 of *A. nomas* to confirm the results on the type of female obtained), and all became micropterous adults. Further experiments should be carried out to show whether or not group size effects the results.

WEBS

The spinning of webs is probably a universal habit in *Archipsocus.* It was observed in all of the species studied. The webs are densely spun of fine strands—much finer than most spider webbing—and occur on tree trunks, branches, vines, sides of buildings, and leaves of palms, magnolias, and oaks, in places protected from rain. Psocids in all stages of development may be found within a single web. The webs are thought to protect the psocids from predators, especially ants (Enderlein, 1912; Gurney, 1939).

Webs of the species treated here range in size from a few millimeters to 610 millimeters in greatest length. The small webs are roughly circular in shape, but an elongate form usually develops as the web becomes larger. On a tree trunk the long axis of the web generally parallels the long axis of the trunk and spreads up and down along a furrow in the bark. Such a web seldom acquires a width greater than 150 millimeters. Webs on small branches are concentrated at points where twigs arise from the branch. In new webs on branches, one such concentration point may be connected to the next only by a few strands, but as the web gets older, enough strands are spun so that the psocids may pass from one concentration point to the next under web. The web spreads as the food supply becomes exhausted, so that the entire area under a large web is not inhabited by the psocids at one time.

The web of *Archipsocus nomas* is constructed mostly of parallel strands laid rather close together so that the web becomes very dense. The webs of the other species are composed largely of crossing strands and do not become as dense as that of *A. nomas*. Web-spinning has not previously been reported for *A. panama*. Its webs are small and have been found on tree trunks, branches, and vines. In two cases they were spun over holes in the bark which were used as retreats by the psocids. Little webbing is spun by *A. frater*.

To determine whether these insects can detect vibrations of the web, the following experiment was conducted. A colony of *Archipsocus floridanus* was placed under a binocular microscope, which was focused on a group of ten nymphs. A small dissecting needle was passed over the nymphs so that its shadow fell on them but the needle did not touch the web. This process was repeated several times but elicited no visible response from them. Then the surface of the web was plucked with the needle near the nymphs, and immediately most of them ran a few millimeters. This was repeated on a smaller group with similar results. A second test was made to eliminate the possibility that the nymphs were reacting to the sight of the needle. The needle was lowered very slowly and carefully through the web into a group of 16 nymphs, then pulled out in the same way. Only three nymphs moved, and then only when the web was disturbed. It is obvious from these experiments that the psocids can detect vibrations of the web; however, plucking with the needle on individual strands above groups of nymphs elicited no movement, indicating either that such fine vibrations did not reach the nymphs or that the nymphs could not detect them.

SOCIAL DEVELOPMENT

The large majority of psocids are not social in the sense usually used by entomologists. Individuals of most species spend a small fraction of their lives in contact with other individuals of their species. Adults usually leave their eggs as soon as they are laid. The beginnings of social development can be seen in a few groups. Nymphs of *Ectopsocopsis pumilis* and *Ectopsocus californicus* occasionally live in small groups under loose webs. Females of the solitary web-dwelling forms of the genera *Reuterella, Palmicola,* and *Aaroniella* remain in their webs with their eggs, but they are usually dead by the time the eggs hatch. Nymphs of *Cerastipsocus* live in dense herds, but the herds break up soon after the insects reach adulthood (personal observations).

In *Archipsocus,* social development has gone much further than in any other psocid group. The nymph emerges from the egg in a web made by its mother or by both of its parents plus their sibs. It remains in this web together with its sibs probably for its entire life, during which it contributes silk and work to the enlargement and repair of the web. Some of the parental generation may still be alive when this individual reaches adulthood.

SEASONAL CYCLE IN NORTH-CENTRAL FLORIDA

Data on the seasonal cycle were obtained throughout a period of 26 months extending from February 1952 to April 1954. The following statements summarize these data. *Archipsocus* colonies are scarce during December, January, and February when they are mostly restricted to hammocks of cabbage palms (*Sabal palmetto*) and mesophytic hardwood trees. Colonies examined during these months have contained a majority of adults and no nymphs in instars earlier than the fourth. First nymphal instars of *A. floridanus* were observed on March 1. From March through June colonies slowly increased in abundance. Nymphs in all instars were found in the webs during this period. From July through October many new colonies appeared, more in open forests than in hammocks, and webs of older colonies grew considerably. During this period small webs were occasionally found containing only a single gravid female or a single female with young nymphs. On five occasions, these single females were macropterous, and all but one of these five females were accompanied by young nymphs. Micropterous females have also been found in such situations; hence, it is probable that during this period gravid females wander out of old colonies to establish new ones, and it is interesting to note that only during this period have I found macropterous females in the field in this region. By late October populations have reached their peak. There they remain through most of November, but by early December they have decreased considerably in abundance. This rapid disappearance may be due to the killing off of all but the best protected colonies by frosts. This is supported by the observation that the obviously poorly protected colonies, those on branches of trees in open forests and hammock borders disappear first.

HABITATS

In Florida, *Archipsocus* generally is found in shady open woodlands, and mesophytic and hydrophytic forests. On the University of Florida campus, colonies are abundant on the north (and occasionally other) walls of brick buildings mostly covered by *Ficus* vines and bordered with foundation shrubs, but where the foundation shrubs are absent, colonies are scarce. On the streets of Gainesville, colonies occur in late summer and autumn on the trunks of large, spreading laurel oaks (*Quercus laurifolia*). In mesophytic and hydrophytic hammocks, colonies are more common on vines and branches of small trees than on trunks of large trees. The trunks of mature cabbage palms in hammocks are often sites of *Archipsocus* webs.

Colonies judges by their large size to be successful are usually located in places protected from sun and rain, where humidity is high, and where there is an abundance of food in the form of small crustose lichens.

Some differences in habitat occur among the species studied. *A. floridanus* and *A. nomas* occur on tree trunks, branches, vines, and walls of buildings. *A. parvulus* has been taken on tree trunks (*Carya* sp., *Liquidambar styraciflua, Magnolia grandiflora,* and *Sabal palmetto)* and the side of a wooden shed. *A. panama* has been taken on the trunk of a large dead pine (*Pinus taeda*), on branches of oak and hickory, and on a *Smilax* vine. *A. gurneyi* is usually found on leaves of cabbage and date palms (*Phoenix canariensis)* but also has been taken on leaves of the southern magnolia (*M. grandiflora*), laurel oak, water oak (*Q. niger*), orange (*Citrus sinensis*), and on stems of arborvitae (*Thuja* sp.) and *Smilax*. Colonies of *A. frater* have been found only on leaves of a dead water oak.

PREDATORS, PARASITES, AND INQUILINES

Several spiders were found living in or very near *Archipsocus* webs. A salticid, *Marpissa undata,* was found with its web in contact with a web of *A. nomas*. A clubionid spider, probably *Clubiona* sp., was found with its web in a small leaf onto which a web of *A. floridanus* extended. On the side of a shed the webs of *A. parvulus* were found under the flat, radiating web of the spider *Filistata hibernalis,* but in this case the psocids are probably much too small to be eaten by the spider.

On several occasions I have observed predatory true bugs of the genus *Empicoris* (=*Ploiariola*) on *Archipsocus* webs. Such an association has already been recorded by Poisson (1951:1743). A species near *E. armatus* was taken on the web of *A. gurneyi*, and unidentified *Empicoris* nymphs were taken on the webs of *A. parvulus* and *A. nomas*.

The only parasites found were tiny myrmarid wasps of the genus *Alaptus*. One culture of *A. panama* was completely destroyed when all of the eggs hatched into *Alaptus* wasps instead of psocids. *Alaptus* wasps were also taken in the webs of *A. floridanus* and *A. gurneyi*.

Mites (Acarina) of several species, and springtails (Isotomidae) are common in *Archipsocus* webs. Apparently they are present as inquilines, i.e., they have no relationships with the psocids other than living in their webs. They probably derive the same protection from the web as do the hosts. The relation is not obligatory in the case of the springtails and probably not with the mites.

SUMMARY

Six species of *Archipsocus* have been found in north-central Florida. Four are oviparous forms of the subgenus *Archipsocus*, and two are viviparous forms of the subgenus *Archipsocopsis*.

Eggs are long-ovoid, smooth-cuticled, and covered sparsely with debris. Eggs of the different species differ in color, size, and pattern of oviposition. Eggs of *A. gurneyi* are laid in large groups, whereas those of the other species are laid singly. Eggs range from 0.33 mm. to 0.50 mm. in length, and 0.15 mm. to 0.28 mm. in maximum width, with minor size differences between species.

Nymphs of the different species differ somewhat in color. A marking technique was used to determine number of nymphal instars for three species. Females in every case underwent six nymphal instars and males usually five.

Sex ratios are unbalanced in favor of females, with values ranging from 2.0 to 11.3. Constant parthenogenesis does not occur in any of these species, and there is no evidence of sporadic pathenogenesis for any of them. Virgin females of the oviparous species lay eggs which do not hatch and which they eat if allowed to do so.

Adults of *A. gurneyi* "guard" their egg clusters.

Polymorphism occurs in adults of all species studied. The different adult forms may be arranged in a series from most neotenic to most adultoid, all species showing approximately the same series. Neoteny is achieved in the females by retention of nymphal characters through the primitive number of nymphal instars, and in the males by reaching adulthood in a normally nymphal instar. Males are all at the extreme neotenic end of the series. Genetic factors probably are not responsible for polymorphism in *Archipsocus*.

Web-spinning was observed in all of the species studied, and some species differences in web structure were noted. The psocids detect disturbances of the webs.

Archipsocus shows the highest degree of social development found among psocids.

Colonies are scarce during the winter, at which time no reproduction occurs in them. Reproduction starts in March, and colonies grow in the spring and summer; many new ones appear in late summer and autumn. In late November and early December many colonies disappear. Colonies are found in mesophytic and hydrophytic forests and in shady clearings, on tree trunks, branches, vines, walls, and leaves. Some specific habitat preferences were observed, the most notable being that of *A. gurneyi* for palm leaves.

Several spiders have been found in and near *Archipsocus* colonies. Some of these undoubtedly prey on the psocids. Predatory bugs of the genus *Empicoris* were found on the webs of the psocids. *Archipsocus* eggs are parasitized by tiny wasps of the genus *Alaptus*. Mites and springtails found in the webs apparently have no trophic relationships with the psocids.

ACKNOWLEDGMENT

The author wishes to acknowledge with thanks much helpful criticism and advice given throughout the course of this work by Lewis Berner of the Department of Biology, University of Florida.

LITERATURE CITED

BADONNEL, A. 1938. Sur la biologie de *Psyllipsocus ramburii* Selys-Longch. (Psocoptères). Bull. Soc. Ent. France, 43:153-158.

———. 1943. Faune de France 42. Psocoptères. Paris: P. Lechevalier et Fils, 164 pp., 375 figs.

———. 1948a. L'effet de group chez *Psyllipsocus ramburii* Selys-Longchamps (Psocoptères), note preliminaire. Bull. Soc. Zool. France, 73:80-83.

———. 1948b. Psocoptères du Congo Belge (2e note). Rev. Zool. Bot. Africaines, 40 (4):266-322, 126 figs.

———. 1949a. Sur le determinisme de l'effet de group chez *Psyllipsocus ramburii* Selys-Longchamps (Psocoptères). Compt.-Rendus Acad. Sci., 228:1517-1519.

———. 1949b. Psocoptères du Congo Belge (3e note). Bull. Inst. Roy. Sci. Nat. Belgique, 25 (11):1-64, 83 figs.

———. 1951. Ordre des Psocoptères. *In,* Traité de Zoologie, vol. 10, pp. 1301-1340, 35 figs.

BROADHEAD, E. 1947. Life history of *Embidopsocus enderleini* Rib. Ent. Monthly Mag., 83: 200-203.

BROADHEAD, E. and B. M. HOBBY. 1944. Studies on a species of *Liposcelis* (Corrodentia, Liposcelidae) occurring in stored products in Britain. Parts I and II. Ent. Monthly Mag., 80: 47-59, 163-173, 22 figs., 3 tables.

ENDERLEIN, G. 1912. Uber die Gespinnste von *Archipsocus recens* End. Leiden Mus. Notes, 34:157-160, 2 tables.

GURNEY, A. B. 1939. Nomenclatorial notes on Corrodentia with descriptions of two new species of *Archipsocus.* Jour. Washington Acad. Sci., 29:501-515, 13 figs.

MOCKFORD, E. L. 1953. Three new species of *Archipsocus* from Florida (Psocoptera: Archipsocidae). Florida Ent., 36:113-124, 30 figs.

———. [MS]. A new *Archipsocus* from Florida. [In press, 1956].

POISSON, R. 1951. Ordre des Hétéroptères. *In,* Traité de Zoologie, vol. 10, pp. 1657-1803, 128 figs.

SOMMERMAN, K. M. 1943a. Bionomics of *Lachesilla nubilis* (Aaron) (Corrodentia: Caeciliidae). Canadian Ent., 75:99-105.

———. 1943b. Description and bionomics of *Caecilius manteri* n. sp. (Corrodentia). Proc. Ent. Soc. Washington, 45:29-39, 11 figs., pls. 1-2.

———. 1944a. Bionomics of *Amapsocus amabilis* (Walsh) (Corrodentia, Psocidae). Ann. Ent. Soc. Amer., 37:359-364, 5 figs., 1 pl.

———. 1944b. Bionomics of *Ectopsocus pumilis* (Banks) (Corrodentia, Caeciliidae). Psyche [Cambridge, Massachusetts]. 50:53-64, 15 figs., pls. 5-6.

WIGGLESWORTH, V. B. 1950. The principles of insect physiology. London: Methuen and Co., 544 pp.

Bulletin of the Florida State Museum, Biological Sciences
Volume I, Number 5, 1957