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## 1.

## Comparative Biology of Salticid Spiders at Rancho Grande, Venezuela. Part I. Systematics and Life Histories in *Corythalia*.<sup>1</sup>

JOCELYN CRANE.

Research Zoologist, Department of Tropical Research,  
New York Zoological Society.

(Plate I; Text-figures 1-15).

[This is one of a series of papers resulting from the 45th and 46th Expeditions of the Department of Tropical Research of the New York Zoological Society, made during 1945 and 1946 under the direction of Dr. William Beebe with headquarters at Rancho Grande in the National Park of Aragua, Venezuela. The expeditions were made possible through the generous co-operation of the National Government of Venezuela and of the Creole Petroleum Corporation.]

[The characteristics of the research area are in brief as follows: Rancho Grande is located in north central Venezuela (10° 21' N. Lat., 67° 41' W. Long.), 80 kilometers west of Caracas, at an elevation of 1,100 meters in the undisturbed montane cloud forest which covers this part of the Caribbean range of the Andes. Adjacent ecological zones include seasonal forest, savanna, thorn woodland, cactus scrub, the fresh water Lake Valencia, and various marine littoral zones. The Rancho Grande area is generally subtropical, being uniformly cool and damp throughout the year because of the prevalence of the mountain cloud cap. The dry season extends from January into April. The average humidity during the expeditions, including parts of both wet and dry seasons, was 92.4%; the average temperature during the same period was 18° C; the average annual rainfall over a 5-year period was 174 cm. The flora is marked by an abundance of mosses, ferns and epiphytes of many kinds, as well as a few gigantic trees. For further details, see Beebe & Crane, *Zoologica*, Vol. 32, No. 5, 1947. Unless otherwise stated, the specimens discussed in the present paper were taken in the montane cloud forest zone, within a radius of 1 kilometer of Rancho Grande.]

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### INTRODUCTION.

Jumping spiders are among the most interesting of all animals for two distinct reasons. First, the epigamic displays and associated

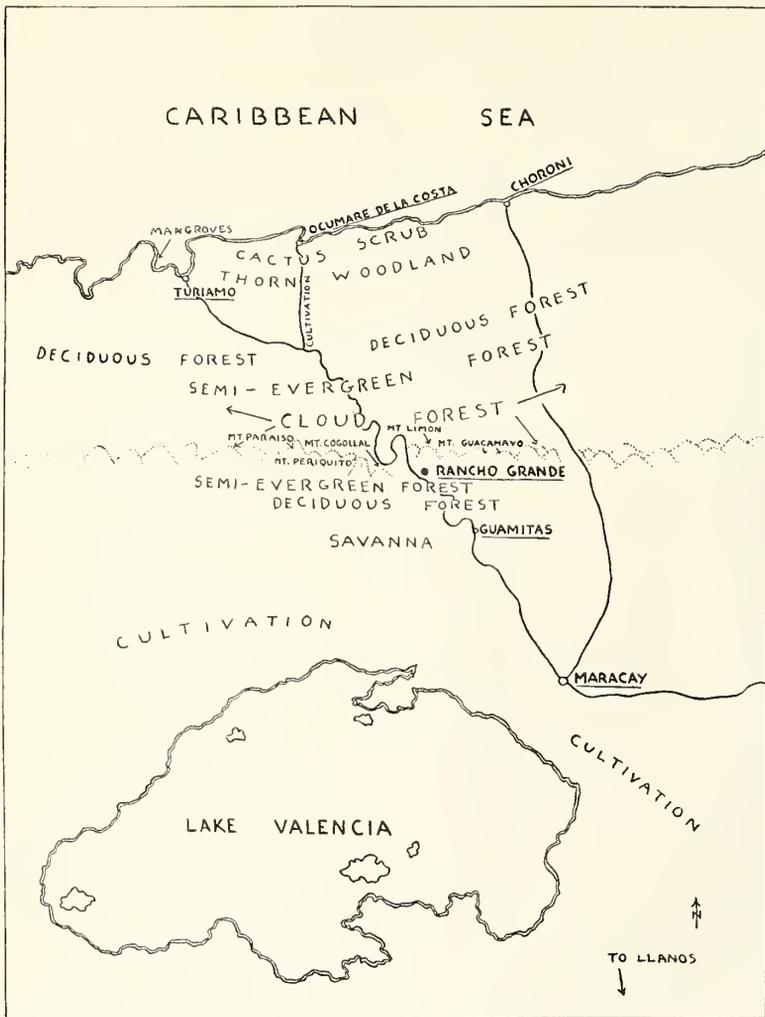
adornments of the males are directly comparable to those of certain fishes, birds and other vertebrates. Second, as all students of spiders have agreed, the family's pattern of evolution is of a challenging complexity. Difficulties in systematics have been increased by the sheer numbers of species, by inadequate series of specimens, by the inability of most workers to study color pattern in living salticids and by the failure of attempts to rear the young and thus gain ontogenetic clues to relationships. Apparently only Bonnet (1933) has reared a salticid through all instars.

The present paper is based on plentiful material representing three new species of the salticid genus *Corythalia*, all studied at Rancho Grande in 1945 and 1946. Each was successfully bred in the laboratory, and all growth stages of both sexes were obtained except for one instar of one species. The report is confined to systematic descriptions of external characteristics of adults and young, accounts of normal display and general life history data. A subsequent paper will present an analysis of display, based both on normal display and on experimental work, and a discussion of evolutionary trends as suggested by development of color and structure, and by behavior. Also to follow is an account of culture and display-study methods.

During the first season at the Rancho Grande station, growth stages and displays of more than forty other species of salticids were also studied in more or less detail. The second year concentrated work was confined to half a dozen of these forms, including *Corythalia*, so that more complete life histories could be obtained and experimental work accomplished.

The three local species of *Corythalia* were among those chosen for special study for the following reasons: first, material of all three species was plentiful and thrived under laboratory conditions; this gave a unique opportunity for comparisons of development, behavior and species barriers in closely related forms. Second, *Corythalia* proved to be highly specialized in many characteristics, particularly in color development and display behavior, and so is an important group for

<sup>1</sup> Contribution No. 783, Department of Tropical Research, New York Zoological Society.



TEXT-FIG. 1. General location of the principal ecological zones near Rancho Grande. The *Corythalia* described in the present paper were taken only in the semi-evergreen and lower cloud forest slopes of the southern watershed. Although only the highest ridge of the coastal range is indicated, the entire region is mountainous except for the Lake Valencia plain.

the study of evolutionary trends, both inside the genus and in comparison with other salticids.

The drawings of *Corythalia* display and the frontal views of females (Text-figs. 12, 13, 14 (part), 15) were made from life by Mr. Kenneth Gosner at Rancho Grande; he also made the preliminary drawings for the growth stage patterns (Text-fig. 2). The final forms of Text-figs. 2 and 14 and the remaining drawings are the work of Miss Pamela Marmont.

The measurement and spine notation systems used are those proposed by Dr. Alexander Petrunkevitch, as outlined in his "Study of Amber Spiders" (1942, pp. 135-139). The standard abbreviations AME, ALE, PME and PLE are used throughout for the various eyes, antero-medial, antero-lateral,

postero-medial and postero-lateral, respectively. "Instar" and "stadium" are used interchangeably. Unless otherwise stated, averaged measurements are from five specimens of each sex or instar considered; length measurements and spine counts include all specimens.

I wish especially to thank Sr. Pedro Infante and Sr. Eduardo Echenagueio, laboratory assistants at Rancho Grande, for their invaluable help in collecting and tending the living salticids.

Deep appreciation goes to Dr. William Beebe and to Dr. Alexander Petrunkevitch for their constructive advice and encouragement.

The types are deposited in the collections of the Department of Tropical Research, New York Zoological Society, New York 60, N. Y.

## CHARACTERISTICS OF THE GENUS *CORYTHALIA* WITH SPECIAL REFER- ENCE TO THREE SPECIES.

### ADULT FORM AND POST-EMBRYOLOGICAL DE- VELOPMENT OF EXTERNAL CHARACTERISTICS.

More than fifty species have hitherto been referred to the American genus *Corythalia*, originally and in synonymy. Several species occur in the United States, but most have been taken in Central America and the West Indies. The few recorded South American forms, all known only from the original series, are the following: From Colombia, *C. dimidiata* Simon, 1901 (color note only), and *C. electa* (Peckham, 1900); from Trinidad (a biological part of South America, rather than of the West Indies), *C. blanda* and *C. placata* (both Peckham, 1900); from French Guiana *C. heliophanina* (Taczanowski, 1871); and from Brazil, *C. fimbriata* and *C. valida* (both Peckham, 1900). Simon, 1901, p. 655, indicated that he took the genus also in the Andes of Venezuela and Ecuador, but descriptions have apparently never been published. Without question, many more South American species remain to be taken and described; our own collections contain at least three more species, in addition to the three with which the present paper is concerned, from other parts of Venezuela and from British Guiana.

It seems equally certain that when adequate knowledge of the group is attained, some of the species in the genus will be reduced to geographical subspecies, or even merged in geographical lines. On the other hand, since the group is obviously subject to high speciation and a radiative type of evolution, it will always remain difficult to divide systematically. As in the family in general, certain characters are present in widely separated species, and absent in closely related ones, while others vary without sharp boundaries.

As is the case with so many salticid genera, the delimitation and understanding of *Corythalia* are complicated by six factors. First, the limits of the genus are apparently not sharply definable. Second, no general survey of the group has been undertaken, to include the extensive series of species now known from both Panama and the West Indies, as well as earlier material from Central and South America. Third, many of the species now referred to this genus are inadequately known, or have been described from a single sex. Fourth, the color and appearance in life have only rarely been recorded. Fifth, the display has not hitherto been described. Sixth, and finally, the post-embryological development has not been previously studied.

Although the present study makes no attempt to review the genus, the following survey of the three new species proposed in this paper should be of aid in a future review of the group. Comparison of these gen-

eral structural characteristics with those given by recent workers in the group, notably Chickering (1946) and Bryant (1942 ff.) show that they are also typical of many Panamanian and West Indian species of *Corythalia*. Some characteristics, in fact, often mentioned in specific descriptions, are shared by many other salticids; examples are the arrangements of facial bristles and trichobothriae. Nevertheless, the data in this paper are based only on the three species to be described, since the earlier authors do not give sufficient data in comparable form to permit complete comparison.

The present survey is given in order to eliminate repetition in the actual specific descriptions, which begin on p. 14, and to form a foundation for the eventual general survey. A résumé of the post-embryological development of each character is given under each.

Two of the proposed species, *chalcea* and *fulgipedia*, are closely related, while the third, *xanthopa*, apparently belongs to a different branch of the genus *Corythalia*. All are characteristic, not borderline, species. For these reasons, a detailed comparison of the three yields enlightening information in regard both to similarities and to directions of variation in the group.

Included in the preliminary discussion are descriptions of the general developmental, behavioristic and ecological characteristics of the three species. Discussion and comparison are reserved for final sections on an Analysis of Display and on Phylogeny, to be published later.

In brief, the three species fit into Chickering's diagnosis of the "*Phiale group*" (1946, p. 34) and of *Corythalia* as given (ibid., p. 112). The retromargin of the chelicera in all our species has a single small tooth (present or absent in other genus members); definite fringes present on the first three or all four legs (present or absent in other genus members); total eye space occupying about half length of carapace; PME slightly closer to PLE than to ALE; lateral sides of carapace nearly vertical and nearly parallel; anterior coxae further apart than width of base of lip; ventral spines on first tibia 1r-2-2, 0-1r-2 or 0-0-2, not, as is more usual in the previously described species, 2-2-2.

The various characters and their development will now be considered in detail.

**Color in Life: Adults.** Integument jet black except for light brown third and fourth, or all, tarsi. A few dark bristles on carapace, described below. Carapace with or without submarginal band and thoracic markings of white scales; ocular quadrangle with or without bronze scales; anterior eyes brownish-black, usually with deep green reflections, always rimmed with yellow or rusty scales; clypeus, chelicerae and palps with or without white or yellow scales and hairs. Palps and legs with plentiful black hairs; male leg fringes black, except for yellow fourth dorsal fringes in *xanthopa*; leg iridescence chiefly purple; white or yellowish

leg scales present in varying amounts in both sexes, better developed in female. Abdomen with transverse bars of black and yellow or white scales (represented subdermally by dark and pale integument) and a pair of terminal spots, all more or less overlaid in males with bronze or yellow scales, or, in female *xanthopa*, with two yellow stripes; dark hairs and bristles arising above scales. This general range of coloration is typical of previously described species in the genus, except that red, occasionally found on faces and abdomens, does not occur in these three species. Sexual dimorphism in color ranges from slight to extreme.

**Young.** Integument: Pigment absent in first instar, which is translucent with a faint greenish or yellow cast; late in this stadium the pale abdominal bands of the second are faintly visible, since the entire spiderling now has a gray tinge from the black cuticle developing subdermally; radiating lines appear on thoracic region. Second instar integument of carapace and abdomen jet black, except for the two pale abdominal bands, one in anterior third, the other behind middle, and a pair of terminal spots; by this stage, too, pigment may or may not be developing in bands on legs; the latter gain full pigment, except for feet, between fourth and sixth stadia, the palps a stage or two later.

**Scales:** Even in second instar, abdominal bands and spots are completely covered with white or yellow scales and intervening portions with black; these primary markings persist throughout at least preadult instar and along with black integument are the most characteristic features of the young compared with those of other genera. A few black scales appear on sides of carapace about the fourth instar, but are usually absent in adult. The most characteristic carapace markings are two spots of white or yellow scales behind PME and a similar pair, or a complete cross-bar, behind PLE; these markings, varying with the species, appear in second or third instar and are traceable at least until sixth; usually they are degenerating and overlaid with bronze scales by the fifth. A strong submarginal band of white scales, characteristic among these three only of *fulgipedia*, appears in third instar; never strong in the other species, it does not appear there until the sixth. AME first rimmed with orange or yellow in second instar, ALE in third or fourth. White scales of face, mouthparts and legs almost absent in *xanthopa*, the yellow frontal hairs of male appearing in rudimentary fashion in preadults of both sexes; white face and appendage scales of the other two species appear in early instars, and are best developed in adult or preadult females.

**Color in Alcohol:** Even after only a few months in 70% alcohol, the distinct color patterns of these spiders are more or less obliterated, and drying the specimens only partially restores them; bronze and gold become dull brown; silvery white scales fade

to gray or creamy; many of the most characteristic scale patches or bars are missing altogether, iridescence cannot be accurately described; finally different individuals fade and lose their scales to very different extents, and this effect of preservation, combined with the normal individual variation in size, structure and pattern, and with sexual dimorphism, would make classification of a few preserved specimens exceedingly difficult; the tendency would be to divide the group into more than the actual number of species. The most constant feature is the light-colored second abdominal band, which, since it is well-marked subdermally, is usually traceable in all three spiders. It cannot be emphasized too strongly that color descriptions should be made from large series of living, displaying specimens, with the details filled in from anaesthetized individuals, and both fresh and worn examples included.

#### **Carapace, General Aspect (Table I):**

**Adults.** Breadth  $7/10$  to  $3/4$  of carapace length in both sexes of all three species, the carapace being slightly longer in females than males and therefore relatively narrower; extra relative length of female carapace almost altogether in postocular region. Greatest width either at insertion of second legs (*fulgipedia* always, *chalcea*, sometimes), or at the slight bulge always present before PLE. Height a little greater or less than width, about one-half to three-fifths of length, least in *fulgipedia*, most in *xanthopa*; females slightly lower than males. Profile rises gently from AME to PLE; from here it either extends as a plateau or descends gently to a point midway between PLE and posterior border; posteriorly the descent is abrupt; postocular plateau best developed in *fulgipedia*; thoracic slope most abrupt in *chalcea*. A shallow transverse, median depression between posterior borders of PLE and a short, median, longitudinal thoracic groove beginning at bottom of depression and extending slightly beyond it. Length of ocular quadrangle about three-fifths to two-thirds of its breadth, and about two-fifths length of carapace; breadth of quadrangle relatively widest in *xanthopa*.

**Young (Text-figs. 3, 4).** Form of carapace changing abruptly from relatively higher and broader than adult in first stadium to much lower and flatter than final form in the second. The final general carapace proportions of the female are almost or quite attained by both sexes in fifth instar, the male keeping female height and breadth proportions until adult (7th) stadium. Text-fig. 3 shows that specific differences in carapace profile are apparent even in second instar, *fulgipedia* being lowest with a longer and flatter postocular plateau. Ocular quadrangle in first stages is wider across its anterior margin than in adult.

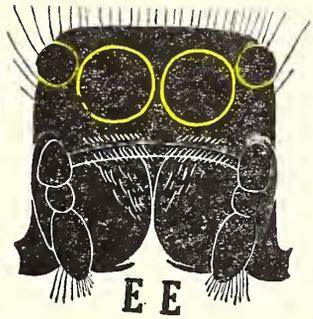
**Eyes (Table I):** **Adults.** Anterior row, viewed from the front, recurved so that a straight line from dorsal borders of AME cuts off one-fourth to one-third of ALE.



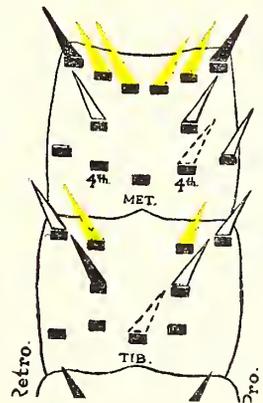
F



DD



EE



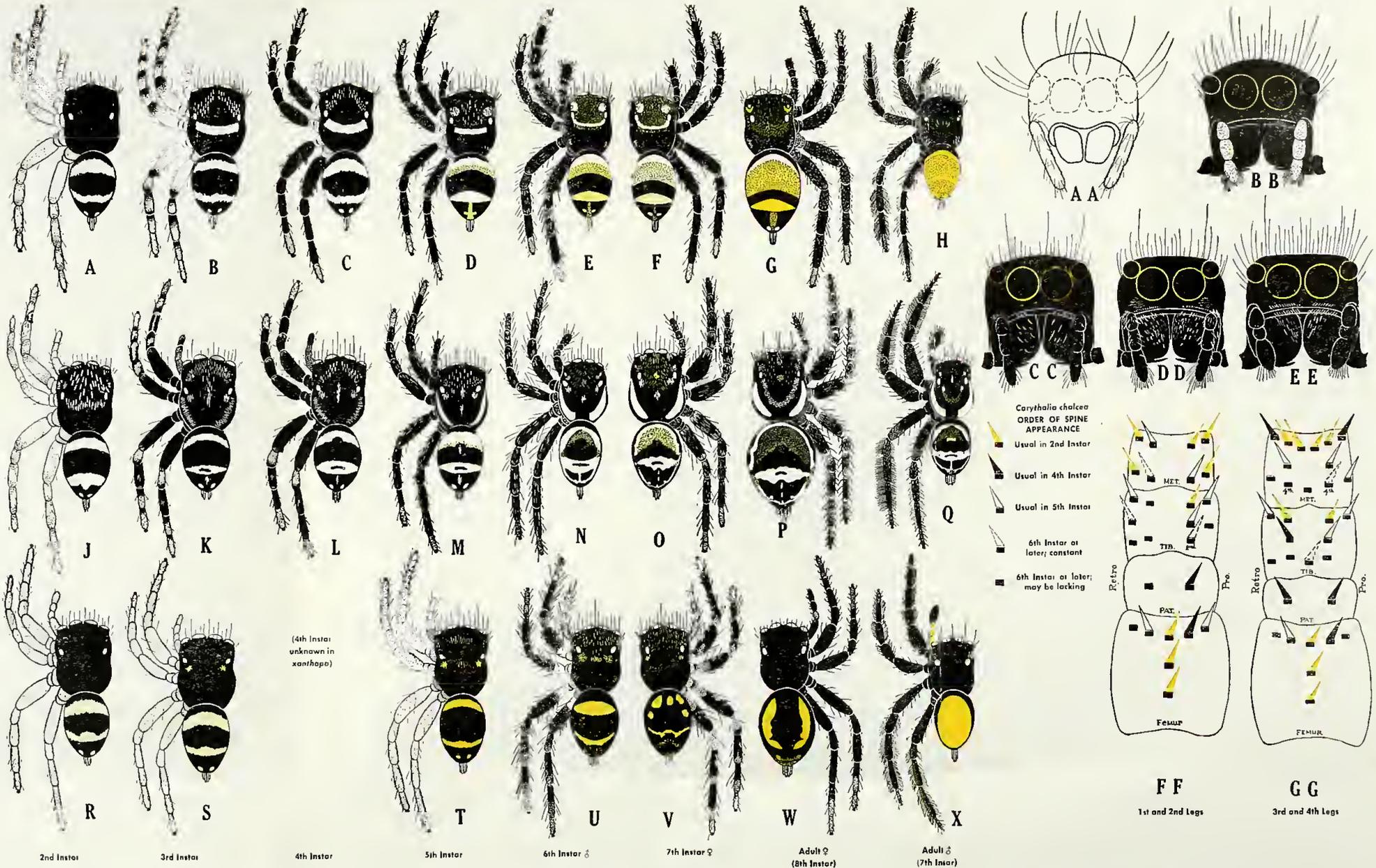


(1st instar in  
chalcona as  
below)



(1st instar in  
xanthopa as  
above)

1st instar



2nd instar

3rd instar

4th instar

5th instar

6th instar ♂

7th instar ♀

Adult ♀  
(8th instar)

Adult ♂  
(7th instar)

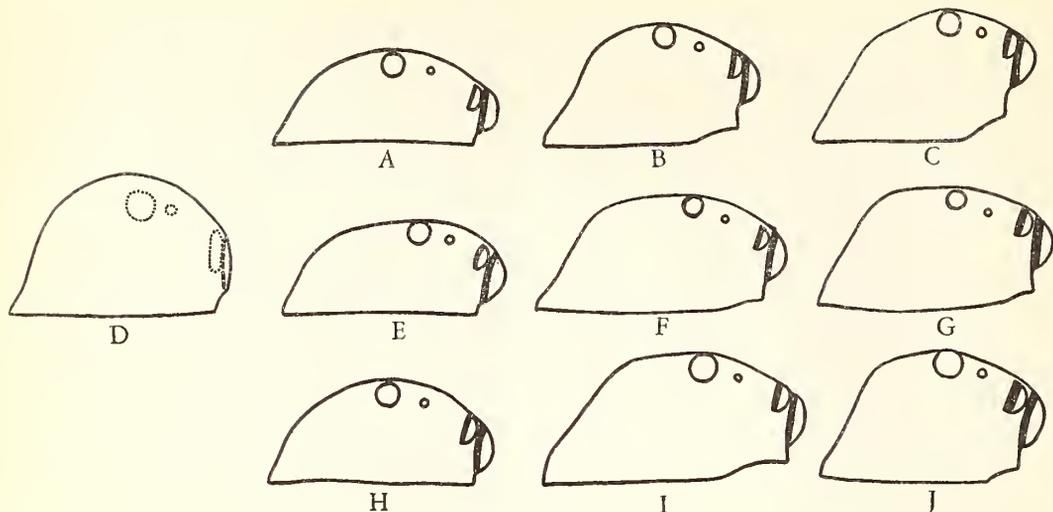
TEXT-FIG. 2. A-X: Growth stages in *Corythalia*, showing comparative development of color pattern and proportions in three species. Color in life is black and white except areas marked in yellow. Clear yellow indicates scales pigmented yellow; yellow stippled with black, or yellow on black, indicates bronze scales. See descriptions for exact colors and variations. Numbers and positions of hairs and bristles not exact; omitted entirely from abdomens. A-H, *Corythalia chalcona*; A, 2nd instar; B, 3rd instar; C, 4th instar;

D, 5th instar; E, 6th instar, ♂; F, 7th instar, ♀; G, 8th instar, adult ♀; H, 7th instar, adult ♂. I-Q, *C. fulvipedia*: I, 1st instar; J, 2nd instar; K, 3rd instar; L, 4th instar; M, 5th instar; N, 6th instar, ♂; O, 7th instar, ♀; P, 8th instar, adult ♀; Q, 7th instar, adult ♂. R-X, *C. xanthopa*: R, 2nd instar; S, 3rd instar; T, 5th instar; U, 6th instar, ♂; V, 7th instar, ♀; W, 8th instar, adult ♀; X, 7th instar, adult ♂. AA-EE, *C. chalcona*. Frontal views, showing development of pigment and scales. The

yellow indicates growth of marginal eye scales; in life the tint varies from pale yellow through orange to rust. AA, 1st instar; BB, 2nd instar; CC, 5th instar; DD, adult ♀; EE, adult ♂. See Text-fig. 6 for total number of primary bristles. FF, GG, *C. chalcona*. Diagrams of typical course of spine development. FF, 1st and 2nd legs; GG, 3rd and 4th legs. Figures under spines indicate their presence on only 2nd or 4th leg. See key at left of diagrams.







TEXT-FIG. 3. Change in carapace profile in *Corythalia*. **A-C, *chalcea***: **A**, 2nd instar; **B**, adult ♀; **C**, adult ♂. **D-G, *fulgipedia***: **D**, 1st instar; **E**, 2nd instar; **F**, adult ♀; **G**, adult ♂. **H-J, *xanthopa***: **H**, 2nd instar; **I**, adult ♀; **J**, adult ♂. Profile of 1st instar practically identical in all species. Adult females drawn to same scale as adult males, to show difference in relative size.

Slightly longer than width at base; basal excavations reaching about two-fifths of length; general shape nearly triangular from distal end of excavations; tip reaches three-fifths of distance to tip of maxillae. Sternal suture slightly procurved.

**Sternum** (Text-fig. 5): *Adults*. Broadly scutiform; width in males three-fourths to four-fifths, in females two-thirds to four-fifths of length; almost as wide or slightly wider at anterior border at base of lip; lateral margins with four excavations on each side well or scarcely developed; widest portion opposite posterior side of second legs; posterior end variable, truncated or bluntly rounded, not extending between fourth coxae, which are separated by about one-fifth to one-seventh of their width.

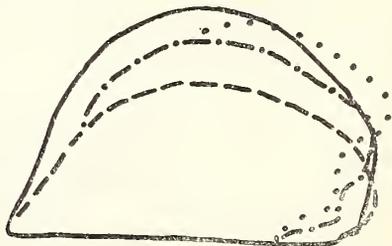
*Young*. Sternum in first instar almost as broad as long (92%); 77% in second instar; flatter in front and more pointed behind.

**Legs. General Proportions** (Tables I, VII): *Adults*. In all three species the third and fourth legs are almost equal and are longer than the first and second, which are also of similar length. They are only slightly longer in males than in females, their actual differences being slightly less than appear in Table I, since the male carapace is shorter than that of the female. In both sexes the third and fourth contrast with the first and second in having shorter patellae but longer metatarsi. Tibial index: first leg, males 23 to 27, females 24 to 33; fourth leg, males 17 to 21, females 18 to 27. Legs are relatively shortest and stoutest in *fulgipedia*.

*Young* (Table VII). Even in the first stadium the legs show these general proportions of the adult, the first two legs being

shorter than the last two; they are much more nearly equal, however, and they measure three-fourths of their adult length in respect to length of carapace. Their tibial index is greater: 27 to 32 (first leg) and 25 to 31 (fourth leg) in the first instar; 24 to 31 (first leg) and 22 to 27 (fourth leg) in the second. The divisions between patella and tibia, and between metatarsus and tarsus, are scarcely discernible in the first stadium, and feebly so in the second in all four legs and the palps. The feet and patellae are noticeably longer in the earliest stages, while the metatarsus elongates chiefly from the fifth instar onward.

**Iridescence**: In adult male only present prolaterally on patella, tibia and metatarsus in all three species in the same relative strengths, being strongest on tibia and metatarsus; it is present on at least the first three legs, in the following relative strengths: 3, 2, 1; in *xanthopa*, in which the fourth leg is also iridescent, the brilliance is equal to that of the third. A slight flattening of the iridescent surfaces is apparent in



TEXT-FIG. 4. Superimpositions of carapace profiles in *C. chalcea*. Solid line, 1st instar; dash line, 2nd instar; dash-dot line, adult ♀; dotted line, adult ♂.

all three species, though to different extents, the greatest flattening being evident on the species and segments showing the highest iridescence. On the patella this flattening is always on the upper prolateral distal surfaces; on the tibia and metatarsus it occurs on the upper half. On the most highly iridescent surfaces hairs are usually scant or absent. In live specimens iridescence is absent on the femora and on all retrolateral surfaces, although in these areas white scales and hairs are often well developed. In preserved specimens, however, a false, slight iridescence is sometimes apparent on anterior tip of femur and on posterior surfaces, while the true areas of iridescent planes are of much reduced brilliance.

#### Special Integumentary Structures.

**Fringes:** In adult males only. At least first three legs conspicuously fringed; *xanthopa* has the fourth legs also strongly fringed. Except in the latter species, in which the fourth fringe is best developed, the fringes occur in the following order of strength on the different legs, from greatest to least: 3-2-1-4. Dorsal and ventral fringes occur on the femur (rudimentary), patella, tibia and metatarsus. Except in the fourth leg fringe of *xanthopa*, in which the dorsal fringe is yellow and longer than the ventral fringe, all fringes are black, and the dorsal fringe is shorter than the ventral. The ventral fringes of femur and patella tend to be each in two distinct rows, prolateral and retrolateral; the remainder, however, are either median, or tend to cover evenly the entire ventral surface. A slight concentration of hairs occurring in preadults of both sexes and in adult females, on lower margins of leg segments, seems to be an adumbration of fringes.

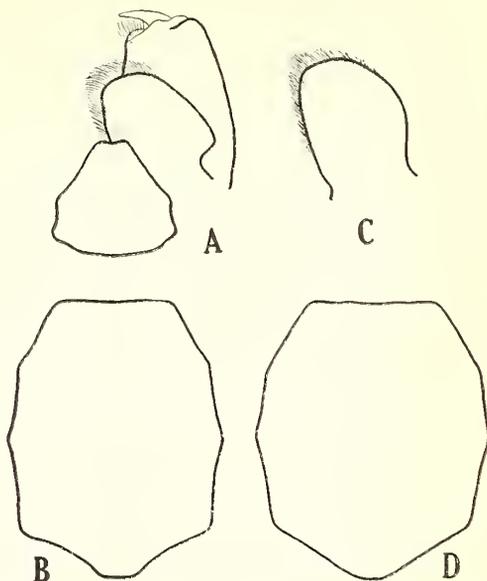
**Spines:** As will be seen from Table II, the following spines are constant in both sexes of all three species:

All legs: femur, dorsal 0-1-1-1; prolateral, upper distal 1; patella, prolateral 1; tibia, ventral distal 2; metatarsus, prolateral and retrolateral, proximal or near-proximal 1, upper distal 1; ventral proximal at least 1p, almost always 1r in addition; ventral distal 2.

First and second legs; tibia, prolateral proximal or near proximal 1, distal 1.

Third and fourth legs: patella, retrolateral 1; metatarsus, prolateral and retrolateral, lower distal 1.

It will be seen also from the Table that some spines, notably in the third and fourth legs, are constant except for rare females, these specimens sometimes having only a single side in one example of one species deficient. Included in this group are the tibial dorsals and the tibial median and distal pro- and retrolaterals. In spite of their rarity, these variables, like the more common ones, apparently indicate a lack of genetic stability in the spine in question, which always is



TEXT-FIG. 5. A, *C. chalcea*, adult ♂; labium, maxilla and chelicera, ventral view; B, same, sternum drawn to same scale; C, *C. chalcea*, adult ♀; maxilla; D, *C. xanthopa*, adult ♂; sternum, at greater magnification, for comparison with *chalcea*.

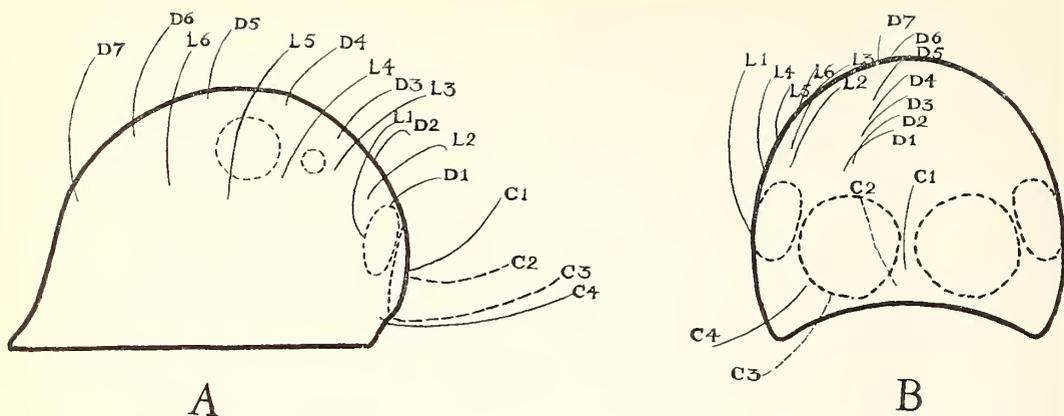
among those appearing late in ontogeny; the constant spines, on the other hand, invariably appear in early instars (see p. 18 and Text-fig. 2, FF, GG).

Constant differences are lacking between adults of both sexes of *chalcea* and *fulgipedia*; *xanthopa* invariably has a few spines fewer than the others.

There are no constant sexual differences within any of the three species, although in each females tend to have fewer spines than males, and their variability is greater.

In regard to exact position of insertion, there is considerable irregularity and variation, especially on the tibia. The dorsal spines on both tibia and metatarsus, and the unpaired tibial ventral proximal, may be inserted either before or behind the midline, although they usually occur behind it. Relative lengths are shown in Text-fig. 7.

**Development of Spines.** The course of development of the leg spines is similar in all three species, the same spines appearing earliest. On p. 18 and in Text-figs. 2 (FF, GG) and 7, is given a survey of the spine development in *chalcea*. Specific differences, aside from the differences in the adults noted in Table II, are confined to earlier or later appearances of some of the spines occurring first in the third, fourth and fifth instars. Compared with *chalcea*, the spines of *fulgipedia* tend to occur one or two stages earlier, and in *xanthopa* one stage later. The second instar is identical in *fulgipedia* and *chalcea*, while *xanthopa* differs from both only in having neither tibial spines nor first and second metatarsal ventral distals, which all ap-



TEXT-FIG. 6. Arrangement of carapace bristles in 1st instar of *Corythalia*. **A**, lateral view; **B**, anterior view. **C1-C4**: clypeal series (C2 and C3, indicated by broken lines, do not appear until 2nd or 3rd instar). **D1-D7**: dorsal series. **L1-L6**: lateral series.

pear instead in the third instar. In *xanthopa* the lag continues in the tibial and metatarsal ventral spines even into the sixth instar. It is this species which tends also to have fewer spines in the adult.

In all species, no spines appear before the second instar, although the femoral dorsals are represented by long hairs in the first. Often, later appearing spines appear to be represented by hairs in a preceding instar, but are never counted as such when in this rudimentary form; these hairs have no trace of the dark chitinous bases which characterize true spines and which, combined with great stiffness, usually obviate indecision as to whether a structure should be counted as a spine. No spines are ever found in any stage of the young which do not appear in at least one sex of the adult, this sex practically always being the male.

By the fifth instar, at least in *chalcea* and *fulgipedia*, all the constant spines found in both adult sexes may be present. No spine developed in or before this instar in any species is inconstant.

In general, the spines in a given series develop from the distal to the proximal end of a segment. (Exceptions are the highly variable first and second tibial retrolaterals). The fourth and third legs not only have more spines than the other two, but tend to develop their late-appearing variables slightly earlier. Among individuals, the retrolateral side of a third or fourth tibia often develops a late-appearing spine before the corresponding proteral; however, the general tendency is for development to be from proteral to retrolateral surfaces.

In general, the latest appearing spines, which are also the most variable, are the lower distal lateral femorals and the proximal spines of tibiae and metatarsi.

**Bristles** (Text-figs. 6, 7): The long stout bristles present on the clypeus and other parts of the carapace are probably homologous with those of the legs, and will be treated, for convenience, along with them.

These bristles, as a group, are of general occurrence in similar though not identical positions in a great many (if not all), salticids, in both sexes, and occur in early instars. I have been unable to detect specific differences in the three species of *Corythalia* under discussion, except that dorsal carapace bristles are more numerous in *fulgipedia* than in the other two species. Individual variation on the ocular quadrangle and thorax is considerable. The bristles are easily broken at the tip, or altogether lost, but their location can usually be detected from pits in the chitin.

**Carapace bristles: Adults.** On the clypeus are three long median bristles, arranged in a triangular formation, of which the upper apical one is longest, and may measure up to two and one-half times the diameter of the AME; two pairs are inserted below the AME, one below their middle and the other external to these (Text-fig. 6B). Bristles in moderate numbers occur above all anterior eyes and between and below the dorsal eyes; there are a few on the ocular quadrangle itself and behind the PLE on the antero-dorsal part of the thorax.

**Young.** Excluding those on clypeus, 13 pairs of carapace bristles are present in first instar and are traceable in some individuals of each stadium including adult. The frequent absence of particular bristles probably always is the result of accident. Later appearing bristles cannot be traced so successfully and are probably variable, as is the case with late-appearing spines; they will be disregarded here. Text-figure 6 shows the positions of the primary bristles. They divide themselves naturally into a dorsal series of seven pairs close to the midline, and a lateral series of six pairs arising near eyes. Three clypeus bristles are always present in first instar, the unpaired median (C1) and the outermost pair (C4); in second instar at least the C3 pair appears, and sometimes the median pair (C2) in addition; the full series of seven is always complete by third

TABLE II.  
Comparative Spine Numbers in *Corythalia*.  
Key: **Bold face**: constant.  
Roman: frequent.  
*Italics*: rare.  
Figures in parentheses: alternates.

		First Leg		Second Leg		Third Leg		Fourth Leg	
		♂	♀	♂	♀	♂	♀	♂	♀
FEMUR	Dorsal	<i>chalcea</i>	<b>0-1-1-1</b>	→	→	→	→	→	→
		<i>fulgipedia</i>	<b>0-1-1-1</b>	→	→	→	→	→	→
		<i>xanthopa</i>	<b>0-1-1-1</b>	→	→	→	→	→	→
	Prolateral (distal only)	<i>chalcea</i>	<b>2</b>	→	→	→	→	→	2(1)
		<i>fulgipedia</i>	<b>2</b>	→	→	→	→	→	2(1)
		<i>xanthopa</i>	<b>1</b>	→	→	→	→	→	1(2)
	Retrolateral (distal only)	<i>chalcea</i>	<b>1(2)</b>	<b>1</b>	2(1)	<b>1</b>	2(1)	→	<b>1</b>
		<i>fulgipedia</i>	<b>1(2)</b>	→	<b>2</b>	2(1)	<b>2</b>	2(1)	<b>2</b>
		<i>xanthopa</i>	<b>0</b>	→	0(1)	→	1(0)	→	0(1)
PATELLA	Prolateral	<i>chalcea</i>	<b>1</b>	→	→	→	→	→	→
		<i>fulgipedia</i>	<b>1</b>	→	→	→	→	→	→
		<i>xanthopa</i>	<b>1</b>	→	→	→	→	→	→
	Retrolateral	<i>chalcea</i>	<b>0</b>	→	1(0)	<b>0</b>	<b>1</b>	→	→
		<i>fulgipedia</i>	<b>0</b>	→	→	→	<b>1</b>	→	→
		<i>xanthopa</i>	<b>0</b>	→	→	→	<b>1</b>	→	→
TIBIA	Dorsal (proximal only; pro or retro)	<i>chalcea</i>	<b>0</b>	→	→	→	<b>1</b>	→	→
		<i>fulgipedia</i>	<b>0</b>	→	→	→	<b>1</b>	→	→
		<i>xanthopa</i>	<b>0</b>	→	→	→	<b>1</b>	→	→
	Prolateral	<i>chalcea</i>	<b>1-1</b>	→	<b>1-1-1</b>	→	→	→	1(0)-1-1
		<i>fulgipedia</i>	<b>1-1*</b>	→	<b>1-1-1</b>	→	→	→	1(0)-1-1(0)
		<i>xanthopa</i>	<b>1-1</b>	→	<b>1-1(1-1-1)</b>	→	0(1)-1-1	→	1-1-1
	Retrolateral	<i>chalcea</i>	1(0)-0(1)	<b>0-0</b>	1(0)-1(0)	→	<b>1-1-1</b>	<b>1(0)-1-1</b>	<b>1-1-1</b>
		<i>fulgipedia</i>	1(0)-0(1)	0(1)-0	1(0)-0	0(1)-0	<b>1-1-1</b>	<b>1(0)-1-1</b>	<b>1-1-1</b>
		<i>xanthopa</i>	<b>0-0</b>	→	<b>0-1</b>	<b>0-1(0)</b>	0(1)-1-1	→	→
	Ventral	<i>chalcea</i>	<b>1r-2-2</b>	<b>1r(0)-2-2</b>	<b>1r-2-2</b>	<b>1r-2(1r)-2</b>	<b>1-0-2</b>	→	1(0)-0-2
		<i>fulgipedia</i>	<b>1r-2-2†</b>	<b>1r-2(1r)-2</b>	<b>1r-2-2</b>	<b>1r-1r-2</b>	<b>1-0-2</b>	→	→
		<i>xanthopa</i>	<b>0-0(1r)-2</b>	<b>0-0-2</b>	<b>0-1r-2</b>	→	<b>1-0-2</b>	→	1(0)-0-2
METATARSUS	Dorsal (proximal only; pro or retro)	<i>chalcea</i>	<b>0</b>	→	→	→	<b>1</b>	→	0(1)
		<i>fulgipedia</i>	<b>0</b>	→	→	→	<b>1</b>	→	1(0)
		<i>xanthopa</i>	<b>0</b>	→	→	→	<b>1</b>	→	→
	Prolateral	<i>chalcea</i>	<b>1-1</b>	→	→	→	<b>1-2</b>	→	<b>1-1-2</b>
		<i>fulgipedia</i>	<b>1-1</b>	→	→	→	<b>1-2</b>	→	<b>1-1-2</b>
		<i>xanthopa</i>	<b>1-1</b>	→	→	→	<b>1-2</b>	→	<b>1-1-2</b>
	Retrolateral	<i>chalcea</i>	<b>1-1</b>	→	→	→	<b>1-2</b>	→	<b>1-1-2</b>
		<i>fulgipedia</i>	<b>1-1</b>	→	→	→	<b>1-2</b>	→	<b>1-1-2</b>
		<i>xanthopa</i>	<b>0-1</b>	→	0(1)-1	→	<b>1-2</b>	→	<b>1-1-2</b>
	Ventral	<i>chalcea</i>	<b>2-2</b>	→	→	→	→	→	2(1p)-2
		<i>fulgipedia</i>	<b>2-2</b>	→	→	→	→	→	→
		<i>xanthopa</i>	<b>2-2</b>	→	→	→	→	→	→

\*-1 side of 1 specimen: 1-1-1

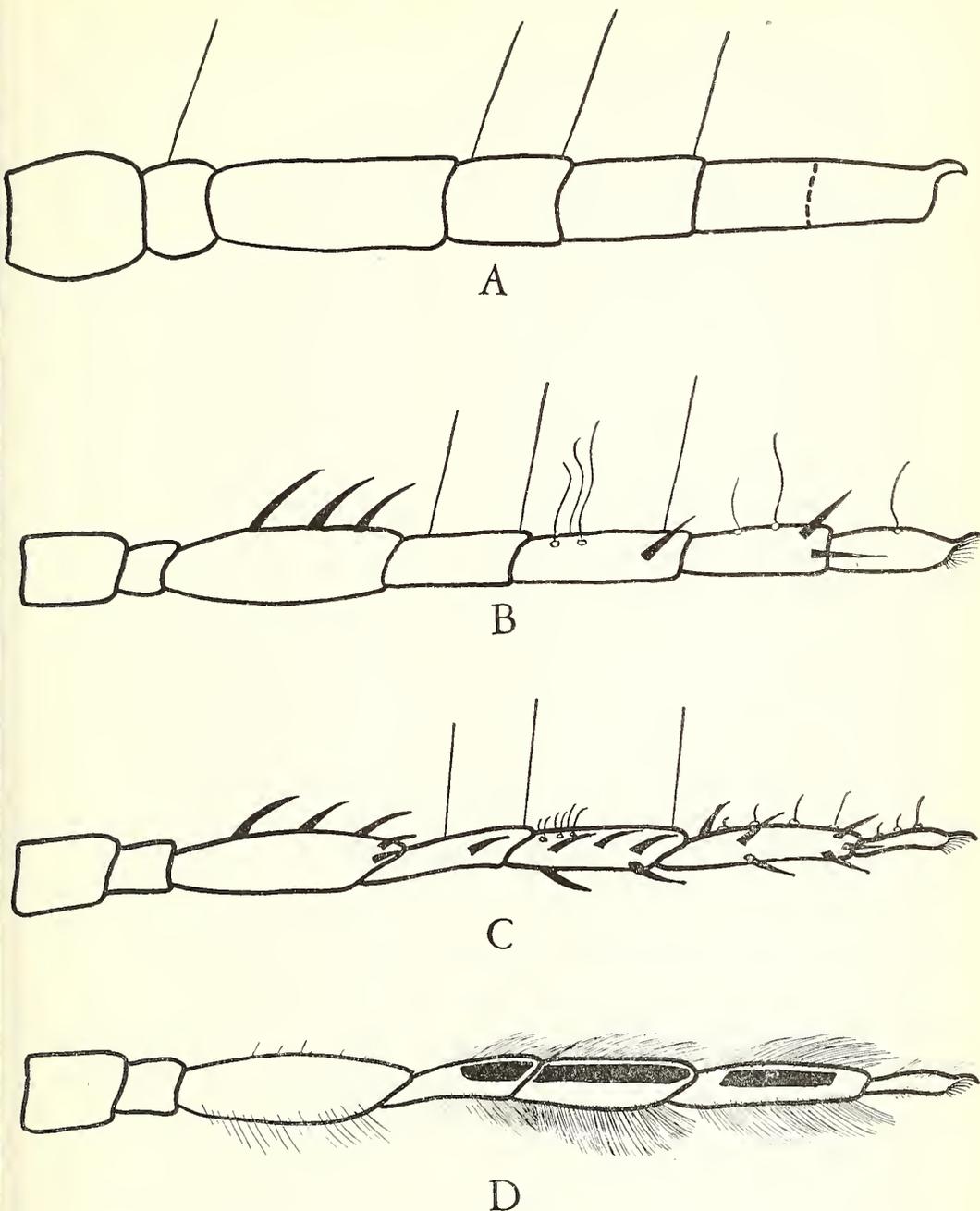
†-1 side of 1 specimen: 2-2-2

‡-1 side of 1 specimen: 0-0-0

§-1 side of 1 specimen: 0

||-1 side of 1 specimen: 1-0-1





TEXT-FIG. 7. Third leg in *C. chalcea*, showing segment proportions, development of primary bristles, spines, trichobothria and fringes. **A**, 1st instar; **B**, 2nd instar; **C**, adult ♂; **D**, same, to show fringes and iridescent areas (in black). Bristles represented by long, straight lines, spines by black triangles, trichobothria by curving lines with circular bases. Structures all drawn relative to total length of leg. Secondary bristles, short pale bristles and general hair covering omitted.

instar. In general the carapace bristles do not change much in relative lengths during development; an exception is the C1 median bristle, which is much shorter than C4 in first instar, but thereafter becomes far longer than all others in the series. Short bristles, very rudimentary and pale, appear on superior edges of chelicerae in fourth instar, 5 to

7 are countable in fifth, and more, now stiff and black, are present in adults.

**Leg Bristles (Long): Adults and Young** (Text-fig. 7). A few of the fairly numerous leg bristles stand out in all instars, beginning with first, and are traceable right through to adults of both sexes. These are located at proximal and distal ends of patella and distal

end of tibia on the palp and all legs. Their frequent absence is obviously due principally to damage; it seems, however, that they may sometimes be naturally lacking, in irregular fashion in various individuals, and varying on the two sides of the same specimen. Of the three bristles, the distal patellar is longest, measuring two or three times width of segment, and the proximal patellar shortest. In addition to these three longest and most constant bristles, a proximal tibial is of frequent and early occurrence on palp, and a more or less paired couple near end of metatarsus on palps and legs; additional tibial bristles also are often conspicuous, but do not appear so early in ontogeny, and are not constant. A trochanter bristle is usually present in first instar only.

**Leg Bristles (Short, Pale):** *Adults and Young.* A different type of bristle altogether occurs, apparently constantly, in adults and young on legs only. They are short, always shorter than trichobothria, and stand out in a fashion which makes them at first glance easily confused with short examples of the latter. They are, however, perfectly distinct, lacking altogether the characteristic bases of trichobothria, never bending at the tip, and occurring not only dorsally but also on sides and ventral surfaces of at least tibiae, metatarsi and tarsi. I have not studied these in detail, except to settle the following points: first appearance in second instar; location apparently fixed, occurring quite regularly in single rows. Especially constant and conspicuous are the following: several median dorsals appearing toward distal ends of tibia and tarsus; at least one on patella; pro-lateral, retrolateral and ventral series on metatarsus and tarsus, consisting of two or three in each series; fewer of latter series on tibia. These bristles occur in very similar fashion on a number of unrelated salticids.

**Trichobothria** (Text-fig. 7): *Adults.* Number and arrangement constant throughout the species under discussion, and apparently typical of a great many salticids which I have examined superficially. In *Corythalia* there are two rows of three (rarely four) on the proximal dorsal half of tibia; a single row of four on metatarsus, well distributed along the crest and increasing in length distally; and a single row of three (rarely four) on proximal half of tarsus, also increasing in length distally. On some legs the pro- or retro-dorsal row on tibia is crowded toward proximal end, but I have not been able to find any specific sexual or special leg distinctions in this arrangement. Naturally, some of each series are frequently missing, but apparently practically always because of injury.

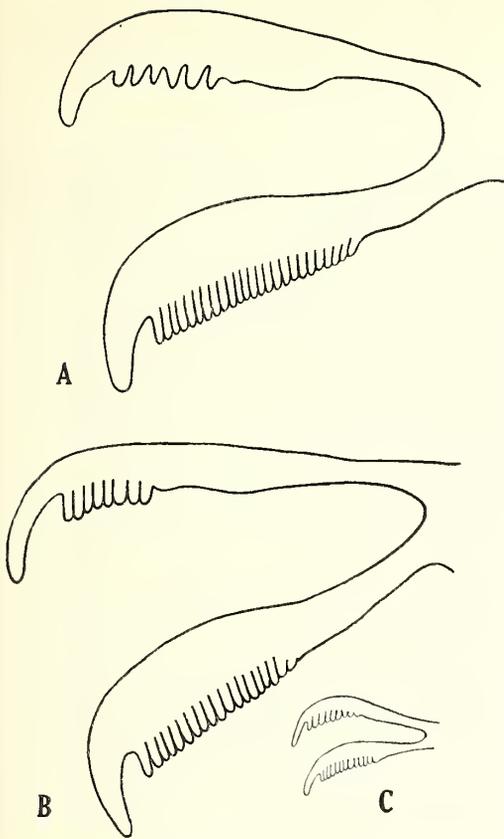
*Young.* Use of the highest power magnification fails to disclose any trichobothria in first instar. In second stadium, one to three in each series usually present, not in any standard order of precedence, even on corresponding legs of same specimen. The distal

metatarsal trichobothrium appears of very constant development in second instar, and is then relatively very long, measuring more than twice width of segment. Tarsal series usually complete by fifth instar, while metatarsal and tibial series lack only one or two trichobothria. In this stage, also, the absences are not constant for particular trichobothria. As late as seventh female instar (preadult), single trichobothria, especially on metatarsus, may be missing on one or more legs.

**Tarsal Claws** (Text-fig. 8; Table III): *Adults.* General type similar on all legs, although first and second differ slightly from third, and particularly from fourth. Proclaw teeth ranging from 13 to 26; very slender, extremely close-set and fine; tips only resolvable (except, sometimes, for one to three distal teeth) except under high power magnification, and then only by transmitted light. Teeth longest and most slender distally; decreasing in size and becoming broader toward proximal end, sometimes abruptly, sometimes in a beautifully graduated series.

Retroclaw teeth 4 to 9, the most proximal one or two being almost always broad, low, often truncate vestiges. All retroteeth shorter, broader and more widely set than pro-teeth, but closer set on fourth leg than on other three, approaching the finely pectinate arrangement of the proclaws, especially in *chalcea* and *xanthopa*. In numbers, proclaw teeth are more numerous on the first and second legs than on third and fourth, while there are one to several more retroclaw teeth on third and fourth legs than on first and second. Individual variation ranging up to about 5 teeth in longest proclaw series, but being only 1 or 2 in a short, retroclaw series. It is not unusual for corresponding claws on different sides of same specimen to vary. Adult males tend to have one or two more teeth on proclaws and one or two fewer on retroclaws, especially on front legs, than adult females. This is not, however, a rigid distinction.

*Young.* Teeth absent, as usual, on claws of first instar (within the cocoon). I am unable to detect a trace of a third claw at this stage, and unguis tufts are undeveloped. Tufts present in second instar though hairs are sparse, and from here on their increase is gradual. In second instar claw teeth also appear, and are of general adult form, being dissimilar, with proclaw teeth finer and more numerous than those of retroclaw, although they are not quite so closely set for their size as in adult. Also, the two claws of each foot are much more nearly alike than in adult, the number of teeth being intermediate to the final form; there are many fewer pro-teeth and usually one or more extra retro-teeth. (Sometimes, however, the number of retro-teeth on posterior legs remains constant). This means that during development pro-teeth increase while retro-teeth decrease. Another interesting point is that in the second instar the retro-teeth of all four legs,



TEXT-FIG. 8. Tarsal claws in *C. chalcea*. **A**, first leg, adult ♂; **B**, fourth leg, adult ♀; **C**, fourth leg, 2nd instar. In each case, the proseries contains the greater number of teeth.

instead of only the fourth leg, are finer and more closely set than in adults, approaching proteeth type. There is only a small increase in proteeth in adults, and no decrease in retreteeth through fifth instar. After that the increases and decreases, respectively, proceed gradually.

In all cases, increase or decrease occurs in the proximal end of a series, the anlagen or vestiges being broad and stumpy. The claw tips are more slender and entire claw more curved in young than in adults, though in *xanthopa* the juvenile shape is maintained and the teeth remain relatively similar, slender and close-set throughout, while the proseries of first and second legs do not attain the high numbers of the other two series.

**Unspecialized Hairs; Scales:** Hairs, apparently unspecialized, are present on all parts of the body in moderate numbers, especially on legs and abdomen. A few leg and abdomen hairs are present even in the first instar, and as in all integumentary structures, are relatively longer than in later stadia. *C. fulgipedia* is the hairiest of the three species. Scales and scale-hairs, because of their special connection with color pattern, are discussed under the heading of Color.

**Palp:** *Adult Male* (Text-fig. 9). Compared with its specific importance in other groups, the *Corythalia* palp is a relatively poor taxonomic character. It tends to great similarity among the three species under consideration, which have the following characteristics: tibia about two-thirds as long as patella, viewed dorsally; tarsus about one-third longer than patella; retrolateral tibial apophysis long or of moderate length, slender or stout, pointed or truncate, serrated or plain. A midventral tibial tubercle. Tarsal bulb overlapping tibia moderately at base; one median loop directed internally and two directed externally are distinguishable, the more proximal external loop being usually only partly visible; the exact proportions and amount of distinctness of the loops are decidedly variable in individuals of the same species. Embolus making about one full turn of spiral, this portion occupying distal one-quarter to two-fifths of bulb; distal part of embolus short or moderate, tip forked or simple. The palp of *fulgipedia* is decidedly more robust (as is the entire spider) than those of the other two species.

*Young.* The male palp is indistinguishable externally from that of the female until the sixth (preadult) instar. In the early stadia the tibia is equal to or longer than the patella, just as in females. In both sexes, unlike the legs, the palp is relatively longer in the first stages; as in the legs, the segments are more nearly equal.

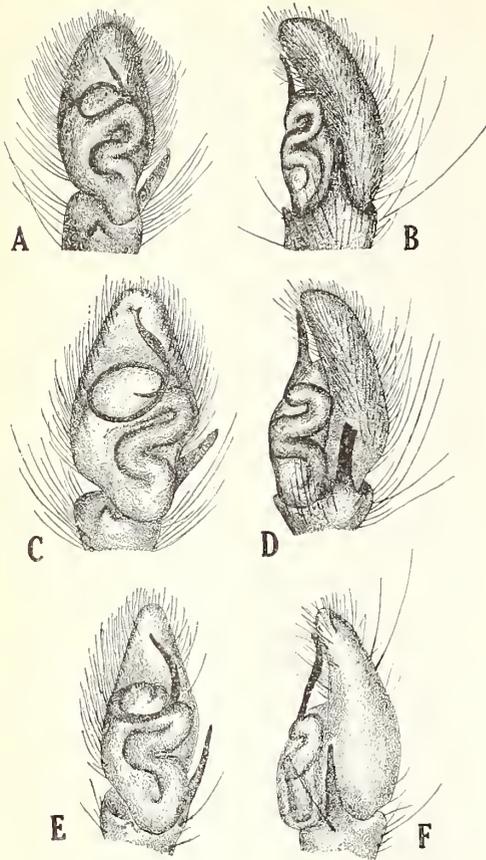
**Epigynum** (Text-fig. 10). Of similar structure in all three species; specific differences lie chiefly in the size of the organ, since the latter is not proportional to the size of the species, and in the relative size and position of the anterior and posterior pairs of subdermal bodies, light and dark brown, respectively. Dissection shows the anterior bodies to consist of a pair of looped ducts, with the openings external and in advance of the genital slit, near the midline; presumably the spermatozoa are inserted here. A bulge

TABLE III.

Tarsal Claws in *Corythalia*\*

	First Leg			Fourth Leg		
	2nd Instar	Adult ♀	Adult ♂	2nd Instar	Adult ♀	Adult ♂
<i>chalcea</i>	p. 13; r. 10	p. 21; r. 7	p. 26; r. 6	p. 13; r. 9	p. 18; r. 8	p. 19; r. 7
<i>fulgipedia</i>	p. 14; r. 8	p. 24; r. 5	p. 24; r. 6	p. 10; r. 9	p. 18; r. 7	p. 18; r. 7
<i>xanthopa</i>	p. 11; r. 7	p. 13; r. 4	p. 17; r. 4	p. 8; r. 6	p. 13; r. 6	p. 15; r. 6

\* From characteristic specimens.



TEXT-FIG. 9. Left palp of adult ♂ in *Corythalia*, ventral and ectal views. A, B, *C. chalcea*; C, D, *C. fulgipedia*; E, F, *C. xanthopa*.

in each duct appears to be a small gland opening into it. The ducts curve to the mid-line, whence they proceed, parallel and contiguous, into the pair of posterior spermathecae, which form the second pair of dark bodies visible externally. The passages to the vagina are a pair of small tubules opening from the anterodorsal section of the spermathecae, near the mid-line. A pair of more or less distinct, smooth, bean-shaped, translucent areas cover most of this tubule-spermatheca system.

In actual size, the epigynum of *chalcea*, one of the larger forms, is slightly smaller than that of *xanthopa*, the smallest species.

*Young.* No trace of the epigynum is visible, at least externally, before the sixth instar (pre-preadult). Then the spermathecae are barely discernible as a pair of minute dark spots just in front of the genital furrow. By the seventh stadium, the spots are clearly distinct.

**Abdomen: Adults and Young.** Ovoid, widest near middle but of exceedingly variable proportions in individuals of both sexes. Anal tubercle a short flattened cone. Spinnerets all of moderate width; anterior pair stoutest, middle pair longest, posterior pair shortest and slimmest. Colulus indistinguish-

able, apparently represented by a few stiff hairs; tracheal spiracle opening near base of spinnerets. Segmentation discernible posteriorly during first instar.

#### SIZE AND GROWTH.

The total length range in adults is from 3.46 to 7.2 mm., that of carapace length 2.05 to 3.83. Sexual dimorphism in size is slight, the carapace length of the largest males in each species exceeding that of the smallest females, while even the total length of some recently molted females (before the eggs have enlarged) may be less than that of males. *C. chalcea* and *fulgipedia* are of almost equal size, although *fulgipedia* is bulkier, being more robustly built, particularly in legs and palps, and is hairier. *C. xanthopa* is a smaller species.

All species have one more instar in the female than in the male; at least in *chalcea* and *fulgipedia* the male has seven instars, including the adult, the female eight. Individuals of both sexes of each of these were reared from the egg. In *xanthopa* the fourth instar, if it exists, is unknown, reared specimens having died in the third instar, a younger stadium than that of the youngest captured field specimens. The smaller size of *xanthopa* makes it possible that there are only 6 male and 7 female instars in this species, although the gap is considerable (Text-fig. 11). However, for convenience in comparison of text-figures and descriptions, this stadium is considered to exist.

Table IV gives average carapace lengths at various stadia. As usual (cf. Bonnet, 1930, p. 469) the length increases are slight in the early instars; during the first, total length actually decreases owing to the absorption of yolk. In both sexes of all species there was found to be great individual variation in the amount of carapace length increase in individuals between the last two instars. As a single example, one male *C. xanthopa* reached 90% of his final carapace length in the preadult instar, while another attained 82%. These variations must be kept in mind in a consideration of Text-fig. 11, p. 20.

TABLE IV.

Comparison of Average Carapace Length in *Corythalia* (mm.).

Instar	<i>chalcea</i>	<i>fulgipedia</i>	<i>xanthopa</i>
1st	.93	.91	.83
2nd	1.2	1.1	1.0
3rd	1.4	1.3	1.1
4th	1.6	1.6	—
5th	2.0	2.1	1.5
6th ♀	2.4	2.4	1.9
6th ♂	2.7	2.6	2.1
7th ♀	2.8	3.0	2.1
Adult ♂	3.1	3.2	2.4
Adult ♀	3.4	3.6	2.6

The durations of the instars proved variable, even when members of the same brood were reared under identical conditions. In the Rancho Grande laboratory, at a mean

temperature of about 70° F., individual instars ranged from about 12 days to more than 8 weeks. In general, the earlier instars lasted around two or three weeks, the later ones around four or more. The longest and the most variable were the preadult stadia. A group of *fulgipedia* carried by ship to New York in the egg stage had all the instar lengths greatly prolonged, although they were never exposed to cooler temperatures than those of the Rancho Grande laboratory, and the average and extreme temperatures of the Zoological Park laboratory were higher. The time required for reaching the adult stage is around five or six months, the males requiring several weeks less than the females. One female *fulgipedia*, reared from the egg, lived to an age of 11½ months, and a male to 11 months. No variations in numbers of instars were found in any species, save in one abnormal *C. chalcona* (p. 16).

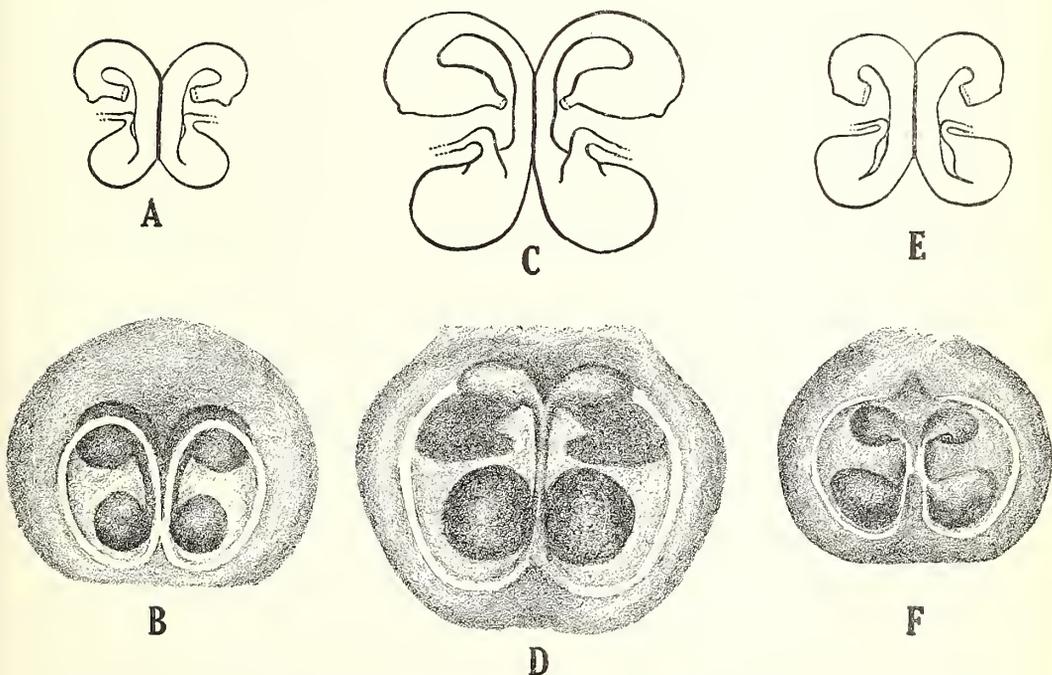
#### BEHAVIOR.

The general habits of all three species of *Corythalia* are exceedingly similar, both to each other and to the general pattern of salticid behavior. All are diurnal spiders which leap on their prey, eat it at once, pass the night in silk shelters, perform special courtship displays as a necessary preliminary to mating, copulate with the male in the dorsal position and guard the eggs in a cocoon spun between the folded edges of leaves.

The first instar is passed within the co-

coon; the spiderling neither eats nor spins, moves about with difficulty, and is helpless when removed from the nest. From the second instar onwards, however, the young engage in all salticid activities except those connected with breeding. From two days to a week or more is passed in the silk shelter before molting; during this time no food is taken; the spider emerges from one to three days or more after molting. Retirement lasts longest during the molt to the adult. In the laboratory the same shelter is used for successive molts and for passing the night, as long as it is not disturbed; the young spider simply enlarges it as needed, sometimes casting out the exuviae, sometimes incorporating them into the cocoon. Brooding females eat and move about very little. When disturbed they knit up a torn cocoon promptly; one female which escaped and was returned to her jar after three days, readopted the cocoon at once. Three clutches of eggs are usually laid, beginning about 8 or 9 weeks after the molt, the first being the largest and containing between 13 and 28 eggs. After mating, the female loses most or all of her attraction for males within less than 24 hours, and in any case will not accept another male. The latter apparently fill their palps in their shelters (I have never seen a sperm web in this group) and will mate with a series of females from two to three days after molting until at least six weeks after that time. After that their display energy diminishes rapidly.

None of the above activities differs re-



TEXT-FIG. 10. Epigyna in *Corythalia*, all drawn to same scale. Upper row, dorsal (internal) views of dissections; lower row, ventral (external) views. A, B, *C. chalcona*; C, D, *C. fulgipedia*; E, F, *C. xanthopa*. Note that dissected epigynum is smallest in *C. chalcona*, although that species is intermediate in average carapace size, and overlaps size range of *C. fulgipedia*.

markably in the three species considered here. The epigamic displays, however, show great specific distinctions. In all, threat and courtship displays are moderately or strongly differentiated; the fringed and iridescent legs play a conspicuous part at least in threat displays and usually in courtship display as well; in *xanthopa*, however, all fringe and iridescence display is excluded from courtship. True fighting is exceedingly rare in *Corythalia*, and probably never occurs under natural conditions. The subject of display will be discussed in detail, including correlated experimental data, in the sequel to the present paper.

I never saw a hint of cannibalism in *Corythalia*, either between mother and young, or between young of similar size; even several pairs of adults of the same species, quite often of various sizes, sometimes lived peaceably together for weeks, as long as they were well fed and uncrowded.

#### HABITAT.

The three species of *Corythalia* at Rancho Grande extend from the deciduous seasonal into the cloud forests, from 700 to at least 1,300 meters; their humidity requirements range from moderate to high, the temperatures from upper tropical to lower subtropical. They are never found in either open country or dense forest, and all are predominantly terrestrial, although *C. chalcea* occasionally lives in epiphytic bromeliads. None was ever taken by shaking bushes or saplings.

#### KEYS TO THE RANCHO GRANDE SPECIES OF *CORYTHALIA* (ADULTS).

The following keys apply equally well to fresh and preserved specimens:

##### MALES.

- A. 4th leg with well-developed fringes; 1st leg with 1 femoral prolateral spine and with clearly fewer than 20 teeth on tarsal proclaw; tibial apophysis of palp pointed, non-serrate; plentiful long yellow hairs on clypeus and palp; no submarginal carapace band.  
..... *C. xanthopa*, p. 29.
- AA. 4th leg with fringes rudimentary or absent; 1st leg with 2 femoral prolateral spines and with clearly more than 20 teeth on tarsal proclaw; tibial apophysis of palp serrated distally; clypeus naked or with a few light scales.
- B. Submarginal carapace band rudimentary or absent; tibial apophysis of palp and tip of embolus pointed  
..... *C. chalcea*, p. 14.
- BB. Submarginal carapace band strongly developed, persistent in alcohol; tibial apophysis of palp truncate; tip of embolus forked  
..... *C. fulgipedia*, p. 22.

##### FEMALES.

- A. Abdomen with 2 broad, longitudinal dorsal pale stripes; no submarginal carapace band; 1st leg with 1 femoral prolateral spine and with clearly fewer than 20 teeth on tarsal proclaw  
..... *C. xanthopa*, p. 29.
- AA. Abdomen without longitudinal stripes, but with a broad, pale band across posterior third; 1st leg with 2 femoral prolateral spines and with clearly more than 20 teeth on tarsal proclaw.
- B. Submarginal carapace band rudimentary or absent; pale clypeal hairs and scales scanty; breadth of epigynal plate less than diameter of one AME  
..... *C. chalcea*, p. 14.
- BB. Submarginal carapace band strongly developed; pale clypeal hairs and scales abundant; breadth of epigynal plate greater than combined diameters of one AME and one ALE  
..... *C. fulgipedia*, p. 22.

#### DESCRIPTIONS OF THE SPECIES.

##### *Corythalia chalcea* sp. nov.

##### DIAGNOSIS.

Adults of both sexes without pale markings on clypeus, chelicerae and palps, or with only a few sparse white scales; submarginal carapace band of white scales present, but sparse, throughout instars. Adult male with abdomen solidly covered with bronze scales above (brownish in alcohol), through which pale basal and median bands and two terminal spots are dimly visible. Adult female abdomen in life with successive bands of silvery-white, bronze, black, golden-yellow and black, the latter marked with a median bronze stripe and a terminal pair of golden-yellow spots; in alcohol these markings are obscured and faded, but at least the second light band is persistent; young with two abdominal bands brilliant silvery white, second through fifth instar. Adults of both sexes with two femoral prolateral spines on first leg, and clearly more than 20 teeth on its tarsal proclaw. Adult male with fringes well developed on first three legs, absent or with mere rudiments on fourth. Tibial apophysis of palp serrated distally, its tip and that of embolus both pointed; breadth of epigynal plate less than diameter of one AME. Second and third legs, but not fourth, elevated during both courtship and aggressive display, although the two are distinct; no rocking in either. Size moderate, total length of adult males around 5.5 mm., of females around 6.5 mm. Terrestrial and arboreal (especially in epiphytes) to a height of at least 8 meters; montane cloud forest only, 1,100 to at least 1,300 meters.

## EXTERNAL CHARACTERISTICS IN ADULTS AND YOUNG.

## COLOR IN LIFE.

(Text-figs. 2, A-X, AA-EE; 12; 15 A).

**ADULT MALE:** *Cephalothorax*. Integument of carapace black, ocular quadrangle with a few long black hairs, almost naked or more or less completely covered with golden bronze scales, which may extend in a triangle over the flattened, postocular region bounded posteriorly by the steep thoracic slope, as well as on the side just below level of dorsal eyes, on the margins of which they are strongly concentrated. On each side a scanty submarginal cephalothoracic border of white starts at level of posterior eyes and extends almost to pedicel.

Anterior eyes with deep green reflections, all four surrounded by hairs varying from cadmium yellow to ochraceous orange, except outer upper margin of antero-lateral eyes. Clypeus with a sparse double row of short white scales and hairs, the marginal longer than the submarginal, the hairs of both rows all directed toward the center. Chelicerae with a moderate sprinkling of white hairs, longest on the internal margins; palps completely black except for the usual terminal patch of grayish short hairs. Sternum black.

All legs black except for very pale straw-colored third and fourth tarsi. All fringes jet black (except white scale-hairs on femora described below). White scales on legs as follows: on at least third and fourth coxae, with usually a few on second, and on all three trochanters; to various extents on dorsal and postero-dorsal surfaces of all femora, but on anterior side only on third and fourth, where they form a conspicuous antero-dorsal distal band of scales and a short anteroventral distal fringe of scale-hairs, longest distally; this fringe is better developed on third than on fourth leg. A few scales, yellow rather than white, on dorso-posterior surfaces of all patellae, and tibiae, and, on the fourth leg, of metatarsus and of anterior sides of these segments as well.

Iridescence present on first three legs as follows: these areas are covered with specially flattened, smooth and completely or practically hairless facets. Patellae: first, second and third; upper distal half of anterior face (demarcated sharply by the diagonal) and bent along it. Tibiae: first, second and third; entire anterior side, but the upper (antero-dorsal) aspect of this being naked and slightly flattened, it is the most effective. Metatarsi: first, second and third; antero-upper sides, especially of third, form narrow, shining strips. No trace of iridescence on fourth leg, or on other surfaces of the first three, which have in the bare spots only the ordinary gloss of unspecialized chitin. Without any question, the most brilliant areas are all three patellae, all three tibiae and the third metatarsus.

**Abdomen.** Integument black, densely cov-

ered except at extreme base with golden bronze scales, through which project relatively few long hairs. Through the scales is more or less dimly visible the typical *Corythalia* band pattern: a sub-basal band of white scales, a post-median band of gold and two terminal gold spots, well separated. Underside of abdomen black, naked save for a variable amount of black pubescence.

Rubbed, old specimens may have the cephalothorax practically or altogether destitute of bronze and white scales, while the bands and spots of the abdomen show plainly. The first scales to be lost are those on the ocular quadrangle and submarginal border of the carapace. Enough of the bronze abdominal coating always remains, however, to make field identification easy. Alcoholic specimens resemble rubbed examples.

**ADULT FEMALE:** *Cephalothorax*. Dorsal and anterior aspect of carapace as in male, except that there is a more decided concentration of the scales into a spot behind each small eye, and sometimes behind each posterior eye as well. Also, the submarginal carapace band is scantier, and the antero-lateral eye may be rimmed completely instead of only partially with orange, the clypeus bands of white and the white hairs on chelicerae are somewhat better developed, there are a few white hairs below inner margin of anterior lateral eyes, and in addition the palps have some white decoration, in a band of close-set scales across tip of femur and with a few scattered scales and hairs on patellae and even fewer on tibia. Sternum black.

All legs black except for very slightly paler coxae and trochanters and first and second tarsi; as in the male, the third and fourth tarsi are very pale. There are white and pale bronze scales to a very variable extent in the following localities: on all coxae, trochanters, femora (especially in a band across tip of latter), patellae and tibiae. On the metatarsi they may be present or absent, sparsely, but are usually found at least on those of the last two legs. Unlike the case of the male, all of these scale groups are developed on the anterior as well as on the dorso-posterior surfaces.

**Abdomen.** Integument black, with a broad, sub-basal band—the width being variable—of solid bronze scales which leave uncovered, at least laterally, along its anterior edge a trace of a narrow silver-white band. Behind this anterior bronze is a narrow band of black, then a band of gold scales closest to a metallic buff yellow (Ridgway), slightly convex anteriorly, and broadly and shallowly scalloped posteriorly. This is followed by a median bronze stripe down the middle of the succeeding black band, which continues to the dark spinnerets. Just in front of the latter is a pair of oval gold spots of the same shade as the second abdominal band. These various bands extend midway down the sides, and the first, bronze band curves back laterally to join the second, gold band. Below this

point the sides are black covered with yellowish-white scales; venter black with a moderately dense coating of light yellow scales.

Rubbed, old specimens, as in the male, may have the carapace and legs practically destitute of white and bronze scales, the first to disappear being from the apex of the ocular quadrangle. Similarly, the anterior bronze band of the abdomen deteriorates to show clearly the entire width of the anterior narrow band of silvery white, while the posterior gold band and spots become so rubbed that they appear almost white, the integument underlying this particular band and the spots being pale.

*Variation.* As has been suggested, the normal, individual variation is considerable in the amount of white scalation on carapace and legs, in the width of the bronze abdominal band, and in the shade of gold of the second band and terminal spots, these differences being visible even in newly molted, unrubbed specimens. The following two examples, however, are distinct enough to warrant separate remarks. The first, No. 5, was reared from the third instar, all the subsequent instars being of normal pattern. In spite of her peculiar appearance, six different males displayed promptly to her and attempted to mate without hesitation, before she was permitted to mate with a seventh, and then killed. She differed from the typical most obviously in: (1) anterior bronze abdominal band extended practically to the second (gold) band, and was actually joined to it by a pair of conspicuous, gold, bronze-outlined chevrons on either side of midline. Hence between the two metallic bands were only three small patches of black, of which the median was triangular. (2) The median stripe behind the second band was pale gold rather than bronze, only slightly deeper in tone than the second band and spots, and was formed of small confluent chevrons. The remaining differences were only relative, and included within the bounds of normal variation, a number of other females having them to the same extent; the second band and posterior spots were very pale gilt and the scales of the carapace border, clypeus and legs developed to maximum extent for this species.

The second abnormal female, No. 16, was reared from the egg; her brothers and sisters were completely typical of the species. This example was peculiar not only in coloration, but also in incomplete spinulation and especially in the fact that she underwent 9 molts instead of 8 and even then was not adult. From the second instar her peculiarities were evident; she had the entire posterior half of abdomen brilliant silvery white, instead of broken into a band and terminal spots, and her legs never developed more than the faintest bandings of pigment.

*YOUNG. FIRST INSTAR.* Typical of *Corythalia*: true pigment lacking, but with the usual two dark abdominal bands clearly visible in latter part of stadium.

*SECOND INSTAR.* Carapace above black, lacking scales entirely. AME with a few yellowish-orange marginal scales. Clypeus, mouthparts and sternum dark gray to black. Palps, legs and spinnerets translucent buff, with slight or no darkening at the joints. Abdomen: the two bands and small pair of terminal spots are shining silvery white, the anterior band usually wider than the posterior. Venter translucent and colorless.

*THIRD INSTAR.* All markings shining silver white. Carapace with a variable number of scales on ocular quadrangle, ranging from a simple spot behind each PME to a pair of bars extending obliquely forward between PME and AME. A strong crossbar, of variable width, is always present across anterior part of thorax behind PLE; in some specimens this has a very faint gilt tinge, which may prove to be a sexual difference. AME and ALE both rimmed with scales ranging from yellowish through orange to deep rust-color, though the ALE rimming is still incomplete on upper outer margins; frontal aspects otherwise unchanged from second instar. Legs strongly barred with dark pigment, usually deposited at all joints except between coxae, trochanters and femora; strength of banding highly variable, even in individuals of the same brood on corresponding days after molting. Abdomen above as in second instar. Venter grayish-black to black.

*FOURTH INSTAR.* Differs from third as follows: a slight yellowish or bronze tinge on some ocular quadrangle scales; clypeus sometimes with a scanty submarginal border of white scale-hairs; femur of palp sometimes darkened basally; its distal end and patella rarely with a few white scales; leg integument darker, usually only coxae, trochanters and tarsi remaining pale; second abdominal band sometimes followed by one or two white scales in the midline.

*FIFTH INSTAR.* Ocular quadrangle with a frosting of bronze or bronzy-gold scales moderately or well developed, although the primary spots and postocular bar are still sharply defined even when reduced in size. ALE sometimes completely rimmed with rust scales. Clypeus with submarginal band of scale-hairs well developed, sometimes with a second line of scales immediately above it and sometimes with a few more scales below each AME. One example had a very few submarginal thoracic scales, but they usually do not appear until the sixth instar. Palp integument dark or pale; all legs usually dark except tarsi, and all, or only third and fourth, coxae and trochanters; leg tibiae and metatarsi sometimes slightly paler; a few white scales on palps, chelicerae and legs. First abdominal band with a trace of bronze across its posterior border and in midline behind second band; second band, at least in male, may have a faint tinge of silver gilt. Venter dark brown or black, with or without one or several darker median stripes; a scattering of white scales present.

SIXTH INSTAR. Ocular quadrangle with a general frosting of bronze or gold scales well developed, usually extending behind ocular quadrangle on anterior thorax to a greater or less extent, and even slightly below dorsal eyes on sides of carapace; the primary scales—white spots behind PME and the bar behind PLE—are still traceable, however, and sometimes persist strongly under the colored scales. Marginal scales of anterior eyes varying from rust to bright orange. Clypeus with at least a submarginal band of white scale-hairs and usually with a second band of scales just above it, as well as a few below each ALE. Thoracic submarginal scales present or absent, sometimes absent in individuals which had them in the preceding stadium. Integument of palp practically black, and of all legs except brown tarsi. White scale or scale-hairs on appendages variable in number, never profuse, usually present at least on patella of palp, and may be present on every leg segment except tarsi, regardless of sex; they tend to be best developed on anterior surfaces. Abdomen with the bronze posterior portion of first band and in midline behind second much better developed than in preceding stadium, but not so extensive or strongly colored as in adult female. There appears to be a definite sexual difference in the brightness of the gilt tinge to the second band: in females it is definitely paler than in males, where it should now be described as pale gold rather than silver gilt. Terminal abdominal spots now usually joining in a white bar. Venter black, usually with a uniform scattering of white scales.

SEVENTH INSTAR. (Female). Differs from adult female only in the usually slightly greater number of white scales on clypeus, palps, chelicerae and legs, in the lesser extent of the bronze portion of the anterior abdominal band, and in the color of the second band and terminal spots, which are still only silver gilt, not golden yellow. It is thus perfectly intermediate between the sixth stadium and the adult. The white scales are as usual highly variable.

SUMMARY OF COLOR DEVELOPMENT IN *C. chalcea*: Integument. Carapace, mouthparts and sternum black in second instar. Palps may begin to darken in fourth, usually not until fifth, pigment not complete until sixth. Legs scarcely banded in second, strongly in third, color complete except for tarsi in sixth. Abdomen black above (with usual two sub-scale bands and paired terminal spots) in second, venter black in third. *Light-colored scales and hairs*: carapace above lacking scales until third instar, when they appear as a pair of ocular quadrangle spots or oblique bars and a postocular bar of silver white, which form the primary carapace scalation; a general frosting of bronze secondary scales begins in fourth on and close behind ocular quadrangle, reaching maximum development in sixth and seventh instars. White submarginal scales on sides of

thorax may appear in fifth, usually not until sixth, and may thereafter persist or disappear. AME first rimmed with yellowish in second, ALE in third, although rimming of latter eyes is not complete until fifth. White scales usually first appear on clypeus, chelicerae and palps in fifth, rarely in fourth; leg scales never appear before fifth; in males these frontal and leg scales usually reach maximum development in sixth (preadult) instar, sometimes in fifth; in females maximum development usually occurs in seventh (preadult). Abdomen with two sharp bands and a pair of terminal spots formed of brilliant silvery white scales until fifth; in this stadium bronze becomes visible in posterior part of first band and in midline behind second; also it seems likely that the faint gilt tinge sometimes apparent on second band is confined to males; if so, it is the only sexual distinction so far found among the three species before the sixth instar; in the sixth, this color distinction is unquestionable, the second band being pale gold in males, scarcely silver gilt in females; the bronze is also better developed in males; the seventh stadium of the female has the bronze and gold about as well developed as in the sixth male, but less strong than in the adult female. The terminal spots tend to be joined by a less distinct silvery band in the fifth. White scales first appear on the venter in the fourth (rarely) or fifth.

### STRUCTURE.

With the characteristics described on p. 3 ff.

In contrast to color development, the course of post-embryological development of structure shows no clear distinctions from the closely related *fulgipedia*, except in the tardiness of the appearance of some of the spines. The general account of postembryological development, under the various structures, is given on pp. 4 ff. The account below, therefore, concerns adults only, unless otherwise noted.

Ranges and averages of proportions of adults are given in Table V, and comparisons with the other species in Table I.

*Carapace*. Height slightly more than half of length; anterior part of thoracic profile descending moderately gently. Anterior width of ocular quadrangle clearly narrower than width of carapace. Width at level of second-to-third coxa scarcely more than that at bulge before PLE.

*Eyes*. All eyes larger than in the closely related *fulgipedia*, and about the same, relatively, as in *xanthopa*, except that ALE and PLE are smaller than in the latter. PME about midway between ALE and PLE.

*Clypeus*. Half or slightly less than half diameter of AME.

*Chelicerae*. Apparently no teeth on pro-margin.

*Maxillae*. Outer margin distinctly concave; tubercle well developed.

TABLE V.  
Relative Proportions in *C. chalcea*.

	Males		Females	
	Range %	Average %	Range %	Average %
Carapace Length: Breadth	71-74	72.6	70-75	72.2
Carapace Length: Height	48-55	51.2	48-54	51.6
Carapace Length: Oc. Quad. Length	36-42	38.8	37-40	38.2
Carapace Length: Oc. Quad. Breadth	57-65	60.6	56-63	59.9
Carapace Length: AME Diameter	18-21	19.2	18-19	18.6
AME Diameter: ALE Diameter	61-64	63.0	57-65	61.4
AME Diameter: MLE Diameter	16-20	18.0	16-18	17.0
AME Diameter: PLE Diameter	56-62	58.4	54-57	55.6
AME Diameter: Clypeus	42-53	48.0	46-54	50.2
Carapace Length: 1st Tibia	35-40	37.2	29-34	30.8
Carapace Length: 2nd Tibia	35-39	36.0	29-31	29.6
Carapace Length: 3rd Tibia	44-48	45.6	35-40	37.6
Carapace Length: 4th Tibia	43-46	44.0	39-41	39.8
Carapace Length: 1st Metatarsus	30-33	31.8	28-28	28.0
Carapace Length: 2nd Metatarsus	29-33	31.0	26-30	27.4
Carapace Length: 3rd Metatarsus	48-54	51.2	40-44	42.0
Carapace Length: 4th Metatarsus	51-55	53.2	44-49	46.2
Carapace Length: Palp	70-81	74.4	80-84	81.2

*Lip*. No distinctive specific characteristics.

*Sternum*. Width three-fourths of length in male, slightly less in female; not quite as wide anteriorly as base of lip; lateral excavations well developed.

*Bristles*. No distinctive specific characteristics.

*Legs*. Third leg longer than fourth leg in all males, but in less than half of females; first leg longer than second in practically all males and in most females. In the formula, Table VI, the alternate order is expressed by the figures in parentheses in the upper row; figures of proportions are averages; for range of variation see Table V. Segments slender like *xanthopa* and unlike *fulgipedia*. Tibial index: first leg, males 25 to 27, females 27 to 28; fourth leg, males 19 to 21, females 18 only. Iridescence strong in adult male, but not as strong as in *fulgipedia*, nor are the segments as sharply modified. Fringes as long as in *fulgipedia*, but not so thick, present on first three legs although sparse on first; there is a rudimentary trace on fourth leg. See description of *fulgipedia*, p. 26, for details of occurrence of iridescence and of fringe arrangement, since in that species these adornments reach their highest development. Table VII shows change in segment proportions with growth.

TABLE VI.

*C. chalcea*: Leg Formula.

	3(4)	4(3)	1(2)	2(1)
Males	2.21	2.08	1.74	1.71
Females	1.96	1.97	1.57	1.55

*Spines*. There are no invariable spine differences separating *chalcea* from *fulgipedia*, nor the sexes from each other. Comparisons of the three species, with variables are given in Table II. The order of spine development in this species follows the general outline given on p. 7. The following paragraphs describe spine development by instars (see also Text-figs. 2 (FF, GG) and 7).

Second Instar. First leg: all three femoral dorsals; tibial distal (usually); metatarsal prolateral distal; metatarsal ventrals, proximals and distals. Second leg: like first except metatarsal proximal proventral lacking. Third leg: like first except for addition of tibial retrolateral distal; metatarsal prolateral and retrolateral distals complete; metatarsal ventral distals rarely present. (Note: these ventral spines may appear on either third or fourth legs, on either side, and in the pro- or retro-series at any time through fifth instar. When present in second instar they are small and weak, scarcely more than bristles). Fourth leg: like third, except that tibial prolaterals and retrolaterals may be lacking.

Third Instar. As in second.

Fourth Instar. The following spines are usually present in fourth instar, in addition to those appearing in second: all legs: femoral distal upper prolateral; patellar prolateral. Second leg: metatarsal proventral proximal (or appears equally frequently in fifth instar). Third and fourth legs: patellar retrolateral. Fourth leg: tibial median retrolateral; metatarsal median retrolateral. Any leg: tibial distal ventral. (The latter spines, however, never appear in all legs in this stadium, and occur rather as a typical fifth instar development).

Fifth Instar. There now appear any of the previous series which did not appear in the fourth instar. In addition, on all legs: femoral distal upper and sometimes lower, retrolaterals; femoral distal lower prolaterals (occasionally; usually not until later, especially on third and fourth legs); tibial distal ventrals and middle prolaterals (latter sometimes absent on third and fourth legs). On first and second legs: metatarsal proximal prolaterals and distal retrolaterals. On third and fourth legs: tibial proximal ventral (rarely in fourth); metatarsal proximal proventrals (or in fourth or sixth); metatarsal

*C. chateaa*: Change of Leg Proportions with Growth.  
(Figures are percentages averaged from leg measurements of three typical individuals in each group).

% of entire leg to all legs.	1st Leg				2nd Leg				3rd Leg				4th Leg			
	1st Instar	2nd Instar	Adult ♀	Adult ♂	1st Instar	2nd Instar	Adult ♀	Adult ♂	1st Instar	2nd Instar	Adult ♀	Adult ♂	1st Instar	2nd Instar	Adult ♀	Adult ♂
Coxa	23.5	22.5	22.3	22.4	23.5	22.5	22.2	22.4	26.5	27.0	27.4	28.6	27.0	28.0	28.1	26.6
Trochanter	14	12	12	10	14	12	12	11	14	11	11	11	14	11	11	12
Femur	8	5	5	7	8	5	5	7	7	5	5	6	7	6	5	6
Patella	24	27	27	26	24	28	29	28	26	25	27	26	26	25	28	28
Tibia	14	13	15	14	14	12	15	14	12	13	12	12	12	13	12	11
Metatarsus	16	15	16	18	16	15	16	17	15	16	16	17	16	16	16	17
Tarsus	24	15	15	15	24	15	14	14	26	16	19	19	25	16	20	18
		13	10	10		13	9	9		14	10	9		13	8	8

proximal pro- and retrolaterals (third leg sometimes) and median pro- and retrolaterals (fourth leg). By the fifth instar all constant spines found in both adult sexes may be present, except for third and fourth metatarsal proximal retroventrals.

Sixth Instar, Male. In this stadium the following spines appear: any of the above mentioned spines not previously present plus the following: First and second legs: tibial median retroventral; sometimes tibial median proventral; usually tibial proximal retroventral; always metatarsal proximal retrolateral. Second leg only: tibial proximal pro-lateral; rarely, tibial distal retrolateral. Third and fourth legs: tibial prolateral proximal (sometimes absent in fourth leg); tibial retrolateral proximal (sometimes absent on third leg); tibial dorsal usually present; metatarsal dorsal present or absent on either or both legs; metatarsal proximal retroventral present on third, sometimes on fourth; fourth metatarsal proximal pro-lateral present or absent; fourth metatarsal proximal retrolateral present or absent. The only spines of adult always absent in this instar are the first tibial retrolateral(s), the second patellar retrolateral, and the second tibial proximal retrolateral; all these spines may be absent in the adult.

Sixth Instar, Female. The female has never added all of the above to her fifth instar spines; most are usually lacking, except the fourth metatarsal proximal retroventral, which is constant in the six specimens examined. Of the others, only the first and second tibial median retroventrals, the first and second metatarsal retrolaterals, the fourth tibial proximal retrolateral and fourth metatarsal proximal pro-lateral ever occur in this stadium.

Seventh Instar, Female. Like sixth in female, except that fourth metatarsal proximal pro-lateral is always present.

*Trichobothria*; Long, Dark Bristles; Short, Pale Bristles. (Text-figs. 6, 7). No distinctive specific characteristics.

*Tarsal Claws*. (Text-fig. 8). First, second and third leg claws strongly differentiated from fourth and from young. Table III gives comparisons with the other species.

*Palp*. (Text-fig. 9, A, B). Slender. Tibial apophysis of moderate length, stout, tip curved inward or straight, bluntly pointed; uneven, scarcely incised serrations in distal half, sometimes indistinguishable. Tibial ventral tubercle well developed. Whole of embolus occupying only distal fourth of bulb; stylus short, scarcely longer than shorter diameter of whorl; tip tapering to a point.

*Epigynum*. (Text-fig. 10, A, B). Smallest of the three forms under discussion, although the species is almost as large as *fulgipedia* and much larger than *xanthopa*. Viewed externally the horizontal extent of the anterior pair of dark spots is broader than that of posterior pair (spermathecae); their diameter is almost as large as that of spermathecae, and extend forward beyond

margin of bean-shaped patches. Breadth of entire epigynal plate less than diameter of a single AME.

*Abdomen.* No distinctive specific characters.

TABLE VIII.

*C. chalcea.*

Length Ranges and Averages in mm.

Instar	Carapace Length		Total Length	
	Range	Av.	Range	Av.
1st	.91-1.02	.93	1.81-2.11	1.94
2nd	1.09-1.27	1.16	1.81-2.69	2.21
3rd	1.23-1.57	1.39	1.91-2.78	2.41
4th	1.33-1.88	1.63	2.5 -3.9	2.94
5th	1.64-2.15	1.95	2.7 -4.4	3.52
6th ♀	2.26-2.57	2.39	3.8 -5.5	4.3
6th ♂	2.47-3.06	2.69	4.0 -6.0	4.8
7th ♀	2.39-3.12	2.83	4.4 -6.0	5.3
Adult ♂	2.67-3.83	3.08	4.5 -6.53	5.26
Adult ♀	3.11-3.56	3.42	5.86-7.0	6.7

mens of *C. chalcea*. Table IV gives comparisons with the other species. The amount of relative growth in each instar is diagrammed in Text-fig. 11. Measurements in millimeters of the male holotype and female paratype are as follows:

Male holotype. Total length in alcohol 5.1 mm.; carapace length 3.1; carapace breadth 2.3; carapace height 1.5; ocular quadrangle length 1.3; ocular quadrangle breadth 1.9; diameter AME, .58; ALE .36, MLE .10, PLE .36; clypeus height .31; 3rd patella breadth .43.

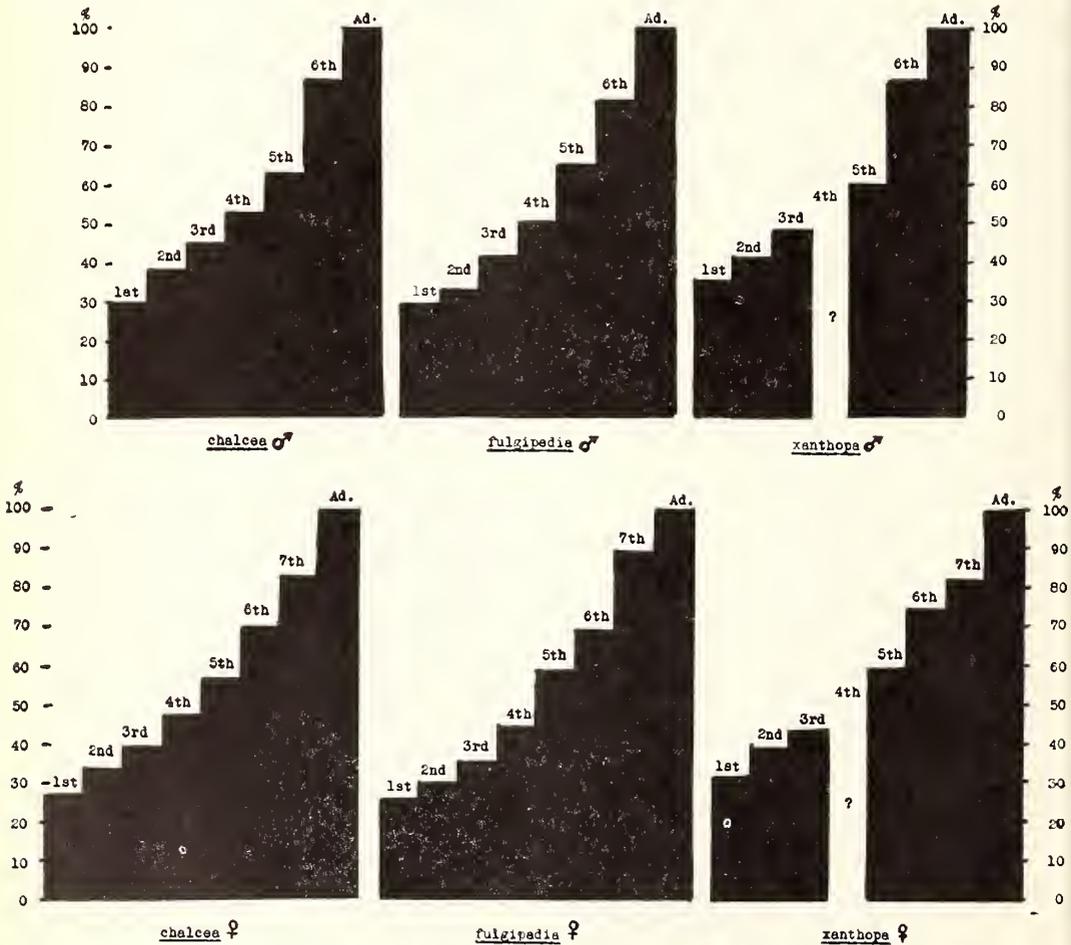
Leg	Femur	Pat.	Tib.	Metat.	Tarsus	Total
1st	1.7	1.0	1.2	.99	.55	5.44
2nd	1.7	1.1	1.1	.99	.51	5.40
3rd	2.4	1.1	1.4	1.6	.62	7.12
4th	2.1	.92	1.3	1.7	.65	6.67
Palp	.89	.41	.31	—	.75	2.36

Female Paratype. Total length in alcohol 5.9; carapace length 3.3; carapace breadth 2.5; carapace height 1.6; ocular quadrangle length 1.3; ocular quadrangle breadth 2.1; diameter AME .64, ALE .38, MLE .11, PLE .36; clypeus height .29; 3rd patella breadth .43.

SIZE AND GROWTH.

MEASUREMENTS.

Table VIII gives the extremes and averages of carapace and total lengths of all speci-



TEXT-FIG. 11. Growth profiles in *Corythalia*. Based on average carapace lengths at each instar.

Leg	Femur	Pat.	Tib.	Metat.	Tarsus	Total
1st	1.7	1.0	1.1	.92	.55	5.37
2nd	1.7	1.1	1.0	.85	.55	5.20
3rd	2.1	1.1	1.3	1.4	.68	6.58
4th	2.1	1.0	1.3	1.5	.65	6.55
Palp	.96	.51	.48	—	.72	2.67

#### RECORDS OF INSTAR DURATION.

*Egg*: About 14 to 23 days; *first instar*: about 15 to 27 days; *second instar*: about 25 to 28 days (records of 5 broods); *third instar*: 4 members of 1 brood: 17, 19, 19, 19 days; other records, 18 days ( $\delta$ ); 32 days ( $\delta$ ); 41, 22-plus days ( $\text{qs}$ ); *fourth instar*  $\delta$ s, 17, 18-plus days;  $\text{qs}$ , 24-plus days; *fifth instar*:  $\delta$ s, 16, 19, 20, 24 days,  $\text{qs}$ , 19, 20, 25 days; *sixth instar*:  $\delta$ s, 23, 25, 27, 29, 52 days;  $\text{qs}$ , 20, 23 days; *seventh instar*:  $\text{qs}$ , 34, 39-plus, 41 days.

#### BEHAVIOR.

(Text-fig. 12; Pl. I, Figs. 1-3).

##### COURTSHIP DISPLAY.

**DIAGNOSIS:** *Stage I.* Body held high. Third legs elevated, extended straight out, and waved up and down in unison above the horizontal, during the rather direct running approach spurts. No posing; no rocking; palps motionless. *Stage II.* First leg held straight out in front, elevated, parallel.

**DESCRIPTION:** *Stage I.* Carapace elevated moderately high, although lower than distal ends of femora. Abdomen horizontal or slightly depressed. All legs except third remain on ground. Third legs elevated, the femur obliquely up as in other legs, and at peak display, raised from horizontal to oblique vertical, with femur-patella joint as hinge, the distal segments remaining straight. When display is not full, the wave arc is from highest point to ground, the tibial joints bending on the downbeat. The rhythm at optimum display consists of several running steps during which the third legs are raised, in unison, and the body held at its highest, followed by a pause while they are lowered (either partially or completely, as described above). Fourth leg braced farther out than in *fulgipedia*. Progress is fairly direct, with little zigzagging. There is no posing, motion being almost constant, nor rocking, and only rarely any vibration (see under *Variation*). The palps hang motionless and relaxed. *Variation.* In one rare individual, an up and down jitter, including a stamping with first feet, occurred at end of every forward movement.

*Stage II.* Cephalothorax elevated as in Stage I, abdomen perfectly horizontal, body sustained on three posterior legs while the first pair are held up and forward. To achieve this position, their femora are directed up, parallel and the legs bent straight forward at femur-patella joint, bringing them on a level with top of cephalothorax. *Variation.* If a not entirely receptive female raises her front legs straight up, the male may raise his vertically also, patting her tarsi with his.

If this completes her acceptance, he slides between hers on to the carapace, patting her as he goes. Even at this stage he may break away.

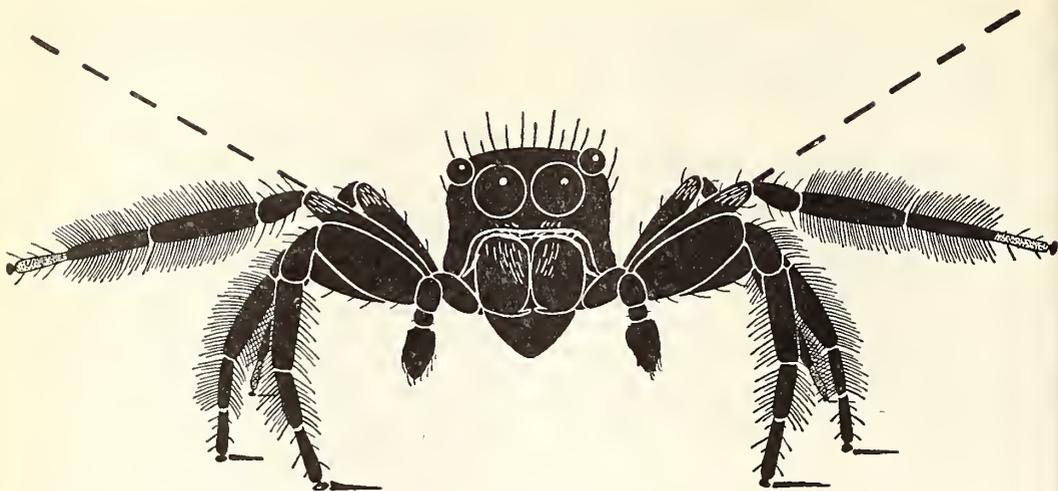
**Female Behavior.** A completely receptive female makes no display attempt at all, but watches closely, sitting crouched, and may or may not run away a few times before accepting male. No more than two or three minutes of display are required. A non-receptive female constantly runs away and/or attacks, leaping at the male again and again. A partially receptive female raises her first front legs forward as the male enters Stage II, and then sometimes upward (see above paragraph) before accepting or rejecting male. One highly receptive individual female, during a series of experiments on several successive days, performed a peculiar, crouching, rocking display toward the end of the male's Stage I and Stage II. All her legs remained on the ground. About the fourth day, still not having been permitted to mate, she gave up the motion, although she remained responsive as ever to the displays of various males, and was finally mated.

##### THREAT DISPLAY.

**DIAGNOSIS:** *Stage I.* Third legs elevated, straight or arched, to horizontal (but not above) and returned in arch to ground, during zigzagging or sidling spurts, which alternate with extended posing. No rocking or vibration. Differs from courtship in that third legs are not brought above horizontal and posing occurs. *Stage II.* First legs held straight overhead, fending off opponent. Differs from courtship in their higher position.

**DESCRIPTION:** *Stage I.* Carapace held moderately high, as in courtship, although in threat the abdomen hangs down. Also as in courtship, all legs remain on ground except third, which are waved up and down. However, these legs are practically never raised above the horizontal plane and usually do not reach this high, while the low point of every wave is the ground. There is more zigzagging and sidling back and forth than in courtship, where the approach is much more direct, the raised leg on the side of the momentary direction of approach being raised higher. Also there is extensive posing, the spider remaining motionless up to a half-minute, with the third legs either more or less elevated, stretched straight, or simply arched, whether touching or clearing the ground. Although this approaches a fan display, at no time is a perfect fan made by the fringes of adjacent legs, as in *xanthopa*. Fourth leg braced far out to side, as in courtship. Palps held more rigidly than in courtship, bent obliquely outward at patella. *Variation.* Some males have swung on the end of a silk thread to the attack. Usually they start display from not more than three inches away, but one individual leapt from a distance of eight inches.

*Stage II.* Usually one or the other of the



TEXT-FIG. 12. Peak of threat display in *C. chalcea*. Dotted lines indicate peak position of legs during Stage I of courtship display. Scales white except for russet eye rims; iridescence not indicated.

opponents retreats when within two inches, but occasionally they meet head-on after short leaps, in which case the third legs remain on ground while the first are raised straight in the air and slightly forward, touching the opponent's tarsi. Chelicerae not opened, nor even seem to touch, and no male has ever been seen to be injured. The meeting is always momentary only.

#### HABITS ASSOCIATED WITH BROODING.

Eggs are laid about seven to nine weeks after the final molt (records inconclusive). The second clutch of individual females is apparently laid about the time the first clutch is ready to molt; the third clutch appears when the second is hatching. The eggs, numbering 20 to 29 (3 perfect first clutches counted) are ivory yellow (Ridgway) and measure 1.06-1.2 mm. in diameter. Eggs of later clutches range from almost normal numbers down to half a dozen. The cocoon is spun in a small dead leaf; a typical example measures  $25 \times 18$  mm., with the oblong inner cocoon surrounding the eggs  $7 \times 9$  mm. The later clutches are apparently always laid in the same leaf, but data are scanty in this species.

#### HABITAT.

*C. chalcea* was taken only in the extreme upper margin of the semi-evergreen seasonal forest and in the lower part of the montane cloud forest at Rancho Grande, from about 1,000 to 1,300 meters. On its lower edges, the habitat overlaps that of *C. fulgipedia*. It was found principally on the ground, on dead leaves along the roadside, well lighted trails, and on the edges of clearings; however, a number of specimens were taken in bromeliads, and on the trunks of trees near these epiphytes, to a height of about 8 meters.

#### RELATIONSHIPS.

*C. chalcea* appears to be most closely related to *C. obsoleta* Banks, 1929, from Panama. It differs in the simpler banding of the female abdomen, in the poorly developed submarginal carapace band, in the lack of grooving in the male embolus and in details of the epigynum.

#### MATERIAL.

A total of 197 specimens of *C. chalcea* have been preserved, including exuviae. They are distributed as follows among the instars; first instar, 45; second, 28; third, 15; fourth, 10; fifth, 11; sixth, ♂s, 12; ♀s, 10; seventh, ♀s, 7; adult ♂s, 35; adult ♀s, 24. All were taken within a radius of half a kilometer of Rancho Grande. The following have been designated as holotype and paratype:

**HOLOTYPE:** Male. Cat. No. 461191, Department of Tropical Research, New York Zoological Society; Portachuelo, Rancho Grande, near Maracay, State of Aragua, Venezuela; 1,200 meters; cloud forest; May 10, 1946.

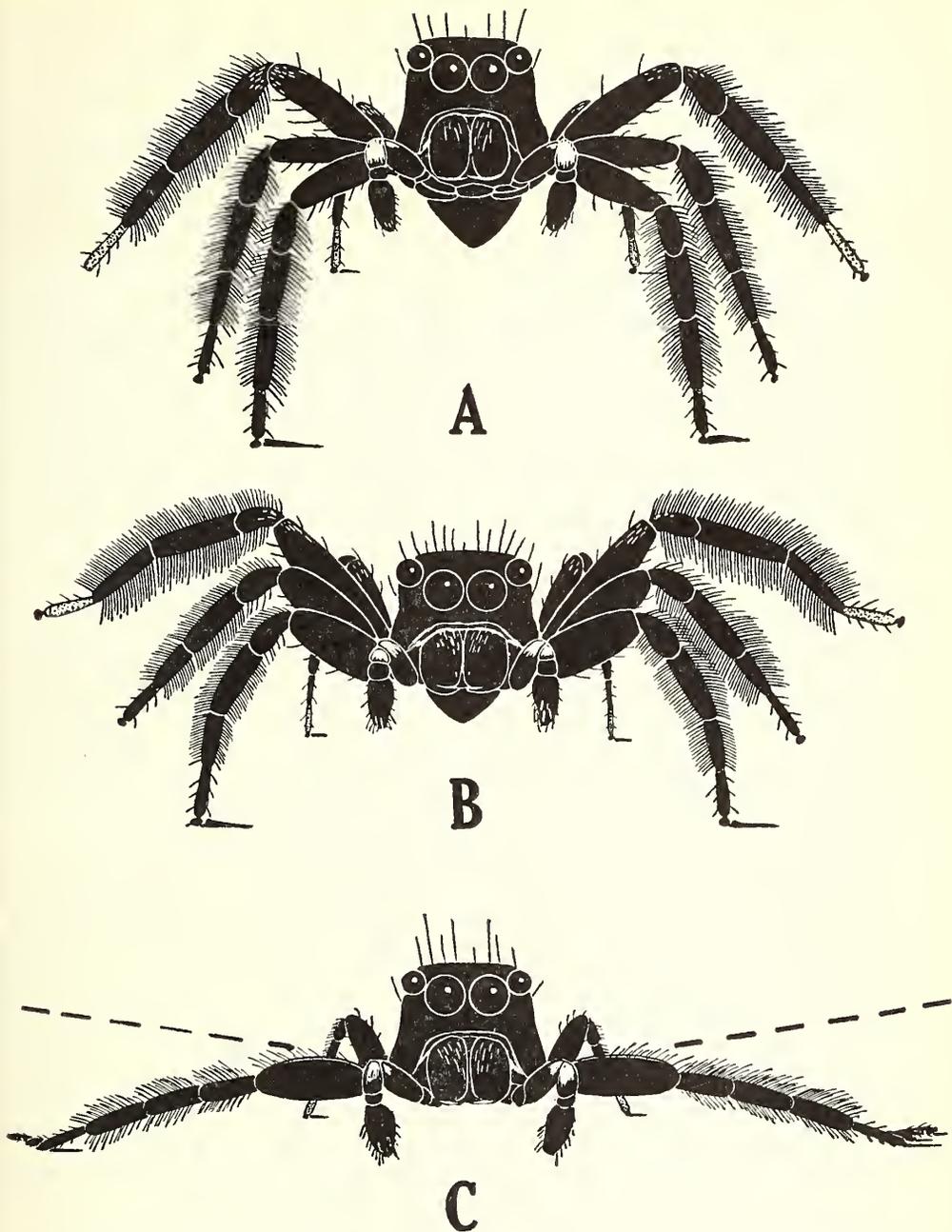
**PARATYPE:** Female. Cat. No. 461192, Department of Tropical Research, New York Zoological Society; same locality as holotype; May 23, 1946.

The name *chalcea* is proposed in reference to the bronze scales covering the male abdomen.

#### *Corythalla fulgipedia* sp. nov.

#### DIAGNOSIS.

Adults of both sexes with a strong, white, submarginal carapace band; at least traces of 5 white spots on carapace plus a thoracic spot or concave band which may be present or absent; male with face and chelicerae almost naked; female with plentiful yellowish and white hairs and scales in these



TEXT-FIG. 13. Display in *C. fulgipedia*. **A**, peak of threat display; **B**, fan phase of threat and courtship; **C**, courtship, Stage 1; dotted lines indicate elevation limit of third legs. Scales white, except for orange or russet eye rims; iridescence not indicated.

areas; abdomen of both sexes banded successively with white, bronze, black, white, black and white, the white bands all confluent on sides; in alcohol only the second white band is usually persistent. Young with two abdominal bands and a pair of terminal spots pure matte white; dorsal carapace scales present from second instar, a strong submarginal band from third. Adults of both sexes with two femoral prolateral spines on first leg, and clearly more than 20 teeth on

its tarsal proclaw. Adult male with fringes well developed on first three legs and with a rudimentary thickening of hair on fourth. Tibial apophysis of palp serrated distally and truncate; tip of embolus forked; breadth of epigynal plate greater than diameter of one AME plus one ALE. Second and third legs, but not fourth, elevated during both courtship and aggressive display; rocking present in aggressive display only. Size moderate, total length of adult males around 5.5 mm.;

of females around 6.5 mm. Terrestrial only on forest roadsides and in open forest clearings in deciduous seasonal and semi-evergreen seasonal forests; occasionally on lower edges of montane cloud forest; about 700-1,100 meters.

## EXTERNAL CHARACTERISTICS IN ADULTS AND YOUNG.

### COLOR IN LIFE.

(Text-figs. 2, I-Q; 13; 15B).

**ADULT MALE:** *Cephalothorax*. Integument black. Ocular quadrangle with or without a sparse scattering of yellowish or bronzy scales, usually concentrated around dorsal eyes. There are always 5 white spots in this general region; a pair in front of PME, a pair behind PLE and a median spot between PLE. In addition yellowish or pale tan scales are present or absent on anterior thorax; in the simplest form they make a median spot at beginning of posterior thoracic slope; in greatest extent they form a crescent in this region merging anteriorly with spots behind PLE. A strong pure white carapace band, beginning at level of PME, stopping short of pedicel. AME and ALE unchanging dark brownish-black, rimmed with rust-colored scales. Clypeus completely naked; a few variable white hairs and scales at base of chelicerae; a moderate number on distal part of femur and on patella of palp with scattered long white hairs near tip of tarsus. Legs: Integument black except for slightly paler third and fourth tarsi. First and second legs with a few white scales on dorso-posterior surfaces of patella and basal tibia and metatarsus, rarely on distal femur as well; third and fourth legs with scales much more plentiful, distinctly yellowish, on posterior surfaces of distal part of femur, entire patella, entire tibia, and base of metatarsus; anteriorly on distal femur and patella only.

**Abdomen.** Anterior band with a variably narrow anterior margin of white, and a broader posterior bronze portion; contiguous to this posteriorly is usually a small median yellowish-white spot; second band white slightly concave forward the anterior edge wavy or plain and the band marked in its center with a short, black bar. Behind second band is a narrow, median, white stripe linking second band to white or yellowish terminal markings, which are usually in form of a wavy narrow band, curving forward or broadly V-shaped. All transverse white bands on abdomen curving to connect with one another high up on the white sides. Venter plentifully clothed in grayish hair.

**ADULT FEMALE:** Like male except that there are more light scales and hairs on ocular quadrangle, face, palps and legs. Details are as follows: *Cephalothorax*. Ocular quadrangle almost always with a general frosting of dull bronze scales often with a

short median line of white scales behind AME; 5 white spots as in male, behind each ALE, each PME and in midline between PLE; anterior thoracic markings, as in male, ranging from none through a median spot (sometimes represented only by several scales) at beginning of thoracic slope, to a complete crescent, concave forward and merging with PLE spots; these thoracic scales usually have a creamy or tan tinge. A strong, pure white submarginal carapace band exactly as in male. Pale tan short hairs and scales all across clypeus below AME and ALE, and a double row of pure white hairs across edge of clypeus. Thick, pure white hairs also on chelicerae and on palp across distal part of femur and entire patella; palp tibia and tarsus heavily covered with tannish-white, except for black tarsal tips. Legs: integument jet black, except for slightly paler first and second tarsi and definitely paler third and fourth. All segments plentifully covered, both anteriorly and posteriorly, with tannish-white scales except coxae, trochanters at joints, dorsal median parts of patellae and tibiae and entire tarsi. However, coxae beneath are well scaled as is underside of the black sternum. **Abdomen.** Like that of male, except that second white band is convex, not concave, anteriorly while the posterior median stripe is often broken. Venter well covered with grayish hair.

**YOUNG; FIRST INSTAR:** Typical of *Corythalia*: true pigment lacking, but with the usual two dark abdominal bands clearly visible in latter part of stadium.

**SECOND INSTAR:** This is the only species in which carapace scales appear before third instar. The black integument and basic pattern of two abdominal bands and a pair of terminal spots are typical of the group. Carapace: large, elongate white scales scattered over entire ocular quadrangle and extending behind it either as a more or less complete band, or as a simple spot behind each PLE. AME bordered with a few rust scales. Clypeus, mouthparts and sternum black. Palps, legs and spinnerets translucent buff with, however, faint dark bands appearing at the leg joints. Abdomen: the bands are dull (not shining) pure white, even, the anterior slightly narrower than the posterior. Venter dark gray.

**THIRD INSTAR:** All markings dull white, except sometimes for a very faint yellowish tinge on scales on anterior part of ocular quadrangle. These scales are concentrated into obscure oblique lines, thickest behind PME; they are very sparse in posterior part of ocular quadrangle and behind ALE. Between and behind PLE is a short median streak, and a well marked spot behind each PLE. A strongly developed carapace band begins at level of posterior eyes, stopping short of pedicel; this band continues, unchanged, except for further broadening and strengthening, and a slight extension forward, from this instar on. Anterior eyes rimmed with rust except outer margin of

ALE. The clypeus has a double row of white scales and hairs, the upper represented only by a short line below each AME, the lower is the usual submarginal band, the hairs directed inward, with longer ones centrally; a few white scales at inner base of chelicerae and many white scales and hairs at tip of palp femur and all over patella. Palp and legs all black with only faint traces of light bands on patellae, tibiae and metatarsi; tarsi may be dark basally. White scales moderately well developed dorsally at tips of all femora, on patellae, and in distal half of third and fourth tibiae. Abdomen above with the usual two bands of dull white, without jagged edges, the second more convex posteriorly than anteriorly; in midline behind second are a very few white scales; in midline in second band a short, curved black bar is indicated; two terminal spots, oval and well separated. Venter black, without light scales.

FOURTH INSTAR: Carapace as in preceding instar; the scalation on ocular quadrangle is rather variable in extent but is never dense except in the spots near PME and behind PLE, as well as the streak between PLE. ALE now completely rimmed with rust scales. Clypeus, chelicerae and palps as in preceding stadium. Legs all dark except for pale tarsi, and sometimes pale posterior patellae; white scales on legs about as in preceding stadium. Abdomen with two even, simple, white bands with a dark horizontal bar in second, followed by a line of midline scales and a pair of terminal spots, as in preceding stadium; in addition, however, there is a slight median, black invagination in posterior margin of first band.

FIFTH INSTAR: In this stadium the coloration becomes almost identical with that of the adult female because of the following additions and changes since the fourth instar: there is now a general coating on the ocular quadrangle of white, faintly yellowish or bronzy scales, through which the primary white spots are still visible near PME and behind PLE; the median streak between PLE is now divided into two spots, one between PLE and one at beginning of thoracic slope, although either one (but not both) may be lacking. White scales and hairs on clypeus, chelicerae, palps and legs are more numerous than in preceding stage, but still not as widespread and thick as in adult female; palp scales are now present on tibia as well as patella and distal femur; leg scales now occur on all segments except tarsi, especially on dorsal and anterior surfaces; palp integument remains pale except for tarsi; legs black except tarsi. Abdomen with bronze now apparent in posterior part of first band, although it is not nearly as well developed as in succeeding stadia; in this instar also appears the small streak or spot of white or yellowish hairs in midline behind the first band. Second band with median bar well marked, median streak following band well developed; posterior markings persisting

either as the primary spots or joining in a wavy band as in later stadia.

SIXTH INSTAR: Although sex can now be told through the form of the palp, there are no differences in color apparent, both sexes being identical with the adult female except that white scales on face and appendages are not so well developed. The carapace markings vary just as in the adult, both in color (from dull white to yellowish) and in extent of scalation, and this is the first stadium in which a crescentic marking outlining the postocular plateau region of the thorax may be present; it seems that if it is to be present in the adult it appears in this stage; if, on the other hand, the thoracic marking is to be a simple median spot, this spot is retained throughout. Tarsi almost as dark as other segments. Median whitish or yellowish patch in midline following bronze portion of first abdominal band present or absent. Terminal abdominal markings variable, the median marking complete or broken, the primary spots completely joined or practically separate; bands curving on sides toward each other, but rarely merging as completely as in final stages. Sternum and abdomen beneath well covered with white scales.

SEVENTH INSTAR: (Female only). Like adult, including amount of variation, except that there is still not quite the profuseness of white scales in frontal aspects and on legs.

SUMMARY OF COLOR DEVELOPMENT IN *C. fulgipedia*: Integument. Carapace, mouthparts and sternum black in second instar, as usual. Palps begin to darken in third, are not completely dark until fifth. Legs moderately banded in second; color complete in fifth. Abdomen black above (with two usual subscale pale bands and terminal spots) in second; venter black in third. *Light-colored scales and hairs*. Carapace above has white primary scale-hairs in second; by third the most prominent 5 patches correspond in position to the 5 constant spots of adult; a general white, yellowish or bronze frosting (secondary scalation) begins in third; separate thoracic spot or crescent, if present in adult, appears in fifth or sixth. Sub-marginal carapace band appears in third and is strong even in that early instar. AME first rimmed with rust in second, ALE in third. Light scales appear first on clypeus, chelicerae, palps and legs in third, reaching maximum development in preadults of both sexes. Abdomen with two sharp bands and a pair of terminal spots pure, dull white until fifth, when a very faint cast of bronze may appear over posterior part of first band; sometimes the bronze does not appear until sixth. Second band with a dark horizontal median bar in third and subsequent instars. Median whitish spots or short stripes following each band appear in fifth; terminal spots merge into an irregular band, and all bands are confluent on lateral margins from sixth on. White or grayish scales appear on venter in fourth or fifth.

## STRUCTURE.

With the characteristics described on pp. 3 ff.

In contrast to color development, the course of post-embryological development of structure shows no clear distinctions from that of the closely related *chalcea*, except in the earlier appearance of some of the spines. The discussion below therefore concerns adults only except where otherwise specified. Ranges and averages of proportions of adults are given in Table IX, and comparisons with the other species in Table I.

*Carapace*. Height less than half of length; anterior part of thoracic profile a plateau. Anterior width of ocular quadrangle much narrower than width of carapace. Width at level of second-to-third coxa much greater than that at bulge before PLE.

*Eyes*. All eyes definitely smaller than in either of the other species. PME about mid-way between ALE and PLE.

*Clypeus*. Half or slightly more than half diameter of AME.

*Chelicerae*. Two minute teeth on promargin.

*Maxillae*. Outer margin distinctly concave; tubercle well developed.

*Lip*. No distinctive specific characters.

*Sternum*. As in *chalcea* width three-fourths of length in male, slightly less in female; not quite as wide anteriorly as base of lip; lateral excavations well developed.

*Bristles*. No distinctive specific characteristics.

*Legs*. Third leg usually longer than fourth leg in both males and females; second leg longer than first leg in all males and in more than half of females. In the formula, Table X, the alternate order is expressed by the figures in parentheses in upper row; figures of proportions are averages; for range of variation see Table IX. Segments thicker and broader in relation to their length, and length relatively shorter than in either *chal-*

*cea* or *xanthopa*, particularly in female. Tibial index: first leg, males 25 to 27, females 27 to 33; fourth leg, males 17 to 21, females 21 to 27.

Both iridescence and luxuriance of fringe reach their highest development in the present species, compared with the other two. Iridescence is present on first three legs, but altogether absent on fourth. The correlated flattening of the surfaces is greater than in either of the other species. Fringes also are present only on the first three legs, although on the fourth there is some thickening and a very slight elongation of the profile hairs. In detail, the fringes are as follows: *First leg*: femur: ventral only; short, downy, chiefly on posterior surface. Patella. Dorsal short and scanty, ventral moderate, anterior, slightly less than length of segment. Tibia: like patella. Metatarsus: no true fringe, but plentiful long hairs. *Second leg*: like first leg, but longer and thicker on all segments,

TABLE X.

*C. fulgipedia*: Leg Formula.

	3 (4)	4 (3)	2 (1)	1 (2)
Males	2.06	2.04	1.70	1.66
Females	1.81	1.86	1.51	1.48

and very well developed on metatarsus. *Third leg*: maximum development. Like second, but longer and thicker, except on femur, where it still does not constitute a true fringe, since it is composed of soft, pale hairs, well separated. Dorsal fringe of the three true, fringe-bearing segments always only about half as long as ventral, and always thinner, the difference being most noticeable on this leg. Dorsal fringe best developed in all three legs on metatarsus. Ventral tibial fringe of graduated length, the longest hairs coming at middle of segment, which is also widest part. This is true also of second tibia. The longest fringe is about as wide as widest part of tibia. *Fourth leg*: the profile hairs of the middle segments, although very short and

TABLE IX.

Relative Proportions in *C. fulgipedia*.

	Males		Females	
	Range %	Average %	Range %	Average %
Carapace Length: Breadth	72-77	74.0	69-75	72.0
Carapace Length: Height	45-51	48.0	47-50	48.4
Carapace Length: Oc. Quad. Length	35-43	37.8	34-38	36.4
Carapace Length: Oc. Quad. Breadth	55-60	57.2	53-58	56.0
Carapace Length: AME Diameter	16-19	17.2	17-18	17.4
AME Diameter: ALE Diameter	59-71	63.2	55-59	57.8
AME Diameter: MLE Diameter	19-23	21.4	18-22	19.4
AME Diameter: PLE Diameter	52-60	56.0	49-53	50.6
AME Diameter: Clypeus	53-56	54.0	53-62	55.6
Carapace Length: 1st Tibia	32-34	32.8	27-30	29.0
Carapace Length: 2nd Tibia	34-35	34.8	28-36	29.8
Carapace Length: 3rd Tibia	34-42	39.2	30-34	32.4
Carapace Length: 4th Tibia	36-42	39.8	36-37	36.8
Carapace Length: 1st Metatarsus	30-33	30.8	23-25	23.8
Carapace Length: 2nd Metatarsus	27-31	29.8	24-27	25.6
Carapace Length: 3rd Metatarsus	44-47	45.8	36-39	37.6
Carapace Length: 4th Metatarsus	46-51	48.4	41-43	42.2
Carapace Length: Palp	77-89	81.0	79-81	79.6

weak, are thickened enough to be termed a fringe, especially on ventral surfaces. There are rudimentary fringes on all tarsi, although the hairs are pale, and longer on dorsal, not ventral surfaces.

*Spines.* There are no invariable spine differences separating *fulgipedia* from *chalcea*, nor the sexes from each other. Comparisons of the three species, with variables, are given in Table II. The order of spine development in this species follows the general outline given on p. 7; details are given for *chalcea* on p. 18 and in Text-figs. 2, 7. Here it is to be noted that although they appear in the same order, certain spines appear one or more instars earlier in *fulgipedia* than in either of the other two species. The *second instar* spines are identical for both species, except that in *fulgipedia* the second metatarsal ventrals are 2-2, not 1r-2, and, in one example, a third patellar prolateral occurs. In the *third instar* appear the following spines, which do not appear in *chalcea* until the fourth or fifth; femoral distal upper pro-laterals; all patellar pro-laterals; third and fourth patellar retrolaterals; some tibial distal ventrals. In the *fourth instar* of *fulgipedia* most spines are present which typically appear in the fifth of *chalcea*; the third and fourth tibial median pro-laterals and corresponding retrolaterals are exceptions, however, since they do not appear until the fifth. In the *fifth instar* of *fulgipedia* the acceleration of development in comparison with *chalcea* loses its impetus, since about the same spines are present in that stage in both species, and the same is true, including the high variability, of the *sixth* (both sexes) and *seventh* (female) instars.

*Trichobothria; Long, Dark Bristles; Short, Pale Bristles.* No distinctive specific characteristics.

*Tarsal Claws.* As in *chalcea*, the first, second and third leg claw-teeth strongly differentiated from those of the fourth and of the young. Table III gives comparisons with the other species.

*Palp.* (Text-fig. 9, C, D). Robust. Tibial apophysis very broad, compressed along dorso-ventral axis, the end obliquely truncate, with the low corner dorsad; tip irregularly serrated. Whorl of embolus large, occupying almost distal two-fifths of bulb; stylus long, broad, tapering; tip shallowly forked, the tines unequal.

*Epigynum.* (Text-fig. 10, C, D). By far the largest of the three under discussion. Viewed externally, the horizontal extent of the clearly visible portion of anterior pair of dark spots is a little less broad than that of posterior pair (spermathecae); they extend to anterior edge of bean-shaped patches. Subdermally, the structure is seen to be almost identical with that of *chalcea*, except for size. Breadth of plate greater than diameter of one AME plus one ALE.

*Abdomen.* No distinctive specific characters.

## SIZE AND GROWTH.

### MEASUREMENTS.

Table XI gives the extremes and averages of carapace and total lengths of all specimens of *C. fulgipedia*. Table IV gives comparisons with the other species. The amount of relative growth in each instar is diagrammed in Text-fig. 11. Measurements in millimeters of the male holotype and female paratype are as follows:

Male holotype. Total length in alcohol 5.7 mm.; carapace length 3.5; carapace breadth 2.5; carapace height 1.7; ocular quadrangle length 1.2; ocular quadrangle breadth 1.9; diameter AME .59; ALE .34, MLE .09, PLE .28; clypeus height .31; 3rd patella breadth .54.

Leg	Femur	Pat.	Tib.	Metat.	Tarsus	Total
1st	1.9	1.1	1.2	1.0	.54	5.74
2nd	1.9	1.1	1.1	1.0	.54	5.64
3rd	2.3	1.2	1.5	1.6	.70	7.30
4th	2.3	1.0	1.3	1.6	.70	6.90
Palp	1.0	.48	.27	—	.97	2.72

TABLE XI.

*C. fulgipedia.*

Length Ranges and Averages in mm.

Instar	Carapace Length		Total Length	
	Range	Av.	Range	Av.
1st	.86-.97	.91	1.72-2.15	1.86
2nd	.96-1.13	1.06	1.54-2.02	1.77
3rd	1.27-1.4	1.32	2.3 -3.0	2.49
4th	1.47-1.81	1.59	2.5 -3.9	3.22
5th	1.88-2.19	2.07	2.9 -4.1	3.68
6th ♀	2.33-2.67	2.41	3.55-4.9	4.23
6th ♂	2.12-2.84	2.62	3.4 -5.28	4.49
7th ♀	2.84-3.15	3.00	4.9 -6.24	5.53
Adult ♂	2.8 -3.63	3.19	4.61-6.14	5.43
Adult ♀	3.28-4.0	3.59	5.76-7.2	6.53

Female Paratype. Total length in alcohol 7.7 mm.; carapace length 3.8; carapace breadth 2.7; carapace height 1.8; ocular quadrangle length 1.3; ocular quadrangle breadth 2.1; diameter AME .59; ALE .34, MLE .11, PLE .28, clypeus height .34; 3rd patella breadth .54.

Leg	Femur	Pat.	Tib.	Metat.	Tarsus	Total
1st	1.9	1.1	1.1	.91	.59	5.60
2nd	1.9	1.2	1.0	1.0	.54	5.64
3rd	2.2	1.1	1.3	1.4	.75	6.75
4th	2.2	1.1	1.3	1.6	.75	6.95
Palp	1.1	.48	.54	—	.86	2.98

### RECORDS OF INSTAR DURATION.

Egg: About 8 to 16 days: *First instar*: more than 12 to less than 31 days (no exact records); *second instar*: 20, 21, 25, 25 and 31 days; *third instar*: 19, 19 and 20 days (specimens taken to New York laboratory: 30, 34 and 42 days); *fourth instar*: the only complete records are of specimens taken to New York: 33, 35 and 37 days; judging by the delayed molting in New York of the other stadia, the normal time is much less, probably around three weeks; *fifth instar*: 22, 27-plus days (both ♂s); in New York laboratory, 67 days (♂); *sixth instar*: ♀s, 20-plus,

27-plus days; ♂s, 26, 26-plus, 34, 34-plus days; New York laboratory, 41 days (♂); seventh instar (♀s); 35-plus, 37, 46, 50 and 61 days.

### BEHAVIOR.

(Text-fig. 13).

#### COURTSHIP DISPLAY.

**DIAGNOSIS.** *Stage I.* Body held low, with legs wide spread laterally; third legs intermittently raised and vibrated in unison with body during or between spurts of progress. No posing; no rocking. Palps jerked, in unison, almost constantly.

*Stage II.* As in *chalcea* but body held lower, and there is vibration.

**DESCRIPTION:** *Stage I.* Cephalothorax held very low with first three pairs of legs stretched progressively farther out to side, so that the femora are parallel with ground and the tarsi show one behind the other; only the fourth legs are extended behind, not laterally, for balance. Abdomen horizontal. All legs left continually on ground except third which are intermittently moderately elevated and vibrated in the air, up and down, in a small arc in unison with vibration in the body, especially the abdomen. The vibration—of about a second's duration—takes place either between or during spurts of rather direct progress. There is no posing and no rocking. The palps are jerked up and down almost continuously, usually with a roughly circular motion, one going clockwise as the other goes counterclockwise, and vice versa; sometimes it is more of a simple jerking up and down. As the female becomes more receptive the elevation of the third legs almost ceases and the male approaches with the cephalothorax even lower, almost touching ground. *Variation.* Some individuals lower the body regularly more than others.

*Stage II.* As in *chalcea*, with first legs out in front, parallel, level with top of cephalothorax, but the body is held lower, and the same type and rhythm of body vibration occurs as in Stage I. He may in this stage, practically touching female, pose utterly motionless if she fences with him, but does not actually run.

#### THREAT DISPLAY.

**DIAGNOSIS:** *Stage I.* Body held exceptionally high, second and third legs raised intermittently, the second just clearing ground, the third higher, bent at patella only, or arched. No vertical vibration, but occasional side-to-side coarse rocking; a moderate amount of posing with raised third legs. Palps jerked at intervals.

**DESCRIPTION:** *Stage I.* Position exactly opposed to courtship display, the cephalothorax elevated to maximum extent through the legs, especially first and fourth, being held in close to body and stretched to maximum vertical; at peak display the first femur slants forward and strongly downward. Sec-

ond legs and third legs extending progressively further laterally. Toes of second legs not touching ground at peak display, and third legs raised and bent only at the femoropatella joint which is raised above level of cephalothorax, the more distal joints held straight at an obliquely downward angle. At less than peak display the cephalothorax is lower, and the leg more arched, its fringes never, however, forming a perfect fan with those of first and second. Fourth leg braced far back. There is no trace of the up-and-down vibration typical of courtship, but some intermittent coarse rocking between spurts of zigzag progress, usually about six rocks (three to each side)—occupying about a second or less—in a series. There is more zig-zagging and sidling than in courtship, and the raised leg on the side of direction of rocking or progress is raised higher. Posing plays a moderate part in threat display, the third legs being usually in the arched, not maximum obliquely bent, position. Palps jerked as in courtship at beginning of threat, but held motionless at peak, with femur bent out and the other segments hanging down.

*Stage II.* As in *chalcea*.

**Female Behavior.** A completely receptive female practically always raises first front legs forward as male enters Stage II, as does the only partially receptive *chalcea* female. A non-receptive female is more combative than a non-receptive *chalcea* female, usually leaping on the male savagely, after hunching her body well down between her close-gathered legs and rocking violently back and forth; if these tactics fail to discourage him—they usually scare him away quite quickly—she will leap, then run away. So far no female has actually hurt a male in this group. A potentially receptive female alternately leaps, sits, and runs away, punctuating these activities with rough versions of the male threat, and as in *chalcea* she raises her first legs first forward and then sometimes upward, although her arched-out second and third legs apparently never actually leave the ground.

#### HABITS ASSOCIATED WITH BROODING.

Each of several females which molted and mated in the laboratory laid eggs between eight and nine weeks after molting, and between three and nine weeks after mating. The second clutches were apparently laid just about the time the first clutch was hatching. Since the former was laid, in its own inner cocoon, within the same leaf and outer cocoon as the first clutch, it was impossible to obtain exact data on these broods without unduly disturbing the female and young. We have two examples of a third clutch also laid in the same cocoon, just about the time the first brood was leaving the nest.

A single leaf is always used for the cocoon, which is more extensive than that of *C. chalcea*. Bits of earth are mixed with the silk binding the edges together. A typical leaf

measures 70 mm. long, and the outer cocoon silk binds its whole length together; each egg packet is about 7 mm. in diameter. The eggs, numbering 13 to 28 (6 perfect first clutches counted) are ivory yellow (Ridgway) and measure .98 mm. in diameter. Eggs of second and third clutches have from 2 to 5 eggs fewer than those in the preceding clutch.

#### HABITAT.

*C. fulgipedia* is typical of relatively open leaf litter in the deciduous seasonal forest, although individuals occur on up through the semi-evergreen seasonal forest across the lower boundaries of the cloud forest along the well-lighted and intermittently dry roadside. In this upper zone its range overlaps that of *C. chalcea*, but it occurs typically only in the drier localities. The altitude range is between 700 and 1,100 meters. It is completely terrestrial.

#### RELATIONSHIPS.

*C. fulgipedia* shares with a large group of species the possession of well-formed fringes on the first three legs and a strong cephalothoracic band; the dorsal cephalothoracic markings in the female check closely with those of *spiralis*, *bicincta* and *opima*, from Central America and Panama (see especially Chickering's keys and descriptions, 1946). The species appears most closely related, however, to *C. blanda* (Peckham, 1900) from Trinidad, and *C. panamana* Petrunkevitch, 1925, from Panama. It differs from *blanda* in the absence of red hairs on the clypeus and in the form of the palpal tibial spine. The abdominal pattern appears identical with that figured by Peckham for *placatus* from Brazil, and the palps are also similar (Peckham, 1901, pls. xxv, fig. 11, xxvi, fig. 2). It differs from *panamana* as follows: the first leg tibial ventral spines are 1r-2-2, not 2-2-2; the tibial spine of the palp is truncate in a lateral view and the embolus is cleft distally; the epigynum is slightly different, although obviously similar to those of both *panamana* and *obsoleta* (cf. Chickering, 1946, fig. 133); and the dorsal carapace markings are apparently better developed. *C. fulgipedia* is smaller than either *blanda* or *panamana*.

#### MATERIAL.

A total of 142 specimens of *C. fulgipedia* have been preserved, including exuviae. They are distributed as follows among the instars: first instar, 35; second, 36; third, 8; fourth, 8; fifth, 7; sixth, ♀, 4; sixth, ♂, 9; seventh, ♀, 6; adult, ♀, 15; adult, ♂, 14. All were taken within a radius of two kilometers of Rancho Grande. The following have been designated as holotype and paratype:

**HOLOTYPE:** Male. Cat. No. 461193, Department of Tropical Research, New York Zoological Society; roadside between Guamitas and Rancho Grande, near Maracay, State of Aragua, Venezuela; deciduous seasonal forest; 900 meters; June 30, 1946.

**PARATYPE:** Female. Cat. No. 461184, Department of Tropical Research, New York Zoological Society; same location as holotype; July 12, 1946.

The name *fulgipedia* is proposed in reference to the brilliant iridescence on the legs of the male.

#### *Corythalia xanthopa* sp. nov.

#### DIAGNOSIS.

All light scales and scale-hairs on carapace and abdomen yellow in life, creamy to brown in alcohol, in both sexes and in young; no submarginal cephalothoracic band in adult of either sex. Adult male with long, thick hairs on palp and clypeus making bright yellow band in life (pale yellow to cream in alcohol); abdomen above entirely bright yellow (brownish in alcohol). Adult female clypeus with pale hairs or scales completely lacking, abdomen black medially, flanked in life by a pair of broad longitudinal yellow stripes, which persist subdermally and in alcohol as pale areas. Both sexes in adult with one femoral prolateral spine on first leg and clearly fewer than 20 teeth on its tarsal proclaw. Adult male with fringes on all legs though they are weak on first; dorsal fringe of fourth leg in life formed principally of yellow hairs. Tibial apophysis of palp non-serrate, pointed; embolus tip pointed. Courtship and aggressive displays sharply distinct, the fourth leg being elevated during aggressive display only. Size small, total length of adult males around 4 mm., of females around 5 mm. Terrestrial on trail and forest edges; semi-evergreen seasonal and lower part of montane cloud forests; 740-1,100 meters.

#### EXTERNAL CHARACTERISTICS IN ADULTS AND YOUNG.

#### COLOR IN LIFE.

(Text-figs. 2, R-X, 14, 15 C).

[All yellow mentioned below is straw yellow (Ridgway)].

**ADULT MALE.** *Cephalothorax:* Carapace integument black with a faint small patch of yellow hairs on each side between AME and ALE. AME and ALE unchanging black rimmed with yellow hairs. Short and fairly long yellow hairs densely covering black integument of clypeus and inner distal half of chelicerae, which may be spotted with brown proximally; yellow hairs all directed toward the center. Mouth-parts and sternum black. Palp integument black except for pale distal half of femur and entire patella and tibia, which are also covered densely with long yellow hairs. All legs black, except for tarsi, including ventral fringes and all dorsal fringes on fourth leg. Fringes on patella, tibia and metatarsus of latter formed mostly of yellow hairs with a few black. All tarsi pale, yellowish or brown, not black, the first

and second pairs darker than third and fourth. No white or yellow scales on legs. Iridescence in usual locations and, in addition, in same positions on fourth leg. *Abdomen*. Integument black, entirely covered dorsally with yellow scale-hairs which appear brighter than straw yellow because of their shininess; a suggestion of a distal yellow chevron; a scattering of long black and pale hairs projecting through scale-hairs. Venter black with dark brown striations in indistinct stripes.

**ADULT FEMALE: Cephalothorax.** Carapace integument black with a few yellow hairs irregularly outlining ocular quadrangle. Eyes black rimmed with yellow. Clypeus naked. Chelicerae and mouthparts black. Palps black except for distal part of femur and entire patellae which are pale. Sternum black. Legs black except for distal half of metatarsi and all tarsi, which are brown. No white or yellow scale-hairs.

*Abdomen.* Above, black, with a pair of long broad stripes of yellow scale-hairs extending two-thirds of distance to posterior tip and beginning at highest point on outer margin of dorsal surface. Behind these a pair of indistinct yellow spots, or, rather, the yellow stripe is interrupted on each side by a black spot joined to its fellow by an indistinct yellow band. Lateral stripes often partly interrupted farther forward by two other, partially isolated spots; a few black and pale hairs as in male. Venter, black except for a pair of ovoid yellowish patches spotted with black.

**YOUNG; FIRST INSTAR:** Typical of *Corythalia*: true pigment lacking but with the usual two abdominal bands clearly visible in latter part of stadium.

**SECOND INSTAR:** From this point on, the species is distinct in having all light carapace and abdominal markings yellow, not white and bronze, and in the tardy development of leg pigment. The black integument (dark brownish-gray on abdomen in early second instar) and basic pattern of two abdominal bands are, however, typical of the group. Second instar, carapace: scales and light hairs lacking except for a very few long pale hairs around lower margin of AME. Clypeus, mouthparts and sternum black. Palps, legs and spinnerets translucent buff. Abdomen: the bands are very pale yellow, each composed of a single row, in this stadium, of large-diametered scale-hairs of unequal length, giving a characteristic uneven, scraggly appearance to the bands; longer hairs in the anterior band near middle project posteriorly; anterior wider than posterior throughout instars; here it is straight, while the second is slightly wavy with an anterior median peak; neither curves forward or back on sides. Two terminal abdominal spots though present, are inconspicuous. As usual, there is pale integument beneath bands and spots. Venter apricot brown.

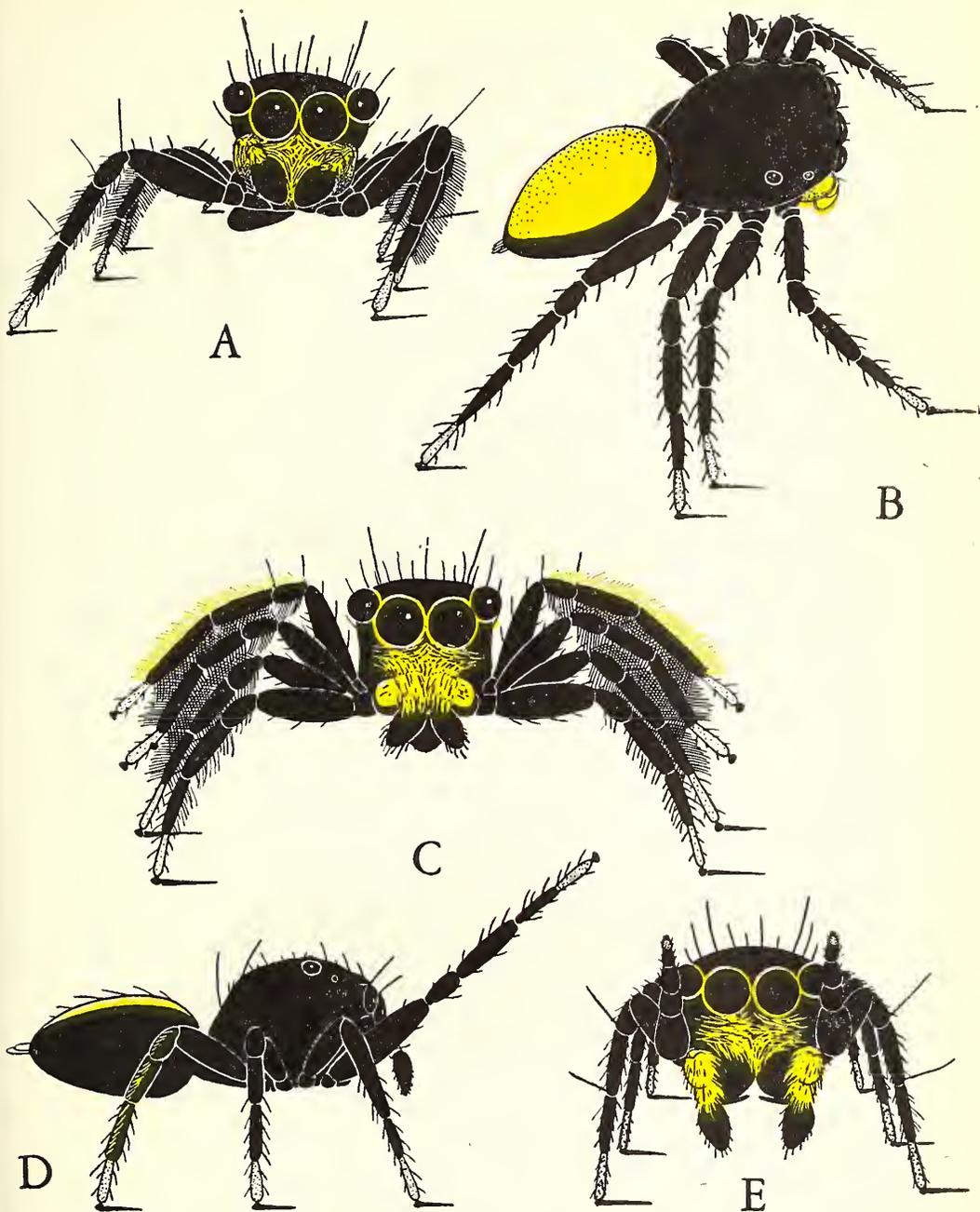
**THIRD INSTAR:** Carapace with a tiny pale

yellow spot behind each PLE, sometimes absent; appendages and abdomen as in preceding stage.

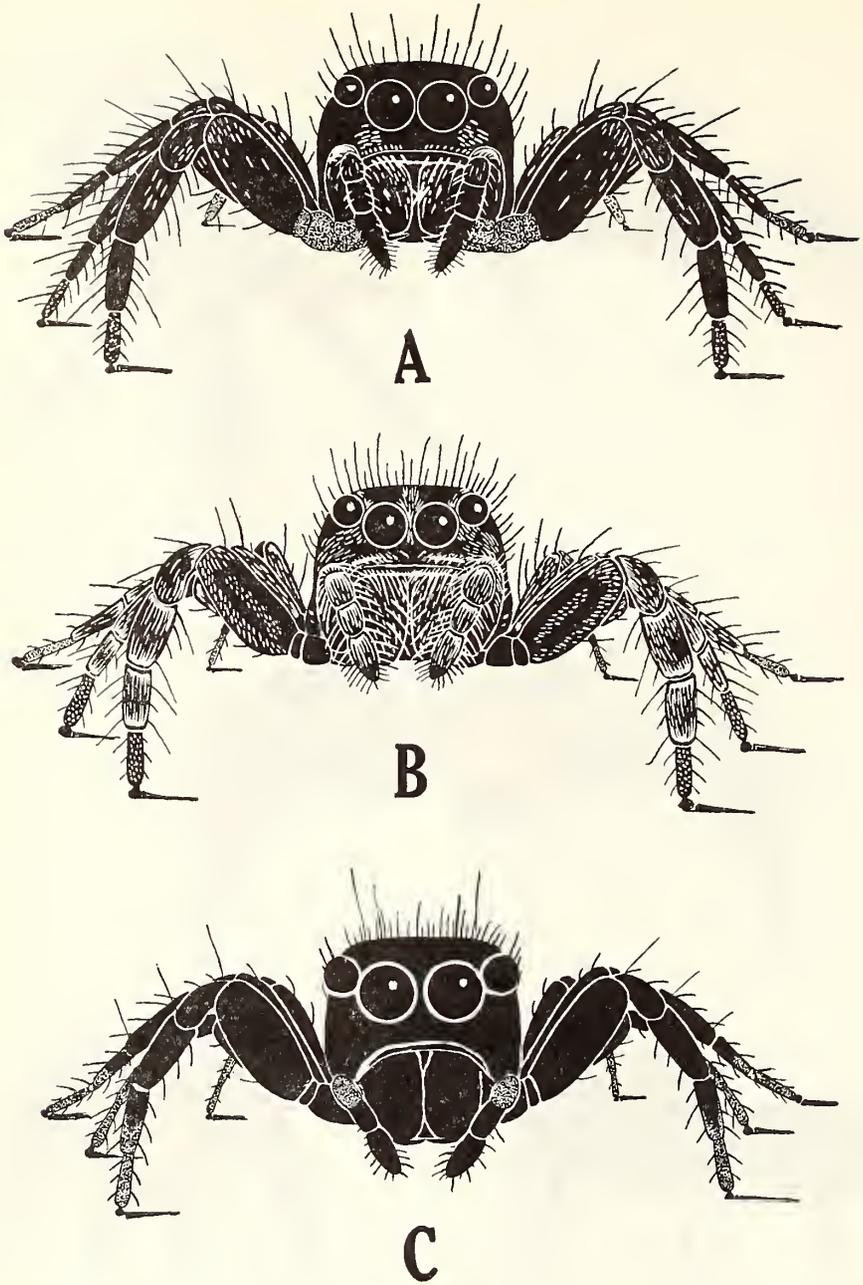
**FOURTH INSTAR:** Unknown.

**FIFTH INSTAR:** Carapace with a few yellow hairs on ocular quadrangle, sometimes numerous enough to form a faint band between PME, or there is only a spot around each PME, with another in middle anterior part of ocular quadrangle; behind each PLE a yellow spot as in preceding stadia, or an almost complete bar. AME and ALE rimmed narrowly with yellow; clypeus still naked; palp translucent; legs either still translucent or banded strongly. Abdomen as in preceding stadia, but bands are now relatively narrower and tend to approach each other on sides. Venter light brown, spotted and blotched irregularly with dark brown.

**SIXTH INSTAR, MALE AND FEMALE:** Cephalothorax: Dorsal part of carapace marked very variably with yellow, the variability depending not only on wear, but on individual differences, since fresh-molted specimens may appear quite different, regardless of sex; in general, however, males tend to have more yellow than females. Scale-hairs of this region now brighter, straw yellow as in adult, than in preceding stadia; at maximum it is a general frosting over of entire ocular quadrangle and extending behind it over anterior thorax in a rough inverted triangle; the minimum development is a small spot around or in front of each PME and around PLE, plus a strong spot behind each PLE; these latter spots are often joined by a faint yellow bar in place of the broad triangle. Scales rimming ALE and AME ranging from rust to chrome yellow. Male has a few submarginal yellow hairs on thoracic part of carapace; this is the only stage in which they appear at all in this sex in this species; also for the only time in males there are a few yellow and white scale-hairs on upper anterior parts of femora, patellae, and tibiae of all legs; in females corresponding hairs appear only on patellae. The characteristic yellow scale-hairs and hairs of adult males first appear, although pale and sparse, in this instar on clypeus, chelicerae and palp patellae. Basal two-thirds of palps either dark or translucent in both sexes; remaining palp segments always translucent except for a few black hairs on the brownish male tarsus. Legs black except at least for coxae, trochanters and tarsi, which are all translucent horn in both sexes; in addition, basal parts of femora, patellae and distal parts of tibiae may be pale, especially in female. Abdomen. Both bands remain very pale, dull yellow in both sexes. Anterior band still broader than posterior, with a slight, posteriorly directed median apex; posterior continuing to have a median bulge directed forward and the ends curve forward laterally. Terminal paired spots either distinct and laterally placed or very obscure; in addition there is usually a median terminal indistinct blotch or band,



TEXT-FIG. 14. Display in *C. xanthopa*. **A**, frontal view of rocking preface to threat and courtships displays; **B**, dorsal view of same; **C**, threat display; **D**, courtship, Stage I, lateral view; **E**, same, frontal view. Yellow scales indicated in color; iridescence of legs not shown.



TEXT-FIG. 15. Frontal views of adult ♀ *Corythalia*. **A**, *C. chalcea*; **B**, *C. fulgipedia*; **C**, *C. xanthopa*.

in place of simple paired spots, this terminal irregularity being typical from this instar onward.

**SEVENTH INSTAR, FEMALE:** Cephalothorax: Ocular quadrangle and thoracic region as in preceding stadium, the yellow scale-hairs being very variable, although in general there is less yellow than in sixth instar. Always, however, there is at least some yellow across anterior part of quadrangle, with spots traceable in front of or around PME. The thoracic region is the most variable,

the yellow ranging from a simple pair of spots behind PLE to an inverted triangle almost as extensive as in some preadult males. ALE and AME rimmed with chestnut. Clypeus with a very few yellow hairs. Palps usually translucent horn; rarely with darkened femora, tips of tarsi dark. Legs strongly banded as in preceding stage; the same segments and degree of variation are involved, though individuals are always darker in the seventh than in the sixth stage. A few yellow scales on dorsal part of fourth

femur; rest of femora, patellae, tibiae and proximal half of metatarsi with a few sparse whitish and yellowish scales, especially at joints, on all except first legs where they are practically absent; these leg scales reach maximum development for this species in this sex and stadium. Abdomen. The most characteristic feature of this stadium is the breaking down of anterior band into a semicircle of variable, asymmetrical, irregular spots. Usually three decided spots occur anteriorly, and another pair, one on each side, behind and lateral to, the outer spots; sometimes, however, the spots are indistinct and tend to merge. The second band is unbroken but slender, usually strongly W-shaped, with a decided median peak and the lateral edges curving strongly forward toward the more posterior spots. The general effect is of a broken circle occupying anterior two-thirds of abdomen. The terminal markings usually consist of a fairly continuous band, just before the spinnerets, triangular, with the apex directed forward, or it may be an arched band; it is never a simple pair of spots. Venter brown, spotted and speckled with black and with a large black irregular central marking; there are some short grayish-buff hairs, especially laterally.

SUMMARY OF COLOR DEVELOPMENT IN  
*C. xanthopa*.

(It must be kept in mind that Fourth Instar is unknown).

*Integument.* Carapace, mouthparts and sternum black in second instar, as usual. Palps remain completely translucent and pale until sixth in male, when basal part of femur may or may not darken; in female basal part of femur may darken to brown in sixth or seventh. Leg pigment develops tardily, two or three instars later than in *chalcea* or *fulgipedia*. There is no trace of

banding before fifth, and then it is present in only two out of three observed specimens. Preadult males and females (sixth and seventh instars, respectively) have the legs still pale at least proximally and distally, and often strongly banded; even the adults have all feet pale, not only the third and fourth. Integument of abdomen does not attain full blackness until third, the second, at least in early part of stage, being dark gray-brown.

*Yellow hairs and scale-hairs:* Throughout the instars the color yellow almost completely replaces the white and bronze of *chalcea* and *fulgipedia*, the only exception being a few whitish or bronze leg scales in the preadult instar. Carapace, like that of *chalcea*, lacking light scale hairs until third. Unlike *chalcea*, the basic pattern of dorsal carapace is two postocular spots instead of a postocular bar. In later instars, from the fifth through the seventh female, there is a considerable and highly variable amount of yellow on and immediately behind ocular quadrangle, especially concentrated around and near PME; only the latter areas survive in adults. Large eyes rimmed as usual with yellowish, varying from rust to chrome, from fifth on. Clypeus and chelicerae remain naked (except for the usual black bristles) until sixth; then the first pale yellow hairs appear on palps, face and chelicerae of male, reaching their full development a stage later in the adult. In females, a few yellow hairs appear on clypeus in the seventh only, being lost in adult. A few white and yellow leg scales in sixth only of males and in seventh only of females. Abdomen. The yellow scales are in the form of two bands and a terminal pair of spots throughout the sixth instar. The preadult (7th instar) female is unique in having the anterior band broken into spots.

STRUCTURE.

With the characteristics described on

TABLE XII.  
Relative Proportions in *C. xanthopa*.

	Males		Females	
	Range %	Average %	Range %	Average %
Carapace Length: Breadth	69-75	71.8	68-74	71.0
Carapace Length: Height	57-65	60.0	55-59	56.2
Carapace Length: Oc. Quad. Length	38-49	43.2	38-44	40.4
Carapace Length: Oc. Quad. Breadth	68-75	71.2	66-68	67.2
Carapace Length: AME Diameter	20-22	21.2	19-21	19.8
AME Diameter: ALE Diameter	66-77	71.2	69-74	71.2
AME Diameter: MLE Diameter	18-20	19.2	19-21	20.4
AME Diameter: PLE Diameter	52-63	60.4	55-67	61.4
AME Diameter: Clypeus	42-50	45.4	43-52	47.3
Carapace Length: 1st Tibia	31-35	33.0	29-31	30.6
Carapace Length: 2nd Tibia	32-35	33.4	30-32	29.6
Carapace Length: 3rd Tibia	42-47	45.0	38-42	40.6
Carapace Length: 4th Tibia	45-48	47.0	42-45	43.2
Carapace Length: 1st Metatarsus	29-32	30.4	30-32	29.8
Carapace Length: 2nd Metatarsus	30-33	31.8	29-31	29.6
Carapace Length: 3rd Metatarsus	47-51	48.8	44-47	45.8
Carapace Length: 4th Metatarsus	52-57	53.6	51-54	52.2
Carapace Length: Palp	74-79	76.8	77-84	81.4

pp. 3 ff. In contrast to color development, the course of post-embryological development of structure shows no clear specific distinctions except in the relative tardiness of the appearance of some of the spines and details of tarsal claw-teeth development. With these exceptions, therefore, the discussion below concerns adults only. Ranges and averages of proportions are given in Table XII; and comparisons with the other species in Table I. In regard to development, see also pp. 4 ff.

*Carapace.* Height clearly more than half of length; anterior part of thoracic profile descending very gently. Ocular quadrangle broad anteriorly, especially in males. Greatest width at bulge before PLE, or width at that point equal to width at level of second-to-third coxae.

*Eyes.* Eyes relatively about as in *chalcea*, except that ALE and PLE are a little larger. PME slightly nearer to PLE than to ALE.

*Clypeus.* Slightly more than half diameter of AME.

*Chelicerae.* Apparently no teeth on superior margin.

*Maxillae.* Outer margin scarcely concave; tubercle faintly indicated.

*Lip.* No distinctive specific characteristics.

*Sternum.* Broader than in other two species, the width in both sexes being four-fifths of its length, and slightly wider anteriorly at base of lip; lateral excavations feebly developed.

*Bristles.* No distinctive specific characters.

*Legs.* Fourth leg usually longer than third in both sexes; first longer than second in both sexes in only about 60% of individuals measured. In the formula, Table XIII, the alternate order is expressed by the figures in parentheses in the upper row; figures of proportions are averages; for range of variation see Table XIII. Segments slender, as in *chalcea*. Tibial index: first leg, males 23 to 25, females 24 to 25; fourth leg, males 17 to 22, females 18 to 20.

Fourth metatarsus longer than third to a greater degree than in other two species. Iridescence feebly developed in this species, though present on same segments as in *chalcea* and *fulgipedia* on first three legs, and on corresponding segments of fourth leg in addition; there is relatively little flattening even of the strongly iridescent third and fourth tibiae and metatarsi. Fringes of first three legs also similar to those found in other two species, the segments of occurrence and relative strength being unchanged (see *ful-*

dorsal and ventral surface. The main specific difference is the presence of a well developed fringe on fourth leg; this is distinguished from that of third in having dorsal fringe composed chiefly of yellow, not black, hairs and in being much longer, not shorter, than ventral; tibial ventral fringe shorter than corresponding width of segment on fourth leg, although it is as thick as on third.

*Spines.* Adults: fewer than in other two species. The following distinctions are constant; for variables consult Table II. Femur: prolateral 1, not 2, at least on first two legs; retrolaterals lacking, at least on first leg. First and second tibiae: proximal ventrals always lacking. First metatarsus: proximal retrolateral always lacking. No constant sexual differences.

Young: compared with *chalcea* and *fulgipedia*, there is a lag in spine development, the spines of tibia and metatarsus which always occur in the second instar in these species (Text-fig. 2, FF, GG) not appearing in *xanthopa* until the third or later. The first and second metatarsal ventrals are not always complete even in the fifth, nor all the constant pro- and retrolaterals of the same segments in the sixth. Details are as follows:

As in *chalcea* and *fulgipedia*, the femur dorsals are present in *second instar*, as are the metatarsal prolateral distals of first and fourth legs and the metatarsal retrolateral distals of third and fourth. The rest of the earliest appearing constants, however, do not appear in *xanthopa* until the third stadium or even later. These delayed spines are the following: tibial prolateral distals, all legs; tibial retrolateral distals, third and fourth legs; metatarsal prolateral distals, second and third legs; metatarsal ventral proximals and distals, first and second legs; metatarsal ventral distals, fourth leg. Although this group of spines usually appears in the *third instar*, some specimens still lack the second leg's tibial prolateral distal, while the metatarsal distals of all legs are usually weak or incomplete. The *fourth instar* is unknown in *xanthopa*. In the *fifth instar* the constant first and second metatarsal ventrals and pro- and retrolaterals of the same segment are still usually incomplete, unlike the usual condition in *chalcea* and *fulgipedia*. In the *sixth* and *seventh* instars, the spines are as well developed as in corresponding *chalcea* and *fulgipedia*, allowing for specific differences, except that the constant metatarsal pro- and retrolaterals are not always complete even in the sixth instar.

*Trichobothria; Long, Dark Bristles; Short, Pale Bristles.* No distinctive specific characteristics.

*Tarsal Claws.* First, second and third leg claws less differentiated from fourth and from young than in other two species. Table III gives comparisons with the other species.

Retroteeth almost as slender, close-set and well graduated as pro-teeth in both first and fourth legs; as usual there are usually one or more broad, truncate rudiments or ves-

TABLE XIII.

*C. xanthopa*: Leg Formula.

	4(3)	3(4)	1(2)	2(1)
Males	2.21	2.18	1.70	1.64
Females	2.07	2.01	1.56	1.55

*gipedia*, p. 26, for details). However, the hairs are less dense than in this species, they are scarcely developed in first leg, and there is less difference in hair length of fringes of

tiges at proximal ends of series, and in individuals there may be variations of one or more teeth in either direction. In one adult female fourth leg, there were 8 completely subdermal proteeth proximal to the usual, well graduated, extruded series of 13.

*Palp.* (Text-fig. 9, E, F). Slender. Tibial apophysis slender, simple, non-serrated, tapering to a point which extends almost to tip of distal external loop. Ventral tibial tubercle not conspicuous, poorly chitinized, close to distal edge. Whorl of embolus occupying distal third of bulb; stylus slender, much longer than shorter diameter of whorl, tip not forked.

*Epigynum.* (Text-fig. 10, E, F). Horizontal extent of anterior pair of dark spots, viewed externally, less than that of posterior pair (spermathecae), and they do not quite extend to anterior edge of bean-shaped patches. In size, the epigynum is a little larger than that of *chalcea*, a much larger species.

*Abdomen.* No distinctive specific characters.

## SIZE AND GROWTH.

### MEASUREMENTS.

TABLE XIV.

*C. xanthopa.*

Length Ranges and Averages in mm.

<i>Instar</i>	<i>Carapace Length</i>		<i>Total Length</i>	
	<i>Range</i>	<i>Av.</i>	<i>Range</i>	<i>Av.</i>
1st	.79-.85	.83	1.44-1.73	1.54
2nd	.99-1.03	1.01	1.34-1.63	1.44
3rd	1.09-1.2	1.14	1.82-2.11	1.96
5th	1.53-1.55	1.54	2.5-3.07	2.78
6th ♀	1.74-1.95	1.86	3.26-3.84	3.56
6th ♂	1.92-2.29	2.09	2.9-3.46	3.13
7th ♀	2.02-2.22	2.14	3.55-4.13	3.91
Adult ♂	2.05-2.73	2.4	3.46-4.99	4.27
Adult ♀	2.33-2.8	2.58	4.32-5.95	5.04

Table XIV gives the extremes and averages of carapace and total lengths of all specimens of *C. xanthopa*. Table IV gives comparisons with the other species. The amount of relative growth with each instar is diagrammed in Text-fig. 11. Measurements in millimeters of the male holotype and female paratype are as follows:

Male holotype. Total length in alcohol 4.8 mm.; carapace length 2.7; carapace breadth 1.9; carapace height 1.5; ocular quadrangle length 1.0; ocular quadrangle breadth 1.9; diameter AME .55, ALE .40, MLE .10, PLE .34; clypeus height .28; 3rd patella breadth .38.

Leg	Femur	Pat.	Tib.	Metat.	Tarsus	Total
1st	1.4	.68	.85	.79	.55	4.27
2nd	1.4	.79	.92	.89	.41	4.41
3rd	1.8	.85	1.2	1.3	.62	5.77
4th	1.9	.62	1.3	1.4	.62	5.84
Palp	.72	.41	.21	—	.68	2.02

Female paratype. Total length in alcohol 4.9 mm.; carapace length 2.7; carapace

breadth 1.9; carapace height 1.5; ocular quadrangle length 1.1; ocular quadrangle breadth 1.8; diameter AME .51, ALE .36, MLE .10, PLE .34; clypeus height .22; 3rd patella breadth .37.

Leg	Femur	Pat.	Tib.	Metat.	Tarsus	Total
1.	1.2	.79	.82	.79	.44	4.04
2.	1.4	.79	.85	.79	.44	4.27
3.	1.7	.79	1.1	1.3	.55	5.44
4.	1.6	.65	1.2	1.5	.58	5.53
Palp	.68	.44	.34	—	.65	2.11

### RECORDS OF INSTAR DURATION.

Egg: About 15 to 18 days (records of 2 broods). *First instar*: 12 to about 16 days (records of 3 broods); *second instar*: about 17 days; *third instar*: unknown, but more than 14 days (all examples died or were preserved before molting); *fourth instar*: unknown; *fifth instar*: the single specimen, a female, allowed to molt from this stage did so on the 18th day after capture; *sixth instar*: a reared female, 17 days; three females captured in this stage molted on 21st, 22nd and 28th days; three males on 17th, 17th and 21st after capture; *seventh instar*: total duration, three females, 22, 24 and 28 days; a fourth, already in seventh instar when captured, molted on the 24th day.

### BEHAVIOR.

(Text-fig. 14; Pl. I, Fig. 4).

#### COURTSHIP DISPLAY.

**DIAGNOSIS:** *Stage 1a.* A short series of rapid, side-to-side rocking jiggles. *Stage 1b.* First legs extended forward, straight, parallel, and raised to 45° angle above the horizontal. Often punctuated with the rocking of Stage 1a. *Stage 2.* The usual forward extension of first legs to horizontal to touch female and creep over her. At no point in courtship are the decorated fourth legs used, or even visible.

**DESCRIPTION:** *Stage 1a.* Carapace moderately elevated, all legs touching ground; abdomen slightly pendent; palps hang down, at outer sides of clypeus. Action is an exceedingly swift rocking motion from side to side. Analyzed from motion picture film, this is seen to consist of (1) alternate shifts of the carapace to right and left and (2) a corresponding, complicated bending and shifting of the legs; those on the side of the tilted body are gathered in a forwardly-directed cluster, the femora bent up and the patellae down at strong angles; those of the opposite side are well extended laterally, the first and fourth legs serving as props fore and aft, while the second and third are variably extended, usually close together, between. A series consists of from a single pair of rocks to about four pairs; they are of such lightning speed that even a 16-mm. camera at 24-frames per second fails to stop the blur of action. The abdomen swings pendulum fashion in the opposite direction from that of the sinking of the carapace.

A series of rocks alternate with approaching zigzags.

*Stage 1b.* Body elevated moderately on second, third and fourth legs; first two legs directed straight out to front, parallel, and elevated to angle of  $45^\circ$  or more above the horizontal; palps hang down at sides of clypeus, motionless; abdomen extended straight out. This stage is often punctuated with rocking of Stage 1a, sometimes with the first legs remaining in air.

*Stage 2.* Typical, the first legs being lowered to the horizontal position to touch the female as she allows it and to creep over her into copulating position. There is practically no preliminary patting.

#### THREAT DISPLAY.

**DIAGNOSIS:** *Stage 1.* The identical rapid, rocking jiggle used in courtship, Stage 1a (p. 35). *Stage 2.* Body elevated high on first legs; second, third and fourth pairs all off ground, raised successively higher forming perfect fan; posing for several seconds in this position.

**DESCRIPTION.** *Stage 1.* Rocking. The rocking motion is less important in threat than in courtship, being almost always confined to one or two jiggles before the fan display, rarely occurring between the fan displays; once or twice I have seen it omitted altogether from threat displays.

*Stage 2.* Carapace supported on tips of first legs, the femora being held at right angles to body, the distal segments arching widely to touch ground far out from carapace; the other three pairs are arched successively higher and more widely, all held free of the ground, suggesting a perfect fan, and held up to several seconds in statuesque immobility. The yellow dorsal fringe of the fourth leg, as well as the pale feet of all are very conspicuous. At the height of display the tip of the abdomen often touches the ground as a prop. The palps are held motionless, their yellow-haired distal-femora, patellae and tibiae touching each other in the midline below the yellow clypeal beard; the black tarsi are often directed outward.

The aggressor advances sidewise from time to time, between fan posing, always facing his opponent, an inch in one direction an inch in the other. For this progress, the second or second and third pairs are lowered, to be raised again into rigid fan position as soon as he stops. The abdomen is never raised to the horizontal in these progressions, but is just cleared of the ground; rocking between fan displays, as has been said, occurs only rarely. Sometimes, at start of the fan phase, the third and fourth legs twitch up and down in the air, before motionless posing; in view of its rare occurrence, it seems likely that only balancing is involved, rather than a peacock-like shimmer of iridescence; on the other hand, since this vibration would seem to increase the play of iridescence, it may be a tendency being en-

couraged in the species by natural selection, which has not reached its full development.

This species was seen actually to fight only once. On this occasion two males were confined much more closely than usual, in a photographic cell only an inch square, under hot lights. Poison injected by his opponent's chelicerae kept one of them incapacitated, upside down, for an hour, but at the end of that time he recovered fully. The second-long fight started and finished so quickly that I missed seeing whether the usual aggressive display preceded it. No such behavior was ever seen in the field, or in the usual roomy observation dishes.

#### HABITS ASSOCIATED WITH BROODING.

Five females which molted and mated in the laboratory laid eggs on the 27th, 28th, 30th, 33rd and 39th day after molting, respectively. Only those laid on the 30th and 33rd day hatched; the parent females of these young were mated on the 9th and about the 19th day after molting, respectively. A sixth female laid eggs on the 44th day after capture as an adult; those eggs also failed to hatch. The second clutch of individual females, were, as usual, laid a few days before the young of the first clutch left the cocoon, that is, about three weeks after the first clutch was laid (two examples); a third clutch was laid by one female 35 days after the second; most of the second lot, however, failed to hatch, and none of the third, nor of the later clutches of other females.

The cocoon is typical, spun on the underside of a dead leaf, flat, with the central mass of eggs, within the fine inner sac, forming a bulge; the dimensions of the whole are about 7.5 x 9.6 mm. The eggs, numbering 14 to 21 (four perfect first clutches counted) are straw yellow (Ridgway), and measure .34-.44 mm. Eggs of later clutches range from almost normal numbers to four or five; none of these small clutches ever hatched. The period of incubation is between 15 and 18 days (two examples).

#### SEASONAL OCCURRENCE.

There was a decided peak of abundance at the beginning of the rainy season in both 1945 and 1946, extending roughly from mid-April to mid-May. However, the species was exceedingly scarce throughout its range in 1946, or perhaps 1945 was a season of abnormal abundance. The chief weather characteristic of early 1946 was an early and chilly wet season. Thanks to a 150-foot stretch of path along the Water Trail near the laboratory, fairly accurate counts could be made throughout each season. Maxima of around 60 were counted on a number of days early in the rainy season during 1945; the following year no more than 6 were ever counted in a single day under apparently identical conditions. Thirty minutes were used to cover exactly the same strip of ground each time, a careful watch being kept

about three feet to each side of the path, that is, to the edge of the cleared space. It was found by sifting experiments (see below) and observation that very few individuals stayed out of sight under the leaves, especially during optimum weather for the species. These conditions included a moderate amount of sun filtering through the canopy following a rainy or densely misty night. Practice made the spiders very easy to see. Curiously, very few young were observed in either year. This observation area was never disturbed by sifting, but about 20 yard-square samples, taken from time to time from adjacent, equally rich pathside leaves yielded practically no early stadia. Before the sifting, it was assumed that very young spiders in particular hunted such prey as collembola in the lower part of the litter. However, more sifting should be done in years of abundance.

#### HABITAT.

This species seems to be confined to semi-evergreen seasonal forest and the lower borders of montane rain forest, from 740 to 1,100 meters; the individuals at the lower levels were found in semi-evergreen seasonal riverbed intrusions into deciduous forests. They were never taken in typical samples of the latter, nor in the immoderately mist-laden slopes of the pure montane cloud forest above Rancho Grande. They are completely terrestrial, among dead leaves on edges of clearings and trails; they never occur in dense undergrowth on the one hand nor in bright, often dried areas like open roadsides on the other.

#### RELATIONSHIPS.

*C. xanthopa* does not appear to be closely related to any species so far described. The strong fourth leg fringes set it apart at once from all described Central American and West Indian *Corythalia*. *Dynamius fimbriatus* Peckham, 1900, from Brazil, has heavy fringes on all legs, but differs in most other respects. The similarity of the male clypeus decorations to those of the otherwise very different *C. canalis* (Chamberlin, 1925) is a good example of the sporadic appearance of male decorations.

#### MATERIAL.

A total of 116 specimens of *C. xanthopa* have been preserved, including exuviae. They are distributed as follows among the instars: the first instar, 13; second, 11; third, 4; fourth, none; fifth, 3; sixth, ♀, 5; sixth, ♂, 7; seventh, ♀, 15; adult, ♀, 28; adult, ♂, 30. All were taken within a radius of two kilometers of Rancho Grande. The following have been designated as holotype and paratype:

**HOLOTYPE:** Male. Cat. No. 461195, Department of Tropical Research, New York Zoological Society; Water Trail, Rancho Grande, near Maracay, State of Aragua, Venezuela; 1,100 meters; lower cloud forest; Mar. 14, 1946.

**PARATYPE:** Female. Cat. No. 461196, Department of Tropical Research, New York Zoological Society; same location as holotype; Sept. 2, 1946.

The name *xanthopa* is proposed in reference to the conspicuous yellow face of the male.

#### SUMMARY.

Three new species of *Corythalia*—*chalcea*, *fulgipedia* and *xanthopa*—are described after detailed study in the field and laboratory. All were taken on a single mountain range of the coastal Andes of Venezuela, at elevations of 700 to 1,300 meters; the niches of all the species overlapped.

Range of variation in color, measurements, proportions and integumentary structures are emphasized in each species, the course of their post-embryological development is traced and display behavior recorded. In these descriptions lie clues to the evolution of the genus and family, to the maintenance of specific barriers and to the evolution of display. Discussion of these subjects will follow in subsequent sections of this study. Here may be noted the following points of general interest to students of spider development and speciation:

1. *Specific differences:* In adults, the greatest specific distinctions occur in color and in display behavior; the principal minor differences involve size, carapace shape, leg length, form and size of palp and epigynum, presence or absence of certain spines and details of the tarsal claw-teeth. In the young, differences are confined principally to color and pattern, and to appearance time of leg pigment, certain scale groups and secondary spines.

2. *Sexual dimorphism:* Color dimorphism ranges from slight to extreme among the three, closely related species. There is little sexual difference in size, the ranges in each species overlapping. The legs, as usual, are slightly longer in the male. Aside from white or colored scales and hairs, the male secondary sexual decorations consist of flattened iridescent areas and fringes on the legs; these structures are closely correlated with display. The sexes cannot certainly be distinguished before the sixth (preadult male) instar.

3. *Instars.* There are seven instars in the male, eight in the female, each of the juvenile stadia lasting from about 12 days to almost two months; the preadult stadium is usually longest. A male and female each lived almost a year from the time of hatching. The first, second, fifth and adult instars show the greatest changes. In the first instar the carapace is about 30% of its adult length; most of the growth occurs in the late stadia.

4. *Proportions.* In the first stadium the carapace is relatively higher, and in the second lower than in the adult. The sternum is broader in early instars. *Corythalia* is unusual in having the two posterior legs longer than the first, correlated with their use in display; this trait is evident even in the first

instar, although the legs are shorter, thicker and more nearly equal at that time. The metatarsi in late stages elongate at the expense of the tarsi.

5. *Eyes*. Theanlagen are unmistakably salticid in arrangement and relative size even in the first instar, and in the second are typical of the *Plexippus* group and of *Corythalia*. They are relatively slightly larger than in adults, less recurved, and project farther laterally.

6. *Integumentary structures, including pigment and scales*:

a. *Appearing in first instar*: Primary bristles of carapace and legs.

b. *Appearing in second instar*: Black integumentary pigment of carapace and abdomen; present on legs, if at all, in bands; two primary scaled bands and terminal spots on abdomen; border scales of AME; primary carapace scales (or in third instar); primary spines (all invariable in adult), including some on each spine-bearing segment, especially distally; a few trichobothria and short, pale bristles, all well distributed; tarsal claw-teeth, those of pro- and retro-series being less differentiated than in adult, and those of first legs less distinct from fourth; facial bristles complete (or in third instar).

c. *Appearing in fourth and fifth instars, or later*: Darkening of legs; highly variable secondary scalation, often including metallic bronze scales, on carapace and abdomen; highly variable scalation of legs; secondary spines, many of them variable in adult, and including certain spines on each segment; remaining trichobothria and short bristles; additional teeth on tarsal proclaws, although retroteeth are reduced, especially on anterior legs; chelicerae teeth in sixth instar or later.

d. *Appearing only in adult males*: In all species, fringes and iridescent areas on legs; in two species, complete yellow or bronze scalation of dorsal side of abdomen; in one species, long yellow facial and palp hairs (anlagen in preadult).

e. *Reduction of structures*: Both primary and secondary carapace and leg scalation of the middle and preadult instars are usually reduced or eliminated in the adult male, and sometimes in the adult female as well. Apparently the only other cuticular structures to be reduced in late instars are some teeth on the retroclaws and the primary trochanter bristle.

7. *Display*: Threat displays between rival males are distinct from courtship behavior in all species. The fringed, iridescent legs are always involved in threat display, but in *C. xanthopa* they are never used in courtship. True fighting, in which poison is injected, apparently does not occur in *Corythalia* except under rare laboratory conditions. Unlike most salticids, in all three species the first legs are less specialized than others, and are elevated only in the final stages of courtship and, sometimes, of threat display. Results of experimental work on the release mechanisms and functions of display will be recorded in a subsequent section.

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## EXPLANATION OF THE PLATE.

### PLATE I.

- Fig. 1. *Corythalia chalcea*. Preliminary posturing of males before threat display.
- Fig. 2. Same. Threat display, Stage I. Lower male is advancing in zigzag motion. Cf. frontal view of climax, Text-fig. 12.
- Fig. 3. Same. Courtship display, Stage II. Female is on vertical wall of box, facing away from male. The male's position, with first legs elevated and extended straight in front of him, is typical of Stage II courtship in all three species. Cf. Stage I, Text-figs. 12-14.
- Fig. 4. *Corythalia xanthopa*. Threat display, Stage I, dorsal view. Cf. Text-fig. 14C.



FIG. 1.



FIG. 2.



FIG. 3.



FIG. 4.

COMPARATIVE BIOLOGY OF SALTICID SPIDERS AT RANCHO GRANDE, VENEZUELA.  
PART I. SYSTEMATICS AND LIFE HISTORIES IN CORYTHALIA.



## 2.

A New Genus and Species of Orneodidae (Moths) from Rancho Grande, North-central Venezuela.<sup>1</sup>

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(Plate I; Text-figure 1).

[This is one of a series of papers resulting from the 45th and 46th Expeditions of the Department of Tropical Research of the New York Zoological Society, made during 1945 and 1946 under the direction of Dr. William Beebe with headquarters at Rancho Grande in the National Park of Aragua, Venezuela. The expeditions were made possible through the generous cooperation of the National Government of Venezuela and of the Creole Petroleum Corporation.

[The characteristics of the research area are in brief as follows: Rancho Grande is located in north-central Venezuela (10° 21' N. Lat., 67° 41' W. Long.), 80 kilometers west of Caracas, at an elevation of 1,100 meters in the undisturbed montane cloud forest which covers this part of the Caribbean range of the Andes. Adjacent ecological zones include seasonal forest, savanna, thorn woodland, cactus scrub, the fresh water lake of Valencia, and various marine littoral zones. The Rancho Grande area is generally subtropical, being uniformly cool and damp all the year because of the mountain cloud cap. The dry season extends from January until April. The average humidity during the expeditions, including parts of both wet and dry seasons, was 92.4%; the average temperature during the same period was 18° C.; the average annual rainfall over a 5-year period was 174 cm. The flora is marked by an abundance of mosses, ferns and epiphytes of many kinds, as well as a few gigantic trees. For further details see Beebe & Crane, *Zoologica*, Vol. 32, No. 5, 1947. Unless otherwise stated, the specimens discussed in the present paper were taken in the montane cloud forest zone, within a radius of 1 kilometer of Rancho Grande.]

## INTRODUCTION.

Four individuals of Orneodidae were collected at Rancho Grande, Venezuela, in 1946. All the specimens belong to a new genus and species. The specimens were captured along the road connecting Rancho Grande with Ocumare de la Costa, between kilometers 24 and 26. This region is approximately 3,400 feet high and is on the ocean side of the pass. The area is usually blanketed in clouds for the greater part of the day with the result that the vegetation rarely fails to be dripping with moisture (see Beebe and Crane, 1947, for maps and ecology).

The specimens were caught at separate times in 1946 but always on foggy days. It was necessary to beat the fog-drenched

bushes to startle the moths into flight, and unfortunately the insects were usually deluged. Three of the specimens were caught at the base of high, moist banks and the remaining specimen less than 15 feet from a similar bank. The pyraustid moth *Lamprosema coeruleonigra* Schaus was very common in the localities where the orneodids were taken and were distinctly partial to the same type of ecological niche. No Orneodidae were taken at lights although we operated lamps in this area in an attempt to collect larger series.

I wish to express my thanks to Miss Pamela Marmont for the venation-figure and to Sam Dunton for the photographs.

***Alinguata***, new genus.

Text-fig. 1.

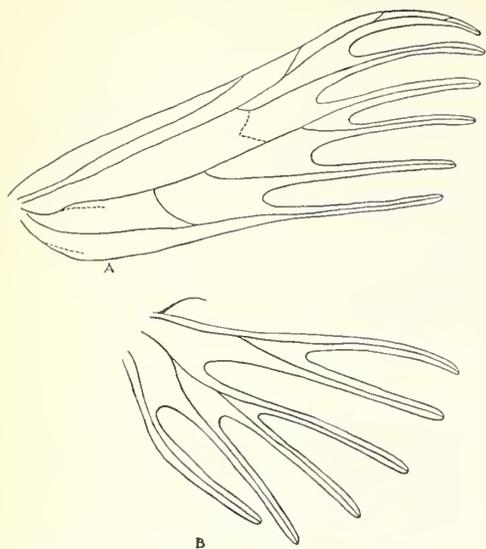
*Tongue and maxillary palpi absent.* Labial palpi decumbent and as long as width of eye. First joint of labial palpi bulbous; at its distal end broader than second and third joints; pedunculate at its juncture with the head. Second joint with a ventro-lateral tuft of specialized scales extending well along the third joint. Third joint of labial palpi acuminate and as long as second joint. Ocelli conspicuous and very slightly separated from eye. Vertex of head with a prominent anterior bulge, conical in outline looking down on head from above. Angle formed by vertex and front of head acute. The above characters have been determined from a detached head with the scales removed.

Legs slender. Epiphysis covered with long scales extending to first tarsal joint. One pair of spurs on mesothoracic legs and two pairs on metathoracic legs, with the outer spurs slightly shorter than inner spurs.

*Forewings not deeply cleft as in Orneodes.* Clefts in cell  $R_5$  and in cell  $M_2$  approximately equal in depth and cleft for one-quarter of wing. Cleft in cell  $M_1$  extends for one-third of wing and cleft in cell  $M_3$  but slightly more. Cleft in cell  $Cu_1$  reaches almost to one-half of wing measured along caudal margin of plume  $Cu_1$ .

Frenulum in hindwing long and prominent. Clefts of hindwing as follows: Cleft in cell R is one-half of length of wing measured along costal margin, cleft in cell  $M_1$  is five-sixths of length of wing measured

<sup>1</sup>Contribution No. 784, Department of Tropical Research, New York Zoological Society.



TEXT-FIG. 1. *Alinguata neblina*. Paratype: (Cat. No. 46132). A, venation of forewing. B, venation of hindwing.

from tip of plume  $M_1$  to base of wing, cleft in cell  $M_2$  is slightly more than one-half of length of wing measured from tip of plume  $M_2$  to base of wing, cleft in cell  $M_3$  is two-thirds of length of wing measured from tip of plume  $M_3$  to base of wing, and cleft in cell  $Cu_1$  is deepest of all, extending almost to base of wing.

In the forewing only vein  $R_1$  of radials completely absent, but vein  $R_3$  and vein  $R_4$ , which are short and located in first plume, very faint. Vein  $R_5$  a strong tubular vein. Traces of upper discocellular vein present. Vein  $Cu_2$  strongly divergent from cell and fuses with vein 2d A well before beginning of plume  $Cu_2$  2d A. See text-figure 1 for venation of fore and hindwing.

*Alinguata* will run to *Paelia* in Meyrick's key (1910, p. 2), from which it may be distinguished by the absence of a tongue. In addition, the third joint of the labial palpi is as long as the second joint in *Alinguata* while the third joint of the labial palpi in *Paelia* is described in the literature as short. If I am correct in interpreting Meyrick's discal cleft (1910, p. 3) as the cleft in cell  $M_2$ , then an additional difference may be noted; this cleft extends to one-half of the forewing in *Paelia* but in *Alinguata* for only a quarter. Walker (1866, p. 1846) in his original description of the genus *Paelia* states that the labial palpi are decumbent, but Meyrick (1910, p. 3) writes that they ascend; in *Alinguata* they are decumbent.

Genotype, *Alinguata neblina*, new species, described below.

***Alinguata neblina*, new species.**

Plate I.

Length of forewing of male 6 mm., of female 7.5 mm.

Head loosely covered with grayish-brown scales. Dorsum of thorax covered with black-

ish-brown scales while the spatulate scales of the patagia have an additional grayish glitter under the microscope. Ventrum of thorax shining, grayish-white. Coxae and femurs silvery gray with scattered brown scales but tibiae brown with scattered gray scales. Prothoracic legs darker than remaining legs. Epiphyses brown. Spurs brown with tan tips. Tarsal segments brown mixed with a few gray scales. A narrow gray band circles each tarsal segment but least prominent on metathoracic legs. Distal band of each leg faintest.

Dorsum of abdomen dark brown and ventrum gray. Abdomen unbanded.

Upper side of wings brownish-black with bluish-white markings in daylight. Under the microscope the color of the wings is bronzy-chocolate brown similar to the colored figure of *Paelia lunuligera* Walker in Meyrick (1910) and the white markings are shining grayish-white. Latter restricted to plumed part of wings and costal margin of forewings.

Forewings with minute patch of grayish-white scales one-eighth from base of wing on costal margin, and a short streak of grayish-white scales approximately one-half from base. Two half circles or crescents composed of grayish-white scales with their centers on the costal margin of the wing are distad of the streak. The three figures are approximately equidistant from each other with the most distal half circle located in the vicinity of the base of the first plume. A very short, grayish-white streak is present in the caudal region of first plume and a grayish-white line distad of the streak runs diagonally across the plume. Another grayish-white half circle follows which is smaller than the half circles previously mentioned and located on the unplumed section of the costal margin. The last figure along the costal margin of the wing is a subterminal streak.

Three V-shaped figures are present on the second plume equidistant from each other and a small irregular patch of grayish-white scales near the base of the plume. These and subsequent Vs mentioned have their apices pointing toward the base of the wing. They are not perfectly shaped Vs like those on the wings of *Paelia lunuligera* Walker and many species of *Orneodes*, as the arms of the V are widespread, and the apices not sharp or pointed.

The third plume also has three equidistant Vs. There is a small patch of grayish-white scales at the base of the third plume on its cephalic margin and another patch on the caudal margin. The latter patch extends over on the fourth plume.

The fourth plume has three Vs but differs from the other plumes in that the two basal Vs are close together.

The fifth plume resembles plumes two and three.

The sixth or last plume has only two Vs. This plume has a small patch of grayish-white figures approximately one-quarter from the base of the plume on the inner

margin of the wing, and another patch at the base of the cephalic margin of the plume.

Ground color of hindwing brownish-black. A patch of white spatulate scales along the costal margin of basal third of wing. A half-circle near the base of the first plume differs from those on the forewing in lying on the inner margin of the first plume rather than on the costal margin. Its center is likewise on the inner margin. There is a V subterminal figure on the first plume. Each of the remaining plumes has four Vs equally spaced from one another, except the last or sixth plume which has only two Vs.

Under side of wings the same as upper, except that the half circle figures along the costal margin of the forewings incomplete on the under side.

Material: A total of four specimens taken as follows: Rancho Grande, north-central

Venezuela: June 24, ♀ holotype (Cat. No. 461069); July 3, ♂ allotype (Cat. No. 461067); March 18, ♀ paratype (Cat. No. 46132); July 7, ♂ paratype (Cat. No. 461068).

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## EXPLANATION OF THE PLATE.

## PLATE I.

- Fig. 1. *Alinguata neblina*. Holotype: (Cat. No. 461069). Upper side of wings and body.
- Fig. 2. Under side.



FIG. 1.



FIG. 2.

A NEW GENUS AND SPECIES OF ORNEODIDAE (MOTHS)  
FROM RANCHO GRANDE, NORTH-CENTRAL VENEZUELA.



## 3.

Prickle Cell Hyperplasia in the Snout of the Redhorse Sucker  
(*Moxostoma aureolum*) Associated with an Infection by the  
Myxosporidian *Myxobolus moxostomi* sp. nov.

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(Plates I-III).

INTRODUCTION.

The corium is the primary site of infection for many histozoic myxosporidians. Tissue responses to such infection are usually manifest as inflammatory reactions and hyperplasia of connective tissue which often form the cysts enclosing the developing spores (Kudo, 1919, 1929, 1930, 1934; Nigrelli and Smith, 1938). The degree of these responses varies with the host, parasite and site of infection. In certain instances the connective tissue cells become highly modified, transforming into epithelioid-like cells. Such a case was reported by Kudo (1929, 1934, 1946) for the connective tissue cells in the corium of the minnow, *Pimephales* (= *Hyborhynchus*) *natatus*, infected with *Thelohanellus* (*Myxobolus*) *notatus* (Mavor). Occasionally a hyperplasia of the epithelium is also associated with these infections (Nigrelli and Smith, 1940), although in most cases there is a tendency for this structure to become thin and sloughed as a result of pressure induced by the enlarging underlying cysts.

The present contribution deals with a new species of myxosporidian, *Myxobolus moxostomi*, found in the corium of the snout of the northern redhorse sucker, *Moxostoma aureolum* (LeSueur), collected in Illinois. Associated with this growth is an hypertrophy of the overlying epithelium in which prickle cells are the main cellular elements involved.

The writer wishes to thank Dr. G. M. Smith for assistance in preparation of the material.

DESCRIPTION OF THE PARASITE.

The affected fish showed a marked swelling in the midregion of the snout just above the maxilla. No external cysts were visible. The fish was sacrificed and the swollen part excised and fixed in 10% neutral formalin. Paraffin sections were cut at six microns and stained with hematoxylin-eosin, Mallory's, Masson's and Giemsa's methods.

The infection was localized in the corium. The cysts were composed of delicately developed connective tissue, and were more or less confluent (Plate I, figure 1). Those that were discrete measured from 0.5 mm. to

4 mm. The central part of the cysts contained numerous spores, a smaller number of developing disporablastic pansporoblasts and cellular debris.

Like the other members of the genus *Myxobolus*, the parasites are polysporous. The spores (Plate I, figure 2) varied in shape from circular to ovoid in front view and were fusiform, with more or less rounded tips in side view. They measured  $6.2-9.4 \times 5.5-9.4 \times 3.1-4.7$  microns (average,  $7.6 \times 7.2 \times 3.9$  microns). It can be assumed that the living spores were slightly larger than the measurements indicated since some shrinkage must have occurred during fixation. The shell was of uniform thickness, with several darkly-staining bodies present in many of the (immature?) spores. The sutural ridge and line were not especially conspicuous. The polar capsules were pyriform in shape, often convergent. They measured  $2.3-3.9 \times 1.6-3.2$  microns (average,  $3.6 \times 2.3$ ). The polar filament, when evident, showed from three to five spiral turns. The sporoplasm was either uninucleate or binucleate. An iodophilous vacuole was evident in many spores.

This parasite was tentatively identified by Nigrelli (1943) as *Myxobolus conspicuus* Kudo. However, a more detailed comparison of the present species with those reported by Kudo (1934) from the same and related fishes is given in Table I. It differs from them in shape and size of spore, details in structure of shell, site of infection and type of tissue responses elicited. The most striking difference is found in measurements of the various parts of the spore. It is for these reasons that it is considered a new species for which the name *Myxobolus moxostomi* is given.

PATHOLOGY.

The actual site of infection with *Myxobolus moxostomi* was in the deeper layers of the corium. Host response in this region was shown by the development of a delicate fibrous growth around the trophozoite and spore masses. There was some invasion and destruction of muscle and periosteal tissues, accompanied by a mild inflammatory reaction. Corial melanophores were at a minimum.

TABLE I.  
Comparison of Species of *Myxobolus* from *Moxostoma*.

PARASITE:	<i>M. moxostomi</i> sp. nov.	<i>M. congesti-</i> <i>cus</i> Kudo, 1934	<i>M. vastus</i> Kudo, 1934	<i>M. gravidus</i> Kudo, 1934	<i>M. conspicuus</i> Kudo, 1929
HOST:	<i>M. aureolum</i>	<i>M. anisurum</i>	<i>M. aureolum</i>	<i>M. anisurum</i>	<i>M. breviceps</i>
SITE OF INFECTION:	Corium of head Deep	Fins  Superficial	Corium, body scales Superficial	Skin, fins  Superficial	Skin of head  Superficial
TUMOR:	Present	Present	Present	.....	.....
SIZE OF CYSTS:	0.5-3 mm.	0.3-1 mm.	2.5-3.8 mm.	0.5 mm.	0.5-4 mm.
CONNECTIVE TISSUE DEVELOPMENT:	Minimum	Minimum	Hypertrophy	.....	Hypertrophy
EPIDERMIS:	Hypertrophy	Thin, broken	Thin	.....	Thin, unicel- lular glands absent
VASCULARIZATION:	Poor (region around tro- phozoites)	Rich	Rich	.....	.....
SPORE SHAPE FRONT:	Circular to ovoid	Circular to oval	Oblong	Oval to oblong	Oval
SIDE:	Fusiform, rounded ends	Lenticular	Lenticular	Fusiform	Fusiform
SPORE SIZE:	6.2-9.4 × 5.5- 9.4 × 3.12- 4.68 micra	9-10 × 8.5- 9.5 × 6 micra	9.5-10.5 × 7.5- 8 × 4-4.5 micra	12-14 × 9.5- 10 × 7 micra	9-11.5 × 6.5- 8 × 4.5-5.5 micra
SHELL:	Mod. thick	Mod. thick, radiating folds	Mod. thick 7 radiating lines	Mod. thick, 4-6 folds in post. part	Mod. thick No striations
SUTURAL RIDGE:	Not promi- nent	Wide	Thickened at ends	Inconspic- uous	Wider than thickness of shell
SUTURAL LINE:	Present	Indistinct	Indistinct	.....	Straight
CAPSULE SHAPE:	Pyriform, slightly divergent	Pyriform, convergent	Pyriform	Pyriform, convergent	Pyriform, dissimilar in size
SIZE:	2.3-3.9 × 1.56- 3.2 micra	5-6 × 2.5-3.5 micra	4.5-5.5 × 1.5 -2.5 micra	5-5.5 × 2.5 micra	5-7 × 2-2.5 micra
FILAMENT:	3 to 5 turns	.....	.....	.....	10 turns

The most striking changes, however, were noted in regions immediately above and adjacent to the actual site of infection (Plate II, figure 3). The fibrous growth here was considerably thickened and more vascularized. In some areas of the growth, the connective tissue appeared to give rise to a supporting stroma of the hypertrophied stratified epithelium. The cellular elements of the latter were mainly prickle cells showing prominent intercellular bridges (Plate III, figure 5). In some parts of the growth the cells appeared as normal polygonal-shaped structures with finely granular cytoplasm and nucleoplasm; the latter occasionally contained several deeply stained, peripherally placed granules of various sizes. The majority of nuclei also possessed a single

nucleolus and few cells showed two such bodies. In most cells the staining reaction of the nucleus was not intense with hematoxylin, but isolated groups of prickle cells were encountered in which this structure was definitely hyperchromatic. Although no mitotic figures were found there was some evidence of activity. In certain regions the cells had broken through the basement membrane and invaded the corium (Plate II, figure 4). The invasion, however, was not extensive.

In other regions of the growth there was considerable evidence of degeneration. The prickle cell growth had crowded and destroyed the mucous gland cells of the skin. The outermost layer of prickle cells showed the greatest changes, manifested metachromatically

with Masson's and Giemsa's stains. The nucleoli of these cells were larger and often filled the entire nucleus. These regions also showed considerable infiltration by macrophages.

#### DISCUSSION.

Kudo (1929) and Nigrelli and Smith (1940) have shown that histozoic myxosporidian parasites may induce a thickening of the epithelium in the regions of the infection. Auerbach (1909) also found that the coelozoic parasite *Myxidium bergense* may cause a thickening of the epithelium of the gall bladder of *Gadus virens*. In these cases the parasites were in more intimate contact with the tissues involved. In the redhorse sucker, the epithelial hyperplasia was immediately above but some distance away from the infection. Whether or not there was any direct association between the infection and the hyperplastic growth is difficult to say.

Intercellular and intracellular cnidosporidians elaborate proteolytic enzymes and other chemical substances which may be responsible for considerable cellular degeneration, cell hypertrophy and other tissue responses noted in these infections. It is altogether possible that chemical substances elaborated by the developing parasites may have a stimulating growth factor which may diffuse to more distant areas either directly or through the circulation.

#### SUMMARY.

A new species of myxosporidian, *Myxobolus moxostomi*, from the corium of the snout of the common redhorse sucker, *Moxostoma aureolum* (LeSueur), is described.

Hyperplasia of the connective tissue and stratified epithelium is associated with the infection. In the hyperplastic epithelium, prickle cells are the main cellular elements involved.

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## EXPLANATION OF THE PLATES.

## PLATE I.

- Fig. 1. Section through cysts showing numerous spores of *Myxobolus moxostomi* together with a few pansporoblasts and other cellular elements. Giemsa.  $\times 75$ .
- Fig. 2. Mature and immature spores of *Myxobolus moxostomi*. Giemsa.  $\times 675$ .

## PLATE II.

- Fig. 3. Section through the overlying growth showing extensive development of corial fibrous tissue and hyperplastic epithelium. Hematoxylin-eosin.  $\times 75$ .
- Fig. 4. Basal columnar cells of the hyperplastic epithelium showing infiltration into the corium. Hematoxylin-eosin.  $\times 675$ .

## PLATE III.

- Fig. 5. Prickle cells of the hyperplastic epithelium. Hematoxylin-eosin.  $\times 675$ .

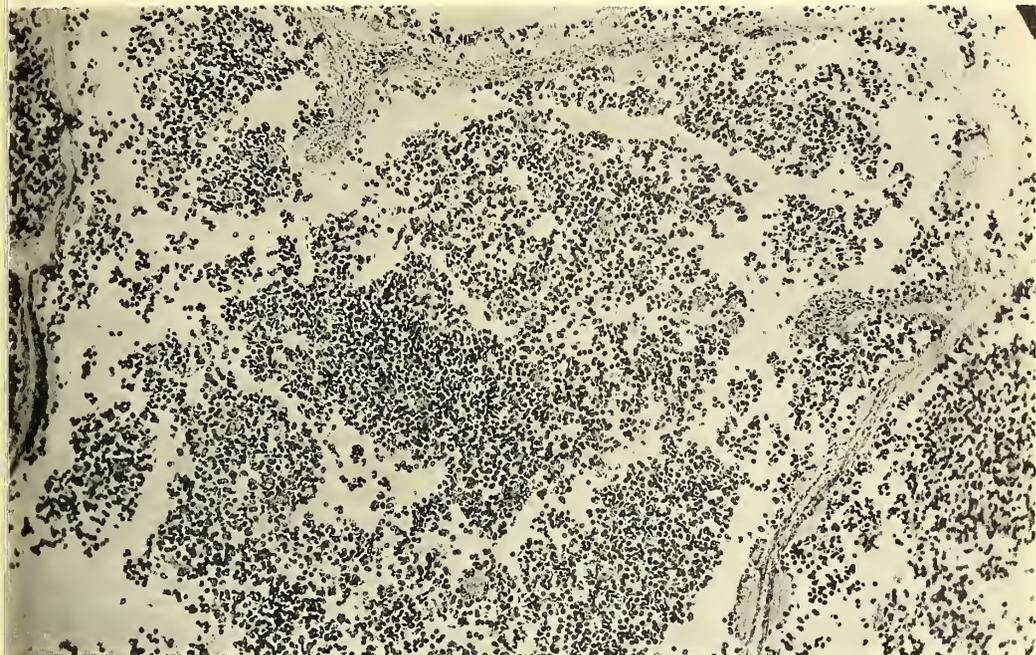


FIG. 1.

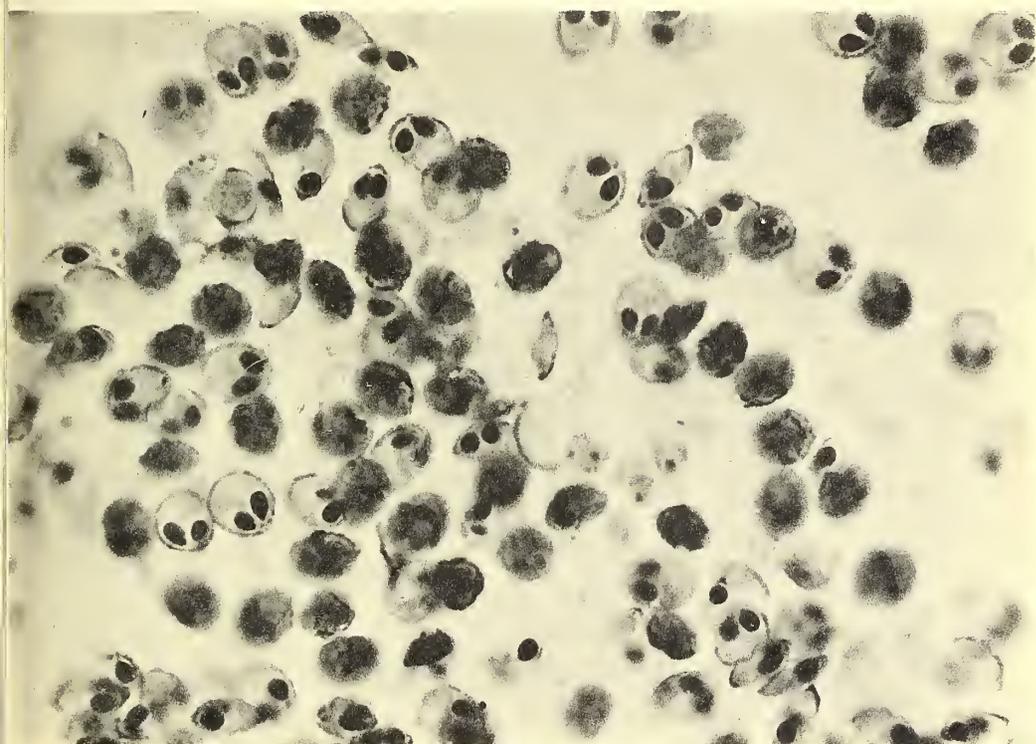


FIG. 2.

PRICKLE CELL HYPERPLASIA IN THE SNOUT OF THE REDHORSE SUCKER  
(*MOXOSTOMA AUREOLUM*) ASSOCIATED WITH AN INFECTION  
BY THE MYXOSPORIDIAN, *MYXOBOLUS MOXOSTOMI* SP. NOV.



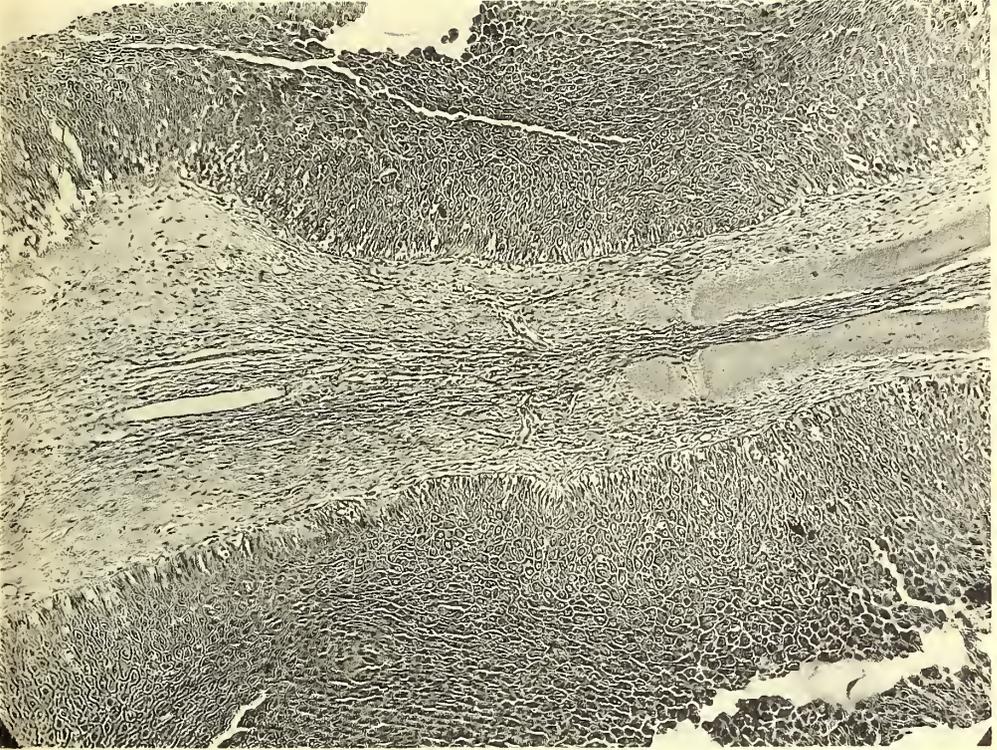


FIG. 3.



FIG. 4.

PRICKLE CELL HYPERPLASIA IN THE SNOOT OF THE REDHORSE SUCKER  
(*MOXOSTOMA AUREOLUM*) ASSOCIATED WITH AN INFECTION  
BY THE MYXOSPORIDIAN, *MYXOBOLUS MOXOSTOMI* SP. NOV.





FIG. 5.

PRICKLE CELL HYPERPLASIA IN THE SNOOT OF THE REDHORSE SUCKER  
(*MOXOSTOMA AUREOLUM*) ASSOCIATED WITH AN INFECTION  
BY THE MYXOSPORIDIAN, *MYXOBOLUS MOXOSTOMI* SP. NOV.



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## 4.

Odonata (Dragonflies) of Kartabo, Bartica District, British Guiana.<sup>1</sup>

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(Plates I &amp; II).

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[This contribution is a result of various expeditions of the Department of Tropical Research of the New York Zoological Society, all made under the direction of Dr. William Beebe. The Guiana trips were made during the years 1909, 1916, 1917, 1919, 1920, 1922, 1924 and 1926. The Kartabo collections and observations were carried on in one-quarter of a square mile of jungle. For detailed ecological and meteorological notes see *Zoologica*, Vol. II, No. 7, 1919, pp. 205-227.]

## INTRODUCTION.

Dr. William Beebe has asked me to report on the Odonata taken at the New York Zoological Society's Tropical Research Laboratory at Kartabo, British Guiana. The collection contains many interesting forms which, in a number of instances, have prompted some excursions into their ecological relations. With Dr. Beebe's consent, I have included smaller lots, hitherto unreported, collected by Dr. Charles Hodge, IV, at Kartabo in July-August, 1926; by Mr. George B. Fox along the Essequibo River; and by the late Dr. William Schaus in French Guiana. The first two lots are in the Academy of Natural Sciences of Philadelphia, the third was sent to me for study some years ago, by the United States National Museum. The

<sup>1</sup> Contribution No. 797, Department of Tropical Research, New York Zoological Society.

types of the new species of Dr. Beebe's collection are deposited in the Academy of Natural Sciences of Philadelphia, as is also the type of one other species. The Odonate fauna of Guiana not represented in these four collections is not considered in this paper.

The only attempt<sup>2</sup> at a list of the Odonata of any of the Guianas known to me is that of W. F. Erichson of 1848, as a section of the Insect part of Richard Schomburgk's "Reisen in Britisch Guiana in den Jahren 1840-1844 im Auftrag Sr. Majestät des Königs von Preussen," Band III, pp. 583-586. Twenty-six species of Odonata are listed, without localities for any of them; fourteen of them are described, ten of the fourteen, including three credited to Hoff-[manse]gg, as new species. Seventeen species of Erichson's list are represented in the collections from Kartabo.

Taxonomic works before and after Erichson—Rambur, deSelys, Hagen, Kirby, Förster, the Williamsons, Montgomery, Borrer, Campion, Martin, Ris, Needham, Geijskes and the present writer—add many other species from the Guianas.

#### DISTRIBUTION OF THE KARTABO ODONATA.

The flora at the Kartabo laboratory is described as consisting of the typical rain forest of eastern South America with swampy areas and clearings made by Dutch and Indian planters.<sup>3</sup> It is of interest to compare the distribution of the Kartabo Odonata, throughout the entire geographic range of each species, with Messrs. Dillon and Smith's Generalized Phytogeographic Map of Latin America.<sup>4</sup> That map divides Latin America, from the northern boundary of Mexico to Cape Horn and including the West Indies, into 14 zones characterized by vegetation features. Kartabo and most of the Guianas lie in Zone 1, "tropical and subtropical rain forest," while a narrow band along the coast, in which Georgetown, Paramaribo and Cayenne lie, is part of Zone 7, "savanna regions."

In making the allocations which follow, it is not to be forgotten that the Odonata of large areas of South America are still unknown. The map employed is indeed generalized, in that its scale does not permit showing the microgeographic details so interpenetrating in a continent of such abrupt

changes in altitude (with all that they imply). Forest and clearings are frequented by different species of Odonata, and even the small area of study at the Kartabo laboratory, 2,000 by 4,000 ft. (650 × 1,300 m.), embraces at least these two kinds of habitat. It must be remembered, too, that the powers of flight of many Odonata are such as to enable them to pass easily from one sort of habitat to another; the correlation of the carnivorous Odonata with the flora must be indirect in most cases, through the intermediation of the phytophagous animals which in turn serve as food for the odonates; and that more direct relations between dragonflies and plants exist where certain plants, such as bromeliads, serve the oviposition needs of certain Odonata (*Mecistogaster*).<sup>5</sup> The real index to odonate distribution is not that of the winged adults but of the aquatic larvae and of the latter we are still almost entirely ignorant.

But with all these considerations, the results of allocating the Kartabo Odonata to the zones of Dillon and Smith's map are striking.

Of the 75 identified species here treated, none falls within zone 4 (palm forests), 5 (sub-antarctic heath forest), 9 (coastal desert of Pacific South America), 10 (Patagonian-Fuegian steppes) or 12 (transitional vegetation of central Chile).

In zone 11 (desert scrub) appears only the widespread *Orthemis ferruginea* (in Sonora), which occurs abundantly in zones 1-3, 6, 7 and 14.

In connection with each of the following lists of species (*a-f*), after indicating the plant zones of Messrs. Dillon & Smith (D.S.) in which they fall, it is pointed out how far these areas agree with the provinces of South American scorpions proposed by Dr. Mello-Leitão<sup>6</sup> (ML) and the districts of South American mammals proposed by Drs. Cabrera and Yapes<sup>7</sup> (CY).

<sup>5</sup> Another case, although not pertaining to the Guianan fauna, is that seen by E. B. Williamson at the Quebrada Sabaleticus, in Antioquia, Colombia, and thus described: "Here for the first time we saw *Cora* and observed its peculiar habit of ovipositing, which it shares with *Miocora*. The eggs are inserted in comparatively solid but barkless horizontal tree trunks or pieces of logs over water. In some cases the logs were scarcely damp, and the eggs were placed as high as six feet above the water." (*Misc. Publ. Mus. Zool. Univ. Mich.*, 3, 17, 1918.) Whether it is merely the physical condition of the logs which determines oviposition in them, irrespective of their kind, is not stated. Still more remote from the Guianan fauna is the case of the European *Aeshna viridis* which is believed by Wesenberg-Lund (*Internat. Revue Gesam. Hydrobiol. Hydrogr.*, 6:191, 389, 1913) and Münchberg (*Ztschr. Morph. Okol. Tiere*, 20 (1): 181-183, 1930) to oviposit only in living plants of *Stratiotes aloides*. Münchberg states that *Anax parthenope*, in Grenzmark, eastern Prussia, oviposits in *Phragmites communis*, less often in *Scirpus lacustris*, never in dead plant tissue (SB. Ges. Naturf. Freunde, Berlin, 1932: 71).

<sup>6</sup> 1945. *Araquívos Mus. Nac. Rio de Janeiro*, 40:9-468, map fig. 185.

<sup>7</sup> 1940. *Historia Natural Ediar Mamíferos Sud-Americanos*. Compañía Argentina de Editores, Buenos Aires, 4to, 370 pp. Map facing p. 14; reproduced as fig. 184 of Mello-Leitão above quoted.

<sup>2</sup> Whether Carl Peter Thunberg's "Fauna Surinamensis" Resp. Collin. 12 Dezbr. 1822. Upsaliae, Acad. Typogr. 4 p. 1-8" and "Fauna Cayenensis, Resp. Kjeller. 4. Juni 1823. Upsaliae, Palmblad. 4. p. 1-11," thus quoted in Horn u. Schlenkling's Index Litteraturae Entomologicae, Band IV, p. 1229 (1929), contain anything on Odonata, I do not know, as I have not seen them.

<sup>3</sup> Beebe, W., 1925; Beebe, W. & Gleason, H. A., 1925, *The Guianas, in Naturalist's Guide to the Americas*. Baltimore, Williams & Wilkins Co., pp. 654-655.

<sup>4</sup> Accompanying Smith, A. C. and Johnston, I. M., 1945. A Phytogeographic sketch of Latin America, *Plants & Plant Science in Latin America*, XVI, pp. 11-18. *Chronica Botanica Co.*, Waltham, Mass.

Passing to Odonata of narrower geographic distribution, there are:

(a) Those at present known only from zone 1 (DS) (tropical and sub-tropical rain forest) of the Guianas and including in some cases the island of Trinidad. These are:

*Argia insipida*<sup>8</sup>  
*Leptagrion beebeanum*<sup>9</sup>  
*Leptagrion* sp.  
*Aeolagrion demerarum*  
*Acanthagrion adustum*  
*Metaleptobasis tetragena*<sup>9</sup>  
*Neonura joana*  
*Protoneura calverti*  
*Aphylla alia*<sup>9</sup>  
*Gomphoides fuliginosa*  
*Macrothemis pumila* (occurs also in zone 7, savannas at Georgetown)

It is quite likely that the apparently limited distribution of these species is due to scanty knowledge on our part.

Kartabo lies within the Carib province (ML) or the Amazonian district (CY). The Carib province roughly corresponds to the Savanna (Sabanico) district but its southern boundary is farther south and extends farther to the east.

(b) Species of the Guianas and the Amazon valley in zone 1 (DS) (tropical and sub-tropical rain forest).

*Hetaerina moribunda*  
*Microstigma maculatum*  
*Megapodagrion macropus*  
*Zonophora batesi*  
*Phyllocycla bartesi*<sup>9</sup>  
*Fylgia amazonica*  
*Micrathyria spinifera*  
*Erythrodiplax angustipennis*  
*E. laurentia*

These species inhabit the Carib and Amazonian provinces (ML) or the Amazonian district (CY). The two maps of these authors are in agreement as to the southern and western boundaries of the Amazonian area.

(c) Species extending across much of the northern part of South America, but not farther north and not farther south than the Amazon valley.

*Hetaerina dominula*  
*Mecistogaster lucretia*  
*Phyllocycla signata*  
*Progomphus dorsopallidus*  
*Archaeogomphus hamatus*  
*Aeschnosoma peruviana*  
*Orthemis aequilibris*  
*Diastatops dimidiata*  
*Zenithoptera fasciata*  
*Oligoclada raineyi*

Five of these species are in our present

knowledge limited to zone 1 (DS), but *M. lucretia* and *P. dorsopallidus* occur also in zone 6 (thorn forest), *Z. fasciata* in 1 and 7 (savannas), *O. aequilibris* in 1, 6 and 7.

These species extend westward into the Incan (Incasica, Incasico) province (ML) or district (CY) which borders the Pacific coast of South America from Panama to Latitude 20° S.; such parts of zone 6 (DS) as they inhabit are along the Venezuelan coast of the Carib province (ML) or Savanna district (CY), while their area of zone 7 (DS) narrowly borders the Atlantic coast of the east end of the Carib and Amazonian provinces (ML) or of the Amazonian district (CY).

(d) Species which extend from the northern coast of South America and in some cases Trinidad (but not farther north) southward beyond the Amazon valley and falling in zones 1 and, mostly, in 7 (DS).

*Mecistogaster linearis* (not in 7)  
*Staurophlebia reticulata reticulata* (also in 6)  
*Gynacantha tenuis*  
*Diastatops pullata*  
*D. obscura* (also in 2, tropical deciduous forest)

*Perithemis thais* (not in 7)  
*Oligoclada pachystigma*  
*Uracis oviposatrix*  
*U. infumata*  
*Erythrodiplax castanea* (also in 2 and 3, south Brazilian forest and savanna zone)  
*E. latimaculata* (also in 2 and 6)  
*E. maculosa* (perhaps also in 2)  
*E. melanorubra* (also in 2 and 6)  
*Rhodygygia cardinalis*  
*Macrothemis polyneura*  
*Idiataphe longipes longipes*

These species add to their distributional areas the Cariri province (ML) which is nearly equivalent to the Tropical district (CY). Some of them invade the Tupi and Guarani provinces (ML) which together correspond to the Tupi and Sub-tropical district (CY) although their respective boundaries in the two maps are different.

(e) Species which extend to the north of South America on the North American continent, to Central America, or to Mexico, or to the United States, but not into the West Indies. They reach in most cases southward below the Amazon valley; the numbers of the DS zones, in addition to zone 1, in which they occur, are added in parentheses.

- i. Not in zone 14 (montane)  
*Hetaerina caja* (2, 6, 7)  
*Megaloprepus caeruleus* (2)  
*Ceratura capreola* (3, 7)  
*Triacanthagyna ditzleri*  
*Gynacantha auricularis* (2, 7)  
*G. gracilis* (2)  
*G. membranalis* (2, 6)

<sup>8</sup> *Argia insipida* was recorded by Kirby from St. Vincent and Grenada in the West Indies (*Ann. Mag. Nat. Hist.*, (6) 14: 268, 1894); the identification should be confirmed.

<sup>9</sup> Species described as new in this paper.

*Orthemis biolleyi*  
*Uracis imbuta* (2, 7)  
*U. fastigiata* (7)  
*Micrathyria eximia* (2, 3)

Some of these species extend southward into the Cariri, Tupi, Guarani and Pampean provinces (ML) or Tropical, Sub-tropical, Tupi and Pampean districts (CY).

ii. Also in zone 14

*Libellula herculea* (Cuenca) (2, 3, 7, 9?)  
*Orthemis cultriformis* (Chiriqui) (2, 8)  
*Erythrodiplax connata fusca* (Cuernavaca, Vilcanota; possibly Huanuco and Colonia del Perene, both in Peru, lie within zone 14)

The Montane zone (DS) includes the higher altitudes of the Incan, Pampean and Chilean provinces (ML) or of the Incan, Andine, Sub-andine and Chilean districts (CY).

(f) Species extending into the West Indies other than Trinidad and Tobago; these are mostly widespread in South America, Central America and Mexico, and some reach the United States; they all occur in zones 1 and 7, most of them also in 2, of the DS map. The numbers of the zones in addition to zones 1, 2 and 7 in which they occur, as well as the most southern geographical limit, are added in parentheses.

*Ceratura capreola* (3) (Rio Grande do Sul)

*Triacanthagyna septima* (6) (Rio de Janeiro)

*Gynacantha nervosa* (6) Porto Suarez, Bolivia)

*Coryphaeschna virens* (6) (Santa Cruz, Bolivia)

*Orthemis ferruginea* (3, 6, 11, 14) (Montevideo)

*Erythrodiplax unimaculata* (Paraguay)

*E. famula famula* (Minas Geraes)

*E. umbrata* (3, 6, 8, 14) (Buenos Aires)

*E. basalis basalis* (6) (Santa Cruz, Bolivia)

*Erythemis peruviana* (6) (Corrientes)

*E. attala* (3, 6, 8, 14) (Buenos Aires)

*Lepthemis vesiculosa* (3, 6, 14) (Corrientes)

*Dythemis multipunctata* (3, 6, 8) (Buenos Aires)

*Tholymis citrina* (6) (Minas Geraes)

*Pantala flavescens* (3, 6, 11, 14) (Sao Paulo)

*Tramea cophysa* (6, 8, 14) (Santos, Brazil)

(See also footnote 8 on *Argia insipida*, page 49).

It will be seen that these species reach southward into the Tupi, Guarani, Cariri and Pampean provinces (ML) or Tropical, Sub-tropical, Tupi and Pampean districts (CY).

#### ODONATA FROM KARTABO.

The species here treated are listed under two sets of relevant subfamily names, the

first that of de Selys and Hagen, dating from their *Revue des Odonates* of 1850 and widely used, the second that of the most recent classification of Tillyard and Fraser (*Australian Zoologist*, 9, 1938-40). Where one of the latter subfamilies is more than a subdivision of one of the former, that fact is indicated by marking it with a roman numeral. All these subfamily names are inserted for the convenience of the reader and do not necessarily imply acceptance of them by the present writer. For each species are given only those bibliographical references pertinent to the present text.

CALOPTERYGINAE S. & H., 1850 (as Calopterygines). HETAERININAE T. & F., 1939.

*Hetaerina dominula* Hagen, 1853.

(Plate I, figs. 3-6).

Selys & Hagen, 1854, *Monog. Calopt.*: 107, pl. 11, fig. 1 (Surinam).

Williamson, E. B., 1923, *Occas. Papers Mus. Zool. Univ. Mich.*, 130: 15, 19 (Brit. Guiana).

Geijskes, 1943, *Ann. Ent. Soc. Amer.*, 36 (2): 168, pl. II, figs. A-G (nymphs, Surinam).

Kartabo, 22.X.1920, one male, lacks abdominal segments 4-10; 1922, one female.

French Guiana, 60 m (iles) up Maroni River, 8.04, Wm. Schaus, U. S. Nat. Mus., one male.

The Maroni River male is of the same species as two males from Wismar, February 16, 1912, and two males from Tumatumari, February 11, 1912, all four from British Guiana, by L. A. and E. B. Williamson and B. J. Rainey and referred by Williamson (1923) to *dominula*. All five, however, differ from Selys and Hagen's figure of the superior appendages (1854) in having the proximal of the two divisions of the "dilatation" of the inner margin rounded, not acute, and from their description in the yellow of the sides of the thorax being well marked, including the stripe on the first lateral suture and the "terminale" stripe. The superior appendages, however, possess what their description of 1854 gives as a character distinguishing *dominula* from *caja*, viz.: "le bord interne supérieur offre, immédiatement après la dilatation, une petite dent analogue à celle de la *divina*."<sup>10</sup> The yellow lateral thoracic stripes are, however, narrower than the "bronze noirâtre" which separates them and hence differ in this respect from the description of *caja*.

On the other hand, the Wismar and Tumatumari males have the postoccipital tubercles angular and well marked, whereas

<sup>10</sup> On comparing pages 106, 112, 114 and 118 of the *Monographie des Caloptérygines* it would seem that in the original draft of the work it was the intention of the authors to recognize *divina* as a distinct species, but they did not do so and did not alter their original references to it.

Williamson says (p. 19) that in *dominula* they are low and rounded. The head of the Maroni River male is distorted and the tubercles can not be seen plainly. This apparent contradiction, as well as the condition of the inner dilatation of the superior appendages, caused me to ask Mrs. Leonora K. Gloyd to make comparisons with Williamson's specimens at the University of Michigan. She kindly replied as follows (February 22, 1943): "The situation seems to be this. Apparently Mr. Williamson (1923, p. 19) meant that the postoccipital tubercles of *dominula* appear low and rounded in comparison to those of *mortua*, as seen in the field without the aid of a microscope (*caja* was not taken in the same locality). I also looked up Hagen's figure of the superior appendages of *dominula* (cited above) and oriented one of E. B. Williamson's specimens so labeled until the appendages looked very much like Hagen's figure. The specimens Mr. Williamson sent you are of the same species as those at Ann Arbor, so there is no mistake in the labeling."

The Kartabo male lacks the appendages essential for determination. It has the postoccipital tubercles as in the Wismar and Tumatumari males, the yellow stripe absent from the first lateral thoracic suture, the yellow on the second lateral thoracic suture and on the metepimeron so reduced as to be much narrower than the intervening black, thus as originally described for *dominula*, but the (pale) reddish spot of the front wings does not reach the costa and is pale brown between costa and subcosta. The basal spot of the hind wings is pale brown, slightly tinged with red (hence this individual is probably not fully aged), its area corresponding fairly well with the original description.

An envelope containing two *Hetaerina* males from Bejuma, Carabobo, Venezuela, February 13, 1920, by J. H. and E. B. Williamson and W. H. Ditzler, sent to me by Mr. E. B. Williamson, was labeled *H. caja* but probably not in his handwriting. One of these in coloring, thoracic pattern and appendages is undoubtedly *caja*; the other is *caja* in coloring and thoracic markings, but its appendages are like those of *dominula* and are shown in our figure 3, Plate I.

The female from Kartabo is small (abdomen 33 mm., hind wing 22 mm.) and agrees with the description of that of *dominula* except that it has the genital valvules and the legs pale brownish-ochre instead of black; the postoccipital tubercles are as in the males described above.

Distribution of *dominula*: Guiana, "Brazil."

#### *Hetaerina moribunda* Hagen, 1853.

Selys & Hagen, 1854, Monog. Calopt., 134, pl. 12, fig. 4 (Para, Cayenne).

Sjöstedt, 1918, *Arkiv Zool.*, 11(15): 39 (Manaos, Brazil).

Geijskes, 1943, *Ann. Ent. Soc. Amer.*, 36 (2): 171 (supposed nymph, Surinam).

Kartabo, 6. VI. 1921, one male.

This male agrees with the appendages as described and figured for *moribunda* by Selys and Hagen (1854), but the wings differ in numbers of antenodals (33-34 on front wings, 31-37 on hind) and in the extent of the basal spots, as follows: on the front wings red from the costa to the hind margin but brownish in the costal cells to the level of the middle of the quadrilateral and in the subcostal cells to the separation of R and M; red ending six cells beyond the level of the quadrilateral. On the hind wings brownish-red from C to Cu (right) or slightly below Cu (left), extending in the costal cells to the 17th antenodal, in the subcostal cells to the 20th or 21st antenodal, and between M2 and Cu to the distal end of the quadrilateral.

The left hind wing is abnormal in the following respects as compared with the apparently normal right hind wing, whose features are noted in parentheses: total length 24.5 mm. (25.5), nodus farther from base 15 mm. (11) but nearer apex 10 mm. (15), maximum width beyond nodus greater 5.9 mm. (5.72), costal area beyond the nodus wider, many of the postnodals anastomosed, stigma smaller, irregular, M2 beginning three cells distad of nodus (at the sub-nodus), cell rows between R1 and M3 distad of nodus irregular.

I have before me for comparison a male from Wismar, British Guiana, January 31, 1912, taken by the late Messrs. L. A. and E. B. Williamson and Mr. B. J. Rainey, with typical *moribunda* appendages and numbers of antenodals (28 front wings) and postnodals (45 front wings), with the basal spot on the front wings nearly as in the Kartabo male except that in the subcostal space the brownish-red reaches beyond the point of separation of R and M to the same level as the red behind it, i.e., to the level of six cells distad of the distal end of the quadrilateral, while on the hind wings the red (less brownish than in the Kartabo male) reaches caudad to one row of cells below Cu and even to the hind margin from the wing base to eight cells distad therefrom, in the costal space to the 21st antenodal, in the subcostal space to the 23rd antenodal and between Rs and Cu to one or two cells beyond the quadrilateral. The hind wing is 25 mm. long.

On the other hand, two males respectively from Manaos, June 16, 1922, and Villa Murtinho, Matto Grosso, April 7, 1922, by J. H. Williamson and J. W. Strohm, with *moribunda* appendages, have the basal spots of the wings very nearly (Manaos) or smaller than (Villa Murtinho) as described for

the Hagenian types. Sjöstedt (1918) also has a note on a male from Manaos.

Distribution: Guiana, Amazon valley.

*Hetaerina* sp.

Kartabo, III. 9. 1926, one female, lacking head and abdominal segments 4-10.

This female has the hind wing 30 mm. long, antenodals on the front wings 24 (right), 23 (left), thoracic pattern similar to that figured by Ris<sup>11</sup> for *H. caja* female except that the dark green median thoracic stripe is wider anteriorly and the green upper metepisternal spot is connected with the green spot at the upper end of the second lateral suture; the middle and hind lobes of the prothorax are almost entirely metallic green and the hind margin of the hind lobe has some slight structural differences from that of *caja*.

Distribution of *H. caja*: Acapulco, Mexico, to Guayaquil, Ecuador, eastward to Trinidad, but not recorded from the Amazon valley or the Guianas.

AGRIONINAE S. & H., 1850 (as Agrionines).  
i. Pseudostigmatinae T. & F., 1938.

*Megaloprepus caerulatus caerulatus* (Drury, 1782).

*Megaloprepus caerulatus* Ris, 1918, *Archiv Naturges.*, 82, A (9); 64. Calvert, 1923, *Ent. News*, 34:129, 168.

Kartabo, Odon. 81, one female, abdomen 77 mm., right hind wing 67 mm., maximum width 17.5 mm., ratio length to width 3.82.

This female agrees better with the characters given by Ris (1918) for *M. c. caerulatus* than for *c. brevistigma*. He remarks: "Die Zahlenreihen ergeben dass eine scharfe Begrenzung von Formen nicht möglich ist. Immerhin ist eine relative Unterscheidung wenigstens der Form *brevistigma* in genügend bestimmter Form zu geben." In a study published five years later (1923) and based on fewer specimens, the present writer said: "An examination of his (Dr. Ris's) data on which these definitions are based clearly shows that one race grades into the other."

Distribution of *Megaloprepus caerulatus* as a whole: Vera Cruz, Mexico, to Demerara and to Yungaz, Bolivia.

*Microstigma maculatum* Hagen, 1860.

(Plate II, fig. 38).

Hagen in Selys, 1860, *Bull. Acad. Roy. Belg.*, (2) 10 (6): 17.

Selys, 1886, *Mem. Couron. Acad. Roy. Belg.*, 38 (4): 12.

Kartabo, 18. III. 1922; 30. III. 1926; V. 7. 1924; VI. 1. 1924; 28. VII. 1920; 8. VIII. 1920; five females, one male, also one male, "Odon. 130," head, left wings and

apex of right front wing lost. Most of these have lost the terminal abdominal segments.

Two species of this genus were at one time (1860), at least, reported from the Guianas by deSelys; they were stated to differ as follows (1860, but with the greater range of size given by him in 1886; italics as in de Selys, 1860):

	<i>M. anomalum</i> Rambur, 1842	<i>M. maculatum</i> Hagen, 1860
Size	medium, abd. ♂ 69-88 mm., ♀ 58-77; hind wing ♂ 47-72, ♀ 45-60	small, abd. 62-74 mm.; hind wing 48-55; sex not stated
Hind margin of prothorax	similar in the two sexes, rounded	much cleft ♂ (not described for ♀)
Wings	quite broad, <sup>12</sup> rounded	quite narrow <sup>12</sup>
♂ Front wings	terminal ninth (to twelfth, 1886) very finely reticulated, forming a dull yellowish, well circumscribed spot, oblique within (adult), yellowish-white (young); stigma slightly reddish (adult), yellowish-white (young), of 3-4 cells	apex very finely reticulated, not opaque or colored
Hind wings	stigma blackish-brown (adult), yellowish-white (young), of 3-4 cells	brown, of one cell; apex not finely reticulated
♀ All wings, apex	narrowly and obliquely white or pale yellow	narrowly and obliquely milky (front) or slightly so (hind)
stigma	blackish-brown, of 3-4 cells, larger on front wings	yellow, of one to several cells (or absent, 1886)

All seven individuals from Kartabo approach the description of *maculatum* more closely than that of any other species. As few specimens of this species have been recorded or discussed in the scanty literature, the presence of these seven from one and the same locality renders it desirable to set down their range of variability in the characters which have been assumed as specific.

In all but one female (V. 7. 1924) the terminal portion of the abdomen is lost; in that female the abdomen measures 78 mm.

Hind margin of the prothorax in both males strongly cleft, in the females with a median, pointed (in profile view), shining,

<sup>11</sup> *Archiv Naturgesch.*, 82, A (9): 53, fig. 24, 1918.

<sup>12</sup> Width not stated numerically.

brown or black tubercle, narrowly yellow posteriorly.

♂. Front wings: denser reticulation at apex beginning .49-.82 mm. proximal to the stigma, denser between C and M1a than caudad, its proximal edge nearly straight, at right angles to C, its color faintly brownish-gray, its length 5.72 mm.; stigma .66-.74 mm., 2-celled, brown. Hind wings: 48-51 mm., denser reticulation at apex beginning at 4 cells proximal to, or .82 mm. distal to, the stigma, denser between C and R1 than caudad, its proximal edge nearly straight, at right angles to C, uncolored or faintly brownish, its length 1.88-5.32 mm. (in the male of 8.VIII.1920 asymmetrical in right and left wings); stigma .41-.74 mm. 1-celled or smaller, brown.

♀. Front wings: denser reticulation at apex beginning 2.2-4.25 mm. proximal to stigma, denser between C and M1a, or M2, or one row of cells posterior to M2, than caudad, its proximal edge convex, its color pale milky brown, faintly gray, faintly brownish-gray, faintly pink, or yellowish, its length 5.50-7.77 mm. (in some individuals asymmetrical in right and left wings); stigma .5-.9 mm. (asymmetrical in all individuals), 1-7-celled (frequently asymmetrical), pale gray to dark brown. Hind wings: 54-56 mm.; denser reticulation at apex beginning 1.5-3.93 mm. proximal to stigma (asymmetrical in four individuals), denser between C and M1a, or one row of cells posterior thereto, than caudad, its proximal edge convex (except in the left hind wing of ♀ V.7.1924 where it is slightly concave), its color pale milky brown or faintly gray, its length 5.3-7.0 mm. (asymmetrical in three individuals); stigma .5-.74 mm., slightly asymmetrical (markedly so in one individual), 1-celled (except 1 + in right wing of ♀ V.7.1924 and 2 + in right hind wing of ♀ 28.VII.1920), white to dark brown.

♂♀. All seven individuals have a yellow humeral stripe. A black, median, longitudinal, pectoral stripe is present in male 130, is present but interrupted in the other male and the female of 28.VII.1920, is very slight and linear in the female of 18.III.1922, is represented by a small blackish quadrilateral spot behind and between the third coxae in two females (V.7.1924 and VI.1.1924) and is absent in the remaining female.

On September 1, 1942, Prof. B. Elwood Montgomery kindly compared the Kartabo male of 8.VIII.1920 with Hagen's type of *maculatum* in the Museum of Comparative Zoology, Cambridge, Massachusetts, at my request. Of this type he wrote: "Under the side label *M. maculatum* in box, a male with following pin-labels: Essequibo Schmid, *M. obliquus* coll. Hagen, red type label Type 12123 and *Microstigma maculatum* Hagen. Tips of all wings somewhat frayed; left fore wing torn or shredded to base; speci-

men otherwise in good condition. Right fore wing is probably complete enough to check any details of venation. Pterostigma, front wing 1-celled, approximate size 1/3 mm.; same, hind wing, seems to fill only one-half cell, as in hind wing of Kartabo male, approximate size one-third mm. Venation at tip of wings more dense in the Essequibo (type) male; color of the tip, front wing, pale pink (due to color of veins as determined under microscope); both rear wing tips torn away. In the costal area of both wings there is a slight cloudiness bordering the cross veins giving the appearance of a slight cream color. Shape of the prothorax, especially its hind lobe, identical or very similar. Thorax of type is somewhat crushed, but markings appear to be identical, especially the yellow humeral stripe, except that it *may* not extend quite so far downward. Fore part of thorax is broken and covered with glue; dark mark on posterior (ventral) portion is same in shape (as in Kartabo male), but less dark in Essequibo male. Length of hind wing about 50 mm. estimated (tip broken off). The wings correspond in width to those of Kartabo male."

Prof. Montgomery also made a camera lucida drawing of a portion of tip of right front wing of the Essequibo male which is here reproduced (Fig. 38). The greater density of the reticulation, as compared with that of the Kartabo male is shown by the following figures:

	♂ Essequibo (type)	♂ Kartabo
Rows of cells between veins C and R	3	mostly 2
Rows of cells between veins R and M1	5-4	3-2-3
Rows of cells between veins M1 and M1a	5-3	3-2-3
Rows of cells between veins M1a and M2	2-3?	2-3

The material of *maculatum* cited in 1860 consisted of a male from Cayenne, a female from Santarem, a female (or a male) from Essequibo and a female from Surinam. In 1886, *maculatum* is quoted from Cayenne, Essequibo, Surinam and "un male de grande taille que je lui attribue est d'Obidos sur l'Amazone." The "patrie" of *anomalum* was given in 1860 as "Le Para, Santarem sur l'Amazone, Cayenne" (the last was the habitat given by Rambur for his *proximum* which de Selys placed as a synonym of *anomalum*); in 1886 as "Amazone (Para, Santarem) . . . exemplaires du haut Amazone (Masari, etc.)."

#### REFRACTIVE BODIES IN CERTAIN WING CELLS OF *Microstigma maculatum*.

In the original description of *Microstigma anomalum* Rambur wrote:<sup>13</sup> "alis hyalinis,

<sup>13</sup> Histoire Naturelle des Insectes Nevropteres, Paris, Roret, 1842, p. 289.

apice reticulatissimis nervis rufis, pterostigmate nullo vel subnullo ♂ . . . avec les nervures et nervules rougeâtres, portant ça et là petites globules très-fins (peut-être accidentels); très-finement réticulées à leur sommet antérieurement qui est blanchâtre sale ou un peu roussâtre . . ." No habitat was given for the single individual of this species.

I have not found any later references to these "petites globules très-fins" in the literature, so set forth the following data on their appearance as shown by the present seven specimens of *M. maculatum*.

Males: The cells of the apex of the front wings are smaller and more numerous than those of the hind wings. The faintly brownish-gray at the apex of the front wings is apparently due to almost colorless, finely granular, refractive bodies,  $\pm$  .013 mm. in diameter, without sharp outlines, located in the membrane of the wing of the cells between the costa and vein M1a. There may be as many as  $100\pm$  of these bodies in a single cell. The cells in which these refractive bodies occur vary in their longest diameters from .2 to .635 mm. The cross veins separating these small cells are wider, e.g., .026 mm., than the cross veins (.017 mm.) which are both farther caudad and proximad. The refractive bodies may occupy the whole or only parts of the cells. Cells at the proximal edge of the gray area do not show a less density of the refractive bodies within them than exists in adjoining cells farther distad in the gray area. The refractive bodies are present in the four larger cells proximal to the first small cells between the costa and vein R1. The hind wings do not show these refractive bodies. The smallest cell observed in the hind wings has a long diameter of .14 mm. and, as in the smallest cell in the front wings mentioned above, is at the wing margin.

Females: Refractive bodies are present in the apical cells of both front and hind wings of all five females. In the front wings they are found in the cells from the costa to vein M2, or to one row, or to two rows, below M2, or to Rs. The smallest apical cell noted was .108 mm. in diameter. In the hind wings these bodies occur in apical cells between the costa and M1a, or M2, or one row of cells below M2. The smallest apical cell noted was .038 mm. in diameter, but the impression was that the cells in the apex of the front wings are on the whole smaller than those in the hind wing.

The following observations were made on the right hind wing of the female of 30.III.1926, under both a binocular Greenough microscope and a compound Leitz microscope. Immersion of the wing apex in 95% alcohol between a slide and cover slip for three hours produced no change in

the refractive bodies. A similar immersion in potassium hydrate (strength unknown) produced a sharply marked polygon, clearer than the refractive body itself, around each body. The wing apex was then transferred to a Syracuse watch glass of the same KOH solution in which it remained bathed for 14½ hours. Examination at the end of that period showed that some cells preserved the polygons as above noted, others were as at first examined in the dry condition, still others had many small air (?) bubbles within them. The wing apex was then washed in water and transferred, still wet, to a slide but without a cover slip; the three sorts of cells as stated for the KOH condition were still visible. The wing apex remained on the slide until it dried, when its appearance in all its cells was the same as that of the apex of a front wing of the same female which had been kept untreated in the dry condition.

At the suggestion of Dr. Rudolf G. Schmieder, the extreme tip of the wing apex which had been treated was cut off through some of the cells containing refractive bodies, mounted dry in a vertical position and the cut edge examined through Leitz objectives 3 and 6 to endeavor to determine whether the refractive bodies could be distinguished, possibly as thickenings of one or other of the two wing membranes. Clusters of granules, of the size seen in the refractive bodies in surface view of the wing apex, were observed here and there, apparently on the outer surface of one or another membrane. These were not found in a similarly mounted fragment of a part of the same wing not containing the refractive bodies. It would appear, therefore, that the outer surfaces of the wing apex, in the refractive body areas, are roughened here and there, and thicker at the site of each refractive body. The thickness of the combined two wing membranes where free from veins and refractive bodies was between .00145 and .00097 mm. in both the fragments examined. At a refractive body the wing section was .0029-.0058 mm. thick; at a cross vein .026-.058 mm. thick.

#### *Mecistogaster* Rambur, 1842.

Two species of this genus are represented in the present material from Kartabo. They may be distinguished from each other as follows:

The pale antehumeral and humeral stripes less unequal in length, their levels overlapping, the former 2.38-3.68 mm., the latter 3.68-4.09 mm. Pterostigma of the front wings longer ( $\text{♂}$  4.91-5.89,  $\text{♀}$  4.91-5.32 mm. or not differentiated), of the hind wings shorter ( $\text{♂}$  4.91-5.73,  $\text{♀}$  4.50 or not differentiated). Males with front margin of hind wing not produced forward before the apex; superior appendages in profile view not bent ventrad,

apex truncated obliquely caudad and ventrad. Females with a yellow spot on each side of hind end of abdominal segments 7-10 or some of them. Abdomen ♂100-125, ♀63-98, hind wing ♂49-60, ♀43-75 mm. (Dimensions according to de Selys 1886) . . .

*linearis*

The pale antehumeral and humeral stripes very unequal in length, the former less than 1 mm., the latter 3.27-4.58 mm., the former not reaching upward as far as the level of the lower (or anterior) end of the latter. Pterostigma of the front wing shorter (♂2.37-4.25 mm., ♀2.37-2.94 mm. or not differentiated), of the hind wing longer in the male (5.97-7.94 mm.) but shorter in the female (3.27-2.94 mm. or not differentiated). Males with front margin of hind wing gradually produced forward in an elliptical curve at the stigma; superior appendages in profile view bent obliquely ventrad beyond mid-length, apex slightly bifid. Females with no yellow spots on abdominal segments 7-10. Abdomen ♂120-130 (117-137), ♀85-110, hind wing ♂58-68, ♀55-70 (♂51-64, ♀49-60) mm. (Dimensions according to de Selys, 1886, but where the Kartabo examples exceed his ranges they are given enclosed in parentheses) . . . . . *lucretia*

*Mecistogaster linearis* (Fabricius, 1777).

*Agriion linearis* Fabricius, 1777,<sup>14</sup> Gen. Insect. :249 (nec Fabr. 1781, Species Insect., 1:528, Nö. 5; 1793, Ent. Syst., 2:388, No. 5). Campion, 1917, *Ann. & Mag. Nat. Hist.*, (8) 19:447.

*Mecistogaster linearis* Selys, 1860, *Bull. Acad. Belg.*, (2) 10 (6) : 22; 1886, *Mem. Couron. Acad. Belg.*, 38 (4) :23. Kirby, 1897, *Ann. & Mag. Nat. Hist.*, (6) 19:615. Ris, 1918, *Arch. Naturges.*, 82 (A9) : 73. Sjöstedt, 1918, *Arkiv Zool.*, 11 (15) :33. Munz, 1919, *Mem. Amer. Ent. Soc.*, 3:74, pl. 8, fig. 50 (venation, hind wing ♀). Needham, 1933, *Amer. Mus. Novit.*, 664:1. Fraser, 1946, *Trans. R. Ent. Soc. London*, 97 (18) :462, figs. 3 c, d (wing tips ♂), 4 b, c (apps. ♂).

*Mecistogaster marchali* var. *selysia* Navas, 1923, *Mem. Pontif. acc. Rom. Nuovi Lincei*, (2) 6:9 (new synonym).

After considering the discussions by de Selys (1860) and Campion (1917) on the type of this species, it seems permissible to regard the Fabrician specimen in the Banks collection of the British Museum as the lectotype,<sup>15</sup> fixed by de Selys (1860) as the first reviser.

In 1860, de Selys distinguished different ages of imago of both sexes of this species.

<sup>14</sup> For 1777, instead of 1776, the usually quoted date of publication, see Hagen, *Biblioth. Ent.*

<sup>15</sup> For definitions of lectotype and references to pertinent literature, see Frizzell, 1933, *Amer. Midl. Nat.*, 14:655; Cresson, 1934, *Ent. News*, 45:124.

The number of specimens from any one locality, as reported in the literature earlier than Col. Fraser's paper of 1946, is smaller than of those present from Kartabo, five males, three females. The latter are listed, therefore, as follows to show both their age, following de Selys, and their seasonal distribution:

Young, front wings, tip white or pale yellow, including the yellowish stigma; hind wings as stated for front wings. Two males, "Odon. 87," 1917, and 22.XI.1920; two females, V.8.1924, and 19.VII.1920.

Semi-adult, front wings, tip whitish, stigma orange above and below; hind wings as stated for front wings. One female, "Odon. 82," 1921.

Adult, front wings, tip smoky or uncolored, stigma orange or ochreous above, dark brown beneath; hind wings, tip faintly smoky, stigma as stated for front wings; abdomen with some pruinosity on hind segments. Three males 3.IV.1924, 24.VII.1920, and 6.XI.1920.

The males have the pterostigma extending from C to M1, with one row of cells between C and R1 and one row between R1 and M1.

It is to the young imago of *M. linearis*, or of *M. lucretia*, or of both species, that the following observations, made by Dr. Beebe on the Aremu River, a right tributary of the Cuyuni, some 25 miles from Kartabo, in late March, 1909, probably refer. "At noon we stopped for breakfast in a primeval forest with rather thin underbrush. . . . Spinning through the aisles made by the giant columns of tree-trunks, were curious translucent pin-wheels, and not until we captured one in the butterfly net did we realize we were looking at the same attenuated forest dragon-flies (*Mecistogaster* sp.) which had deceived us so completely five years ago in Mexico.<sup>16</sup> The movement of the long, narrow wings, with the spot of white at the tips was, to the eye, a circular revolving whirl, with the needle-sized body trailing behind. The white spots revolved rapidly, while the rest of the wings became a mere gray haze. These weird creatures, apparently so ethereal and fragile, were hunting for spiders, and their method was regular and methodical. From under leaves or from the heart of widespread webs, good-sized spiders were snatched. A momentary juggling with the strong legs, a single nip and the spider minus its abdomen dropped to the mould, while the dragon-fly alighted and sucked the juices of its victim. If we drew near one of these spiders on its web, it instantly darted away, sliding down a silken cable to the ground or dashing into some crevice, but the approach of the hovering dragon-fly, although rather deliberate, was unheeded,

<sup>16</sup> Two Bird-lovers in Mexico, pp. 239-241.

the spider remaining quiet until snatched from its place."<sup>17</sup>

Geographical distribution of *M. linearis*: The Guianas, Amazon Valley from Para to the Rio Bobonaza in Ecuador, Muzo, etc., in the eastern Cordillera of Colombia; Venezuela; one male from Matto Grosso (Ris, 1918).

#### THE SEASONAL DISTRIBUTION OF *Mecistogaster linearis* THROUGHOUT ITS RANGE.

It will be noted that of the specimens from Kartabo dated for day and month, both young and adult have been collected in July and November; July in the long wet season, November at the end of the long dry season. The remaining two dated individuals are from April and May, at the end of the short dry and the beginning of the long wet season respectively.<sup>18</sup>

Among Schaus's material from French Guiana, in the U. S. National Museum, are two young females from Cayenne, December, 1903, and the Maroni River, June, respectively.

The records of occurrence at Kartabo and in French Guiana indicate that *linearis* imagoes are to be met there during much of the year and are not limited to any one season, but the data are not yet full enough to make more precise statements.

Kirby (1897) records *linearis* taken in forest at Santarem, lower Amazons, February 27, 1896, in the wet season. Sjöstedt (1918) has briefly described a semi-adult male, a young male and three young females from the Amazons (Rio Autaz, Sept.-Nov., Rio Purus, Jan., and Manaos, July). In the collection of the Academy of Natural Sciences of Philadelphia is a semi-adult male taken at Manaos X.18.1919. July to November represent the relatively dry season, January the height of the wet season.<sup>19</sup>

Ris (1918) has described very adult males and females from Muzo in October, 1910, a very adult male from Llanos de Medina in June, 1910, and an adult male and young and adult females taken at Villavicencio, in January, 1911, all in Colombia. Villavicencio,

at 450 meters elevation, lies at the entrance to the llanos (Ris, p. 3), where January falls in a dry period, June in the wet season.<sup>20</sup>

Navas (1923) has described females from Muzo of July and October, 1918, under the name *Mecistogaster marchali* var. *selysia*. His account of the membrane of the apex of apparently all the wings as "opalino sive lacte picta" seems to apply better to *M. linearis* than to *marchali* (= *lucretia* Selys, 1890).

Prof. Needham (1933) has recorded a male of *linearis* from Mt. Duida, Venezuela, November 23, 1928. If we may use the precipitation records of Ciudad Bolivar, this would be in the wet season (Reed, 1928, p. 10).

Quite recently (1946) Col. Fraser has published a list of *linearis* taken at localities in Colombia and Peru in the valleys of the Putumayo, Amazons and Huallaga rivers. His largest series of specimens (12♂, 27♀) is that from Mishuyacu, Peru, described as being "near Iquitos" (t. c. (2): 11); the males were taken from Feb. 2 to July 10, the females from Jan. 25 to Dec. 20, except, apparently, Sept. and Oct., all in 1931; one male, Oct. 31, is cited from Yumbatos, Peru, in the Huallaga valley. Brooks says:<sup>21</sup> "On the Amazon side of the Andes the rainy season last[s] from October to April, and the dry season from May to Sept. but July is the only really dry month." The seasonal range of the Mishuyacu *linearis* extends through a wet season with two maxima, March and December, and a dry with a minimum rainfall of 4.6 inches in August, if we may use the Iquitos data.

In these extra-Guianan records of *linearis*, the wet season is represented by those from Santarem, Rio Purus, Llanos de Medina, Muzo, Mishuyacu and Mt. Duida, the dry from Villavicencio and relatively dry from Manaos, the Rio Autaz, Muzo and Mishuyacu.

*Mecistogaster lucretia* (Drury, 1773).

*Libellula lucretia* Drury, 1773, Illustr. Nat. Hist., 2:87, pl. 48, fig. 1, Index p. 2. Sulzer, 1776, Abgekurtz. Gesch. Insec. 1: 169, tab. 24, fig. 4.

*Lestes lucretia* Westwood, Drury, 1837, Illustr. Nat. Hist., 2: tab. 48, fig. 1.

*Agrion lucretia* Burmeister, 1839, Handb. Ent., 2:818.

*Mecistogaster lucretia* Rambur, 1842, Ins. Nevrop.: 286. Kirby, 1890, Cat. Odon., 121

<sup>20</sup> Kendrew, p. 323. Reed, p. 12, data for Puerto Berrio, nearest station to Muzo. Muzo lies in one of the north to south interandine valleys where in July there is less, in October more, rain. Haurwitz & Austin, p. 235 (Bogota, Medellin). "From the llanos there are no long series of records, but all accounts tell of an almost rainless period from the end of November till the middle of March." (Kendrew, p. 323.)

<sup>21</sup> Climate, p. 167. Precipitation figures for each month at Iquitos are given by Reed, p. 17; Kendrew, p. 343; Miller, p. 89.

<sup>17</sup> M. B. & C. W. Beebe: Our Search for a Wilderness, New York, Henry Holt & Co., 1910, pp. 270-1. Spiders form at least part of the food of *Megaloprepus caerulatus*, ally of *Mecistogaster*, listed on page 52 antea; Calvert, Ent. News, 34:171-4, 1923.

<sup>18</sup> Climatic data from Beebe, British Guiana in the Naturalist's Guide to the Americas: 649-652 (Baltimore, The Williams & Wilkins Co.), 1926; Reed, Monthly Weather Review, Suppl. 31:8, 1928; Miller, Climatology, London, Methuen, 1931, pp. 75, 88-89. Haurwitz & Austin, Climatology, New York & London, McGraw-Hill, 1944, p. 234. "There is considerable variation in these seasons, and occasionally a short season is almost eclipsed." (Beebe).

<sup>19</sup> See data by Reed (1931) for Taperinha, near Santarem, and for Manaos, in Yearbook U. S. Dept. Agric., 1941, pp. 674, 675. White, O. E., The Amazon Valley in the Naturalist's Guide to the Americas, p. 675, 1926. Kendrew, W. G., Climates of the Continents, 2nd edit. (Oxford, Clarendon Press, 1927), pp. 325-6, 343. Brooks, C. E. P., Climate (New York, Scribners, no date, subsequent to 1928), pp. 142, 144. Miller, A. A., Climatology, p. 89. Haurwitz & Austin, Climatology, 234, 1944.

(in part). Selys, 1890, *Compt-Rend. Soc. Ent. Belg.*, pp. cxix, clxiv. Fraser, 1946, *Trans. R. Ent. Soc. Lond.*, 91(18):452, fig. 3b (tip of hind wing ♂).

*Preia lucretia* Gistel in Gistel & Bromme, 1850, *Handb. Naturges.*, 452. Cowley, 1934, *Entom.*, 67:202.

*Agrion linearis* Fabricius, 1781, *Spec. Ins.*, 1:528, No. 5; 1793, *Ent. Syst.*, 2:388. (Nec Fabr., 1777, *Gen. Ins.*, 249).

*Libellula linearis* Gmelin, 1790, *Syst. Nat.*, 1(5):2625, No. 45. Olivier, 1792, *Encyc. Meth. Ins.*, 4:567, No. 41 (in part).

*Libellula longissima* Fée, 1832, *Vie de Linné*, 365.

*Mecistogaster marchali* Rambur, 1842, *Ins. Nevrop.*, 283. Selys, 1860, *Bull. Acad. Roy. Belg.*, (2) 10 (6):25; 1886, *Mem. Couron. Acad. Roy. Belg.*, 38 (4):25. Kirby, 1890, *Cat. Odon.*, 121.

*Mecistogaster filum & pedicellatus* Rambur, 1842, *Ins. Nevrop.*, 284.

The changes made by de Selys in 1890 in the nomenclature of *M. lucretia* and *marchali* were subsequent to the publication of Kirby's Catalogue. The revised synonymy of what he earlier called *lucretia* Drury, later *amalia* Burmeister, is given in *Biologia Centrali-Americana, Neuroptera*, 354, 1907, and to it I now add a new synonym, *Agrion linearis* Blanchard (1840, *Hist. Nat. Ins.*, 3:64, *Nevrop. pl. 2*, fig. 1.). The revised synonymy and references for de Selys' earlier *marchali*, later *lucretia*, have not been detailed and therefore are given above, after an examination of all the passages quoted. Dr. Ris (1913, *Mem. Soc. Ent. Belg.*, 22:59) has retained the Selysian nomenclature of 1860 and 1886 for *lucretia* and apparently cites only the second reference to *lucretia* by de Selys in 1890, i.e., p. clxiv, quoting McLachlan's opinion, and overlooking the first reference, p. cxix, with the original suggestion by Hagen. I see no reason to change my arrangement in the *Biologia* just quoted and which Dr. Ris doubted.

In 1860, page 20, de Selys distinguished young and adult imagos of this species, under the name of *M. marchali*. As in the case of *M. linearis*, the material present from Kartabo is more extensive than that hitherto recorded in the literature from any one locality. It and two males from nearby Rockstone are, therefore, listed here to show the age and the seasonal distribution.

Young, abdomen not pruinose; front wings, tips whitish or pale yellow, including the stigma; hind wings, tips uncolored except the pale brown stigma. Three males, 5.VIII.1920, 17.VIII.1920, and "Odon. 122;" two females, 1.III.1920, 6.XI.1920.

Semi-adult, abdomen not pruinose; front wings, tip slightly smoky, stigma yellow or ochre; hind wings, tip uncolored, stigma

darker brown. One male, 23.VIII.1920; two females, 16.VIII.1920, and no date. Rockstone (Schaus) one male, no date.

Adult, abdomen with some pruinosity on hind segments; front wings, tips slightly smoky, stigma reddish-brown or darker brown; hind wings, tips uncolored, stigma dark brown. Four males, 13.III (no year), 5.VIII.1920, 18.VIII. (no year), 20.XI.1920. Rockstone (Williamson & Rainey) one male, Feb. 12, 1912.

The males here listed have the pterostigma extending from C to M1 (or to a fraction of a cell below M1 on the front wings); on the front wings it consists of two rows of cells between C and R1 and one or two rows between R1 and M1; on the hind wings it consists of only one row of cells between C and R1 and one row between R1 and M1.

Geographical distribution of *M. lucretia*: Northern Venezuela, the Guianas and the lower and middle Amazon valley (Selys, 1886).

#### THE SEASONAL DISTRIBUTION OF *Mecistogaster lucretia* THROUGHOUT ITS RANGE.

Considering the ages and dates of the British Guiana imagos, the greatest number of individuals (five males, one female) taken in any one month is in August, wherein young, semi-adults and adults are equally represented. Young and adult were collected also in March and in November. *Lucretia*, like *linearis*, is, therefore, apparently to be found as imagos throughout the year. Except for November, however, the months in which the two species have been collected are not the same, although not far apart. The British Guianan seasons in which *lucretia* imagos have been obtained are the short dry (Feb., March), the end of the long wet (July) and the end of the long dry (Nov.). Finally, a very adult female was taken by Dr. Schaus at Cayenne, in December, 1903 (U. S. National Museum), which is in the beginning of the wet season, only two seasons being recognized here as against the four in British Guiana.<sup>22</sup>

In the Academy of Natural Sciences of Philadelphia are two adult males from Cariaquito, Venezuela, collected by Stewardson Brown on Jan. 22, 1911. In an account of his expedition by Stone,<sup>23</sup> Cariaquito is located on the south shore of the peninsula of Paria. Judging from the rainfall records from the nearest localities, Rio Caribe and Ciudad Bolivar, January is at the end of a wet season at Cariaquito.<sup>24</sup>

These discussions of the seasonal distribu-

<sup>22</sup> Reed, 1928, pp. 5, 7-8. Miller, 1931, p. 75. Carlson, *Geography of Latin America*, revised edition, p. 352, 1943 (New York, Prentice Hall).

<sup>23</sup> 1913, *Proc. Acad. Nat. Sci. Phila.*, 65:189.

<sup>24</sup> Reed, l. c., p. 10; Carlson, l. c., p. 336.

tion of *M. linearis* and of *M. lucretia* are prompted by the results of one year's observations in Costa Rica which seemed to indicate that imagos of *M. modestus*<sup>25</sup> fly in that country only at the beginning of the wet season.

ii. Megapodagriinae T. & F., 1938.

*Megapodagrion megalopus* (Selys, 1862).

Kangaruma, 15.II.1921, one male, abdominal segments 6-10 lost. Distribution: Amazon valley (Selys, 1862, 1886).

iii. Argiinae T. & F., 1938.

*Argia*

By Leonora K. Gloyd

(I have asked Mrs. Gloyd, as the one best acquainted with this genus, to examine and report on the material in question. This she has kindly done as follows. P. P. C.)

*Argia* sp. A, group of *oculata* Hagen.

Kartabo: 12.III.1924, one male; III.9.1926, one female; III.26.1926, one female; 3.IV.1924, one male (abd. segs. 7-10 lost); 8.VI.1921, one male; 20.IX.1920, one male (abd. segs. 6-10 lost); not dated, one female, No. 20357, abdomen lost; also July-August, 1926, by Dr. Charles Hodge IV, one male.

These males are not quite the same as my specimens of Sp. 26<sup>26</sup> from Venezuela which were compared with the type of *oculata* at the M. C. Z. in 1935, nor of Sp. 19<sup>26</sup> from Colombia (which may prove the same as Sp. 26. Segments 3-5 of this series have much more blue and there are slight differences in the superior appendages which are difficult to describe. Neither are they the same species as either of two belonging to the *oculata* group Dr. Geijskes sent me from Dutch Guiana. This group is going to take a tremendous amount of study and it may be that by the females we shall know them! Dr. Geijskes's males had such slight differences from Sp. 19 they could have easily been identified as the same *but* the females are quite distinct. So if these three females from Kartabo belong to the five males from the same locality, and I think they do, then here is another member of the near *oculata* group.

These females have a low tubercle with a depression mesad which forms a shallow pit beneath the short overhanging projection of the mesostigmal lamina; *oculata* has neither pit nor tubercle.

*Argia* sp. B.

Kartabo: 1922, one male (left front wing lost).

<sup>25</sup> Calvert, 1911, *Ent. News*, 22 (9): 402-411; Calvert, A. S. & P. P., 1917, *A Year of Costa Rican Natural History*: 230-243. See also Picado, C., 1913, *Bull. Sci. France & Belg.*, (7) 47 (3): 346-7.

<sup>26</sup> Temporary numbers given by me to species in sorting and making a preliminary study of the huge amount of *Argia* material accessible to me. L. K. G.

Same as my Sp. 16,<sup>26</sup> "Near *sordida* and *ulmeca* in Calvert's keys. May be undescribed species. P. P. C. & L. K. G. Sept. 10, 1934."

*Argia* sp. C.

Kartabo: 22.X.1920, one female, not dated; nos. 20340 and 24449, two females; Hadas Clearing 14/6/22, one female. All four females have lost abd. segs. 7-10 or more.

To me these specimens look like my Sp. No. 1<sup>26</sup> or No. 14<sup>26</sup> of the *indicatrix* group. Species 1 is from Belem, State of Para, Brazil, and is near, or, *indicatrix*; Sp. 14 is from British Guiana and as nearly as I can make out is what Sjöstedt redescribed as *Argia impura* but Rambur's type of *impura* has abdominal segments 7-10 missing and without a more critical study of several other species which are similar in size, coloration and general appearance, I can neither agree nor disagree with his determination.

*Argia* sp. D.

Kartabo: IV.6.1924, one female (abd. segs. 6-10 and left front wing lost).

My Sp. 8.<sup>26</sup> Color pattern, wings (postquad. cells 3-3), shape of pterostigma, mesostigmal lamina, etc., agree very well. Species 8 according to our mutual studies is still an undescribed species. My sample specimen is from Manaus, Amazonas, Brazil.

*Argia insipida* Hagen, 1865.

Essequibo River below [between?] mouths of Potaro and Rupinuni, IV-V, 1920, George B. Fox, one teneral female in collection of the Academy of Natural Sciences of Philadelphia.

Males of this species are very near *pipila* but differ in extent of blue in color pattern as well as in appendages. Here again it is the females which are most easily distinguished. *A. ierea* Geijskes is a synonym. *A. pipila* females, as stated in the original description, have no mesepisternal tubercles, *A. insipida* does have them.

Distribution of *insipida*: British and Dutch Guiana. See footnote 8, antea, page 49, on the reported occurrence of this species in the West Indies.

iv. Coenagriinae T. & F., 1938.

*Leptagrion beebeanum* n. sp.

(Plate I, figs. 1, 2).

Kartabo, V.4.1924, one male, holotype, collection of Dr. William Beebe, deposited by him in the Academy of Natural Sciences of Philadelphia, No. 9275.

Wings: Anal vein separating from the hind margin of the wing slightly proximal to the cu-a cross-vein by a distance one-fourth or less of the length of that cross-vein, which is a little nearer to the level of the second than of the first antenodal. Cross-

vein descending from the subnodus not continued directly to the hind wing-margin, the marginal cell against which it ends pentagonal (hence like *Leptagrion*, Williamson, *Ent. News*, 28:242, 1917) but not high and the adjoining marginal cells not high (hence not like *Leptagrion*, l. c.). M2 arising at the 7th postnodal (front wings) or 6th (hind wings), Rs and M3 widely separated at the proximal cross-vein between them. Pterostigma with both proximal and distal ends oblique, nearly parallel, the proximal slightly more oblique than the distal; brown, surmounting less than one cell, costal edge 1.09 mm. (front wing), 1.18 mm. (hind wing). Postnodals 13 (right), 14 (left), M1a arising at the 10th (front wings); 13 (right), 12 (left), M1a arising at the 9th (hind wings). Upper side of the quadrilateral, front wings, subequal to the inner (proximal) side and .3 as long as the lower side; hind wings, twice as long as the inner side, half as long as the lower side. Three ultra-quadrilateral, antenodal cells on all four wings.

Most of the legs missing, only one tarsal claw (probably of a first leg) preserved, with a distinct tooth much shorter than the tip of the claw beyond the tooth.

General color black, in many places with a metallic blue or violet reflection, as on the nasus, vertex near each eye and abdominal segments 2-6. Labrum shining black. Labium and rear of head near the "pale clay yellow" of Smith's Glossary.<sup>27</sup> Labium cleft in its apical .46. No pale postocular spots.

Hind margin of prothorax convex, somewhat flattened; propleura pale, faded (color in life?).

Mesepisternum at its anterior (inferior) end with a pale yellowish or greenish antehumeral vitta about .7 mm. long. Mesepimeron for most of its length with a pale greenish stripe. Most of the metapleuron, of the metinfraepisternum and of the pectus pale greenish, with a brownish-black streak on the upper half of the second lateral (metapleural) suture and a short transverse blackish streak near the hind end of the pectus.

Abdomen: Intersegmental articulations of segments 1-5 narrowly pale cadmium yellow (Smith, l. c.), mid-dorsally interrupted on 4 and 5; sides of 1-6 inferiorly pale yellowish, rising higher at the bases of 3-6. Dorsal surface of 7-10 partly covered by an incrustation of foreign material which conceals their color pattern, but apparently black, unmarked. Tenth segment not elevated at its hind end, which latter, in dorsal view, is widely emarginated for two-sevenths of the segment's length. On view-

ing the hind surface of 10 from above and behind, there is seen, immediately below the hind dorsal margin, a distinct, sharply margined groove which extends from the level of the middle of one superior appendage to the level of the middle of the other superior appendage; each end of this groove is closed.

Superior appendages one half as long (in profile view) as segment 10, in dorsal view directed nearly straight caudad and showing an infero-internal lamella in the proximal two-thirds of their length; this lamella rounded at its apex and ending nearly at right angles to the remaining superior part of the appendage, which latter tapers to a slender apex bent mesad at its tip and ending in a slight hook. In profile view, the appendage is two-branched, upper branch twice as long as the lower; the distal end of the lamella above mentioned terminates as a convex projection at three-fifths the appendage-length, beyond which the upper branch tapers to an acute tip directed slightly dorsad; lower branch half as long as the upper branch and about three-sevenths as high thereof at base, forming a slender tapering process, curved slightly dorsad and ending a little short of the terminus of the lamella of the upper branch.

Inferior appendages, in profile view, hardly shorter than the lower branch of the superior appendages; the height of one appendage equal to one-half of the height of the tenth segment; upper third of the appendage produced as a blunt cone directed nearly straight caudad.

Abdomen 49, hind wing 32 mm.

This species, named in honor of the Director of the Kartabo Station, belongs in de Selys' group of *L. andromache* and *elongatum*, but differs from both of them in the form of the abdominal appendages and by the oblique pterostigma surmounting less than one cell; *andromache*, moreover, has the pterostigma "presque carré."

#### *Leptagrion* sp.

Kaieteur, British Guiana, 18.II.1921, one male, abdominal segments 8-10 lost.

Related to *L. elongatum* Selys, but differing therefrom in the (oblique) shorter pterostigma which surmounts only one cell on all four wings, the presence of a black stripe on the humeral suture for its entire length, only half as wide as the middorsal black stripe, and a still narrower brown stripe on the whole length of the second (metapleural) lateral suture. Abdominal segments 1-7 37 mm., hind wing 26 mm. Owing to the absence of the specifically important abdominal appendages, I give this insect no specific name.

#### *Aeolagrion demerarum* Williamson, 1917.

Williamson, E. B., 1917, *Ent. News*, 28 (6):244, figs. (male apps.), pl. XVIII, fig.

<sup>27</sup> Smith, John B. Explanation of Terms used in Entomology, plate IV, fig. 22. Brooklyn Entom. Soc., 1906. The title here given is that of the two title pages of the writer's copy, but the back of the original buckram binding reads "Glossary of Entomology."

22 (venation). Geijskes, 1941, *Ann. Ent. Soc. Amer.*, 34:722, fig. 2 (nymph).

Kartabo, two males, one dated, 8.VI.1921; both lack heads.

There is a male from Paramaribo, Surinam, by Miss Katherine Mayo, in the collection of the Academy of Natural Sciences of Philadelphia.

All three males have been compared with a paratype from Georgetown, British Guiana, Jan. 25, 1912, by L. A. and E. B. Williamson and R. J. Rainey, received from Mr. E. B. Williamson, with which they agree.

All four males show a structural feature not mentioned in the original description: On each mesepisternum, at its anterior end, near its lateral margin, is an erect triangular process (mesostigmal lamina), about .14 mm. high, when viewed in profile and slightly from below; directed dorsad and laterad, blue anteriorly, its apex black; it is situated directly behind the "round lateral wing" of the same side of the hind prothoracic border.

Since writing the preceding paragraph, I have received three males and two females of *demerarum* from the Botanic Garden at Paramaribo, collected and sent to me by Dr. D. C. Geijskes. They are dated 19.VI.1939, 10 Oct. and 20.Dec.1938. The females also possess a mesostigmal lamina, less prominent (.09 mm. high) than in the male, the apex (which is triangular and directed laterad in the male) rounded off, the black of the apex continued caudad as a minute metallic green spot on to the anterior surface of the mesepisternum; this minute spot absent in all seven males.

Distribution: British and Dutch Guiana.

***Acanthagrion adustum* Williamson, 1916.**

Williamson, E. B., 1916, *Ent. News*, 27 (7):320, pl. XVII, figs. 1, 2 (male apps.), 10 (mes. stigma female). Geijskes, 1943, *Ann. Ent. Soc. Amer.*, 36:180, pl. VI (nymph).

Kartabo, Odon. 19, LAMA 17, one specimen, abdomen lost.

Agrees well with the description and with a paratype from Wismar, British Guiana, Feb. 15, 1912, by L. A. and E. B. Williamson and R. J. Rainey, received from Mr. Williamson, with which it has been compared.

Distribution: British Guiana.

***Metaleptobasis tetragena*<sup>28</sup> n. sp.**

(Pl. I, figs. 20-22).

Kartabo, July-August, 1926, by Dr. Charles Hodge IV, one female, not fully matured, holotype, to be placed in the collection of the Academy of Natural Sciences of Philadelphia, by the kindness of Dr. Hodge, No. 9274.

Wings: M2 arising at the sixth postnodal (front wings), at the fifth (hind wings); A and Cu2 in the same straight line<sup>29</sup> (all wings). Pterostigma longer than wide, grayish, surmounting less than one cell on all four wings, costal margin .71 mm. (front wing), .66 mm. (hind wing), proximal end oblique, distal end less so. Twelve postnodals (all wings), M1a arising at the 10th (all wings), Cu2 ending at the level of the 6th postnodal (3 wings) or 7th (left hind wing). Antenodal ultraquadrilateral cells on all wings three.

Legs yellow, with black or brown spines, 6 on the outer row of the third tibia, 8-9 on the inner row; tarsal claws without a tooth.

Labium as noted by Williamson for *M. mauritia* and *M. manicaria*. Labrum obscure ochre; rhinarium and nasus dark brown; frons anteriorly ochreous, superiorly black, a transverse yellowish stripe laterad to each paired ocellus; vertex dark metallic green and violet; occiput and postero-superior margin of vertex yellowish; rear of head ochraceous; antennae: first and second segments pale cream (?), anterior surface of the first and distal end of the second brown.

Prothorax ochraceous; hind margin with two erect processes, each about .07 mm. wide and a little longer, apex almost transversely truncate, processes separated by a subrectangular interval of about .11 mm. width. (Pl. I, figs. 20, 21).

Thorax with a mid-dorsal metallic violet stripe about .57 mm. wide, remainder of thorax pale brown becoming yellowish on the sides; on each lateral margin of the violet stripe, at its anterior end in dorsal view, is a straight, slender, tapering process ("horn") .45 mm. long, diverging widely cephalad from its fellow; in profile view each process is directed upward at its base, but soon directed cephalad and overhanging the prothorax; at their bases these horns are .24 mm. apart. (Pl. I, figs. 20-22).

Abdomen brown dorsally, with a metallic reflection, a transverse, basal, pale green ring at the anterior end of segments 2-6, interrupted mid-dorsally by the brown and confluent with an inferior stripe of the same pale green on the same segments; posterior third of 8, half of 9 and all of 10 dorsally paler, yellowish. Appendages of 10 reaching to the level of the hind end of 11. Genital valves barely projecting caudad beyond the level of 11; serrulations on their ventral margins about six in number, located in the distal third of the valves, each one wider than high, rounded at apex, first to third separated from each other by 2-3 times the width of each, fourth to sixth separated by

<sup>29</sup> Cf. Williamson, 1915, *Proc. U. S. Nat. Mus.*, 48 (2089):637, lines 26-28, in which is an easily overlooked statement of this peculiarity as a venational generic character of *Metaleptobasis*.

<sup>28</sup> τέτρα = four, γέν = be born, in allusion to the four thoracic horns.

the width (or less) of each, first to third each bearing a seta, fourth and fifth each two, sixth (which is close to base of palp) none.

Abdomen 35 mm., hind wing 22 mm.

This female differs from the females of other described species of *Metaleptobasis* or *Leptobasis* in having subparallel processes on the hind margin of the prothorax and longer, cylindrical, diverging "horns" at the anterior end of the mesothorax. The nearest species is *quadricornis* Selys of Para, whose thoracic armature is thus described: "Prothorax roussâtre, le bord postérieur presque droit et chacun de ces côtés portant une corne aplatie, redressée et penchée vers le thorax dont le bord antérieur porte aussi deux petites pointes coniques, redressées plus courtes, une de chaque côté, mais assez rapprochées et dirigées vers le prothorax," and again: *quadricornis* "les deux cornes du thorax et celles du prothorax presque égales coniques, assez courtes," (Selys, 1876). The italics are mine to emphasize the differences. *Quadricornis* is described also as having the pterostigma covering one cell, the internal side hardly oblique.

*Ceratura capreola* (Hagen, 1861).

Geijskes, 1941, *Ann. Ent. Soc. Amer.*, 34 (4):729, fig. 5 (nymph).

Kartabo, VRS, Odon. 6, one male; Odon. 40, one citrus female.

Both male and female have seven postnodals on the front wings, six on the hind wings, thus agreeing with "the individuals from Brazil, of both sexes, (which) have usually one more postcubital (postnodal) on both front (7) and hind (6) wings than the majority of Mexican and Central-American examples possess." (Biol. Centr.-Amer. Neur. 132, 1903). The dorsum of the eighth abdominal segment of this male has the anterior .57 mm. black, the posterior .4 mm. blue.

Distribution: Cuba, Jamaica, Puerto Rico, Martinique and Vera Cruz, Mexico, to Rio Grande do Sul, Brazil, and Jujuy, Argentina.

v. *Protoneurinae* T. & F., 1938.

*Neoneura joana* Williamson, 1917.

Williamson, 1917, *Trans. Amer. Ent. Soc.*, 43:213, 215, 242, 7 figs.

Kartabo, VI.4.1924, one male lacking abd. segs. 7-10; 9.VIII.1920, one male lacking abd. segs. 4-10.

Both specimens were compared with a male paratype from Tumatumari, British Guiana, Feb. 9, 1912, at the Academy of Natural Sciences of Philadelphia. The remaining portions of the June male agree well with Williamson's detailed description and figures, except that the black bar running from either side of the median ocellus does not quite reach the antenna of the same side, although the remainder of this bar,

forward and backward from the antenna, agrees. The August male has the longitudinal black bar on either side of abdominal segment 2 reaching both base and apex of that segment, the black markings on the sides of abdominal segment 1 are not symmetrical.

Distribution: British Guiana.

*Protoneura calverti* Williamson, 1915.

Wilmsn., 1915, *Proc. U. S. Nat. Mus.*, 48 (2089):620, 619, 632-635, pl. 41, fig. 1 (venation), pl. 43, figs. 11, 12 (thoracic color pattern), pl. 44, figs. 23, 24 (apps.).

Kartabo: July-Aug., 1926, Chas. Hodge IV, one male.

The Kartabo male differs from Williamson's description and figures and from two of his male paratypes from Tumatumari, British Guiana, Feb. 11, 1912, with which it has been compared, by having the orange red spots on the mesepisternum reaching farther dorsad and caudad, attaining a length of 1.65 mm. as compared with 1.18 mm. in the paratypes, by the longer yellow area, 1.65 mm., on the metepisternum, vs. 1.18 mm. in the paratypes, and by the black on the second lateral thoracic suture being narrower (.19 mm. vs. .33 mm.). In the two paratypes the inferior appendages project as far caudad as do the superiors; in Williamson's figures and in the Kartabo male the inferiors extend beyond the level of the superiors; the shape of the appendages appears to be the same in all three males. The Kartabo male has all surfaces of the middle third of the third femora yellow. The three males have 9-10 postnodals on the front wings, 8-9 on the hind.

Distribution: British Guiana, Trinidad.

GOMPHINAE S. & H., 1850 (as Gomphines).

i. *Ictinogomphinae* T. & F., 1940.

*Zonophora batesi* Selys, 1869.

Selys, 1869, *Bull. Acad. Belg.*, (2) 28 (8): 198. Needham, 1944, *Trans. Amer. Ent. Soc.*, 69: 219, pl. XVI, fig. 19a (genit. 2d abd. seg. ♂).

*Zonophora bodkini* Campion, 1920, *Ann. Mag. Nat. Hist.*, (9) 6:136, pl. VII, figs. 10-14 (venation, vulv. lam., mand., max.).

"Essequibo R(iver) below [between?] mouths of the Potaro and Rupinuni, British Guiana, V.1920, George B. Fox," one male, in coll. Acad. Nat. Sci. Phila.

The mouths of the Potaro and Rupinuni (also spelled Rupununi and Raponunni) Rivers, where they empty into the Essequibo, are about 100 miles (150 km.) apart.

This male has abdomen 58 mm., hind wing 48, its maximum width 13, pterostigma of front wing 5.48, width of head 9.5, 1st femur 4.66 long, 2d femur 5.72, 3d femur 7.93 mm.; antenodals, front wings, 23 and 24, 1st and 6th or 8th thicker, hind wings, 16, 1st and 8th thicker; postnodals, front wings, 15 and 16, hind wings, 17 and 18.

Compared with Selys' description of *batesi*, from Fonte Boa, Upper Amazons, Brazil, this male has the abdomen slightly longer (type 55 mm.) the hind wing slightly shorter (type 50 mm.), pterostigma slightly shorter (type 6 mm.), the ante- and postnodals fewer. Pale markings of the thorax not distinct but apparently not different. Abdominal segment 1 with an orange or yellow spot each side in the posterior half; two yellow or orange spots on each side of 2, one anterior, the other posterior; basal yellow or orange spot on each side of 3 from base to transverse median suture, where it rises almost to the mid-dorsal line, behind this suture a narrower stripe to .9 of the segment's length; a narrower basal stripe each side of 4-6, pointed posteriorly, reaching to the transverse suture on 4, not as far on 5 and 6; the basal ring on 7 reaching to the same suture, interrupted by a mid-dorsal black line. No orange or yellow marks on 8-10. Branches of the inferior appendage spread far wider apart (3.44 mm.) than are the superiors (2.70 mm.). The hamules, penis and especially its vesicle agree fairly well with the figures for this species given by Needham (1944), although the cornua of the penis are extended farther.

The single female from Tumatumari, Potaro River, British Guiana, described by Mr. Campion (1920) as *Zonophora bodkini*, is nearly the same size as the present male, but the hind wing is longer (52 mm.), and in most respects, other than those of sex, this male agrees with Mr. Campion's description, including the stout tubercle behind each of the paired ocelli. The hind margin of the occiput of this male, however, is almost straight, barely concave, the ante- and postnodals are slightly fewer, the pterostigma decidedly shorter and there is a brace-vein at its proximal end.

I think the differences above listed between the present male and the description of *batesi* are not specific and that *bodkini* is the corresponding female.\*

Distribution: Guianas, Amazon valley.

***Progomphus dorsopallidus* Byers, 1934.**

Byers, 1934, *Occas. Papers Mus. Zool. Univ. Mich.*, 294:1, pls. I, II.

Kartabo: one female, lacking abd. segs. 4-10.

The female of this species has not been described. The present specimen agrees fairly with the description of the male, especially with the thoracic color pattern. The

\* Subsequent to the reading of the first proofs of this article, I received from Dr. Erich Schmidt, of Bonn, Germany, proof sheets of a paper by himself entitled "Revision der Gattung *Zonophora* Selys Deutsche Entom. Zeitschrift 1941, Heft I-II (9 Juli 1941) p. 76ff." Dr. Schmidt has not distributed his separata as yet. His paper is included in the Insecta section of the Zoological Record for 1945. In it he has the same conception of *Z. batesi* as set forth above and has likewise concluded that *Z. bodkini* Campion is the female of *Z. batesi*. This note is inserted here to record that he and I—have independently reached the same conclusions.

posterior margin of the occiput has a slight tendency to form a median excision. Wings colorless, hind wing 20 mm. Pterostigma pale clay yellow, smaller than described, 2.83 mm. long on costal margin, surmounting 4-4½ cells. Antenodals, front wings, 15 and 13, hind wings 10 and 11; postnodals, front wings, 10 and 9, hind wings, 10; all the triangles 2-celled.

*Dorsopallidus* was described from San Estéban, Venezuela.

***Gomphoides fuliginosa* Hagen, 1854.**

Needham, 1944, *Trans. Amer. Ent. Soc.*, 69:195, 197, pl. XV, fig. 8e, pl. XVI, fig. 8f. Kartabo: one nymphal exuvia, 7.IX.1920.

I have asked Prof. Needham to study this exuvia in the belief that he would be more able than I to identify it in the course of his examination of allied material. His results are contained in his paper cited above.

Distribution: British and Dutch Guiana.

***Phyllocycla* new generic name**

for *Cyclophylla* Selys preoccupied. Type species: *signata* Hagen, as for *Cyclophylla*, fixed by Kirby, 1890, *Cat. Odon.*, p. 74.

Cowley (*Ent. Mo. Mag.*, 70:244, 1934) pointed out that the name *Cyclophylla* Selys, 1854, was preoccupied by Brandt, 1837, in *Coelenterata*<sup>30</sup> but demurred to giving a new name for *Cyclophylla* on the ground that it was unnecessary, since the three genera or subgenera, *Gomphoides*, *Cyclophylla* and *Aphylla*, had been combined into one for which he accepted Muttkowski's 1910 name, *Negomphoides*.

Now that Prof. Needham has resurrected these three genera (*Trans. Amer. Ent. Soc.*, 65:365, 388, 389, 1940) on partly new characters, it seems necessary to adopt a new name for *Cyclophylla*, hence the present proposal of *Phyllocycla*. However, the distinctness of the three groups, based on Needham's new characters drawn from the anal field, is still not sharp, as attention is called below to variations in *Phyllocycla signata*, *Ph. bartica* and *Aphylla alia* in the number of cells in the anal loop and in the course of vein A2 which are not in accord with his characters for *Cyclophylla* (*Phyllocycla*).

***Phyllocycla signata* (Hagen, 1854), (new combination).**

*Cyclophylla signata* Needham, 1943, *Bolet. Entom. Venezol.*, 2(4):201.

Kartabo, 13.iii, one male.

Abdomen 37 mm., hind wing 27, pterostigma (right front wing) 3.30, third femur 5.10, width of head 6.5, width of hind wing 7.85 mm.

<sup>30</sup> Neave, Nomenclator Zoologicus, 1939, I:920, gives the reference for Brandt's name as 1837, *Bull. Sci. Acad. Imp. Sci. St. Petersburg.*, 1 (24): 187, which I have examined. The title of Johann Friedrich Brandt's paper in question is "Remarques sur quelques modifications dans l'arrangement de l'ordre des Acalephes discophores ou umbrellaifères," in which the "Subgenus [Carybdea] Cyclophylla Nob." is briefly characterized and two species, *Carybdea periphylia* Per. et Les. and *Carybdea bicolor* Quoy et Guim., are referred to it.

This male corresponds closely with de Selys and Hagen's descriptions and figures of 1854 and 1858 of *signata*, based on a male from "Bresil" in the Berlin Museum and a female from Venezuela by Appun in Hagen's collection. Such differences as I have found (in addition to slight ones in size which the above dimensions indicate) are: Occiput dark brown, hind margin nearly straight (shown as slightly bilobed in Hagen's pl. 12, fig. 4d of 1858); markings of the abdomen not very distinct; on moistening the insect with alcohol, the pale basal spots reach apparently to one-tenth of the segment's length on 3, one-fifth on 4, .15 on 5 and 6 and .17 on 7; 10 is dark brown dorsally; discoidal triangle of front wings 3-celled by 3 veinlets, one from each side, which meet in the center; discoidal triangle of hind wings and internal triangle of front wings each 2-celled, internal triangle (sub-triangle) of hind wings free; antenodals on the front wings 20 and 19, on the hind wings 14; postnodals on the front wings 12, on the hind wings 13.

The following particulars may be added: Pale green antehumeral stripe .8 mm. wide at its lower (anterior) end, just above its union with the green mesothoracic "half-collar" and where it is separated from the brown mid-dorsal carina by exactly its own width, the right and left antehumerals converging upward. The much narrower (.25 mm.) pale humeral stripe complete. A pale green stripe (.5 mm. wide) on most of the length of the brown mesepimeron; a sub-equally wide pale green stripe on most of the length of the brown metepisternum; between it and the green of the metepimeron is a brown band, about 1 mm. wide, on the second lateral suture; by far the larger part of the metepimeron is pale green to the small brown triangle at its postero-inferior angle.

Anal loop of 3 cells (1 in front, 2 behind) not sharply defined posteriorly, A1 and A2 approximating slightly behind it, thence diverging to the hind margin of the wing; distal portion of A2 convergent with A3. A basal subcostal cross-vein on all wings.

*Signata* has not appeared in the literature since de Selys and Hagen's Monographie des Gomphines of 1858 until it was compared with *C. anduzei* by Needham (1943).

Distribution: Venezuela, Guiana, Brazil.

***Phyllocyba bartica*, new species.**

(Plate I, figs. 7-15).

?*Cyclophylla* sp. No. 6, Needham, 1940, *Trans. Amer. Ent. Soc.*, 65:379 (nymph).

Kartabo: III.4.1926, one female; III.9.1926, one male holotype; III.11.1926, one female; 18.5.1919, one male; July-Aug. 1926, one female by Dr. Charles Hodge IV, in the collection of the Academy of Natural Sciences of Philadelphia, paratypes. Holotype ♂ No. 9277 Acad. Nat. Sci. Phila.

Also, I have had the opportunity to include in the following description one pair taken in copula, the female with a cluster of eggs at the vulva, four other males and one other female from Itaituba, on the Rio Tapajos, Brazil, I, III, and V, 1922, by A. H. Fassl, from the collection of the late Dr. F. Ris (Senckenberg Museum, Frankfurt am Main), and one male from Kartabo, British Guiana, taken by Dr. W. T. M. Forbes, between November 1 and 5, 1920, now in the Cornell University collection—all lent to me by the Museum of Zoology, University of Michigan, through the kind interest of Mrs. Leonora K. Gloyd; these likewise are paratypes.

♂. Face (except rhinarium=anteclypeus), labrum, vertex and occiput reddish brown. Rhinarium, frons, above its transverse carina, pale green, but a narrower reddish-brown band on its upper surface immediately in front of the ocelli. Hind margin of occiput almost straight. Rear of head and labium perhaps pale green in life.

Prothorax reddish-brown. Pterothorax dark brown, mesothoracic "half collar" united broadly with an antehumeral stripe on each side to form a green figure "7", the antehumeral stripe widest (.5-.8 mm.) at its lower end just above where it joins the half-collar and where it is once to nearly twice as far from the green-lined mid-dorsal carina as its own width; right and left antehumerals converging toward their upper ends where each is .42-.65 mm. distant from the same carina. Sides of thorax mostly dark brown, the following green: a complete stripe .3-.4 mm. wide, immediately in front of the humeral suture, a mesepimeral stripe .42-.65 mm. wide at mid-height, for almost the whole length of the sclerite, a metepisternal stripe .57-.66 mm. wide, close to the second lateral suture, and most of the metepimeron and pectus.

Abdominal segments 1 and 2 brown, a dorsal basal spot on each side of 1 (or the two united), a mid-longitudinal stripe and the auricles on 2 and the sides inferiorly of both 1 and 2, pale green; 3-10 blackish, a longitudinal reddish-yellow stripe on each side of 3-7, reaching .8 of the length of the segment on 3, .86 on 4, .7 on 5, .3 or more on 6, .83 on 7 (for shorter distances on other males); some reddish on each side of 8 and 9, and a small yellowish spot on each side of 10 near its hind margin.

Lateral margins of 7 widening gradually from base to apex. In profile 8 shows a distinct lamellate expansion of the ventral tergal margin for its entire length, increasing in depth caudad to a maximum of .25-.38 mm. at three-fourths' the segment's length and terminating in a circular quadrant, ventral margin with 12-14 denticles; expansion on 9 having a maximum of .1 mm. at mid-length of the segment.

Superior appendages 1.70-2 mm. long, longer than 10, subequal to 9, blackish or reddish-brown; in dorsal view each directed nearly straight caudad in its proximal .6, then curved mesad; at .4-55 length there is an acute, pale-tipped tooth on the upper, carinate margin; opposite this tooth is a slight convexity or a straightness on the otherwise concave mesal ventral margin; at seven-eighths' to nine-tenths' length the outer margin is strongly angled mesad and thence extends in a nearly straight line to the apex; the extreme apex is rounded and finger-like and slightly proximal to it the inner margin is excised, but convex proximal to the excision; the inner (mesal) surface of the appendage is grooved for its entire length, the groove passing under (ventral to) the ante-apical convexity just described. In profile view each appendage as a whole is directed slightly dorsad and its height regularly decreases, especially on its ventral margin, from base to apex; the terminal sixth or more is obliquely truncated ventrad and caudad; the upper margin shows two shallow concavities, the first from base to the superior tooth (above described) at .4-55 length, the second, shallower, from the tooth to the strong superior angulation at seven-eighths' length or more where the truncation of the apex begins; the inferior margin shows a sharp, conical, basal tooth, whence the margin is slightly convex, thence slightly concave, ascending to the beginning of the apical truncation.

Inferior appendage visible in dorsal, but hardly in profile, view; in dorsal view about one-fifth as long as the superiors, a little wider than long, distal margin with a slight median notch, not always present.

Auricles with 7-10 black, marginal denticles. Genitalia of 2 as shown in figs. 8-10, Plate I. Posterior cleft of the "gaine" (Hagen, 1858, pl. 12, fig. 4j) = "hood of the penial peduncle" (Needham, 1943, p. 202) with a tooth at the bottom, as in Hagen's figure cited. Cornua of the penis finely serrate as figured by Hagen (l. c., pl. 12, fig. 4i).

Legs reddish, distal ends of the femora and the tarsi reddish-brown.

Wings faintly smoky, stigma brown, surmounting  $4\frac{1}{2}$ -7 cells, a basal subcostal cross-vein<sup>31</sup> on all wings, all triangles (except the free internal of the hind wings) 2-celled (or the discoidal triangle of the front wings 3-celled in seven out of sixteen wings), two ultra-triangular rows (preceded by three cells on the hind wings) increasing to three rows beyond the level of separation of the subnodal sector (Rs bridge) and median vein (M1-2), anal loop of two cells, A1 and A2 converging behind it, thence diverging to the hind margin of the wing (see Pl. I, fig. 13), with one (1♂) or two (7♂) cells

between them immediately posterior to the anal loop. Antenodals on front wings 14-19 (17), on hind wings 11-15 (13). Postnodals on front wings 9-13 (10), on hind wings 10-13 (11), numbers in parentheses the most frequent. First and fifth or sixth antennodals stronger on the front wings, first and fifth on the hind wings. Venation dark brown.

Dimensions of ♂: abdomen 37.5-40.5 mm., hind wing 27-29, pterostigma, front wing 3.59-3.68, third femur 4.87-5.0, width of head 6.25-7.70, width of hind wing 7.00-8.00 mm.

♀. Differs from the male as follows: Pale antehumeral stripe at its upper end .47-.8 mm. distant from mid-dorsal carina, its maximum width at lower end .9 mm. Sides of thorax apparently the same. Reddish-yellow on the sides of abdominal segments reaching to the full length of 3-7. Lateral expansions of 8 to .09-.14 mm., of 9 to .05-.09 mm. Segment 11 .36 as long as 10, conical, yellowish, Appendages 1-1.4 mm. long, subequal to 10, yellowish or ochre, straight, slender, tapering to an acute apex. Vulvar lamina (Pl. I, fig. 14) .38-.5 mm. long, .24-.28 as long as the sternum of 9, 1.0 mm. wide at base, bifid in distal half or two-thirds, lobes triangular, interval between lobes nearly 90°, interval between apices of lobes .47-.57 mm. Discoidal triangle 3-celled in right front (2♀) or both front (2♀) wings. Antenodals on front wings 16-20 (16 and 18 equally frequent), on hind wings 12-14 (13). Postnodals on front wings 11-12 (11), on hind wings 12-15 (13). The female of III.11.1926 has the first and sixth antennodals on the hind wings thicker.

Dimensions: abdomen 34-39 mm., hind wing 29.5-31, pterostigma of front wing 3.40-4.09, third femur 4.91-5.20, width of head 6.5-7.20, width of hind wing 6.5-8.34 mm.

The younger female, taken by Dr. Charles Hodge, also may belong to this species. Its colors are paler. Head pale brown, the following pale green: a curved stripe on each side of the labrum close to the free margin, rhinarium (anteclypeus), a spot on each side of the nasus (postclypeus), frons above the carina but leaving a wider brown stripe in front of the ocelli. Most of the prothorax pale green, hind lobe pale brown. Pterothorax with a mid-dorsal yellow or pale green stripe .33 mm. wide, each green antehumeral stripe .5 mm. wide where it joins the mesothoracic half-collar, its upper end only .33 mm. distant from the mid-dorsal carina. Sides of thorax pale reddish, the pale green stripes present but not so clearly seen, owing to the partial wrinkling of the surface.

Abdomen pale greenish or reddish with blackish-brown markings as follows: an indistinct oblique line on each side of dorsum

<sup>31</sup> Two on the left front wing of one male.

of 2, a narrow mid-dorsal stripe on 3 and 4 from the transverse antemedian carina to four-fifths of each segment's length, a similar stripe on 5 and 6 for the entire length of each, a pair of oblique streaks diverging caudad on the hindmost fifth of 3-6; 7 largely pale with some blackish near its hind end and some for much of the length of 8-10.

Vulvar lamina more exposed, .42 mm. long, .21 as long as the sternum of 9, bilobed in its distal half, lobes widely triangular, each lobe a little more than 90° at tip and rounded, interval between lobes a little more than 90°, width of lamina 1.09 mm., distance between tips of lobes .42 mm.; the 9th segment has been accidentally flattened and more of the sternite of 9 immediately behind the vulvar lamina has been exposed, showing a transverse ridge, concave caudad in the middle and followed by a transverse low tubercle bearing many hairs; on each side of the middle line, immediately in front of this ridge is a small, shallow, darker brown pit. (Pl. I, fig. 15).

Wings clear, pterostigma pale clay-yellow (Smith's "Explanation"), surmounting 6-8 cells, discoidal triangle of both front wings 3-celled, internal triangle of front wings and discoidal triangle of hind wings 2-celled, also the internal triangle of right hind wing, that of left hind wing free. Three ultra-triangular cells precede the two rows on the left front wing and on both hind wings, the increase to three rows is at the level of separation of Rs bridge and M1+2 on both front wings and on left hind wing. Anal loop of two cells, shaped as in the above described 7♂, 4♀, with only slight differences in the lengths of the sides. Antenodals on front wings 19 and 20, first and seventh thicker on the right, on the hind wings 14, postnodals on hind wings 13 and 14.

Otherwise this female is as in the four females above described.

Dimensions of this ♀: abdomen 37 mm., hind wing 31.5, pterostigma front wing 4.0, third femur 4.58, width of head 7.2, width of hind wing 9.0 mm.

The venation of the present material of *bartica* agrees fairly well with that described by Needham (1940) for a nymph, *Cyclophylla* sp. No. 6, American Museum of Natural History, "Acc. 3928: came in with fishes from British Guiana." However, in these five female imagos, the distal portion of vein A2 is parallel, not convergent, with A3 on the hind wings of both sides, hence departing from one generic character for *Cyclophylla* as given by Needham (1940, p. 365); the eight males, on the contrary, agree with this character. There are five postanal<sup>32</sup> cells, three of them posterior to

the anal loop in three females, four postanal cells, two of them posterior to the anal loop in the remaining female and the males. There are two rows of cells between A2 and A3 from A to the wing margin on the right hind wing of the July-Aug. female, while on its left hind wing two rows begin one cell below A; in three females two cells between A2 and A3 begin only at two cells from the wing margin, i.e., two cells below A; in the males and one female there is but a single row of cells between A2 and A3, although the female has two marginal cells. Considerable variation in the cells of the anal area is, therefore, to be expected, although the anal loop is 2-celled in all thirteen imagos.

The specific name *bartica* here proposed is that of the district in which Kartabo lies.

In size and coloring *Ph. bartica* is very similar to *Ph. signata* Hagen. The males of *bartica* differ from that of *signata* in the smaller lateral dilatations of abdominal segments 8 and 9, in the shape of that of 9, in the superior appendages having a superior tooth at .4-.55 length, a more distinct angulation of the outer margin at seven-eighths' length, the ante-apical excision of the inner margin more abrupt and in having the acute, conical, inferior, basal tooth; and in the 2-celled anal loop of the hind wings. As mentioned under *signata* (antea), the Kartabo male of that species has the discoidal triangle of both front wings 3-celled, whereas in the types of *signata* it is 2-celled. Of the males of *bartica* here described, seven out of sixteen wings have this triangle 3-celled, the remaining nine 2-celled. Of the five females here referred to *bartica*, three have this triangle 3-celled symmetrically, the remaining two have it 3-celled and 2-celled asymmetrically. These five females are referred to *bartica* because of their symmetrically 2-celled anal loop, as in the *bartica* males, while in the single male of *signata* the anal loop is symmetrically 3-celled. The anal loop is not mentioned in the previous descriptions of *signata*.

The descriptions of other species referred, or referable, to *Cyclophylla* (*Phyllocycla*) or *Aphylla*, differ from *Ph. bartica* as follows:

In the absence of a superior tooth near the mid-length of the superior appendages: *ambigua* Selys, 1873, *anduzei* Needham, 1943, *brevipes* Selys, 1854, *caraiiba* Selys, 1854, *cristatus* Needham, 1944, *cubana* Navas, 1917,<sup>33</sup> *curvata* Navas, 1933, *dentata* Selys, 1859, *distinguendus* Campion 1920, *edentata* Selys, 1869, *elongata* Selys, 1857, *gladiata* Hagen, 1854, *hesperus* Calvert, 1909, *molossus* Selys, 1869, *ophis* Selys,

<sup>32</sup> As marked by Needham, 1944, *Trans. Amer. Ent. Soc.*, 69: pl. XVI, fig. 4c, here including the two cells of the anal loop

<sup>33</sup> *Cyclophylla cubana* Navas, 1917, *Mem. Pont. Acc. Romana*, 3:3, may be the same as *Aphylla caraiiba* Selys, 1854.

1869, *pachystyla* Needham, 1944, *producta* Selys, 1854, *protracta* Selys, 1859, *signata* Hagen, 1854, *sordida* Selys, 1854, *tenuis* Selys, 1859, *theodorina* Navas, 1933, *volSELLA* Calvert, 1905, and *williamsoni* Gloyd, 1933. Of these, *ambigua* differs also in the possession of a median notch in the hind dorsal margin of abdominal segment 10, *anduzei* in the form of the lateral margin of segment 7; *brevipes*, *cristatus*, *dentata*, *distinguendus*, *edentata* and *molossus* have the pale antehumeral stripe not united with the mesothoracic collar to form a figure 7; *cubana*, *gladiata*, *ophis*, *signata* and *sordida* have no stout, inferior, basal tooth on the superior appendages; in *gladiata* and *sordida* the pale humeral stripe is incomplete; *hesperus* and *protracta* differ in the lateral margins of abdominal segments 8 and 9; *ophis* has no angulation at seven-eighths the length of the superior appendage; still other differences are indicated in the respective descriptions.

Ris 1904<sup>34</sup> says of the superior appendages of *Cyclophylla argentina* Hagen, 1878, "dessen obere Kante nahe der Basis und an der Stelle der stärksten Krümmung gegen das Ende je ein ziemlich stumpfes Zähnen trägt. Das Ende stumpf." His 1913<sup>35</sup> figure of the appendages shows the tooth "nahe der Basis" at about .36 of the appendage length.

For *Cyclophylla diphylla* Selys, 1854, it is stated of the superior appendages: "Le bord supérieur porte une tubercule à son premier tiers," but no mention is made or shown (in 1858) of an inferior basal tooth, and the lateral margins of 8 and 9 are different from those of *bartica*.

*Gomphoides eugeniae* Navas, 1927, has the superior appendages with a superior tooth before mid-length; in dorsal view rounded, not angulate, exteriorly where the appendage changes its direction; lateral margins of 8 and 9 differently shaped.

*Cyclophylla pegasus* Selys, 1869, has the superior appendages "portant en dedans à leur moitié un petit tubercule," the lateral margins of 8 and 9 almost rudimentary.

In *Gomphoides viridipleuris* Calvert, 1909, "at about half length the inner surface (of the superior appendages) bears a small blunt tubercle near the upper edge of the appendage," but in dorsal view the appendages are rounded, not angulate, exteriorly where the change in direction of the appendage occurs.

*Phyllocycla bartica* female differs from the descriptions of the following species of which the female only has been described:

*andromache* Selys, 1869, which has no pale mesothoracic collar and has short pale antehumeral bands;

*Aphylla cornutifrons* Needham, 1944, which has a pair of frontal horns;

*Gomphoides ictinia* Selys, 1878, which has the vulvar lamina reaching abdominal segment 10.

The description of *Cyclophylla obscura* Kirby, 1899, is insufficient to enable its specific recognition.

#### *Aphylla alia* n. sp.

(Plate I, figs. 16-19).

Kartabo, 19.VII.1920, one male, abdominal segments 5-10 and left hind wing beyond the triangle lost, holotype, No. 9276, Acad. Nat. Sci. Phila.

This male agrees with the first character for *Cyclophylla* listed by Needham, 1940 (*Trans. Amer. Ent. Soc.*, 65:365), viz.:

(a) Anal loop of two cells sharply defined at its rear by convergence of A1 and A2, but not with the second character, as

(b) the distal portion of A2 is not convergent with A3 but diverges somewhat from it and also from A1. (Pl. I, fig. 18.)

It agrees with the following Selys-Hagen (1858, pp. 216-217) characters for *Cyclophylla*:

(c) internal triangle (subtriangle) of the front wings of two cells;

(d) the same of the hind wings free;

(e) discoidal triangle of all wings 2-3 celled (here 2-celled); but disagrees with the following Selys-Hagen characters:

(f) labium (i.e., the median lobe or ligula) as long as wide (here wider than long);

(g) "pièce supérieure des parties génitales" (=anterior lamina) emarginate at middle (here a quadrangular plate narrowed posteriorly, reaching caudad against the anterior hamules) (Pl. I, fig. 17);

(h) anterior and posterior hamules, in profile view, almost equally prominent, the anterior more slender, curved strongly caudad and dorsad; in oblique view, an acute, posterior, basal tooth is visible near the floor of the genital fossa; posterior hamule, in profile view erect, at least twice as thick as the anterior hamule, with a bunch of long (.85 mm.) hairs, its apex acute and directed mesad (Pl. I, figs. 16, 17);

(j) "gaine du penis" (vesicle or first segment thereof), in profile view, acutely pointed ventrad; in rear view, this acute point corresponds to a transverse lamella whose margin is trifid, the teeth about .047 mm. long (Pl. I, figs. 16, 19);

(k) glans of penis (=4th segment) with two very long cornua (here the cornua are absent and the glans, in ventral view, is subquadrangular, .6 mm. long, .38 mm. wide at base, .57 mm. at apex, membranous, pale, near its mid-length with two very black denticles in an oblique line on each side of its median line) (Pl. I, figs. 16, 17);

(l) "cueillère" (=sheath of penis, Tillyard, 1917) elongate, slightly wider at apex

<sup>34</sup> Hamburger Magalhaensische Sammelreise, Odonaten, p. 19.

<sup>35</sup> *Mem. Soc. Ent. Belg.*, 22:74.

with the merest suggestion of a median apical notch (Pl. I, fig. 17, sh).

The characters above lettered (*b*), (*f*), (*g*), (*h*), (*j*), (*k*), which differ from those given by Needham and by Selys-Hagen for *Cyclophylla*, approach or are identical with those of *Aphylla* and hence render doubtful the distinctness of these two "genera."

Other features of this male from Kartabo are: vertex, anterior surface of frons, nasus (postclypeus) except for a small yellow spot each side, lower margin of rhinarium (anteclypeus), labrum except for a yellow spot each side, rear of head except for a yellow spot each side near middle of eye-margin—dark brown (near Cologne earth or Roman sepia of Smith's Explanation, pl. iv, nos. 37 and 38). Occiput (its hind margin a straight line), superior surface of frons except a dark brown basal band in front of the ocelli, most of the rhinarium, genae, outer surface of mandibles—greenish-yellow. Labium near pale clay yellow (Smith, pl. iv, no. 22).

Prothorax: fore lobe brown pink (Smith, no. 21), middle and hind lobes greenish-yellow. Pterothorax predominantly darker brown than that on head, the following greenish-yellow: mid-dorsal carina, a transverse stripe ("collar") at anterior end of each mesepisternum for its entire width, an antehumeral stripe .8 mm. wide at mid-height, separated by a distance less than its own width from the mid-dorsal carina, diverging therefrom and from its fellow of the opposite side forward and downward, widened laterad at its upper end where it borders the ante-alar sinus, pointed at its lower end which does not touch the transverse mesepisternal stripe (hence *not* forming a figure 7), a stripe .57 mm. wide at mid-height on the mesepimera, a stripe passing through the metastigma around which it is enlarged but above which it is narrowed to .33 mm., a stripe on the metepimeron .98 mm. wide at mid-height, these three stripes wider at their upper ends which attain the upper margins of their respective sclerites. Interlar tergites with a mid-dorsal row of greenish-yellow or (on the scutella) gamboge spots. Pectus brown pink.

Abdominal segments 1-4: ventral surface dull yellow. Dorsal surface of 1 and 2 dark brown, a mid-dorsal stripe on 2, widened just posterior to the level of the yellow-tipped auricles, thereafter narrowed and confluent at its hind end with a transverse band which borders the entire width of the segment, yellow, auricles moderately prominent with 25-30 minute, posterior, black denticles; 3 largely orange but obscured with dull brownish at anterior end, the submedian transverse carina, an obliquely transverse ante-apical band and a longitudinal stripe on each side of the mid-dorsal carina uniting the former two, black; 4 orange each side for the anterior two-

sevenths of the segment's length, black from the submedian transverse carina as far caudad as a narrow, transverse, ante-apical, orange stripe, and with a slender, blackish prolongation forward on each side of the mid-dorsal carina almost to the anterior end of the segment; intersegmental articulations of 2-3, 3-4, 4-5 black; an inferior, longitudinal, brown stripe on each side of 3 and 4 for their entire lengths.

Legs: femora brown, superiorly reddish, tibiae and tarsi darker brown to black.

Wings (in addition to the features given at the beginning of this description): slightly brownish at the extreme bases of the subcostal and submedian spaces, venation dark brown or black except for the pale yellow costa, stigma pale ochre, surmounting  $5\frac{1}{2}$ -7 cells, 16 (right), 17 (left) antenodals on the front wings, the 1st and 6th thicker, 12 on the hind wings, 1st and 5th thicker, 11 (right), 12 (left) postnodals on the front wings, 13 (right), 14 (left) hind wings; one basal subcostal, one cubito-anal and one supratrangular cross-veins on all four wings, the cubito-anal nearly at the level of the first antenodal; post-triangular cells, front wings, two rows from the triangle out to the level of the point of separation of M1 and M3 (left) or one cell more remote (right), on the hind wings 3, then two rows to the level of the point of separation of M1 and M3 (left) or of M1 and the bridge of Rs (right). Hind wings with 4 paranal cells (Needham, 1944), of which the first two are also the proximal cells of the anal triangle and the fourth is also the first postanal; 5 postanal cells (Needham, 1944); sequence of cells between A1 and A2 behind the 2-celled anal loop: 1, 2, 3 (right), 2, 2, 4 (left), anal triangle 4-celled.

Dimensions: abdominal segments 1-4 13.5 mm., hind wing 28 mm., costal edge of stigma, front wing, 3.6 mm.

At least five species referred, or referable, to *Aphylla*, viz.: *brevipes* Selys, *dentata* Selys, *distinguenda* Campion, *edentata* Selys and *molossus* Bates Mss. Selys, are described as having the pale antehumeral stripe not connected with the pale mesothoracic "half collar;" in this respect the present male resembles them, but is smaller, has a shorter pterostigma and no pale humeral stripe; some other data concerning these five are given antea in the discussion of *Phyllocyca bartica*. The genitalia of the second abdominal segment of none of these five species have been described and owing to the absence of the last six abdominal segments and appendages of this specimen, it is not possible to say whether it is or is not conspecific with any of the five.

## ii. Gomphinae T. & F., 1940.

*Archaeogomphus hamatus* (Willmsn., 1918).  
*Agriogomphus hamatus* Williamson, 1918,

*Occas. Papers Mus. Zool. Univ. Mich.*, 59:4, pls. i, ii.

*Archaeogomphus hamatus* Williamson, 1919, op. cit., 63:5, pl. I, fig. 2; 1923, op. cit., 134:7.

Kartabo, 3 males, 1 female; two of the males without most of the abdomen, one male labeled 2.8.1919, another 6.III.1924, the remaining male and the female not dated.

In his paper of 1923 Williamson distinguishes *A. hamatus* female from *A. furcatus* female by the latter having the "rear of the occiput armed with two posteriorly directed spines or horns," while *hamatus* has the "rear of the occiput not armed with posteriorly directed horns." The present female has a horn .09 mm. long on each side of the occiput in the position in which rudiments are shown in his figure 10, pl. i of 1918 for *hamatus*. Since at least two of the present males are *hamatus* by the seminal vesicle (first joint of the penis), the principal character relied upon by its describer, I refer this female to the same species.

Distribution of *A. hamatus*: Dept. Magdalena, Colombia; British Guiana.

Of the thirteen features shown for *Archaeogomphus* in Prof. Needham's Verification Table for the neotropical Gomphinae (*Trans. Amer. Ent. Soc.*, 65:389, 1940) the following show deviations in these four individuals:

Postnodals in fore wings 6, without exception;

Antenodals in hind wings 9, without exception;

Postnodals in hind wings 5-7 (6 most frequent, in 5 wings out of 8);

Cross-veins between the sectors of the arculus proximal to the middle fork in fore wings 3-4 (4 more frequent, in 5 wings out of 8);

The same in hind wings 2, without exception;

Length of hind wing ♂ 15.5-17 mm., ♀ 18 mm.

The remaining seven features show no deviations in the present material.

AESHNINAE S. & H., 1850 (as Aeschnines).

i. Gynacanthaginae T. & F., 1940.

*Staurophlebia reticulata reticulata*  
(Burmeister, 1839).

E. M. Walker 1915, *Can. Ent.*, 47:390.

Rockstone, Essequibo, 9.04, Wm. Schaus, one female in the U. S. National Museum.

The colors of this female agree with the description of those from British Guiana given by Prof. Walker, t. c., p. 388. The venational features which he tabulated on page 389 show some variations in this female as follows: antecubitals, front wings, 34 (right), 33 (left), hind wings, 22 (r),

23 (l); postcubitals, front wings, 27 (r), 26 (l), hind wings, 28 (r), 30 (l); marginal cells between Rs and M3, front wings, 46 (r), 42 (l), hind wings, 49 (r), 47 (l); cross-veins in triangle, front wings, 6 (r), 7 (l), hind wings, 6 (r), 5 (l); cross-veins in supratriangle, front wing, 9, hind wings 7; cubital cross-veins, front wings, 8 (r), 9 (l), hind wings, 6 (r), 5 (l); cells in anal loop, hind wings, 21 (r), 18 (l); position of fork of Rs (number of first postnodal cells before stigma, front wings, 9, hind wings, 11 (r), 12 (l). Abdomen exclusive of apps.) 70 mm., hind wing about 70 mm. (extreme apices broken).

To aid in determining the geographical distribution of the Guianan form of *Staurophlebia*, which Prof. Walker considered to be *S. reticulata reticulata*, I have re-examined the Honduras and Chiriqui males cited in the *Biologia Centrali-Americana*,<sup>36</sup> which presumably are duplicates of specimens in the René Martin collection in the Paris Museum. The Honduras male has a very narrow, reddish line representing the stem of the T-spot of the frons, a faint brown line on the fronto-nasal suture, thorax dull greenish with a narrow (linear) faint reddish-brown streak bordering the ante-alar sinus anteriorly and on each side of the mid-dorsal carina; abdomen faded, its anterior segments reddish-brown, inferior appendage one-half as long as the superiors, elongate, triangular, as shown in Prof. Walker's figure 2, page 396.

The Chiriqui male has a distinct, black, linear stem to the T-spot, a narrow dark brown line on the fronto-nasal suture and along the base of the labrum, thorax dull greenish, discolored in front of the ante-alar sinus, a narrow reddish-brown stripe on each side of the mid-dorsal carina, abdomen faded, its anterior segments reddish-brown, inferior appendage as in the Honduras male except that it is two-thirds as long as the superiors.

I have examined also two males of *Staurophlebia* from the Florida road in the forest near Guapiles, Costa Rica, one taken by myself June 4, 1909, the other by Messrs. Schaus and Barnes on June 5 or 6, 1909, and one female taken by Prof. F. Tristán and myself in forest north of Santa Cruz, Costa Rica, January 29, 1910. The first male has a reddish-brown linear stem to the T-spot, barely the suggestion of a line on the fronto-nasal suture, thorax green, no darker markings in front of the ante-alar sinus or along the mid-dorsal carina, green of the thorax continued caudad as far as the extreme base of abdominal segment 3, anterior half of 3 otherwise reddish-brown, inferior appendage reaching to .55 of the length of the superiors. The other Guapiles male was

<sup>36</sup> *Neur.*, p. 179, 1905.

apparently similarly colored although the stem of the T-spot is still fainter, the thorax and first two abdominal segments more faded, the inferior appendage of the same extent. The Santa Cruz female is the only one of the three for which I have notes of the living colors; they are as follows: Eyes bright green with black pseudopupillae (6 horizontal rows in profile view, as follows from above downward: 2, 5, 6, 6, 5, 4, those of 2nd and 3rd row largest, decreasing in size from 3rd to 6th row). Remainder of head pale greenish-blue a rather faint pale brown T-spot on frons. Thorax and abdomen pale blue, the former a little grayish from pruinosity, abd. segments 1 & 2 and anterior half of 3 green. Thoracic sutures faintly brown. Abdominal intersegmental articulations dark brown, especially 7/8 and 8/9. Abdominal appendages brown, pale at base. Legs pale blue, tarsi and 3rd tibiae inferiorly black.

The Honduran and Costa Rican individuals thus approach Prof. Walker's *St. reticulata guatemalteca* more closely than either of the other two forms which he has differentiated; the Chiriqui male's living colors may have been such as to place it here also, although its present dried condition might seem to refer it to *St. reticulata obscura*.

René Martin<sup>37</sup> is the only author who has described and figured the inferior appendage of a *Staurophlebia* as "triangulaire conique du quart environ des supérieurs," although he adds "plus long chez certains sujets." Where this appendage is mentioned elsewhere in the literature, its length is given as half or more than half as long as the superiors, as it is in the four males mentioned above and in a male from Rockstone, British Guiana, which I received from Mr. E. B. Williamson. Prof. Walker has not discussed variations of the inferior appendage in his paper of 1915.

"The inferior appendage has a superior, basal, triangular process which projects upward and backward between the right and left superior appendages at their base; although well developed it is not mentioned in the descriptions; its morphological significance will, doubtless, be interesting."<sup>38</sup> It was subsequently described and figured by Prof. Walker (1915, pp. 392, 394, fig. 1), and by Navas for *St. platyura*.<sup>39</sup>

How it escaped the careful eye of E. Menger, artist of Martin's Aeschnines in the Catalogue of the Selys Collections, it is difficult to understand.<sup>40</sup>

<sup>37</sup> Cat. Coll. Zool. Selys-Longchamps, fasc. XX: 210, fig. 216, 1909.

<sup>38</sup> Biol. Centr. Amer. Neur. p. 178, 1905.

<sup>39</sup> Bol. Soc. Ent. Esp., 3: 91, fig. 1, "por encima". Mayo-Junio, 1920.

<sup>40</sup> A similar process exists on the inferior appendage of *Aeshna (Coryphaeschna) luteipennis* Burm. and has escaped description, although several times figured: Brauer, 1866. *Novara Reise Neurop.*, tab. I fig. 19 (as *Ae. excisa*);

Geographical distribution of *S. reticulata reticulata*: Porto Cabello, Venezuela, the Guianas, Para and perhaps farther south in Brazil and Argentina.

#### *Triacanthagyna* AND *Gynacantha*.

The identifications and the geographical distribution of the following species of these two genera are according to E. B. Williamson's paper of 1923 (*Univ. Mich. Mus. Zool. Misc. Publ. No. 9*) and that of Mr. W. D. Hincks of 1934 (*Entom. Record*, 46:77-81).

#### *Triacanthagyna septima* (Selys, 1857).

Kartabo: one male, "Odon. 83," abdomen lost; one male, abd. segs. 9-10 lost; one male, July-August, 1926, by Dr. Charles Hodge IV; Penal Settlement, 1917, one female, abd. segs. 6-10 lost. Georgetown, British Guiana, 15.3.1919, one female, appendages in part lost.

Anal loop with two vertical rows of cells in the hind wings of the three males and the left hind wing of the Georgetown female, with three vertical rows in the remaining three hind wings of the females; the second Kartabo male, however, has a central cell in the midst of the two vertical rows. There are three rows of cells between M4 and M5pl of both front and hind wings of all five individuals. The anal triangle is 2-celled in the three males, except in the left hind wing of ♂ 83.

Distribution: Mexico to Bolivia and Rio de Janeiro, Brazil, including previous records from Dutch and French, but not British, Guiana; also Trinidad and Cuba.

#### *Triacanthagyna ditzleri* Williamson, 1923.

Georgetown, British Guiana, Broad Street, Head Office, 10.12.28. L. D. Cleare, Jr., one male in alcohol, lacking both left wings and abd. seg. 6, sup. apps. detached and at bottom of vial; sent by Prof. J. G. Needham.

Probable length of abdomen (excl. apps.) 35 mm., sup. apps. 5.56 mm., hind wing 33, costal edge of pterostigma, front wing, 3.35 mm.

Distribution: Guatemala to Mishuyacu, Peru, and Rio Grande do Sul, Brazil, including a record from Bartica, British Guiana (H. S. Parrish). Williamson, however, thought (l. c., p. 9) that the "similar but larger specimens from southern Brazil" which he referred to this species "will probably be found to be specifically distinct." Geijskes has reported *ditzleri* also from Trinidad, West Indies.<sup>41</sup>

Calvert, 1895, *Proc. Calif. Acad. Sci.*, (2) IV, pl. XV fig. 27; Martin, 1908, Cat. Coll. Zool. Selys, fasc. XVIII, p. 74, fig. 72 (dorsal view); Navas, 1911, *Revista Mus. Paul.*, 8:480, fig. 3a (as *Remartinia barbiellina*). Calvert, 1941, *Ann. Ent. Soc. Amer.*, 34 (2): 393, fig. 1.

<sup>41</sup> Zool. Meded. Mus. Nat. Hist. Leiden, 15 (1-2): 99, 1932.

*Gynacantha tenuis* Martin, 1909.

Georgetown, British Guiana, one female.

Abdomen 45, hind wing 46, costal edge of perostigma, front wing, 3.60 mm.

Abdominal segment 10 in dorsal view 1.04 mm. long, 1.80 mm. wide; a shallow transverse groove at .36 of length of segment, interrupted mid-dorsally; anterior to this groove is a pair of low rounded elevations .24 × .42 mm., separated by a median depression .28 mm. wide; posterior to the transverse groove are two shallow smooth depressions each .28 × .60 mm., separated by a low mid-dorsal ridge, .24 wide, bearing short blackish hairs or fine lines; each of these depressions extends laterad to as far as the level of the lateral margin of the respective appendage. In the proximal anterior angle of each of these two depressions is a transversely elongated "crater," .19 × .25 mm., abutting on the mid-dorsal ridge just mentioned. Although these features of segment 10 are bilaterally symmetrical, it is doubtful whether they are specifically constant—some *T. septima* and *G. auricularis* are similar. The supra-anal tubercle (11th tergite) is .66 mm. long.

Anal loop separated from the hind margin of the wing by only one row of cells; the loop of three vertical rows of cells, except that the first transverse row of cells in the right hind wing consists of 4 cells, where there are but 3 cells in the left wing. Between M3 and M4 on all only one row of cells except where M4 makes a slight curve caudad, at which place there are two double cells on the right front wing, 1½ double cells on the right hind wing, one double cell on both left wings.

Distribution: Colombia to French Guiana and Putumayo district, Peru, including a single female from "Essequibo, British Guiana, Schneider," also two females from Chapada, Matto Grosso, Brazil. This species also has been recorded from Trinidad by Dr. Geijskes.<sup>42</sup>

*Gynacantha auricularis* Martin, 1909.

Kartabo: IV.4.1926, one male; V.8.1924, one male; V.12.1924, one male; VI.14.1924, one male; one female, not dated. Mt. Everard, Br. Guiana, one male.

The male of IV.4.1926 shows plainly a thin mid-ventral vertical plate between the right and left hamular processes and between the right and left spines of the anterior lamina but not reaching as far cephalad as the anterior end of the anterior lamina. This is the appressed "anterior parts" (Williamson) of the right and left hamular processes, and is well developed in *G. gracilis* and in *G. membranalis* (but not as strongly in *T. septima*), hence used by Williamson in his key (1923, p. 12) as one of the characters

separating *Triacanthagyna* from *Gynacantha*.

The most frequent condition of the anal loop is to have three vertical rows of cells in its anterior half and two vertical rows in its posterior half, but the three rows extend to the hind edge of the loop in the right hind wings of ♂ IV.4 and of the Mt. Everard ♂. In all six individuals the membranule of the hind wings is very narrow, its maximum width being only .14-.19 mm.

Distribution: Costa Rica to Chapada, Matto Grosso, Brazil, including a record from Bartica, British Guiana (H. S. Parrish).

*Gynacantha nervosa* Rambur, 1842.

Kartabo, V.17.1924, one female.

The anal loop has three vertical rows of cells, but in the left hind wing there is a transverse row of 4 cells at mid-height.

Distribution: California and Florida to Matto Grosso, Brazil (including a record from Rockstone, British Guiana—Williamson), Cuba, Haiti, Jamaica and Trinidad.

*Gynacantha gracilis* (Burmeister, 1839).

Kartabo: III.6.1926, one male; 2.VI.1921, one male, abd. segs. 4-10 lost; not dated, one male. Sixty m (iles) up Maroni R (iver), French Guiana, J 04, Wm Schaus, one teneral male, U. S. National Museum.

The prevalent tendency in these four males, is for the anal loop to have four vertical rows of cells (6 wings out of 8), but ♂ III.6. has both hind wings with three such rows except for one transverse row of four cells at mid-height, ♂ 2.VI. right hind wing, at one cell below the level of point of separation of Cu2 and A1, are three vertical rows, and in the undated male the right hind wing has three, then four, vertical rows.

The articular area between abdominal segments 1 and 2 in the Kartabo males is almost black around the body except at the genital fossa, but in the teneral Moroni River male this area is not black dorsally.

Distribution: Costa Rica to Bolivia and Rio de Janeiro, Brazil (including a record from Kartabo, British Guiana, October, 1920, W. T. M. Forbes).

*Gynacantha membranalis* Karsch, 1891.

Kartabo: 3.V.1924, one male; VI.9.1924, one female; VI.20.1924, one male; 11.7.1919, one male; undated, one male. Georgetown, British Guiana, one male.

The Kartabo, VI.20, and the Georgetown males are smaller than the dimensions given for this species in Williamson's paper of 1923, the hind wing being 53 mm. long in the former and 52 mm. in the latter. All my measurements of the superior male appendages of this material are lower than Williamson's, ranging from 5.4 to 5.81 mm., and

<sup>42</sup> 1932, paper above cited, p. 97.

some of those for costal margin of the stigma, front wing, are lower: 4.9 and 5.1 mm.

The anal loop of the hind wings of the five males has three vertical rows of cells throughout, except the left hind wing of ♂ 11.7, which has four vertical rows with three intermixed and the right hind wing three vertical rows in the anterior half, four such rows in the posterior half; both hind wings of the female have three vertical rows in the anterior half, four in the posterior half.

Distribution: Costa Rica to "Prov. del Sara," Bolivia, and Para, Brazil (including records from Bartica, H. S. Parrish, and Rockstone, E. B. Williamson, in British Guiana). Dr. Geijskes has reported this species from Trinidad.<sup>43</sup>

## ii. Aeshninae T. & F., 1940.

### *Coryphaeschna virens* (Rambur, 1842).

Kartabo: "Odon. 22," one female. R. Supenaam<sup>43</sup> British Guiana, September, 1930, G. Brinsley, one female, sent by Prof. J. G. Needham. Cayenne, French Guiana, Jan. 04, Wm. Schaus, one male, U. S. National Museum.

Distribution: Tamaulipas, Mexico, to Santa Cruz, Bolivia, Chapada, Matto Grosso, and the Amazons, Brazil; Cuba, Haiti and Trinidad.

### CORDULINAE Selys & Hagen, 1850 (as Cordulines).

#### Corduliinae T. & F., 1940.

### *Aeschnosoma peruviana* Cowley, 1934.

(Plate II, figs. 39-41, 43).

Cowley, 1934, *Stylops* 3 (4): 92-94.

Kartabo, 13.iii, one male, lacking abd. segs. 5-10 and the 2nd pair of legs.

Mr. Cowley has presented a description of, and a key to, the species of this genus, according to which the present male is *peruviana*. His description of *peruviana* was based on a single teneral female from "Peru: Rioja, Prov. Moyobamba, Dep. San Martin (Dr. P. Martin). . . . Rioja lies at an altitude of 848 metres between two tributaries of the Rio Mayo, itself a tributary of the Rio Huallaga."

From his description this male differs as follows: Frontal and dorsal parts of head dark metallic blue, not very brilliant. Right antenna 2.93 mm. long, left antenna broken. Thoracic pale markings present but indistinct, those on the meso- and metanotum more distinct, pale green. Coxal pale spots partly faded. Wings slightly smoky throughout, no yellow or other color at the bases,

membranule brown, reaching by a narrow prolongation to the anal angle, about 1.18 mm. beyond the apex of the 2-celled anal triangle; stigma dark brown, its costal edge on the front wing 2.13 mm.; antenodals on the front wings 15 (right), 14 (left); under the last costal antenodal on each front wing, but not actually in line with it, is a sub-costal antenodal placed slightly distad (right), distinctly proximad (left); arculus on all the wings proximal to the second antenodal by .24-.33 mm.; supratrangular cross-veins 3 on the front wings 1 (right), 2 (left) on the hind. Abd. segs. 1-4 13 mm., the pale spots on the segments are indistinct; hind wing 34 mm.

The small rounded auricles on abd. seg. 2 occupy about the anterior third of the lateral length of the segment; in ventral view each projects about .33 mm. beyond the surface of the segment; the accessory transverse carina of this segment, directed cephalad and ventrad, meets the auricle a little posterior to its antero-dorsal angle.

Genitalia of abd. seg. 2, profile view: anterior lamina hardly visible but bearing a tuft of hairs .7 mm. long; hamule hardly more prominent than genital lobe, its antero-posterior dimension .66 mm., its dorso-ventral dimension (penis not protruded) .42 mm., its most prominent part is the obtuse apex of the anterior (inner) branch; genital lobe wider (antero-posterior dimension .76 mm.) than high (dorso-ventral dimension .42 mm.), shape as shown in Pl. II, figs. 40, 41.

Supplementing the data on tibial carinae of Corduliinae given by Dr. St. Quentin,<sup>45</sup> the lengths of these carinae on the first and third legs, in mm. and in percentage of tibial length, are respectively (1) .71 mm., 20%, (3) 5.9 mm., 86%.

As Mr. Cowley points out, the presence of two cubito-anal cross-veins in the hind wings of *Ae. peruviana* necessitates an alteration in the statement of generic characters. A similar condition is found in the Malagassy genus *Libellulosoma* Martin, 1906, which that author placed next to *Aeschnosoma*, and in *Platycordulia* Williamson 1908<sup>46</sup> and *Neurocordulia* Selys<sup>46</sup> of North America.

The difference in the color of the frons of this male from that of the female type of *peruviana* is paralleled in *Ae. forcipula* Hagen. *Forcipula* is placed next to *peruviana* in Cowley's key; the length of its male hind wing (33-36 mm., Selys, 1871) is nearer to that of the present male than is that of the latter to the length of the hind wing of the type female of *peruviana* (38-39 mm.); however, the hind wing of *forcipula* female is given by de Selys as slightly

<sup>43</sup> 1932, loc. cit., p. 98.

<sup>44</sup> The Supenaam River is a left tributary of the Esse- quibo, near its mouth; see map, p. 24, of Beebe, Hartley & Howes, *Tropical Wild Life in British Guiana*, New York, 1917.

<sup>45</sup> *Zool. Anzeig.*, 121 (9-10): 225-239, 1938.

<sup>46</sup> *Ent. News*, 19 (9): 431, pl. xviii, 1908.

longer than that of *forcipula* male (35-37 vs. 33-36 mm.).

*Forcipula* is reported from Para, Ega and Sao Paulo in the Amazon valley, probably also Bahia (Selys, 1871) and Surinam (Martin, 1906, 1914<sup>47</sup>); *Ae. rustica* Selys from Bahia and Dutch Guiana (Martin, 1906, Cowley, 1934). If our identification of the present male be correct, the distribution of *peruviana* is Peru and British Guiana.

LIBELLULINAE Selys & Hagen, 1850 (as Libellulines).

The sequence of genera is according to Ris, Libellulinae, 1909-1919.

i. Libellulinae T. & F., 1940.

*Libellula herculea* Karsch, 1889.

Kartabo: VI.10, VI.12, 16.VI, all 1924, three females.

In a male from Cayenne, by Wm. Schaus, in the U. S. National Museum, abd. 32 mm., hind wing 40 mm., the pointed frontal tubercles, measured in dorsal view, project .09 mm. from the anterior surface of the frons; the corresponding rounded tubercles of the three females from Kartabo (abd. 31-34, hind wing 47-49) project .02-.05 mm.

Distribution: Vera Cruz, Mexico, to Cuenca, Ecuador, Iquitos, Peru, and Sapucay, Paraguay.

*Orthemis ferruginea* (Fabricius, 1775).

Kartabo: 30.VI.1924 and 11.7.1919, two males; three males numbered "Odon." 4, 85 and 105, and one female "Odon. 41."

Distribution: Florida, Texas and Arizona to Montevideo, Uruguay, Tucuman, Argentina (and Chile, Hagen, 1861), West Indies.

*Orthemis aequilibris* Calvert, 1909.

Kartabo: 5.V and 2.VI, both 1924, two females.

The vertex and frons of these two females approach the purple madder (of Smith's Explanation, pl. iv, fig. 7) and have a metallic violet reflection, but the reflection is not very brilliant; that of 2.VI is the brighter of the two. The same parts in the female from British Guiana by A. F. Porter, Jan. 18, 1912 (cited by Ris,<sup>48</sup> given to me by E. B. Williamson) are Roman sepia (Smith, l. c., fig. 38) with a metallic blue reflection. The female type of *aequilibris* from Paramaribo, undated (Acad. Nat. Sci. Phila. No. 9264), has the frons nearest burnt sienna (Smith, fig. 35), but somewhat duller, less vivid. The dated female paratype from Paramaribo (Dec. 18, 1904), and a third female of the same locality and date, not cited in the original description but marked at that time "faded-identif. doubt-

ful" have the frons a little darker than the pale brown of Smith (fig. 40).

Distribution: Valencia, Venezuela, to the Amazons.

*Orthemis biolleyi* Calvert, 1906.

Camaria, 27.VII.1920, one female.

The frons approximates the brown pink of Smith (fig. 21), the vertex is a little darker and has a slight metallic violet reflection. In this female and in that from British Guiana by A. F. Porter, Jan. 15, 1912, cited by Ris<sup>49</sup> and given to me by E. B. Williamson, the distal margin of the vulvar lamina is almost straight in ventral view. In the females of *O. ferruginea* and of *O. aequilibris* this margin is concave caudad in ventral view.

Distribution: Guatemala to Manaos, Brazil, and Iquitos, Peru.

*Orthemis cultriformis* Calvert, 1899.

Kartabo: 11.VI.1921, one male, abd. segs. 6-10 lacking.

Distribution: Chiriqui, Panama, to Agamo, Ecuador, Mishuyacu, Peru, and San Isidro near Buenos Aires.

ii. Diastatopidinae T. & F., 1940.

*Diastatops*.

Identifications and geographical distribution according to Prof. B. E. Montgomery, *Lloydia*, 3: 213-280, 1940. "The known distribution of *Diastatops* extends from the lower Magdalena (Sevilla, Colombia) and Orinoco (Cano d'Vagre, Venezuela) basins to the lower Parana basin (Sta. Fe, Argentina)," Montgomery, p. 221.

*Diastatops pullata* (Burmeister, 1839).

Montgomery, 1940, p. 238.

G(eorgetown): one specimen, head and abdomen lost.

The "light area" of the wings is not at all conspicuous and is hardly paler than the distal brown.

Distribution: The Guianas to Matto Grosso, Brazil, and eastern Peru.

*Diastatops obscura* (Fabricius, 1775).

Montgomery, 1940, p. 249, pl. III, figs. 1-3.

Kartabo: one male "Odon. 23," abd. segs. 5-10 lost; one male "Odon. 51," head, abd. seg. 10 and apps. lost.

Prof. Montgomery says, p. 251, of this species: "Cephalic surface of anterior lamina [of male] smooth." Both these males, under Zeiss binocular, oc. 4, obj. a<sub>0</sub>, show minute spinules here, which are still more evident under a Leitz compound microscope, oc. 10 ×, obj. 3, in this case used with the lower lens of the objective removed; these spinules are about .009 mm. long.

<sup>47</sup> Cat. Coll. Selys-Longchamps, fasc. xvii, pp. 57, 60, 1906; Gen. Insect., 155, p. 14, 1914.

<sup>48</sup> Cat. Coll. Zool. Selys, fasc. 16 (2):1103, 1919.

<sup>49</sup> For *Camaria*, on the Cuyuni River, see M. B. & C. W. Beebe, Our Search for a Wilderness, New York, 1910, pp. 248-250.

Distribution: Colombia and Guiana to Paraguay and Bolivia.

*Diastotops dimidiata* (Linnaeus, 1758).

Montgomery, 1940, p. 257.

Kartabo: 3.VI.1924, one male; 8.VI.1924, one male, abd. segs. 7-10 lost; 11.VI.1924, one male, abd. segs. 5-10 lost; not dated, two males, abd. segs. 4-10 and 6-10 lost respectively.

St. Laurent, Maroni River, French Guiana, March, one teneral female, coll. Wm. Schaus, U. S. National Museum.

Tendencies to form more densely reticulated areas are visible in the post-triangular area of both front and hind wings, between Cu1 and Cu2 near their origins and in the anal loop of the hind wings.

Distribution: Venezuela and the Guianas to Para (Brazil).

*Zenithoptera fasciata* (Linnaeus, 1758).

(Plate II, fig. 42).

1. Kartabo: "Odon. 53," one specimen, abdomen lost. 2. Hoorie:<sup>50</sup> "Odon. 16," one specimen, abdomen lost.

With these two specimens I have compared the following material:

3. Cayenne, French Guiana, Dec. 03, one male.

4, 5. Hermina Falls, Maroni River, Surinam, Aug., one male, one female.

6. Surinam River, one male. Nos. 3-6, coll. Wm. Schaus, U. S. National Museum.

7-9. Guinipa (error for Guanipa) River,<sup>51</sup> Ven[e]zuela, Feb., 1911, S. Brown, two males, one female (male 7 lacks the head, male 8 abd. segs. 5-10).

10. Para, 21.10.92. ex Selys coll., one male.

11, 12. Brazil, two males, with labels "Palp. americana L" in Hagen's handwriting and printed labels "Mus. Berol.," "From P. R. Uhler's coll." and "Coll. of P. P. Calvert."

13-23. Rumococha, Rio Amazonas, near Iquitos, Aug. 1939, José Schunke, through Mr. Joseph Hocking.

24. Costa Aguaray, Paraguay, one male, ex coll. Foerster.

Nos. 7-24 are in the Academy of Natural Sciences of Philadelphia.

Nos. 1-10, 12-23 have five yellow, lateral, thoracic stripes and are, therefore, the *Zenithoptera americana* of Ris, 1910.<sup>52</sup> No. 24 has two orange, lateral, thoracic bands, occupying almost all of the mes- and metepimera respectively—hence as in Ris's *viola*—but also a mesepisternal, distinctly antehumeral, orange stripe, .33 mm. wide at mid-

height, parallel to and distant .7 mm. from the mid-dorsal carina, .47 mm. distant at its upper end and .85 mm. distant at mid-height from the humeral suture, not quite attaining the ante-alar sinus above; this stripe is not mentioned by Ris for *viola* and is decidedly more anterior than the first of the five stripes of his *americana*. This male, No. 24, was labeled by Foerster "Z. fasciata? an americana, an subspecies nova?"; it agrees with the description of *Z. lanei* recently published by Dr. N. Dias dos Santos<sup>53</sup> except for some neuration details which I do not believe to be significant.

No. 11 is much faded so that the thoracic markings are not visible. No. 12 has a distinct yellow antehumeral stripe in the same position as the red antehumeral of No. 24. Traces of ill-defined antehumeral red are visible on Nos. 2, 7-9, 13-18, 20 and 21.

The range of size of specimens Nos. 1-23 is abdomen ♂ 14-17 mm., ♀ 14, hind wing ♂ 19-24, ♀ 22-23; in the eleven males from Rumococha the range is abd. 14.0-16.0, hind wing 21-23.5 mm. The largest male is that from Surinam River, the Cayenne male is almost as large, the smallest is from Rumococha, but the mutilated Brazil males (Nos. 11 and 12) have the hind wing 19.5 and 19 mm. The Kartabo and Hoorie specimens (Nos. 1 and 2) have the hind wing 23 and 21.5 mm. respectively.

The width of the white postnodal band, as measured on the right front wing, between veins M1 and M2, varies from 1.10 (Para) to 2.17 (Kartabo) mm.; in the Rumococha series from 1.32 to 1.89 mm., but is not correlated with wing-length. In the Hoorie specimen it is 1.74 mm. wide.

The maximum width of the pale apical or ante-apical spot, measured in the long axis of the wing, varies from 0 (one Guanipa River, Para, one Rumococha, No. 22) to 1.87 mm. (Brazil No. 11). In the first six Rumococha males (Nos. 13-18) its width is 1.18-1.46 mm. and it is separated from the apex by brown which is as wide as the pale spot; in four other Rumococha males (exclusive of No. 22) its width is .3-3.71 mm. and it is situated at the wing apex with no marginal brown; the collector of the Rumococha series gave one number to specimens 13-18, another to Nos. 19-23. In the Kartabo and Hoorie specimens the width of the white postnodal band and of the apical pale spot is 1.27 and .60 mm., respectively, with no marginal brown.

The width of the external branch of the genital hamule varies from .34 (No. 12) to .47 (Nos. 4, 6, 17, 20) mm., and hence is not correlated with locality; the ventral margin of this branch varies from nearly straight to strongly convex, but again is not characteristic geographically. On comparing

<sup>50</sup> For the location of Hoorie, on the Barama River, British Guiana, see "Our Search for a Wilderness" by M. B. & C. W. Beebe, New York, 1910, map, page 110.

<sup>51</sup> See Stone, W., *Proc. Acad. Nat. Sci. Phila.*, lxxv:189, 1913. The altitude is 0-200 m., the mouth in the Golfo de Paria, 10° N., 62° 20' W.

<sup>52</sup> *Cat. Coll. Selys-Longch.*, fasc. XI:312, 1910.

<sup>53</sup> *Revista Brasil. Biol.*, 1 (2):207, figs. 1-12, Rio de Janeiro, Junho, 1941.

the extruded penes of Nos. 3 (Cayenne), 11 ("Brazil") and 24 (Costa Aguaray), I find no difference.

In profile view, the inferior margin of the male superior appendages is armed with a row of denticles, one of which is usually larger than the others and may consequently be described as a tooth; the position of this tooth varies from one-half to two-thirds of the appendage-length and again is not correlated with locality. In the Rumococha series, however, a correlation between the position of this tooth and the wing markings appears: males Nos. 13-18, which have the pale *anté*-apical spot, have this tooth at 64-68% of the appendage-length, while Nos. 19-23 with the pale spot at the *apex*, or absent, have the tooth at 50-55% of the appendage-length. Nos. 12 and 24 have the tooth at 67%, No. 10 at 57%, Nos. 6 and 7 at 50% of the appendage length.

For his *americana*, Ris (1910) gives as a female character "im Hinterflügel eine longitudinale, oft nicht complete Aufhellung von A3 bis in die Mitte des Discoidalfeldes," with no mention of the male in this respect. For his *viola* (1910) he states of the eight males he examined: "Alle Exemplare mit longitudinale Aufhellung in Hinterflügel wie das ♀ *americana*." At that time the female of *viola* was unknown to him. In 1919, from a larger series of *viola*, he figured both sexes with the "Aufhellung" on the hind wings. It is also to be noted that his 1910 figure, 173 ter, showing the Aufhellung on the hind wing, is labeled "*americana* ♂."

Of the present material, in which at least the base of the abdomen is preserved, Nos. 4, 5, 6, 7, 8, 9, 11 and 12 have the "Aufhellung" well developed, No. 3 has it feebly indicated, in Nos. 10 and 24 it is absent. It would appear, therefore, that the presence or absence of this "Aufhellung" is not a sexual character in *Zenithoptera* and that it is impossible to determine the sex of specimens 1 and 2.

Distribution of *fasciata* L.: Pacific slopes of Colombia from less than 200 meters elevation to Trinidad and the Guianas, the Amazon from Para to Umbria, Colombia, and Balsapuerto, Peru.

Montgomery (*Lloydia*, 3:233, 1940) has reported *Zenithoptera*, without particulars, from Nicaragua.

#### THE TYPES OF THE LINNAEAN SPECIES OF *Zenithoptera*.

The specific status of the forms of *Zenithoptera* was discussed by Ris (1910, 1919), but he was not able to examine George Edwards' "A Natural History of Birds" (Part IV, 1751) on which the Linnaean names are based. I have studied a copy in the library of the Academy of Natural Sci-

ences of Philadelphia and present my results.

In the *Systema Naturae*, edit. X, p. 545 (1758), Linnaeus named two "species" now in question. His full statements are as follows:

"*fasciata*. 12. L. alis planis fuscis: fascia alba lineari. *Edw. av.* 174, t. 174. *Habitat in India. DeGeer.*"

"*americana*. 16. L. alis purpurascensibus: fascia alba, primoribus apice albis; posticis linea baseos alba. *Edw. av.* 174, t. 174. *Habitat in America. Corpus viride. Alae fusco-purpurascens.*"

Edition XII of the *Systema*, "reformata," 1767, pp. 903 and 904 respectively, has the same statements except that for *fasciata* has "av." for "aw." and that for *americana* has "Edv." for "Edw."

It will be noted that Linnaeus refers to the same plate in Edwards' work for these two species. Edwards' plate 174 contains only two figures: one is of a bird, The Lory Parrakeet, the other is of a "Fly," a photograph of which is here reproduced as our figure 42, Plate II. Linnaeus does not refer to any specimens of either *fasciata* or of *americana* which he may have seen. It would appear, therefore, that each of these specific names is based solely upon one and the same figure and that *americana* was from the very start a synonym of *fasciata*. There is no basis for a suggestion that reference to some other plate in Edwards' work was intended by Linnaeus in one or other of his two species, as an examination of all of Edwards' plates fails to show any other than his 174 to which the Linnaean descriptions could refer. Since only one figure by Edwards is concerned, Ris' 1910 (p. 315) suggestion that *fasciata* Linnaeus might be the same as *tullia* Drury has no standing.

How did Linnaeus arrive at the idea of two species? I can only suggest that he may have seen, in 1758 or earlier, the specimen which his compatriot, DeGeer, later described and figured in 1773 (*Mem. Hist. Ins.*, III:559, pl. 26, fig. 7) as *Libellula violacea* and of which DeGeer then wrote "que je crois originaire des Indes," and on that basis added to his description of *fasciata* "Habitat in India. DeGeer." On difference in habitat, Linnaeus may have separated his *americana* from his *fasciata*, but the basis for the two "species" still remains one and the same figure of Edwards. DeGeer placed *fasciata* Linn. as a synonym of his own *violacea* and subsequent writers have followed him except in recognizing the priority of Linnaeus's name. Sjöstedt has this note on DeGeer's type: "DeGeer's *Lib. violacea* (*Mem. Ins.* III, p. 559, No. 6 t. 26, fig. 7, 1773) deren Typus vorliegt, ist mit *americana* L. (Ris, o. c.), nicht mit *viola* Ris identisch. Auf der Etiquette des erwähn-

ten Typus in DeGeer's hier im Stockholmer Reichsmuseum aufbewahrter Typus-Sammlung seiner Memoiren steht: '6 *L. violacea* D. G.-L. *fasciata* L., p. 559' " (*Arkiv för Zoologi*, 11 (15) : 40, 1918.

Edwards' description of the insect is as follows (p. 174): "The Fly engraved on this Plate has the Head and body of a dull Green; the wings are of a dirty purplish Brown, with some transparent Spots in them. I drew it from Nature, but forgot to note from whence it was brought; but I think it was from the *West-Indies*." On page 26 of his Part I, Edwards says: "I do not pretend to have any Skill in the Description of Insects, not having at all study'd them; nor do I know the Terms by which their Parts are distinguished: But they being no Part of my Design, I have added them only as Decorations to fill up some void spaces in the Plates where the Birds were small, so that if my Descriptions are obscure, I hope the Justness of the Figures will help to clear them." Pages 236-243 of Edwards' Part IV are occupied by "A Catalogue of the Names of all the Birds, Beasts, &c. contained in the four Parts of this *Natural History*, ranged in a *Generical Order*," insects are on pages 242-243 and among them are "Flies with very long Bodies, and four pretty long Wings, that fly swiftly over watery Places, vulgarly call'd with us *Horse-flies*, or *Horse-stingers*. The green Horse-fly 112 The purple and brown Horse-fly 174." [Incidentally, The green Horse-fly 112, in Edwards' Part III, 1750, is *Neurobasis chinensis* (Linn.).

No information is afforded by Edwards' figure or description as to stripes or bands on the thorax, nor are the abdominal appendages sufficiently distinct to determine the sex; the wings agree better with Ris' photographs of his *viola* than of *americana*.

Hagen has a two-page article, "Die Neuroptera der Linneischen Sammlung" (Stett. Ent. Zeit., 6:155-156, 1845), in which the following statements occur: "Hr. Buchhändler Dr. J. R. Schulz in London hat auf meine Bitte die Güte gehabt, an Ort und Stelle die noch vorhandenen Arten zu notiren. Seiner gefälligen Mittheilung verdanke ich folgende Bemerkungen: In Linne's eigenem Exemplar der ed. XII der Syst. naturae sind folgende Arten mit Tinte von Linne unterstrichen und sämmtlich noch vorhanden. Die Etiquetten sind nach der Anspruch des Herrn Richard Hippist, Sekretair der Linnean Society, ebenfalls sicher von Linne's eigener Hand." [There follows a list, names only of 33 species, 14 of which are *Libellula*, but not including *fasciata* or *americana*.] Hagen's article continues: "Ausserdem sind in selben Buche mit Bleifeder unterstrichen und mit Etiquetten, welche wahrscheinlich vom Käufer der Linne'schen Sammlung, Herrn Smith her-

rühren und den gelegentlich Zusatz: E description Linn. führen, noch folgende 17 Arten vorhanden: *Libellula fasciata* [and 16 species of non-Odonata]. . . . Leider konnte ich über die Insekten selbst keine nähere Auskunft erhalten." This specimen of *fasciata*, marked in Linnaeus' copy of the 12th edition of the *Systema Naturae* (1767), may or may not have been in Linnaeus' hands when the 10th edition was published (1758).

Summing up, like Ris, Erichson, Rambur and Burmeister, I consider Linnaeus' *fasciata* and *americana* to be one and the same species, but unlike Ris—although in agreement with Erichson and Rambur—I use *fasciata* as the specific name by reason of its priority over *americana* on page 545 of the 10th edition of the *Systema Naturae*.

Ris (1910, p. 313) has briefly discussed also the justifiability of the acceptance of the generic name *Zenithoptera* Bates in Selys (1869) in preference to that of *Potamothemis* Kirby (1889), on the ground of insufficiency of de Selys' characterization. As de Selys' two statements are not generally accessible, they are reproduced here.

"Quant aux deux Palpopleura de l'Amérique méridionale à peine distinctes l'une de l'autre: *P. americana* L. et *fasciata* F. [sic] (*violacea* De Geer) elles ont un faciès tout différent, leur abdomen est grêle et selon M. Bates elles portent comme les Agrion les ailes relevées dans le repos. Il convient d'adopter pour elles le genre *Zenithoptera* proposé pour elles par le célèbre voyageur dans les notes manuscrites qu'il m'a gracieusement adressées, lorsqu'il m'a cédé sa riche collection d'Odonates de l'Amazonie." (Recherches sur la faune de Madagascar et ses Dépendances, d'après les découvertes de François P. L. Pollen et D. C. Van Dam. 5me partie, 1re livraison, pp. 15-16. Leyde, Stenhoff, 1869).

"*Palpopleura*, Ramb. — Presque exclusivement africain; une seule espèce aberrante (*P. sexmaculata* Fab.) est asiatique. *L'Americana* a formé le G. *Zenithoptera*, Bates." (Assoc. Française Avanc. Science, 10e Session 1881, p. 667. 1882).

After Karsch (Berlin. Ent. Ztschr. 33 (2) p. 355, 1890) had pointed out the identity of Kirby's *Potamothemis* with Bates' *Zenithoptera*, Kirby placed his *Potamothemis* as a synonym of *Zenithoptera* (Cf. Kirby, Cat. Odon., pp. 9 and 178, 1890) and used *Zenithoptera* in his paper in the *Annals and Magazine of Natural History* (6) 19:602, 1897.

#### *Perithemis thais* Kirby, 1889.

Kirby, 1889, *Trans. Zool. Soc. Lond.*, 12 (9):324.

Ris, 1930, *Misc. Publ. Univ. Mich. Mus. Zool.*, 21:38.

Kartabo, one specimen, abdomen lost, 20.X (?) .1920; one male, undated.

The male has the triangle of the right front wing and of both hind wings 2-celled, of the left front wing free, internal triangle of both front wings 3-celled; discoidal (post-triangular) cells on the right front wing 3, then 2 rows to beyond the level of the nodus, then 3 rows increasing to 6 marginal cells; on the left front wing they are 3.2.2.3, then 2 rows to beyond the level of the nodus, followed by 3 rows increasing to 5 marginal cells; there is 1 (right) and 2 (left) single cells reaching from M4 to Cu1 on the hind wings. The black markings of the abdomen and the brown markings on the wings are as in Kirby's original description of 1889, except that there is no brown border at the tip of the hind wings.

The dated specimen has the triangles of both front wings free, of both hind wings and the internal triangle of both front wings 2-celled; the post-triangular cells of the front wings are: (right) 2.2.2.3.3.2, then 3 rows increasing to 7 marginal cells, (left) 3.2.2.3.2.3.2, then 3 rows increasing to 6 marginal cells; there is a single cell reaching from M4 to Cu1 on both hind wings. The brown bands on the wings are greatly reduced and paler than in the male, that at the triangle of the hind wings broken into two clouds, one at the triangle, the other behind Cu2-A1, the ultra-nodal bands of all wings very tenuous at M3.

Distribution: Recorded by Ris (1930) from Trinidad to the Amazons and Matto Grosso, and by Snhr. Dias dos Santos (1944) from Ilha Seca, São Paulo.

### iii. Brachydiplacinae T. & F., 1940.

#### *Fylgia amazonica* Kirby, 1889.

Kalacoon, Bartica District, one specimen, Odon. 111, lacking head and abdomen.

This specimen is probably a female since the only coloring on the wings is a slight smoky trace in the most proximal row of cells along the anal margin of the hind wings. I have compared this specimen, as far as its mutilated condition permits, with a male from Para, Dec. 26, 1892, by Schultz, given to me by Baron E. de Selys-Longchamps, with which it agrees.

Distribution: The Guianas, Para.

#### *Oligoclada pachystigma* Karsch, 1890.

Borrer, 1931, *Misc. Publ. Univ. Mich. Mus. Zool.*, 22:24, figs.

Kartabo, one male, 2.VI.1921; one male, VrS, Odon. 56; one male, LAMA 17, Odon. 39, abd. segs. 6-10 lost.

The occiput in male 56 is intermediate between Borrer's figures 48 and 49, the spines very acute; in male 39 and the dated male it is like his figure 51, but wider posteriorly and without spines.

Distribution: Orinoco Venezuela, the

Guianas, Amazon and Madeira valleys from Para to Porto Velho, Rio Sao Lourenço in Matto Grosso (Borrer).

#### *Oligoclada raineyi* Ris, 1919.

(Plate II, fig. 37).

Ris, 1919, *Cat. Coll. Zool. Selys-Longch.*, fasc. 16 (2): 1134.

Borrer, 1931, *Misc. Publ. Univ. Mich. Mus. Zool.*, 22:34.

Kartabo, 20.V.1924, one female.

The female of this species has not been described hitherto. The present individual agrees so well with the described males in all but sexual characters that I do not hesitate to refer it to this species. It falls at once into the nearest rubrics for *raineyi* in the keys of Ris (l. c., p. 1132) and of Borrer (l. c., pp. 16-17).

The only differences detected between the venation of this female and Ris' figure 650 of that of a male from Tumatumari, British Guiana, are: antenodals  $9\frac{1}{2}$ <sup>54</sup> on both front wings, 9 (right), 8 (left) postnodals\* in the hind wings, one row of 6 (right front and hind wings) or 5 (left front and hind wings) cells between Rs and Rspl, 2 rows of post-triangular cells from the triangle out for 4 cells, followed by 3 rows for at least 4 cells in both front wings (beyond this point the wings are torn); the single row between M4 and Cu1 on the hind wings for 2 cells only, thence increasing; cells bordering the proximal side of the bisector of the anal loop (A2 of Ris and of Borrer) 7 (right), 8 (left\*) hind wing; the anal margin of both hind wings, proximal to A3, is torn so that an exact count of rows of cells can not be made, but enough remains to show that no great difference here from Ris' figure can have existed.

Following are other features of this female: Vertex brown ochre;<sup>55</sup> frons anteriorly nearest cadmium yellow,<sup>55</sup> above darker brown, with a metallic blue reflection; clypeus pale blue-green;<sup>55</sup> labrum blue-green at base, becoming brown distad and finally black along the free margin; labium near gamboge,<sup>55</sup> "with a median band of black as wide as ligula proximally and narrowing to" (Borrer) .28 mm. distally. Occiput burnt sienna,<sup>55</sup> darker in the center, triangular in dorsal view with a pair of finger-like projections on the caudal margin, similar to Borrer's figure 50 for *O. pachystigma*, but each directed laterad, not at all caudad.

Hind lobe of prothorax 1.65 mm. wide in dorsal view, slightly wider than any other part of that segment, bilobed, with a row of marginal gray hairs up to .94 mm. long.

Pterothorax bluish-pruinose with some metallic reflection on the sides. Legs black-

<sup>54</sup> The differences here marked with an asterisk fall within the range of variation for *raineyi* as given by Borrer.

<sup>55</sup> Of Smith's "Explanation of Terms used in Entomology," 1906, pl. 1V.

ish, first femora pale brown inferiorly in the proximal half, third femora 5.4 mm. long, with 15 spines in the outer (anterior) row, increasing in length distad, last spine nearly twice as long as the penult; following the last spine is a shorter hair or slender spine; 13 more slender spines in the inner (posterior) row; between these two rows, but much nearer to the inner row, is a ventral row of 6 (left femur) — 9 (right femur) spines shorter than, but equally stout as, those of the outer row. Only the merest hint of a tooth on the tarsal claws and even that not visible on all claws.

Abdomen narrowing slightly from 2-8, more abruptly on 9-10, a distinct additional transverse carina on the anterior half of 3 and 4; indian red<sup>55</sup> dorsally, margins of 8 and all of 9 and 10 blackish; ventral surface darker red, lateral margins and a spot at each postero-lateral angle of 5-8 and sternite of 8 blackish.

Vulvar lamina not projecting caudad as far as the level of the hind tergal margin of 8, its free margin bilobed, its anterior margin defined by a low transverse carina which, in ventral view, is convex anteriorly (Pl. II, fig. 37).

Appendages .19 mm. long, straight, a little longer than 10, and than the anal tubercle (tergite of 11) between them.

Abdomen 13.5, hind wing 20 mm.

Distribution: British Guiana, Surinam, Para (Borror).

#### *Uracis imbuta* (Burmeister, 1839).

Calvert, 1906, 1907, Biol. Centr.-Amer. Neur.: 218, 402.

Ris, 1911, 1919, Cat. Coll. Zool. Selys-Longch., fasc. XII: 411, 419; fasc. XVI (2): 1139, figs. 657, 658 (venation).

British Guiana: Kartabo, eight males, six females, four specimens lacking abdomen, eight of them dated March 1-11, 1926, June 1, 1921, June 3, 1924, June 8 and 16, 1920, July-Aug., 1926 (Dr. C. Hodge IV); those not dated numbered Odon. 48, 74, 89, 117, 123, VRS Odon. 20 and 30. Kaieteur, Feb. 2, 1921, one male, abd. segs. 5-10 lost. Essequibo River below [between?] mouths of Potaro and Rupinuni Rivers, May, 1920 (Geo. B. Fox), one female (Acad. Nat. Sci. Phila.).

French Guiana: Cayenne, June, one female; 60 m(iles) up Maroni River, 8.04, one male; St. Laurent, Maroni, March, one male, two females (all by Dr. Wm. Schaus, U. S. Nat. Mus.).

The female from the Essequibo River has the proximal side of the triangle of the hind wings distal to the arculus; the anal field of the same wings between A3 and the anal margin has at base 4 rows of cells, but in its distal half only 3 rows, decreasing to 2 rows and then 1 cell.

Of the 20 individuals from British Guiana, 8 (=40%) have the proximal side of the triangle of the hind wings at the arculus, the remainder have it more distal. Of the 5 individuals from French Guiana, the 3 females have this side at the arculus or very slightly distal, the 2 males more distal. Of the 11 males, 7 females tabulated for taxonomic characters for the Biologia Centrali-Americana, 15 of the 36 hind wings (=41.7%)<sup>56</sup> had the proximal side of the triangle of the hind wings at the arculus, the remainder more distal. The B. C.-A. material of *imbuta* studied was a much less homogeneous group, geographically, than that here recorded from British Guiana, as it extended from the Isthmus of Tehuantepec to Venezuela and included 3 males and 3 females as the largest number of individuals from any one lot (i.e., the indefinite locality "Panama" M. C. Z.). Of other species of *Uracis*, tabulated at the same time as the B. C.-A. *imbuta*, and which appear in the *Annals of the Carnegie Museum*, 6 (1): 227-229: *siemensi* 1 male, *ovata* 1 male, 3 females,<sup>57</sup> *infumata* 2 males, *fastigiata* 17 males, 7 females (including those of this last species in the B. C.-A.)—all had the proximal side of the same triangle distal to the arculus.

These facts suggest that the fewer individuals of *imbuta* with the proximal side of the triangle of the hind wings at the arculus represent a more primitive state for this genus, while those *imbuta* with the distally placed proximal side of the triangle, and also the other species of this genus, display a more specialized condition. This view is strengthened by the fact that *imbuta* has the triangle of the front wings placed more nearly at 90 degrees with the supratriangle, while the other species have that triangle more obliquely placed, as Ris pointed out (1911, pp. 410-411). This interpretation of the positions of the proximal side of the triangle of the hind wings in *Uracis* as primitive and as specialized is a contradiction to the recession of the triangle as set forth by Prof. Needham<sup>58</sup> and perhaps not in harmony with Col. Fraser's ideas<sup>59</sup> as to this triangle. Neither of these authors deals with the obliquity of the triangle of the front wing in this connection and the question involves the relationship of *Uracis* to other genera, briefly touched on by Ris (1911, p. 409). A similar obliquity in a much less densely veined wing occurs in *Brachygonia oculata* of Borneo (Ris, fasc. XI, p. 352, 1910).

I have not found any other features (color, venation, genitalia of the second abdom-

<sup>56</sup> These data have not been published hitherto.

<sup>57</sup> *Ovata* is referred to *infumata* by Ris, 1911, p. 414.

<sup>58</sup> *Proc. U. S. Nat. Mus.*, 26 (1331): 721, 1903.

<sup>59</sup> *Australian Zoologist*, 9 (4): 393 and 394, 1940, under Brachydiplacinae and Onychotheminae, respectively.

inal segment or appendages of the male, vulvar lamina) correlated with these differences in the position of the triangle of the hind wings of *Uracis*.

Distribution of *U. imbuta*: Mexico to Buenos Aires, Trinidad.

***Uracis ovipositrrix* Calvert, 1909.**

Kartabo, III.4.1926, one male; one specimen, not dated, abdomen lost, possibly a female because the brown at the apex of the wings has the centres of the cells paler and the hind wings, between A3 and the anal margin, have 4 rows of cells for 4 cells, then 2 rows almost to the apex of the anal loop, while the male, in the same area, has 4 rows, followed by 3 rows almost to the apex of the anal loop.

Distribution: British Guiana, including Mt. Roraima, Surinam, the Amazons from Santarem to Iquitos; Matto Grosso.

***Uracis infumata* Rambur, 1842.**

British Guiana: Waratuk, 19.ii.1921, one female.

Distribution: British Guiana, Cayenne, Para, Fonte Boa, Bahia and Matto Grosso, Brazil; Mishuyacu, Peru.

***Uracis fastigiata* (Burmeister, 1839).**

Kartabo, I.VIII.1920, one male, abd. segs. 5-10 lost; IV.1.192?, one female.

Hind wing, male, 34 mm., female, 29.5 mm. The last antenodal of both front wings of the female is united with the penult antenodal at an oblique angle at the subcosta; it is more slender than the other antenodals.

Distribution: Mexico to Yumbatos, Peru, east to Trinidad, Bahia and Matto Grosso.

***Micrathyria spinifera* Calvert, 1909.**

Kartabo, 22.II.24, one male.

Distribution: Subsequent to its original description from Surinam, this species has been recorded by Ris (1911) from Para, Villanova and Obidos, all in the Amazon valley, where it was first taken by Henry Walter Bates.

***Micrathyria eximia* Kirby, 1897.**

Kirby, 1897, *Ann. Mag. Nat. Hist.*, (6) 19:609, pl. xiii, fig. 4 (not 3) (body and left wings).

Ris, 1911, *Cat. Coll. Zool. Selys-Longch.*, fasc. XII:450, figs. 285, 286 (apps. ♂).

Kartabo, 20.VI.1924, one specimen (female?), abdomen and the posterior part of the right hind wing proximal to the bisector of the anal loop and as far forward as the anal vein, lacking.

The venation differs from that of *Oligoclada* in the presence of two bridge crossveins on all four wings, in this respect resembling *Fylgia*, *Nephepeltia*, *Edonis* and *Micrathyria* as figured by Ris (*t.c.*, pp. 391,

393, 395, 397, 426, 449). It differs from *Fylgia*, *Nephepeltia* and *Edonis* in showing not the slightest trace of breaking in the costal side of the triangle of the front wings; from *Edonis* also in having a maximum of only 2 rows of cells between A3 of Ris and the anal margin of the left hind wing.

In Ris' key to the species of *Micrathyria* (1911, pp. 426-429), this specimen falls under rubrics E (except that the arculus is very close to the second antenodal in both front and the right hind wings and at that antenodal in the left hind wing instead of "ungefähr in der Mitte zwischen 1. und 2. Anq.") *ee* and *éé*. These exceptions from E are also found in the following eximiae in the Academy of Natural Sciences of Philadelphia: Chapada, Matto Grosso, two males, one of which lacks the left front wing, and Puerto Barrios, Guatemala, one male, in which the arculus is near the second antenodal on the front wings and at the second antenodal on the hind wings. Kirby's original figure of *eximia* shows the arculus between antenodals 1 and 2 but nearer to 2 on both front and hind wings. In the David female shown in fig. 30, tab. 9, *Biologia Centrali-Americana*, Neuroptera, the front wing has the arculus slightly proximal to the second antenodal, the hind wing a little distal to the second antenodal.

Distribution: Guatemala to Santa Catarina, Brazil.

iv. Sympetrinae T. & F., 1940.

***Erythrodiplax* Brauer, 1868.**

The following identifications and statements of geographical distribution are based on the recent excellent Revision<sup>60</sup> of the genus by Dr. Donald G. Borror. As stated in its preface: "In this revision of the genus the fundamental criteria of species have been the characters of the male genitalia, particularly those of the penis." In preparing penes for examination, Dr. Borror removed them from the insects, treated them with cold potassium hydroxide and after studying and drawing them, placed each in a small vial of glycerine and the vial in an envelope with the insect from which the penis was removed.

<sup>60</sup> Graduate School Studies, Contributions in Zoology and Entomology, No. 4, The Ohio State University, 1942, xvi + 286 pp., 41 pls. The following changes in Dr. Borror's key to the species seem desirable:

Page 29, couplets 3 and 3': for "Lateral keel" read "Transverse keel" (compare page 13).

P. 30, couplet 8: transpose "truncate, with distal edge nearly or quite straight" to immediately follow "Genital lobe," and thus make this couplet correspond more exactly to couplet 8'.

P. 30, couplet 9 and p. 42, couplet 68: for "anal edge" read "anal angle."

On reaching couplet 23', page 32, penis "with a more or less distinct posterior lobe," it should be noted that triplet 27' p. 34 (to which 23' leads in some cases), states "Penis with posterior lobe poorly developed and in some cases apparently lacking." A similar case is furnished by the series of couplets 38', 40', 41', 42' and 43'.

In making the present identifications of pinned dry specimens, I have not separated the penes from the insects, for only an infinite series of meticulous curators can assure the continued association of an insect and its detached parts and the possibility of later students examining *all* parts of a specimen. I have, therefore, proceeded as follows, following a suggestion for certain other Odonata which I owe to Mrs. Leonora K. Gloyd. A tiny wad of raw cotton wool, soaked in a weak solution of household ammonia, was placed on the ventral surface of the second and third abdominal segments of the inverted, pinned dragonfly and allowed to remain for one, two, or three hours. When convenient, and if the genitalia were still moist, the insect was placed under a binocular dissecting microscope, Greenough model, the penis gently lifted with fine needles, and even fine forceps, so that it was completely protruded but still attached to the abdomen. A small triangle of white paper (white as being conspicuous),  $< 1 \times 2-3$  mm., was then inserted, with the same instruments, between the second and fourth segments of the penis and the insect laid aside to dry. The penis thus remains visible and distinct from neighboring parts. This method is more expeditious than Dr. Borror's.

It is not pretended that penes treated by this method show all the details revealed in Dr. Borror's figures of penes prepared with potassium hydroxide and *kept moist*. This is especially true for the details of the internal and posterior lobes of the penis. It is believed, however, that sufficient detail is preserved in the penes, as here treated, to permit safe identification, leaving the finer details for comparative anatomical studies and the potassium hydroxide or similar techniques.<sup>61</sup>

To what extent the penes, as here prepared, fall short of Dr. Borror's figures, may be seen by comparing our figures with his for the same species.

***Erythrodiplax castanea*** (Burmeister, 1839).

(Plate II, fig. 23).

Kartabo, V.4.1926, one male, abdomen lost; V.11.1924, one male; 7.VII.1922, one female, No. 56. Abary<sup>62</sup> [River, near the coast]; 2.V.1924, one male.

The males have the brownish-yellow spot on the base of the front wings larger (reaching to the cubital cross-vein) than in the female (only half-way to that vein). The first and third males listed have two cubital

cross-veins on the hind wings, the other male and the female have only one. The female has 4 cells in the subtriangle of the left front wing.

Distribution: Trinidad and Colombia to S. Paulo, Brazil, Paraguay and central Peru.

***Erythrodiplax angustipennis*** Borror, 1942.

(Plate II, fig. 24).

Borror, 1942, Revis. Erythrodiplax: 68, figs.

French Guiana: 100 (?) mi (les) up Maroni River (Dr. Wm. Schaus), one male (U. S. Nat. Mus.).

This male belongs to the *longitudinalis* group of Borror, pp. 64-65. It agrees with *E. anatoidea* Borror, 1942, in having the frons metallic bluish-dark reddish brown<sup>63</sup> anteriorly and dorsally, where it is coarsely punctate-rugose, sides glabrous and almost blackish, except for a small, triangular, yellow spot at each latero-ventral angle; thorax with no yellow lateral stripe; abdominal appendages nearest to brown pink (No. 21) of Smith's glossary.

It agrees better with Borror's figures of the genital hamule, genital lobe and penis of *angustipennis* than with those for *anatoidea* or *longitudinalis*.

Thorax blackish dorsally, indian red (Smith No. 33) on the sides. Abdomen cologne earth (Smith No. 37) to blackish, an indistinct brown ochre longitudinal streak on each side of dorsum of segments 4-7, no pruinescence. The venation and dimensions fall within the ranges given for *angustipennis*.

Of the three species of this group, Dr. Borror saw one male (Bejuma, Venezuela) of *longitudinalis* (Ris), one male, one female (Porto Velho, Brazil) of *anatoidea* Borror and three males, two females (Cachuela Esperanza,<sup>64</sup> Bolivia, and Villa Murinho, Brazil) of *angustipennis* Borror, while a male of the last named from "Alcobaza, R. Totantias" (Alcobaca, Rio Tocantins?) is quoted, page 70, from Ris. No other definite localities for these three species have been published; much is still to be learned concerning them.

Distribution of *angustipennis*: French Guiana, tributaries of the Amazon in Brazil and Bolivia as stated above.

***Erythrodiplax unimaculata*** (De Geer, 1773).

(Plate II, figs. 25, 26).

Kartabo, VRS Odon. 2, 29, 62, three males; Odon. 33, one female, front wings lost; LAMA 17, one female; VRS Odon. 18, 113, two males; Georgetown, one male.

French Guiana: Cayenne, Jan. 04 (Wm. Schaus) one mature male (U. S. Nat. Mus.).

<sup>61</sup> Both Dr. Borror and I will, I fear, fall under the censure of Dr. G. Fankhauser, who writes: "One of the characteristics that should be included in the description of every species of plant or animal is the number of chromosomes that are to be found in its cells." *Quart. Rev. Biol.*, 20 (1):20, March, 1945.

<sup>62</sup> See M. B. & C. W. Beebe, *Our Search for a Wilderness*, New York, 1910, map, p. 110.

<sup>63</sup> Dragon's blood 34, or burnt sienna 35, of Plate IV of Smith's Explanation of Terms used in Entomology, from which other color terms are here taken.

<sup>64</sup> Probably Cachuela Esperanza of the National Geographic Society's map of South America of 1942.

The first three males above listed are immature, wing spots yellowish-brown, thorax and abdomen marked with yellow; the second three males are mature, thorax, abdomen and basal wing spots dark brown to black. The LAMA 17 female has the vulvar lamina in caudal view a little more widely rounded than that of No. 33 and may be *laurentia* in view of Dr. Borrór's remarks on pages 40 and 85.

The penes of the two males treated with ammonia are not as much expanded as in Dr. Borrór's figure 97, ventral view, but all seven males agree with the other characters of this species. These two penes have more the appearance shown in his figure 116, ventral view, of *latimaculata*, but the lateral view of the terminal joint is not at all like that of *latimaculata*. The lateral view of what I here identify as *unimaculata* differs from Dr. Borrór's figure 97 in having the apical lobe less projecting, much as in his figures of *fervida* and *ochracea*, 95 and 96, but even the teneral male No. 62 has some bluish reflection on frons and vertex. His figures 227 and 237 are referred on his page 252 to *unimaculata* and both are stated to be of the same specimen, "No. 116b, Georgetown, British Guiana, Oct. 10-15, 1920." On page 63, figure 227 is referred to *E. venusta*.

Distribution: Jamaica, Martinique and Trinidad, Guiana to Matto Grosso, Brazil, Paraguay and central Peru.

***Erythrodiplax laurentia* Borrór, 1942.**

(Plate II, fig. 27).

Borrór, 1942, Revis. Erythrod., 83, figs.

Kartabo, 21.V.1924, one male, abd. segs. 6-10 lost, genitalia of 2 obscured by gum; 6.VI.1924, one male; VI.11.1924, two males.

The male of 6.VI. agrees with *laurentia* in Dr. Borrór's key, page 31, wing spot, fig. 22, appendages, fig. 190, hind prothoracic lobe, fig. 371, and profile of frons, fig. 335, but is more like *kimminsi* in penis, fig. 100, lateral view, hamule and genital lobe, fig. 242, and in size, abdomen 21, hind wing 26 mm.; the internal lobes of the terminal segment of the penis are not dilated in this ammonia-treated male. The two males of VI.11 agree with *laurentia* in wing spot, appendages, hind prothoracic lobe as far as visible and in size, abdomen 20, 21 mm., hind wing 23, 24.5 mm.; one of them is like fig. 241 of the hamule and genital lobe of *laurentia*, but is a little more like *kimminsi* in the profile of the frons, fig. 333; its penis is not protruded; the other of these two males has the profile of the frons as shown for *laurentia*, but is more like *kimminsi* in hamule and genital lobe and in the lateral view of the penis, the internal lobes of the terminal segment of the penis not dilated.

Distribution: Guiana to Para, Brazil.

***Erythrodiplax famula famula* (Erichson, 1848).**

(Plate II, figs. 28, 29).

Kartabo, ten males, five females, some dated from III.9.(1926) to VI.1.(1924), and 27 and 29.X.1920, the male with the last date No. 20773, others numbered Odon. 49 (one male), VrS Odon. 50 (one female), Odon. 54 (one male, Kalacoon 1916), Odon. 109 (one male), Odon. 121 (one female).

In all of these males the basal yellow or brown spot fills only part of the triangle on the hind wings.

Distribution: Cuba, Trinidad, Venezuela, the Guianas to Minas Geraes, Brazil.

***Erythrodiplax latimaculata* Ris, 1911.**

(Plate II, figs. 30, 31).

Kartabo, one immature male, with labels Odon. 38, LAMA 17.

This male is apparently *latimaculata* by its characteristic penis (Borrór, fig. 116), genitalia of the second abdominal segment (B., fig. 250) and hind lobe of the prothorax (B., fig. 374), but is very small: abdomen 15 mm., hind wing 18 mm., stigma of the front wing 2.22 mm. Basal spot of wings brownish-yellow, on the front wings to the second antenodal for the entire width of the wing, on the hind wings to the fourth antenodal, apex of triangle and to the hind margin 1-2 cells proximal of the apex of the anal loop. Venational details within the ranges given by Dr. Borrór for this species.

Neither Ris nor Dr. Borrór describe immature males of this species. The differences in coloration are considerable as the following show: Vertex brown with a transverse darker line connecting the lateral ocelli, frons red without blue or purple reflections (frons and vertex of the shape and punctuation as in an adult male from Pirassununga, S. Paulo, Brazil); clypeus, labrum and labium reddish-yellow without dark markings; thorax brown above, pale greenish on the sides; abdomen pale brown, an ill-marked, narrow, darker, mid-dorsal stripe or line on 3-10, appendages pale brown, legs pale brown. Similar teneral males, distorted after removal from alcohol, are in the lot from Pirassununga.

Distribution: Venezuela, Bolivia (Santa Cruz), British Guiana, Brazil (Amazonas, Minas Geraes, S. Paulo).

***Erythrodiplax umbrata* (Linnaeus, 1758).**

Kartabo, twelve males, six females, some dated from III.9.(1926) to August (1920, 1926, Dr. C. Hodge IV), some numbered Odon. 73 (one male), VrS Odon. 125 (one male), Odon. 61 (one female), LAMA 17 Odon. 3 and 64 (two females), Odon. 31 (one male). Georgetown, one male, one female. Essequibo River below [between?] mouths of Potaro and Rupinuni, V.1920

(Geo. B. Fox), one female (Acad. Nat. Sci. Phila.).

Two males from Kartabo, 11.VI.1924 and July-Aug., 1926, are teneral. All eight females are heterochrome, i.e., lack the broad dark band on the wings between nodus and stigma.

Distribution: Indiana and Ohio (U.S.A.) to Argentina (Santa Fe and Buenos Aires) and central Peru and Bolivia (Santa Cruz), including the West Indies but not Chile.

***Erythrodiplax maculosa* (Hagen, 1861).**

(Plate II, figs. 32-34).

Ris, 1911, Cat. Coll. Zool. Selys-Longch., fasc. XII:526, fig. 316.

Borrer, 1942, Revis. *Erythrodiplax*, 119 (with bibliography and synonymy).

Dias dos Santos, 1945, *Ann. Ent. Soc. Amer.*, 37 (4):389-392, pl. I.

Borrer, 1945, *Ann. Ent. Soc. Amer.*, 37 (4):393-395, figs.

Kartabo, one male, abd. segs. 6-10 lost, labeled LAMA 17 Odon. 63.

This male agrees in many respects with the recently (1945) published descriptions and figures by Senhr. Dias dos Santos and Dr. Borrer, but also shows the following differences: occiput black above, yellow behind, basal spot on front wings confined to the cubital and anal spaces but not reaching the first anal cross-vein or its level in the cubital space; basal spot on hind wings darkest in the subcostal and cubital areas and triangle (nearest to the brown ochre of Smith's glossary, pl. IV, No. 36, but darker), remainder of the spot paler, fading out at the fifth antenodal and at two cells beyond the triangle, anal area behind A not as markedly paler than the rest of the spot as shown in Dr. Borrer's (1945) figure 3; front wings with 6(\*)<sup>65</sup> antenodals, the last continued to R1, costal side of triangle broken so that the distal piece is slightly longer(\*) than (right) or equal(\*) to (left) the proximal piece; hind wings with 4(\*) postnodals, base of the triangle a little distal of the arculus, only 1 cell between the bases of A2 and Cu2; size smaller(\*): hind wing 13 mm. vs. 16-17.5 mm.; fewer cells between Rs and Rspl: 6(\*) (front wings), 5(\*) (right hind wing), 4(\*) (left hind wing), symptomatic of other details in the distal half of the wings and perhaps correlated with their smaller size. The variation in the origin of the nodal sector, M2, in this male is shown in our figure 34; its condition in the left front and right hind wings is to be considered normal, in the other two wings abnormal (compare Dr. Borrer's 1945 figure 3).

It is of interest to note the points of resemblance between this male and the male

type of *Edonis helena* Needham (1905)<sup>66</sup>: the black lips, all triangles and the subtriangle free, the non-development of Mspl, 1 cubital cross-vein, the brown basal, although much smaller, spots on the wings, the 6 antenodals on the front wings, all continued to R1, the venation of the area between A3 and the hind wing margin, and only 1 cell between the bases of A2 and Cu2. There are, of course, many differences, *Edonis* having 2 bridge cross-veins, the costal side of the triangle of the front wings not broken, Rspl more sharply defined, the differently shaped genitalia of the second abdominal segment, without considering all those venational features of *maculosa* for which the latest two authors give variation data.

The single male deters me from attempting a caustic potash-glycerine preparation of its penis, but I have made two drawings of the dried organ for comparison with Snhr. Dias dos Santos' figure 9. The resemblances here, those mentioned above and absence of the appendages from this male, all deter me from regarding it as specifically distinct from *maculosa*.

Distribution of *maculosa*: British Guiana, Minas Geraes and S. Paulo, Brazil, Paraguay; the original locality (Georgia, U.S.A.) reported by Hagen is almost certainly erroneous.

***Erythrodiplax basalis basalis* (Kirby, 1897).**

(Plate II, figs. 35, 36).

Kartabo, one male, abd. segs. 6-10 lost, labeled Kalacoon 1916 Odon. 115, three females, labeled VrS Odon. 21, Odon. 59 and Odon. 90, respectively.

The abdomens of the three females measure 16-16.5 mm., hind wing of the male 17.5, of the females 18.5-19, stigma of the front wings, male 2.13, of the females 2.36-2.64 mm. The front wings have the triangle free in the male and in two females, and once-crossed in female 21; the subtriangle 3-celled except in the right front wing of female 59 where it is 2-celled, two post-triangular rows from the triangle out in the same three, three post-triangular cells, then 2 rows in female 21. The hind wings have Cu1 separating from the triangle a little distad of its hind angle and only 1 cell between that angle and A2 in all four individuals. The arculus is proximal to the second antenodal in all wings except in the left hind of female 21. The basal spot of the wings of the females is yellow, reaching to the cubital cross-vein or less on the front wings, to the arculus or less on the hind wings.

Distribution: Jamaica, Trinidad, the Guianas, Colombia to Matto Grosso, Brazil, central Peru and Santa Cruz, Bolivia.

<sup>65</sup> Differences marked with a (\*) are also differences from Ris' 1911 description and figure of Hagen's type of *maculosa* in the Zürich Museum.

<sup>66</sup> *Proc. Biol. Soc. Washington*, 18:113.

***Erythrodiplax connata fusca* (Rambur, 1842).**

*Erythrodiplax connata* Burm. e (*fusca* Ramb.) ♂, Calvert, 1906, Biol. Centr.-Amer. Neur., pl. IX, fig. 41 (penis, untreated).

Kartabo, seven males, two females, some dated from 3.5 to VI.15.1924, one male is XI.1920, others are labeled VRS Odon. 13 and 128 (two males), Odon. 120 and VrS Odon. 9 (two females). Essequibo River below [between ?] mouths of Potaro and Rupununi, IV-V.1920 (George B. Fox), two males, one has lost abd. segs. 6-10 (Acad. Nat. Sci. Phila.).

French Guiana: 60 mi(les) up Maroni R(iver), 8.04 (Collection Wm. Schaus), one teneral male in bad condition, abd. segs. 5-10 lost (U. S. Nat. Mus.).

A Kartabo male of 6.VI.1924, has the frons reddish but with a purplish tinge which would incline me to refer it to *E. c. connata*. Dr. Borrer, however, refers all British Guiana material of *E. connata* to *E. c. fusca*. It is not *melanorubra* (cf. his Revision, page 163) because of the shortness of the terminal joint of the penis: 1.09 mm.

Distribution: Mexico and Trinidad to southern Peru, Bolivia (Santa Cruz), Argentina (Tucuman) and Uruguay.

***Erythrodiplax melanorubra* Borrer, 1942.**

French Guiana: St. Laurent, Moroni River (Collection Wm. Schaus), two females, undated. (U. S. Nat. Mus.).

One female has the vulvar lamina apparently normal, its antero-ventral margin in profile view .95 mm. long, almost equal to the lateral tergal margin of abdominal segment 9; abdomen 16 mm., hind wing 21, costal edge of stigma of front wing 2.74 mm. The second female has the dimensions of the vulvar lamina, abdomen, hind wing and stigma as in the preceding individual, but the ninth segment appears to be retracted slightly into the eighth, so that its visible lateral tergal margin is slightly shorter. The nearest localities to French Guiana, recorded by Dr. Borrer for *melanorubra*, are in the states of Aragua, Carabobo and Yaracuy of Venezuela, so that this species should appear in British Guiana also.

Distribution: French Guiana, Venezuela to central Peru, Bolivia (Santa Cruz), Paraguay, Brazil (S. Paulo) and Argentina (Entre Rios).

***Erythemis peruviana* (Rambur, 1842).**

Kartabo, one male, 1.V.1921, one female, 7.VI.1924; LAMA 17 Odon. 92, one male; Abay (Abyary ?, on the coast) Odon. 32, one male; G(eorge)town, one male, abd. segs. 5-10 lost. Male Odon. 32 and the female bear pin labels "*Erythemis peruviana* (Rambur) Cur" presumably in Mr. R. P. Currie's handwriting; male 32 lacks head and abdomen.

Distribution: Tamaulipas, Mexico, to Corrientes, Argentina; Jamaica.

***Erythemis attala* (Selys, 1857).**

Kartabo, 6.5.1924, one female, right hind and left front wings lost.

Distribution: Guadalajara, Mexico, to Buenos Aires; Cuba, Haiti, Martinique.

***Leptthemis vesiculosa* (Fabricius, 1775).**

Kartabo, eight males, four females, some dated from III.7 (1921) to 17.VIII (1920), including two males by Dr. C. Hodge IV (1926), one male numbered Odon. 115, one male labeled LAMA 17 Odon. 129, one female VRS Odon. 119 (?). Most of the specimens have lost some segments of the abdomen.

Distribution: Sanibel Island (Westfall, 1941), Florida and southern Texas to Corrientes, Argentina.

***Rhodopygia cardinalis* (Erichson, 1848).**

Kartabo, two males, terminal abdominal segments lost, one labeled Odon. 28, the other Odon. 110.

Distribution: Guiana to Matto Grosso, Brazil, and eastern Peru (?).

**v. Trithemiinae T. & F., 1940.*****Dythemis multipunctata* Kirby, 1894.**

Ris, 1919, Cat. Coll. Zool. Selys-Longch., fasc. XVI (2):1202, 1206.

Kartabo, 3.VI.1924, one male.

French Guiana: Cayenne, Dec. 03 (Collection Wm. Schaus), one male (U. S. Nat. Mus.).

These identifications are according to Ris' revision of the species of 1919, without further study on my part. These two males agree with his description (p. 1207) of a series of seven males from Tumatumari, British Guiana, 7.12.II, except that there are no pale spots on abdominal segment 7 of the Kartabo male and none on segment 8 of both males. His description of the Guiana examples is comparable with that of six males from Guatemala wherein is stated: "meist ein schwarzes Bogenstreifen über den Postelypeus;" in the Kartabo male the black arched streak is on the lower margin of the postelypeus (nasus).

Distribution: Guatemala and the Guianas to Peru and Buenos Aires; St. Vincent, Grenada and Trinidad in the West Indies.

***Macrothemis polyneura* Ris, 1913.**

Ris, 1913, Cat. Coll. Zool. Selys-Longch., fasc. XV:888; 1919, XVI (2):1214.

Kartabo, VI.17.1924, one female, abd. segs. 6-10 lost.

Ris (1913) described this variable species from one male each from Poco Grande (Estado S. Paulo), and Parana, Brazil, from one female each from Surinam, Jurimaguas

and Jatahy (Goyaz) and from two females from Espirito Santo; in 1919 he added the description of a male from Kaieteur Ravine, British Guiana (11.IV.1912).

The present female differs from the description of the five females as follows: Lips nearest Van Dyke brown of the colors shown on Plate IV of Smith's Explanation of Terms used in Entomology; frons Van Dyke brown with metallic bluish reflection anteriorly and superiorly. The "gelbliche Längsbinden . . . der Dorsalkante genäherte auf Segment 5-7" of the abdomen appear to be present on segment 4 also. Yellow at base of front wings reaching to 2 cells beyond the triangle, at base of hind wings to antepenult antenodal and 4 cells beyond the triangle, paler where it reaches the hind margin of the wing proximal to the anal loop, remainder of all wings faintly brownish. Two cells in the widest part of the anal loop on the distal side of A2 opposite the external angle, but only 1 row of cells on the proximal side of A2, i.e., between A2 and A3; 4 rows of cells between A3 and the anal margin; post-triangular (discoidal) cells on the right hind wing 2 rows from the triangle distad for 5 cells, thence increasing; on the left hind wing they are 1, 2, 1, 1, 1, 2, 2, 2, 3. . . . Antenodals front wings,  $14\frac{1}{2}$ , arculus slightly proximal to the 2nd, hind wings, 11 (right), 10 (left), arculus distal to the 2nd. Abdominal segments 1-5 15 mm., hind wing 32 mm., stigma, front wing 2.13 mm., Cologne earth of Smith's glossary, *loc. cit.*

Distribution: The Guianas to Parana, Brazil, Jurimaguas (Yurimaguas?), Peru.

***Macrothemis pumila* Karsch, 1890.**

Karsch, 1890, Berl. Ent. Zeitsch., 33 (2): 364, 368. Ris, 1913, Cat. Coll. Zool. Selys-Longch., fasc. XV:895; 1919, fasc. XVI (2): 1218. Geijskes, 1932, *Zool. Meded.*, 15 (1-2): 125.

Kartabo, two females, both lacking abd. segs. 7-10, one dated 20.X.1920.

Both females agree well with Karsch's original description of this species from Bahia. Ris figured (1913) the appendages and the genitalia of the 2nd abdominal segment of the male and in 1919 described both sexes from British Guiana and Trinidad with figures of their venation. Dr. Geijskes (1932) also has notes on Trinidad examples.

Distribution: Trinidad, British Guiana, Amazon valley from Para to Umbria, Colombia, and Porto Velho on the Rio Madeira, Bahia.

vi. *Zyxommatinae* T. & F., 1940.

***Tholymis citrina* Hagen, 1867.**

Kartabo, July-Aug., 1926 (Dr. Charles Hodge IV), one male (Acad. Nat. Sci. Phila.).

Distribution: Vera Cruz, Mexico, to Mi-

nas Geraes and Matto Grosso, Brazil; Cuba, Jamaica.

***Pantala flavescens* (Fabricius, 1798).**

Bartenef, 1931, Zool. Jahrb. Abt. Syst. Ökol. Geog. Tiere, 60 (5-6):471-488 (geographical distribution with world map).

Kartabo, four males, V.4.1924 to July-Aug. 1926 (including one by Dr. C. Hodge IV in Acad. Nat. Sci. Phila.).

French Guiana: St. Laurent, Maroni River, M[ar]ch (collection Wm. Schaus), one male (U. S. Nat. Mus.).

Distribution: The most wide-spread of all *Odonata*: circumtropical, extending northward to North Dakota and Maine, Egypt, Transcaucasia, Turkestan, the Himalayas, Amur region of Siberia and Kamtschatka and southward to Sao Paulo, Natal and New South Wales (Bartenef, 1931).

***Tramea cophysa* Hagen, 1867.**

Ris, 1913, Cat. Coll. Zool. Selys-Longch., fasc. XVI (1):988, fig. 570 (genit. male); 1919, fasc. XVI (2):1223.

Referred by implication to *Trapezostigma* Hagen, 1849, by Cowley, 1935, *Entom.*, 68: 283.

Kartabo, 2.V.1921, one male, hind wing 41 mm., abdomen (excl. apps.) 28 mm.

French Guiana: Cayenne, two males 12.03, 2.04, one female Jan. 04 (collection Wm. Schaus, U. S. Nat. Mus.).

The Kartabo male is puzzling, with features agreeing with *cophysa* on the one hand and approaching *onusta* on the other.

Those agreeing with *cophysa* are: Head (if it belongs here, left eye considerably damaged) with vertex and frons metallic violet; thorax with well-marked yellow stripes on mes- and metepimera, reaching more ventrad than the level of the metastigma; (labium discolored); face greenish-yellow along the eyes; thoracic dorsum reddish-brown, no black markings (apices of superior appendages broken off); hamule pressed against the genital lobe so as to be no more prominent than the lobe, its shape like that in Ris' figure 570; wings, other than the basal spots, hyaline, venation somewhat reddish-brown except in the basal spots where it is yellowish; basal spot of front wing yellow half-way to first antenodal; only 1 row of cells between A2 and A3.

Those features approaching *onusta* are: Basal spot of the hind wings brown reaching to: in C and Sc one-half way between 1st and 2nd antenodals, in R and M to arculus, in supratriangle and triangle to level of 2nd antenodal, filling the hindmost cell of the first row of post-triangular cells, the first 2 cells between Cu1 and Cu2, to nearly the same level between Cu2 and A2, behind A3 nearly to the level of the distal angle of the triangle, thence curving slightly

proximad and caudad to the anal angle of the wing; the distal margin of this basal brown spot, therefore, serrate in its anterior half; one row of cells between Cu1 and Cu2; the pale area posterior to the membranule and along the anal margin of the wing occupies a maximum width of 7 cells at right angles to that margin, hence far from A3. This present specimen has the most extensive basal spot on the hind wings for any *cophysa* yet described.

Ris (1913) recognized three forms of *cophysa*: (a) with the basal spot of the hind wing "relativ gross von reichem gold braun, gelb geädert und meist mit breitem gelbem Hof"; (b) with the basal spot "sehr klein" or (c) "klein." This Kartabo male falls in his form (a).

As to the three examples from Cayenne, although the lateral, yellow, thoracic stripes, if present, have faded, I believe them also to be *cophysa* form (a); otherwise they agree fairly closely with Ris' description. The lengths of the superior appendages, of segments 9 + 10, and of segments 8 + 9 + 10 (measured along the mid-dorsal line) of these three specimens are, respectively, 3.19, 2.21, 4.90; 3.52, 2.62, 4.91; 2.69, 2.54, 4.66 mm. The genital hamules do not project quite as far beyond the genital lobe as shown in his figure 570 from a male from Guayaquil. The dark brown basal spot of the hind wings extends to the cubital cross-vein or to the origin of A2 (males), or half-way between the origins of A2 and Cu2 (female).

Distribution of form (a): Tennessee and Texas (Williamson, 1914), and from Ocotlan, Mexico, and Cuba to Guayaquil, Ecuador, and Santos, Brazil.

*Idiataphe longipes* (Hagen, 1861).

Cowley, 1934, *Ent. Mo. Mag.*, 70 : 243 (*Ephidatia* preoccupied).

*Ephidatia longipes* Calvert, 1906, *Biol. Centr.-Amer. Neur.* 216, tab. ix, figs. 1-5. Ris, 1913, *Cat. Coll. Zool. Selys-Longch.*, fasc. XVI (1) : 1013. Klots, 1932, *New York Acad. Sci. Surv. Porto Rico, etc.*, XIV (1), pl. II, fig. 16 (genit. male).

*Ephidatia longipes longipes* Ris, 1913, op. cit. : 1014 and 1919, fasc. XVI (2) : 1227.

*Ephidatia longipes cubensis* Ris, 1913, 1919, op. cit. : 1013, 1226.

*Ephidatia cubensis* Needham & Fisher, 1936, *Trans. Amer. Ent. Soc.*, 62 : 108 (nymph), figs.

*Idiataphe cubensis* Garcia - Diaz, 1938, *Journ. Agr. Univ. Puerto Rico*, 22 (1) : 60, pl. VII, fig. 3 (venation).

LAMA 17, Odon. 1 and 60, two males.

Both males have lost abdominal segments 5-10, both have the outer branch of the genital hamule "breit, fast quadratisch," one of the characters by which Ris (1913, p.

1012) distinguished *longipes* from *batesi*. This quadrate form is shown by Calvert (1905, fig. 4) and by Mrs. Klots (1932). Ris further gave 7½-8½ antenodals on the front wings for *longipes*, 6½ for *batesi*. Both of these males have 6½ antenodals; they show a faded pale (yellowish?) stripe on the ventral inflexed part and, more narrowly, on the adjacent dorsal part of the tergite of the third abdominal segment only, this stripe reaching from the anterior end to three-fourths' length of the tergite; basal brown spot of the hind wings reaches in Sc half-way to the first antenodal and in Cu to the origin of A2; labium yellowish-brown in distal half, almost black in the proximal half; labrum black, clypeus nearest Van Dyke brown of plate IV, No. 39, of Smith's glossary; vertex almost black, frons very dark metallic violet blue, thorax blackish, no pale markings visible (faded?); hind wing 27, 28 mm.

These two males, therefore, do not agree completely with either of the two subspecies of *longipes*, *longipes longipes* and *longipes cubensis*, recognized by Ris.

Distribution of *longipes longipes*: British Guiana; Para (?), Minas Geraes, Espiritu Santo, S. Joao del Rey (Rei) and Rio de Janeiro, Brazil. (Ris). Kirby adds Colombia (*Trans. Zool. Soc. Lond.*, 12 (9) : 331. 1889).

Distribution of *longipes cubensis*: Bahamas, Cuba, Isle of Pines, Puerto Rico, Trinidad, Mexico, Guatemala, Panama, Colombia; Santarem, Brazil (Ris, 1913, 1919; Needham & Fisher, 1936; Garcia-Diaz, 1938).

It is of interest to note that Ris, 1919, p. 1227, records both *E. longipes longipes* and *E. batesi* from Wismar, British Guiana, as taken on the same days, 15, 16.II.1912, by the same collectors, Williamson and Rainey.

ADDENDUM:

*Dicterias cothurnata* (Foerster) new combination.

*Neocharis cothurnata* Foerster, 1906, *Jahresber. Mannheim. Ver. Naturk.*, 71-72 : 68. Ris, 1918, *Arch. Naturgesch.*, 82 A (9) : 12. Munz, 1919, *Mem. Amer. Ent. Soc.*, 3 : 47, 73, pl. VI, fig. 31 (venation ♂).

*Charitopteryx cothurnata* Cowley, 1934, *Entom.*, 67 : 201.

Subsequent to the proof-reading of this paper, a single female of this species was found among a miscellaneous lot of unstudied Odonata at the Academy of Natural Sciences of Philadelphia, wherefore the following for completeness' sake.

Bartica, British Guiana, 12.17.1913, H. S. Parish, 1♀; allotype, A.N.S.P.

Distribution: Surinam, British Guiana. Until the specific characters of forms referred to *Dicterias* are better known, *D. cothurnata* is to be added at the top of list *a* on preceding page 49 of this paper, "Dis-

tribution of the Kartabo Odonata." *Dictérias* is placed in the Calopterygidae by deSelys and Hagen, 1853, in the family Heliocharitidae by Tillyard and Fraser, 1939.

The present female (this sex has not been described hitherto) differs from Foerster's description and Munz's figure of the venation of *cothurnata* male as follows:

Arculus nearest and proximal to the third costal antenodal on the right front wing, midway between the 2nd and 3rd on the left front wing, slightly distal to the 2nd on both hind wings. One double cell between Cu2 and the hind wing margin at less than half distance from the quadrilateral to the distal end of Cu2 on both hind wings; 21 right, 22 left costal antenodals on the front wings, 16 right, 17 left on the hind wings; antenodal length 14 mm., postnodal length 20 mm. on the hind wings, apices of the front wings beyond the stigmata destroyed. Two basal subcostal cross-veins on both front wings and the left hind, one on the right hind. The single cubital cross-vein nearly as far proximal of the arculus as the arculus is long on all the wings, separation of vein A from the hind margin of all the wings as far proximal of the cubital cross-vein as the arculus is long. Nodal sector (M2) separating from M1  $\frac{1}{2}$ - $1\frac{1}{2}$  cells beyond the nodus, M1a at  $6\frac{1}{2}$ - $8\frac{1}{2}$  cells beyond the nodus on the front wings, at  $6\frac{1}{2}$ -7 cells on the hind wings, and 6 cells beyond the origin of M2 on the front wings and the right hind, 5 cells on the left hind.\* Supplementary sectors as in Munz's figure, rather than in Foerster's lines 26-29, page 68. Postnodals, front wings, 22 right, left broken; hind wings 17 right, 18 left.

Abdominal appendages 1.14 mm. long, subequal to abdominal segment 10, straight, simple, tapering to a very acute apex. Distal half of ventral margin of genital valves serrulate. Palps of genital valves .74 mm. long, cylindrical, divergent in dorsal or ventral view, but curved slightly mesad in terminal fourth, extreme apex slightly thickened, reaching to beyond the level of abdominal segment 10 but not as far as that of the apex of the abdominal appendages.

Third femur 11 mm., 3rd tibia 15 mm., 3rd tarsus 2 mm. Abdomen 39, hind wing 34 mm.

Pterostigma of the front wings total

\* Lines 21-23, page 68, of Foerster's description should apparently read: "Der Sektor subnodalis entspringt 10 Zellängen nach dem Arculus, der Nodalsektor 1 Zelle und der Ultranodalis 7 Zellen nach dem Niveau des verdickten Nodus."

length 5.32 mm., costal margin 4.74 mm., brown, a brace vein present on the front wings and the left hind, but not on the right hind, not thicker than adjacent cross-veins and not continued in the same oblique line as the proximal side of the stigma. Apex of the wings hyaline, not brown.

No distinct pale band across the ocelli.

Pterothorax olive with the mid-dorsal carina black and reddish-brown (Van Dyke brown of Smith's Glossary) stripes ca. .57 mm. wide on the mesepisternum, humeral (mesopleural) suture and on the metepimeron and ca. .4 mm. wide on the mesepimeron and the 2nd lateral (metapleural) suture; the two sutures named are each finely lined with yellow.

Abdomen olive green, segments 2-8 (or -10?) with an inferior longitudinal Van Dyke brown stripe for the entire length.

Legs reddish-brown.

This female is of nearly the same size as those of *D. umbra* Ris, 1918,<sup>†</sup> of *D. peruviana* Navas, 1920,<sup>‡</sup> and perhaps of *D. provera* Hagen, 1859,<sup>§</sup> (dimensions not given), but larger than that of *D. atrosanguinea* Selys, 1853.<sup>¶</sup>

*Cothurnata* differs from all these four species in having two cross-veins in the quadrilateral of all four wings; this is the second of two characters given by Munz as separating *Neocharis* from *Dictérias*; the first is negated by *D. umbra*.

The position of the arculus with respect to the antenodals, the number of basal subcostal cross-veins (*i.e.*, proximal to the first thickened antenodal), the extent to which M1+3 approximate R, the point of separation of M1+2 from M3, the point of separation of M2 from M1, the exact position of cu c-v and of the point of separation of A from the hind margin of the wings are features which vary even in specimens referred to the same species, so that it is impossible, in the present paucity of material of *Dictérias* recorded in the literature, to determine how many of these venational details have specific significance.

<sup>†</sup> *Arch. Naturgesch.*, 82 A (9):12, pl. 1, figs. 1, 2 (venation ♂, ♀).

<sup>‡</sup> *An. Soc. Cient. Argent.*, 90:34; Cowley, 1937, *Proc. Roy. Ent. Soc. London*, (A) 12 (8-9): 24, fig. 2 (1st leg).

<sup>§</sup> Hagen in Selys, *Bull. Acad. Belg.*, (2) 7:444; Needham, 1933, *Amer. Mus. Novitat.*, 664:4, fig. 2 (venation).

<sup>¶</sup> *Syn Calopt.*:56; *Monog. Calopt.*:191, pl. 5, fig. 6 (venation), pl. 8, fig. 12 (mouth parts), pl. 14, fig. 6 (abd. apex), 1854; *Bull. Acad. Belg.*, (2) 37:662, 1869. Munz, 1919, *Mem. Amer. Ent. Soc.*, 3, pl. VI, fig. 32, has copied the figure of the venation of the *Monog. Calopt.*

## EXPLANATION OF THE PLATES.

Abbreviations on some of the figures:

al, anterior lamina  
 gl, genital lobe  
 gs, glans of penis  
 h, hamule  
 hl, first (anterior) hamule  
 h2, second (posterior) hamule  
 p1-p4, first (vesicle) to fourth joints of penis  
 pr, hind lobe of prothorax  
 sh, sheath of penis  
 A1, A2, A3, C, M1, M1a, M2, M3, R1, Rs,  
 veins according to the Comstock-Needham notation.

Most of the drawings have been made with the aid of a Zeiss camera lucida, the majority in connection with a Zeiss-Greenough binocular microscope using paired oculars 2 or 10, paired objectives F55 or a<sub>0</sub>. Drawings of the penes of *Erythrodiplax* and figures 1, 2, 20, 21 and 22 have been made under a Leitz compound microscope, ocular 10X, objective 3 with its lower lens off for the camera lucida, adding this lens to complete the details by free hand.

## PLATE I.

- Fig. 1. *Leptagrion beebeanum* n. sp. Dorsal view of abdominal segment 10 and appendages of ♂ type, Kartabo, British Guiana, 6.24.1924.
- Fig. 2. *Leptagrion beebeanum* n. sp. Right profile view of the same.
- Fig. 3. *Hetaerina dominula* Hagen. Left superior appendage ♂ Bejuma, Venezuela, February 13, 1920. t indicates the small tooth on the internal superior margin, referred to in the text as being a distinguishing character of *dominula* according to de Selys and Hagen.
- Fig. 4. *Hetaerina dominula* Hagen. The same from Tumatumari, British Guiana, February 11, 1912.
- Fig. 5. *Hetaerina dominula* Hagen. The same from Maroni River, French Guiana, 8.04.
- Fig. 6. *Hetaerina dominula* Hagen. Outline of head ♂ to show the occipital tubercles. Kartabo, 22.X.1920.
- Fig. 7. *Phyllocycla bartica* n. sp. Left profile view of abdominal segments 8-10 and appendages, ♂, holotype, Kartabo, III.9.1926.
- Fig. 8. *Phyllocycla bartica* n. sp. Left profile view of genitalia of second abdominal segment ♂ holotype. One cornu is directed cephalad for clearness' sake. At a is shown a piece of a cornu of the penis more highly magnified.
- Fig. 9. *Phyllocycla bartica* n. sp. Rear view of vesicle (first joint) of penis, ♂ holotype.
- Fig. 10. *Phyllocycla bartica* n. sp. Ventral view of hamules and anterior lamina, ♂ holotype.
- Fig. 11. *Phyllocycla bartica* n. sp. Dorsal view of tenth abdominal segment and appendages, ♂ holotype.
- Fig. 12. *Phyllocycla bartica* n. sp. Right hind wing base, ♀, Kartabo, III.11.1926.
- Fig. 13. *Phyllocycla bartica* n. sp. Right hind wing base, ♂ holotype.
- Fig. 14. *Phyllocycla bartica* n. sp. Ventral view of vulvar lamina and ninth abdominal segment, ♀ Kartabo, III.4.1926.
- Fig. 15. *Phyllocycla bartica* ? n. sp. The same, ♀ Kartabo, July-August, 1926.
- Fig. 16. *Aphylla alia* n. sp. Left profile view of genitalia of second abdominal segment, ♂ holotype, Kartabo, 19.VII.1920.
- Fig. 17. *Aphylla alia* n. sp. Ventral view of hamules, ♂ holotype.
- Fig. 18. *Aphylla alia* n. sp. Right hind wing base, ♂ holotype.
- Fig. 19. *Aphylla alia* n. sp. Rear view of vesicle (first joint) of penis, ♂ holotype.
- Fig. 20. *Metaleptobasis tetragena* n. sp. Dorsal view of mesothoracic horns and hind lobe of prothorax, ♀ holotype, Kartabo, July-August, 1926.
- Fig. 21. *Metaleptobasis tetragena* n. sp. Frontal view of same, ♀ holotype.
- Fig. 22. *Metaleptobasis tetragena* n. sp. Left profile view showing left mesothoracic horn and left tubercle of hind lobe of prothorax, ♀ holotype.

## PLATE II.

- Fig. 23. *Erythrodiplax castanea* (Burmeister). Right profile (lateral) view of last joint of penis, Kartabo, 2.V.1924.
- Fig. 24. *Erythrodiplax angustipennis* Borrer. Right profile view of last joint of penis, Maroni River.
- Fig. 25. *Erythrodiplax unimaculata* (De Geer). Right profile view of last joint of penis, Kartabo, VRS. Odon. 62.
- Fig. 26. *Erythrodiplax unimaculata* (De Geer). Ventral view of apex of last joint of penis, Kartabo, VRS. Odon. 18.
- Fig. 27. *Erythrodiplax laurentia* Borrer. Right profile view of last joint of penis, Kartabo, 6.VI.1924.
- Fig. 28. *Erythrodiplax famula famula* (Erichson). Ventral view of apex of last joint of penis, Kartabo, 20.IV.1920, not fully colored.
- Fig. 29. *Erythrodiplax famula famula* (Erichson). Right profile view of last joint of penis, Kartabo, 1.VI.1924.
- Fig. 30. *Erythrodiplax latimaculata* Ris. Ventral view of apex of last joint of penis, LAMA, Odon. 38.
- Fig. 31. *Erythrodiplax latimaculata* Ris. Right profile view of last joint of penis of same.

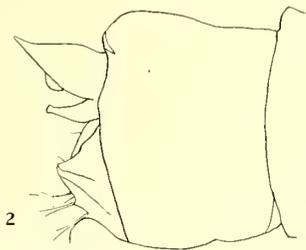
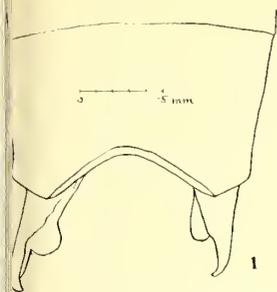
- Fig. 32. *Erythrodiplax maculosa* (Hagen). Ventral view of apex of last joint of penis, LAMA 17, Odon. 63.
- Fig. 33. *Erythrodiplax maculosa* (Hagen). Right profile view of genitalia of second abdominal segment of same.
- Fig. 34. *Erythrodiplax maculosa* (Hagen). Nodal region of the four wings of same.
- Fig. 35. *Erythrodiplax basalis basalis* (Kirby). Ventral view of last joint of penis, Kalacoon, 1916, Odon. 112.
- Fig. 36. *Erythrodiplax basalis basalis* (Kirby). Right profile view of last joint of penis of same.
- Fig. 37. *Oligoclada raineyi* Ris. Ventral view of vulvar lamina and abdominal segment 9, Kartabo, 20.V.1924.
- Fig. 38. *Microstigma maculatum* Hagen. Apex of right front wing, Essequibo ♂, type of Hagen, in the Museum of Comparative Zoology; from camera lucida drawing by Prof. B. Elwood Montgomery.
- Fig. 39. *Aeschnosoma peruviana* Cowley. Rear view of vesicle (first joint) of penis, Kartabo. 13. iii.
- Fig. 40. *Aeschnosoma peruviana* Cowley. Left profile view of genitalia of second abdominal segment of same male.
- Fig. 41. *Aeschnosoma peruviana* Cowley. Ventral view of hamules and genital lobes of same male.
- Fig. 42. *Zenithoptera fasciata* (Linnaeus). Photographic reproduction, by Mr. A. D. Warden, of George Edwards' figure, pl. 174, of his Natural History of Birds, quoted by Linnaeus as the basis for his *Libellula fasciata* and also *Libellula americana*.
- Fig. 43. *Aeschnosoma peruviana* Cowley. Photograph, by Mr. Herman A. Walters, of male from Kartabo, 13.iii.

#### Corrections to Plates.

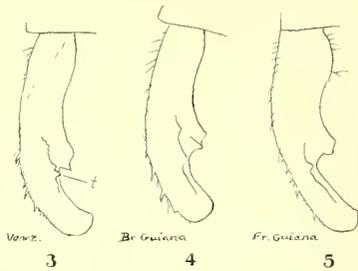
Plate I, Fig. 16. For h2 read h1; for h1 read h2.

Plate II, Fig. 38. Following are the abbreviations marking the wing-veins from above downward: C, R1, M1, M1a, M2, Rs, M3.

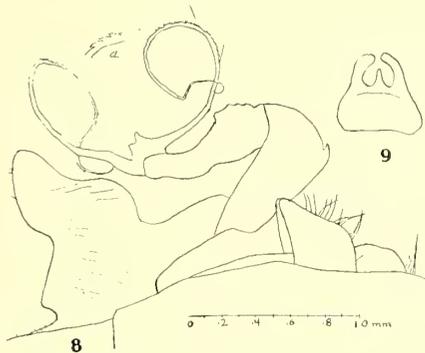
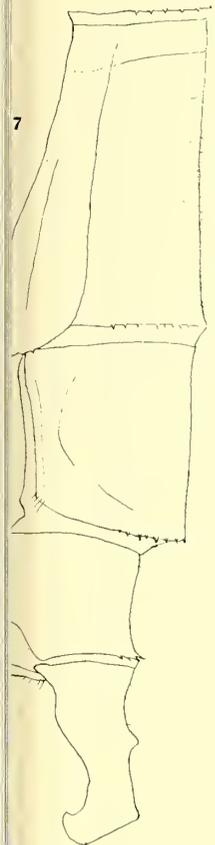




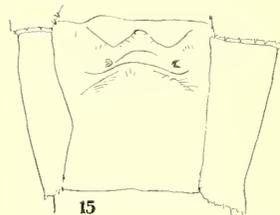
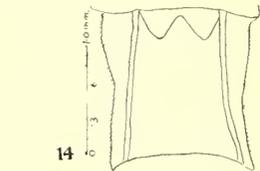
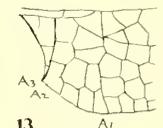
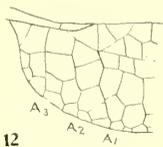
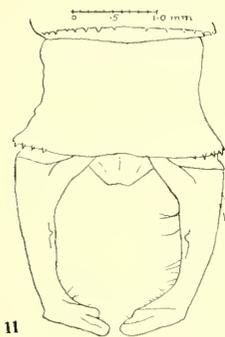
1, 2 *Leptagrion beebeanum* n. sp.



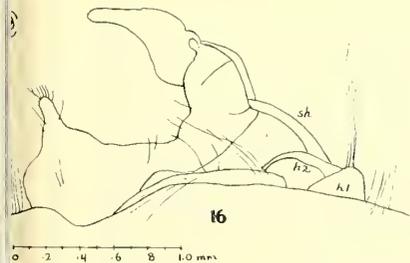
3-6 *Hetaerina dominula* Hagen



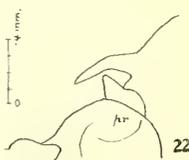
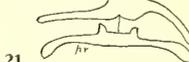
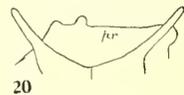
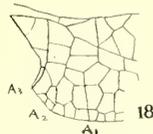
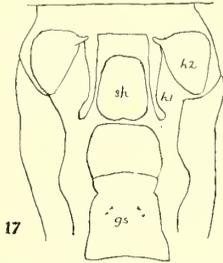
7-15 *Phyllocycla bartica* n. sp.



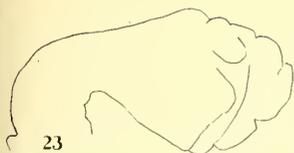
20-22 *Metaleptobasis tetragena* n. sp.



16-19 *Aphylla alia* n. sp.



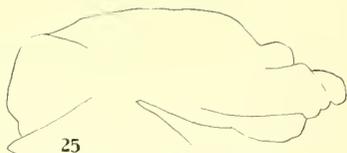




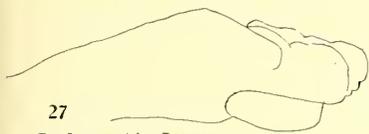
23 *Erythrodiplax castanea* (Burm.)



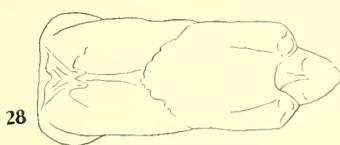
24 *E. angustipennis* Bor.



25,26 *E. unimaculata* (DeGreer)



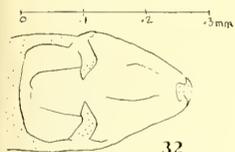
27 *E. laurentia* Borrer



28



26



32

0 .1 .2 .3 mm



29

0 .3 .5 1.0 mm

28,29 *E. famula*  
*famula* (Erichson)

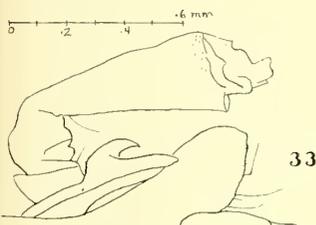


30

30,31 *E. latimaculata* Ris



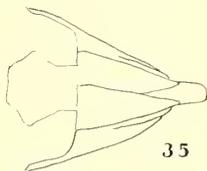
31



33

0 .2 .4 .6 mm

35,36 *E. basalis*  
*basalis* (Kirby)

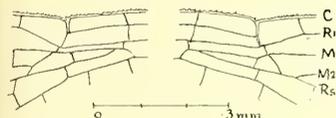


35



37

*Oligoclada*  
*raineyi* Ris



34

32-34 *E. maculosa* (Hagen)

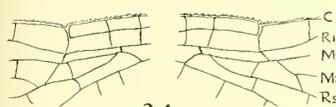


36



38

38 *Microstigma maculatum* Hagen



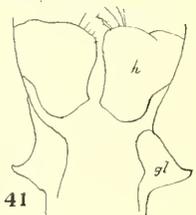
34

32-34 *E. maculosa* (Hagen)

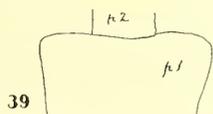


40

39-41 *Aeschnosoma peruviana* Cowley



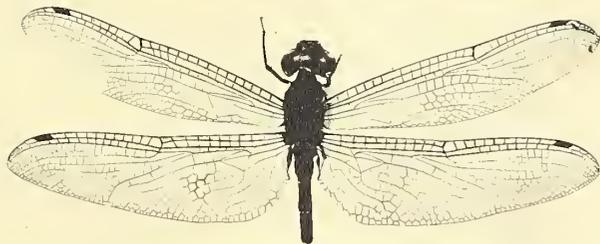
41



39



42 *Zenithoptera fasciata*  
(Linnaeus)



43 *Aeschnosoma peruviana* Cowley



## 5.

Army-ant Life and Behavior under Dry-season Conditions  
with Special Reference to Reproductive Functions.

## II. The Appearance and Fate of the Males.

T. C. SCHNEIRLA.

*The American Museum of Natural History.*<sup>1</sup>

(Plate I; Text-figure 1).

## INTRODUCTION.

In keeping with the marked deviations of the doryline ants from most other ants in their general behavior pattern, there are extensive differences in their mode of reproduction. The close relationship which exists between general reproductive pattern and colony behavior in the American subgenus *Eciton* (*Eciton*), has been described in previous reports (Schneirla, 1938, 1944). The present paper represents an attempt to throw further light upon *Eciton* reproductive processes by inquiring into dry-season events and particularly the appearance and function of *Eciton* males.

The wasplike winged males of the dorylines, which contrast sharply with the curiously-structured wingless dichthadiigynes or fertile females of these ants, have been described by various authors (Gallardo, 1920; Mukerji, 1926; Wheeler, 1921; Smith, 1942), yet the manner in which these reproductive forms are produced and the nature of their functional relationship to colony activities have remained obscure to the present time.

The elusiveness of this problem is suggested by my failure to find any trace of developing *Eciton* male forms during the rainy season, notwithstanding the fact that an extensive search of the nests was carried out in the rainy months of four different years. The studies (Schneirla, 1933, 1938, 1944) were made in the Caribbean area of Panama, in a region that has well marked and fairly regular annual rainy and dry seasons. It would seem by elimination that young reproductive individuals of both sexes must appear during the latter part of the rainy season or in the course of the annual dry season.

Most of our previous evidence on the fertile forms of *Eciton* has come as we shall see (in the "Discussion" section of the present paper) from the occasional capture of males and females in scattered localities, under seasonal and colony conditions which are generally very incompletely reported.

<sup>1</sup> This investigation was carried out while the writer was a Fellow of the John Simon Guggenheim Memorial Foundation. Supplementary studies have been supported by a grant to the Department of Animal Behavior from the Committee for Research in Problems of Sex, National Research Council.

The desirable procedure to clarify the confusion is a comparison of data from areas with similar annual climatic changes. A beginning was made by the writer in the dry season of 1945, in a sampling of *Eciton* colonies in various rain-forest localities in southern Mexico through the latter two-thirds of the regular dry season (Schneirla, 1947). This general area was selected because its annual rainy-dry seasonal cycle approximates that of the Atlantic rain-forest area of Panama. In that study various well-separated localities were visited successively, a procedure calculated to give a broad view of *Eciton* conditions through the period. A predominance of worker broods was found, with but limited evidence on the reproductive forms. Just one brood of developing males was found, under conditions somewhat resembling the single male brood previously found by Wheeler (1921). It is clear that a cross-sectional survey is not adequate for the study of events as elusive as the production of *Eciton* fertile forms appears to be.

The present survey represents a longitudinal or relatively continuous survey of conditions in the locality of the original Panama studies. As was anticipated, male forms appeared in the *Eciton* broods and an extensive study of their relations to the colonies became possible. Among the questions to which the study was directed were these: Do the males appear in distinctive broods or in mixed broods (e. g., with worker forms)?—How many males may be produced by a given colony, and do all colonies produce them?—Is the production of males synchronized in some manner with the ordinary production of worker broods by *Ecitons*, or does this process occasion interruptions or irregularities in the ordinary reproductive rhythm? Such questions are of interest not only from the standpoint of *Eciton* reproductive functions, but also with regard to the general problem of caste determination in insects.

We are of course interested in learning the relationships of males to colony behavior, both when they are in broods and after they have emerged as alate adults. We have found that worker broods have a regular and important causal function in the occurrence of the periodic nomadic and stary changes in colony behavior which are consistent

features of *Eciton* life under rainy-season conditions (Schneirla, 1938; 1944). Is it possible that the appearance of developmental forms other than workers is reflected in a different set of relationships between brood and colony?

Finally there is a whole set of questions concerning the behavior and function of the males, in particular the conditions of their dispersal as winged individuals and the manner of their eventual meeting with the unique wingless *Eciton dichthadii*gynes. Problems such as the last, concerning the process of mating, will be touched upon only circumstantially here in relation to the dispersion of the males from their colonies of origin.

#### LOCALITY AND GENERAL CONDITIONS OF THE INVESTIGATION.

This paper is based upon a systematic investigation of *Eciton* behavior and related colony conditions in a given general locality, Barro Colorado Island, C. Z., through the principal part of a given dry season.

The survey extended over roughly the last three-fourths of the dry season of 1946 into the early part of the next rainy season, in all from February 7, 1946 to June 16, 1946. Until near the end of this period rains were exceptional and generally very light, with numerous sequences of rainless days until after mid-April. These circumstances are typical of the locality.

That there is a sharp seasonal difference in rainfall on Barro Colorado Island (as in the Caribbean area generally) is clear from the fact that in a summary of monthly averages and deviations for a period of fifteen years on the Island during which records were kept by the same method, the smallest monthly rainfall probable in the wet months from May through November (6.3 in. for September) clearly exceeds the largest monthly fall probable in the dry months from December through April (5.0 in. for April).<sup>2</sup> Thus the Island itself may be considered a very satisfactory region in which to investigate the seasonal differences in ecology and behavior of tropical American rain-forest animals. With respect to dry-season conditions in the spring of 1946, it should be added that the preceding wet season had brought an exceptionally large fall of rain before dry weather set in about mid-December; consequently even the rather high ground of Barro Colorado, well-forested as most of it is, may have retained more moisture than is usual during the dry season. Only the terrain in the eastern section of the Island, with its lighter forest cover than other sections, approached in dryness the conditions generally encountered in southern Mexico in the spring of 1945 (Schneirla, 1947, areas 1, 3 and 4).

The study is mainly concerned with two terrestrial species of the subgenus *Eciton*

(*sensu stricto*), which are among the most frequently encountered members of the genus *Eciton* in Central America.

The general method involved surveys of behavior and biological conditions of *Eciton* colonies in the field, with special field and laboratory tests introduced when feasible. The plan was to keep as complete a record as possible of army-ant colonies present in the eastern and southeastern half of the Island (the drier section). Two colonies, one of *Eciton (E.) burchelli* (colony B-I) and one of *E. (E.) hamatum* (colony H-B) were kept on record throughout the four months of the study, and numerous other colonies of these two species were studied for shorter intervals of time.

At intervals of about three days through the period of investigation, when accessible the bivouacs of colonies under observation were broken into as carefully as possible for brood samples. Periodically the bivouacs of colonies other than the two principal cases (B-I and H-B) were ransacked for a thorough inspection of their brood and adult population. A large part of the collected brood material was fixed in a modified Bouin's solution before preservation in 70% alcohol.

Live *Eciton* material was kept at the laboratory for special behavior observations and tests arising from the field work. For sampling the population of flying *Eciton* males, occasionally a small light trap was set at various places in the general forest and a larger light trap was placed in the forest near the laboratory clearing. Also, a white illuminated board just outside the main laboratory building was inspected each night for alate males.

#### RESULTS.

##### *General Results: The Nature and Occurrence of Eciton Male Broods.*

It has developed from numerous seasonal investigations on Barro Colorado Island (Schneirla, 1933, 1938) that in the regular season of rains in that locality *Eciton* colonies produce only worker forms in immense broods. No sexual forms were found in a great number of broods examined during the period from May through September. Our present results indicate that the production of males is seasonally conditioned, and evidently limited to the dry season.

The general findings are summarized chronologically in Table I. From the time the study was begun on February 7 until the latter part of February, only broods containing worker forms were found in the bivouacs of *Eciton burchelli* and *E. hamatum*. In agreement with the 1945 results from southern Mexico, such broods resembled those of the rainy season in containing the entire polymorphic series of worker types, and from general inspection seemed to approach them in numbers of individuals (ca. 25,000). The first brood containing male forms was found on February 16 in a colony of *E. burchelli* (No. B-III), chanced upon

<sup>2</sup> The writer is grateful to Mr. James Zetek, Resident Manager of the Barro Colorado Island laboratory, for having made this data available, and for the many other ways in which he generously facilitated arrangements for these investigations.

late in the evening during the early part of its bivouac-change movement. It was observed that some rather bulky larvae were being carried by workers in the column. Samples of these larvae were taken, and later at the laboratory were found to be all of the characteristic sub-cylindrical male type and all nearly the same size, about 14 mm. in length. On February 20, when the bivouac of this colony was examined carefully, the brood was estimated to contain 3,000 larvae, all of the male type and not very different in size. The last distinct brood of males found in the investigation was a lot of alate males discovered in a colony of *E. hamatum* (H-L) on April 16. As Table I indicates, male broods were discovered in various other colonies of both *E. burchelli* and *hamatum* during the intervening period of about two months.

Representative stages of development in *Eciton* males, from early larval to mature forms, are illustrated in Plate I.

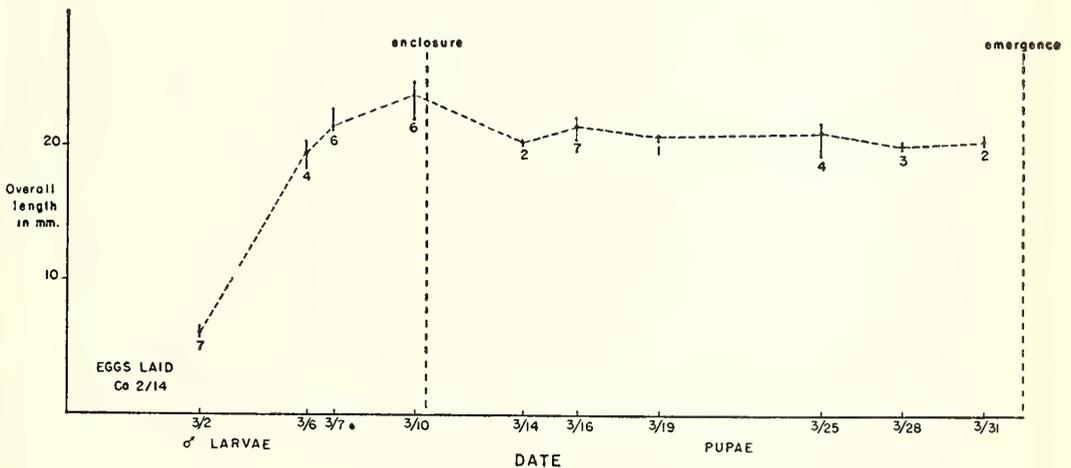
Altogether, male broods were found in 5 of 26 different colonies of *E. hamatum* under observation at different times from mid-February to late April, and in 6 of 21 different colonies of *E. burchelli*. Dealate males in limited numbers were found at intervals in the colonies of both species up to the time when the study ended in mid-June. In these species the production of males seems to be confined to the dry months.

The results summarized in Table I suggest that a species difference exists in the time of male-production. Inspection of the captures shows that male broods of *E. burchelli* were found from shortly after mid-February, when early larval broods were discovered in the bivouacs, to the end of March when only alate forms were found. In contrast, larval male broods of *E. hamatum* were not found until the middle of March, and alate broods of this species were not taken until mid-

April. Notwithstanding the relatively small number of cases, in view of the fact that numerous colonies of these two species were investigated with approximately equal frequency during the period, it is quite possible that we are dealing with a reliable difference in the timing of male production. Especially suggestive is the fact that all of the respective stages of *E. hamatum* males from early larvae to dealate forms were taken later than were the corresponding male types of *E. burchelli*. The *burchelli* colonies on the Island evidently begin their production of males earlier than do *hamatum* colonies, and finish earlier. Judging from the fact that winged males of various species of *Eciton* (*Labidus*) and *E. (Neivamyrmex)* were taken at lights from the early part of February, it is possible that males are produced still earlier in the season in some of these species.

In this study, two colonies of different species of *Eciton* (*Eciton*) were kept on record for approximately four months after early February. All of the principal activities such as raids and nomadic movements were investigated, and whenever possible samples of their broods were taken at 3-day intervals. In one of these colonies, H-B of *E. hamatum*, four all-worker broods were produced during the interval, but this colony produced no males of its own. Within the same time, colony B-I of *E. burchelli* brought forth three worker broods and in addition one all-male brood of its own. There follows a résumé of the latter case, which as various other results indicate is representative of the circumstances of male-production in species of *Eciton* (*Eciton*).

*The record of colony B-I, E. burchelli.* The colony was found on February 6, through chancing upon its raiding system. At the time its bivouac cluster was established within a large hollow tree, about 2.5 meters from the ground, one side of it visible



TEXT-FIG. 1. Sketch of representative stages in the development of a male brood of *E. burchelli* (colony B-I), from larva to mature pupa. Size at each stage is represented by the overall length of specimens taken in small samples. The number of individuals in each sample is indicated below the short vertical line representing range and average of lengths in the sample.

through a huge knothole. This was clearly a statory site into which the colony had moved within the preceding few days, for an immense brood of probably more than 25,000 mature worker larvae newly enclosed in cocoons was present. On February 16 unsuccessful attempts were made to discover and sample a new brood of eggs which, in the regular cycle of Eciton events, would be expected at about that time (Schneirla, 1944). On February 28, with the greater part of the now mature worker brood removed as callows from cocoons, the colony set off upon a nomadic period in which raids were larger than before and successive nightly bivouac-change movements occurred.

Larvae of the new brood, which later proved to be an all-male brood, were taken from the temporary bivouac of March 2. These larvae were all nearly the same size, about 6.4 mm. in length. In the following days they grew with surprising rapidity. For example, on March 10 a small sample of six of them approximated 23 mm. in length. At that time these larvae evidently were nearly mature, for the first spinning was observed on March 9. The growth rate of this brood is represented in Text-figure 1.

On March 10, when the colony spent its first day of a new statory period clustered within the basal trunk cavity of a large hollow tree, cocoon-spinning appeared to be widespread among the mature male larvae. The spinning evidently lasted about six days in all. On March 19 approximately 200 of the enclosed larvae were dragged by workers to the outer edge of the tree-opening, where they were discarded. All larvae in the heap of discards were found to be dead at the time. A general examination disclosed no clue as to possible causes of death.

On March 29, when all members of the male brood seemed to be nearly mature pupae in a well-pigmented condition, the colony began to shift away from its statory site in the hollow tree.<sup>3</sup> At this time laboratory tests showed that most of the males were capable of antennal, tarsal, and trunk reflexes of sufficient amplitude to be readily observable with the naked eye. Large numbers of newly emerged alate males were seen nightly in the columns after this time, together with many unopened cocoons which were lugged along by workers. On the night of March 31 the "shucking" of mature male pupae from their cocoons was observed in full swing at both old and new bivouacs. At the time it was estimated that more than three-fourths of the males had emerged as callows.

On April 1 the presence of a new brood of very young worker larvae in colony B-I was established. The nightly bivouac-change columns of the colony now were thronged with many hundreds of alate males, passing

along the trails under their own power in single file or in small groups, generally surrounded and closely followed by workers in large groups. Successive nightly movements were observed in which for periods of two hours or more the alate males ran in column with workers from the old to the new bivouac site. The males appeared only during the nightly removals; in the daytime they remained within the bivouac cluster and never were seen among the workers on the raiding trails.

On April 2 the emergence of this brood from cocoons seemed to be complete. Judging by a count of empty cases collected from the statory site and first few nomadic bivouacs, this brood of males numbered close to 3,000 individuals.

Each evening after April 3, within a few hours after dusk in the early beginning of the bivouac-change, as many as a few dozen winged males were to be seen in the vicinity of the bivouac of the day, running circuitously about on the ground and on low vegetation and other objects close to the ground. Generally each male had a few workers hanging to his body or running in close contact with thorax or gaster. No departure flights were observed until after April 5, then on succeeding nights the male take-off flights were observed frequently, from the vicinity of the old bivouac and sometimes from the new site, but never from the moving column. (No movements of the colony occurred on the nights of April 4, 6, and 8.)

On April 14, when colony B-I entered a further statory period (with its larval worker brood now mature and engaged in spinning), alate males were not very numerous, and it was judged that not more than 600 of them remained with the colony. A few nightly departures of males were observed during the statory period, from the large lightning-split tree in which the colony was clustered, until in the first bivouac-change movement of the new nomadic period it was not possible to observe any alate males at all. (At this time the major part of a new brood of mature pupal workers had emerged from cocoons.) Since no alate males were observed in the B-I columns during subsequent nightly removals, it was judged that the last of them had left the colony.

To sum up the life of this male brood in colony B-I in which it was produced, its growth stages (cf. Text-figure 1 and Plate I) may be timed approximately as follows:

Probable midpoint date of egg-production: (During the early third of a statory phase). February 14

Presence ascertained as very young larvae: (In the early days of a new nomadic period). March 3

Mature male larvae at height of cocoon-spinning: (At beginning of a further statory period). March 10

<sup>3</sup> The nightly bivouac-change movements through which this colony shifted from the statory site of March 10-31 were complex and rather exceptional, involving as they did a process of true colony-division which will be discussed in a forthcoming paper.

TABLE I.  
Principal records of male Eciton broods in the 1946 dry season at Barro Colorado Island.

Date found	Colony symbol and species	Condition of male brood	Estimated brood population	Other broods present	Colony behavior	Remarks
Feb. 22	B-II-X <i>E. burchelli</i>	Nearly mature larvae	3,000	Large brood of callow workers	Nomadic; four nightly moves observed	No movement on second night after large part of male brood was taken away
Mar. 1	B-III <i>E. burchelli</i>	Mature pupae, largely emerged alates	3,000	Large brood, very young worker larvae	Newly nomadic; three successive nightly moves observed	Evidently found on day following the first nomadic move
Mar. 2	B-I <i>E. burchelli</i>	In early larval stage	3,000	Large brood newly emerged callow workers	Nomadic; on move until larvae mature, enclosed	Nomadic activity rose considerably in following days
Mar. 6	B-IV <i>E. burchelli</i>	Adult alates	500	Large brood nearly mature larval workers	Nomadic; four successive moves, then stately	No males remained after stately period of 22 days
Mar. 29	B-V <i>E. burchelli</i>	Adult alates	1,000	Large brood fairly mature larval workers	Nomadic; two successive moves observed	Exodus of males observed from bivouac area
Mar. 31	B-VI <i>E. burchelli</i>	Adult males	500+	Large brood mature larval workers	Nomadic; moved that night into stately bivouac	No alate males remained after stately period of 21 days
April 3	H-J <i>E. hamatum</i>	Very young larvae	3,000	Large brood newly emerged callow workers	Nomadic; large raids, two successive moves seen	Just three days after stately period
April 4	H-K <i>E. hamatum</i>	Larvae more than two-thirds grown	3,000	No other broods observed	Nomadic; two successive moves observed	Raids exceptionally large; movements long
April 9	H-L <i>E. hamatum</i>	Newly emerged callow alates	2,000	Large brood very young worker larvae	Nomadic	Queen contracted; two de-alated males found in bivouac
April 10	H-M <i>E. hamatum</i>	Newly emerged callow alates	2,000	Immense brood very young worker larvae	Nomadic	250 meters from H-L; possibly from same base colony

Mature males emerging from cocoons: (At beginning of a new nomadic phase). March 31  
 Alate males probably all gone about April 20

Provided that the eggs of this brood were laid on or about February 14, as there is reason to believe was the case, the total development time of this male brood was close to 46 days, with 22 days of this time for growth from the stage of larval maturation to pupal maturation. The males left the colony in nightly lots, and practically all of them appeared to have flown off within little more than three weeks from the time of their emergence as callow alates. Actually, the major part of this brood got away during the nomadic period of about 12 days which followed directly upon their emergence from cocoons. However, no departure flights were witnessed on the first three nights after emergence from cocoons had begun.

Colony B-I had but one brood of males, preceded by one immense all-worker brood and followed by two others, all broods appearing at regular intervals during the period of study. The total developmental time of the male brood was roughly the same as that of worker broods.

*Evidence from briefer studies of male production.* In all, 11 male broods were found in 47 colonies of *E. burchelli* and *E. hamatum* studied during the season of investigation. The chief characteristics noted above in the evidence from the production of a male brood by colony B-I were confirmed in briefer investigations of the other cases. The gist of the evidence from the other ten cases is presented in Table I, in chronological order, and further relevant facts from other colonies are given below, roughly in the sequence of developmental stages.

Colony H-J (*E. hamatum*) was found at 11:00 a. m. on April 3, engaged in a large three-system raid from a temporary bivouac 100 meters to the east of the Shannon trail, opposite Station 6.<sup>4</sup> There was a brood of many thousands of newly emerged callow workers, relatively few of which were to be seen outside the bivouac. Near the rear center of the cylindrical bivouac cluster were found two walnut-sized clumps which contained relatively small sub-cylindrical larvae (later identified as Eciton male larvae) all roughly the same size. The colony was definitely nomadic, since it moved to a new bivouac site late that evening, and staged a new 3-system raid on April 4. Two broods: a large brood of callow workers, and a brood of young male larvae.

Colony H-K (*E. hamatum*) was found at 10:00 a. m. on April 4, about 200 meters to the east of Wheeler trail near station 22. A large 3-system raid was in progress; the bivouac was a very broad irregular cylinder beneath a large log. Well distributed through

the walls and interior of the mass was a brood of male larvae considerably more mature than the brood of colony H-J, and estimated to number between 2,500 and 3,500 individuals. That evening the colony moved to a new bivouac site about 200 meters distant. One brood: a relatively small brood of moderately developed male larvae.

Colony B-II-X (*E. burchelli*) was found on the move into Lutz ravine on the evening of February 20, crossing Barbour trail near station 2. In the column were observed many thousands of newly emerged callow workers, distinguished from older workers by their light pigmentation, and large numbers of rather advanced male larvae lugged along by workers. The bivouac of February 21 could not be investigated; however the move of that evening was traced to the new site, and on February 22 the bivouac contents were examined. The brood of callow workers was relatively immense; that of male larvae was much smaller and was close to maturity. The new bivouac of February 23 was an unusually tall structure. It was a regular cylinder 90-100 cm. in height and about 35 cm. in width at the top (depending to the ground from the undercut upper edge of a broad buttressed root) and tapering inward toward the bottom which touched the ground. The male larvae were evenly distributed throughout the walls of the cluster, held by workers, and heaped in occasional pockets in the interior meshwork of workers. Nightly moves were observed until February 25, when the colony held its position within the base of a small partially open hollow tree, occupied the night of February 24. Late in the day on February 25 signs of larval cocoon-spinning were observed. On the night of February 26, after a very large raid during the day, the colony moved across Donato trail beyond station 3, about 160 meters to the north where a cluster was formed against the upper interior wall of a great hollow tree. Cocoon-spinning by larvae was greatest on February 27, judging by the rate at which wood dust fell to the ground from the elevated cluster of ants, and by the same sign this activity was completed on February 29 (as far as transportation of larvae to spinning places by workers was concerned). On the evening of March 21 the colony moved away, leaving a large heap estimated to contain more than 2,000 male pupa cases on the tree floor. Two broods: one immense brood of callow workers, one relatively small brood of males. Presumably a further brood of eggs was laid early in the 22-day statary period.

Colony B-III (*E. burchelli*) was discovered at 8:30 a. m. on March 1, about 300 meters to the north of the Van Tyne trail near station 8. At the time the last ants were leaving in column from what was evidently the previous bivouac site of the colony beneath the overhung side of a somewhat raised log, for under the log in one spot was found a sizeable heap of empty male pupa cases. (These were later counted at the laboratory, and

<sup>4</sup> See special map of Barro Colorado Island prepared by 11th Engineers, Office of Department Engineer, Panama Canal Department U. S. Army.

totalled 2,740). The column itself was thronged with alate males, and other alates were huddled in small groups at occasional caches along the route where workers were seen with small numbers of male cocoons, some in the process of being opened. The alate males were strung out at intervals in the column, each running with an entourage of workers. The new bivouac was about 100 meters distant from the log under which the previous site evidently had been, and was a large exposed cylinder depending from low vines to the ground. The alate males remained within this cluster once they entered. The bivouac was found to contain several hundreds of alates, more than 100 unopened or partially opened male cocoons, and an immense brood of very young worker larvae gathered into a few masses in the very center of the bivouac. The described column evidently took the route of a protracted bivouac-change movement which had lasted through the preceding night. This route was not used after the movement was completed at 9:25 a. m. During the day a vigorous raid developed southward, and that night the colony moved to a new site over the principal trail of this raiding system. Further raids and bivouac-change movements were observed on March 2 and 3. The last male cocoons were opened on March 3. Two broods: a newly emerged brood of callow alate males estimated to number about 3,500; and an immense worker brood in the early larval stage at the time of study. With the appearance of the callow males the colony clearly had terminated a statary period at the time it was discovered.

Colony B-V (*E. burchelli*) was found at 11:40 a. m. on March 29 on Ocelot Hill about 350 meters to the southeast of station 8 on the Shannon trail. The colony formed an elongated cluster wrapped around the trunk of a small tree, its bottom clearing the ground by about one meter. The ants were staging a large raid. Distributed through the bivouac walls and interior was a brood of alate males estimated to contain not more than 1,000 individuals, and an immense brood of nearly mature worker larvae. That evening the colony moved about 150 meters to occupy a site in the upper interior of a small hollow tree. On the following day the ants staged a large raid, but their bivouac-change movement that night had to go unobserved and the colony "escaped." Since some spinning had been observed in the essentially mature larval worker brood, it is probable that the colony became statary on March 30 or 31. Two broods: a brood of alate males, evidently reduced to a few hundred by previous departures, and an immense brood of nearly mature larval workers. The colony was nomadic, but evidently about to enter a statary phase.

Colony H-L (*E. hamatum*) was found at 9:40 a. m. on April 9, bivouacked about 50 meters to the south of the cut-off trail between Wheeler 14 and Armour 3. A large 3-system raid was in progress. The bivouac,

a cylindrical cluster formed against a buttressed tree root, contained many hundreds of recently emerged alate males (but no male cocoons), and an immense brood of very young worker larvae massed in a few boluses in the very center of the cluster of ants. (The queen was found in the contracted condition; also, two dealated males were discovered in the cluster.) The colony did not move that night (possibly because of my having thoroughly disrupted the bivouac); however, after a large 3-system raid on April 10, a bivouac-change movement over more than 250 meters occurred in the evening. The colony evidently was in the early stages of a nomadic period. Two broods: a newly emerged brood of callow alate males estimated at 2,000 individuals, and an immense brood of very young worker larvae.

Colony H-M (*E. hamatum*) was discovered at 10:00 a. m. on April 10 about 75 meters to the north of Armour 2. A large 3-system raid was in progress, distinctly separated from the raiding system of colony H-L. In the bivouac, an irregular mass under low vines, there were found hundreds of alate males and a brood of many thousands of very young worker larvae. Despite the separation of raiding trails, this colony and H-L may have been divided from the same colony within the days just preceding, a possibility supported by the similar status of their two broods and by their presence in the same area. Two broods: hundreds of alate males, and a large brood of very young worker larvae.

Colony B-IV (*E. burchelli*) was found on March 6 at 10:15 a. m., bivouacked 150 meters southeast of Barbour 3, and raiding vigorously to the northward. The large irregular bivouac cluster, massed beneath some vines, contained hundreds of alate males and a huge brood of half-matured worker larvae. On each of the following days until March 11 this colony carried out large daily raids and successive nightly movements. On the night of March 8 one dealated male was seen in the bivouac-change column, moving along under his own power closely followed by groups of workers. In each of the nightly movements the column was crowded with alate males, and numerous males were observed in take-off flights from the vicinity of the bivouac. On the night of March 11 a dealated male was seen in the column within a few meters of the old bivouac, running toward the cluster with numerous workers clinging to his gaster. On the night of March 12, when the colony moved into a hollow tree near Wheeler 2, which was to be its statary bivouac for the next 21 days, it was estimated that perhaps 300 alate males remained. (At that time the mature larval worker brood was spinning cocoons.) On March 22, when the colony was etherized and the bivouac ransacked (to check the time of egg-laying in the queen) no winged males were seen. On April 1 the first signs of cocoon-opening were noted, and on the evening of April 3, with the greatest part of

the new worker brood removed from cocoons, the colony moved off. No males were seen in this movement; very probably none remained. Three broods: a callow alate male brood; then a huge worker brood; and a further brood of worker larvae.

Colony B-VI (*E. burchelli*) was found on March 31 at 4:30 p. m., bivouacked under some heaped-up branches in the lower part of Lutz Creek. An extensive raid was in progress at the time. When the bivouac cluster was opened a considerable number of alate males (estimated at more than 500 individuals) was found, together with an immense brood of nearly mature worker larvae. In the latter brood numerous indications of spinning activity were observed. When the bivouac-change movement was well under way at 10:00 p. m., alate males were numerous in the procession. Considerably before the termination of the movement a queen (contracted) was observed in the column. In this movement the colony passed to a clustering site high in a large fig tree between Snyder-Molino 2 and Pearson 2, where it entered a stately phase. Thus there was no opportunity to check the departures of the remaining males. On the night of April 20 when the colony again became nomadic, an immense brood of newly emerged callow workers was seen, but no males were observed in the bivouac-change column. Two broods: the remnant of an alate male brood; and an immense brood of workers.

*General summary of male production.* This evidence from shorter studies of *burchelli* and *hamatum* colonies corroborates the results of the extensive survey of colony B-I in every important respect. The males appear in distinct lots of that sex alone, and at given points in the regular Eciton brood-production cycle, when worker broods might otherwise appear. Thus the male larvae of a given brood exhibit a limited size range at any given time and pass through the respective phases of their development closely in step with one another so that all eventually emerge from their cocoons as callow individuals within a short period of a few days. In other words, a given male brood appears to have essentially the same time relations with the worker brood which preceded it and the one which follows it as would a worker brood under ordinary conditions (cf. Schneirla, 1938, 1944). We have reported three cases (colonies B-I, B-II and H-J) in which male broods were preceded by worker broods, and it may also be noted that in colonies B-I and B-II the male brood was followed by a brood of workers as was the case in colonies B-III, B-IV, B-V, B-VI, H-L and H-M. The conclusion seems inescapable that the eggs of a given male brood must be laid by a single functional queen in each colony, and that this queen delivers a male brood after having produced one or more worker broods. These facts raise some interesting questions for the student of insect genetics.

There is a striking difference between male broods and worker broods, in that while

our single batches of developing worker forms are all very large with a population of probably more than 20,000 individuals in each, the male broods are all relatively small and number close to 3,000 individuals each. However, rough calculations (based on the relative bulks of preserved material) suggest that we should not be surprised to find the total "tissue bulk" of a male brood at maturity closely approaching or even exceeding that of a worker brood at maturity. The reader should be reminded here that none of the investigated male broods were sampled in the egg or earliest larval condition<sup>5</sup>, so that the number of potential males could be compared with the number of potential workers in respective newly delivered broods.

The chief reason for this hiatus in our evidence is readily understood when the complex but regular relationships between brood-production phases and the stately-nomadic changes in colony behavior (Schneirla, 1944) are recalled. The eggs of a new brood are produced when the colony is roughly one-third through a stately phase, at a time when the bivouacs are located in relatively inaccessible places such as hollow trees or logs, all too easily passed by since the raids then generally are small and in the dry season frequently are absent (Schneirla, 1947). Even when a stately bivouac is located, one must go to the heart of the bivouac to sample the eggs or young brood concentrated there, a procedure which for instance was out of the question when the male brood of our record colony B-I was in the earliest developmental phase. To obtain such material a concentrated collecting procedure will be essential, directed at the sampling of brood populations rather than at the gathering of normative behavior data.

#### *Behavior and Behavioral Relationships of Males.*

*Activities of the male brood considered as a colony energizing factor.* When the male larvae are still very small they are packed into boluses in the very center of the bivouac cluster, much as are worker larvae at comparable early stages. This is certainly true of the stately bivouac in which they begin their life, and also of the earliest part of the ensuing nomadic period, except for the time each night when the brood is scattered about in small packets through the new bivouac after having been transported over the bivouac-change trail.

There is no reason to believe that when very young the male larval brood is an important factor in raising the general colony excitation threshold to the level of large raids which can pass over at nightfall into the bivouac-change process. Thus when colony B-I took to the march on February 28, it was presumably a sharp rise in tactuo-chemical stimulation from the immense brood of cal-

<sup>5</sup> However, an eventual cytological examination of other preserved brood samples in very early stages may bring further male broods to light.

low workers circulating through the community which set off the new behavior developments, rather than stimulation from the small male larvae then packed into a few centrally-located masses. Hypothetically, we may believe that the stimulative role of the male larvae increases rapidly in keeping with their rapid growth rate in the nomadic period (cf. Text-figure 1), so that they take over the principal excitatory function after that of the callow brood has lapsed somewhat.

In this connection it appears significant that the fourth and fifth raids of colony B-I (March 3 and 4) were noticeably smaller than the three first raids of the nomadic period which began on February 28, and that the distance of the nightly bivouac-change movements was considerably reduced as compared with the preceding ones. The movement of March 2 carried over only 30 meters, that of March 3 over 19 meters, and on the night of March 4 the colony shifted its bivouac only 8 meters, as compared with movements of 110 and 75 meters on the first two nights respectively. It is probable that the noticeable decline in the vigor of raids and in the extent of nomadic movements at this time was based upon a reduction of effective stimulation from the broods. We have suggested previously (Schneirla, 1944) that the stimulative effect exerted by new callows drops off sharply within the few days after their emergence. At that time a very young larval male brood (relatively small as it is in numbers) may be still rather weak in energizing the colony, although both of these brood factors may act together in keeping the colony above the statory level of activity.

For the remainder of the nomadic period during which the B-I male larvae were growing rapidly, the daily raids were large and all of the nightly bivouac-change movements were relatively lengthy affairs carrying over more than 100 meters of ground. Then, as we have seen, the colony became statory on the day when most of the mature larvae had become enclosed. It remained statory with small daily raids or no raids on given days, until identifiable reflex activities of the enclosed but nearly mature male pupae occurred. Then the daily raids became increasingly extensive and vigorous, and the colony became nomadic at the time when the major part of the male brood had emerged as callows.

This is the same type of coincidence of brood condition and colony behavior which we have identified when worker broods are present in *Eciton* colonies. It indicates that male broods have much the same trophalactic (i. e., social-stimulative) relationship and colony-energizing function as have worker broods. A consideration of the general behavior evidence concerning males further supports this view.

*Responses of workers to the male larvae.* When they are very young, the male larvae are gathered together into a few packets generally kept near the center of the bivouac.

These boluses of larvae thereby are somewhat isolated from the workers of the general colony, although they are the scene of much activity on the part of the diminutive workers minor. The minima not only crowd upon the external surface of the massed larvae, but also push into the interior through narrow galleries among the larvae. Presumably, as with young worker broods, the workers minor are more or less consistently occupied with licking the tiny larvae of the young brood and palpating them with antennae. Presumably also, at some time before the colony leaves its statory bivouac (e. g., before February 28 in colony B-I), larval feeding also begins. Although direct evidence upon these early events is very scanty at the present time as far as male broods are concerned, the state of affairs probably is similar to that previously observed with young larval worker broods.

We have some direct observational evidence for the colony relations of male larval broods after the colony takes to the march, when there is a much more rapid increase in body size than with worker larvae and a proportionately rapid increase in the scope and vigor of larval activities. The almost incessant twisting and squirming movements of the larvae, which are increased noticeably as workers touch them antennally or run across them, act in turn to increase the activities of the workers. The result is that, as these stimulative relationships increase to the point of involving workers through the intermediate types, the workers frequently pick up the larvae and hold them individually, or carry them about. As the brood advances in development, it is thereby more widely distributed through the bivouac cluster. This change obviously increases the stimulative scope of the brood, and as with worker broods, that development is related causally to wide increases in the extra-bivouac activities of the colony (cf. Schneirla, 1938).

Thus it seems that a male larval brood enters into trophalactic relations with the adult membership of the colony which serve to increase colony "drive" much as does the stimulative effect of a worker brood. The fact that the population of a male brood in species of *Eciton* (*Eciton*) contains only about one-tenth as many individuals as do worker broods is not contradictory on this score. To resolve the difficulty it is only necessary to consider that, at comparable growth stages, the body size of any male larva in the nearly homogeneous brood is many times that of the median size larvae in a worker brood. Accordingly, we should expect that the stimulative effect of each male larva (both in tactual effects through movements and chemostimulative effects through cuticular secretions) would be much greater than that exerted by worker larvae with their much smaller size, strength, and body area. From our observations, such is undoubtedly the case. For instance, while in the bivouac even the largest worker larva generally is

held by no more than one or two workers, it is not uncommon to see a bulky male larva held in place by a dozen or more workers. Based upon such differences, interesting variations appear in certain extra-bivouac activities when a male brood in a fairly advanced larval stage is present.

*Behavior involved in the nomadic transfer of a larval male brood.* The transportation of a young larval worker brood by a nomadic colony occasions no particular difficulties, since the tiny larvae are carried in small packets by individual workers, and in the night-time hours following the movements are gathered together into the center of the new bivouac. When the worker larvae are larger and even when they are nearing maturity and are close to maximal size, they are carried readily by individual workers, each larva slung beneath the body of a carrier, the anterior segments of the larva gripped in the mandibles of the carrier. Little difficulty is involved except in starting out from the old bivouac, when a single larva often is gripped by numerous workers pulling against one another. This often happens when a worker has grasped a larva much too large for it to carry in straight-forward progress, and a circuitous tugging results which attracts other workers to the scene. Usually as a result of these tussles one of the larger intermediate workers large enough to deal with the burden finally keeps possession of the larva, and notwithstanding her load moves unobstructedly ahead as a member of the column. Even in the absence of quantitative data it is safe to say that in the Eciton bivouac-change column there exists a direct relationship between bulk of burden and size of the worker carrying it.<sup>6</sup>

Difficulties due to excessively bulky burdens do not occur in the first few nomadic movements of a colony with an early brood of male larvae. In fact, despite a vigilant observation of the first three bivouac-changes of colony B-1 when its male larval brood was small, the brood escaped my notice and was first sampled from the bivouac on the fourth day. The observation of an increasingly striking set of events in the eighth and ninth movements of the period on the nights of March 7 and 8 first brought out some notable differences between the transportation of larval worker and of larval male broods.

In the early stages of the bivouac-change movement lugging of the bulky male larvae from the bivouac begins when each larva becomes the center of much worker activity. A very circuitous, hit and miss process then is involved in getting a larva into carriage on the trail. At first the unwieldy object is pulled around haphazardly in different directions near the bivouac by numerous workers tugging at it, so that it is yanked and

dragged on and off the trail repeatedly. There is much bumping and colliding of bodies moving variously at "cross purposes," in a hectic time-consuming process. In the course of this largely random activity, more and more workers come to mill about with increasing numbers of larvae at the trail-base close to the bivouac. Added to the difficulty of somehow attaining a coordination of worker activities in carrying individual larvae, many special interferences are presented by an irregular terrain complicated by leaves, brush and tangled vines. But gradually, in the course of two or more hours as the bivouac-change movement gets under way, a development arises from the tussle and struggle which in the end helps to resolve the whole difficulty very nicely.

In the yanking and pulling about of larvae by groups of workers, by degrees more and more of the workers drop out of the activity and huddle or stretch out motionless on the spot where a summation of swarming-under or rough treatment occurs. By small steps and very slowly a layer of clustered ants thereby forms over the trail itself and at the sides of the trail near the bivouac. Over this "ant roadway" other workers run and pull larvae about, incidentally smoothing the substratum further by forcing protruding parts of the cluster to shift position. Of course the roadway is not of uniform thickness, since the ants cluster most readily at the edges of leaf obstacles and at terrain depressions and similar points of obstruction where the greatest amount of pellmell struggle and bumping about of bodies is certain to occur.

The early stages of this complicated process must be observed in detail and in sequence, if one is to appreciate just what causes workers to form the "roadway." Watching individual workers in the push, we note that the elements of the roadway are recruited from among those individuals that are repeatedly buffeted and overrun within limited intervals of time. Once they are out of general activity, such workers lie motionless except for a vibration of antennae, stretched in place by catching with their tarsal hooks into objects such as leaf edges or the projecting body parts (generally legs) of other workers. Workers may thus lie in place immobilized for hours as the procession rushes over them. Evidently a repetition of tactual stimulation is essential to keep the workers immobilized in the pavement of bodies. For as the column gets under way and side eddies of traffic cease to pass over ants clustered at places away from the main line or in remote depressions where larvae happened to roll in the early struggle, workers in such isolated clusters presently begin to stir, disengage themselves, and run off.

The roadway of clustered workers is widest close to the bivouac and progressively narrower in trail sections farther out. An even more striking reminder that the roadway arises indirectly out of difficulties in

<sup>6</sup> Lutz (1929) reported essentially the same conclusion for the carrying of leaf-segments by workers of *Atta cephalotes*. The average load under the conditions of Lutz's survey was roughly five milligrams more than twice the weight of the carrier.

transporting bulky objects over rough ground, is the fact that it is started at the old bivouac site and laid down progressively over the trail toward the new site. In the outermost stretches of trail (e. g., more than 75-100 meters from the old bivouac) the band is thin and narrow or even absent, except where irregularities and obstructions in the route such as upturned leaves have produced serious interferences with the transportation of larvae. When a male larval brood nears maturity and occasions the greatest difficulties in transportation, the roadway is most likely to be clearly formed as a meandering ribbon of clustered workers extending perhaps the entire distance from old to new bivouac sites. The adaptive significance of the roadway, as a relatively even surface over which the huge male larvae can be moved to the new clustering site, does not require much emphasis here.

The indirect manner in which the ant roadway comes about is further revealed by observations upon changes in the carrying of larvae. In some respects the changes are similar to those involved in the transportation of worker larvae as first described above. The building of the roadway is the result of hours of laborious changes during which a directionalized column arises. To indicate how the shift from inefficiency to efficiency occurs in larva-carrying, for the sake of clarity it is best to choose a time after the drift from the old bivouac is fairly well under way. Then each male larva is dragged from the bivouac by several workers of nearly all sizes except majors, clutching and tugging at it on all sides. In the course of much thrashing about with the burden most of these are shuffled off and rolled underfoot, to furnish a source of recruits for the roadway. Finally, as a rule only two of the larger intermediate workers retain their holds and carry the larva in the direction of general movement. Characteristically they run in tandem with the larva slung beneath their bodies, straddling it with their legs, one clutching the burden in her mandibles at the anterior segments while the other catches hold behind the midsection. Relatively immature male larvae may be transported in other ways as well, and in carrying these the smaller workers may participate all of the way; however, with bulky, advanced larvae there is least variation in the size of burden-bearers since smaller workers are largely eliminated during the initial tussle. Although both early and late in the movement difficulties such as those described occur at the start of the journey, once the eventual carriers are under way with their burden on a fairly well-formed "roadway," they make surprisingly good headway and there is a minimum of stoppage. The occurrence of the roadway, typical of bivouac-change movements when advanced male larvae (but generally not worker larvae) are transported, is an expression of the high stimulative effect which the maturing and bulky males, individually and collectively,

exert upon the worker membership of the colony.

*Behavior associated with enclosure and pupation of the male brood.* Colonies of *E. burchelli* and *E. hamatum* cease nomadic movements when their male larval broods mature and become enclosed, and remain stately until the colony's male brood has completed its pupation. In these respects the results for case B-I coincide with data from numerous other colonies of both species.

The spinning of cocoons by male larvae resembles in general outline the process as described by Beebe (1919) and by Schneirla (1934) for *Eciton* worker broods. The difference is that all phases of the process occur in a much more striking way when male larvae are involved. Some of the highlights from the B-I record will stand as representative.

The last nomadic nest of colony B-I, when its male brood was at maturity, was established in a shallow mammal burrow. Larval spinning must have occurred during this day (3/9/46) since many of the larvae picked out from the bivouac-change column of the same night were provided with thin envelopes. Later that night scattered instances of spinning were observed on the interior floor of the large hollow tree into which the colony passed. However, the bivouac cluster was formed within the cavity of the tree just above the wide opening at its base, and most of the spinning evidently occurred in the upper spaces. Much of the time during the first three stately days (March 10-12) the cavity walls and the ground both within and immediately around the tree were covered with throngs of milling ants. Both day and night, occasional concentrations of workers were observed around larvae which had been lugged to the floor of the cavity where spinning took place on a carpet of wood dust. Evidently the enclosure of only a minor part of the male brood was begun in this way, judging by the number of similar groups observed by flash-light in activity around the bivouac, and by a constant downward drifting of fine wood detritus through the air. This fall continued for about five days, until there had accumulated on the broad floor of the cavity a wide conical heap of finely divided woody material more than 15 cm. deep in one or two places.

Some notes on events in colony B-I typify the details of behavior. "On the floor of the tree hollow (6:15 p. m., March 12) here and there are groups of a dozen or more workers gathered around one of the large larvae, touching it at intervals with antennae and mouth parts as its anterior end twists about in spinning, and tugging at it intermittently. Each larva is the center of much commotion, particularly when the joint tugging of numerous workers shifts or rolls it about on the gently sloping sides of the wood-dust mound. Other similar groups can be seen stationed at intervals on the nearly vertical back interior wall of the tree, with a variable number of workers holding fast to each larva

engaged in spinning. This number often grows into a sizable mass of squirming bodies around a larva which (through its own movements or because of a flurry among the ants) happens to slip momentarily from the mandibles of workers which have been holding it in place."

None of the larvae thus engaged in spinning outside the bivouac were enclosed by more than thin transparent envelopes, whereas after March 11 the bivouac contained a rapidly growing number of larvae with heavier and translucent brownish cases. The inference is that the early stages of enclosure take place outside the bivouac, whereas once the envelope is started it may be completed while the larva is held within the mass of ants in the bivouac cluster itself. The ants seem to drag out only naked larvae or larvae in the early stages of spinning.

When spinning is completed, colony activity decreases markedly. For example, on March 14 practically all of the B-I brood was enclosed in brown cases, and no spinning was observed outside the bivouac. At 8:30 a. m. a few hundred ants were running about over the floor of the cavity, and there were two or three columns which extended only a meter or two outside the tree. No raiding system was formed on this day; only a limited raiding system formed on March 15, and there was none on March 16. Judged in terms of amount of activity outside the bivouac, particularly the frequency and the size of raids, the general activity of the colony fell to a low point after the larval brood was enclosed. It is significant that although daily raids occurred during the first four days of the statory period, in which brood-enclosure evidently was completed, no raids developed and colony activity was minimal on the three following days. Activity in B-I remained at a relatively low ebb, with no raids occurring on half of the days, through the central part of the statory period until March 26. This was the quiescent period of pupation in the male brood.

Thereafter raids occurred daily, increasing in vigor, until on March 30 a recognizable nomadic condition arose. The increase in colony activity appeared coincidentally with certain new brood developments. On March 27 there were reflex movements of antennae and tarsi, as well as general trunk contractions in some of the pupae, readily perceptible to the naked eye. A few empty male pupa cases were found below the bivouac on that day. The number was considerably greater on March 29, when cocoon-opening by workers was found. This process is similar to that previously described for the delivery of a worker brood (Schneirla, 1934, 1938). The difference is that each male cocoon is the center of a far greater commotion as it is held by struggling workers stationed in the bivouac structure.

As is the case with worker broods, the colony begins its nomadic movements when the major part of the mature pupal brood has emerged. Also, as with worker broods,

a critical species difference appears in that in the first movement of *burchelli* colonies a considerable part of the brood (nearing one-third in given instances) may be carried along in column in unopened cases, whereas in *hamatum* colonies the unemerged increment is much smaller or even absent. Hence in the first *burchelli* movements one may observe numbers of bulky male cocoons carried along in a bivouac-change column which is thronged by newly emerged callow males.

*Behavior of callow males and colony responses to them.* We have set forth the principal facts with respect to the behavior relations of callow males to the colony, in records condensed in an earlier section of this paper. Within the period of about three weeks required for the complete discharge of a male brood from its parent colony, only after dusk do the callow males appear outside the bivouac. In the daytime the males hang in the cluster, among the workers, but in the hours after nightfall they may be seen in small numbers as a rule running about close to the bivouac. Each of them is attended by a small group of workers which follow him closely as he runs about circuitously and erratically, a few of them clinging to his wings and gaster, others riding upon him. From time to time a relatively free male may take short hopping runs, flit his wings nervously and even leave the ground in short flights, frequently after having mounted a stalk or vine. At intervals, as the night advances, the males take off in flight from low vegetation. Although one gets the impression that the worker "hangers-on" impede the flight escape of males, it is possible that males sometimes fly off carrying workers with them. A few such escapes were observed in the present study.

As a rule, not many of the callow males leave the bivouac until the workers have begun their regular exodus in the bivouac-change movement. Then the alates take their exit from the cluster among the workers, each of them followed rather closely in the procession by a group of workers. Clumsy behavior in beginning the movement is typical of males, with frequent stops and returns occurring before they get under way in the column from the bivouac. During traffic interruptions which are occasioned by such behavior, males with their worker retinues may separate from the column and enter the zone around the bivouac where males are skipping and flitting about more or less independently.

Once they are under way in the regular bivouac-change columns, the alate males move along under their own power, at a regular pace and with closed wings. One gets the impression, from watching the movements of a given colony evening after evening, that the trail-running of males undergoes an improvement in the course of time in that after a few nights progress seems to be more regular than at first and there are fewer returns and interruptions. The

males often run in single file with workers; often males run together in file. The clinging and crowding workers generally retard the pace of the alates somewhat, and the path is blocked variously (by the slowness of other males in particular), so that colonies with alate male broods sometimes require the entire night and perhaps the early daylight hours as well to complete their movements.

When the new bivouac cluster is reached, most of the alates stream directly into it with the workers. It is the first males to reach the new site, before the cluster has been well started, that may get away from the main group of workers and run about in the vicinity. Some take-off flights may result.

*Events after departure from colony of origin.* Our findings show that after a brood of perhaps 3,000 winged males has emerged, these alates leave the parent colony by flying. However, in the colonies for which emergence of callow alates was observed, no escapes were recorded on the first three or four nights after the cases were removed. Then, a given number of males takes off nightly by flying away in the course of excitatory activity in the vicinity of the bivouac, until in the course of about three weeks after emergence most or all of the winged males have left the bivouac of origin.

Direct observations show that *Eciton* males are capable of strong maintained flight once they are under way, so that with the assistance of air currents some of them must get several hundred meters if not greater distances from the parent colony. From early February of 1946 at Barro Colorado the winged males of various *Eciton* (*Labidus*) and *E. (Neivamyrmex)* species were taken nearly every night at the laboratory lights and often on the white reflecting board at the laboratory clearing, as well as in the small light trap set at various places within the forest. The alates of these groups also were taken occasionally by hand when attracted at night to the reflector of the 5-cell headlamp which I used in the forest. However, our study concerns male-production in the species of *Eciton* (*Eciton*) particularly, and for some reason the alates of species in this subgenus were almost never taken at lights in these ways. The exceptions occurred when I worked with a light within the area around a colony from which alates were known to be issuing at the time.

Special field and laboratory tests show that the males are able to follow the chemical trails of their own colony or another colony of their species. Alate males ordinarily do not leave the bivouac of their colony in the daytime. On the other hand dealate males

TABLE II.

Dealate males of *Eciton* (*Eciton*) species found on Barro Colorado I. during the period February—June of 1946.

Date of capture	Colony and species	Time of day	Locality and general circumstances	Alates present in the colony	No. taken
March 3	B-I <i>E. burchelli</i>	8:00 p.m.	Running in bivouac-change column with workers, en route toward new bivouac	None; only males in early larval stage	7
March 4	B-I <i>E. burchelli</i>	9:00 p.m.	Running with workers in bivouac-change column	None; only males in early larval stage	3
March 8	B-IV <i>E. burchelli</i>	7:40 p.m.	Approaching old bivouac in column of workers	Remnants of alate brood present	1
March 11	B-IV <i>E. burchelli</i>	9:00 p.m.	Approaching new bivouac in column of workers during bivouac-change	Remnants of alate brood present	1
March 27	H-B <i>E. hamatum</i>	10:45 a.m.	Moving with workers in column a few cm. from the bivouac	No male brood produced by H-B	1
April 6	B-I <i>E. burchelli</i>	8:40 p.m.	Running toward the old bivouac in column of workers	Own alates present in bivouac	1
April 9	H-L <i>E. hamatum</i>	10:00 a.m.	Captured from central part of colony bivouac cluster	Newly emerged alates present	1
April 12	H-H <i>E. hamatum</i>	10:15 a.m.	Captured from central part of colony bivouac cluster	No male brood produced by H-H	2
May 5	B-I <i>E. burchelli</i>	10:30 p.m.	Taken from bivouac-change column en route toward new bivouac	Few if any alates remain from own male brood	1
May 13	H-B <i>E. hamatum</i>	7:45 p.m.	Standing among workers on log close to bivouac, among larvae (cocoon-spinning)	No male brood produced by H-B	1

have been taken on occasion in the present study and by others (Wheeler, 1912; Reichensperger, 1926), running about on the raiding trails of their species in the daytime. Appropriate tests show that after their flight males are accepted into groups of workers of their own or other colonies of their species. It is probable that the chief means of getting into some colony after the flight is through the following of a chemical trail which is crossed accidentally as the scattered males run about over the forest floor.

Although we have little direct evidence on what happens to alate males once they leave the parent colony on their flights, from certain facts the general nature of events may be suggested. In the first place, laboratory tests indicate that a considerable amount of flying leads to loss of the wings within a few hours, hence our attention turns to occurrences involving dealate males.

Table II shows that dealate males were discovered in association with Eciton colonies on ten different occasions in this study. In five of these instances (B-I, March 3; B-I, March 4; H-B, March 27; H-H, April 12; and H-B, May 13), the dealates clearly must have originated in another colony of the species. For example, a limited number of dealates was found in the bivouac-change columns of colony B-I on two successive evenings at a time considerably before the male brood of this colony had even completed the larval stage, but at a time when a *burchelli* colony with alate males was known to be located in bivouac relatively close by. On the night of March 3 seven dealate *burchelli* males were captured while running at intervals of a few meters apart in the B-I column. Obviously these males must have come from some other *burchelli* colony, since at the time the male brood of colony B-I was in its early larval stage. The most likely source was another *burchelli* colony with a large brood of escaping alate males which at the time was bivouacked only about 350 meters from the location of colony B-I. On the following night, when the colonies were still no more than 450 meters apart, three additional dealate males were found in the B-I column. Subsequently these colonies moved divergently, and no further dealates were observed in colony B-I until May 5. The capture of dealate males from two different *hamatum* colonies (H-B, on March 27 and May 13; H-H, on April 12) took place when no alates were present and only worker broods had been produced. In four of the cases (B-IV, March 8; B-IV, March 11; B-I, April 6; and H-L, April 9) the dealate individuals were found at times when alate males produced by the same colony were also present, and may have been returned males of the same brood. The case of colony B-I on May 5 is more doubtful. Although a few survivors of the alate male brood may have been present at the time, none had been seen during the preceding week. Our cases divide nearly equally into those in which the dealate males must have come from another colony of the spe-

cies, and those in which they may have originated in the colony in which they were taken. Although, in some instances males evidently return to their own colonies after the flight, the surprising thing is that so few dealates were found in colonies known to contain alates. Evidently post-flight returns into the colony of origin are exceptional.<sup>7</sup>

As Table II shows, dealate males were taken in this study both in bivouac-change columns at night and in raiding columns in the daytime (and under the latter condition also by Wheeler, 1912, and by Reichensperger, 1926). There is no evidence that dealate males leave the bivouac of the host colony in the daytime to run the raiding trails, and it seems more probable that instances of dealates on raiding trails involve newly dealated individuals that have encountered the chemical routes of a colony after alighting but have not yet entered its bivouac. Some of our night-time captures of dealates on bivouac-change trails may similarly involve newly alighted individuals; however, it is also very likely that in others of these instances the males were running in the movement after having spent one or more days in the host colony. The case of the males found in the B-I column on the nights of March 3 and 4, as the circumstances described above suggest, seems the clearest instance of probable night entrance into a column. Other facts suggest that such entrances may occur either by night or by day, when stray males chance upon and follow trails.

As mentioned above, our laboratory and field tests show that males of *E. burchelli* and *E. hamatum* are capable of following the chemical trails of their own colony or another colony of their species. For instance, on numerous occasions dealate males were placed close to a circular column formed in the laboratory by workers of a strange colony of their species. In virtually all cases the male finally entered the column more or less readily after chancing upon the trail, and soon was running on the endless route among the workers, although typically with a clumsiness that contrasted notably with the typical stereotyped precision of the ordinary workers. For their part the workers generally accept any stray dealates one may present from other colonies, on occasion nipping at the newcomer for a time, but generally indicating in their behavior that he exercises a considerable chemo-receptive attractive effect upon them. When the new male is set down experimentally at a raiding trail in the field, as a rule he is taken into column by the workers. Typically they are soon clustered around him and, when he eventually moves off on the trail, he has an entourage of closely following workers some of whom cling to his body or even ride upon him. The attractive effect of Eciton males upon work-

<sup>7</sup> The latter type of case very probably appears with misrepresentative frequency in our records, since colonies with male broods were examined more frequently in detail than were others.

ers resembles that of the queen (Schneirla, 1944), with the difference that the latter appears to be definitely more powerful.

#### SUMMARY AND DISCUSSION.

It is clear that in the area of this study and for the *Eciton* species investigated, the production of males is limited to the dry season. In studies on Barro Colorado Island confined to the rainy season (Schneirla, 1933, 1938, 1944) only worker forms have been found in *Eciton* broods, but in the dry season of 1946 male broods at all stages were discovered in colonies of the same species (*E. hamatum* and *E. burchelli*). Moreover, there appears to be a species difference in susceptibility to whatever conditions account for male-production. In our records for the 1946 dry season male broods appeared roughly one month earlier in colonies of *E. burchelli* than in colonies of *E. hamatum*.<sup>8</sup> This difference may be added provisionally to other differences previously described in the raiding, bivouacking and general behavior of these two species of subgenus *Eciton* (*Eciton*).

The discovery of immature male *Eciton* broods has been reported in three instances from other localities. The first of these is not strictly comparable to our results, since it concerned a species of the hypogaecic subgenus *Neivamyrmex* (= *Acamatus*). The engineer Hubrich sent to Carlos Bruch (1924) specimens of advanced male pupae of *E. (Neiv.) hetschkoi* taken at the end of July (in "winter") 1924 in the Sierra Alta Gracia of northern Argentina. Numerous enclosed male pupae approximately 13 mm. in length were found in the bivouac cluster, which was beneath a large tree trunk. This finding, together with various discoveries of mature male broods to be noted below, suggests that in *Neivamyrmex* species also the males appear in distinctive broods of their own sex alone.

The first discovery of a developing male brood in any species of *Eciton* (*Eciton*) was reported by Wheeler (1921). The find was made at the Kartabo station in British Guiana on July 17, 1920, at the end of a short semiannual wet period. A colony of *E. burchelli* which Drs. Wheeler and Emerson drove with smoke from its bivouac in a hollow tree was found to have a brood of a few hundred mature male pupae in cocoons. A brood of male pupae somewhat less advanced than in the above instance was found by Schneirla (1947) during early April of 1945 in a colony of *E. hamatum* in the area of the upper Coatzacoalcas R. in southern Mexico. The conditions in this case were similar to those of our 1946 Panama records given in the present paper, in that a brood of more than 1,000 pupae was found during the latter half of a well-marked annual dry season,

in a colony which was definitely "statory" at the time. A further resemblance is found in the fact that in the Kartabo and S. Mexico cases a large brood of very young (evidently worker) larvae was present in addition to the male pupal brood, a relationship of broods which holds uniformly in our 1946 Panama records.

The present study involved the investigation of particular colonies of *E. hamatum* and *E. burchelli* over considerable intervals of time while male broods were undergoing their development. The results from the respective instances, which represent all stages of male development, indicate that a given male brood appears at a predictable time in the colony brood-production process, that is, occurs in a definite temporal relation to preceding and following (worker) broods. Thus the present results for male broods fit the timing of the *Eciton* reproductive process as previously described for the rainy season (Schneirla, 1944). Our results indicate the prevalence of a pattern of events which is adequately represented by the case of *E. burchelli* colony B-I. Numerous other evidence given above supports this fully investigated case in showing that the eggs of a male brood must be laid (in both our test species) in the first part of a statory period when an enclosed brood of worker forms entering pupation is present, and that when this male brood enters its pre-pupal phase during the next statory period of the colony, a huge new brood of (worker) eggs is then laid by the queen.

The expression "the queen" is used advisedly here, since from our results it is evident that the eggs of an all-male brood must be laid by the single functional dichthadiigyne responsible for the delivery of the large worker broods which precede and follow the males in a given colony. Our results invariably indicate a high degree of regularity in the time relationships of male and worker broods found in particular colonies, without any evidence that more than one functional queen is present in a given case.<sup>9</sup>

There is one report in the literature which suggests that conditions in other *Eciton* subgenera may be similar to those evidently prevalent in species of *Eciton* (*Eciton*). That is the discovery of a large colony of *E. (Lab.) praedator* by Luederwaldt (1918) on October 23, 1916, bivouacked in an old termite nest in a garden at São Paulo, Brazil. This colony possessed a brood of enclosed worker pupae, as well as numerous empty cocoons about 20 mm. in length from which males were thought to have emerged. Furthermore, the queen was physogastric at the time and masses of newly laid eggs were found—a set of circumstances suggesting a regular succession of broods, with one of them evidently a male brood.

<sup>8</sup> It is well known that seasonal production of males as well as females is common among the other subfamilies of ants. Characteristic differences in the time of year at which fertile forms are produced have been described by Talbot (1945) for four temperate-zone species representing two ant subfamilies.

<sup>9</sup> In a subsequent paper the conditions under which a second queen was found in colony B-I will be reported. Various reliable circumstances made it clear that she was not the functional queen of this colony but a new supernumerary dichthadiigyne.

Our findings on the male broods in species of *Eciton* (*Eciton*) indicate that such broods contain only male individuals. They also suggest that very possibly no colony has more than one such brood in a given season and that otherwise worker broods are produced.<sup>10</sup> It is also quite probable that some of the colonies produce no males whatever. At any rate we have the record of colony H-B (*E. hamatum*) which produced four large worker broods but no male broods during the 1946 dry season. In this survey more than fifty colonies of *Eciton* (*Eciton*) species were studied for intervals of a few days or for longer intervals, yet indications of male-production were found in but eleven of these cases. Although the possible errors of sampling were much greater when *Ecitons* were searched for in five different localities of southern Mexico in the dry season of 1945 (Schneirla, 1947), it is worth repeating here that only one of more than 20 *Eciton* (*Eciton*) colonies then studied had a male brood at the time. The Panama results suggest that very few if any colonies of this subgenus have more than one male brood per season.

From our evidence the influence of a male brood upon colony behavior is very similar to that which we have described for worker broods (Schneirla, 1944). As with worker broods, the energizing or "drive" function of a male brood is introduced and is removed in an essentially all-or-none fashion, in dependence upon the growth stage reached by the brood. Clearly the basis of this factor is the capacity of the queen to complete laying the eggs of a given male brood within a few days, so that the entire brood passes through the successive stages of development in step. Consequently, at any given time all individuals in the male brood exert similar effects upon the general colony.

We have found that when male broods appear in *Eciton* (*Eciton*) colonies there are no important interruptions or differences in the nomadic-statory cycle of colony behavior, which occurs substantially as when worker broods are present. Colonies with fairly advanced broods of male larvae are found in the nomadic condition, staging large daily raids that terminate each night in a bivouac-change movement of the entire colony. As with worker broods, the colony shifts from nomadic to statory behavior precisely at the time when its male brood has completed larval development and is spinning cocoons. Then later, when the enclosed male brood has completed its pupation, a further nomadic period begins with the emergence of the callow males from their cocoons.

The occurrence of male broods evidently does not disturb the timing of nomadic-statory phases in any important way, since we have found no identifiable differences in the duration of the phases and in the total developmental time of male and of worker broods. We have inferred that the inclusive

developmental period of a male brood requires about 45 days, and have found in the case of three *burchelli* colonies that the males spend close to 21 days of this time enclosed in cocoons, just as do worker broods. From the routine facts alone, as concerns the intensity of daily raids and the occurrence or non-occurrence of night-time movements, it would be difficult to tell which type of brood, male or worker, was present.

As we have suggested above, the basis of the concomitant changes in male brood and colony behavior is found, as with worker broods, in the trophallactic relationships of workers and brood (Wheeler, 1928; Schneirla, 1941). Our field observations and specific laboratory studies show that male larvae stimulate the workers both tactually and chemically, and thereby exert a distinctive energizing effect upon the workers. We have found "nomadic" colonies somewhat sluggish when their male larvae are still small, and have interpreted this condition as an insufficiency of the energizing effect of a male larval brood to maintain colony activity at its peak early in the nomadic period, at the time when the stimulative effect of a callow worker brood (which initiated the period) has waned. The stimulative effect of the male larvae soon increases greatly in keeping with a rapid advance in their size and activities, a change which evidently provides the essential basis for a marked rise in general colony activity. In the daytime the large larvae are spread well throughout the bivouac, each held by a group of workers as the center of a rather extensive zone of stimulation in the cluster. And at night in the colony movement, the bustle and complexity of events in the transportation of the bulky larvae emphasize the great stimulative effect which the brood exerts upon the colony. One outstanding event that is peculiar to the relations of the male brood to worker behavior is the formation of the "ant roadway." We find that although a male brood is roughly only one-tenth as numerous as a typical worker brood, after early development its total stimulative effect appears to equal or even exceed that of a worker brood at corresponding stages.

There is no support in *Eciton* behavior for the assumption of Brauns (1901) and others that doryline colonies must remain in place while breeding the sexual forms because it is impossible to transport the large larvae of these forms. We have ample evidence that *Eciton* colonies are able to carry along the male larvae nightly in bivouac-change movements so long as these larvae are immature and unenclosed, even when the larvae are maximal in size and very unhandy to lug along in column. The eventual stoppage of colony movements when the male larval brood is mature depends upon quite different causes than mere bulkiness of the brood.

The manner in which *Eciton* colonies drop to minimal activity once their male broods are enclosed contrasts strongly with the

<sup>10</sup> The circumstances of queen-production are unknown at the present time.

crescendo which occurs in colony activity as the maturing pupae begin their reflex stirring within cocoons. These activities arouse the workers to a mounting pitch of activity within and outside the bivouac, which eventuates in the shucking of callow males from their cases and the transition of the colony into a new nomadic phase. It is during this period of about two weeks that most of the few thousand males leave the colony. This concurrence of events has a particular adaptive value, as we shall see.

The exodus of winged doryline males from their nests has been reported in numerous instances in the literature. For Old World dorylines, Brauns (1901) reported the notes of G. A. Marshall on a colony of *Dorylus* observed in Rhodesia (Africa). In this case, large numbers of alate males emerged from the extensive subterranean excavations of the colony, with the workers evidently driving out the males or even pulling them from the nest. In India, Wroughton (1892) saw the workers of *Aenictus wroughtoni* on two successive days apparently driving winged males from the nest of the colony beneath a verandah floor. Santschi (1908) discovered beneath a dye-shop oven in Tunis a large *Typhlopone fulvus* nest from which hundreds of males took flight in the late afternoon on six consecutive days.

The previous *Eciton* observations are relatively few, and are limited to the hypogaecic species. A number of winged males was found by Hetschko (Mayr, 1886) in the subterranean galleries of an *E. (Acam.) hetschkoi* nest excavated by him at Paraná, Brazil. Wheeler (1900) reported witnessing the exit of males in numbers from a nest of *E. (Acam.) schmitti* in dry soil, near Austin, Texas. In the Sierra de la Ventana of Argentina on February 16, 1916, Bruch (1916) saw numerous male individuals erupting one evening from a nest of *E. (Acam.) strobeli* under the foundation of a building. In a colony of *E. (Acam.) spagazzinii* found in a comparable situation at Bella Vista, Argentina, by Gallardo (1915) in April, 1914, eight days after a group of about 50 winged males had been dug out from one part of the nest the workers opened a second exit between stones, from which numerous males presently emerged and flew off. Workers of this species were observed in the same locality in February of 1917, 1918 and 1919, but appeared to be without males; however, in December of 1916 an exodus of males was observed from an *E. (Acam.) spagazzinii* nest in another section of Buenos Aires province (Gallardo, 1920).

These observations support the conclusion that males of the hypogaecic subgenus *Acamatus* (= *Neivamyrmex*) develop in specific broods which emerge from their cocoons within limited periods of time, as do those of *Eciton (Eciton)* species. Smith (1927) concluded, that since alate *Neivamyrmex* males were taken by Wheeler in Texas during October of different years, and since he himself received specimens from the mid-

dle South captured in mid-November, "the males do not reach maturity until late in the season." We may suspect that the males of these species characteristically develop seasonally and leave the parent colony in considerable numbers at given times.

Doryline males of certain species are readily taken at lights in the tropics at given times of year. Vosseler (1905) reported the impression that the males of African species swarm to lights in numbers at times when major changes in humidity occur. Wheeler and Long (1901) reported that the males of *E. (Acam.) schmitti* fly to lights during the spring and early summer in Texas; later Wheeler (1913) noted that males of *E. (Lab.) coecum* are common about lights in the Austin area from early March to late in April. Males of *E. (Acam.) carolinense* were taken by W. Davis in Georgia in June, 1908 (Wheeler, 1921). Von Ihering (1912), who kept a colony of *E. (Lab.) coecum* under observation for about four months while it occupied the same site, stated that in Brazil flights of *Eciton* males generally come in midsummer, particularly in the months of December to February. Also, he noted that the annual flights varied; for example, whereas large numbers of males representing at least six species were taken at lights in the year 1910-1911, the results were sparse the following year. As noted by Gallardo (1920), the males of *E. (Acam.) strobeli* are frequently seen in the Argentine around house lights during the spring and summer, where Strobel (Mayr, 1886) took them in numbers during the summer months of December to February. Sumichrast (1868) reported capturing numerous *Eciton* males at lights during the first rains, in the Cordoba area of Vera Cruz in Mexico. At the lights of the Kartabo Laboratory in British Guiana, Wheeler (1921) took a few males of different *Eciton* species each night between July 26 and August 31, 1920. Of 41 alate male specimens, two were identified as *E. burchelli* males, and 39 were attributed to a colony of *Cheliomyrmex nortoni* nesting close behind the laboratory building.

It will be noted that with the exception of Wheeler's capture of two *E. burchelli* males in British Guiana, all of these reports concern *Labidus* and *Acamatus* species. The difference cannot be attributed to chance, for at Barro Colorado Island during the spring months of 1946 males of the hypogaecic species were commonly taken at the lights of the laboratory, a few dozen meters from the forest edge, and at light traps within the forest itself, whereas no males of the *Eciton (Eciton)* species were taken at the laboratory and few were taken at forest light traps. The difference may be due in part to typical habitat differences among the subgenera, perhaps to unknown differences in flight (e. g., range) and responses (e. g., to light) of the males.

The present study has furnished some direct evidence concerning the manner in which alate *Eciton* males are dispersed from

their parent colonies. The alates ordinarily remain within the bivouac during the day, emerging only after nightfall. One important factor as laboratory tests show is their withdrawal from very bright light. The males of *Eciton* (*Eciton*) species have large compound eyes as well as dorsal ocelli, and reactions to light may play more than one rôle in their behavior.

The departure flights of males, once they begin, always occur after nightfall. However, very few flights are to be observed within the first nights after a given brood has emerged. Possibly after emergence there are certain maturational processes which must run their course before the flight can occur, comparable to those reported by Snodgrass (1925) for the drone honeybee. In addition there are certain extrinsic circumstances which appear to operate in favor of a certain detention of *Eciton* males in their colony of origin.

We have seen that, within the first nights after the main part of a male brood has emerged from cocoons, the alates begin to appear outside the bivouac in limited numbers. A few of them at a given time may be seen in action on the surface close to the bivouac, alternately engaged in short spurts of running or (more frequently on further nights) in bursts of wasplike wing-vibration and in clumsy short flights. The way in which each active male is closely followed and actually gripped by workers may serve as a deterrent to premature departure flights. Another factor which would appear to retard the depletion of a brood of alate males is their involvement in the bivouac-change exodus. Most of them, when they leave the bivouac, pass almost at once into a directionalized stream of workers, and once in the column they make their way more or less directly to the new home site. Seldom are they free to run or flit about and to mount low vegetation (that is, to enter the pre-flight condition) except on rare occasions as when a major traffic interruption occurs (e. g., crossing of the route by a night-raiding hypogaecic *Eciton*). The new bivouac is entered directly by most of them, with little opportunity to stray.

The result is that probably not more than a few dozen or at most a few hundreds of the alates leave the colony on a given night, and hence the male brood is not entirely gone until three weeks or perhaps a longer time after its emergence from cocoons. Hence our findings confirm the hypothesis of M. R. Smith (1942) that *Eciton* males do not remain long in the parental bivouacs after emerging as callows. Since they fly off in greater numbers on moonlight nights, it may be that the males are all away sooner when a brood emerges during a period of full moon. The fact that male broods leave the colony in nightly lots inevitably increases the chances that at least a few of the males may get into colonies of their own species. Within a period of three weeks it is reasonably certain that any "loaded" colony will

come within male-flight range of one or more conspecific colonies.

Preliminary ground activity appears to be prerequisite to flight. Much excited running about and intermittent bursts of wing action are regular preliminaries to the take-off flight of *Eciton* males. In the case of any given male such behavior may last as long as thirty minutes before he actually flies away. We have mentioned the possibility that the retinue of workers may function incidentally to prevent premature flights. The existence of an organic build-up process of given duration is suggested by the fact that, up to the moment of actual departure, there appears to be little actual flying other than occasional short hopping flights.

Evidently, the take-off generally involves a clear departure from the vicinity of the home colony. Some of our results indicate that the flights carry over distances of at least a few hundred meters from the parent colony. Thus it may be possible for an *Eciton* colony to distribute males widely through a fairly large area around each bivouac site occupied during the period when nightly flights are being made by males. The process of dispersion must be assisted considerably by the influence of air currents and wind. Furthermore, the area which can be "seeded" with males from a given colony is greatly augmented through the fact that from the time the male alates first emerge their colony is nomadic, i. e., through about 12 days in *E. burchelli* and 17 days in *E. hamatum*. This of course means that each night finds the colony in a new focus of distribution relatively distant from the preceding site. These positive factors operate against numerous hazards of the flight which must tend to reduce greatly the chances that any given male will survive and eventually reach a scene of possible reproductive function. For, as we shall see, flight (or its equivalent) and dealation appear to be prerequisites for sexual response and function in *Eciton* males.

In view of the fact that a male *Eciton* brood probably contains a minimum of two or three thousand individuals as a rule, and that dozens or even hundreds of alates may leave a loaded colony on a given night, we are impressed by the rarity with which dealate males are observed in association with colonies. In contrast to the great frequency with which *Eciton* males (of hypogaecic species) are taken at lights, a survey of the doryline literature shows that dealate males are found only exceptionally.

The first discovery of this kind on record occurred in western Africa near the Gaboon R., in April of 1847, when Savage (1849) observed a few large insects later identified as dealated males of *Dorylus nigricans*, running back and forth in the columns of a colony of this species. These dealates were able to return and were readily accepted by the workers when displaced from the route. The first *Eciton* male dependably referred to its species was a male with only remnants of wings taken by W. Müller (1886) on

March 1, 1885, from a column of *E. burchelli*. The ants evidently were engaged in a bivouac-change movement in which the male was participating, for Müller noted that his find was partially running and partially nudged along by workers. On October 21, 1905, K. Fiebrig took a single dealate male from a column (also evidently migratory) of *E. (Lab.) praedator* in San Bernardino, Paraguay (Forel, 1906). Reichen-sperger (1926) reported a "developed" male and single queen of *E. (E.) mattogrossensis* sent to him in 1924 from Monte Alegre, Pará, after having been captured from the nest of the same colony. The finder, P. Cherubim Mones O. F. M., judged that a migration was in progress at the time. On November 29, 1911, Wheeler (1912) took two winged males of *E. (E.) vagans* near San Jose, Costa Rica, in a column of workers. Since these last males were taken in the daytime and evidently from raiding columns, presumably they were recent post-flight individuals. From a long file of *E. (Acam.) pilosum beebei* at Kartabo, British Guiana, in July of 1920 Beebe took two partially dealated males, and a little later on the same day Wheeler (1921) removed two additional males from the same column in which they "were being conducted along by the workers." Smith (1942) reported that D. E. Read found three dealate males in a nest of *E. (Acam.) carolinense* which was excavated in the vicinity of Spartanburg, S. Car.

My own experiences, based upon a concerted searching of Eciton bivouacs, further suggest that very few Eciton males reach colonies after their flights. In the first place, their seasonal occurrence is indicated by the fact that despite countless chances for discovery, only one dealate male has come to light during four rainy season surveys.<sup>11</sup> Further, in more than twenty Eciton colonies which were examined by me in southern Mexico during several months of the regular dry season of 1945, only one dealate male was found in any of the bivouacs. This male was found on May 1, 1945, in the midst of a mainly subterranean *E. hamatum* bivouac in a dry forest in northeastern Oaxaca (Schneirla, 1947). Relatively few dealate males were found in the present study.

It seems very probable that under ordinary conditions most of the few thousand alates in a given Eciton male brood are lost through the flight, and that only a small handful of them succeeds in getting into colonies. The possibility must also be considered that some of those which reach colonies of their species may be killed by work-

ers when first encountered on raiding trails or in other ways may have their span of life cut short after entering the bivouacs. It is probable that the greatest part of the male output is lost after landing from the flight, through the action of hazards such as predators, exposure and desiccation.

It is apparent from our evidence that very few of the males re-enter their own parental colonies, confirming the surmise of Gallardo (1920) that the flight operates against inbreeding and in favor of cross-fertilization.

Evidently the males can get into other colonies only by chance after their flight through happening to cross chemical trails in the course of their running about. Observations and appropriate tests show that Eciton males can follow the chemical trails of other colonies of their species. Hence, among those males that survive for any length of time after the flight, the ones that happen to encounter a chemical trail of their own species while wandering about on the ground may thereby reach a bivouac. (This wandering process is of course inferentially inserted here, since Eciton males have not been captured, either as alates or dealates, on the ground except with columns of workers or in bivouacs.) The process of such trail discovery, if it actually occurs, must be highly fortuitous. For example, the trail would have to be crossed near a bivouac or the male might get lost in its ramifications, must be a recent one or it might be too faint to be followed, and so on. Casualties must be numerous.

It should be noted that the ability of males to follow chemical routes thus encountered may be the outcome of a habituation to their own colony (and species) chemical during their initial stay of some days in the parent bivouacs. Also these chemical stimuli have been followed when the colony bivouac-change routes are travelled by the male callows during nightly bivouac-change movements. Furthermore, the pre-flight stay of males in their parent bivouacs may operate to insure the adequate impregnation of cuticular surfaces with the species chemical, thereby increasing the chances that in possible post-flight arrival at the trails of other colonies they will not be attacked by the foraging workers.

Since the males retain their wings through a rather lengthy stay in their parent colony, and since we find them without wings relatively soon after the flight, it would appear that through the flight itself physiological changes are set up which lead to dealation. The process may resemble the characteristic post-flight dealation of queens which prevails widely among most species in ant subfamilies other than the dorylines. The matter deserves special study.

It may be that the flight is essential for the occurrence of mating behavior and reproductive function in the Eciton male. The Ecitons exhibit the predominant tendency among ants for a full male flight under ordinary natural conditions.<sup>12</sup> However, at

<sup>11</sup> On June 13, 1932, in the early weeks of the rainy period, a single dealate male was found running in a column of *E. hamatum* workers. The male was in the last section of a bivouac-change movement which had been delayed by rain and was completed shortly after the find, at 9:00 a.m. He ran under his own power, although occasionally the workers which crowded closely around and after him nipped and tugged at his legs when he paused or started to reverse directions. This was the only dealate male observed in three periods on Barro Colorado Island in the early months of rain, when, presumably, dealate males might still be present in some of the colonies.

present we do not know whether under any conditions the males may go flightless without impeding their eventual fertility. In the present investigation a few tests of preliminary nature were made in which alate Eciton males were found not especially responsive to queens. But on the other hand in just two opportunities to test the behavior of dealates placed together with queens, coupling occurred within a period of minutes. Gallardo (1920) considered it unlikely for hypothetical reasons that fertilization may be carried out by Eciton males that have not made their flight. He observed that males of *E. (Lab.) praedator* taken at lights by E. Caride had the genital organs completely distended, a condition noted also by the present writer in the case of *E. (Lab.) coecum* males taken around lights at Barro Colorado in May of 1933. It is barely possible that the flight itself may set up physiological changes prerequisite to mating, as Goetsch (1933) has suggested for termites. However, in certain termites Grassé (1942) has obtained dealation and successful mating through isolation without benefit of any flight, and C. P. Haskins (personal communication) has obtained comparable results with the alates of certain ponerine ant species.

By and large, male flight appears to be the rule among the Ecitons, presumably insuring a predominance of cross-fertilization of apterous young queens in foreign colonies. However, we must reserve the possibility that on occasion short flights or the activity-equivalent of flight may permit a return into the parental colony, and subsequent inbreeding.

Finally, let us consider whether our findings cast any light on the problem of when, how, and by what individual or individuals the male eggs are produced. The last question would seem to have priority. If the Dzierzon rule holds for Ecitons as it holds widely among other social insects (Phillips, 1915; Snodgrass, 1925), then army-ant males arise from unfertilized eggs which might be laid by workers or by a regular queen. Of course workers as possible male-producers cannot be excluded without good reason, since production of males from worker eggs has been demonstrated in numerous species of bees (Plath, 1922; Snodgrass, 1925), is known to be common among ant species particularly when colonies are old and well-fed (Fielde, 1905; Emery, 1918; Wheeler, 1928; Weyer, 1929), and is even believed by Verlaine (1926) to be virtually the rule among social insects. In fact, Haskins and Enzmann (1945) have reported evidence that in certain ponerine species not only males but also females may arise

from impatentate worker eggs. Worker ants of many species are known to possess ovarioles (Bickford, 1895; Holliday, 1904), although in virtually all investigated cases workers have fewer than in the queen. Mukerji (1933) discovered ovaries in two of twelve workers of the Old World species *Dorylus (Alaopone) orientalis* examined by him, with indications that one of these workers might have been capable of producing eggs. At present evidence is lacking that the workers of New World doryline species may be functional. The anatomical evidence is meagre and negative, since Miss Holliday found no evidence of ovarioles in several workers of *E. (Acam.) schmitti* which she studied histologically.

The findings reported in this paper flatly oppose the possibility that in *Eciton (Eciton)* species male broods result from worker eggs. These broods number in the few thousands, and in our experience always appear as distinct all-male broods in which all individuals are approximately of the same age. There are far too many eggs in such broods, far too similar in time of production, to be conceivably the product of workers. A sporadic egg-production in small lots but not in precise broods, would be expected of workers. Moreover, such broods are always found to be exactly synchronized with other (worker) broods just as would be expected were the egg-laying cycle of a single colony queen responsible for all (Schneirla, 1944). In many laboratory observations of *hamatum* and *burchelli* workers in lots varying from a few dozens to a few hundreds, housed in artificial nests and given all possible care as to food and moisture in particular, the writer has found no evidence that eggs were ever laid. Contrary to the state of affairs existing rather widely among other ants, it is exceedingly doubtful that Eciton workers play any direct role in species genetics by functioning as reproductives.

We have concluded that Eciton male-production is a seasonally-conditioned process, limited (at least in the area and under the conditions of this study) to the dry season. From our previous evidence (Schneirla, 1944; 1947), the Eciton colony queen at regular intervals throughout the year produces huge batches of inseminated (i. e., functionally diploid) eggs, resulting in successive large worker broods through the rainy season and most of the dry season. In the present investigation we have found that during the early part of the dry season there arises somehow as a regular delivery episode in the given queen's cycle a much smaller batch (and probably only one) of male-producing eggs.<sup>13</sup>

On the Dzierzon rule these eggs which produce males are presumably unfertilized, functionally haploid eggs. What can account for this seasonally-conditioned and time-limited change in the queen's function? It might be thought that these eggs are laid

<sup>12</sup> Whether or not a flight is indispensable, pre-nuptial flying evidently occurs in the males of all ant subfamilies, except for the minority of species in which the male lacks wings (e.g., certain species of *Ponera* and *Cardiocondyla*—Wheeler, 1913). Thus the males went aloft in all four of the myrmecine and camponotine species investigated by Talbot (1945). In these same species female flight also appeared to precede mating, although it was limited mainly to wing action on the ground in the bulky females of *Prenolepis imparis*.

<sup>13</sup> How young queens are produced in Eciton colonies is unknown at present.

by old queens whose sperm supply is exhausted. Male-production by old queens is known to occur in honeybees, and Goetsch (1939) has reported it for certain ants. However, it is very doubtful that this can be the regular mode of male-production in the Ecitons. We have found several male broods in *E. burchelli* and *hamatum* which were followed (and some of them known to have been preceded) by regularly-spaced worker broods. Although the writer has a little (unpublished) evidence for the possible referentialization of functional colony queens in *E. hamatum*, there is no good reason to believe that such events occur widely as sequels to an annual exhaustion of sperm accounting for male broods. In the absence of direct evidence, it seems wiser to hypothecate a temporary process of blocked insemination of eggs by virtue of seasonal and time-limited causes.

The possibility that at given times the effective fertilization of eggs by sperm is prevented temporarily through a reflex-physiological change in the queen has been made plausible by the recent studies of Flanders (1946) on the honeybee and by earlier work on other insects. Flanders finds significant evidence justifying the idea long known as the "Wagner theory" (cf. Phillips, 1915, p. 188). In the queen honeybee it is probable that under certain conditions of extrinsic stimulation (e. g., small comb cells) the sperm valve may open, permitting the release of sperm from the spermatheca and the fertilization of eggs; whereas under other stimulative conditions (large cells; old comb) the valve remains closed and unfertilized male eggs are laid. In the fertile females of other insects, equivalent stimulative conditions may control fertilization in a corresponding manner (see Flanders, 1939). The seasonal production of males with species differences in the timing is an occurrence widely present among ants (Talbot, 1945), and male-producing eggs are commonly laid in the autumn by honeybee queens (Vandel, 1930). Insects in general are known to be rather delicately affected metabolically by changes in environmental conditions such as prevalent temperature and humidity (Uvarov, 1931; Chapman, 1931; Buxton, 1932; Himmer, 1932; Mellanby, 1935). Their reproductive processes are known to be affected by ecological conditions (Alpatov, 1932; Wigglesworth, 1934). Since, as Ezikow (1926) and others (Wheeler, 1913) have shown, the ovaries of queen ants react in a fairly sensitive manner to the prevailing metabolic condition of the individual, it is conceivable that a delicately adjusted process such as that which must underlie the impressive egg-production rhythm of the Eciton queen might be affected temporarily by an abrupt change in general conditions. A reasonable hypothesis would appear to be that seasonally the Eciton queen is so influenced by the first impact of dry-season conditions that the fertilization process is temporarily blocked. Despite the occurrence of a vertical

shifting of Eciton bivouac sites in dry terrain (Schneirla, 1947) which may act as a partial buffer for the queen against non-optimal atmospheric conditions, it is possible that a time lag may exist in the queen's readjustment to these or related seasonal changes (such as available water in food,—Buxton, 1932) sufficient to account for a temporary inhibition of insemination. While these considerations may seem reasonable, they must be regarded as highly tentative in the absence of direct evidence concerning the ecological relationships of Eciton reproductive processes.

#### RÉSUMÉ AND CONCLUSIONS.

Males of the two investigated species of *Eciton* (*Eciton*) appear during the first half of the regular dry season, in distinctive broods of about 3,000 individuals each. Male-production in the 1946 season began a few weeks earlier in *E. burchelli* than in *E. hamatum*.

The production of one male brood per colony in a given season appears to be the rule, with some colonies having none. Results indicate that the male brood is the progeny of the regular colony queen, since it appears that the all-male brood of a given colony generally arises as a regularly synchronized episode in the reproductive cycle, spaced between worker broods.

It is suggested that the impact of dry-season conditions operates to inhibit the insemination process of the queen completely so that a batch of male-producing unfertilized eggs is laid before a readjustment to dry-season conditions somehow occurs.

Results show that a male brood has trophalactic stimulative relationships with workers comparable to those ordinarily exerted by a worker brood. Once larval development is well under way, the energizing effect of a male brood is comparable to that exerted by a worker brood roughly ten times its population size. Since male developmental phases are largely the same as those of worker broods, the appearance of male broods occasions no substantial modification of the (nomad-statory) cycle of colony behavior changes.

The complete dissemination of alate males from the parental colony begins a few nights after emergence and ordinarily requires about three weeks for its completion. The alates escape in nightly lots, which perhaps are larger on moonlight nights than at other times. The expenditure of a given brood of alates in flight may be retarded both through the behavior of workers and through participation of males in bivouac-change movements.

The male flight operates largely in favor of cross-breeding of colonies, although inbreeding evidently is not excluded. The "seeding" of males from a given colony is widened greatly in scope by the fact that (in the species studied and probably also in others) colonies are nomadic for a number of days after the alates emerge.

Most of the alate males evidently are lost through the flight, and few reach a situation of possible reproductive function. It is suggested that upon landing after the flight, males generally get into other colonies through chancing upon and following the chemical trails established in the daily colony raids. The pre-flight stay of alates in their parental colonies may operate to prepare them for this process, by habituating them to species chemical as in trail-following, and by insuring the saturation of their cuticle with species chemical. Thus acceptance of males into other colonies of their species may be facilitated through the chemically conditioned responses of workers to them much as to nestmates rather than as to booty.

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## EXPLANATION OF THE PLATE

## PLATE I.

Representative growth stages in males of  
*Eciton burchelli*.

- Fig. 1. Larvae from the brood of colony B-I, taken at four-day intervals (cf. Text-fig. 1). Left, sample of March 2 (range of lengths, 5.6-6.6 mm.); middle, March 6 (range of lengths, 18.3-20.4 mm.); right, March 10, at larval maturity (range of lengths 22-24.8 mm.).
- Fig. 2. Post-larval male specimens from the brood of colony B-I. Left, pre-pupa of March 14, removed from cocoon; middle, pupa of March 25, removed from cocoon; right, enclosed pupa of March 25.
- Fig. 3. Mature males of *E. burchelli*. Left, alate post-flight males, preserved a few minutes after flight in laboratory cage; right, dealate males, preserved several hours after laboratory flight and loss of wings.

All specimens twice natural size.

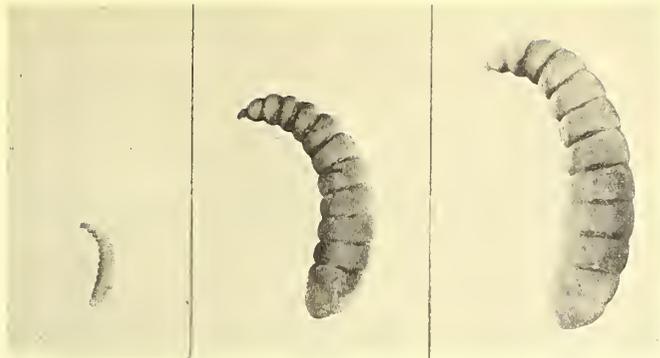


FIG. 1.



FIG. 2.



FIG. 3.

ARMY-ANT LIFE AND BEHAVIOR UNDER DRY-SEASON CONDITIONS WITH SPECIAL REFERENCE TO REPRODUCTIVE FUNCTIONS. II. THE APPEARANCE AND FATE OF THE MALES.



## 6.

Notes on the Display of the  
Three-wattled Bell-bird (*Procnias tricarunculata*).

LEE S. CRANDALL.

(Plate I).

When Charles Cordier, Staff Collector for the New York Zoological Society, arrived at the Zoological Park from Costa Rica on August 31, 1947, he brought with him three specimens of the Three-wattled Bell-bird (*Procnias tricarunculata*). It is believed that these were the first representatives of the species to be seen alive outside their native habitat, which includes the mountains of Nicaragua, Costa Rica and Panama.

The trio consisted of an adult male with chestnut body and white head and throat, an immature male in mottled green plumage, its back slightly blotched with chestnut, and an adult female. The adult male, unfortunately, escaped soon after arrival but the younger bird remained available for observation. In writing of this particular bird<sup>1</sup>, Cordier states that he was calling regularly at the time of his capture in mid-May, 1947. After being placed in a flight cage at the Zoological Park in September, 1947, he quickly resumed his demonstrations. At this time, although calling was frequent, there was no noticeable enlargement of the wattles, the three appendages remaining black and shrunken. The nasal wattle was about  $\frac{3}{4}$ " in total length, the basal  $\frac{1}{4}$ " being approximately  $\frac{1}{8}$ " in diameter, the distal  $\frac{1}{2}$ " about  $\frac{1}{16}$ " in diameter. When in this condition, the slightly thickened basal  $\frac{1}{4}$ " was faintly erectile. The lateral wattles were estimated to be 1" in length and  $\frac{1}{16}$ " in diameter, each with two or three sharply angular kinks.

In January, 1948, it was noted that there was some extension of the wattles when the bird was calling. This enlargement increased gradually, reaching a maximum about May 1, when the following notes were made. Certain plumage changes had occurred by this time, the chocolate of the upper parts having increased, the head having become thickly mottled with white and the throat almost entirely white, with a strong wash of yellow.

The bird begins its display by bringing its body into a stiffly horizontal position, held high on the legs, much as in *P. nudicollis*. The mouth is opened widely, until the lower

mandible approximates a right angle to the upper. The wattles remain shrunken. The body is then pumped rapidly up and down for about five seconds. This movement then ceases and with the body, legs and wings rigid, a violent convulsion of the throat and neck is followed by the sharp, metallic "bell" sound. Frequently, but not invariably, this initial effort is followed by a series of five or six lesser ones, in regularly decreasing volume.

Pumping and calling may alternate continuously for periods of an hour or even longer. As calling continues, the wattles gradually enlarge until, after several efforts, the maximum is reached. At this point, the following dimensions were estimated: nasal, length  $3\frac{1}{4}$ ", diameter,  $\frac{1}{4}$ "; laterals, 3", diameter,  $\frac{3}{16}$ ". All wattles are completely sessile at the maximum and move from side to side as though weighted, when the convulsive calls are given.

At this stage, the display is frequently preceded by head shaking and experimental opening of the mouth. This seems to be related to the position of the heavy nasal wattle, which causes the bird obvious annoyance. It may fall at either side and frequently drops within the widely opened mouth, which sometimes closes upon it.

While several efforts are required before the wattles reach their maximum, any sudden disturbance of the bird will cause them to shrink almost instantaneously. If activity is promptly renewed, enlargement takes place visibly, so that the maximum is regained within a few seconds.

During the period under consideration, the female has continued to occupy the same cage. Her general reaction seems to be one of mild alarm, although on several occasions she appeared to be attracted by the dangling wattles. At least once, she was seen to reach out as though to peck at them. This action caused the male to move quickly, with immediate retraction of the wattles.

Often, following several displays, the male darts rapidly at the female, which flies in alarm. No attempt at copulation has been noted.

<sup>1</sup> *Animal Kingdom*, November-December, 1947, pp. 175-6.

## EXPLANATION OF THE PLATE.

## PLATE I.

Photographs by Sam Dunton, Staff Photographer, New York Zoological Park.

Fig. 1. *Procnias tricarunculata*, ♂, sub-adult. Showing wattles in normal resting condition.

Fig. 2. *Procnias tricarunculata*, ♂, sub-adult. Calling position, wattles somewhat less than fully extended.

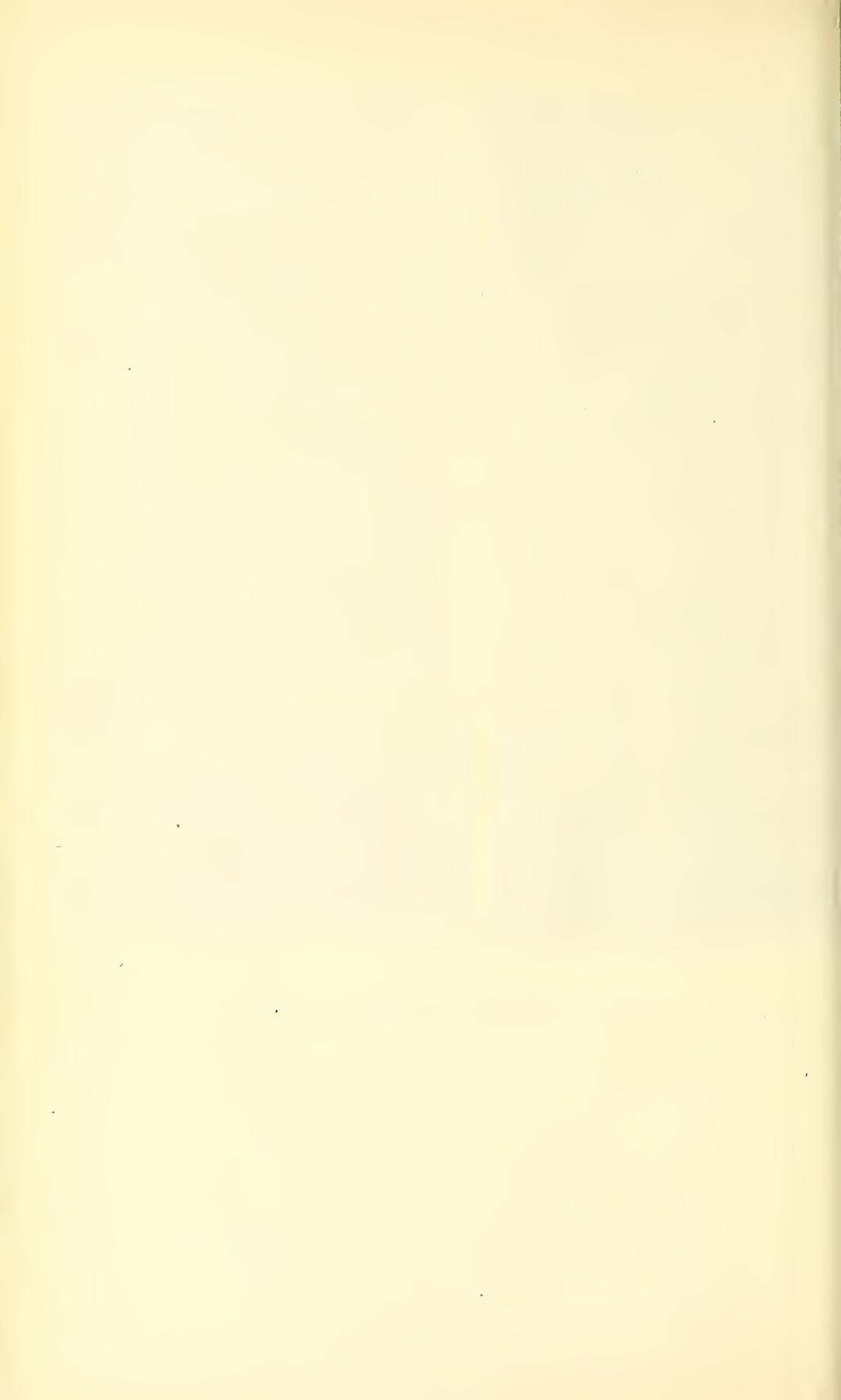


FIG. 1.



FIG. 2.

NOTES ON THE DISPLAY OF THE THREE-WATTLED BELL-BIRD  
(*PROCNIAS TRICARUNCULATA*).



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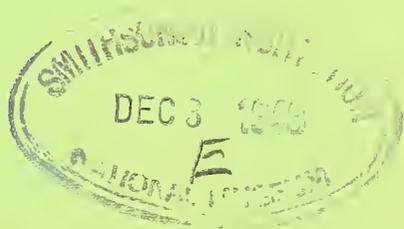
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## 7.

## The Cephalopoda Decapoda of the *Arcturus* Oceanographic Expedition, 1925.<sup>1</sup>

BY THE LATE G. C. ROBSON, M.A.

*Formerly Deputy Keeper, British Museum (Natural History).*  
(Published by permission of the Trustees of the British Museum).

(Text-figures. 1-18).

[This paper is based on the collections taken on the *Arcturus* Oceanographic Expedition to the eastern Pacific in 1925. This, under the direction of William Beebe, was the seventeenth expedition of the department of Tropical Research of the New York Zoological Society. For detailed data on localities, dates, dredges, etc., refer to *Zoologica*, Vol. XXII, No. 2, pp. 33-46].

### PREFACE.

This report was prepared by the late G. C. Robson in 1932 but his last illness prevented the paper from being completed. His successors, Mr. G. I. Crawford and Dr. W. J. Rees, have made a few minor corrections, prepared a list of species and a revised bibliography, but it has been deemed advisable to leave the text as written by the author.

The paper is of considerable interest as it deals with a hitherto little-known cephalopod fauna and also presents the views of an acknowledged authority on the status of many important genera of squids.

An appreciation and a full list of Robson's cephalopod researches by Dr. W. Adam of Brussels has been published in the *Proceeding of the Malacological Society of London*, Vol. 27, pp. 131-136, 1946.

N. B. KINNEAR,  
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### INTRODUCTION.

The decapod cephalopods collected by Dr. Beebe during the spring and early summer cruises of the *Arcturus* in 1925 were examined by Mr. J. F. W. Pearson and made the subject of a preliminary report. This was submitted as a thesis for a Degree in the University of Pittsburgh, but was never published. Mr. Pearson was unable to continue his work on the collection and in 1928 Dr. Beebe invited me to complete the study of the material. A copy of Mr. Pearson's thesis was sent to me and I have found it very useful as a preliminary survey. It contained much information concerning the gear used on the *Arcturus*, the stations at which cepha-

lopods were taken, and a general discussion on the research problems involved. Of these sections I have unfortunately not been able to make any use. As regards the systematic work Mr. Pearson evidently considered his identifications very provisional. In spite of the limited time at his disposal, however, and the difficulty he obviously experienced in getting the necessary literature, whenever he ventured on a specific diagnosis his judgment was rarely at fault.

The bulk of the collection consists of juvenile specimens with no associated adult stages, and it has proved quite impossible to determine the generic position of two or three forms. There are also a good number of fragments and badly mangled specimens of which the identification is very dubious.

As regards the juvenile stages of uncertain status, I have given here full particulars in the hope that when such stages are better known in the decapods as a whole, the relationships of these specimens may be understood from my descriptions.

The collection of Decapoda is represented by some 30 species and is therefore an unusually rich one. I have been compelled to describe five new species and a new genus. The majority of the species here described come from the waters near the Galápagos Archipelago and it would have been very interesting to compare this fauna with those of adjacent areas, e.g. the coast of Central America and Colombia and the more remote regions of the Pacific. Unfortunately the lists available for such a study are so meagre in contents that by the time the doubtful identifications have been eliminated, the basis for a reasonable comparison has disappeared. That 16% of the species here mentioned are new, may be a little surprising, but it must be remembered that the cephalopod fauna of the equatorial Pacific is very poorly known. There is another important fact to bear in mind. Many of the species of teuthoid decapods are regarded as cosmopolitan and the chief students of the group (notably Pfeffer), adopting a conservative attitude, have refrained from creating new species out of the obvious variants that turn up from time

<sup>1</sup> Contribution No. 815, Department of Tropical Research, New York Zoological Society.

to time. Perhaps there is some justification for this attitude when the study of a group is in the stage when material is being amassed and before the extent of the variation is fully realized. But at present the assumed genetic homogeneousness of cosmopolitan marine species (seen in other groups as well, e.g. in Copepoda, etc.), if it is not a mere product of taxonomic conservatism, is a challenge to our curiosity. It implies not only that the natural "divides" (such as the Agulhas Divide) in the ocean and the regional changes of temperature and salinity, etc., have no modifying effect on the natural population (which in the case of planktonic forms such as *Liocranchia reinhardti* seems very surprising), but also that such mutations as do arise are readily suppressed and have no effect in producing the local modifications that we see in widely-ranging terrestrial animals. One is bound to view this alleged homogeneity with some suspicion. If it is, however, substantiated, it is a matter of considerable importance. As far as the Cephalopoda are concerned, the statistical analysis of natural populations is still very much limited by the smallness of the catches made, and there is great need for the intensive study of variation in the commoner and more widely ranging species.

My best thanks are due to Dr. Beebe for the opportunity of studying this interesting collection.

#### LIST OF SPECIES OBTAINED

##### Order Decapoda

##### Sub-order Teuthoidea

##### Family Loliginidae

*Septoteuthis occidentalis* Robson  
(?subsp. nov.)

##### Family Bathyteuthidae

*Bathyteuthis abyssicola* Hoyle  
*Bathyteuthis* sp.

##### Family Enoploteuthidae

*Abraliopsis hoylei* (Pfeffer)  
*Abraliopsis* ?*hoylei* (Pfeffer)  
*Abraliopsis* sp.  
*Pyroteuthis giardi* (Fisher)  
Genus and species uncertain.

##### Family Octopodoteuthidae

Genus and species uncertain.  
*Octopodoteuthis nielsenii* n. sp.  
? *Octopodoteuthis* sp.

##### Family Onychoteuthidae

*Onykia* sp.  
*Onykia* ?*appellofi* (Pfeffer)  
*Onychoteuthis* ?*banksi* (Leach)  
Genus and species uncertain (subfam.  
Lycoteuthinae)

##### Family Histiototeuthidae

*Stigmatoteuthis arcturi* n. sp.  
*Histiothauma oceani* n. gen., n. sp.  
Genus and species uncertain.

##### Family Ommatostrephidae

Genus and species uncertain (subfam.  
Illicinae)  
*Stenoteuthis pteropus* (Steenstrup)  
*Stenoteuthis bartrami* (Lesueur)

?*Stenoteuthis* spp. (*Rhyncoteuthion*  
stage)

*Hyaloteuthis pelagica* (Bosc)  
*Symplectoteuthis oulaniensis*  
(Lesson)

Genus and species uncertain.

##### Family Chiroteuthidae

*Chiroteuthis* sp. (*Planctoteuthis*  
stage)

*Mastigoteuthis* sp.  
*Mastigoteuthis* sp.

##### Family Cranchiidae

*Liocranchia reinhardti* Steenstrup  
*Galiteuthis* sp.  
*Taonidium pacificum* n. sp.  
*Helicocranchia beebei* n. sp.  
*Helicocranchia* sp.

#### DESCRIPTIVE SECTION.

##### FAMILY LOLIGINIDAE.

*Septoteuthis occidentalis* Robson  
(? subsp. nov.).

One (♂) from Station 22; 1,000 miles south of Bermuda; (No. 3). Taken in dip-net at night (attracted by electric light). This specimen is rather immature, measuring only 60 mm. in dorsal mantle-length. Its main features resemble my *S. occidentalis* (Robson, 1926), but it tends to draw near to *S. ehrhardti* in the width of the fins (index: *occidentalis* 26, the present specimen 22, *ehrharti* 21). In its mantle-index (38), form of teeth of the tentacular and brachial suckers and shape of the first arms it agrees with *occidentalis* very well and differs from the other western Atlantic species. There is one marked difference, however, viz., the tentacle is like that neither of *occidentalis* nor of *ehrharti*, as it is only slightly longer than the mantle.

I note in this specimen the approximation to double hectocotylization observed in the type of *occidentalis* (Robson, 1926, p. 354, fig. 3). The only difference from the type in the *Arcturus* specimen is that the reduced suckers are continued over rather a wider area in the former.

Since the appearance of my paper on *S. occidentalis*, Boone (1928, p. 16) has revived the ambiguous *S. sloanei* Gray (Leach MS) for specimens obtained in tropical eastern American seas. The type of this West Indian form cannot be found. Boone's well-described form is quite different from my species in fin-proportions, sucker-dentition, etc.

##### FAMILY BATHYTEUTHIDAE.

##### *Bathyteuthis* Hoyle.

I agree with Naef and Grimpe in regarding Hoyle's name (Hoyle, 1885) as having priority over Verrill's *Benthoteuthis* (Verrill, 1885). Hoyle's date of publication was evidently May, 1885. Although the sheet on which Verrill's generic name appears is dated "April, 1885," there seems no escape from the conclusion that the actual publication was in or after the June of that year

(i.e. the date given by the last sheet of the part).

***Bathyteuthis abyssicola* Hoyle.**

1 specimen from Stn. 33; N.E. of Galápagos; PT-1 (No. 86); 600-0 fms.

1 specimen from Stn. 39; Galápagos Is.; PT-1 (No. 109); 500-0 fms.

1 specimen from Stn. 50; S.E. of Galápagos; T-2 (No. 146); 400-0 fms.

1 specimen from Stn. 59; S. of Cocos Id.; T-5 (No. 36); 600-0 fms.

1 specimen from Stn. 59; S. of Cocos Id.; T-5 (No. 35); 600-0 fms.

1 specimen from Stn. 59; S. of Cocos Id.; T-9 (No. 143); 500-0 fms.

1 specimen from Stn. 74; S. of Cocos Id.; T-21 (No. 119); 400-0 fms.

1 specimen from Stn 74; S. of Cocos Id.; OT-2 (No. 38); 750-0 fms.

1 specimen from Stn. 84; Galápagos Is.; PT-4 (No. 89); 400-0 fms.

1 specimen from Stn. 86; Galápagos Is.; T-9 (No. 37); surface.

Nos. 86, 36, 35, and 119 are well-preserved specimens, 22-7 mm. in mantle-length and of normal structure. Of the remaining specimens all are fragmentary or otherwise in poor condition, but I do not hesitate concerning their identity. One specimen (No. 146), which measures 5 mm. in mantle-length, has remarkably small fins. The width of the head, the eyes and the arm-circlet of this example remind one of the form described below. Pfeffer (1912, p. 327) regards all the described forms of *Bathyteuthis* as conspecific. Between the type specimen of *B. abyssicola* (S. Ocean), the original example of Verrill's *Benthoteuthis megalops* (regarded as synonymous) (N. Atlantic), Chun's specimens (Indian Ocean and 36° and 170° E.) and Hoyle's E. Pacific forms (Cape Mala), there are some important differences which are carefully analyzed by Pfeffer. As the matter stands now I have no option but to adopt the latter's treatment of these forms, though I am not entirely satisfied with it.

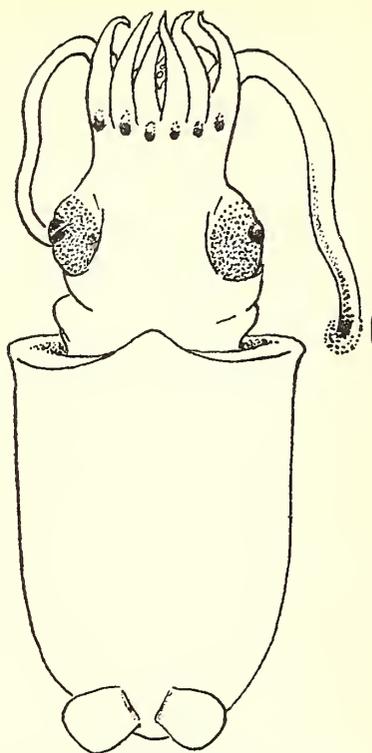
***Bathyteuthis* sp.**

(Text-figure 1).

One specimen (??) from Stn. 84, off Narborough Id., Galápagos Is. Young Fish Trawl; (No. 88); 700-0 fms.

This is represented by a small and juvenile specimen about 7 mm. long in mantle-length; it is in fairly good condition, though the body is a little distorted and the eyes somewhat damaged.

The mantle, which measures 7×5 mm., is much broader than in the equivalent stage of *B. abyssicola* ("megalops") (Chun, 1910, pl. XXIV, fig. 4). The head is narrower than at the corresponding stage of that form, in which the interocular width exceeds the mantle-width and the arm-circlet is distinctly



TEXT-FIG. 1. *Bathyteuthis* sp. from Stn. 84, (No. 88); circa×8.

narrower. One of Hoyle's Cape Mala specimens (1904, p. 33) has a broad body, the width of the latter being about two-thirds of the length. It also has a narrow arm-circlet. This specimen was 23 mm. long in mantle-length. Actually Pfeffer (1912, pl. 27, f. 13) shows a figure of a specimen from the Plankton Expedition with a narrow circlet of arms, but the shape of the body, fins and head in this specimen are very different from that seen in our Galápagos example.

The fins are diminutive, but not noticeably smaller than those of some specimens previously figured. The arms and tentacles and their suckers do not seem to differ from those of *abyssicola*. There is a very marked difference in the cephalic component of the adhesive-organ, which is very narrow in *abyssicola* (Chun, 1910, pl. XXV, fig. 7) and much wider in this form. It must be noted, however, that Chun's figure is of an adult. The tentacular manus is rather more compact than that figured by Chun.

On the whole the features agree fairly well with those of *abyssicola*. But it is impossible to treat a form so different in head- and body-shape and in general proportions as referable to that species. All the same I am unwilling to describe such a young and immature specimen as the type of new species.

Actually from Pfeffer's figures (1912, pl. 27) and Chun's it seems that there is a very great deal of variation within the forms referred to *abyssicola*. It must be noted that

undoubted *abyssicola* of approximately this size (Chun 1910, pl. XXIV, fig. 4) has the large eyes and arm-circlet of the adult.

***Abraliopsis* Joubin.**

Having had no opportunity of seeing original specimens and revising this genus, I refrain from criticizing Pfeffer's treatment (1912) in detail. It seems to me very unsatisfactory, especially as he does not state what the status of the well-figured and fully-described "*A. morisii*" of Chun (1910) is. I feel very uncertain as to the real relationships between *A. hoylei*, *A. morisii* and Hoyle's eastern Pacific "*hoylei*" (= *affinis* Pfeffer). For the time being I confine myself to describing the *Arcturus* specimens and pointing out their relationship to the various forms previously described.

***Abraliopsis hoylei* Pfeffer.**

1 specimen (?♀) from Stn. 51; S. of Galápagos Is.; T-2, (No. 154); 165-0 fms., young, 0.14 mm. long.

1 specimen (♀) from Stn. 61; W. of Cocos Id.; T-5, (No. 170); 600-0 fms., a head only.

1 specimen (♂) from Stn. 68; N. of Cocos Id.; PT. 1, (No. 24); 600-0 fms.

1 specimen (a fragment) from Stn. 68; N. of Cocos Id.; PT 1, (No. 171); 600-0 fms.

1 specimen (♀) from Stn. 74; S. of Cocos Id.; OT-4 (No. 26); 625-0 fms., discolored and without tentacles but apparently referable to this species.

1 specimen (?♀) from Stn. 74; S. of Cocos Id.; T-7 (No. 118); 450-0 fms., damaged.

2 specimens (♀) from Stn. 74; S. of Cocos Id.; (Nos. 30 & 31); 750-0 fms., a head and arm only, a good deal damaged.

The specimens as originally measured ranged from 42 mm. to 5 mm. The body in head and mantle length, and the fins in shape, tend to resemble in shape those of *hoylei* (Pfeffer, 1912, pl. 17) and differ from Chun's "*morisii*." Hoyle's fig. 3, pl. 1, is doubtless badly drawn. The ocular light-organs exactly resemble those of Chun's "*morisii*," as do the tracts on the head. The latter, but not the ocular organs, are like those figured by Hoyle (1904, pl. 10, fig. 1). The tentacular manus resembles that seen in Pfeffer's fig. 9, pl. 17, in having four neat distal rows of suckers. But it has 3 large and 3 small hooks (unlike all the others) and agrees with Chun's fig. 5, pl. VIII, in having five carpal pads and suckers. There is one sucker between the distal and middle small hooks. The structure of the hectocotylus is more or less intermediate between that seen in Hoyle's figure and that illustrated by Chun. There is no large triangular basal lappet as in Hoyle's specimens. The arrangement of the fringe on the ventral side is otherwise very like that figured by Hoyle. Hoyle figures, probably in error, the large hooks as on the ventral side, whereas in our specimen and in Chun's they are on the dorsal side. Both Hoyle and Chun

figure a number of papillae at the base of the hectocotylus; but here I most certainly found a number of small suckers.

I think this is undoubtedly a member of the polymorphic species indicated by Chun, Pfeffer and Hoyle and as such I prefer to use Pfeffer's name *hoylei* rather than that proposed by him for Hoyle's eastern Pacific specimen.

***Abraliopsis ?hoylei* Pfeffer.**

One specimen (♂) from Stn. 74; S. of Cocos Id.; (No. 23); trawl; 0-844 fms.

This is represented by a specimen 25 mm. in dorsal mantle-length. Each fin is 11.5 mm. wide by 18 mm. long (over all). They are thus well over half the mantle-length. The anterior border is convex.

The mantle is slender with some evidence of the aperture having been flared outwards. It measures 10-11 mm. at the aperture and ca. 6 mm. half way along.

The tentacular manus resembles that of Chun's "*morisii*"; but the distal rows of suckers are more numerous and the extremity is thicker and shorter.

The "Seitenbrücke" of the hectocotylized arm which are enclosed in the web are nearly five times as long as the arm is wide and the unenclosed ones are closer than in Chun's figure. Though it is damaged one would say that the hectocotylus resembles that of *hoylei* figured by Hoyle (1904, pl. 8, fig. 5).

The specimen is not very well preserved and I would not care to dogmatize about its position.

The following specimens are indeterminate:

***Abraliopsis* sp.**

1 specimen (?sex) from Stn. 51; S. of Galápagos Is.; T-3, (No. 96); 274-0 fms. A very small specimen devoid of the tentacles.

1 specimen (?♀) from Stn. 74; S. of Cocos Id.; OT2 (No. 32); 750-0 fms. Shrivelled up; unrecognizable.

***Pyroteuthis giardi* (Fischer).**

1 specimen from Stn. 38; Tower Id. Galápagos; PT. 1 (No. 70); 300-0 fms.

1 specimen from Stn. 51; S. of Galápagos Is.; T-3 (No. 99); 274-0 fms.

1 specimen from Stn. 53; S. of Galápagos Is.; T-2 (No. 100); 800-0 fms.

1 specimen from Stn. 59; S. of Cocos Id.; T-8 (No. 28); 300-0 fms.

1 specimen from Stn. 74; S. of Cocos Id.; T-56 (No. 152); surface.

1 specimen from Stn. 84; Galápagos Is.; PT-4 (No. 93); 700-0 fms.

2 specimens from Stn. 84; Galápagos Is.; T-8, 9, 10 (No. 157); 500-0 fms.

3 specimens from Stn. 84; Galápagos Is.; T-20 (No. 90); 500-0 fms.

2 specimens from Stn. 84; Galápagos Is.; T-1 (No. 149); 300-0 fms.

3 specimens from Stn. 86; Galápagos Is.; T-1 (No. 57); 400-0 fms.

3 specimens from Stn. 86; Galápagos Is.; T-2 (No. 59); 500-0 fms.

1 specimen from Stn. 86; Galápagos Is.; T-8 (No. 62); 500-0 fms.

1 specimen from Stn. 86; Galápagos Is.; T-11 (No. 69); 1,000-0 fms.

1 specimen from Stn. 86; Galápagos Is.; T-5 (No. 78); 1,000-0 fms.

2 specimens from Stn. 87; W. of Galápagos Is.; T-3 (No. 83); 450-0 fms.

The following young forms are possibly referable to this species:

from Stn. 86, Galápagos Is.; T-11 (No. 77), 1,000-0 fms.

from Stn. 86, Galápagos Is.; T-11 (No. 64), 1,000-0 fms.

from Stn. 49, off Hood Id.; T-2 (No. 107), surface.

The largest of these specimens has a mantle-head length of 30 mm. Several are in a fragmentary condition and their identity is very doubtful.

Many of these are clearly referable to *P. giardi*. There is, however, a frequent difference from the described forms in the possession of long and narrow tentacular manus. The proximal (carpal) suckers are enlarged as in the Galápagos variety (var. *hoylei* Pfeffer, 1912), described by Hoyle (1904); but there are no carpal pads and the manus is much more slender. The arrangement of the arm hooks and suckers and of the "Schutzsaüme" (which are usually damaged) is very much the same, though slight differences occur in the number of hooks. The arrangement of the ocular light organs exactly resembles that figured for *giardi*.

The shape of the body is distinctly more slender than that shown in Hoyle's figure, though the latter is actually of a larger specimen, and is more like that seen in Chun's figures (Pl. XII, figs. 1-2) which are more of a size with ours. The shape of the fins, on the other hand, is very like that seen in Hoyle's figure and unlike that in Chun's.

It is very remarkable that these specimens should show such a definite difference in the form of the manus from Hoyle's examples from the same locality. It is a pity that none of my specimens are males.

#### Genus and species uncertain.

One specimen from Stn. 51; S. of Hood Id., Galápagos; T-3 (No. 97); 274-0 fms.

The mangled specimen has hooks on the thin upper arm-pairs and the tentacles. There are no light organs on the eyes but there are traces of very small organs on the ventral surface of the head and mantle. The surface has, however, been scraped fairly clean and few of these organs are left. As their distribution is the chief diagnostic feature, the status of this form cannot be discussed.

#### FAMILY OCTOPODOTEUTHIDAE.

##### Genus and species uncertain.

One specimen from Stn. 28; E.S.E. of Cocos Id.; T-1 (No. 141); surface.

This specimen is in fairly good condition. It has hooks on the three upper arms and none on the tentacles. The suckers on the latter are of dubious arrangement (?2-3 rows). The absence of hooks on the tentacles and the biserial (?) disposition of the suckers might induce one to place it in the Octopodoteuthidae. The fins are very small, about one-quarter of the mantle-length. The head is enormous. There is a row of light-organs round the top of the eye-ball. I could distinguish none on the body or head.

##### *Octopodoteuthis* Rüppel.

Pfeffer (1912, p. 124) subdivided the Octopodoteuthidae into two groups, in a key translated (with some omissions) below.

- A. Arms (?always) with a spindle-like termination and long, small-based, "sich zum Teil deckenden" hooks which are arranged in two straight series mostly with suckers opposed ("zusammenhängenden"). Some normal suckers are found between the tip and the hooks, except in the ventral pair which is devoid of them and has rudiments of "Basalpolster." Fins terminal..... *Octopodoteuthis*
- B. Arms devoid of spindle-like end. "Die Haken sich nicht Deckend." Apparently no normal suckers.
1. Tentacle stumps persistent ..... *Cuciototeuthis*
  2. Tentacles stumps not persistent ..... *Octopodoteuthopsis*

*Octopodoteuthopsis* further has its hooks widely alternating and with broad bases. The oral surface shows a median groove or line. The fins are terminal, but not reaching the tip of the mantle.

The character of the two specimens before me make this classification very questionable. To begin with, though clearly conspecific, they vary a good deal *inter se*. One has a well-marked spindle-like termination of the arms; in the other it is almost imperceptible. In one there is a number of microscopic normal suckers between the hooks and the end of the arms. In the other I could not find them. These features do not present such a correlation of characters as would suggest that the two individuals are representatives of *Octopodoteuthis* and *Octopodoteuthopsis* respectively, as the one specimen with the end swelling (as in *Octopodoteuthis*) is devoid of the normal suckers (as in *Octopodoteuthopsis*).

Over and above these anomalies we must note a further incompatibility with Pfeffer's scheme. In one specimen the fins do not reach to the tip of the mantle (*Octopodoteuthopsis*), but the specimen has the end swelling of *Octopodoteuthis*. Similarly both seem to show the latter feature, yet in both the suck-

ers are arranged in a zig-zag and enclose a median groove (*Octopodoteuthopsis*). In short I believe Pfeffer's grouping breaks down and, though distinct groups may be found in this family, they are not revealed by his key. I place these forms provisionally in *Octopodoteuthis*, though there are some marked differences that might justify the creation of a new genus for them.

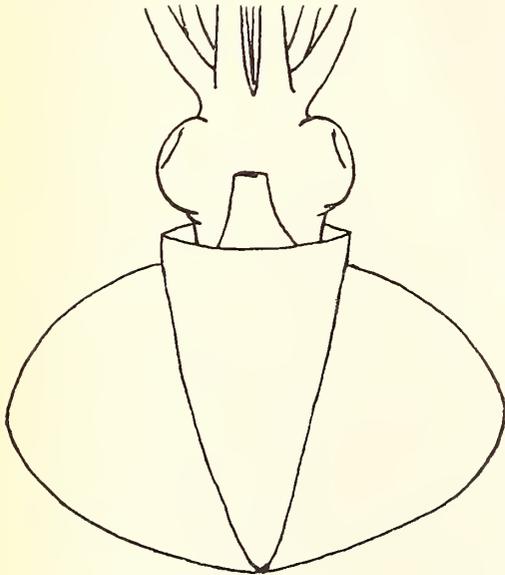
***Octopodoteuthis nielseni*, n. sp.**

(Text-figs. 2-4).

Two specimens from Station 74; Cocos Id.; T-69 and T-70; 400-0 and 500-0 fms. respectively. (Nos. 33 and 34).

- Dorsal length of mantle ..... 26 (?+) mm.
- Maximum width of mantle ..... 12+mm.
- Maximum length of fins ..... 22 mm.
- Total width of fins ..... 34 mm.
- Length of head (mantle edge to base of dorsal arms) ..... 9 mm.
- Width of head ..... 11 mm.
- Length of third left arms ..... 36+mm.

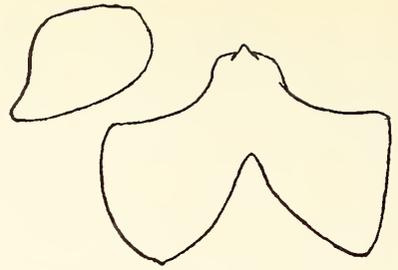
*O. sicula* has been many times described and figured. I shall at a later date give a full analysis of its variation, but confine myself now to pointing out the chief points of difference of *O. nielseni* from the eastern form.



TEXT-FIG. 2. *Octopodoteuthis nielseni* n. sp.; outline of body.

In *O. nielseni* the suckers and hooks are arranged in a zig-zag about a median furrow. So much damage has been done to the arms that it is not easy to say how many hooks there were. On one arm there are at least 20 pairs.

The hooks are, as in *sicula*, sheathed in fleshy casings and are upright and columnar. The fins are 84% of the body-length and their total span is 130% of the mantle-length



TEXT-FIG. 3. *Octopodoteuthis nielseni* n. sp.; funnel organ.

(both figures are the same as in *sicula*). The cephalic component of the adhesive-organ is not like that of *sicula* as shown in Pfeffer's fig. 9, pl. 19 (1912); there is a far wider and less distinctly channelled groove. Unlike those of *sicula* the arms are rounded and have neither "Schwimmsaume" nor "Schutzsaume." The latter are found in the oceanic form of *sicula* (Pfeffer) and both types occur in Sasaki's form. The funnel organ (Text-fig. 3) is not like that of *sicula* figured by Jatta (1896) though it is a little more like that shown by Sasaki (1929). The radula is quite unlike that of *sicula* (Jatta, 1896, pl. 13, fig. 8) in its tall rhachidian tooth, with an extraordinary small base and square admedian tooth. The radula is very unlike those of such enoploteuthids as I know. The admedian and first lateral are not unlike those of *Alluroteuthis* (Odhner, 1923, pl. I, fig. 18).

*Remarks:* This form is somewhat of a difficulty. The general shape and the form of the fins are not particularly different from those of *sicula* (e.g. as given by Pfeffer and Sasaki). The adhesive-organ, radula and the entire lack of membranes on the arms (which cannot be due to damage) are, however, features which preclude our ranking it with *sicula*. The adhesive-organ is of uncertain importance. Another point of diagnostic value is the great length of the third arms. The following table sets forth the relationships of the forms in question.



TEXT-FIG. 4. *Octopodoteuthis nielseni* n. sp.; radula.

*sicula*. Jatta. Longest arms 30 mm., mantle 25 mm.

Pfeffer. Longest arms equal mantle.

Sasaki. Longest arms slightly shorter than mantle.

*nielsenii*. Longest arms 36 mm., mantle 26 mm.

On the whole it seems best to regard the Galápagos form as a distinct species. At the same time it must be noted that *sicula* is rather variable and the status of the various forms called by this name is by no means clear.

This species is dedicated to my friend, E. Nielsen of Copenhagen.

**?*Octopodoteuthis* sp.**

A fragment from Stn. 1, PT-3 (No. 104), from the surface was labelled "*Octopodoteuthis*" by Mr. Pearson. It is now unrecognizable.

**FAMILY ONYCHOTEUTHIDAE.**

***Onykia* (*Teleoteuthis*, Auctt.) sp.**

4 specimens from Stn. 33; N.E. of Galápagos Is.; T-1, T-2 (Nos. 105, 144); surface; 5-6.5 mm.

1 specimen from Stn. 52; S. of Hood Id.; T-1 (No. 136); surface; 4.5 mm.

1 specimen from Stn. 59; S. of Cocos Id.; T-1 (No. 114); surface; 10 mm.

50 specimens from Stn. 74; S. of Cocos Id.; T-31-33, 35-36, 45-7, 50-65, 66 (Nos. 94, 101, 134, 67, 102, 140, 112, 81, 72, 129); surface; up to 13 mm.

13 specimens from Stn. 77; S. of Cocos Id.; T-1, T-2 (Nos. 124, 132); surface; up to 6 mm.

20 specimens from Stn. 78; N.E. of Galápagos Is.; T-1 (No. 126); surface; 4.5 mm.

2 specimens from Stn. 84; Galápagos Is.; T-1, 8, 9, or 10 (Nos. 151, 164); surface; up to 7 mm.

I am unable to assign this large assemblage of young forms, which range in size from just under 3 mm. up to about 13 mm. in mantle-length, to any known species. The Pacific species of this genus are very imperfectly known. If Pfeffer's figures (1912, pl. 1, figs. 12-13) of the tentacle of early stages of *O. caribaea* are at all representative of that species (which may possibly have a cosmopolitan distribution, but see Pfeffer), they differ markedly from the specimens under investigation in which at the stage represented in Pfeffer's figure 12 the tentacular suckers are far more irregularly arranged. At a stage more or less the same as Pfeffer's figure 13, the two marginal rows of suckers are enlarged and are not unlike those of *Thelidoteuthis* (Pfeffer, 1912, pl. 18, fig. 29). Indeed were it not for the absence of light-organs and other features in all the 91 specimens, I would be tempted to imagine that this might be referable to that genus. Unfortunately there are no signs of the dif-

ferentiation of the suckers into hooks except in one specimen 12 mm. long and in this the manus is so badly preserved that its precise arrangement cannot be made out.

***Onykia ?appellofi* (Pfeffer).**

A single (♀) specimen from Stn. 61; T-5 (No. 113); 600-0 fms.

The general shape of the head, body, manus and fins of this specimen agree very closely with *Onykia appellofi*. The manus is particularly like that of *appellofi* figured by Pfeffer (1912, pl. 3, fig. 9). The specimen measures 27 mm. in mantle-length.

***Onychoteuthis ?banksi* Leach.**

A very immature example 8 mm. long from Stn. 51, S. of Hood Id., T-2 (No. 156), 165-0 fms., may be referable to this species. It is very like the young specimens figured by Pfeffer.

**SUBFAMILY LYCOTEUTHINAE.**

**Genus and species uncertain.**

One specimen from Stn. 84, T-8, 9 or 10 (No. 163), in 500, 400-0 fms.

This is a small, well-preserved specimen measuring about 5 mm. in mantle-length. There are no hooks on any of the arms and none on the tentacles. The arm-suckers are in 2 rows, the tentacular ones in four rows, there being very little difference in size between the suckers. The adhesive apparatus is of the simple type found in the Architeuthidae, Enoploteuthidae and Onychoteuthidae. The fins are very small and terminal. Three light-organs occur on the ventral periphery of the eye-ball and on the under surface of the head and mantle. There are none inside the pallial cavity.

This is a very interesting specimen. It was originally labelled by Mr. Pearson as "Enoploteuthidae; genus undetermined." I think, however, that in young enoploteuthids of this size, the arm-suckers, and probably the tentacular suckers as well, are modified as hooks (cf. Pfeffer 1912, pp. 120 and 141). We ought, therefore, to regard it as an onychoteuthid (the Architeuthidae being ruled out by the occurrence of light-organs). In the Onychoteuthidae the hooks of the tentacles (when they occur) seem to be developed late, since in the specimen of *Teleoteuthis caribaea* over 5 mm. long figured by Pfeffer (1912, pl. 1, fig. 12), the hooks are not yet seen. This might be held to be an early stage of any onychoteuthid genus. The only group of this family, however, that have light-organs are the Lycoteuthinae. As (a) the equivalent stage of the other genera show a sign of size-differentiation in one of the marginal rows of tentacular suckers, which is lacking in this specimen, and as (b) the Lycoteuthinae have no hooks at all, I am inclined to regard this specimen as representing a new group of this subfamily differing from the typical forms in having ocular but no tentacular or intrapallial light-organs.

## FAMILY HISTIOTEUTHIDAE.

*Stigmatoteuthis* Pfeffer.

In his key to genera of Histioteuthidae, Pfeffer distinguishes *Stigmatoteuthis* from *Calliteuthis* by its possession of denticular arm and tentacle-suckers and the lack of accessory chitinous structures on the manus. I am not altogether certain that this is a satisfactory distinction, as there are some marked deviations in the form of the manus in the species which by this definition fall into *Stigmatoteuthis*.

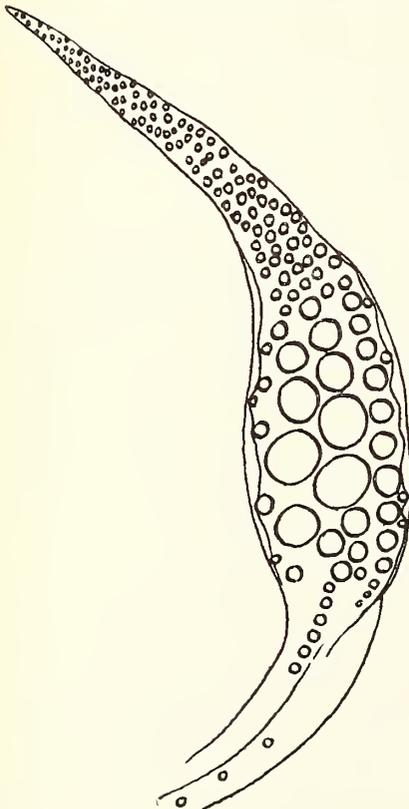
*Stigmatoteuthis arcturi* n. sp.

(Text-figs. 5-6).

One specimen (♀) from Stn. 7 (No. 18); (26° 54' N; 51° 15' W.); PT-1; 1,640 fms.-surface.

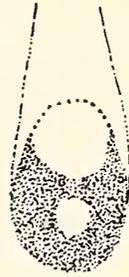
Dorsal Mantle, length:	32± mm.
“ , width:	16± mm.
Fins, length:	11± mm.
“ , width:	11± mm.
1st. arms, length:	ca. 64 mm.
2nd. “ “ :	ca. 64 mm.
3rd. “ “ :	ca. 66 mm.
4th. “ “ :	ca. 62 mm.

The head region has been badly damaged and the epidermis has been removed from all the arms save the ventral. The body is rela-



TEXT-FIG. 5. *Stigmatoteuthis arcturi* n. sp.; tentacular manus.

tively small and broadly conical. It differs in its greater width from *S. verrilli* (= *C. reversa* Verrill). The arms are subequal, but in their present condition it is not easy to specify their exact length.



TEXT-FIG. 6. *Stigmatoteuthis arcturi* n. sp.; cephalic light organ, ×13.

The chitinous rings of the majority of the arm-suckers are equipped with a number of low, broad and closely-set teeth. These are usually better marked on the distal periphery and on some they are virtually absent on the proximal part of the ring.

There is no trace of the excrescence on the proximal circumference noted by Pfeffer in *S. goodrichii*.

The fins are rather torn and their exact shape is uncertain. They seem to be sub-circular. The apical margin projects beyond the end of the body. The surface of the tentacular manus is roughly divisible into two areas, a proximal expanded part bearing the large suckers and a narrow and very much longer distal part bearing very minute suckers (Text-fig. 5). The general shape reminds one of that of *Calliteuthis meneghini* (Pfeffer, 1912, pl. 22, fig. 13), though the resemblance ceases there. There seem to be six rows of suckers in all, but two (the outer marginal of each side) are represented only by 2-3 very minute ones. The first two rhachial pairs are small and are followed by four very large pairs which decrease slowly outwards. After about the seventh rhachial pair the order becomes confused but the distal region seem to consist of 4 or 5 rows. The outer margin is occupied by a single row of suckers which are very minute to begin with, and then increase up to the eighth, after which they decrease and become of a size with the distal ones. There is a carpal row of six suckers and knobs. There is no trace of any accessory chitinous pieces. The rim of the sucker-rings is beset, in the majority of the suckers, with a complete series of small distinct and acute teeth. The light-organs (Text-fig. 6) differ from those of *S. goodrichii* as figured by Pfeffer, (1912, pl. 22, fig. 9). The gladius has the lateral areas narrow and not wide as in *S. dofleini*.

This species differs clearly from those previously described, principally in the character of the manus. Differences from *S. goodrichii* and *verrilli* have already been noted. From *S. hoylei*, which it resembles in a gen-

eral way, it differs in the arrangement of the suckers of the manus. Also the teeth of the arm-suckers of that species are said to be sharp. From *S. japonica* it differs very distinctly, particularly in the tentacles. From *S. ocellata* it differs in that the suckers of the latter are "finely spinous" and from *S. dofleini* it differs in the tentacles (Sasaki, 1929, pl. XXII) and in having the lateral area of the gladius narrow and not wide.

#### *Histiiothauma* n. gen.

Histioteuthid forms without any trace of a web and with very small fins. The peduncles of the suckers are enlarged to form large pyramidal structures. Arm-membranes of both kinds absent. The distribution of light-organs, as far as density is concerned, is midway between *Histioteuthis* and *Meleagroteuthis*. No light-organs on the dorsal surface of the mantle and fins. The tentacular suckers small and undifferentiated in size; no carpal system.

Type of the genus: *H. oceani* (see below).

For some time I was convinced that *Histiiothauma* was a juvenile form of *Meleagroteuthis*. Not only is there a vague general likeness, but in some respects, notably in the disposition of the light-organs on the dorsal arms, the agreement is close. The geographical distribution of the forms also favours this view. On comparing the following list of differences it seems to me, however, that *Histiiothauma* cannot be a young *Meleagroteuthis*. The difference between Pfeffer's specimen (26 mm. mantle-length) and Berry's (up to 59 mm.) are inconsiderable as compared with the differences between these two and the Galápagos specimen. Even if we disregard the condition of the suckers as problematical, so many points of difference still remain of an order not associated with growth-changes, that I have no option but to provide a new genus for the *Arcturus*'s specimen.

Mantle-length (dorsal): 7.2

Mantle-width: 8

Fins, length: 3.8 (±)

Fins, breadth: 2.6 (±)

Arms 1st: 16.0 (±2)

Arms 2nd: 16.0 (±2)

Arms 3rd: 16.0 (±2)

Arms 4th: 16.0 (±2)

Tentacles: ca. 42

The body is broadly conical and nearly as wide as long. The apex is rounded and blunt. The fins are very small relative to the size of the mantle and do not project beyond the apex and sides as in the other members of the family. They are very much crumpled and their exact shape is not certain but they seem to have been longer than wide.

The arms are subequal. They are devoid of swimming membranes and "Schutzsaüme." The suckers on all the arms are represented by their bases alone which are rather large (usually pyramidal) structures at the apex of which is sometimes seen the vestige of a thread-like stalk (?). On some of the arms a very minute adoral sucker persists. This is quite normal and its chitinous ring seems to be edentulous. Owing to their scarcity I have removed some of these for closer examination.

At first sight one would assume that the suckers had been lost by accident; but if they had been stripped by contact with some foreign body one would expect to find one or two persisting here and there over the arm generally as is often seen. One cannot speak for certain but it seems to me that this is no case of accidental loss. The "cartilaginous" tubercles found by Pfeffer on the dorsum of the three upper arm-pairs are present in this form. But I could find no median pallial row. Berry (1912, p. 308) could find neither and surmises that this may be a juvenile character.

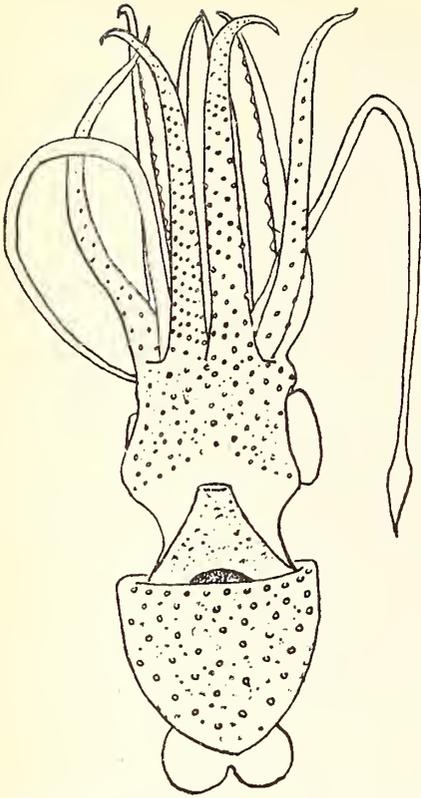
	<i>Meleagroteuthis</i>	<i>Histiiothauma</i>
Light organs	Close, numerous. Dorsal and ventral.	Less numerous. Very few dorsal.
Web	Present between upper arms.	Absent.
Arm suckers	Normal.	? Absent.
Manus	Suckers clearly differentiated in size. Carpal suckers present.	Suckers more or less equal. No carpal suckers.
Arm membranes	Both types present.	Absent.
Fins	Over 1/2 length of mantle. Projecting beyond apex.	Well under that length. Not projecting beyond apex.
Light-organs	Complex.	Simple.

#### *Histiiothauma oceani* n. sp.

(Text-fig. 7)

One example (♂) from Stn. 51; S.E. of the Galápagos; T-2, (No. 29); in 165-0 fms.

The tentacle-manus exhibits a number of minute suckers which show even less size-differentiation than *Meleagroteuthis*. They seem to be in six irregular rows. The rims exhibit a number of low knobs or plates which



TEXT-FIG. 7. *Histiothauma oceanii* gen. et sp. nov.; ventral aspect,  $\times 3$ .

in some seem to be raised here and there into what would pass for teeth, though on the whole one would call them edentulous.

There is no trace of a web on any of the arms.

*Light-organs:* On the first three pairs of arms, there are two disposed irregular (dorsal and ventral) rows of these organs. Occupying the sagittal line on the 1st-3rd arms is a single series of subcutaneous white masses which may also be luminous. On the fourth pair there are five rows of organs, at least to begin with. The organs are rather openly distributed over the ventral surface of the mantle, below a line drawn diagonally from the edge of the mantle, opposite the eye, to a point on the ventral surface, just short of the apex. There are very few on the funnel or fins. The organs are simple and consist (macroscopically) of a simple globular body surmounted by a dark pigment mass.

The left eye, as in examples of other species in this family, is very much larger than the right. This is noted in *Meleagroteuthis hoylei* (Berry, 1912, p. 305; Pfeffer, 1912, p. 295), *Histioteuthis bonelliana* (Robson, 1924, p. 608) and in *Hymenoteuthis macrope* (Berry, 1912, p. 273). This curious phenomenon has never had sufficient attention paid to it. It may be the prelude to a general change of symmetry.

On the two ventral arms the reduction of the suckers is carried to a further extreme. The pedicels are over the greater part of the arm so reduced as to be almost imperceptible. Whether this is to be interpreted as hectocotylization I cannot say. Unfortunately the animal is very immature and it is not possible to determine the sex from the internal organs.

#### Genus and species uncertain.

One specimen (? sex) from Stn. 74; S. of Cocos Id.; T-2 (No. 68); in 620-0 fms.

This specimen is very much damaged and does not permit of exact study. It measures 11 mm. in mantle-length. It cannot be readily accommodated in any of the known genera. It has light-organs of the scattered type, the suckers are edentulous, the manus is devoid of accessory chitinous pieces and has about 7 rows of smallish suckers. This combination of characters seems to exclude it from the genera hitherto known. As it is so young and may not represent the adult condition I refrain from describing it as a new genus. As a matter of fact, according to the figure of a young *Calliteuthis* given by Chun (1910, pl. 19, figs. 1 & 2, as *Histioteuthis*, determined as *Calliteuthis* by Pfeffer, 1912, p. 268) the manus in that genus of a specimen with mantle-length 10 mm. is undifferentiated. On the other hand the fins of this form are quite unlike those of *Calliteuthis*.

One specimen from Stn. 86; Galápagos Is.; (No. 20); in 600-0 fms.

The remarks made about the preceding form are applicable to this specimen. It has scarcely any web, non-denticulate suckers, the tentacles are devoid of accessory chitinous pieces and the light-organs are small and far more separated than in *Meleagroteuthis*. By the ordinary procedure it is placed in the group of *Calliteuthis* and *Stigmatoteuthis*. But its characters (toothless suckers, no accessory pieces on manus) cut across Pfeffer's classification. It measures 18 mm. in dorsal mantle-length and may be a young form of either of these genera.

#### FAMILY OMMATOSTREPHIDAE.

##### Genus and species uncertain.

Two specimens (? sex) from Stn. 74; S. of Cocos Id.; T-7 (Nos. 82 and 73); ? Depth.

These are small specimens measuring 15 mm. in mantle-head length. Their position is rather enigmatic. The foveola is undifferentiated, which immediately ranks them with *Illex* and *Todaropsis* and yet the tentacular manus being clearly undeveloped (it consists of a few small suckers), it is impossible to say if they should go into *Illex* or into *Todaropsis*. Mr. Pearson originally diagnosed them as "*Symplectoteuthis*." Actually I found a very loose strand of tissue connecting the two parts of the adhesive-organ on one side of our specimen but it was really impossible to say if this was adventitious or not. The entirely undifferentiated foveola puts this suggestion out of court at once. In shape,

size of fins, etc., it is not at all unlike the young *Illex* figured by Pfeffer (1912, pl. 29, figs. 3-4). The adhesive-organ also is more like that of *Illex* than it is to *Todaropsis*; but the longitudinal cleft of the cephalic component is not nearly so open as in that genus. The denticulation of the suckers is very obscure.

#### SUBFAMILY STHENOTEUTHINAE.

##### *Sthenoteuthis pteropus* Steenstrup.

Seven specimens (6♀, 1♂) from Stn. 74, D. 1; (No. 803).

These specimens have typical tentacular manus, siphonal foveola and "adhesive-organs." The largest has a dorsal mantle-length of 110 mm., the smallest 49 mm.

##### *Sthenoteuthis bartrami* Lesueur.

One specimen (♀) from unknown station, (? CN 2).

A fairly typical form 144 mm. in dorsal mantle-length with 6-7 suckers on the proximal side of the first modified sucker of the manus. The cephalic element of the locking-apparatus is somewhat different in detail from that figured by Pfeffer (1912, pl. 35, figs. 8-9).

##### [?] *Sthenoteuthis* sp. (*Rhynchoteuthis* stage). (Text-figs. 8-10).

4 specimens from Stn. 40; off Albemarle Id., Galápagos; T-1 (Nos. 120 and 137); from surface.

1 specimen from Stn. 50; S. of Hood Id.; T-2 (No. 147); 400-0 fms.

1 specimen from Stn. 52; S. of Hood Id.; T-1 (No. 135); surface.

1 specimen from Stn. 53; S. of Hood Id.; T-2 (No. 103); 800-0 fms.

8 specimens from Stn. 62; off Malpelo Id.; T-1 (No. 138); surface.

1 specimen from Stn. 65; N. E. of Cocos Id.; T-3 (No. 121); surface.

1 specimen from Stn. 68; N. of Cocos Id.; T-1 (No. 108); surface.

15 specimens from Stn. 74; S. of Cocos Id.; T-66 (No. 130); surface.

9 specimens from Stn. 74; S. of Cocos Id.; T-45 (No. 139); surface.

5 specimens from Stn. 74; S. of Cocos Id.; T-66 (No. 131); surface.

13 specimens from Stn. 77; S. of Cocos Id.; T-2 (No. 133); surface.

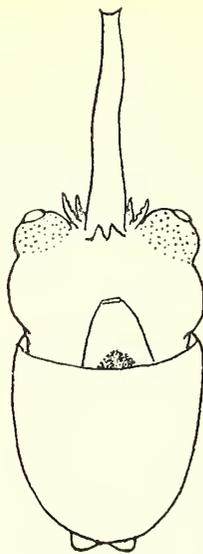
12 specimens from Stn. 77; S. of Cocos Id.; T-1 (No. 123); surface.

7 specimens from Stn. 78; N.E. of Galápagos Is.; T-1 (No. 128); surface.

13 specimens from Stn. 78; N.E. of Galápagos Is.; T-1 (No. 127); surface.

1 specimen from Stn. 84; Galápagos Is.; T-3 (No. 173); surface.

4 specimens from Stn. 84; Galápagos Is.; T-8, 9, or 10 (No. 161); 500-0 fms.

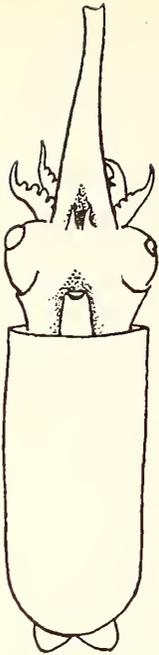


TEXT-FIG. 8. *Sthenoteuthis* (?), *Rhynchoteuthis* stage; larva with a mantle-length of 2.5 mm. from Stn. 53 (No. 103).

This interesting series of 102 individuals varying in size from 10 mm. (mantle-length) down to about 1.9 mm. seems to contain representatives of two species. The whole series was measured and the mantle-width and "spout" width was expressed as a percentage of length from the apex to the center of the eye. On the whole there is manifest a distinct correlation between small size and greater width of the mantle; in other words, younger specimens tend to be wider than older ones. They also tend to have a shorter "spout."



TEXT-FIG. 9. *Sthenoteuthis* sp. (?), *Rhynchoteuthis* stage; larva with a mantle length of 8.4 mm., from Stn. 74 (No. 130).



TEXT-FIG. 10. *Sthenoteuthis* (?), *Rhynchoteuthis* stage; larva with a mantle length of 3.5 mm. from Stn. 74 (No. 131).

Nevertheless the correlation is by no means absolute and two specimens (131/1 and 147/1) are far narrower than the average for their group-size and have a shorter "spout." These seem to me to be representatives of a different species. Chun (1910) noticed a similar dimorphism and Pfeffer (1912, p. 390) considered it evidence of the fact that two distinct species have a *Rhynchoteuthion*-stage. I suspect that the difference between No. 130/3 (width index 50) and No. 139/3 (index 34), of which one is but a millimetre longer than the other, is of systematic importance. Like Degner (1925, p. 42) I could find no clear indication of a differentiation into large- and small-eyed types (Chun, 1910). As far as I can see at present, it is by no means easy to assign any of the various *Rhynchoteuthion* stages to a particular species of the *Sthenoteuthidae*. On the whole specimens obtained by the *Arcturus* do not tend to resemble the early stages figured by Pfeffer (1912, pl. 37, figs. 8-10), though some later stages are like Pfeffer's pl. 37, figs. 2-3.

The most valuable information to be gleaned from these measurements relates to the "spout." Apparently it is developed at an earlier stage than any represented here, as in the smallest it is long and fully developed and the two moieties are nearly completely fused up. Chun (1912, p. 203) found it developed in a specimen 0.8 mm. long. Pfeffer (1912, p. 380) found a specimen of 3.2 mm. mantle-length still covered by an "embryonale Haut." Specimen from Stn. 84 (No. 173),

which measured under 2 mm. in mantle-length, was similarly covered in a membrane and was described by Mr. Pearson as an "egg." The spout is very well developed in this specimen. Its relative length gradually decreases until at about 9.0 mm. length it is not more than 10 or 12% of the body-length. At about this period the two elements which at the earliest stages are completely fused have gradually come apart and are found separated for  $\frac{1}{2}$ - $\frac{3}{4}$  of their length. They eventually separate when the animal is 9-10 mm. long. It is quite evident that the fused moieties actually separate. A limited number (13) of these forms of sizes varying from 4.0 to 6.1 mm. in size do not show the spout at all. The tentacles which are very small are completely separated and seem to be mere stumps. It remains to be seen whether these are (1) members of a species distinct from those having the *Rhynchoteuthion* stage; (2) forms which have prematurely lost the funnel; or (3) forms in which it has not yet developed. The development, etc., of this organ suggests several interesting and important questions which are outside the scope of the present paper.

On the whole my results agree with those of Degner, as far as the formation of the spout is concerned. In the early stage it shows a complete fusion of the two moieties and at about 7 mm. long the latter are in contact towards the extremity only. I differ from Degner in finding that at about 7 mm. the area of fusion is in some individuals as much as half the length of the spout. Nor do I find the separation at the apex figured by Degner (1925, fig. 32).

#### *Hyaloteuthis pelagica* (Bosc).

One specimen (? ♀) from Station 54, off Hood Island, Galápagos (No. 55), taken at the surface from the ship.

This is a small and very slender specimen 25 mm. long by 5 mm. wide with fins 6 mm. long or nearly a quarter of the mantle-length. The ventral white patches have an arrangement much more like that shown by Férussac and d'Orbigny (1835-48, "Calmars," pl. 18, figs. 1 & 2; and "Ommastrèphes," pl. 1, figs. 17, 18) than that illustrated by Pfeffer. The structure of these patches does not agree with the descriptions already given, in two respects. (1) They are not raised above the surface as "petits tubercules blancs, à peine saillants" (Férussac and d'Orbigny, p. 348); (2) nor are they "feache punktionmigen Gruben, welche im ihrem Grunde je einen . . . Tuberkel tragen" (Pfeffer, 1912, p. 463). They are simply dense white and semi-lustrous patches lying evenly with the surface. A section through one shows no sign of special organization. I assume that, as this specimen is young (Férussac and d'Orbigny's specimen and that in the Hamburg Museum measured 55 mm. in mantle-length according to Pfeffer, 1912, p. 464), the light-organs may not be fully developed.

***Symplectoteuthis oualaniensis* (Lesson).**

One specimen (♀) from stomach of *Germolunga pelamis*, Stn. 74 (No. 5), S. of Cocos Id.

This specimen is very badly damaged and in particular the epidermis has been completely stripped off the ventral surface so that it is not possible to say if the ventral luminous streaks given by Sasaki (1929) as the only diagnostic difference between *S. oualaniensis* and *S. luminosa* are present or absent. Berry has placed the latter in a different genus, *Eucleoteuthis*.

The animal is a small one and measures only 70 mm. from the base of the dorsal arm to the apex of the body. It is remarkably slender as compared with the thicker specimens (e.g. that figured by Pfeffer), but agrees with *oualaniensis* in general shape and not with *luminosa*.

It further differs from *oualaniensis* in (1) the profile of the keel on the 3rd arms, which is lower and not triangular; (2) the shallower "Schutzsaüme" of that arm; and (3) the marked compression of the tentacular manus. I do not know how far all these characters might not be produced by maceration, etc.

**Genus and species uncertain.**

A very much mangled and fragmentary specimen identified by Mr. Wesley as *S. oualaniensis* does not appear to me to be referable to either of the species of that genus. The fins are well under 1/3 of the mantle-length.

**FAMILY CHEIROTEUTHIDAE.*****Chiroteuthis* (*Planctoteuthis* stage).**

(Text-fig. 11).

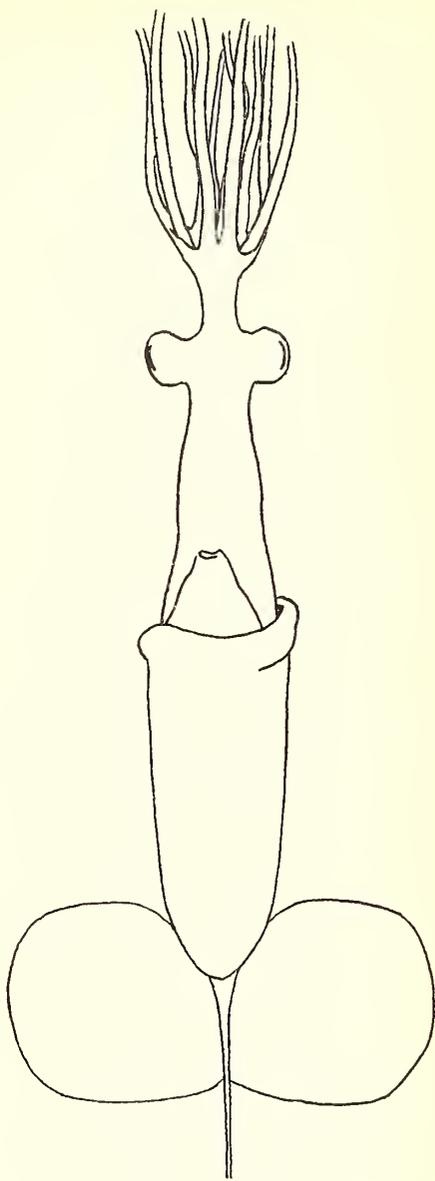
One specimen from Stn. 74; S. of Cocos Id.; T-70 (No. 40); in 500-0 fms.

This specimen, which is very much distorted and mangled, measured ca. 30 mm. from the upper edge of the fins to the eyes. The arms are in the order 4.3.2. (?3=2).1. The manus exhibits four equal rows of suckers which are not differentiated distally as in the "*Doratopsis*" stage. The cephalic component of the adhesive-organ has a basal projection, as in Chun's "*Doratopsis exophthalmica*" (1910, pl. XLVII, fig. 2). Like that species it also has a very slender "Hals" just above the eyes. But its fins are much larger and the body is wider. In the size of the fins it resembles the stage described by me as *Doratopsis* sp. A (1924). The form and length of the terminal spine is uncertain.

This seems to be a new juvenile form.

One specimen from Stn. 45, T-3 (No. 21), from 200-0 fms.

This specimen resembles the above very closely and is better preserved. The head and "neck" (above and below eyes) measure just about the same as the distance from the edge of the mantle to the posterior edge of the fins. This seems to have a complete "spine" 1½ times as long as the fins.



TEXT-FIG. 11. *Chiroteuthis* sp., (*Planctoteuthis* stage), ventral view of specimen from Stn. 74 (No. 40).

One specimen from Stn. 74, PT. 2 (No. 27), from 600-0 fms.

A larger specimen, very much crumpled. It measures 36 mm. in mantle-length. The fins are not quite so large.

Two specimens (fragments) from Stn. 68, PT.-1 (No. 172), from 600-0 fms.

Specimens very much mangled. Fins and mantle only, measuring 26 and 19 mm. in mantle-length.

One fragment from Stn. 74, PT.-1 (No. 201), from 600-0 fms.

Diagnosed by the characteristic fins. 35 mm. long.

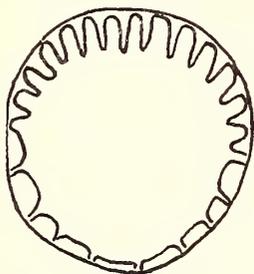
**Mastigoteuthis sp.**

(Text-figs. 12-13).

One specimen (? or two) (? sex) from Stn. 86; (No. 11); S.W. of Narborough Id., Galápagos Archipelago; (No. 17); surface-1,000 fms.

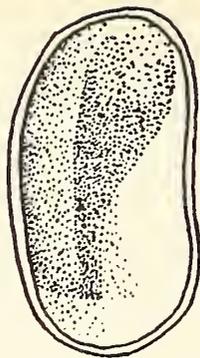
This specimen is in very bad condition. The skin has been entirely stripped off the muscles. It is represented by a head, body and fins all separate, and some fragments of tentacles. I am in fact very uncertain whether the body and fins belong to the same animal. For that reason I refrain from describing it as a new species, which I would most certainly be compelled to do if I were convinced that the fragments were referable to the same animal. The following are such data as I feel qualified to record.

Mantle-length:	65 mm. (?90).
Mantle-width:	24 mm.
Fins, length:	70 mm.
Fins, total width:	62 mm.
Arms R. 1 length:	70 mm.
“ 2 “ :	90 mm.?
“ 3 “ :	90 mm.?
“ 4 “ :	—
Tentacles:	280?+



TEXT-FIG. 12. *Mastigoteuthis* sp., sucker ring from the third arm,  $\times 33$ .

It is uncertain how long the mantle actually is, as the fins with what looks like the apical part of the gladius have been torn from it. The fins may have been 7/9 of the length of the mantle. They are only slightly longer than wide. The body is rather slender. The arms are probably in the order 4.3.2.1. as usual, but a very unusual feature is the great length of the upper arms which are longer than the mantle. The suckers of the third arm have their distal edge armed with about 14 longish teeth; proximally these become low, broad plates. The cephalic component of the adhesive-organ is moderately wide, its width being 53% of its length. Its rim is very narrow. This form differs from Hoyle's *M. dentata* (1904, p. 34) which was recorded from near the Galápagos in the size of its fins and arms, the dentition of the suckers of the latter and the shape of the adhesive-organ. Nor can I associate it with any other recorded species.



TEXT-FIG. 13. *Mastigoteuthis* sp., cephalic component of adhesive organ,  $\times 5\frac{1}{2}$ .

**Mastigoteuthis sp.**

A single tentacle just over 29 cms. long from Station 12; 27° 58'N. 46° 52'W.; (No. 166); "found on sounding-wire" (sounding of 2,840 fms).

This fragment is not like any previously described tentacle of *Mastigoteuthis*. The suckers are excessively minute and very numerous. They seem to be sessile or at least to have very short stalks. I could not distinguish any teeth on the rings.

One specimen (very much damaged) from Stn. 33, PT.-1 (No. 84); from 700-0 fms.

One specimen (very much damaged) from Stn. 50, T-2 (No. 145); from 400-0 fms.

One specimen (very much damaged) from Stn. 33, PT.-1 (No. 85).

Nothing very useful can be said regarding these damaged specimens.

**FAMILY CRANCHIIDAE.**

***Liocranchia reinhardi* Steenstrup.**

4 specimens from Stn. 38; off Tower Id., Galápagos; PT.-1 (No. 71); 300-0 fms.

1 specimen from Stn. 38; off Tower Id., Galápagos; Pt.-2 (No. 53); 500-0 fms.

1 specimen from Stn. 33; N. E. of Galápagos; Pt.-1 (No. 8); 700-0 fms.

1 specimen from Stn. 59; S. of Cocos Id.; PT.-1 (No. 52); 600-0 fms.

1 specimen from Stn. 74; S. of Cocos Id.; T-21 (No. 98); 600-0 fms. (shrivelled).

1 specimen from Stn. 74; S. of Cocos Id.; T-76 (No. 51); 500-0 fms.

1 specimen from Stn. 84; Galápagos Id.; PT.-1 (No. 61); 500-0 fms.

1 specimen from Stn. 84; Galápagos Id.; T-1 (No. 150); 300-0 fms.

1 specimen from Stn. 84; Galápagos Id.; T-8, 9 or 10 (No. 158); 500-0 fms.

1 specimen from Stn. 84; Galápagos Id.; T-5 (No. 47); surface.

7 specimens from Stn. 84; Galápagos Id.; PT.-1 (No. 7); 500-0 fms.

7 specimens from Stn. 84; Galápagos Id.; PT.-3, 4 (No. 54); 700-0 fms.

? specimens from Stn. 84; Galápagos Id.; T-14, 20 (No. 54); 500-0 fms.

1 specimen from Stn. 86; Galápagos Id.; T-11 (No. 48); 300-0 fms.

1 specimen from Stn. 86; Galápagos Id.; T-8 (No. 16); 500-0 fms.

1 specimen from Stn. 87; Galápagos Id.; PT.-1 (No. 46).

The following table gives the length  $\times$  width ratio and the length of the fins.

Coll. No.	Mantle-length	Mantle-width % length	Fins length % mantle-length
16	42	33	23
48	32	27	21
51	26	34	21
71a	26	28	12
71b	25	36	16
46	22	40	13
71c	19	36	13
71d	19	36	14
541	15	40	13
542	14	50	14
543	14	45	12
544	14.3	41	12
47	14	42	14
52	14	46	15
545	13.5	45	14
546	13.2	53	13
61	13	38	11
150	11.5	47	12
547	11	45	19
53	10.5	52	14
158	10+	50	18

From this it seems pretty clear that longer specimens tend to be narrower and to have longer fins. Nearly all the forms in the *Arcturus* collection are relatively narrow and only four attain or exceed an index of 50. The actual form of the body varies from a regularly narrow ovoid to a vase-like form with the greatest width situated anteriorly and slender apical region.

*The fins:* The apex of the body extends half way or rather less down the fins. I found no specimens like those figured by Pfeffer (1912, pl. 48, fig. 21) in which the apex scarcely overlaps with the fins. The fins are relatively very small and in no case exceed 23% of the mantle-length.

They tend to occur in two phases—one in which each fin has an outline representing the large part of the circumference of a circle and another in which they are rather wider than long.

*Arms:* In the largest specimen (No. 16) there are 16-17 pairs of regularly biserial suckers on the 3rd arms (cf. the very dif-

ferent arrangement in Sasaki's description). The tentacles differ from those usually encountered in that there is a very marked and abrupt difference in size (manifest at or about the 10th row) in the suckers, there being a small apical region of very small suckers and a larger proximal area having a number of very large ones.

*"Ventral Bands:"* Pfeffer (1912, p. 666) gives as a difference between this species and *globulus* Berry, that there is a double tubercle at the apex of the angle formed by the bands. I have found in these specimens that the tubercle is sometimes double, sometimes single and that sometimes there are two separate tubercles.

*Remarks:* *L. reinhardti* is manifestly a very variable species and I am not at all sure that all the forms which have been included in it are conspecific. Not only does the bodily shape and that of the fins vary enormously (though an age-factor is undoubtedly influential here), but also the arrangement of the suckers on the arms and tentacles, the relation between the fins and the body-apex, and other characters, etc., differ considerably in the described specimens.

The specimens here recorded seem to be a more or less homogeneous population; but until the variation of this species and of *valdiviae* is more thoroughly understood, the status of the various described forms is determined and the effects of age and sex evaluated, not much can be said.

#### *Galiteuthis* sp.

One specimen (?♀) from Stn. 86; off Narborough Is., Galápagos; T-2; 500-0 fms.

This very interesting form is badly damaged and in poor condition and I am unable, in the absence of several important features, to speak with certainty as to its status.

The form of the fins and the smooth arm-suckers ally it with *Galiteuthis*. Unfortunately the arms have been wholly stripped of their integument and one cannot find any trace of the support-membrane from which to see if the characteristic trabeculae are present. On the other hand the tentacles are absent, which Pfeffer (l.c.) makes a diagnostic feature of *Taonius*. It should be noted that Sasaki gives a description of a *Taonius* with complete tentacles. The outstanding feature of the present specimen, as in Joubin's specimen and one of Sasaki's, is the enormous length and remarkable slenderness of the body. Actually it measures 241 mm. from the centre of the eye to the apex and its width was probably about 22 mm. or under 10% of

	Length	Width nearly	Width: Length %	Fins % Length
<i>phyllura</i> (Berry, 1912)	230	35	nearly 15	49
<i>armata</i> (Chun, 1910)	121	20	16	42
(Sasaki, 1929)				
larger spec.	270	27	10	51
(Joubin, 1898)	350±	—	10	50

the length. The fins measure about 92 mm. from the tip of the gladius to the anterior insertion-point. They are thus nearer a third than a half of the mantle-length (actually 37%). These proportions may be compared with the other species.

The fins, as in Sasaki's figured specimen, but unlike those of Joubin and Chun, are continued right to the apex and there is no protruding "Schwanzfaden" as in the two latter. Differences in this respect as well as in the width of the body make it very likely that all the specimens recorded as *armata* are not actually referable to the same species.

Besides the features above indicated there are no others in a suitable condition for description.

***Taonidium pacificum* n. sp.**

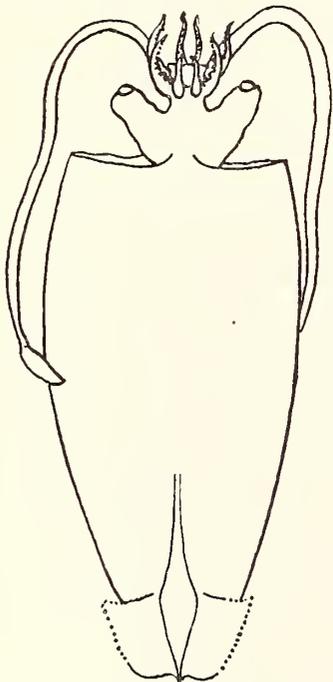
(Text-fig. 14).

One specimen from Stn. 66; N. of Cocos Id.; PT-1 (No. 49); 600-0 fms.

One specimen from Stn. 68; N. E. of Cocos Id.; PT-1 (No. 81); 600-0 fms.

*Measurement* (mm). (Larger specimen).

Dorsal mantle-length:	29±
Mantle, width:	14±
Head, length:	3
Fins, length:	4
Arms length, 1st:	2.2
2nd:	3.2
3rd:	4.4
4th:	4.0(?)
Tentacles, length:	25.0



TEXT-FIG. 14. *Taonidium pacificum* n. sp.; dorsal view, circa  $\times 2\frac{1}{2}$ .

The body in both specimens is elongate and broadly conical. The fins in the larger specimen are about  $\frac{1}{8}$  of the total length and together form a rather broad oval. They are distinctly longer than wide. In the smaller specimen they are much smaller and narrower and though it is likely that this small size may be due to damage, both fins are equal in width and there is no apparent damage.

The tentacles are about as long as the mantle (smaller specimen) or a little shorter than it (in the larger). The manus consists of four series of sub-equal suckers with smooth rings. There are about 10 rows of these. The tentacle stem bears two rows of minute suckers.

In the larger specimen the arms seem to be in the order  $3 = 4.2.1$ . The funnel-organ is more or less crescentic.

*Remarks:* According to Pfeffer's key this should be *P. chuni* but it differs from that obviously juvenile form (a) in the greater length of the arms and tentacles, (b) in the shape of the body and (c) in the size and shape of the fins.

***Helicocranchia beebei* n. sp.**

(Text-figs. 15-18).

1 specimen from Stn. 74; S. of Cocos Id.; Petersen Fish Trawl No. 1 (No. 144); 600 fms. to surface.

1 specimen from Stn. 86; off Galápagos; T-8 (No. 9); from 500-0 fms.

1 specimen from Stn. 28; S.E. of Cocos Id.; T-1 (No. 142); from surface.

1 specimen from Stn. 74; S. of Cocos Id.; OT-3 (No. 63); from 833-0 fms.

1 specimen from Stn. 74; S. of Cocos Id.; PT-1 (No. 39); from 600-0 fms.

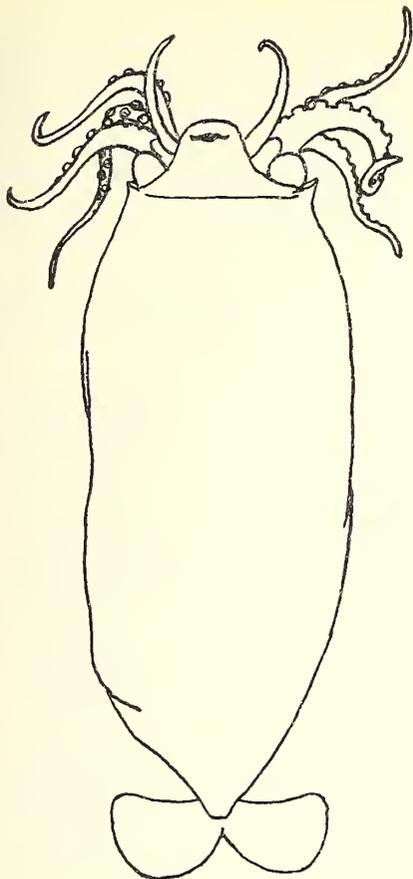
1 specimen from Stn. 74; S. of Cocos Id.; PT-3 (No. 58); from 620-0 fms.

*Dimensions.*

Dorsal length of mantle:	54	mm.
Width of mantle		
(round the curve):	26	mm.
Length of fins (maximum):	4.9	mm.
Width of fins (total):	13.0	mm.

	R.	L.
Length of 1st arm:	16	16
Length of 2nd arm:	16	17
Length of 3rd arm:	14	14
Length of 4th arm:	11	10

The mantle region is stouter than in *H. pfefferi*. The fins are peculiar and may constitute a ground for excluding this form from Massy's genus. She states in her generic definition (1904, p. 34) that the fins are attached to the end of the dorsal surface and are pedunculate. In our form they are certainly not pedunculate nor are they attached as in *H. pfefferi*. On the other hand there do not seem to be available any detailed drawings of the fin-insertion of *Teuthowenia*. On



TEXT-FIG. 15. *Helicoeranchia beebei* n. sp.;  
 $\times 1\frac{1}{2}$ .

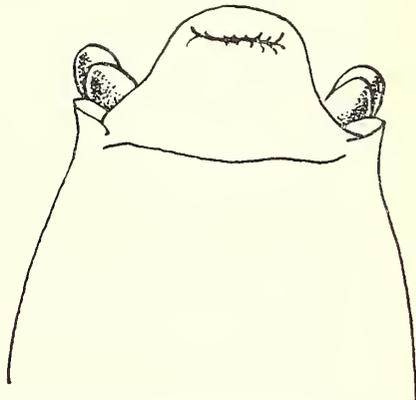
the whole in *H. beebei* the general plan of the insertion of the fins is not unlike that figured by Pfeffer (1908a, p. 105, fig. 120) for *T. megalops*. The shape of the fins and the angle at which they are set to the main axis are very characteristic.

The cephalic region, on the other hand, is very like that of *Helicoeranchia*. The arms are in the order 1 = 2.3.4., the longest arms are one-third the length of the body as in *Helicoeranchia*, though the order is different. The funnel rises well above the eyes as in Massy's genus, but it is thicker and not so pointed as in the latter. The median part of the funnel-organ is of the same type as in *Helicoeranchia*, but its three sections are all more angular and form a less symmetrical trefoil-pattern. The lateral portions are markedly different, as they are L-shaped and very remote from the median part. The suckers have been damaged, so that it is impossible to discuss their number and arrangement. The oral surface has apparently undergone some violent pressure and I find it a little hard to distinguish the real character of the surface.

For example most of the adoral suckers have an ovoid or squareish aperture and I am

unable to determine if this is the result of lesion or if it is natural.

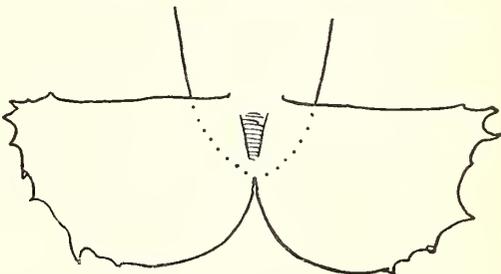
The tentacles are absent. They are represented by two exactly symmetrical stumps on each side. I believe that their absence is not due to accidental destruction, but resembles the similar abortion of the tentacles in *Octopodoteuthis* and *Taonius*. It would be necessary to obtain other specimens of the species before speaking with certainty on this matter.



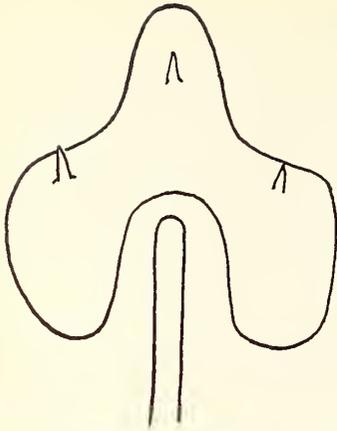
TEXT-FIG. 16. *Helicoeranchia beebei* n. sp.;  
 funnel,  $\times 3$ .

The eyes are large and placed on very short stalks, their longest axis being at right angles to that of the stalks. I do not find any obvious structure comparable to the ocular light-organ of *Helicoeranchia* and *Teuthowenia*. I have compared the eye of my species with that of the type of *H. pfefferi* and find that the light-organ is very conspicuous and unmistakable in the latter.

This form is distinct from *H. pfefferi* in the fin-shape and attachment, eyes and in certain features of the funnel-organ, and from Berry's *Helicoeranchia* sp. (1912) in the shape of its fins and arm-formula. It differs from *Teuthowenia* in the length of its arms and the position of the eyes relatively to the funnel. The apparent absence of ocular light-organs and possibly of tentacles may ultimately necessitate its elevation to sub-generic or even generic rank. The relationship of the genera and subgenera placed in



TEXT-FIG. 17. *Helicoeranchia beebei* n. sp.;  
 dorsal aspect of fins,  $\times 5\%$ .



TEXT-FIG. 18. *Helicocranchia beebei* n. sp.; funnel organ.

the group of *Teuthowenia* by Pfeffer requires further elucidation. I do not know why more stress was not placed by him on the marked divergences in the relationship between the height of the funnel and the level of the eyes.

#### *Helicocranchia* sp.

One specimen from Stn. 28; S.E. of Cocos Id.; T-1 (No. 142); from the surface.

Differs from the above in the lower funnel and shallow and more divergent fins. The specimen is very much distorted.

In addition there are two very much damaged and shrivelled specimens labelled "*Teuthowenia*" from Stns. 80 (No. 116) and 61 (No. 117).

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## 8.

Hyperplastic Epidermal Disease in the Bluegill Sunfish,  
*Lepomis macrochirus* Rafinesque.

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(Plates I-VII).

## INTRODUCTION.

Hyperplastic epidermal disease has been reported frequently among European freshwater cyprinids, but only rarely from other species in this and other parts of the world. This disease, variously called carp-pox, Pockenkrankheit des Karpfens, varioles des carps, cutaneous warts and epithelioma papillosum, has been known since the Middle Ages. It is characterized by white or grayish, irregular, raised patches scattered over the skin. Histologically there is a striking hyperplasia of epithelial cells and other epidermal elements, supported by a delicate stroma. According to Hofer (1904), the first accurate description probably was given by Wierzejski in 1887. This atypical growth was restudied and recorded from carp and related fishes by the following: Hofer (1896 a, b; 1901; 1904), Doflein (1898, 1928), Plehn (1906, 1924), Loewenthal (1907), Fiebiger (1909), Thomas (1931) and Schäperclaus (1935).

A somewhat similar hyperplastic disease has been recorded for marine fishes. Johnstone (1925) reported skin lesions in dabs and plaice taken off the coast of England. He referred to these lesions as cutaneous warts or epitheliomata. Smith (1935) described a hyperplastic epidermal disease in winter flounder (*Pseudopleuronectes americanus*) caught in Long Island Sound. This was the first report of such a disease occurring in fishes of American waters.

The present report, insofar as known, is the first description of an epidermal hyperplasia in a freshwater fish of North America. The disease was found in bluegill sunfish, *Lepomis macrochirus* Rafinesque, taken from a lake near New Preston, Connecticut.

The writer is indebted to the late Mr. L. Beeman, former owner of the Warmaug Black Bass Hatchery, at New Preston, for collecting the fish; to George M. Smith, Yale Medical School, for some of the histological preparations, photographs and suggestions incorporated in this paper, and to Mr. James Atz, of the New York Aquarium staff, for criticism in the preparation of this paper.

## MATERIAL AND METHODS.

The hyperplastic epidermal growths were

found in bluegill sunfish for four consecutive years from 1938 to 1941. During this period about 200 diseased fish were examined. What percentage of the total population this number represented was not determined. All of the fish studied were sexually mature, measuring from 13 cm. to 24 cm. in standard length. Of this diseased group, 75% were females and 25% were males. Most of the fish were collected during the spring, at which time the epidermal growths were most extensive. Fish caught during this period were kept in aquaria and observed for over a year. They showed no further extension of the growths; instead there was a tendency for the hyperplasia to regress.

The fish were collected and stored in the pools of the Warmaug Black Bass Hatchery. Some were sacrificed, fixed and preserved in 10% neutral formalin. Others were shipped alive and placed in reserve tanks of the New York Aquarium at Battery Park, where the progress of the disease was studied. Skin lesions and various organs of the body were prepared for histological examination from preserved material. They were blocked in paraffin, sectioned at 3 and 6 microns and stained with hematoxylin-eosin and by Mason's, Giemsa's and Willhite's methods. Some scales with the growth were stained and mounted *in toto*.

Attempts at transmission were made, but in all cases negative results were obtained. Diseased fish were kept in tanks with normal-appearing bluegills and other fishes from the same area and with bluegills taken from a pond near Red Bank, New Jersey, for more than a year and a half. The New Jersey fish remained normal throughout the entire period of exposure. Dermal and intraperitoneal transplants of fresh and glycerinated material had no effect. Bits of the epidermal growth were transplanted into the anterior chamber of the eye of both normal and diseased bluegills. The tissue remained intact for several weeks but eventually was absorbed. No regeneration of the growth took place in regions where scales with the overgrowths were removed.

## DESCRIPTION OF THE HYPERPLASIA.

The epidermal hyperplasia is quite similar to the disease described from other fishes.

The disease appears as whitish papillomatous-like nodules or mucoid overgrowths on the skin of any part of the body (Figs. 1 and 3), but more frequently on the dorso-lateral surface (Fig. 2). They vary in size from that of a pin-point to 2-3 cm. in length and about 2-4 mm. in thickness (Figs. 3, 7 and 8). Some of the nodules are black or grayish in appearance due to the presence of melanophores (Fig. 5). The latter are not especially increased in amount.

The whole mounts of scales (Fig. 5) also show numerous needle-like crystals usually radially arranged and superficially placed. They measure from 10-25 microns in length, and are not alcohol or xylol soluble, nor do they stain with hematoxylin-eosin. Rod-shaped magnesium phosphate crystals were reported by Johnstone (1925) as impregnating the cutaneous warts of a plaice. The significance of these crystals in the epidermal hyperplasia of the sunfish and those found in the plaice is not known.

Histologically, the growth shows a great hyperplasia of epithelium without keratinization (Figs. 6-10). The hyperplasia appears to arise from the epithelium lining the scale pockets (Fig. 8). Here the cells may vary from the normal three or four layers to many layers as they grow over the scales (Figs. 4 and 7). The proliferating cells seem to follow the paths formed by the scale rings (Fig. 5). The hyperplasia consists of closely packed epithelial cells and epidermal elements around a central core originating from the corium (Figs. 6-8). Melanophores, capillaries, nerve elements and fibrous material are found in this core. In some areas the corium is edematous (Fig. 7) but no inflammatory reaction is evident.

The cells in the normal regions of the epidermis are typically flattened epithelial elements with mucus and sensory cells interspersed. As the cells proliferate along the surface of the scale they take on a more or less spindle shape (Figs. 5 and 9). They are eventually forced up into folds (Figs. 7 and 8), with the corial tissue growing into them (Fig. 8). Along these folds the epithelial cells are columnar with a somewhat thickened basement membrane (Figs. 7, 8 and 10). These cells form the basal elements of the hyperplasia. The outermost cells take on a polyhedral and squamous appearance, and seem to be connected with each other by intercellular bridges, which probably accounts for the rigidity of the growth (Fig. 10). In hematoxylin-eosin and Giemsa's preparations the cells stain homogeneously, each with a typically appearing nucleus. No nuclear or cytoplasmic inclusions are seen in these or in Willhite preparations made for this purpose. Pro-chromosomes are evident in many of the nuclei (Figs. 9 and 10), and typical mitotic figures occur frequently (Fig. 10). Numerous mucus cells are present (Fig. 8). These are more prominent around the

periphery but they may be clustered in any area of the growing tissue. Occasionally they are arranged around a central lumen forming a follicle-like structure (Fig. 11). The secretion within the lumen stains pink or yellowish with Giemsa's and green with Masson's. Sensory cells in the epithelium are not involved in the hyperplasia.

Fishes caught later in the year show many regressive changes. The orderly formation of cell layers, as seen in Figs. 6 and 10, gives way to a disorganized growth. Many of the epithelial cells appear oval in shape with scanty or vacuolated cytoplasm, pyknotic nuclei and with karyorrhexis evident here and there. With Masson's, the tissue gives a metachromatic picture. There is a tendency for the peripheral cells to slough (Fig. 14), and those in the interior of the growth to form epithelial cyst-like bodies (Fig. 12). In some areas there is an abortive attempt to regenerate as evidenced by the presence of cells undergoing mitosis in regions showing considerable degeneration. Eventually, the hyperplastic tissue is invaded by macrophages and degeneration becomes more extensive.

The ecto-parasitic ciliates, *Trichodina* and *Ichthyophthirius*, are found associated with the disease in every preparation studied. The *Ichthyophthirius* is encysted in the growth, while *Trichodina* is found free on the surface (Figs. 13 and 14).

There is no evidence of invasion into the sub-dermal region, nor is there any evidence of metastatic growth. Sections of the various internal organs appear normal. The indications are, then, that the hyperplastic epidermal disease of the bluegill sunfish, as in other freshwater and marine fishes, is a benign regressive disease.

#### DISCUSSION.

Epidemiologically, the epidermal hyperplastic disease in cyprinids and in the bluegill sunfish gives evidence that an infectious process may be involved. The occurrence of the hyperplasia in the same species of fish, and in the same pond or lake year after year would point in that direction. In the European fish, the disease is usually endemic during the warmer months. In certain years epidemics have been reported throughout the continent, but more often it occurs only sporadically. In one lake, Jasmunder Bodden, in northwest Germany, 20% of the cyprinids (carps, ides, breams, etc.) collected during the summer were found affected (Plehn, 1924). In the bluegill sunfish, the disease was found more commonly during the spring. Fish caught in this period showed more extensive growths than those collected later in the year. In addition, stained sections of material collected in the spring presented more mitotic figures than that prepared from material collected in the summer. The hyper-

plastic growths in the latter group showed considerable degeneration and regression.

The exact cause of the hyperplasia, however, still remains unknown. It is interesting to report that in every instance a parasite has been found associated with the disease. Thus Hofer (1904) and Doflein (1898, 1928) recorded the presence of a histozoic myxosporidian, *Myxobolus cyprini*, and inferred that this organism might have been responsible for the hyperplasia, even though the protozoan infection was localized in the kidney, liver and spleen. Related cnidosporidians (myxosporidians and microsporidians) associated with tissue hyperplasia in other fishes have been demonstrated by several investigators: Kudo (1919, 1924), Nigrelli and Smith (1938, 1940), Nigrelli (1948). As pointed out by the latter, "Intercellular and intracellular cnidosporidians elaborate proteolytic enzymes and other chemical substances which may be responsible for considerable cellular degeneration, cell hypertrophy and other tissue responses noted in these infections. It is altogether possible that chemical substances elaborated by the developing parasites may have a stimulating growth factor which may diffuse to more distant areas either directly or through the circulation."

Other parasites have been associated with the lesions in cyprinids and other fish. Thus, Plehn (1924) reported that the fish louse, the copepod *Argulus*, occurred frequently on the diseased fish, while Smith (1935) showed that winter flounders with hyperplastic epidermal disease were infected with the metacercarial larvae of the digenetic trematode *Cryptocotyle lingua*. In the diseased bluegill sunfish the ciliates *Trichodina* and *Ichthyophthirius* were present in the overgrowths.

Plehn (1924) believed bacteria to be the primary agent responsible for the hyperplasia, as interpreted by her statement, "Durch infektion gesunder Fische mit Karpfenläusen von den kranken konnten solche Wundpocken experimentell hervorgerufen werden. Da der stich des *Argulus* gewöhnlich diese Wirkung nicht hat, liegt die Annahme nahe, dass der Parasit nur als Ueberträger einer anderen Infektion wirkt; vielleicht sind es Bakterien, die die Hautwucherung veranlassen." It is also possible that *Argulus* and other parasites encountered in fishes showing these lesions may be the vector for a virus. A viral agent was indicated by Loewenthal (1907), who found inclusion bodies in the epithelial cells of diseased European cyprinids. The possibility that *Argulus* transmitted a virus was discussed by Thomas (1931), who attributed this suggestion to Plehn. Smith (1940) considers the disease to be caused by a virus on the basis of Loewenthal's findings. That parasites can and do transmit viral disease is known for higher animals, e.g. swine influenza and salmon poisoning in dogs and men. The former is

transmitted by the larvae, which occur in earthworms, of the nematode *Metastrongylus elongatus*; and the latter by the metacercarial larvae, which encyst in the flesh of salmon, of the digenetic fluke *Trogloctrema salmonicola*.

It should be pointed out that ectoparasites are found frequently on fishes (Nigrelli, 1943) and in many instances a simple thickening of the skin (corium and/or epithelium) is involved. This is particularly so in the case of infections with *Ichthyophthirius*, a parasite of world-wide distribution. These Protozoa obtain nourishment by feeding on the host tissue cells. Fishes are susceptible to them during periods of varying temperature, which probably accounts for their presence in large numbers, at least in the temperate zone, during the spring. Under these temperature conditions the parasites enter the skin and may be overgrown with epithelium. Whether or not the simple hyperplasia of the epithelium often noted in these infections takes place at the time of active feeding or during the encystment process is not known. It is well known, however, that many parasites are capable of inducing the development of host fibrous tissues, especially during their process of encystment, and it is also probable that a hyperplasia of epithelial tissue may be another manifestation of this response, as in the case of papillomatous diseases associated with parasites (Nigrelli and Smith, 1940).

Schäperclaus (1935) suggested that the hyperplastic epidermal growth occurring in European cyprinids was a manifestation of a nutritional deficiency, but gave no evidence to support this. Nevertheless, this hypothesis finds some support in the work of Wolf (1945) on the "gill disease" of trout. This disease was manifest as a hyperplasia of the epithelium of the gills of trout fingerlings. Wolf considered this hyperplasia a response to chemical irritants, fish waste products, present in hatchery waters. He further pointed out that the susceptibility to the irritants was increased in those fish kept on a pantothenic acid deficient diet. A similar process may be involved in the epidermal hyperplasia of the bluegill sunfish and in other fishes in which this disease has been reported.

One consistent feature of the hyperplastic epidermal disease of fishes is the presence of parasites. Bacterial, protozoan, helminthic or arthropod parasites have been reported in all cases. Only in one instance (Loewenthal, 1907) were inclusion bodies described. Also, with one exception (Plehn, 1924), all attempts to transfer the disease to normal fish gave negative results. The infective agent in this exceptional case was bacterial, but the evidence was not conclusive. It may be concluded, then, that the epidermal hyperplasia found in fishes, is the response of sus-

ceptible hosts to toxic or mechanical irritants produced by parasites.

SUMMARY.

A hyperplastic epidermal disease, similar to "carp-pox," is described in bluegill sunfish, *Lepomis macrochirus*. The disease was endemic in a lake near New Preston, Connecticut, for the four consecutive years from 1938-1941. During this period 200 diseased fish were collected and studied. The lesion is characterized by papillomatous-like nodules or patches and histologically consists of an extensive hyperplasia of epithelial cells and other epidermal elements supported by a delicate stroma. Parasitic infection of the skin with the ciliates *Trichodina* and *Ichthyophthirius* is present, the latter embedded deep in the epithelium. All attempts to induce the disease in normal fish from this and other localities were negative. The disease is a benign regressive hyperplasia, since no invasion of the underlying structures or metastases were found.

The possible role of parasites, chemical irritants and dietary deficiencies in the production of this and similar hyperplastic epidermal growths in fishes is discussed.

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## EXPLANATION OF THE PLATES.

## PLATE I.

- FIG. 1. Bluegill sunfish, *Lepomis macrochirus*, with epidermal hyperplastic mucoid-like patches. Such extensive growths are present especially in the spring. Slightly less than natural size.
- FIG. 2. Fish with patches in the dorso-lateral region, the usual position of these abnormal growths. Such fish are caught frequently during the summer months. Slightly less than natural size.

## PLATE II.

- FIG. 3. Hyperplastic epidermal growth, showing papillomatous-like arrangement. About 3 X.
- FIG. 4. Isolated scales showing the nature of the overgrowth. Note that each scale's nodule is discrete. About 7 X.

## PLATE III.

- FIG. 5. Scale mounted *in toto*. Note the distribution of melanophores, extension of the hyperplastic growth along pathways formed by the scale rings and needle-like crystals interspersed throughout. **n**, needle-like crystals; **e**, extension of growth. Hematoxylin-eosin. 75 X.
- FIG. 6. Hyperplastic epidermis with stroma penetrating from the corium. This is a section of growth taken from a fish caught in the spring. Note the orderly arrangement of the cells and lack of any degenerative changes. **c**, corium; **s**, scale. Hematoxylin-eosin. 75 X.

## PLATE IV.

- FIG. 7. Section showing the upfolding of the growth. Note the cellular arrangement and thickened basement membrane of the columnar cells. The corium is slightly edematous. **c**, corium; **s**, scale; **bm**, basement membrane. Hematoxylin-eosin. 80 X.
- FIG. 8. Section of nodule. The light vacuolated bodies are mucus cells. Giemsa. 75 X.

## PLATE V.

- FIG. 9. Epithelial cells as elongate, fibroblastic-like elements, growing out from the base of the growth. Note the mass of blood elements on the right. Hematoxylin-eosin. 675 X.
- FIG. 10. Details of the growth shown in Fig. 6. From the corium in the lower left, the columnar epithelial cells radiate out and become polyhedral and flattened elements towards the periphery. Most of the nuclei are in the pro-chromosomal stage, but some mitotic figures can be seen. Hematoxylin-eosin. 675 X.

## PLATE VI.

- FIG. 11. Follicle-like arrangement of mucus cells. Masson. About 1,000 X.
- FIG. 12. Cyst-like body formed by epithelial cells. Hematoxylin-eosin. 1,000 X.

## PLATE VII.

- FIG. 13. A single *Ichthyophthirius* embedded deep within the hyperplastic epithelium. Note the numerous ingested epithelial cells. Masson. 900 X.
- FIG. 14. *Trichodina* on the surface of the growth. Note the degeneration of peripheral cells, pyknotic nuclei and sloughing. Hematoxylin-eosin. 675 X.



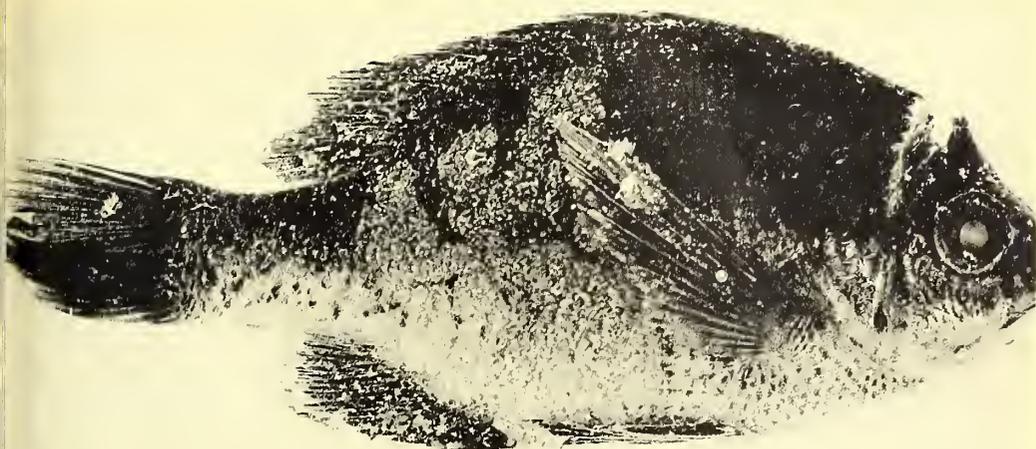


FIG. 1.

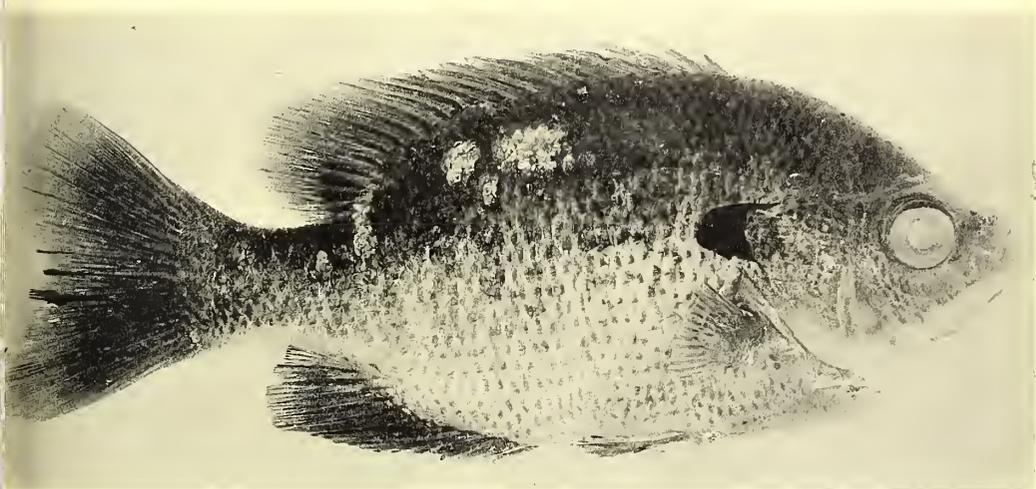


FIG. 2.

HYPERPLASTIC EPIDERMAL DISEASE IN THE BLUEGILL  
SUNFISH, *LEPOMIS MACROCHIRUS* RAFINESQUE.



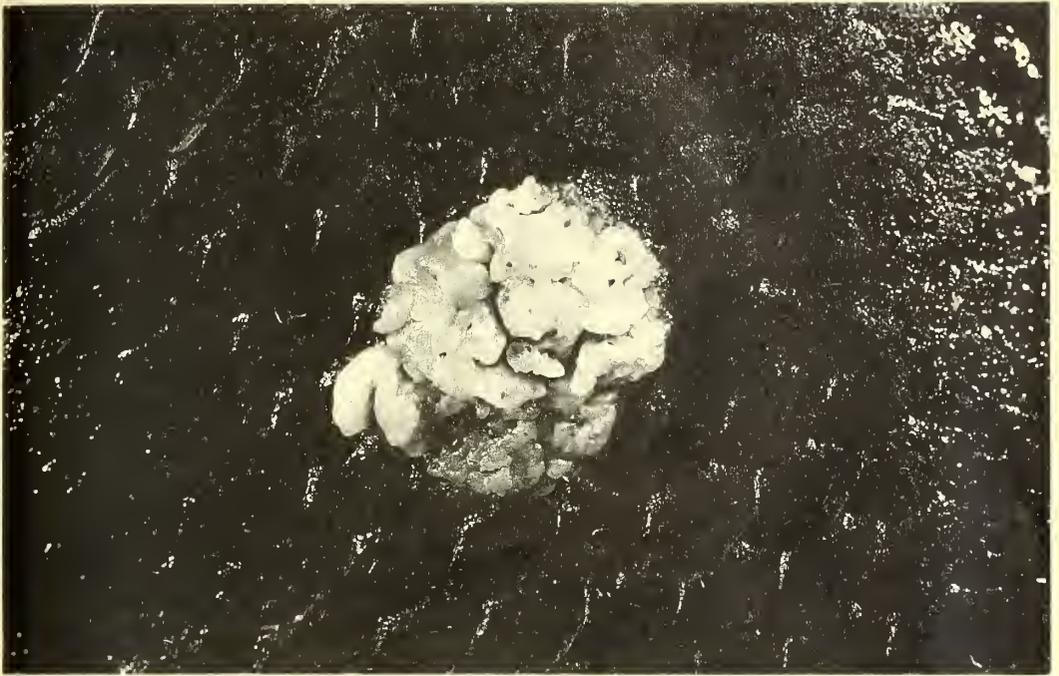


FIG. 3.

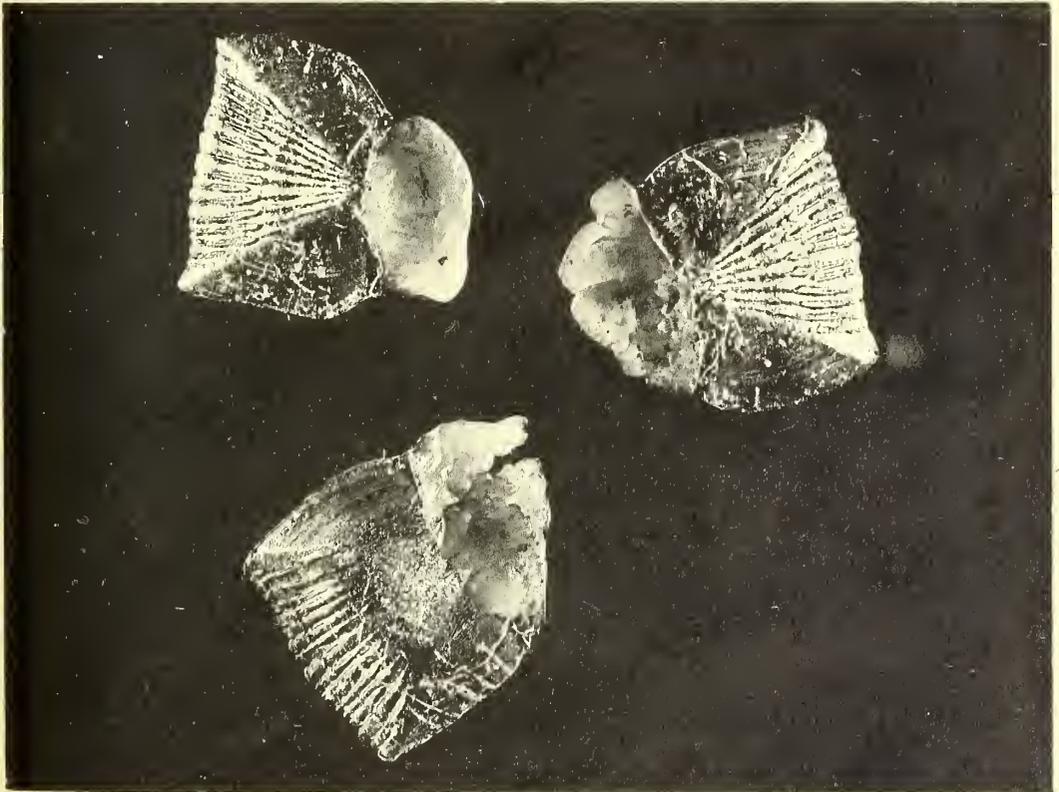


FIG. 4.

HYPERPLASTIC EPIDERMAL DISEASE IN THE BLUEGILL  
SUNFISH, *LEPOMIS MACROCHIRUS* RAFINESQUE.



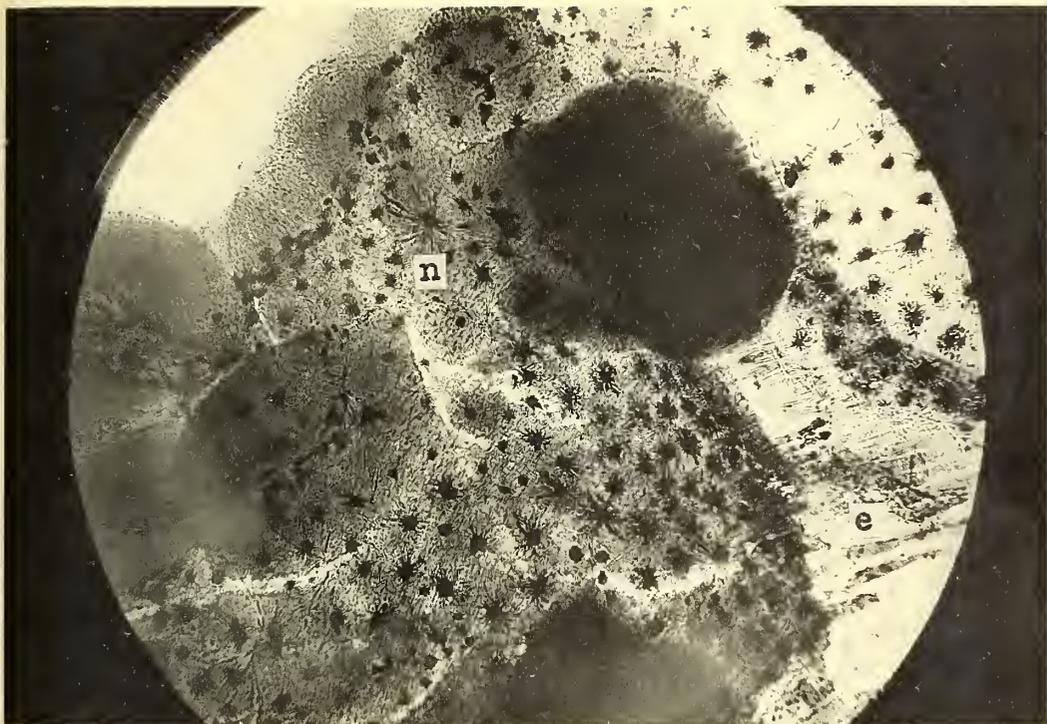


FIG. 5.

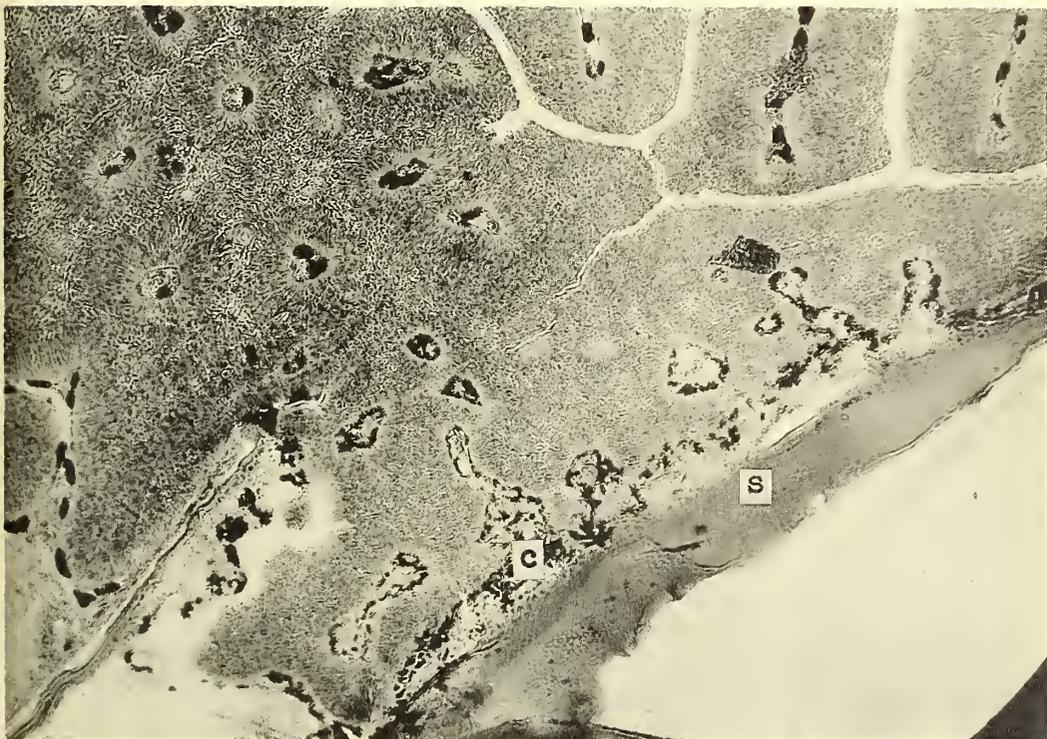


FIG. 6.

HYPERPLASTIC EPIDERMAL DISEASE IN THE BLUEGILL  
SUNFISH, *LEPOMIS MACROCHIRUS RAFINESQUE*.



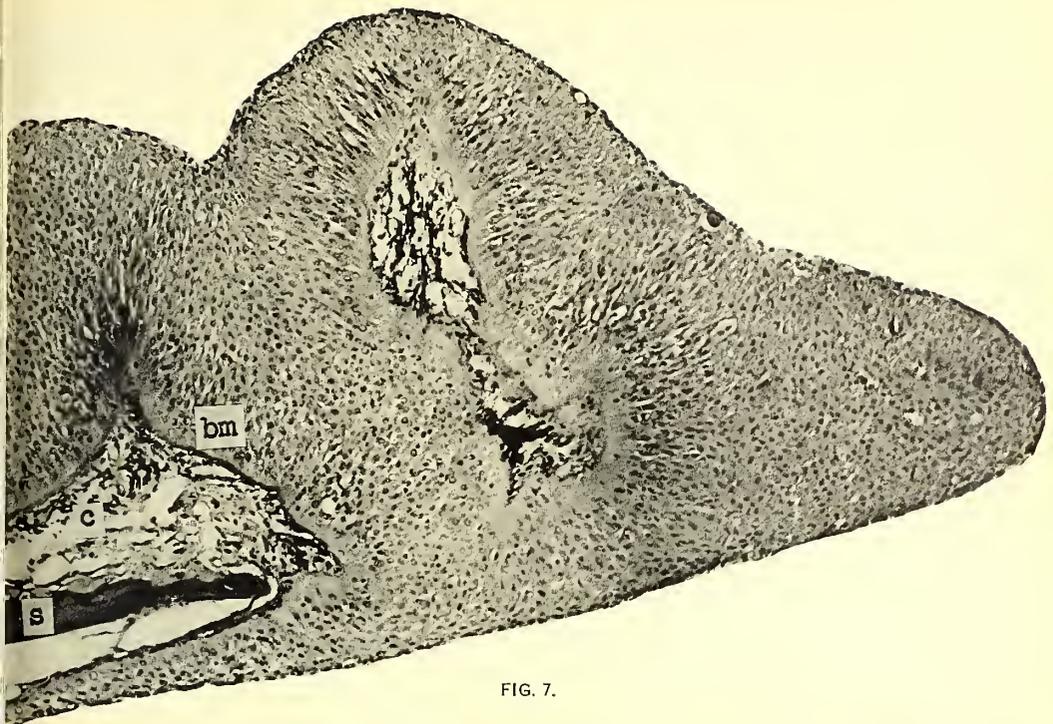


FIG. 7.

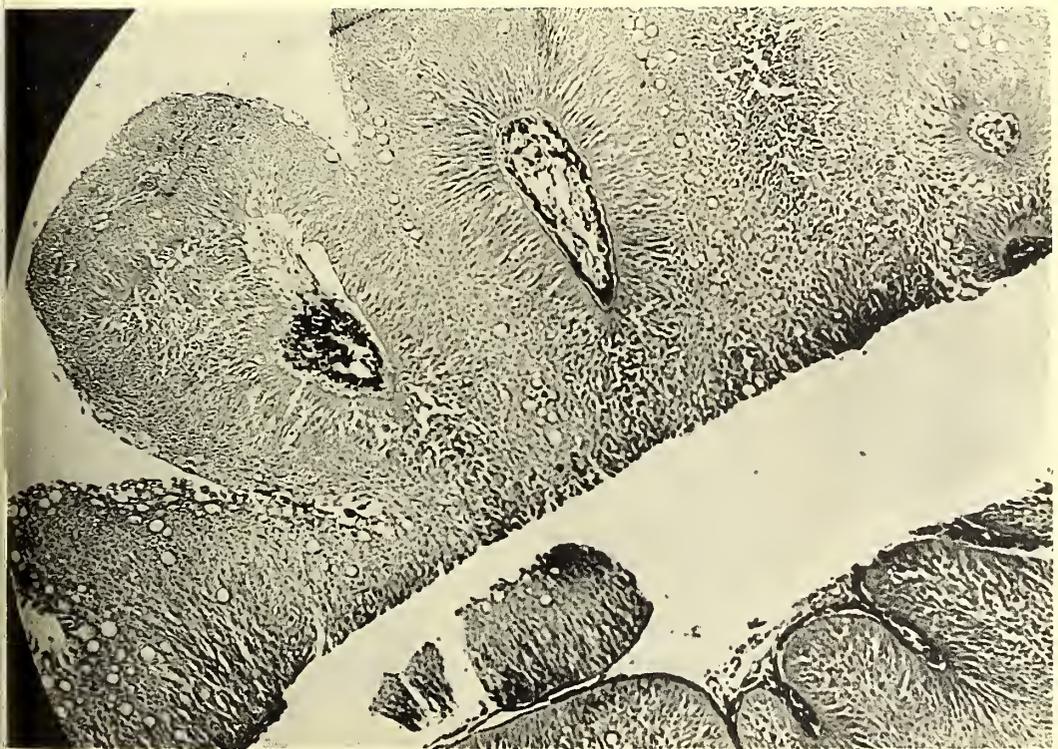


FIG. 8.

HYPERTROPHIC EPIDERMAL DISEASE IN THE BLUEGILL  
SUNFISH, *LEPOMIS MACROCHIRUS* RAFINESQUE.



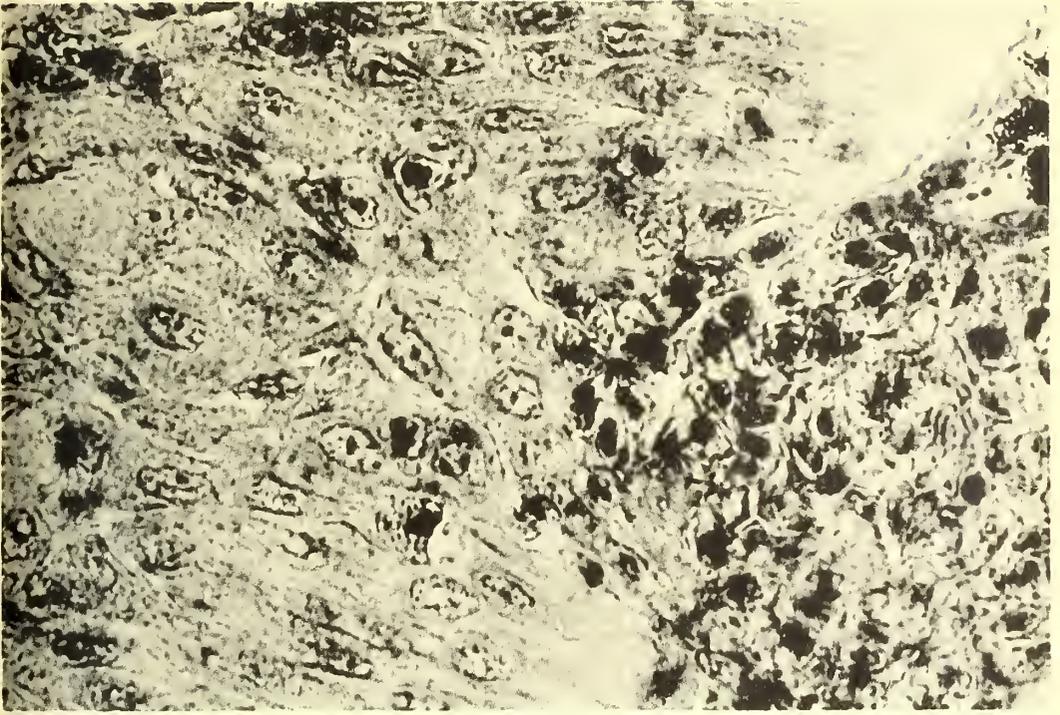


FIG. 9.

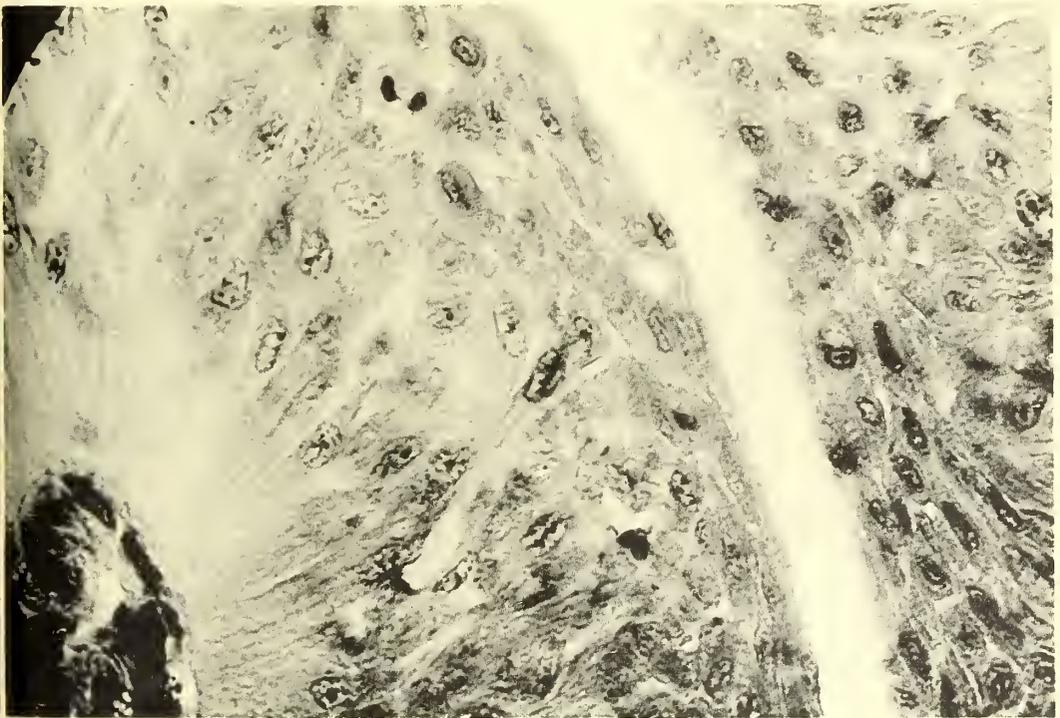


FIG. 10.

HYPERPLASTIC EPIDERMAL DISEASE IN THE BLUEGILL  
SUNFISH, *LEPOMIS MACROCHIRUS RAFINESQUE*.



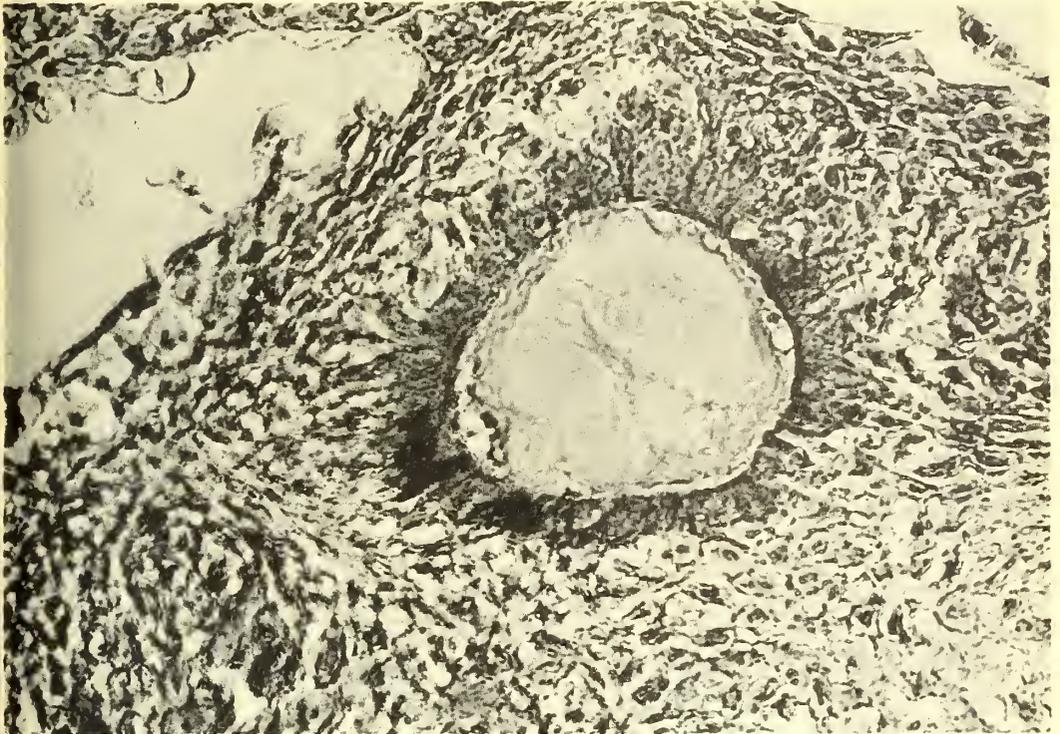


FIG. 11.

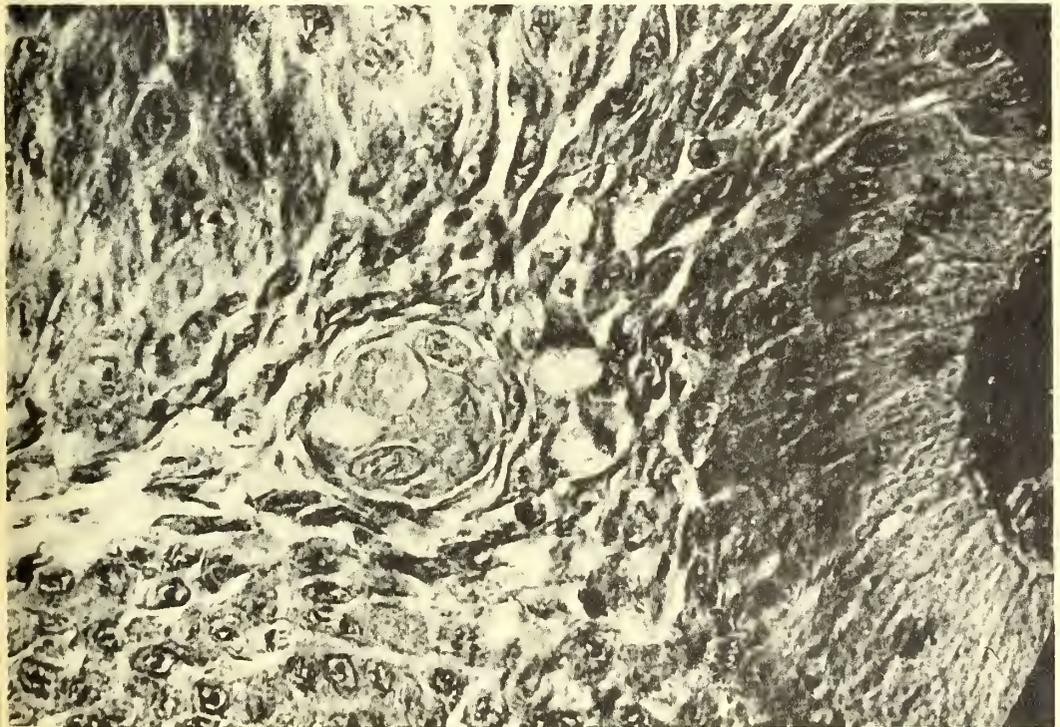


FIG. 12.

HYPERPLASTIC EPIDERMAL DISEASE IN THE BLUEGILL  
SUNFISH, *LEPOMIS MACROCHIRUS RAFINESQUE*.



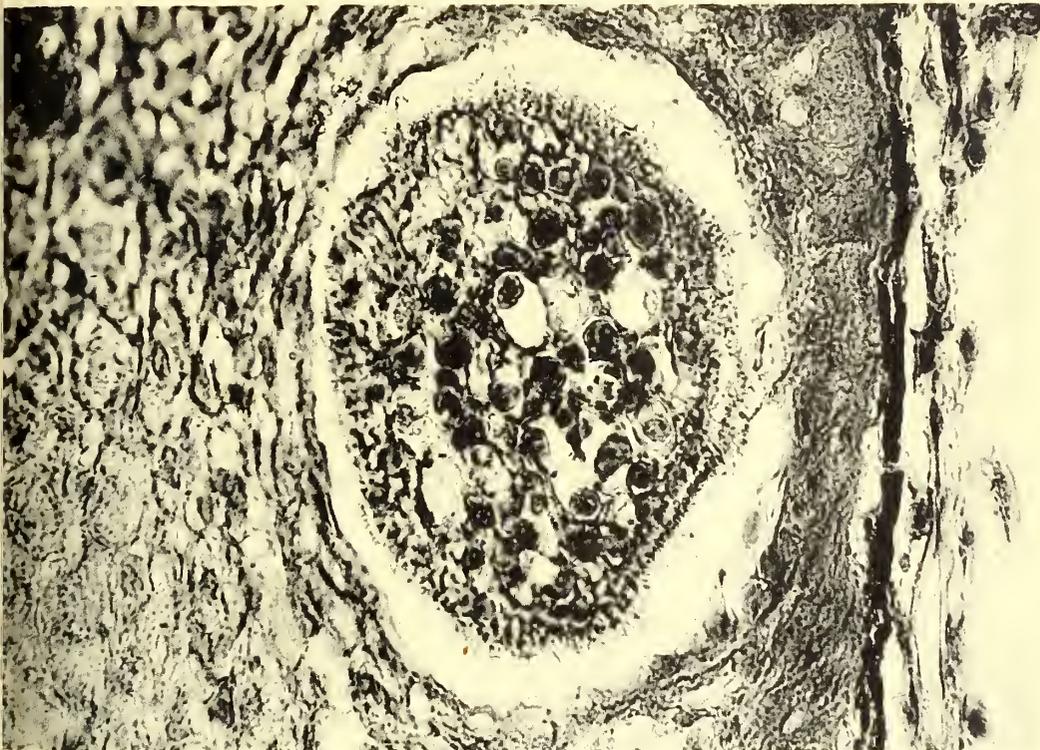


FIG. 13.

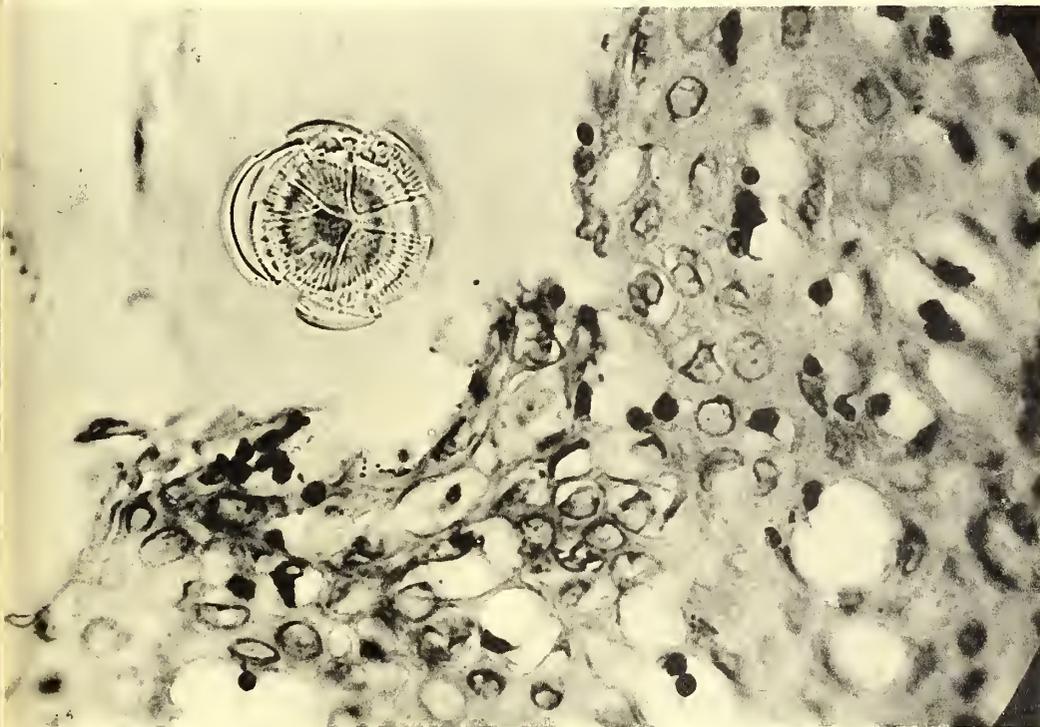


FIG. 14.

HYPERPLASTIC EPIDERMAL DISEASE IN THE BLUEGILL  
SUNFISH, *LEPOMIS MACROCHIRUS* RAFINESQUE.



## 9.

Comparative Biology of Salticid Spiders at Rancho Grande, Venezuela.  
Part II. Methods of Collection, Culture, Observation and Experiment.<sup>1</sup>

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[This is one of a series of papers resulting from the 45th, 46th and 47th Expeditions of the Department of Tropical Research of the New York Zoological Society, made during 1945, 1946 and 1948 under the direction of Dr. William Beebe, with headquarters at Rancho Grande in the National Park of Aragua, Venezuela. The expeditions were made possible through the generous cooperation of the National Government of Venezuela and of the Creole Petroleum Corporation.

[The characteristics of the research area are in brief as follows: Rancho Grande is located in north central Venezuela (10° 21' N. Lat., 67° 41' W. Long.), 80 kilometers west of Caracas, at an elevation of 1,100 meters in the undisturbed montane cloud forest which covers this part of the Caribbean range of the Andes. Adjacent ecological zones include seasonal forest, savanna, thorn woodland, cactus scrub, the fresh water Lake Valencia, and various marine littoral zones. The Rancho Grande area is generally subtropical, being uniformly cool and damp throughout the year because of the prevalence of the mountain cloud cap. The dry season extends from January into April. The average humidity during two expeditions, including parts of both wet and dry seasons, was 92.4%; the average temperature during the same period was 18° C.; the average annual rainfall over a 5-year period was 174 cm. The flora is marked by an abundance of mosses, ferns and epiphytes of many kinds, as well as a few gigantic trees. For further details, see Beebe & Crane, *Zoologica*, Vol. 32, No. 5, 1947.]

experimental work (Crane, 1948). The applications and results of the techniques outlined in the final section of this paper will be reported in future publications. All of the experimental salticid work at Rancho Grande has been concerned with a comparative study of the innate releasing mechanisms of the epigamic displays in various genera. The ultimate aim is two-fold: first, to work out evolutionary patterns within the family, with particular attention to the relationships between function and structure; second, to compare and correlate the mechanisms in this family with those in unrelated groups, in accordance with the stimulating work of Lorenz, Noble, Lack, Tinbergen and their associates, who have been concerned almost exclusively with vertebrates (e.g., see Tinbergen, 1948, with bibl.).

The study of living salticids is one of the most continuously fascinating and ultimately rewarding of zoological pursuits. Nevertheless, the pioneering Peckhams were quite right when they warned enthusiastic readers, some sixty years ago, against going in for such a study casually. Deep appreciation is due them and all the more recent students of live salticids, including particularly Bristowe, Bonnet and Kaston, who, working patiently in the brief northern summers, have recorded and studied many salticid displays.

The tropics have the great advantage of leisurely seasons combined with large numbers of species. Nevertheless, just as in the north, it is essential to be on familiar terms with the local forms, with their restricted niches, relative abundance and specific idiosyncracies. Also, it is most important to remain in a single locality for as many months of as many years as possible: tropical salticids, although they may be carried north successfully, have their innate rhythms disturbed, becoming irregular in their moults and erratic in activity after the trip.

In some ways tropical salticids are ideal experimental animals. The variety of behavior and correlated structures in closely related forms makes them of peculiar interest in the study of basic evolutionary problems. They are, under proper conditions, exceedingly hardy. Their food supply is usually easily arranged. Individuals have an active

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## I. INTRODUCTION.

The following pages describe the general methods of working with jumping spiders at Rancho Grande, Venezuela. Although some of the field techniques are axiomatic to experienced arachnologists, they are included here for completeness, since they may be helpful to new students of the group, or to those who have not worked in the tropics.

Part I of this series dealt with systematics and life histories in *Corythalia*, excluding

<sup>1</sup> Contribution No. 816, Department of Tropical Research, New York Zoological Society.

adult life of at least one month and usually two or more. The breeding seasons of most species extend over months, and sometimes throughout the year. Most important, these spiders are extremely adaptable to captivity, and adequate comparative observations in both field and laboratory indicate no differences whatever in basic behavior patterns.

Nevertheless, rearing and experimenting with salticids is a finical business. Although the adults are giants compared to *Drosophila*, they are pygmies to a guinea pig, and any trainer of jumping fleas would feel more promptly at home with them than a gifted researcher accustomed to monkey and mice. Rare or experimentally important spiders escape, get squashed or eaten, and inexplicably die at the most inopportune moments. Cloud forest species may be killed in a night if moisture is withheld; xerophytic forest forms can die in three days through too much humidity. An extra whiff of chloroform during some simple operation may ruin forever the future display performance of a valuable male. A rare and delicate female, reared, mated, fed and tended with difficulty through half a year, to secure an evolutionarily significant first instar, ultimately laid nothing but three bad eggs.

Not the least of the exasperations of behavior students in tropical localities is the fact that most salticids turn out to be little known or altogether new, necessitating a great deal of fundamental taxonomic work. Two exceptional neotropical regions are Panama and the West Indies, their spider fauna having been clarified in the excellent recent reports of Chickering (e.g., 1946) and Bryant (e.g., 1943), respectively.

Genetical work is greatly needed in the group and is almost an untouched field. As subjects, however, salticids are only moderately suitable. Few species so far tested breed reliably in captivity. The usual length of a generation averages perhaps six months, and so is too long to be convenient. The broods are small, the total number of eggs laid by a female of average size in many genera never reaching more than thirty, and sometimes numbering less than ten. To rear to maturity even four or five young of a given brood has so far been accomplished only several times at Rancho Grande, and second generation offspring of captive specimens have only been secured twice. However, these mechanical rearing difficulties are directly traceable to the fact that many species were under simultaneous observation, and that no stay in the laboratory was longer than six months; a geneticist who restricted his choice of work species with knowledge and care, and could keep the broods going continuously through, say, two years, would have results of great value.

Finally, any zoological investigator who is fortunate enough to pass sufficient time in a permanent tropical laboratory, will find a field of immense interest in salticid spiders, if he has an inclination for studying complex

behavior and evolutionary problems in a relatively unfamiliar group. Although he will quickly work out his own improved techniques, the following suggestions may save him a number of time-consuming trials and errors.

## II. COLLECTING METHODS.

The principal collecting method was the shaking of bushes and branches into a large, inverted umbrella, the specimens being caught in vials as they ran up toward the rim. Because of the steep terrain and tangled, chronically damp vegetation around Rancho Grande, the umbrella method was more efficient and convenient than the equally popular systems of spreading a sheet under the foliage to be shaken, or sweeping the shrubs with a net. *Corythalia* and other primarily terrestrial forms were located by simple visual searching in the right habitats, and were secured in inverted vials, this method proving more effective for the surface-living jumpers than the sifting of leaves. A few salticids were collected on tree trunks and in epiphytic bromeliads. The latter were detached by our tree-climbing Venezuelan assistants, lowered carefully upright to the ground with a light rope, and either dissected over a poncho on the spot or wrapped up and brought intact to the laboratory.

Salticids wanted for study alive should never be risked in the same vial with any other spider, even though their sizes appear so nearly equal that there seems to be small danger of one's eating the other; different species and even individuals differ greatly in aggressiveness and voracity. The most convenient way of carrying a sufficient number of vials up and down mountains is in two light-weight cotton bags—snake-collecting bags are excellent—with drawstring tops; they can be slung over each shoulder, or hung at the belt. With empty vials in one bag and used ones in the other, there is neither delay nor confusion when a single umbrella-shake suddenly yields a half dozen much-desired and extremely agile jumping spiders.

Collecting during or soon after a rain is not rewarding, since salticids then cling their tightest or even go into their night-time shelters, and the water from the shaken leaves is likely to drown whatever spiders there are. Nevertheless, in choosing seasons for tropical collecting, the drier months should be avoided, since salticids are then often impossible to find in deciduous woods, scrub and savanna, and are relatively scarce even in rain and cloud forests.

The richest collecting areas for salticids in northern South America have always proved to be neglected clearings and the edges of forest roads or paths. The forests themselves are uniformly poor, as are open savannas. Unfortunately, no collecting has yet been done high in the forest canopy; that well-lighted niche should prove remarkably rich whenever an adequate system of arboreal locomotion can be devised.

Although many salticids live in the temperate zone, the display season is usually brief and the winter a period of inactivity. In contrast, the great majority of salticids are tropical, so that far more material is available to the student in low latitudes. More important for behavior studies, the tropical breeding season is always prolonged and sometimes, it seems, perennial, so that growth and display may be observed throughout the year in sufficiently humid localities.

### III. MAINTENANCE AND CULTURE.

A number of excellent methods have been worked out for keeping various families of spiders alive in the laboratory, among which may be mentioned those of Bonnet (1930), Branch (1942) and Brown (1945). The salticids, however, have always proved difficult. The Peckhams (1889) reared one female salticid through ten molts, but she died before becoming mature. Wagner (1888) also had some success, but does not give details. Moles (1916) reared various families, but could not bring salticids through the early instars. Bonnet's first attempts to rear salticids failed, although he had great success with other groups; finally, however (1933), he reared a brood of *Philaeus regius* to maturity and was able to breed the resultant adults with each other.

The method described below is an adaptation of various techniques of spider and insect culture, and was necessitated both by the sensitivity of the spiders to drought and by the special conditions at Rancho Grande. High humidity was essential to these cloud forest spiders, while the laboratory was relatively dry; yet the spiders could not be kept in stoppered vials with moistened corks, because excessive mold often developed overnight.

The method which eventually proved successful was the following. It involved the care of an average stock of about 75 individuals, exclusive of first and second instar broods. All spiders, except mated pairs, were kept in individual cylindrical specimens jars, measuring  $1\frac{1}{2} \times 2$ ",  $2\frac{1}{4} \times 3$ " or  $3 \times 3\frac{1}{2}$ ", depending on the size of the spider. The largest size was reserved for large mated pairs or for females with egg cases; individuals did not do better in ample space than in the minimum-sized jars assigned, and to save space and for convenience they were given the smallest size feasible. Strong, fine-mesh, khaki-brown mosquito netting, of regular army grade, was used for covers and secured by rubber bands. The most convenient jar labels proved to be a self-adhesive type put out by the Avery Adhesive Label Corporation of Los Angeles, California; pencilled data in regard to molts, etc., could be erased and changed repeatedly. The jars were kept on a special table near the laboratory windows, in excellent light but away from the direct sun. Jars of experimental adults were kept well

separated, in order to avoid the effects of summation, reinforced stimuli and overstimulation before experiments, since some individuals display on a visual sign-stimulus alone, even through the distortion of two curved glass walls.

Each jar contained a small cylinder of cotton dental wadding 10 or 15 mm. long by about 6 mm. in diameter. This was saturated, although not to the dripping point, every two to four days. The optimum condition seemed to be that it should be practically dry before remoistening. The spiders could all stand prolonged fasting; some survived after several hours in the refrigerator and a few could withstand moderate heat; drought, however, killed all kinds rapidly.

The spiders were fed on *Drosophila* and other small flies several times a week. Since wild *Drosophila* and houseflies were practically absent at Rancho Grande, while small flies of other groups were abundant in the caretakers' cottages, only two or three jars of breeding *Drosophila* were maintained, and were used for emergencies only. Vials full of the other flies were easily captured at night, attracted to a flashlight from the cottage walls and ceilings where they roosted. The quickest feeding methods for our collections proved to be the following: a vial of flies was lightly chloroformed with a moistened cork and decanted onto white cardboard. About three to six flies were then brushed lightly into each jar, after the dental wad had been dipped in water. Where reared *Drosophila* were used, a large group was allowed to escape into a jar inverted over the breeding bottle, and a card with a chloroform-saturated bit of cotton slipped across the aperture; afterwards the stupefied flies were brushed as before into the spider jars. This proved simpler and faster than permitting the requisite number to escape directly into each jar through a small opening in the top of the fly bottle. The spiders became so tame that they were completely undisturbed by the routine. A light tap sent them away from the netting tops. The young, when about to molt, usually spent at least two or three days in their cocoons, never eating at this time; these were disturbed as little as possible, but the wad had to be dampened. Even when the cocoon was spun at the junction of netting and glass, a little care avoided injury. The jars were cleaned about every ten days.

Naturally there were frequent accidents and escapes, especially during transfers to and from observation dishes (see below). One source of trouble was the rubber bands which rotted quickly in the climate and tended to break without warning. Another was an occasional incursion of small ants, who scavenged among the dead flies in the jars, leaving tiny holes in the netting large enough for the escape of small spiders. In a lowland tropical laboratory, ants would be a real nuisance which, however, could easily be prevented by the time-tested custom of

standing table legs in kerosene or wrapping them in poisoned "ant tape." Major and unexplained pests were the mites which often appeared in egg cases. It now seems certain, however, that they attack only bad eggs or dead spiderlings; dead flies in the jars were never touched. Their method of dispersal is a puzzle; infected jars were always carefully cleaned before re-use.

Young spiders were usually removed from their mothers as soon as they emerged from the cocoon, although there was not a single case of cannibalism between mother and young, or between first or second instar spiderlings, in any of the salticids under observation. Two or three second instar spiders could be kept in a single small jar, but were usually segregated before the next molt. A few individuals of placid-tempered species were reared together almost to the adult stage.

No food is taken during the first instar, but is essential during the second. Incidentally, none of the tropical salticids studied spend more than the first instar in the cocoon. During the second, tiny live creatures from the leaf litter were given, collembola and minute worms being the most acceptable to small forms such as *Corythalia xanthopa*. This is the most crucial period of rearing and few individuals were brought through it. As soon as a spider had eaten one meal, it was ready to tackle a wriggling but de-winged *Drosophila*, even though the fly was always considerably larger than the spider. Larger species could seize de-winged *Drosophila* as their first food. Dr. Ernst Mayr and Dr. T. Dobshansky, in conversation, have made the sensible suggestion that a culture of wingless *Drosophila* mutants would be helpful in feeding the youngest specimens on a large scale. Before the second instar was over, the sturdiest individuals could catch normal *Drosophila*, and several *Corythalia chalcea* in one brood caught them as first food. Certain aphids were acceptable to the very young in emergencies, but were not good as a steady diet. I had no success in inducing young salticids to feed on freshly killed and punctured insects, since they never showed any interest in a motionless body (cf. Mole's successful rearing of other families by this method, 1916).

#### IV. METHODS OF STUDY AND EXPERIMENT.

*Color Records.* It was essential to record colors from living specimens. The general aspect was described from non-anaesthetized examples in vials under a binocular microscope. Details of scalation were recorded after a specimen was chloroformed. Variations proved to be so great in some species that it was essential to make complete descriptions of a number of examples of each available instar; this was particularly important since, to begin with, nothing was known of the number of instars, their appearance, sexual differences in the young, or even the identity of many examples. The

latter differed so greatly from the adult, or so resembled the young of various species in a single genus, that they had to be reared and only the exuviae preserved. Detailed descriptions and pattern sketches of the young were particularly important since evanescent color patterns are proving exceedingly helpful in working out phylogenetic relationships.

*Drawings.* Sketches of displays and color pattern were made from the living spider, the exact proportions being worked out from preserved examples. All display drawings were completed in the field, so that final details could be checked from other displaying individuals.

Attention may be called here to an excellent technique recently reported by Dr. Kaston (1948, p. 47), giving credit to Miss Kathryn Sommerman. Palps and other parts may be easily held for hours in any desired position by first placing a bit of vaseline in the bottom of the dry observation dish. The specimen is then partly imbedded before alcohol is flowed in.

*Study of Exuviae.* The cast skins are best preserved dry, each in a separate vial with a bit of absorbent cotton. They become entangled in the strands just enough to cling when the cotton is removed with forceps. They can be repeatedly taken out for study, comparison and drawing, without damage and with minimum danger of being blown off the stage by an unwary breath. Yet the tangling is so slight that they can be easily manipulated, or legs and other parts detached at will and mounted for high-power study.

*Preservation.* Except for exuviae, all specimens are preserved directly in 70% alcohol. Early instars needing repeated removal from vials during study are also best tangled in a few strands of cotton.

*Display Observation.* Fortunately, the displays of a number of the reared species, belonging to widely separated genera, were observed in the field, in various degrees of completeness. In every case, the threat and courtship display behavior was identical with that recorded under laboratory conditions. Some of the experiments were also repeated successfully, using uncaptured spiders in their natural environment; the results of these corresponded closely to those in the laboratory. They will be described in detail in subsequent reports. The important point here is that captivity has no apparent effect on the display behavior patterns of salticids.

The most convenient vessel for display study in the laboratory is a shallow glass dish, measuring at least  $4 \times 4 \times 2$ " and covered with a piece of window glass. The aeration system described by the Peckhams (1889, p. 37) is unnecessary in these studies, since the spiders are kept in the dishes for a few hours at most. Transfers from jar to dish are made with a  $3 \times 1$ " vial, the spider being gently prodded when necessary with a camel's hair brush. Spiders in display condition (see below) never need more than a

few minutes to settle down in their new surroundings. The glass dishes are particularly suitable for experiments, since they can so easily be scalded, wiped with alcohol and aired, in order to remove chemical traces of previous occupants.

A simpler display study technique is applicable to some salticids which, while having especially good eyesight, depend relatively little on chemotactic and/or smell stimuli. Their displays may be studied on an open table, the danger of persistent chemotactic stimuli being eliminated by using a fresh sheet of white or light-colored paper for each test. Various tints of blue, green, yellow and gray made no perceptible difference in the responses. These spiders, of which examples are *Corythalia*, *Eustiromastix*, *Mago* and *Hypaeus*, are all highly developed literal jumpers; even their normal progress is usually a series of hops, and they are invariably less restless—to human eyes less “nervous”—than other groups of the family. Their attention is easily attracted by appropriate visual stimuli and, even in the absence of a stimulus, they do not tend to race off and get lost in a frenzy of multisensory exploration.

The dish-study method will, however, be found to be more practicable for the majority, at least of tropical salticids, which are runners except during the emergencies of hunting and of progress over chasms. These genera include *Semorina* and other ant-like salticids, *Menemerus*, *Ashtabula* and *Sassacus*. This subject of basic behavior variation will be fully discussed in a subsequent paper.

During observation in both field and laboratory, magnifying spectacles were most useful; they consisted of small lenses, about  $\times 5$ , mounted several inches in front of empty frames.

When unfamiliar males and females were taken, trial-and-error was the only way of determining, while they were still alive, whether they belonged to the same species. Members of the *Phidippus* and *Plexippus* groups are particularly difficult since not only is sexual dimorphism often extreme but also the females are frequently voracious. Extreme vigilance failed to prevent all accidents when I guessed wrong and placed together a male and female of different species. Yet the risk was worthwhile, because sometimes only a single adult pair of a given species in breeding condition was taken during the season. For example, in 1945 the only adult male *Eustiromastix* was kept alive for three months and tried with four different kinds of females before the right one, caught in an early instar, finally molted to the adult form and stimulated the male to display.

In most species, as Bonnet (1933) found with *Philaeus*, there is little danger of cannibalism so long as the spiders are well fed. Our specimens were always given flies not more than 24 nor less than three hours before display experiments.

A vital factor in spider experiments, as in those with other animals, has proved to be the fluctuating physiological condition of both sexes. The only part of this subject which belongs properly in this account of methods is the fact that its influence must always be kept in mind by the investigator. A male taking no interest in a certain female on one day may display and mate promptly with her twenty-four hours later, under conditions as exactly similar as it is possible to make them. Also, the behavior of a male not in top display condition is often not typical of the species; for this reason salticids are best studied when at their physiological peak, that is, when their threshold to display stimuli is low. Under natural conditions it is usually only males in this condition which have sufficient persistence to carry through display to successful mating. Therefore, unlike many vertebrates (cf. Tinbergen, 1948, p. 39), the most easily stimulated spiders give the most typical responses; concomitantly, positive reactions of these individuals to incomplete or abnormal stimulus situations should not be underestimated in determining the relative importance of various releasers.

In discovering the condition of a given male, for use in experiments concerning sign stimuli, one or two stimuli were presented, with known effects on his particular species in different physiological states. For example, a mirror was moved in a certain way for a certain length of time and/or a particular mounted specimen was similarly manipulated. During a series of experiments the condition of the spider must be frequently rechecked by these standards, especially in the case of negative responses. For instance, if a male will not display to a new mount (see below) with a white spot painted on the clypeus, his condition must be rechecked immediately with the standard stimuli, since the spiders tire and/or become overstimulated very suddenly and completely.

This brings up the point of rest periods, the importance of which has been recently reemphasized by Tinbergen in regard to vertebrates (idem, p. 43). It is essential to rotate the members of the test group during each experimental session, in order to avoid the after-effects of stimulation. This principle has been observed in all the experiments with Rancho Grande salticids.

The above remarks have applied equally well to the study of typical display patterns of salticids and to experiments performed to determine their innate releasing mechanisms. The following paragraphs give a survey of general methods used in strictly experimental work. In subsequent papers details of particular experiments will be given where advisable, to substantiate the validity of certain conclusions.

*General Position of Experimental Table.* In order to minimize possible effects of phototropisms, the observer always sat with back to the window. All experiments concerning releasing mechanisms were con-

ducted in daylight, within a certain range of temperature, brightness and humidity.

*Mounted Specimens.* L-shaped pieces of cardboard, such as may be cut from library cards, are very useful in experimental work. Individual spiders are chloroformed and at once fastened with glue or paper cement to the short arm, in any desired position. The color of the card is immaterial if it is a fairly light tint, and so contrasts in brightness with the spider. Whether or not it matches the background of the table over which it is manipulated has no apparent effect: a test spider never responds to an L alone. However, to reduce the variables, the procedure was standardized, to use only light green cards on a background of similar hue, brightness and saturation. The tip of the long end is bent up to form a convenient handle. A number is written on the card, and the whole dried (in order to eliminate odor stimuli), protected from pests by paradichlorobenzene crystals; odors from the latter are quickly dissipated before experiments, and in any case have no apparent effect on the subjects. Such a mount becomes a standard and can be used indefinitely. When it is manipulated before a test spider, the latter takes no notice of either the observer's hand, which is usually behind him anyway, because of the length of the L-arm, or of the L itself; his attention, if any, is captured only by the mount. L-cards are also useful in manipulating lightly chloroformed spiders, for example females, where it is desired only to test the effect of her odor as opposed to chemotactic stimuli; the card insulates her from the background, so that she does not leave a "trail" during the manipulations. Finally, painted cardboard models of spiders are likewise glued on L-cards for ease of handling and storing.

*Anaesthesia.* Ether, refrigeration and chloroform have been tested, and of the three chloroform is the most satisfactory. Recovery from ether is too quick, whether the specimen is anaesthetized for testing reactions to immobility of another individual, or for painting or mutilating; also, ether itself is often highly disagreeable to the observer. Recovery from refrigeration is almost instantaneous or, if it has been prolonged in a tropical spider, normal behavior may never be resumed. A special cold technique, however, is sometimes preferable to chloroform during a long operation: the spider is first chilled to immobility in the refrigerator, then promptly brought to the microscope and the work performed on top of a cheesecloth-wrapped ice cube. Recovery of complete display reactions can never be assured by this means.

Chloroform, when handled carefully, is the most satisfactory anaesthetic. For moderately swift recovery with unimpaired reactions, the spider should be placed in a vial with a chloroform-dipped cork; there it should stay just long enough to make its legs

go rigid *after* its removal from the fumes; that is, it should be taken out before stupor appears complete. In the case of a long operation, several repeated short doses of chloroform are better than a single long one. Different salticid species, even when closely related and of similar size, vary considerably in their reactions to the various methods. The use of carbon dioxide is a possibility still to be tested in this group.

*Paint.* A number of different kinds of paint were tested for marking and altering patterns in salticids. Uniformly satisfactory for all indoor experimental work except blinding were opaque water colors. In blinding, a base coat of the above water color was given, followed by an overcoat of light-colored Flopaque paint (see below) or even fingernail polish. The base coat is necessary to insulate the spider against harmful effects of the strong chemical varnishes and their removers; the spider may die if paint is allowed to seep around the eye margins; more important, the powerful removers are invariably poisonous. The base coat of water color is stuck with difficulty on the shiny convex surfaces and is easily removed by the spider if not covered with the more adhesive paint; however it is completely harmless, protects the margins from the covering paint, and both layers are sponged off easily and simultaneously with a water-soaked brush. Light colors are used so that complete eye-coverage may be easily checked. Shellac, used by the Peckhams and others, seems to share difficulties with other non-water-colors: although it is not necessarily poisonous in itself and will largely wear off in time, turpentine or other removers are harmful; the importance of this lies in the technique of modern experiments, since a negative reaction, for validity, should be promptly supported by positive reactions to the same stimuli after sight has been restored, to eliminate the factors of post-operative or post-anaesthetic effects.

Water color obviously will not serve for marking spiders to be liberated. For this purpose Flopaque paint (manufactured by Floquill Products, Inc., New York 23, N. Y.), is ideal. It is waterproof, dries almost instantly, and adheres well to either scales or naked chitin. Also, it is thinner than any insect-marking mixture I have tested, so that a variety of identification patterns are easily painted. It is harmless to the spider when applied on top of either carapace or abdomen, but all appendage joints, especially near the body, as well as the eye margins, should be avoided.

Cards were painted with samples of various tints and shades of the opaque water colors, as well as colors straight from jars. These were used to determine their relative brightness with a Weston exposure meter. A similar set of cards with grays of corresponding values, as well as whites, was then made up. Finally the cards were photo-

graphed through a filter (Wratten No. 18A) reflecting substantially all rays except the ultra-violet, in order to determine which of the colors involved an ultra-violet factor; the reds were also tested visually through a blue-green filter for blue and violet content. Obviously these tests can give only approximate results; their value lies in preliminary color vision studies in a field laboratory, in the absence of precision instruments.

In regard to the actual painting technique, nothing need be said except that even the finest paintbrush obviously must be trimmed to paint a successful spot on a half-millimeter clypeus. The spider is best held on the dissecting microscope stage in the bare fingers, but protected by an enfolding wisp of cotton.

*Mutilations.* A dissecting needle with a tiny distal blade is ideal for quickly removing palps or legs at any desired joint, or for shaving off hairs and scales.

*Distance Measurements.* Distances at which reactions to a stimulus were initiated were measured conveniently as follows: A piece of green oilcloth was marked with black ink into 12 numbered, concentric circles an inch apart. The whole was varnished with an alcohol-proof preparation, so that chemotactic trails could be removed with alcohol after every use. A sheet of glass might be used, instead of varnish.

#### V. SUMMARY.

This paper is devoted primarily to methods of studying salticid spiders alive in the tropics. Shaking, visual searching, and examination of airplants are the primary collecting methods. Dry season fauna is scanty, even in rain forests. Specimens are maintained and reared successfully in small jars with mosquito netting tops. Continuous but non-constant moisture is supplied with dampened, cotton, dental wads. Food consists of *Drosophila* and other small flies, reared and wild. Second instar young are fed small leaf litter organisms and de-winged *Drosophila*. Displays are studied in natural habitats, on open tables and in glass-covered dishes. Colors and display positions are recorded from living specimens. Dried or chloroformed examples, for experimental manipulation, are conveniently mounted on the short ends of L-shaped pieces of cardboard. Chloroform, carefully controlled, is a successful anaesthetic. Color and pattern are usually altered with opaque watercolors. Mutilations are performed with a bladed needle. Painted, concentric circles are convenient for measuring distances of responses to stimuli. Precautions against confusion of experimental results are discussed, as well as the general suitability of salticids as subjects for experimental research.

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## 10.

Fish Fauna of Rancho Grande, Venezuela.<sup>1</sup>

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## INTRODUCTION.

[This is one of a series of papers resulting from the 45th and 46th Expeditions of the Department of Tropical Research of the New York Zoological Society, made during 1945 and 1946 under the direction of Dr. William Beebe with headquarters at Rancho Grande in the National Park of Aragua, Venezuela. The expeditions were made possible through the generous co-operation of the National Government of Venezuela and of the Creole Petroleum Corporation.

[The characteristics of the research area are in brief as follows: Rancho Grande is located in north central Venezuela (10° 21' N. Lat., 67° 41' W. Long.), 80 kilometers west of Caracas, at an elevation of 1,100 meters in the undisturbed montane cloud forest which covers this part of the Caribbean range of the Andes. Adjacent ecological zones include seasonal forest, savanna, thorn woodland, cactus scrub, the fresh water lake of Valencia, and various marine littoral zones. The Rancho Grande area is generally subtropical, being uniformly cool and damp throughout the year because of the prevalence of the mountain cloud cap. The dry season extends from January into April. The average humidity during the expeditions, including parts of both wet and dry seasons, was 92.4%; the average temperature during the same period was 18° C; the average annual rainfall over a 5-year period was 174 cm. The flora is marked by an abundance of mosses, ferns and epiphytes of many kinds, as well as a few gigantic trees. For further details, see Beebe & Crane, *Zoologica*, Vol. 32, No. 5, 1947. Unless otherwise stated the specimens discussed in the present paper were taken in the montane cloud forest zone, within a radius of 1 kilometer of Rancho Grande.]

## INTRODUCTION.

Within the limits of our researches at Rancho Grande living conditions for fish were so poor that only three species were represented. Two of these were characins, which without special adaptations could make their way up low rapids to the limit of permanent pools in the upper middle reaches of the brooks feeding the Rio Limon, south of the Portachuelo Pass watershed.

The smaller and more precipitous streams on the north side of the divide were inhabited by a single species of catfish, *Pygidium*. This, like most members of its family, was adapted for life and progress in

swift currents and restricted pools. The opercles and interopercles were armed with rows of projecting spines, and by alternate movements of these gill covers the fish could cling to steep rocks, and progress against gravity and force of water with remarkable success. The mobile, eel-like body and flattened fins were all of help.

Under laboratory conditions these fish showed pronounced ability to leap, yet I never saw any salmon-like jumps in nature, whereas several times the fish were observed hitching themselves, little by little, up the steep sides of rocks and through water trickling from one small pool to another.

Brown-spotted *Pygidium*.*Pygidium b. banneai* Eigenmann.

*Pygidium banneai* Eigenmann; *Indiana Univ. Studies*, no. 16, 1912, p. 19; *Mem. Carnegie Mus.*, vol. 7, 1918, no. 5, p. 318.

These catfish belong to the subfamily Pygidiinae, which are mostly of small size, and have unpleasant reputations of being parasitic on the skins of other fish, and actually entering and living within the gill cavities of large catfish. The catfish of Rancho Grande must seek more normal methods of livelihood, for there are no other fish in the upper reaches of these mountain streams. Their habitat is typical, for *Pygidium* as a whole is confined to streams of the higher Andes, living as high as three miles above sea level.

*Habitat.* Ten minutes away from Rancho Grande brings us to a small brooklet. It crosses the main road by a stone and cement culvert, and from here on down the valley it drops steeply, enters the Rio Ocumare and finally ends, six miles north, in the Caribbean. Near the culvert we found specimens of this fingerlong catfish, the only fish able to ascend this steep succession of falls and small pools, to exist in periods of drought when the stream becomes a drop-by-drop trickle, and to withstand the change to a roaring torrent resulting from cloudbursts during the height of the rains.

*General.* The first of this species were taken on April 17, 1946. There were two large ones (60 mm. standard length), and three small (20 mm.).

In seventeen other pools of this same

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stream, small individual catfish were taken in twelve; large, apparent adults in three more; while two pools were without fish.

When disturbed, the fish wriggled along the bottom, and when alarmed pushed under dead leaves. Fear was a minor sensation with them, perhaps due to the absence of kingfishers and herons. Nevertheless I came suddenly upon a large *Belostoma* water-bug, a three-inch menace to fish and frogs.

On May 22 more small fish were taken from four other small brooks crossing the road along the same stretch as catfish brook number one, all within a half kilometer. None were taken more than thirty meters above the culverts.

On July 4 I collected a number of fish with a few explosive caps. The first pool above the culvert measured two feet by a foot and a half, by a few inches deep, half filled with leaf debris, over a gravelly bottom. The explosion sent a small geyser of water into the air, but for a time there were no visible results. Then several catfish came into view, moving slowly close to the bottom. The only effect was a complete disregard of the hand net. We scooped up twelve in a few minutes. None of them came to the surface as do tide-pool fish, but only swam about slowly, pushing under pebbles and leaves. The largest ones showed subdermal congestion when examined closely, and ultimately died. All of small and medium size recovered. The largest was 73 mm. in standard length.

*Color in Life.* In a large specimen the upper surface down to the lateral line was cinnamon buff, below fleshy white, immaculate. A line of very faint darker buff marks extended down midline of back, ending at dorsal. On each side a series of unconnected, irregular, dark blotches of all shapes extended to tail. Below this, on the midsides, an almost solid line of dark buff, breaking up posteriorly, reached the tail. On top of head two distinct longitudinal lines were behind the eyes, greenish in life. Two irregular, dark buff blotches on gill covers.

The pattern and colors of the young fish were like those of the larger, except that they were more distinct and linear, less broken into blotches. After three weeks in an aquarium the pigment showed a decided tendency toward breaking into unconnected blotches.

*Eye.* In the larger fish the eye was 1 mm. in diameter, protuberant, and when at rest directed outward. In extreme movement the eyeball had a vertical rotation of at least 50 degrees, the direction of vision changing from almost lateral to more nearly superior.

*Position in Life.* The fish rested flat on the bottom of the pool, often beneath a leaf or stone. Pectorals spread wide, flat on bottom, outer elongated ray (ca. 8.6 mm. in length) 45 degrees out from body. Between it and the body the fin fanned out. Lower maxillary

barbel flat, curved obliquely back; upper one slightly raised, obliquely forward, tip curved backward; narial barbel forward, 20 degrees out and back from longitudinal.

*Gill Covers in Life.* These were divided into two lobes, one above the other, the lower one larger. There were at least thirteen opercular spines projecting through the skin of the lower lobe, arranged in two irregular rows. The distal row, eight in number, penetrated the skin in the shape of slender, curved, sharp, tooth-like spines. Four or five, considerably smaller, projected from the lesser, upper lobe. When the fish was frightened and moved toward the shelter of pool debris, the gill covers could be seen to move independently, and apparently aided the pectorals in forward progression. They must be of decided help in clinging fast to rock crevices and vertical surfaces in swift currents.

*Viability.* In August we killed the last of the small catfish taken in May. It had increased three mm. in length, and had become somewhat darker in color. For three months it had lived in perfect health, without provided food, in a glass laboratory dish two and a half, by three and a half, by one inch deep, loosely covered, half filled with unchanged water which was thick and opaque with green algal scum.

*Terrestrial Locomotion.* A fish of medium size (35 mm.) when placed on a dry cement floor instantly flipped a distance of twenty-three inches. It rested four seconds and then cleared twenty-five inches, then fifteen more; ten seconds rest, and two leaps of six and fourteen inches. Two minutes' rest was followed by three flips of two, four and thirteen inches; then a period of wriggling and futile flipping within an area of five inches; a final high effort of eighteen inches and I returned it to its aquarium, very dusty but quite unharmed. For two minutes it hid beneath a leaf and then leaped out upon the floor. A characin under the same conditions merely twisted and wriggled for a minute and then gave up.

*Food.* In addition to much comminuted vegetable matter, we recorded as additional food an aquatic dragonfly larva, together with two small beetles and a fly which had probably fallen into the pool.

## Characins.

Directly in front of Rancho Grande several small streams had their origin, streams which made their way down the steep valley to the south of Portachuelo Pass. Far down at the bottom all of these merged with the Rio Limon, which reached a width of several meters as it flowed over the relatively flat lowlands, and finally emptied into Lake Valencia miles away. The upper reaches of these brooklets were too small for any fish, but before they lost themselves in the larger stream the small pools, connected by less precipitous falls, were inhabited by two spe-

cies of characins. These were *Hemibrycon dentatus metae* and *Creagrutus beni*. Both were found in equal abundance just before the junction of the tributaries and main stream, but higher up, even past the culvert and on up the northern slopes, *Creagrutus* still persisted in rather swift currents.

### Dark-tailed Characin.

#### *Hemibrycon dentatus metae* Myers.

*Hemibrycon dentatus metae* Myers, *Proc. Biol. Soc. Washington*, vol. 43, 1930, p. 68; Schultz, *Proc. U. S. Nat. Mus.*, vol. 95, 1944, p. 363.

A single discharge of a small explosive cap on July 22, 1946, in a lower pool, yielded sixteen of these small but colorful characins. They varied from 60 to 105 mm., in standard length, the largest weighing thirteen grams.

*Color in Life.* Dark silvery blue above, changing to bright silver. Below silvery white. Five specimens had a dark, diffused, shoulder spot, absent in the others. All showed a broad, pale lateral band, and a lateral, jet-black band on the caudal peduncle, extending back to the tips of the mid-caudal rays. Caudal fin either clear or with distinct dusky area above and below, with a strong tinge of lemon yellow or pink on the proximal portion of the fin. In the largest specimens there was a dusky area on the dorsal fin. Anal strongly dusky along the tips of the rays, bright pink on the anterior rays. Upper part of eye bright red.

*Food.* The largest fish (105 mm.) had just eaten a large (50 mm.) brightly colored sphinx caterpillar, not quite dead. Three other fish had the following in their stomachs: (a) dragonfly larva, cicadellid, membracid, beetle larva, dipteran, vegetable matter and quartz grains; (b) Cassidini, caddisfly larva, dipteran larva, dragonfly larva, a fly and an aphid; (c) small moth and dragonfly nymph.

### Pink-tailed Characin.

#### *Creagrutus beni* Eigenmann.

*Creagrutus beni* Eigenmann, *Ann. Carnegie Mus.*, vol. 7, 1911, no. 1, p. 142; Schultz, *Proc. U. S. Nat. Mus.*, vol. 95, 1944, p. 336.

Many of these were collected in the lower and middle reaches of the southward flowing streams. Twenty-nine were taken with a single cap on July 22, 1946, measuring from 21 to 80 mm.

*Color in Life.* Dark olive above and on sides, except for a broad, very pale silvery blue lateral band. Below, anteriorly whitish with body organs showing through; posteriorly olive. Faint, indistinct peduncular duskiness. Basal half of caudal greenish-yellow, then a large dusky area. Distal portion, especially under lobe, pink, varying to scarlet in some individuals. This tail pattern the same in all sizes, small and large. In small fish and some of medium size the lateral silvery band was dusky on the posterior third. Distal parts of pelvic and anal rays bright lemon. Iris scarlet on upper fourth, silvery and dusky elsewhere.

*Food.* Two specimens contained the following: (a) firefly larva and unknown insect; (b) small caterpillar, beetle and unknown aquatic larva.

*Viability.* A 40 mm. *Creagrutus* was kept for five weeks in a quart jar in the laboratory, with unchanged water and no provided food. When killed at the end of this period it was as active as ever, with no diminishing of coloration. The only change was a dense growth of green algae on the rays of the caudal.

Note: I have to thank Dr. Leonard P. Schultz for the identification of the three species. The specimens are divided between the United States National Museum and the collections of the Department of Tropical Research of the New York Zoological Society. The department catalogue numbers are, *Pygidium banneavi banneavi* 30627, 30716, 30831, 30941. *Hemibrycon dentatus metae* 30868, 30892, 30986. *Creagrutus beni* 30869, 30870, 30940.



## 11.

The Species of *Bathystoma* (Pisces, Haemulonidae).

By ISAAC GINSBURG.

U. S. Fish and Wildlife Service.

The genus *Bathystoma*, first established by Scudder (*Bull. Mus. Comp. Zool.*, 1:12, 1863), differs from *Haemulon* only in normally having 13 dorsal spines, instead of 12. In other characters the two genera essentially agree. As shown in Table III, of 166 specimens of *Bathystoma* examined only 2 variants have 12 spines. In contrast, 62 specimens examined representing 5 species of *Haemulon*, namely, *plumieri*, *sciurus*, *parra*, *macrostomum* and *flavolineatum*, have 12 spines. Therefore, this difference seems sufficiently constant to be used as a generic or subgeneric character.

Jordan and Swain (*Proc. U. S. Nat. Mus.*, 7:308-313, 1884) revised the species of *Bathystoma* which they included in *Haemulon*, used in a broad sense. They recognized three species, as follows, with the geographic distribution as determined by them: *rimator*, North Carolina to Trinidad; *aurolineatum*, Florida Keys to Cuba; *quadrilineatum*, Bermudas to Brazil. Later, Jordan and Fesler (*Rep. U. S. Comm. Fish.*, 17:477-79, 1893) designated the third species *striatum*, instead of *quadrilineatum*; this substitution being a necessary nomenclatorial emendation in their opinion. They also give the distribution of *aurolineatum* as "Florida Keys to Brazil," the latter and San Domingo being the two localities given in the original description. Still later, Jordan and Evermann (*Rep. U. S. Comm. Fish.*, 21:385, 1896) treated *Bathystoma* as an independent genus.

According to the revisers mentioned, therefore, *Bathystoma* comprises three sympatric species. Later authors have followed this conclusion (using the amended nomenclature as noted above), and as occasion required, some of them recorded three species from the same locality, distinguishing *striatum* by the higher scale count and *rimator* from *aurolineatum* by its deeper body, as was done by Jordan and Swain. The data determined in the investigation here recorded prove that this treatment is in error. *Bathystoma* comprises only two known sympatric species, *aurolineatum* and *striatum*, and not more than two occur at any given place. One of these species, *aurolineatum*, differs markedly in body depth with the local populations; but there is no evidence of a bimodal frequency distribution in that character in

any given locality. The local populations are roughly divisible by body depth into three major groups which, for taxonomic purposes, may be treated as three allopatric subspecies. One subspecies, *aurolineatum*, occurs in the West Indies and South and Central America. All specimens examined by me from the coast of the United States belong to only one species, *aurolineatum*, sensu lato. The other species, *striatum*, might possibly occur in the Florida Keys, but this remains to be proved. The composite U. S. population may be designated as a distinct subspecies, *rimator*, which is confined to the coast of the United States. The Bermuda population constitutes a third subspecies, *angustum*, which is formally established below.

I am not satisfied that the nomenclature currently applied to the species (or subspecies) of *Bathystoma* is correct. For instance, the body depth given by Jordan and Swain (above citation), as determined by Sauvage, for the type of *aurolineatum* applies more nearly, judged by my data, to that species which is designated currently by authors, and in this paper, as *striatum*. Also, the locality of *striatum* is given in the original description as North America. If by "America Septentrionali" Linnaeus meant the coast of the United States, the name *striatum* should replace *rimator*. However, the proper use of these names, and the synonymy of the species, could be determined only by a comparative study of the original material. Pending such a study, I continue to use the nomenclature in the sense it is currently applied.

***Bathystoma aurolineatum*** (Cuvier and Valenciennes), sensu lato.

The frequency distribution of body depth is given in Table I, expressed as a percentage of the standard length, segregated into 6 size groups and by population. The depth differs considerably with size and it also differs with the local populations. The size and population differences indicated apparently are only rough approximations, as I was limited by the available material which to a certain extent determined the grouping of the data as given in the table. The minor population differences especially are indicated in a very limited way. Because of the paucity of speci-



mens from most restricted localities, the data to a large extent are grouped by major geographic regions. The local samples comprised in the composite groupings exhibited in the table are shown in the next paragraph. A figure following a locality gives the number of specimens examined, and the next figures in parentheses give the range of their standard length.

*United States, Miscellaneous*: off Albe-  
marle Sound, North Carolina, 3 (88-97);  
Cape Lookout, N. C., 1 (161); Browns Inlet,  
N. C., 1 (166); off Cape Fear, N. C., 4 (160-  
189); Charleston, South Carolina, 12 (124-  
242); off Savannah, Georgia, 5 (76-183);  
Fernandina, Florida, 1 (196); New Smyrna,  
Florida, 1 (134); off Pine Island, Florida, 7  
(83-118); Charlotte Harbor, Florida, 2 (136-  
149); Gasparilla Light, Florida, 5 (41-89);  
off Choctawhatchee Bay, Florida, 2 (53-55);  
Pensacola, Florida, 3 (103-108); Galveston,  
Texas, 1 (165). *Florida Keys*: Biscayne Bay,  
1 (71); Big Pine Key, 1 (74); Bahia Honda,  
3 (131-135); Boca Grande, 6 (73-117).  
*Southern Florida*: the Florida Keys as given  
above, and Key West, 23 (54-171). *Tortugas*,  
5 (78-144). The preceding specimens are  
here referred to the subspecies *rimator*; the  
following to the subspecies *aurolineatum*.  
*Hispaniola*: Haiti, 8 (67-143); Samana Bay,  
Dominican Republic, 5 (141-158). *American  
Tropical Atlantic*: Includes Hispaniola as  
stated and the following, Bahamas, 6 (124-  
172); Cuba, 12 (65-132); Jamaica, 2 (110-  
123); Puerto Rico, 2 (94-149); St. Thomas,  
Virgin Islands, 1 (124); St. Lucia, Wind-  
ward Islands, 3 (86-94); Colon and Porto  
Bello, Panama, 2 (78-88); Bahia, Recife and  
Rio de Janeiro, Brazil, 6 (105-155).

To display some minor population differ-

ences indicated by the data, groupings are  
not the same in all three tables. In Table I  
"Key West" and "Cuba" are stated separ-  
ately from "Southern Florida" and "Ameri-  
can Tropical Atlantic," respectively, in order  
to show some apparent minor differences in  
those two populations. In Table II "His-  
paniola" and in Table III "Hispaniola" and  
"Cuba" are stated separately from the rest  
of "American Tropical Atlantic" for the  
same purpose.

Table I shows that the combined sample  
from the coast of the United States, except-  
ing perhaps the smallest size group and also  
the Tortugas population, diverges from that  
of tropical America to a subspecific degree,  
and it seems appropriate to treat the two  
major groups of population as two coordinate  
subspecies, *rimator* with a relatively deep  
body and *aurolineatum* with a more slender  
body. The Bermuda population is at the other  
extreme and should be treated as an inde-  
pendent subspecies.

Within the major groups of populations  
there also appear to be some population dif-  
ferences of a minor degree. Although the  
samples examined are not sufficiently exten-  
sive to elaborate the minor differences satis-  
factorily, the following seems tentatively  
indicated. The southern Florida populations,  
as compared with the more northern United  
States populations, average the body some-  
what deeper in the smaller specimens; but  
more slender in the large-size group, over-  
lapping the subspecies *aurolineatum* to a  
greater extent, especially the Key West popu-  
lation. The Cuba population seems to average  
a slightly more slender body as compared  
with the other American tropical populations.  
(The latter comparison is made for the com-

TABLE II.—FREQUENCY DISTRIBUTION OF THE NUMBER OF SCALES SEGREGATED BY MINOR POPULATION, SUBSPECIES AND SPECIES.

Population	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	
<i>aurolineatum</i> sensu lato U. S., Miscellaneous				2	3	3	6	1	7	4	4	2	4	1	1								
Southern Florida		2	3	1	5	1	3	6	4	5	1	1		1									
Tortugas			1		1	1				2													
American Tropical Atl.		2	2	5	2	6	4	4	3		1	2		1									
Hispaniola	1	1	1	2	1	4	2		1														
<i>rimator</i>		2	4	3	9	5	9	7	11	11	5	3	4	2	1								
<i>aurolineatum</i>	1	3	3	7	3	10	6	4	4		1	2		1									
<i>angustum</i>					1	2	4	3	2	1													
<i>striatum</i>																		1	1	1		1	



bined size group data as the specimens for each separate size group are too few to draw even tentative conclusions.)

The five specimens examined from Tortugas approach the subspecies *aurolineatum* even more closely than the other southern Florida populations. The two larger specimens fall at the mode of the distribution of that subspecies. It is possible that the study of an adequate sample from Tortugas will show that that population is more appropriately grouped with *aurolineatum* rather than *rimator*. If this contingency proves so, such a rather unexpected population difference will find a parallel in *Bathygobius curacao* (see *Jour. Washington Acad. Sci.*, 37: 278, 1947). However, in the absence of satisfactory proof, the 5 Tortugas specimens are tentatively grouped with *rimator*.

Omitting the two extreme size groups, one at each end, the combined data for the other 4 size groups are given under geographical groupings and the subspecies heading in Table I. In the absence of adequate data for each size group separately, this combination gives a roughly approximate measure of the degree of subspecies divergence.

The combined data for the 4 size groups show to some extent a gradual transition in decreasing body depth from the more northern U. S. localities to the Florida Keys to Key West to Tortugas to Cuba. Hence, the pertinence of separating the populations into two distinct subspecies might be questioned. However, this is rather the general rule in subspecies distinctions. That is, subspecies, as a rule, are not homogeneous entities; but the constituent local populations differ in a minor way and in variable degrees. Omitting the Tortugas sample which is discussed above, there is a slightly but perceptibly abrupt transition between the U. S. populations and those from tropical America and this seems to be the proper geographical boundary to draw between the subspecies.

Differences in the scale, gill raker and fin ray counts, shown in Tables II-III, are of minor degrees, less than subspecies magnitude. The subspecies *angustum* averages low soft dorsal and pectoral counts; while *aurolineatum* averages a somewhat high gill raker count on the lower limb. Other differences are indicated for the minor constituent populations within the subspecies as follows: The southern Florida populations, as compared with the more northern United States populations, average lower scale and gill raker (on upper limb) counts, and a slightly higher pectoral count. The Hispaniola population averages somewhat lower scale and soft dorsal ray counts, and the Cuba population averages a high gill raker count on upper limb and a slightly lower pectoral count, within their subspecies.

The color pattern of the subspecies *aurolineatum* and *rimator* is essentially as that described below for *angustum*. The dark

lines disappear with growth, and most of the smaller specimens have two more dark lines than the partly faded specimens of *angustum* examined, one close to the dorsal contour and another on the head, behind the eye.

***Bathystoma aurolineatum angustum*, new subspecies.**

Depth modally 29 (in specimens 74-113 mm.), varying 28-31. Dorsal rays predominantly 14, very often 15. Pectoral rays with the mode decidedly at 17, varying 16-18.

Specimens examined more or less faded and color pattern rather faint or hardly perceptible; a dark blotch at caudal base moderately marked; with rows of small pearly spots along rows of scales, horizontal below lateral line, about 12, oblique above; each spot at anterior part of exposed portion of scales, their periphery darker colored; often shades reversed, the spot darker, the periphery lighter, resulting in rows of darker spots against a lighter background, forming nearly continuous streaks in gross effect; the latter phase more often present on lower part of body and in the larger specimens; a median dark streak from snout to within a variable distance of caudal blotch, interrupted by eye; a second streak above lateral line on dorsal aspect of snout and interorbital space, continued to end of dorsal fin; traces of streaks present in largest specimens examined.

The color pattern, as judged by these faded specimens, is essentially as in the other two subspecies of *aurolineatum*, except that the dark streaks appear to persist to a larger size. The other two subspecies usually have two more streaks, as noted above; but this seeming difference is possibly due to the faded condition of the specimens.

Holotype:—U. S. N. M. 20178 Bermuda; 127 mm. in standard length, about 160 mm. in total length (caudal broken at end).

Other 29 specimens 74-138 mm. in standard length examined from Bermuda.

This is a highly divergent subspecies. It diverges from the other two subspecies of *aurolineatum*, *sensu lato*, to a higher degree than the latter diverge from each other. The divergence in body depth, shown by the determined data, is about of species magnitude. However, *angustum* nearly agrees with the other two subspecies in the scale count, color pattern and other characters, and its treatment as a coordinate subspecies seems the best course to take, judged by available evidence. In two characters, body depth and soft dorsal count, *angustum* bridges the depression in the distribution between *striatum* and the other two subspecies of *aurolineatum*.

***Bathystoma striatum* (Linnaeus).**

This species evidently is not as common as *aurolineatum*. Only 4 specimens were found in the National Museum, 3 from Cuba and 1

from Haiti, and these were the only specimens examined during this study.

Typically with 6 longitudinal dark streaks; the uppermost at a little distance below upper contour, beginning on nape and ending before end of spinous part of dorsal; the second on dorsal aspect of snout and inter-orbital space and continued to end of dorsal; the third short, not continued behind head, converging forward with second on snout; the fourth from upper margin of eye continued backward along lateral line to an area under end of dorsal; fifth median in position, from eye backward, merging with fourth under anterior part of soft dorsal; sixth wider and fainter than others, from pectoral base to within a moderate distance of caudal base; an unpaired streak on midback in front of dorsal; no definite caudal blotch in specimens examined. The streaks are present in the largest specimens examined and possibly do not disappear with growth.

This species, then, has a different color pattern than *aurolineatum*, sensu lato. The streaks occupy somewhat different positions, typically they number 2 more, and they possibly do not disappear with growth. The specimens examined also lack the caudal spot. The structural differences are indicated in the tables. The most divergent character is found in the scale count. The determined data show a slight gap between the two species; but some degree of intergradation may reasonably be expected when more specimens of *striatum* are examined. This species also differs in averaging more gill rakers on the lower limb, fewer anal rays, more pectoral rays, a more slender body and fewer dorsal rays, the degrees of divergence of these overlapping characters perhaps being in the order named. On the whole, it is not difficult to distinguish single specimens of *striatum* from *aurolineatum* sensu lato.

## 12.

The Morphology of the Pituitary Gland of the South African Clawed Toad, *Xenopus laevis* Daudin.

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(Plate I).

## INTRODUCTION.

In recent years much interest has been shown in the South African clawed toad, *Xenopus laevis* Daudin, because of its sensitivity to anterior pituitary hormones. On the basis of this sensitivity, Bellerby ('33) suggested *Xenopus* as a test animal for determining pregnancy. Landgrebe ('39) made such tests and described the technique in detail. The validity of the test was further evaluated by Weisman, Snyder and Coates ('42) and Weisman and Coates ('44). Hogben, Charles and Slome ('31), Bellerby and Hogben ('38) and Berk ('39) described sex factors related to pituitary function in this animal. During a somewhat earlier period a hypophyseal-chromatophore mechanism also received considerable attention (Slome and Hogben, '28).

Thus far while there appears to be agreement on the physiological aspects of the hypophysis of *Xenopus*, the morphological descriptions of the gland to be found in the literature (Rimer, '31; Hogben, Charles and Slome, '31; Levenstein and Charipper, '39; Atwell, '41) seem to be rather incomplete. The purpose of the present report is to describe the normal morphology and histology of the pituitary gland in *Xenopus laevis*, in an effort to augment and clarify the subject.

We wish to acknowledge with sincere appreciation the opportunity to examine the original preparations made by Dr. Irving Levenstein, in collaboration with the senior author during a preliminary survey, also the cooperation of Mr. Christopher W. Coates who through the New York Zoological Society and the New York Biologic Research Foundation generously contributed much of the material used in the current investigation.

## MATERIALS AND METHODS.

Sexually mature males and females of *Xenopus laevis* were used in this investigation. The pituitary glands were obtained following decapitation, and, usually, removed from the brain case along with a portion of the midbrain.

The tissues were fixed in Bouin, Zenker,

Formol sublimate, and formalin (10%) for studies of the microscopic anatomy of the gland. To demonstrate the finer cellular details, the tissue was placed in Champy's fluid for twenty-four hours, then in 2% osmic acid at 35° C. for three to six days. The Golgi apparatus was best demonstrated after the longer period of osmication.

Horizontal, longitudinal and cross-sections were then cut serially in paraffin at 3 and 4 micra. These were stained by Masson method with modifications (Foote, '33) and checked with hematoxylin and eosin. The Dawson and Friedgood ('38) method and the Severinghaus ('32) technique were used for further cellular differentiation.

## DESCRIPTION.

## a. Gross Morphology.

*In situ*, the pituitary gland when observed ventrally is a flattened disc-like structure with lateral elongated projections. The anterior portion of the gland is bounded ventrally by the presphenoid cartilage which extends forward from the basisphenoid bone. When these structures are removed, the gland is seen to be suspended from the *tuberculum cinerum* by the infundibulum just dorsal to the optic chiasma (Fig. 1).

The *pars anterior* is ventro-caudal to the rest of the gland. In some specimens this portion is ovoid in outline with its longer dimensions antero-posterior while other specimens exhibit a greater diameter in the dextri-ventro axis. Dorsal to this ovoid structure is the flattened, elongated, dumb-bell shaped extensions of the *pars intermedia*, which extend transversely across this anterior lobe. No large blood vessels are observed entering the pituitary body, but a good sized blood vessel is seen embedded in both sides of the brain, lateral to these elongate projections.

## b. Microscopic Anatomy.

## 1. General.

A histological study of the *hypophysis cerebri* of *Xenopus laevis* reveals a structure, similar, in general, to that described for most vertebrates. In serial sections, and at the

several planes, this gland shows an anterior portion with a cellularly differentiated area (the anterior process of Atwell '41), a *pars intermedia*, a *pars nervosa* and, lying on either side of the median line, two epithelial plaques embedded in the walls of the infundibulum—the *pars tuberalis*.

The *pars anterior* is ventro-caudal to the rest of the gland (Fig. 2) and is ovoid in shape. It is the largest lobe of the complex and is firmly embedded in a thickened median eminence of the infundibulum. The rostral area of the *pars anterior* is heavily vascularized and distinct from the anterior lobe proper. The area consists chiefly of weak staining basophile cells with few acidophiles.

Dorsal to the anterior lobe is a flattened elongate structure which extends transversely across the anterior lobe (Fig. 3). These projections consist of two clearly demarcated areas, a ventral portion, the *pars intermedia* and a dorsal portion, the *pars nervosa*. The intermedia is very closely applied to the *pars nervosa* and only separated by a thin connective tissue septa. The *pars nervosa* is continuous with the infundibulum.

Anterior to and continuous with the infundibulum on either side are thickened extensions of the hypothalamus, the *tuber cinereum*. These structures completely enclose the infundibular cavity which, in some sections, is continuous with the third ventricle of the brain.

In transverse and frontal sections of the *tuber cinereum*, two epithelial plaques (*pars tuberalis* of Atwell '41), one on either side, are found embedded in the ventral surface (Fig. 5). These structures are bounded on the ventral surface by the *pia mater* and on the dorsal side by blood vessels.

## 2. Pars Anterior.

Of the several structures which make up the pituitary gland, the *pars anterior* is the most complex in its cellular elements. It is seen as nests in transverse sections. These nests are separated by delicate connective tissue partitions (Fig. 4). Very often a capillary can be seen penetrating the center of the nest of cells. In median sagittal sections, the gland is somewhat tubular and consists of cords of cells which are separated by capillary channels containing numerous erythrocytes.

The *pars anterior* fixed in Bouin's, Champy's, or formalin and stained in Masson's stain consists of three general cell types, acidophiles, basophiles and chromophobes. These cells can be distinguished by size, granulation, and staining reaction.

With the Dawson-Friedgood technique ('38), it is possible in some sets of slides to distinguish four cell types on the basis of staining reactions. Two types of acidophiles may be distinguished; an "Azure-carmine" cell and an "Orange G" cell. The "Azure-carmine" cell is larger than the "Orange G," and

contains granules which are coarser and more numerous than those present in the "Orange G" cell. The cytoplasm of the "Orange G" cell is homogenous in appearance, containing very fine acidophilic granules evenly distributed throughout the cell. The nuclei of both of these cells are identical; ovoid with some chromatin material and a very definite acidophilic nucleolus. The third cell type is a deeply staining basophile; the fourth cell type is very much like the "Orange G" cell in size and cytoplasmic granulation, but is distinguishable by lightly staining purple cytoplasm. These cells are sparse.

The distribution and staining intensity of the cells is not uniform throughout. The periphery of the gland appears to contain poorer staining cells. In the rostral portion of the anterior pituitary, below the anterior process, only a very few deeply stained acidophilic cells occur. It was noted, however, that acidophilic cells become more numerous near the center of the gland and diminish toward the periphery. Few well stained basophile cells are encountered in the anterior portion of the gland, but many occur in nests deeper in the anterior pituitary, a condition very much similar to that described for the pituitary gland of *Necturus maculosa* (Charipper, '31).

The acidophile cells are completely filled with coarse spherical granules, and show definite cell outlines (Fig. 10). They contain an ovoid vesicular nucleus within which is a central acidophilic nucleolus. When exposed to osmic acid, the Golgi apparatus appears as a network capping the nucleus.

The basophile cells, though relatively few in the anterior lobe, show a tendency to group and form nests. The granules in the basophile are not as coarse or as numerous as those found in the acidophiles. These cells when exposed to osmic acid demonstrate many clear vacuoles within the cell. The nucleus is not as large as that of the acidophile and is indented or somewhat kidney-shaped. This nucleus is usually clear and contains a definite acidophilic nucleolus. The typical Golgi found here is similar to that described by Severinghaus ('33) for the pituitary of the rat. It occurs in the cytoplasm away from the nucleus. The Golgi network does not appear as a continuous structure but rather as though made up of heavy plates (Fig. 8).

The third type of cell, the chromophobe, in osmicated preparations is light brown in color and takes neither the acidophilic or basophilic stain even after post-chromatization. This cell is more like the acidophile than the basophile in shape, and is found distributed throughout the gland but is the dominant cell in the rostral part of the anterior pituitary. The cytoplasm of these cells is finely granular. The nucleus is vesicular and contains a central nucleolus similar to those found in acidophiles and basophiles. In some

of these cells, Golgi of the acidophilic cell type is found. In others, Golgi characteristic of the basophile cell occurs.

### 3. Anterior Process.

The terminology adopted here is that suggested by Atwell ('41) although this structure was described by Rimer ('31) and Hogben and Slome ('31) as the *pars tuberalis*.

The anterior process is embedded in the median eminence of the infundibulum. This area, which is continuous with the *pars anterior*, is the point of attachment of the anterior lobe with the infundibulum. The cells of the anterior process are arranged in very definite cords, giving this area a lobular appearance. In transverse sections, these cords appear as nests, each of which is completely within a thin connective tissue septa (Fig. 6). A small lumen may be seen in the center of each nest. Each of these acinar-like structures contains two types of cells. One of these cell types is similar to that found in the *pars tuberalis*. It is chromophobic with a vesicular nucleus and a central acidophilic nucleolus. The cells are ovoid in outline with very little cytoplasm and show poor cell boundaries. The second cell type found within these nests is basophilic, columnar, and contains a nucleus similar to that found in the chromophobe. This basophilic cell is larger than the chromophobe and the nucleus is always basally placed.

The anterior process is heavily invaded by blood vessels from the infundibulum. These vessels penetrate the anterior process and make their way to the anterior lobe proper.

### 4. Pars Tuberalis.

The center of each plaque forming this part of the gland is pierced by fair sized blood vessels and is well vascularized (Fig. 7). The cells of the *pars tuberalis* in some sections appear to be arranged in cords and separated by thin connective tissue septa (Fig. 9). This cord-like arrangement, however, is not as clear as that found in the anterior processes. The cells of the *pars tuberalis* are quite different from those found elsewhere in the gland. They are comparatively small and the cells are chromophobic with scant cytoplasm. The nucleus which is vesicular occupies the greater portion of the cell. Unlike the cell membrane, the nuclear membrane is well defined. Within the clear nucleoplasm is a large, distinct, usually centrally placed, acidophilic nucleolus.

### 5. Pars Intermedia.

The *pars intermedia*, as seen in transverse section, is situated between the *pars anterior* and the *pars nervosa*. In frontal section, this portion of the gland is thickest at either lateral end, but only three to four cells in width where the *pars intermedia* forms a concavity into which the oval region of the *pars anterior* fits. The *pars intermedia* is characterized

by its compact irregular cord-like arrangement. These cords are separated from each other by thin connective tissue. This lobe of the pituitary is separated from the *pars anterior* and the *pars nervosa* by well defined connective tissue partitions. No evidence of direct vascularization could be found.

The cells making up the cords of the *pars intermedia* are very tall, columnar, with small basal, ovoid nuclei. When stained with aniline blue after routine fixation, these cells react as basophiles. In cross section the cells are ovoid and have poor cellular outline. The nucleoplasm stains weakly with acid fuchsin but contains a deep staining acidophilic nucleolus. The cells of the *pars intermedia* are very rich in osmophilic material (Fig. 11). Some Golgi configurations such as described for the acidophiles and basophiles of the *pars anterior* are present, but more often the osmophilic material is found either as small rings or thick short filaments, distributed throughout the cell.

### 6. Pars Nervosa.

This portion of the gland lies dorsal and adjacent to the *pars intermedia* and is separated from the latter only by a connective tissue membrane. The *pars nervosa* is continuous with the infundibulum and consists almost entirely of rather compact basophilic fibrous tissue. These fibres are arranged in cords giving the *pars nervosa* a lobular appearance. Distributed throughout this fibrous mass are several different cellular elements. Especially abundant are the ependymal cells similar to those which line the anterior wall of the infundibulum and the *tuber cinerum*. Mossy neuroglia cells also are present with a scattering of some spindle-shaped cells with a process at each end of their long axis. Many basophilic cells resembling those of the *pars intermedia* can be distinguished here. The *pars nervosa* is well vascularized and contains many blood sinuses and capillaries. The presence of these sinuses give the *pars nervosa* a very sacculated appearance. These blood vessels enter the *pars nervosa* at the region where this portion of the pituitary comes off the infundibulum.

### DISCUSSION.

The pituitary gland of *Xenopus laevis* Daudin, in relation to its neurocranium, is similar to that found among the anurans. The entire gland is suspended from the hypothalamus and although when exposed on its ventral surface it is easily movable, the anterior lobe—unlike that of other anurans—is firmly attached to the brain. No major blood vessels penetrate the gland although even macroscopically the anterior lobe is seen to be richly vascular. This concurs with the report of Patterson ('39), who described the vascularization of the brain of *Xenopus* as being similar to that of urodeles and other anurans.

The ramus posterior, a branch of the internal carotid arteries, divides and one of its branches is distributed to the optic lobe while the other vascularizes the pituitary body. Blood is carried to the jugular vein from the pituitary by two very thin-walled veins. These connect with each other by transverse vessels. In the anurans these thin-walled veins are described by Ecker (1889) as small venous plexi on either side of the pituitary body.

The general structure of the pituitary of *Xenopus* is similar to that described by other investigators (Atwell '19, '41; DeBeer, '26; Charipper '31; Rimer '31; and Sato '35). The four characteristic lobes found in all amphibians are present in this animal. As pointed out by Charipper ('37), the pituitary body of amphibians is not compact. This is especially true of *Xenopus* where two elongate lateral extensions are found projecting transversely across and beyond the ovoid anterior pituitary.

The *pars anterior* of *Xenopus laevis*, like that of other amphibians, is ventro-caudal to the rest of the gland. This is transversed on its dorsal side by the *pars intermedia* and *pars nervosa* which are dumb-bell shaped. The *pars tuberalis* in this animal is located in a position similar to that described by Atwell ('19) for *Rana pipiens* and *Rana catesbeiana*. This lobe is described by DeBeer ('26) as consisting of a pair of epithelial plaques "plastered" on the floor of the *tuber cinereum* in front of and separate from the rest of the pituitary body.

The anatomical relationships of these parts, therefore, do not vary from those described in other amphibians. In microscopic preparations, however, *Xenopus laevis* displays an area of cells not occurring in either urodeles or anurans. This particular area is found at the rostral portion of the *pars anterior* and is embedded in a thickened portion of the floor of the infundibulum which Atwell ('41) designates as the median eminence. The cells of this area are of two types, basophilic and chromophobic. The area is well vascularized. This portion of the anterior pituitary, because of its cellular arrangement, cell types and heavy vascularization, is suggestive of the *pars tuberalis* of urodeles described by Atwell ('21) and DeBeer ('26). On the basis of this description Rimer ('31) and Hogben, et al. ('31) have called this area the *pars tuberalis* and concluded that *Xenopus laevis* displayed a "zalamandrine" type of pituitary. As a further confirmation of this, Rimer ('31) reports that despite a careful study of serial sections he was not able to locate the *pars tuberalis* as described for anurans. Atwell ('41), in discussing the anterior margin of the *pars anterior*, is of the opinion that it is not the *pars tuberalis* but rather a differentiated area of the *pars anterior*. He describes the *pars tuberalis* of *Xenopus* as epithelial plaques in the ventral

wall of the infundibulum. Dawson ('40) also reports a similar region in the anterior margin of the *pars anterior* in the pituitary of the African lungfish. This region being single and median in position, does not fit any phylogenetic description of a true *pars tuberalis*.

In this work both the anterior margin of the *pars anterior* as well as the infundibulum were studied serially in transverse, sagittal and frontal planes. The cells were also stained with several techniques to demonstrate cellular detail. As a result, both the anterior process and the paired epithelial plaques as described by Atwell ('41) for *Xenopus laevis* were seen and confirmed. The study of the anterior process is in agreement with that described by Rimer ('31) and Hogben, et al. ('31) for this area. The cell types and arrangement of cells in cords is similar to that described by Atwell ('21) and DeBeer ('26) for the *pars tuberalis* of urodeles. The *pars tuberalis* in *Xenopus laevis* is located in a position similar to that described by Atwell ('19 and '41). However, the present findings differ in that this area showed some tendency to be lobular and definitely vascularized. This is in accord with Sato ('35) and D'Angelo ('41). The latter investigator suggests that the vascularization of the *pars tuberalis* in the frog is appreciable when measured in terms of capillary length.

Atwell ('41) points out that morphogenetic and cytologic studies are necessary to determine whether the anterior process represents the region of earlier attachment of the *pars tuberalis* and whether these two areas are related histologically. In this connection he describes the cells of the anterior process of *Xenopus* to be larger and more definitely chromophilic than those of the *tuberalis*. In this investigation, however, we are able to demonstrate many chromophobic cells within the cords of the anterior process which are identical with the cells of the *pars tuberalis*. However, no valid cytological criteria could be found for further confirmation of the relationship unless negative results be considered. Golgi material could not be demonstrated in the cells of the anterior process or in the cells of the *pars tuberalis*.

The tubular arrangement of the cells in the *pars anterior* of *Xenopus laevis* seems to be peculiar to this form since similar conditions are not described in the literature for other amphibians. Poris and Charipper ('38) report this condition common to all reptilian forms and an outstanding feature of the *Anolis carolinensis* pituitary. In amphibian pituitary, three types of cells are distinguished; acidophiles, basophiles and chromophobes. In their distribution the chromophobe cells are found in all parts of the *pars anterior* and are the dominant cell in its anterior portion. The acidophiles are scant in this area but are more numerous in the center of the gland. There are few true baso-

philes present in the anterior lobe and these are found only in its posterior region. A study of the osmophilic material in these cells reveals bizarre configurations. Many acidophile cell demonstrate Golgi apparatus capping the nucleus, similar to the acidophiles in the rat's pituitary (Severinghaus, '33). This configuration in *Xenopus laevis* is not constant for all acidophiles. Basophiles treated with osmic acid also displayed osmophilic material. The Golgi apparatus is usually away from the nucleus and ring-shaped. This cell, unlike the acidophile, contains many clear vacuoles. Among the chromophobes both types of Golgi configurations are found. This condition is similar to that described by Severinghaus ('33) for the rat and Levenstein ('39) for the pituitary of goldfish.

The *pars intermedia* of *Xenopus*, in general, conforms with that found in other amphibians. As described for most amphibians this lobe of the pituitary contains only one cell type which stains basophilically. Atwell ('19), however, maintains that the cell type of the *intermedia* is chromophobic and further that that part is well vascularized. The present investigation yields no evidence of direct vascularization in this lobe. This agrees with the work of DeBeer ('26) and D'Angelo ('41) for *Anura*. The cells of the *intermedia* are very rich in osmophilic material. Seldom, however, do these assume definite configurations but, rather, appear scattered as short rods throughout the cell.

The *pars nervosa* is continuous with the infundibulum and is composed chiefly of coarse basophilic fibres. This portion of the gland contains cords which give it a somewhat lobular appearance. The several cell types present here are chiefly nervous in origin. However, these cells are similar to those present in the *pars intermedia*. The *pars nervosa* is very conspicuously vascularized and contains many large blood sinuses. This is in general agreement with all such previous investigations.

#### SUMMARY AND CONCLUSIONS

1. Confirmation is offered for the presence of five anatomical parts of the pituitary gland in *Xenopus laevis* Daudin; *pars anterior*, anterior process, *pars intermedia*, bilateral plaque-like *pars tuberalis* and a *pars nervosa*.

2. The *pars tuberalis* in *Xenopus* is described as definitely vascular.

3. The *pars anterior* contains the usual three cell types: acidophiles, basophiles and chromophobes.

4. Two varieties of chromophobes are described on the basis of their Golgi configuration. One with a compact Golgi capping the nucleus similar to that described in the acidophile; the other with a looser, thinner, band-like arrangement not closely applied to the nucleus and similar to the condition found in

the basophile. This arrangement is very much like the configurations described by Severinghaus ('33) for the rat and Levenstein ('39) for the goldfish.

5. The cell types found in the anterior process, compared to those occurring in the *pars tuberalis*, indicate a possible histogenetic relationship and lend positive weight to Atwell's ('41) question concerning the anterior process as a point of attachment of the *pars tuberalis*.

6. The confirmation of the presence of the *pars tuberalis* as definitely bilateral epithelial plaques further strengthens Atwell's ('41) contention that the pituitary of *Xenopus* is definitely not of the "zalamandrine" type.

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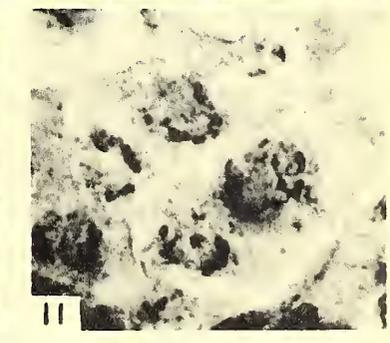
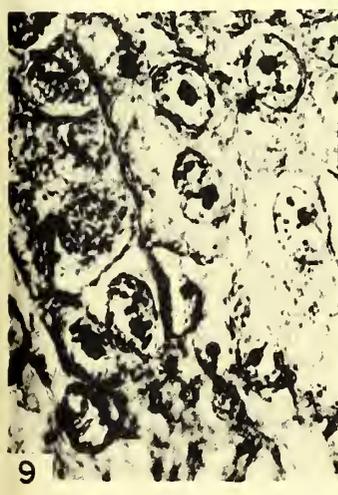
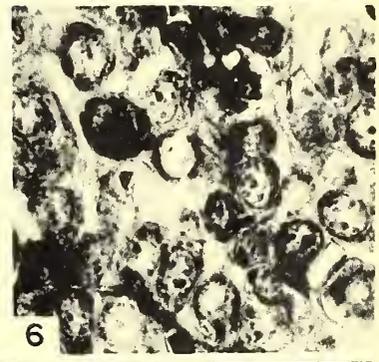
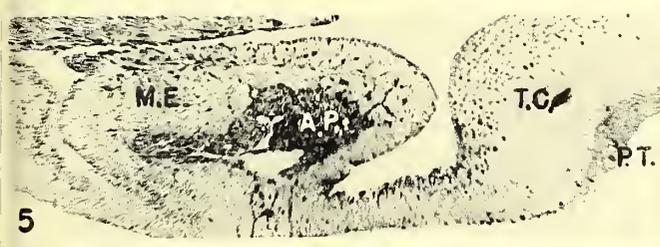
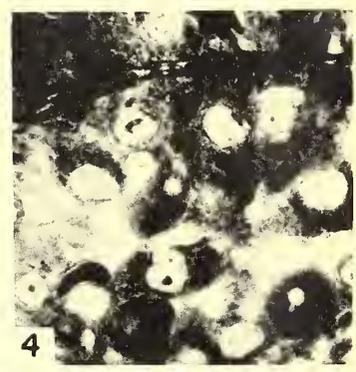
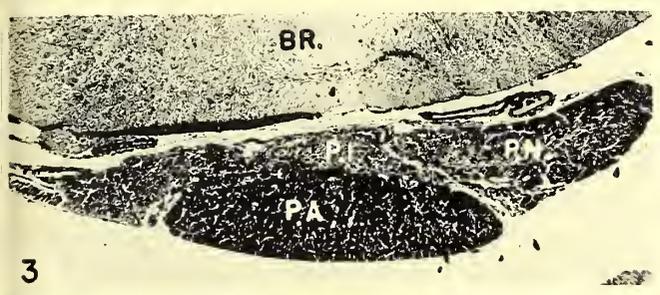
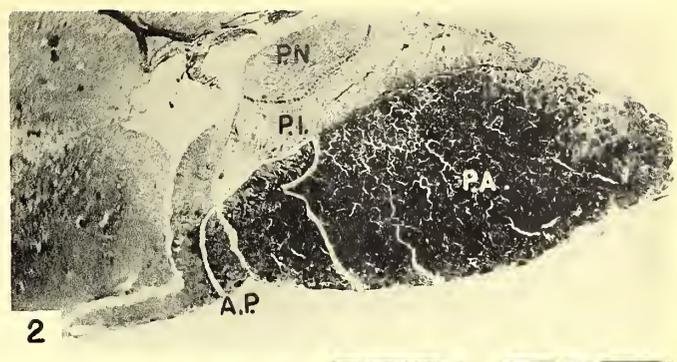
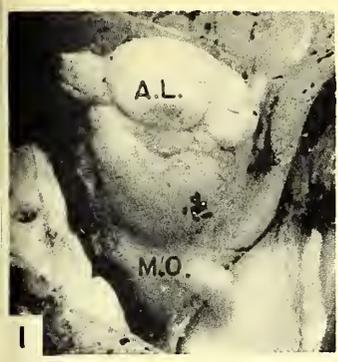
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## EXPLANATION OF THE PLATE

## PLATE I.

- FIG. 1. A ventral view of the pituitary gland of *Xenopus laevis* Daudin, in its relation to the brain. Note the ventrocaudal position of the anterior lobe and the lateral elongated projections dorsal to this structure. **A. L.**, Anterior lobe; **M. O.**, Medulla oblongata.
- FIG. 2. A median sagittal section of the pituitary showing the relationship of the *pars nervosa* (**P. N.**) *pars intermedia*, (**P. I.**) *pars anterior* (**P. A.**), and the anterior process (**A. P.**) in its relationship to the infundibulum. Formalin-sublimate; Dawson-Friedgood,  $\times 135$ .
- FIG. 3. Transverse section through the pituitary gland. Note the wing-like arrangement of the *pars intermedia* and the *pars nervosa*. Formalin; Mallory modification.  $\times 50$ .
- FIG. 4. Section through the *pars anterior* showing nesting arrangement, three types of cells and in addition the heavily stained connective tissue system. Bouin; Masson.  $\times 1080$ .
- FIG. 5. Anterior process (**A. P.**) embedded in this median eminence (**M. E.**). Note the epithelial plaque, the *pars tuberalis*, (**P. T.**) in the broad arm-like tuber cinerum (**T. C.**). Formalin; Mallory modification.  $\times 200$ .
- FIG. 6. Section showing two cell types present in the anterior process, the darker basophilic cells and the lighter chromophobic cells. Mann-Kopsch; Masson.  $\times 650$ .
- FIG. 7. A higher magnification of the *pars tuberalis* showing its vascularization. Formalin; Mallory modification.  $\times 650$ .
- FIG. 8. A highly magnified region of the *pars anterior* showing the loose Golgi network of a basophile. Mann-Kopsch; Masson.  $\times 1800$ .
- FIG. 9. Section through the epithelial plaque forming part of the *pars tuberalis*, showing the chromophobic nature of the cells and their striking similarity to the chromophobes of the anterior process drawn in Fig. 6. Formalin; Mallory modification.  $\times 1440$ .
- FIG. 10. Section through the *pars anterior* showing the vesicular nature of the nuclei. In addition the different Golgi configurations may be observed. Mann-Kopsch; Masson.  $\times 1440$ .
- FIG. 11. A section through the *pars intermedia* showing the amount and distribution of the osmophilic substance and to some extent the nature of the Golgi configuration. Osmo-sublimate; Dawson-Friedgood.  $\times 1800$ .



THE MORPHOLOGY OF THE PITUITARY GLAND OF THE SOUTH AFRICAN CLAWED TOAD, *XENOPUS LAEVIS* DAUDIN.



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## 13.

Eastern Pacific Expeditions of the New York Zoological Society. XXXIX.  
Mollusks from the West Coast of Mexico and Central America. Part VI.<sup>1</sup>

LEO GEORGE HERTLEIN &amp; A. M. STRONG.

California Academy of Sciences.

(Plates I &amp; II).

[This is the thirty-ninth of a series of papers dealing with the collections of the Eastern Pacific Expeditions of the New York Zoological Society made under the direction of William Beebe. The present paper is concerned with specimens taken on the Templeton Crocker Expedition (1936) and the Eastern Pacific Zaca Expedition (1937-1938). For data on localities, dates, dredges, etc., refer to *Zoologica*, Vol. XXII, No. 2, pp. 33-46, and Vol. XXIII, No. 14, pp. 287-298].

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## INTRODUCTION.

This is the sixth of a series of papers dealing with collections of mollusks taken on the Templeton Crocker Expedition (1936) and the Eastern Pacific Zaca Expedition (1937-1938). The general plan of presentation followed in the present contribution is that mentioned in Part II of this series of papers<sup>2</sup>. Formal headings and keys are given for the species collected by the expeditions of 1936 and 1937-1938. Occasionally additional species are included in the keys for convenience but in such cases it is indicated

<sup>2</sup> Hertlein, L. G., and Strong, A. M. Eastern Pacific Expeditions of the New York Zoological Society. XXXII. Mollusks from the West Coast of Mexico and Central America. Part II. *Zoologica*, New York Zool. Soc., Vol. 23, Pt. 3, December 6, 1943, pp. 149-168, pl. 1.

<sup>1</sup> Contribution No. 820, Department of Tropical Research, New York Zoological Society.

which species do not occur in the present collection.

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### Superfamily Veneracea.

#### FAMILY VENERIDAE.

This large family is represented in the present collection by 51 species and subspecies which are assigned to 15 genera.

Four important papers published by Dall<sup>3</sup>, Jukes-Browne<sup>4</sup>, Palmer<sup>5</sup> and Frizzell<sup>6</sup> are especially useful to anyone studying the west American Veneridae. The paper by Frizzell contains much important information, including references to the supraspecific names applied to the Veneridae and a preliminary reclassification of this large group.

#### KEY TO THE GENERA OF THE VENERIDAE.

- A. Left valve with an anterior lateral tooth or denticle
- a. Inner margin strongly crenulated  
*Antigona*
- aa. Inner margin not crenulated
- b. Shell orbicular; large, polished  
*Dosinia*
- bb. Shell trigonal or elongated
- c. Shell with reticulate sculpture; pallial sinus slight or lacking  
*Gouldia*
- cc. Shell with concentric sculpture only
- d. Beaks subcentral; shell usually higher than long (sometimes anterior end longer); trigonal...*Tivela*<sup>7</sup>
- dd. Beaks usually decidedly anterior; shell longer than high

<sup>3</sup> Dall, W. H. Synopsis of the Family Veneridae and the North American Recent species. *Proc. U. S. Nat. Mus.*, Vol. 26, No. 1312, December, 1902, pp. 335-412, pls. 12-16.

<sup>4</sup> Jukes-Browne, A. J. A Synopsis of the Family Veneridae. *Proc. Malacol. Soc. London*, Vol. 11, Pt. 1, March, 1914, pp. 58-74; Pt. 2, June, 1914, pp. 75-94.

<sup>5</sup> Palmer, K. Van Winkle. The Veneridae of Eastern America, Cenozoic and Recent. *Palaontogr. Americana*, Vol. 1, No. 5, pp. 209-522 (1-213), March, 1927, pls. 32-76 (1-45), February, 1929.

<sup>6</sup> Frizzell, D. L. Preliminary Reclassification of Veneracean Pelecypods. *Bull. Mus. Roy. d'Hist. Nat. Belgique*, Tome 12, No. 34, December, 1936, pp. 1-84.

See also Tomlin, J. R. le B. Some synonyms in the Veneridae. *Proc. Malacol. Soc. London*, Vol. 15, Pt. 6, October, 1923, pp. 310-313.

<sup>7</sup> The subgenus *Eutivela* Dall has crenulated inner margins but is not known to occur in west American waters.

- e. Ventral margin (interiorly) with oblique grooving; small  
*Transennella*

- ee. Ventral margin without oblique grooving

- f. Pedal retractor impression deeply excavated; shell large, thick and smooth  
*Megapitaria*

- ff. Pedal retractor impression not deeply excavated; shell smaller and thinner

- g. Anterior lateral small and situated near anterior margin of hinge plate  
(subgenus)

*Agriopoma*

- gg. Anterior lateral large and situated close to or nearly midway between anterior cardinal and anterior margin of hinge plate  
*Pitar*<sup>8</sup>

#### B. Left valve without an anterior lateral tooth

- a. Inner margin crenulated
- b. Shell elongate (anterior end often narrow) or subquadrate; small; concentric sculpture very prominent .....*Irus*<sup>9</sup>
- bb. Shell roundly trigonal or ovately quadrate; usually large
- c. Concentric sculpture of coarse, rugose ridges...*Anomalocardia*
- cc. Concentric sculpture of fine or coarse lamellae (sometimes much reduced)
- d. Escutcheon well developed on left valve
- e. Left posterior cardinal elongate; middle cardinal thick; hinge plate triangular; pallial sinus usually short .....*Chione*
- ee. Left posterior cardinal short; middle cardinal not thickened (strongly bifid) hinge plate narrow and long; pallial sinus usually long  
*Protothaca* s.s.<sup>10</sup>
- dd. Escutcheon lacking or nearly so on left valve  
(subgenus) *Callithaca*

<sup>8</sup> The subgenus *Tinctora* Jukes-Browne has an irregularly crenulated margin and is represented in west American waters by one species, *Pitar vulnerata*.

<sup>9</sup> The type species of *Irus* has a smooth inner margin.

<sup>10</sup> Not represented in the present collection.

- aa. Inner margin not crenulated
- e. Shell suborbicular or roundly subquadrate  
*Cyclinella*
- ee. Shell obliquely elliptical or trigonal
- f. Pallial sinus present
- g. Obliquely elliptical; pallial sinus narrow  
*Compsomyax*
- gg. Trigonal; pallial sinus wide; small, length not exceeding 8 mm.  
*Psephidia*
- ff. Pallial sinus lacking (in type); anterior and middle cardinal teeth formed by a thin bent lamina, with two pits on ventral side  
*Callocardia* s.s.<sup>10</sup>

Genus *Dosinia* Scopoli.

Key to the subgenera of *Dosinia*.

- A. Escutcheon present ..... *Dosinia* s.s.<sup>11</sup>
- B. Escutcheon lacking ..... *Dosinidia*

Subgenus *Dosinidia* Dall.

Key to the species of *Dosinidia*.

- A. Orbicular, very large, usually longer than high; expanded posteriorly..... *ponderosa*
- B. Ovately or triangularly orbicular, smaller, usually as high or higher than long; not expanded posteriorly
- a. Pallial sinus pointing toward middle of anterior adductor impression  
*dunkeri*
- aa. Pallial sinus pointing toward ventral margin of anterior adductor impression; ribs subobsolete medially  
*annae*<sup>12</sup>

*Dosinia* (*Dosinidia*) *dunkeri* Philippi.

*Cytherea dunkeri* Philippi, Abbild. u. Beschreib. Conchyl., Bd. 1, Heft 7, October, 1844, *Cytherea*, p. 170 (4), pl. 2, fig. 5. "Patris: Mare Pacificum Mejico alluens."

*Artemis simplex* Hanley, Proc. Zool. Soc. London, April, 1845, p. 11. "Hab. Panama, St. Elena. Mus. Cuming, Hanley."—Hanley, Cat. Rec. Biv. Shells, Ap., p. 357, ?1856, pl. 15, fig. 41, 1844. Panama.

*Artemis dunkeri* Reeve, Conch. Icon., Vol. 6, *Artemis*, 1850, species 34, pl. 6, fig. 34. "Hab. St. Elena and Panama, Central America (from sandy mud at low water); Cuming."—Adams & Reeve, Zool. Voy. Samarang, Moll., 1848, p. 78, pl. 21, fig. 17. Not the record "Hab. Eastern Seas."

*Dosinia dunkeri* Philippi, Carpenter, Cat. Mazatlan Shells, September, 1855, p. 61. Mazatlan, Mexico, also earlier records cited.

—Grant & Gale, Mem. San Diego Soc. Nat. Hist., Vol. 1, 1931, p. 354. Earlier records cited. Pliocene and Recent.

*Type Locality*: West coast of Mexico.

*Range*: Magdalena Bay, Lower California, to the Gulf of California and south to Zorritos, Peru, and the Galápagos Islands.

*Collecting Stations*: Mexico: Tenacatita Bay; Manzanillo (184-D-2), 30 fathoms, gravelly sand; 17 miles S.E. of Acapulco (189-D-3), 13 fathoms, mud; Port Guatulco; Nicaragua: Potosi and Monypenny Point, Gulf of Fonseca; Corinto (200-D-11, 19), 8-13 fathoms, sand, mangrove leaves, also beach drift, also Isla Encantada; Costa Rica: Port Parker; Culebra Bay; Isla Cedro, Gulf of Nicoya; 1 mile South of Golfo Bay; Panama: Isla Parida; Bahia Honda; Colombia: Gorgona Island.

*Description*: Shell white, somewhat ovately or triangularly orbicular, often slightly higher than long, beaks strongly projecting; lunule ovately oblong, moderately depressed; exterior regularly concentrically grooved, sometimes faint superficial radial striae are present; pallial sinus angular, usually projecting slightly beyond the middle of the shell and pointing toward the middle of the anterior adductor muscle impression.

A specimen from the Gulf of California in the Henry Hemphill collection in the California Academy of Sciences, measures: length, 56 mm.; height, 55 mm.; convexity (both valves), 30.6 mm.

The form described as *Dosinia annae* by Carpenter<sup>13</sup> is very similar to *D. dunkeri* but the concentric ribs are flatter and more nearly obsolete in the middle portion of the valves and the pallial sinus points more nearly toward the base or ventral portion of the anterior adductor impression.

Compared to *Dosinia ponderosa*, *D. dunkeri* is smaller, higher in proportion to the length, less expanded posteriorly, umbos more ventricose, beaks more projecting, and it is sculptured by finer and more regular concentric grooves.

*Dosinia brasiliensis* White from the Miocene of Brazil is very similar to *D. dunkeri*, and *D. mathewsonii* Gabb from the Miocene of California also has some features in common.

*Distribution*: *Dosinia dunkeri* was collected at a number of localities from west Mexico to Colombia on beaches and dredged at depths of 8 to 30 fathoms. It is also known to occur from Pliocene to Recent in the Gulf of California region.

*Dosinia* (*Dosinidia*) *ponderosa* Gray.

*Arthemis ponderosa* Gray, Analyst, Vol. 8, 1838, p. 309. [No locality cited].

*Artemis ponderosa* Gray, Reeve, Conch. Icon., Vol. 6, *Artemis*, 1850, species 4, pl. 1, fig. 4. "Hab. Gulf of California (in sandy mud at low water)."

<sup>13</sup> *Dosinia annae* Carpenter, Cat. Mazatlan Shells, September, 1855, p. 61. "Mazatlan; very rare."—Römer, Mon. Molluskengattung *Dosinia*, Scopoli, (Cassel), 1862, p. 18, pl. 4, fig. 1.

<sup>11</sup> Not represented in west American waters.

<sup>12</sup> Not represented in the present collection.

*Dosinia ponderosa* Gray, Grant & Gale, *Mem. San Diego Soc. Nat. Hist.*, Vol. 1, 1931, p. 351, pl. 15, figs. 1a, 1b, 1c. Earlier records cited. Pleistocene and Recent.

*Type Locality*: Gulf of California (here designated as type locality). No locality cited originally.

*Range*: Scammon Lagoon, Lower California, to the Gulf of California and south to Paita, Peru, and the Galápagos Islands.

*Collecting Stations*: Mexico: Santa Inez Bay, Gulf of California (144-D-1-4 and 145-D-1-3), 4-20 fathoms, sand, sandy mud, crushed shell, weed, calcareous algae, also on beach; Tenacatita Bay; Santa Cruz (195-D-21), 33 fathoms, mud; Nicaragua: Corinto (200-D-10,11,16), 4-8 fathoms, sand, mangrove leaves; Costa Rica: Port Parker (203-D-1,2,3), 18.2-27 fathoms, sandy mud, crushed shell, shelly mud, algae.

*Description*: Shell large, orbicular, longer than high, slightly angulated posterior to the ligament, gently convex, thick, cream colored and covered by a shining horn-colored periostracum; lunule cordate, depressed; exterior concentrically grooved but these are usually weaker in the median portion of the valves, faint superficial radial striae are sometimes present; pallial sinus angular and projecting to a point about midway between the anterior and posterior adductor impressions.

A large specimen from the Gulf of California, in the collections of the California Academy of Sciences, measures: length, 145 mm.; height, 139 mm.; convexity (both valves), 75 mm.

Compared to *Dosinia annae* Carpenter, the shell of the present species is larger, the posterior dorsal margin is more expanded, the beaks are less projecting, the posterior portion of the hinge plate is wider and the pallial sinus points toward about the middle rather than toward the base of the anterior adductor impression.

The shell of *D. ponderosa* is larger, thicker, more orbicular in outline, the beaks are less projecting, the dorsal outline is broader, the concentric sculpture is coarser, and the posterior portion of the hinge plate is wider than that of *D. dunkeri*. The Atlantic species *Dosinia concentrica* Born is somewhat similar, and related species occur in the Miocene and Pliocene of California, Peru, and the Caribbean region.

*Distribution*: Specimens of *Dosinia ponderosa* were collected from the Gulf of California to Costa Rica on beaches and dredged at depths of 4 to 33 fathoms. It also is known to occur in the Pleistocene of southern California, the Gulf of California region, Oaxaca, Mexico, and Ecuador.

### Genus *Tivela* Link.

Key to the species of *Tivela*.

- A. A broad, shallow, radial furrow present posteriorly; yellowish-white *argentina*  
 B. Radial furrow slight or lacking posteri-

orly; usually brown or brown with cream colored stripes, or purplish coloration

a. Very convex; high; thick *byronensis*

aa. Gently convex or compressed; longer than high (slightly produced anteriorly); thinner; dorsal margins meeting at a greater angle

b. Height usually exceeding 30 mm.; compressed, triangular, thin

c. Shell gaping posteriorly *hians*<sup>14</sup>

cc. Shell closed posteriorly *planulata*<sup>14</sup>

bb. Height usually not exceeding 30 mm.; more convex, thicker *delessertii*

### *Tivela argentina* Sowerby.

*Cytherea argentina* Sowerby, *Proc. Zool. Soc. London*, June 1, 1835, p. 46. "Hab. ad Sinum Nicoiyo, Americae Centralis." "Found in sand banks at low water."—Sowerby, *Thes. Conch.*, Vol. 2, 1851, p. 622, pl. 129, fig. 62 (as *Cytherea argentina*). Original locality cited.—Reeve, *Conch. Icon.*, Vol. 14, *Cytherea*, 1864, species 11, pl. 4, fig. 11. Central America.

*Type Locality*: Gulf of Nicoya, Costa Rica, in sand banks at low water.

*Range*: Mazatlan, Mexico, to Panama.

*Collecting Stations*: Nicaragua: Corinto (200-D-10,11,19), 7-13 fathoms, sand, mangrove leaves, also in beach drift; Costa Rica: 1 mile south of entrance to Golfito Bay.

*Description*: Shell trigonal, rather thin, moderately convex, yellowish-white, ventral margin arcuate, somewhat attenuated at both ends; a broad, shallow, radial sulcus is present posteriorly; periostracum thin, light brown in color. A large valve from Costa Rica measures approximately: length 61 mm.; height 58 mm.; convexity 16.5 mm.

*Distribution*: *Tivela argentina* was collected by the expedition at Corinto, Nicaragua, where it occurs fairly commonly, and south of the entrance to Golfito Bay, Costa Rica. This species has been reported as occurring in the Pliocene of Argentina<sup>15</sup> but according to von Ihering<sup>16</sup> that record can be referred to *Tivela fulminata oblonga* Philippi.

### *Tivela byronensis* Gray.

*Cytherea radiata* Sowerby, *Proc. Zool. Soc. London*, April 16, 1835, p. 23. "Hab. ad oras Columbiae Occidentalis. (Salango and Xipixapi)." "Found in sandy mud at a depth of nine fathoms."—Sowerby, *Thes. Conch.*, Vol. 2, 1851, p. 615, pl. 128, figs. 28,29,30,31 (as *Cytherea radiata*). Original locality cited.

Not *Trigona radiata* Megerle von Mühl-

<sup>14</sup> Not represented in the present collection.

<sup>15</sup> *Tivela argentina* Sowerby, Borchert, *Neues Jahrb. f. Miner. Geol. u. Palaeo.*, Beil. Bd. 14, 1901, p. 204, pl. 8, figs. 9, 10. "Paraná." Argentina, Pliocene.

<sup>16</sup> von Ihering, H., *An. Mus. Nac. de Buenos Aires*, Vol. 14 (Ser. 3, Vol. 7), 1907, p. 384.

feld, 1811. [Referred to *Tivela mactroides* Born, 1778, by Dall, 1902].

*Trigona byronensis* Gray, *Analyst*, Vol. 8, 1838, p. 304. "Inhabits Pacific Ocean. Capt. Lord Byron."

*Venus solangensis* d'Orbigny, *Voy. Amér. Mérid.*, Vol. 5, Moll., 1846, p. 564. New name for *Cytherea radiata* Sowerby, "(non *V. radiata*, Chemn., 1795; Risso, 1826)." Sowerby's locality for *C. radiata* cited.

*Tivela radiata* Sowerby, Römer, *Monogr. Molluskengattung Venus*, Linné, Bd. 1, 1865, p. 13, pl. 6, figs. 1a-g. Mazatlan, Salango, Xipixapi, Panama, Guayaquil.

*Type Locality*: Salango, Ecuador (here designated as type locality). "Pacific Ocean" originally cited.

*Range*: Lagoon Head, Lower California, to the Gulf of California and south to Guayaquil, Ecuador.

*Collecting Stations*: Mexico: Banderas Bay; Chamela Bay; Tenacatita Bay; Guatemala: 7 miles West of Champerico (197-D-1,2), 14 fathoms, mud; Nicaragua: Corinto (200-D-10, 11, 16, 19), 4-13 fathoms, sand, mangrove leaves, also Isla Cardon; Panama: Gulf of Chiriqui (221-D-1-5), 35-40 fathoms, sandy mud.

*Description*: Shell triangularly ovate, solid, gibbous, often somewhat produced posteriorly, lunule large; colored by reddish-brown radial and concentric bands; perios-tracum olive brown.

A specimen from Tiburon Island in the Gulf of California, in the collections of the California Academy of Sciences, measures: length, 58 mm.; height, 54.5 mm.; convexity (both valves together), 37 mm. Another from the same locality measures: length, 59.1 mm.; height, 50.4 mm.; convexity (both valves together), 39 mm.

This shell is very variable in shape and color. It may be nearly equilateral or quite inequilateral and ventricose or flattened and somewhat attenuated at each end. The color varies from the white variety, *semifulva* Menke, to all varieties of radially banded brown and white patterns to nearly all brown. Some of the specimens in the present collection could be referred to the striped and latticed color form *hindsii* Hanley<sup>17</sup> but when a large series of specimens is examined so much variation in form and color can be observed that there seems to be but little use to apply names to the various color varieties. Carpenter came to the same conclusion after examining over 600 specimens of this species, as did Römer in his study of this species.

*Tivela mactroides* Born, in the Caribbean region, is a similar species.

*Distribution*: *Tivela byronensis* was collected at a few localities along the west coast from Mexico to Panama. It occurs commonly in tropical West American waters. It

also has been recorded as occurring in the Pleistocene of Lower California, and Oaxaca, Mexico, and in the Pliocene of Ecuador.

*Tivela delessertii* Deshayes in Sowerby.

Plate II, Figure 10.

*Cytherea nitidula* Lamarck, Sowerby, *Thes. Conch.*, Vol. 2, 1851, p. 616, species No. 14, pl. 128, fig. 25. "Locality uncertain."

*Cytherea delessertii* Deshayes in Sowerby, *Thes. Conch.*, Vol. 2, 1854, p. 785. "*C. nitidula* (14) is not the true species of Lamarck, but M. Deshayes has named it *C. Delessertii*."

*Tivela delesserti* Deshayes, Dall, *Proc. U. S. Nat. Mus.*, Vol. 26, 1902, p. 386. "Scammon's Lagoon (young?); Cape St. Lucas, the Gulf region, and south to Acapulco."

*Type Locality*: Santa Inez Bay, east coast of Lower California (here designated as type locality). No locality cited originally.

*Range*: Santa Inez Bay, Gulf of California, to Oaxaca, Mexico.

*Collecting Stations*: Mexico: Santa Inez Bay, Gulf of California; Cape San Lucas.

*Description*: Shell broadly trigonal, slightly inequilateral, slightly attenuated anteriorly, moderately convex, a trace of a faint radial sulcus at about the posterior third of the valve present on most specimens; colored light chestnut brown with darker stripes or purplish-brown stripes on a cream colored ground.

A fine specimen from Santa Inez Bay measures: length, 30.9 mm.; height, 23.5 mm.; convexity (one valve), 8.8 mm.

The shell of *Tivela delessertii* is thicker and not as high as that of *T. planulata* Broderip & Sowerby. It is smaller, much more elongated, not as high in proportion to the length and flatter than *T. byronensis*, with striped varieties of which, at times, it has been confused.

*Distribution*: *Tivela delessertii* was collected by the expedition at Santa Inez Bay in the Gulf of California and at Cape San Lucas. It apparently does not occur nearly so commonly as *T. byronensis*.

#### Genus *Gouldia* C. B. Adams.

*Gouldia* C. B. Adams, *Cat. Gen. and Spec. Rec. Shells in Coll. of C. B. Adams* (Middlebury: Justus Cobb, printer), 1847, p. 29. Species cited, *G. cerina* Adams and *G. parva* Adams, both from Jamaica. Footnote states: "Syn. *Thetis*. Ad. This name having been preoccupied by Mr. Sowerby for two fossil species in the Green Sand formation of England, I propose the above in honor of my friend Dr. A. A. Gould."—K. V. W. Palmer, *Palaeontogr. Amer.*, Vol. 1, No. 5, p. 307 (99), 1927. "Genoholotype.—*Gouldia cerina* (Adams)."

Not *Gouldia* Bonaparte, 1849. Aves.

*Type*: *Gouldia cerina* C. B. Adams. [Designated by Dall, *Jour. Conch.*, Vol. 4, No. 2, April, 1883, p. 61. Referring to the two species originally cited by Adams, Dall stated,

<sup>17</sup> *Cytherea hindsii* Hanley, *Proc. Zool. Soc. London*, December, 1844, p. 110. "Hab. Guayaquil. Mus. Cuming, Hanley."—Hanley, *Cat. Rec. Bivalve Shells*, Ap., p. 356, 1856, pl. 15, fig. 35, 1844. Guayaquil.—Reeve, *Conch. Icon.*, Vol. 14, *Cytherea*, 1864, species 39, pl. 9, figs. 39a, 39b. Bay of Guayaquil, Ecuador.

... "I have taken the first, largest, and most conspicuous species of the two as a type." On page 62 he mentioned ... "the typical *Gouldia cerina*." Illustrated by K. V. W. Palmer, text fig. 14, p. 307 (99), 1927, pl. 52 (21), figs. 1, 5, 9, 11, 21, 1929. North Carolina to the Antilles, Bermuda, and south to Cape San Roque, Brazil].

Shell small, beaks minute; lunule long, bounded by an impressed line; no escutcheon; pallial line simple or with a slight sinus; ornamented with fine concentric or reticulate sculpture (Palmer).

Palmer cited the occurrence of three species living in east American waters, six species and subspecies occurring in the Miocene, and two species in the Pliocene of eastern North and Central America.

So far as known this genus is represented by only one species in west American waters. It also is known to occur in the Pleistocene of the Gulf of California region.

#### *Gouldia californica* Dall.

*Gouldia californica* Dall, *Proc. U. S. Nat. Mus.*, Vol. 51, No. 2166, January 15, 1917, p. 579. "Gulf of California near La Paz, in 21 fathoms."

*Gafrarium (Gouldia) stephensae* E. K. Jordan, *Contrib. Dept. Geol. Stanford Univ.*, Vol. 1, No. 4, November 13, 1936, p. 136, pl. 19, figs. 10, 11. "Magdalena Bay, Lower California." "Pleistocene."

*Type Locality*: Gulf of California near La Paz, Lower California, Mexico, in 21 fathoms.

*Range*: La Paz, Lower California, Mexico, to Port Parker, Costa Rica.

*Collecting Stations*: Mexico: Manzanillo (184-D-2), 30 fathoms, gravelly sand; Costa Rica: Port Parker (203-D-1,3), 12-15 fathoms, sandy mud, crushed shell, shelly mud.

*Description*: Shell small, thin, white, with touches of brown along the dorsal border, ovate-triangular, the anterior lateral tooth large and prominent, the pallial line hardly sinuated; sculpture reticulate, the concentric sculpture more prominent in the middle of the disk, the radial toward the ends of the valves; the inner valve margins smooth. Length 6 mm.; height, 5.5 mm.; diameter, 3 mm. (Dall).

*Distribution*: This species was taken off Manzanillo, Mexico, in 30 fathoms and more abundantly at Port Parker, Costa Rica, in 12 to 15 fathoms. It also occurs in the Pleistocene of Magdalena Bay, Lower California.

#### Genus *Megapitaria* Grant & Gale.

Key to the species of *Megapitaria*.

- A. Margin below beaks broadly rounded;  
periostracum dull golden brown  
*aurantiaca*
- B. Margin below beaks flattened;  
periostracum shiny purplish-brown,  
often mottled ..... *squalida*

#### *Megapitaria aurantiaca* Sowerby.

*Cytherea aurantiaca* Sowerby, Gen. Rec.

and Foss. Shells, Vol. 2, Pt. 33, 1831, pl. 196, ng. 3. [No locality cited].

*Cytherea aurantia* Hanley, Sowerby, *Thes. Conch.*, Vol. 2, *Cytherea*, 1851, p. 628, pl. 132, fig. 97 bis. "From Mr. Cuming's collection."

*Dione aurantia* Deshayes, Reeve, *Conch. Icon.*, Vol. 14, *Dione*, 1863, species 12, pl. 3, fig. 12. "Hab. Acapulco, South America".

*Macrocallista aurantiaca* Sowerby, E. K. Jordan, *Contrib. Dept. Geol. Stanford Univ.*, Vol. 1, No. 4, 1936, p. 142. Magdalena Bay, Lower California, Pleistocene. Gulf of California to Ecuador, Recent.

*Type Locality*: Bay of Panama (here designated as type locality). No locality cited originally.

*Range*: Gulf of California to Salinas, Ecuador.

*Collecting Stations*: Mexico: Port Guatulco (195-D-4,6), 3-4.5 fathoms, sand, algae, crushed shell, also on shore; Tangola-Tangola Bay (196-D-14,15), 5 fathoms, crushed shell, also on shore; Costa Rica: Port Parker; Culebra Bay; Ballenas Bay; Golfito, Gulf of Dulce; Colombia: Gorgona Island.

*Description*: Shell large, ovate, convex, thick, smooth, the anterior end the shorter, indistinctly angled posteriorly; sculptured only with concentric lines of growth; periostracum dull orange pink brown beneath which the shell is orange pink or pinkish-brown; margin smooth.

Large specimens from the Gulf of California in the collections of the California Academy of Sciences measure 115 mm. in length.

The shell of this species is more broadly rounded in outline than that of *Megapitaria squalida*. The dull orange brown periostracum and orange pink shell is different from that of *M. squalida* in which the periostracum is a shiny purplish-brown, often mottled or striped, and the shell is a drab light brown.

*Distribution*: This species was collected on shore and dredged in 3 to 5 fathoms from west Mexico to Colombia. It also has been recorded as occurring in the Pliocene and Pleistocene of Lower California.

#### *Megapitaria squalida* Sowerby.

*Cytherea squalida* Sowerby, *Proc. Zool. Soc. London*, April 16, 1835, p. 23. "Hab. ad Sanctam Elenam." "Found in sandy mud at a depth of six fathoms."

*Cytherea squalida* Sowerby, Sowerby, *Thes. Conch.*, Vol. 2, *Cytherea*, 1851, p. 629, pl. 131, figs. 87, 88, 89 [Lower] "California." [Not the record cited "from the Philippine Islands"].

*Dione squalida* Sowerby, Reeve, *Conch. Icon.*, Vol. 14, *Dione*, 1863, species 10, pl. 3, fig. 10. Locality record same as cited by Sowerby, 1851.

*Pitar (Megapitaria) squalidus* Sowerby, Grant & Gale, *Mem. San Diego Soc. Nat. Hist.*, Vol. 1, 1931, p. 347. Earlier records cited. Pliocene to Recent.

*Type Locality*: Santa Elena, Ecuador, in 6 fathoms, sandy mud.

**Range:** Scammon Lagoon, Lower California, to the Gulf of California and south to Mancora, Peru.

**Collecting Stations:** Mexico: East of Cedros Island (126-D-2), 38 fathoms, mud; Arena Bank (136-D-15,16,26,30), 35-45 fathoms, mud, muddy sand, crushed shell, weed, rock; Cape San Lucas; Arena Point area; Ceralbo Channel (137-D-3), 46 fathoms, rock; Ceralbo Island, shore; Santa Inez Bay (141-D-1-4), 7-20 fathoms, sand, sandy mud, crushed shell, weed, calcareous algae, (143-D-1), 29 fathoms, mud, crushed shell, weed, (144-D-2), 2½ fathoms, sand, weed, rocks, (145-D-1,3), 4-13 fathoms, sand, also at Santa Inez Point and at Monument Station, shore; Port Guatulco (195-D-1,2,21), 2.5-18 fathoms, sand, algae, crushed shell, mud; Tangola-Tangola Bay (196-D-17), 23 fathoms, mud; Costa Rica: Port Parker (203-D-1,2,3), 12-15 fathoms, sandy mud, crushed shell, shelly sand and mud, algae, also on beach; Port Culebra (206-D-1-3, 14 fathoms, sandy mud, also on shore; Cedro Island, Gulf of Nicoya; Golfito, Gulf of Dulce; Panama: Gulf of Chiriqui (221-D-1-5), 35-40 fathoms, sandy mud; Bahia Honda (222), shore; Colombia: Gorgona Island, shore.

**Description:** Shell large, attaining a length of 120 mm., smooth, convex, somewhat produced anteriorly and posteriorly and somewhat roundly angulated along the posterior umbonal slope; periostracum shiny purplish-brown often somewhat mottled or striped and beneath this the shell is colored a drab light brown.

The shell of this species differs from that of *Megapitaria aurantiaca* in the coloration and in that it is more produced both anteriorly and posteriorly. Although there appears to be nearly complete intergradation between the two, typical forms are quite distinct.

*Macrocallista orcutti* Dall, described from the Pleistocene of Magdalena Bay, is a similar species but possesses a much larger and thicker shell. *Macrocallista maculata* Linnaeus, which occurs in the Caribbean region, is another similar species.

Other names which have been applied to *M. squalida* include *Chione biradiata* Gray, 1838, and *Cytherea chionaea* Menke, 1847, which was proposed for a mottled, rounded form.

**Distribution:** *Megapitaria squalida* is very commonly found in the Gulf of California region and south to Peru. It was collected at many localities from off Cedros Island, Lower California, to Gorgona Island, Colombia, on the beach and dredged at depths of 2.5-46 fathoms. The largest number of specimens found at any one locality was at Port Parker, Costa Rica. It is also known to occur in the Pliocene and Pleistocene of the Gulf of California region and has been recorded<sup>18</sup> as occurring in the Pleistocene of the Newport Bay area in southern California.

### Genus *Transennella* Dall.

Key to the species of *Transennella*.

- A. Shell faintly concentrically grooved exteriorly
- a. Length exceeding 10 mm.
- b. Angle at beaks 90°; thick  
*pannosa*<sup>19</sup>
- bb. Angle at beaks 120°; more produced anteriorly; moderately thin  
*puella*
- aa. Length not exceeding 10 mm.
- c. Angle at beaks 90°.....*tantilla*<sup>19</sup>
- cc. Angle at beaks 110°  
*galapagana*<sup>19</sup>
- B. Shell strongly concentrically grooved exteriorly; lunule more broadly cordate  
*sororcula*

### *Transennella puella* Carpenter.

*Callista* (? *pannosa*, var.) *puella* Carpenter, *Ann. & Mag. Nat. Hist.*, Ser. 3, Vol. 13, April, 1864, p. 313. Described from "Cape St. Lucas." Reprint in *Smithson. Miscell. Coll.*, No. 252, 1872, p. 211.

*Transennella puella* Carpenter, Hertlein & Strong, *Proc. Calif. Acad. Sci.*, Ser. 4, Vol. 23, No. 24, 1939, pp. 377-378 (in text), pl. 32, figs. 14, 15, 16. Cape San Lucas on beach, also dredged.

**Type Locality:** Cape San Lucas, Lower California.

**Range:** Guadalupe Island, Lower California, to the Gulf of California and south to Nicaragua and probably to Panama.

**Collecting Stations:** Mexico: Cape San Lucas; Arena Bank in the Gulf of California (136-D-16), 45 fathoms, muddy sand, weed; Santa Inez Bay (145-D-1-3), 4-13 fathoms, sand; Port Guatulco (195-D-9), 7 fathoms gr. sand, crushed shell; Tangola-Tangola Bay (196-D-13), 10 fathoms, gr. sand, crushed shell.

**Description:** Shell roundly ovate, small, large specimens attain a length of about 18 mm.; hinge normal for the genus; color pattern consisting of various amounts of brown or brownish zigzag markings on a cream ground or whitish triangular areas surrounded by brown; pallial sinus only slightly ascending, rounded at end, projecting anteriorly to about one-half the length of the shell; interior whitish and purple; interior margin obliquely grooved; apical angle of beaks about 120°.

*Transennella puella* differs from *T. pannosa* Sowerby, which occurs off western South America, in the thinner shell, which is more produced anteriorly, and in that the apical angle is approximately 120° as compared to about 90° in Sowerby's species.

*Macrocallista (Chionella) omissa* Pilsbry & Lowe, 1932, described from San Juan del Sur, Nicaragua, was said to possess a shorter and more triangular shell than that of *Transennella puella* as well as different sculpture and color pattern.

<sup>18</sup> See Bruff, S. C., *Univ. Calif. Publ., Bull. Dept. Geol. Sci.*, Vol. 27, No. 6, 1946, p. 232.

<sup>19</sup> Not represented in the present collection.

*Distribution*: Specimens of *Transennella puella* were collected at several localities from Santa Inez Bay in the Gulf of California to Tangola-Tangola Bay, Mexico, on the beach and dredged in 4 to 45 fathoms.

***Transennella sororcula* Pilsbry & Lowe.**

*Transennella sororcula* Pilsbry & Lowe, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 84, May 21, 1932, p. 102, pl. 9, figs. 12-16, text fig. 4. "San Juan del Sur, Nicaragua."

*Macrocallista sorocula* Pilsbry & Lowe, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 84, May 21, 1932, p. 143, pl. 9, figs. 12-16.

*Transennella sorocula* Pilsbry & Lowe, Hertlein & Strong, *Proc. Calif. Acad. Sci.*, Ser. 4, Vol. 23, No. 24, 1939, p. 377 (in text), pl. 32, figs. 11, 12. Dredged in 20-220 fathoms due east of San Jose del Cabo, Lower California.

*Type Locality*: San Juan del Sur, Nicaragua.

*Range*: Santa Inez Bay, Gulf of California, to San Juan del Sur, Nicaragua.

*Collecting Stations*: Mexico: San Lucas Bay (135-D-25), 7 fathoms, sand; [?] (135-D-16), 6-20 fathoms, sand; Arena Bank (136-D-27), 50 fathoms, sand, calcareous algae, rock; Santa Inez Bay.

*Description*: Shell roundly ovate, varying in size from 16 to 35 mm. in length, glossy, rather deeply but unequally concentrically grooved, this character most strongly developed anteriorly and posteriorly; color cinnamon brown, or cream with radial markings or a network of chocolate-colored lines or various combinations of such patterns; interior white tinged with purple; the pallial sinus extends forward nearly one-half the length of the shell; inner margins obliquely grooved.

The more rounded outline, stronger concentric grooves, larger size and more broadly cordate lunule are characters which serve to separate *Transennella sororcula* from other species of the genus in west American waters.

*Distribution*: This species was taken by the expedition at a few localities from San Lucas Bay to Santa Inez Bay in the Gulf of California, on the beach and at depths of 6 to 50 fathoms.

**Genus *Pitar* Römer.**

Key to the subgenera of *Pitar*.

- A. Shell with spines or scales along posterior umbonal angulation.....*Hysteroconcha*
- B. Shell without spines or scales along posterior umbonal angulation
  - a. Shell with fine zigzag sculpture  
*Hyphantosoma*
  - aa. Shell without zigzag sculpture
    - b. Shell suborbicular; inner margin irregularly crenulated.....*Tinctora*
    - bb. Shell ovate or subtrigonal; inner margin smooth
    - c. Shell smooth or with fine concentric threads

- d. Left middle cardinal decidedly longer and thicker than anterior cardinal
- e. Left anterior lateral very small and distant from cardinals

*Agriopoma*<sup>20</sup>

- ee. Left anterior lateral larger and close to cardinals.....*Pitarella*
- dd. Left middle cardinal only slightly longer than anterior cardinal.....*Pitar* s.s.
- cc. Shell with strong concentric ribs or lamellae *Lamelliconcha*

**Subgenus *Pitar* s.s.**

Key to the species of *Pitar* s.s.

- A. Shell decidedly elongated; with brown zigzag concentric markings; smooth, very thin.....*newcombianus*
- B. Shell roundly trigonal or suborbicular
  - a. Anterior lateral tooth of left valve higher than others.....*consanguineus*
  - aa. Anterior lateral tooth of left valve not higher than others.....*unicolor*

***Pitar (Pitar) consanguineus* C. B. Adams.**

*Cytheraea consanguinea* C. B. Adams, *Ann. & Lyceum Nat. Hist. New York*, Vol. 5, July, 1852, pp. 496, 545 (separate pp. 272, 321). "Panama."—Römer, *Monogr. Molluskengattung Venus*, Linné, (Cassel), Bd. 1, *Cytheraea*, December, 1867, p. 108, pl. 28, figs. 5, 5a, 5b. Panama.

*Cytheraea consanguinea* C. B. Adams, Sow-erby, *Thes. Conch.*, Vol. 2, 1853, p. 743, pl. 163, fig. 203. Panama.

*Type Locality*: Panama.

*Range*: Port Guatulco, Mexico, to Panama.

*Collecting Stations*: Mexico: Port Guatulco (195-D-1), 2.5 fathoms, sand, algae; Guatemala: 7 miles west of Champerico (197-D-2), 14 fathoms, mud; El Salvador: La Libertad (198-D-2), 14 fathoms, mud; Nicaragua: Monypenny Point, Gulf of Fonseca; Corinto (200-D-8, 9, 19), 6-24 fathoms, mangrove leaves, also on shore; Costa Rica: Port Parker (203-D-1, 2, 3), 10-15 fathoms, sandy mud, crushed shell, shelly sand, algae, shelly mud; Cedro Island, Gulf of Nicoya; Golfito, Gulf of Dulce.

*Description*: Shell roundly trigonal, beaks a little anterior to the center, smooth but with fine concentric lines of growth; ornamented with brown radial markings which often do not reach the ventral margin, in some specimens the beaks faintly pinkish colored; hinge with the anterior lateral of the left valve larger and higher than the others; interiorly the umbonal area is usually pink, the remainder of the shell white.

The largest specimen in the collection measures approximately: length 33 mm.; height, 26.4 mm.; convexity (one valve), 9.5 mm.

<sup>20</sup> *Agriopoma* has been placed in this key for convenience although it is also cited under *Callocardia*.

The shell of *Pitar consanguineus* is more rounded in outline and possesses a much larger anterior lateral tooth in the left valve in comparison to that of *P. mexicanus*.

The more rounded trigonal form and longer anterior dorsal margin serve to separate this species from *Pitar inconspicuus* Sowerby<sup>21</sup> and *P. purus* Deshayes<sup>22</sup>, both described from Peru, and *P. tomeanus* Dall, described from Chile.

**Distribution:** Specimens referable to *Pitar consanguineus* were taken by the expedition from west Mexico to Costa Rica on the beach and dredged at depths of 2.5 to 24 fathoms. The largest number of specimens collected at any one locality, mostly small, was at Corinto, Nicaragua, in beach drift and dredged in 12-13 fathoms.

#### *Pitar (Pitar) newcombiana* Gabb.

*C[irce]. L[ioconcha]. newcombiana* Gabb, *Proc. Calif. Acad. Nat. Sci.*, Vol. 3, January, 1865, p. 189. "Hab. two valves, Catalina Island, 120 fms. Dr. Cooper."

*Pitaria newcombiana* Gabb, I. S. Oldroyd, *Stanford Univ. Publ. Ser. Geol. Sci.*, Vol. 1, 1924, p. 151, pl. 57, fig. 2. Monterey, California, to Lower California. Also Pleistocene and Pliocene.

**Type Locality:** Catalina Island, California, in 120 fathoms.

**Range:** Monterey, California, to the Gulf of California, and south to Port Guatulco, Mexico, and Clarion Island.

**Collecting Stations:** Mexico: Cape San Lucas; Port Guatulco (195-D-9), 7 fathoms, gr. sand, crushed shell.

**Description:** Shell thin, trigonally ventricose, polished, marked by minute concentric striae; beaks large, subcentral; anterior end prominent, narrowly rounded, posterior a little the widest, base convex; lunule not excavated, bounded by an impressed line; color yellowish-white, variously lined with brown angular lines; interior whitish; internal margin smooth; hinge teeth delicate (Gabb).

A specimen from Port Guatulco, Mexico, measures approximately: length, 17.3 mm.; altitude, 14 mm.; convexity (both valves together), 9 mm.

**Distribution:** One specimen of this species was taken at Cape San Lucas and one was dredged by the expedition at Port Guatulco, Mexico, in 7 fathoms. It also is known to occur in the Pliocene and Pleistocene of southern California and in the Pleistocene of Lower California.

<sup>21</sup> *Cytherea inconspicua* Sowerby, *Proc. Zool. Soc. London*, June 1, 1835, p. 47. "Hab. ad Paytam, Peruviae." "Found in sandy mud at low water."—Sowerby, *Thes. Conch.*, Vol. 2, 1851, p. 638, pl. 133, figs. 133, 134 (as *Cytherea inconspicua*). Payta, Peru.

<sup>22</sup> *Dione pura* Deshayes, *Cat. Conch. Biv. Shells in Brit. Mus.*, Pt. 1, 1853, p. 68. "Hab. Callao (Hinds)."

*Cytherea pura* Deshayes, Römer, *Monogr. Molluskengattung Venus*, Linné, (Cassel), Bd. 1, *Cytherea*, September, 1867, p. 84, pl. 23, figs. 1, 1a, 1b. Callao, Peru.

*Cytherea (Caryatis) pudicissima* E. A. Smith, described from the coast of India, was compared to *Dione pura* Deshayes (see *Ann. & Mag. Nat. Hist.*, Ser. 6, Vol. 14, September, 1894, p. 169, pl. 5, figs. 3, 4. "Hab. off Ganjam coast, 24 miles south-east of Gopalpur, in 89-93 fathoms").

#### *Pitar (Pitar) unicolor* Sowerby.

*Cytherea unicolor* Sowerby, *Proc. Zool. Soc. London*, April 16, 1835, p. 23. "Hab. ad Real Lejos Americae Centralis." "Found in coarse sand at a depth of six fathoms."—Sowerby, *Thes. Conch.*, Vol. 2, 1851, p. 629, pl. 131, figs. 90, 91 (as *Cytherea unicolor*). "Xippixapi, West Columbia; coarse sand, at 6 fathoms. Cuming."

*Chione badia* Gray, *Analyst*, Vol. 8, 1838, p. 306. [No locality cited].

*Cytherea ligula* Anton, *Verzeichniss der Conchyl.*, 1839, p. 7. [*Cytherea* cited as a subgenus of *Venus*.] [No locality cited.]—Philippi, *Abbild. u. Beschreib. Conchyl.*, Bd. 1, Heft 6, *Cytherea*, July, 1844, p. 149 (1), pl. 1, fig. 2. "Patria . . ."

*Dione unicolor* Sowerby, Reeve, *Conch. Icon.*, Vol. 14, *Dione*, 1863, species 33, pl. 8, figs. 33a, 33b. "Hab. West Columbia."

**Type Locality:** Real Lejos [near Corinto], Nicaragua, in 6 fathoms, coarse sand.

**Range:** Humboldt Bay, Lower California (Dall) [Panama]. Acapulco, Mexico, to Jipijapa, Ecuador.

**Collecting Stations:** Costa Rica: Culebra Bay; Piedra Blanca Bay; Uvita Bay; Golfito; 1 mile south of the entrance to Golfito, Gulf of Dulce.

**Description:** Shell triangularly elongately rounded, somewhat compressed, thick, concentrically ridged but these are obsolete in the medial portion of the valves, fine radial striations are present on unworn specimens; color white or chestnut brown or some shade between the two. The pallial sinus extends forward more than half the length of the shell, the end is rounded.

The largest specimen collected measured approximately: length 46 mm.; height, 40.5 mm.; convexity (one valve) 10 mm.

Characteristic features of this species are the smooth medial areas externally and the long pallial sinus which extends forward more than half the length of the shell.

**Distribution:** This species was taken by the expedition only along the coast of Costa Rica.

#### Subgenus *Pitarella* Palmer.

*Pitar (Pitarella) mexicanus* Hertlein & Strong, sp. nov.

Plate I, Figures 3 and 8.

*Pitar lenis* Pilsbry & Lowe, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 84, May 21, 1932, p. 100, pl. 16, fig. 6. "Acapulco, 20 fathoms" (type). Also, "Guaymas, 20 fathoms" (paratypes).

Not *Cytherea lenis* Conrad, *Jour. Acad. Nat. Sci. Philadelphia*, Ser. 2, Vol. 1, 1848, p. 130, pl. 14, fig. 19. Marlborough, Hanover County, Virginia, Eocene. Referred to "*Pitaria (Pitaria) lenis* Conrad by Van Winkle Palmer, *Palaeontogr. Amer.*, Vol. 1, No. 5, p. 218 (10), 1927, pl. 35 (4), fig. 7, 1929.

**Type Locality:** 4 miles south-southwest of Maldonado Point, Mexico, in 26 fathoms, mud.

**Range:** Santa Maria Bay, west coast of

Lower California, to Santa Inez Bay in the Gulf of California and south to the Gulf of Chiriqui, Panama.

*Collecting Stations*: Mexico: Arena Bank (136-D-2), 45 fathoms, mud, *Arca* conglomerate; Santa Inez Bay (143-D-4), 25 fathoms, sand, (146-D-1), 35 fathoms, mud, crushed shell; 19 miles west of Mazatlan (153); Manzanillo (184-D-2), 30 fathoms, gravelly sand; 4 miles ssw. of Maldonado Point (192-D-1), 26 fathoms, mud; Port Guatulco (195-D-1, 20), 2.5-23 fathoms, sand, algae, mud; Guatemala: 7 miles west of Champerico (197-D-1, 2), 14 fathoms, mud; El Salvador: Meanguera Island, Gulf of Fonseca (199-D-1), 16 fathoms, sand, mud, crushed shell; Nicaragua: (exact locality unknown); Costa Rica: Port Parker (203-D-1, 2, 3), 12-15 fathoms, sandy mud, crushed shell, shelly sand, algae, shelly mud; Port Culebra (206-D-1, 2, 3), 14 fathoms, sandy mud; Cedro Island, Gulf of Nicoya (213-D-1, 10), 8-10 fathoms, mud; off Ballenas Bay, Gulf of Nicoya (213-D-11, 17), 35 fathoms, mud.

*Description*: Shell elongately oval, rather thin, white, exteriorly resembling *Compsomyax subdiaphana* Carpenter; ornamented with close, fine, concentric riblets over the whole valve or subobsolete medially; lunule large, cordate, bordered by an incised line; hinge of left valve with 3 cardinals and an anterior lateral tooth, the anterior and middle cardinals are joined dorsally, the middle one is longer and thicker, a pit occurs at the base, the posterior cardinal is elongate and thin, the lamella forming the middle and anterior cardinals bears slight irregularities or cusps, the anterior lateral with 2; hinge of right valve with a high thin anterior cardinal connected with a bifid posterior cardinal, the middle cardinal is separated from the anterior cardinal by a narrow space but separated from the posterior cardinal by a much wider space, anteriorly there are two low laterals separated by a pit; pallial sinus short, wide, ascending, rounded at the end. Dimensions: length, 42.3 mm.; height, 33.3 mm.; convexity (both valves together), 25 mm.; pallial sinus projects forward approximately 20 mm. from the posterior margin.

Holotype (Calif. Acad. Sci. Paleo. Type Coll.), from Station 192-D-1, Lat. 16° 16' 30" N., Long. 98° 37' W., 4 miles south-southwest of Maldonado Point, Mexico, in 26 fathoms (47 meters), mud.

The species described as *Cytherea lenis* by Conrad was referred to the genus "*Pitaria*" [= *Pitar*] by K. V. W. Palmer. This necessitates a new name for the west American species described under the name of *Pitar lenis* by Pilsbry & Lowe and the name *Pitar mexicanus*, based upon a specimen off Maldonado Point, Mexico, is here proposed.

The shell of this species is somewhat more elongated and less rounded and the left anterior lateral is less elevated than that of *P. consanguineus* C. B. Adams. It is variable in thickness and in the amount of rounding or subangulation of the posterior end.

The ornamentation of some large specimens is similar to that of *Pitar (Pitarella) gatunensis* Dall and *P. (P.) tumbezianus* Olsson, both of which are tropical American Miocene forms. The character of the hinge of the present species, which has the left middle cardinal more elongated and thicker than the anterior cardinal, together with the shape and ornamentation, are so characteristic of *Pitarella* that we have been led to place it in that subgenus.

*Distribution*: Specimens of this species were taken from Santa Inez Bay in the Gulf of California to the Gulf of Chiriqui, Panama. Usually only one or two specimens were found at each locality but about 75, many of them small, were dredged in 12 fathoms at Port Parker, Costa Rica. This species also has been recorded as occurring in the Pleistocene of Panama.

#### Subgenus *Hyphantosoma* Dall.

Key to the species of *Hyphantosoma*.

- A. Lunule broadly cordate; pallial sinus projecting forward considerably less than half the length of the shell; white *alates*
- B. Lunule elongately cordate; pallial sinus projecting forward nearly half the length of the shell; brown markings...*pollicaris*

#### *Pitar (Hyphantosoma) alates* Hertlein & Strong, sp. nov.

Plate I, Figures 9, 11, 12 and 13.

Shell solid, roundly trigonal, plump, uniformly white; beaks prominent, anteriorly directed over a large cordate lunule defined by a fine impressed line; anterior dorsal margin short, straight, posterior dorsal margin sloping, arched, with a shallow depression on each side of the hinge line and extending to the posterior end; ends and ventral margin rounded; exterior surface ornamented by fine lines of growth, strongest near the margins, very faint near the beaks, crossed by numerous, almost microscopic, radial grooves which divaricate along radial lines extending from the beaks to the posterior and anterior ends of the basal margin, obsolete near the beaks; hinge and ligament strong, normal for the genus and subgenus; pallial sinus short, fairly wide, rounded at the end, ascending, projecting forward to about one-third the length of the shell; interior white; margin smooth. The type measures: length, 53.8 mm.; height, 46 mm.; convexity (both valves together), 34.2 mm.; pallial sinus projects forward 21 mm. from the posterior margin.

Holotype (Calif. Acad. Sci. Paleo. Type Coll.), dredged at station 136-D-13, Lat. 23° 29' N., Long. 109° 24' W., Arena Bank, Gulf of California, in 45 fathoms (82 meters), mud, *Arca* conglomerate. Another single valve without information as to locality probably came from the same general region. A small right valve was dredged at Station 214-D-1-4, Lat. 9° 19' 32"—9° 17' 40" N., Long. 84° 29' 30"—84° 27' 30" W., 14 miles S. × E. of Judas Point, Costa Rica, in 42-61 fathoms, mud, shell, rocks.

A single left valve without information as to locality measures approximately: length, 46 mm.; height, 41 mm.; convexity (one valve), 16 mm. The specimen is slightly eroded but except for the absence of zigzag sculpture it is identical with *Pitar aletes*. Zigzag sculpture is lacking on small specimens and it seems likely that this type of sculpture may disappear with slight erosion of the larger shells or it may be missing on some specimens.

In general features the new species is somewhat similar to *Pitar pollicaris* but is higher in proportion to the length, more convex and trigonal in outline.

*Pitar (Hyphantosoma) aletes* bears a close resemblance to *Pitar (Hyphantosoma) carbaseus* Guppy,<sup>23</sup> described from the Miocene of Jamaica, but appears to be less broadly rounded posteriorly.

The species described by Dautzenberg as *Meretrix (Pitar) intricata*,<sup>24</sup> believed to occur in the East Indian region, resembles in general features the west American species here described. Dautzenberg's species differs in color and in other details. *Pitar (Hyphantosoma) sculpturatus* Marshall<sup>25</sup> from the Miocene of New Zealand is another member of this group.

#### *Pitar (Hyphantosoma) pollicaris* Carpenter.

*Dione prora* Conrad, Reeve, Conch. Icon., Vol. 14, *Dione*, October, 1863 species 45, pl. 10, fig. 45. "Cape St. Lucas, Xantus, California." [Specimen received by Reeve from Carpenter].

*Callista pollicaris* Carpenter, *Ann. & Mag. Nat. Hist.*, Ser. 3, Vol. 13, April, 1864, p. 312. "Figured by Mr. Reeve (Conch. f. 45) as '*Dione prora*, var.'" Reprint in *Smithson. Miscell. Coll.*, No. 252, 1872, p. 210.—Verrill, *Amer. Jour. Sci.*, Vol. 49, 1870, p. 219. Near La Paz, Lower California.

*Pitaria pollicaris* Carpenter, Dall, *Proc. U. S. Nat. Mus.*, Vol. 26, 1902, p. 387. Gulf of California, Cape St. Lucas, and south to Callao, Peru.

*Type Locality*: Cape San Lucas, Lower California.

*Range*: Gulf of California to Callao, Peru.  
*Collecting Stations*: Mexico: Port Guatulco (195-D-9), 7 fathoms, gr. sand, crushed shell; Colombia: Gorgona Island.

*Description*: Shell large, elongately oval, moderately inflated; anterior end somewhat projecting and roundly pointed, ventral margin rounded, posterior end somewhat roundly truncated; a shallow groove is present just

ventral and roughly parallel to the posterior dorsal margin; lunule elongate and bounded by an impressed line, escutcheon narrow; perfect specimens are sculptured by fine zigzag grooves, young shells usually are sculptured in this manner especially on the anterior portions of the valves; the whole colored drab white but in young specimens often with brown zigzag markings which may be somewhat strengthened in radial bands; hinge normal, with a strongly developed anterior lateral tooth in the left valve; pallial sinus extends forward nearly to the middle of the shell, the end is broadly angulated; interior white; margin smooth.

A large specimen in the collections of the California Academy of Sciences from Carmen Island, Gulf of California, measures approximately: length 80 mm.; height, 60 mm.; convexity (both valves together), 39 mm.

The exterior of the shell of this species is often partially covered by a white powdery substance, apparently some form of algae.

This species bears a resemblance to *Pitar prorus* Conrad<sup>26</sup> from the western Pacific, but the anterior end is less acutely pointed, the posterior dorsal area bears a much stronger radial groove and the posterior margin is more truncated. No fine divaricate grooving is present on specimens of *Pitar prorus* collected by Ted Dranga at Vambia, Island of Ono, Fiji, which we have examined. Römer<sup>27</sup> discussed the relations of the west American and related species of this group in the Indo-Pacific region.

*Distribution*: Only a few specimens of *Pitar pollicaris* were collected by the expedition at Port Guatulco, Mexico, and at Gorgona Island, Colombia.

#### Subgenus *Hysteroconcha* Fischer.

Key to the species of *Hysteroconcha*.

- A. Posterior umbonal angulation bearing spines
  - a. Shell large; spines well spaced  
*lupanarius*
  - aa. Shell small; spines more numerous and crowded; concentric ridges thinly lamellate ..... *multispinosus*<sup>28</sup>
- B. Posterior umbonal angulation bearing scales ..... *roseus*

#### *Pitar (Hysteroconcha) lupanarius* Lesson.

*Cytherea lupanaria* Lesson, *Centurie Zool.*, 1830, p. 196, pl. 64 [four figs.]. "Cette belle espèce est très-commune sur les grèves entre Colan et Payta sur la côte du Pérou."—Lesson, *Voy. Coquille, Zool.*, Vol. 2, Pt. 1, 1830, p. 430. Original locality cited.

*Dione semilamellosa* Gaudichaud, Reeve, *Conch. Icon.*, Vol. 14, August, 1863, species 20, pl. 6, figs. 20a, 20b, 20c. "Hab. Central America."

<sup>23</sup> See *Pitar (Hyphantosoma) carbaseus* Guppy, *Woodring, Carnegie Inst. Washington, Publ. No. 366*, May 20, 1925, p. 153, pl. 20, figs. 15-19. Bowden, Jamaica, upper Miocene.

<sup>24</sup> *Meretrix (Pitar) intricata* Dautzenberg, *Journ. de Conchyl.*, Vol. 55, No. 4, March 30, 1908, p. 333, pl. 6, fig. 1. Exact locality unknown but believed to have come from the region of the Celebes.

<sup>25</sup> *Macrocallista sculpturata* Marshall, *Trans. & Proc. New Zealand Inst.*, Vol. 50, July 15, 1918, p. 272, pl. 20, figs. 6, 6a. Pakaurangi Point, New Zealand. Mid-tertiary. See also *Pitar (Hyphantosoma) sculpturatus* Marshall, *Laws, Trans. & Proc. Roy. Soc. New Zealand*, Vol. 71, Pt. 2, September, 1941, p. 135.

<sup>26</sup> *Cytherea prora* Conrad, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 7, 1837, p. 253, pl. 19, fig. 18. "Inhabits the Pacific, probably towards the coast of New Holland."

<sup>27</sup> Römer, E., *Monogr. Molluskengattung Venus*, Linné, (Cassel), Bd. 1, *Cytherea*, 1867, p. 108.

<sup>28</sup> Not represented in the present collection.

*Pitaria (Hysteroconcha) lupanaria* Lesson, Dall, *Proc. U. S. Nat. Mus.*, Vol. 26, 1902, p. 388. Ballenas Bay, Lower California, to the Gulf of California and south to Payta, Peru.

*Pitar (Hysteroconcha) lupanaria* Lesson, R. H. Palmer & Hertlein, *Bull. South. Calif. Acad. Sci.*, Vol. 35, Pt. 2, May-August (issued September 10), 1936, p. 73. Oaxaca, Mexico, Pleistocene.

*Type Locality*: Between Colan and Paita, Peru, on the strand.

*Range*: Ballenas Bay, west coast of Lower California, to the Gulf of California and south to Negritos, Peru.

*Collecting Stations*: Mexico: Chamela Bay; Tenacatita Bay; Sihuatanejo Bay; Tangola-Tangola Bay; Nicaragua: Potosi and Monypenny Point; Corinto (200-D-16, 19), 4-13 fathoms, mangrove leaves, also at Isla Cardon; Costa Rica: Golfito, Gulf of Dulce.

*Description*: Shell triangularly ovate, rather ventricose, concentrically ridged, these are somewhat laminated anteriorly and often somewhat obsolete posteriorly; one or two rows of long spines occur along the posterior dorsal umbonal angulation; color whitish and purple-violet, with violet spots at the base of the spines.

This species is very similar to *Pitar dione* Linnaeus which occurs in the Caribbean region. The shell of *Pitar lupanarius* is larger than that of the Antillean species and the ornamentation differs in that violet spots occur at the base of the spines. *Dione expinata* Reeve, described from Central America, is a form of *P. lupanarius* in which the spines are greatly reduced in size.

A form bearing more numerous, more slender, crowded spines and thinner, more lamellate concentric ridges than typical *P. lupanarius*, was named "*Cytheraea multi-spinosa*" by Sowerby. The shell described as *Callista (Dione) longispina* Mörch<sup>29</sup> appears to be somewhat similar to the form described by Sowerby.

*Distribution*: Specimens of this species were taken from Chamela Bay, Mexico, to the Gulf of Dulce, Costa Rica. It also has been recorded as occurring in the Pleistocene of Oaxaca, Mexico.

***Pitar (Hysteroconcha) roseus* Broderip & Sowerby.**

*Cytheraea rosea* Broderip & Sowerby, *Zool. Jour.*, Vol. 4, No. 15, January, 1829, p. 364. "Hab. ad Littora Oceani Pacifici." "From St. Blas."—Sowerby, *Zool. Beechey's Voy.*, 1839, p. 151, pl. 43, fig. 7. "Found abundantly at St. Blas."

*Dione rosea* Broderip & Sowerby, Reeve, *Conch. Icon.*, Vol. 14, 1863, *Dione*, species 29, pl. 7, fig. 29. "Hab. Panama."

*Pitaria (Hysteroconcha) rosea* Broderip & Sowerby, Dall, *Proc. U. S. Nat. Mus.*, Vol. 26, 1902, p. 389. Gulf of California to Panama.

<sup>29</sup> *Callista (Dione) longispina* Mörch, *Malakozool. Blätter*, Bd. 7, January, 1861, p. 196. "Realejo specim. plura."

*Type Locality*: San Blas, Mexico.

*Range*: Gulf of California to Panama.

*Collecting Stations*: Costa Rica: 1 mile south of the entrance to the Gulf of Dulce; Panama: Gulf of Chiriqui (221-D-1-5), 35-40 fathoms, sandy mud.

*Description*: Shell obliquely heart-shaped, compressed, rose-purple, obscurely banded, concentrically closely ridged, ridges here and there lamellated on the anterior side, on the posterior prickly lamellated along the margin, scarcely spined (Reeve).

Short scaly spines occur on the shell of this species in a white radial streak along the posterior umbonal angulation. A right valve collected in the Gulf of Dulce, Costa Rica, measures: length, 44 mm.; height, 34.4 mm.; convexity (one valve), 10 mm.

A subspecies, *Pitar roseus wiedenmayeri* H. K. Hodson, 1931, has been described from the Miocene of Venezuela. *Pitar vanwinkleae* Olsson, 1922, described from the Miocene of Costa Rica, is also said to be similar to *P. roseus*.

*Distribution*: One right valve of this species was collected by the expedition on the beach one mile south of the entrance to the Gulf of Dulce, Costa Rica, and one specimen was dredged in the Gulf of Chiriqui, Panama, in 35-40 fathoms. It also has been recorded as occurring in the Pliocene of Ecuador.

**Subgenus *Lamelliconcha* Dall.**

Key to the species of *Lamelliconcha*.

- A. Shell somewhat rostrate and pointed posteriorly ..... *concinus*
- B. Shell broadly rounded or subtruncated posteriorly
  - a. Concentric lamellae uniform in height ..... *frizzelli*
  - aa. Concentric lamellae not uniform in height
    - b. Lamellae evenly spaced and alternating in height ..... *alternatus*
    - bb. Primary lamellae separated by 1 to 3 lower lamellae ..... *callicomatus*

***Pitar (Lamelliconcha) circinatus alternatus* Broderip.**

*Cytheraea alternata* Broderip, *Proc. Zool. Soc. London*, June 1, 1835, p. 45. "Hab. ad Columbianam Occidentalem. (Monte Christi.)" "Dredged up in sandy mud at a depth of seven fathoms."

*Dione alternata* Broderip, Reeve, *Conch. Icon.*, Vol. 14, *Dione*, 1863, species 28, pl. 7, figs. 28a, 28b. Broderip's types illustrated.

*Cytheraea circinata* Born, Reeve, *Conch. Icon.*, Vol. 14, *Dione*, August, 1863, species 25, pl. 7, figs. 25a, 25b. "Hab. Mazatlan."

Not *Venus circinata* Born, *Test. Mus. Caes. Vindob.*, 1780, p. 61, pl. 4, fig. 8. "Patria ignota."

*Type Locality*: Monte Christi, Ecuador, in 7 fathoms, sandy mud.

*Range*: Gulf of California to Paita, Peru.

*Collecting Stations*: Mexico: Chamela Bay; Tenacatita Bay (183-D-2), 30 fathoms,

muddy sand; Tangola-Tangola Bay; Nicaragua: Corinto (200-D-11, 17, 19), 7-13 fathoms, sand, mangrove leaves; Costa Rica: Uvita Bay; 1 mile south of Golfito Bay.

*Description*: The shell of this species is ornamented by sharp raised concentric ribs which, in perfect specimens, alternate in height. The color is white with radial chestnut rays and the lunule and escutcheon violet chestnut or in some specimens the entire shell may be entirely violet chestnut or white. The interior is white with violet chestnut on the dorsal portion.

A specimen collected by the senior author at Corinto, Nicaragua, measures: length, 37.5 mm.; height, 31 mm.; convexity (one valve), 11.6 mm.

Young specimens of this subspecies are remarkably similar to the east American *Pitar circinatus* Born. Large specimens are said to attain a greater size, greater convexity, and with the ribs somewhat more widely spaced than those on the east American form.

The shell of *Pitar circinatus alternatus* is more rounded in outline and lacks the decided posterior rostration of *P. concinnus* Sowerby.

*Pitar (Lamelliconcha) petersoni* Olsson, 1932, described from the Miocene of Peru, is a similar form.

*Distribution*: This subspecies was taken by the expedition on beaches and in shallow water from west Mexico to Costa Rica. It was found fairly abundantly at Corinto, Nicaragua.

***Pitar (Lamelliconcha) callicomatus* Dall.**

*Pitaria (Lamelliconcha) callicomata* Dall, *Proc. U. S. Nat. Mus.*, Vol. 26, No. 1312, December, 1902, pp. 389, 402, pl. 16, fig. 8. "Bay of Panama, in 14 fathoms, mud." Also in 7-30 fathoms.

*Pitar callicomata* Dall, Strong, Hanna & Hertlein, *Proc. Calif. Acad. Sci.*, Ser. 4, Vol. 21, No. 10, 1933, p. 118. Acapulco, Mexico.

*Type Locality*: Bay of Panama, in 14 fathoms, mud.

*Range*: Acapulco, Mexico, to Panama.

*Collecting Stations*: Mexico: Port Guatulco (195-D-20), 23 fathoms, mud; Panama: Gulf of Chiriqui (221-D-1-5), 35-40 fathoms, sandy mud.

*Description*: Shape similar to but more oval than that of *Pitar circinatus alternatus*. It is ornamented by prominent concentric lamellae between which occur from one to three low secondary lamellae. The shell is of a dull white color.

The dimensions of the type specimen of this species, were given as: length, 47 mm.; height, 36 mm.; convexity, 22 mm.

*Distribution*: Only single valves of this species were taken at Port Guatulco, Mexico, in 23 fathoms, and in the Gulf of Chiriqui, Panama, in 35-40 fathoms.

***Pitar (Lamelliconcha) concinnus* Sowerby.**

*Cytherea concinna* Sowerby, *Proc. Zool. Soc. London*, April 16, 1835, p. 23. "Hab. ad

Panamam." "Found at a depth of ten fathoms in fine sand."

*Cytherea concinna* Sowerby, Sowerby, *Thes. Conch.*, Vol. 2, 1851, p. 630, pl. 132, figs. 99, 100. Original locality cited.

*Dione concinna* Sowerby, Reeve, *Conch. Icon.*, Vol. 14, *Dione*, 1863 species 31, pl. 8, figs. 31a, 31b. "Hab. Panama, Mazatlan."

*Cytherea affinis* Broderip, *Proc. Zool. Soc. London*, June 1, 1835, p. 45. "Hab. ad Colombiam Occidentalem. (Xipixapi.)" "Dredged up from sandy mud at a depth of ten fathoms."

*Dione affinis* Broderip, Reeve, *Conch. Icon.*, Vol. 14, *Dione*, 1863, species 30, pl. 8, fig. 30. Original locality cited.

*Cytherea tortuosa* Broderip, *Proc. Zool. Soc. London*, June 1, 1835, p. 45. "Hab. ad Panamam, et ad Xipixapi." "Dredged up from sandy mud at a depth of six fathoms."

*Dione tortuosa* Broderip, Reeve, *Conch. Icon.*, Vol. 14, *Dione*, 1863, species 61, pl. 12, fig. 61. Original locality cited.

*Venus paytensis* d'Orbigny, *Voy. Amér. Mérid.*, Vol. 5, 1846, p. 565. "*Cytherea affinis*, Broder., 1835, *Proceed. Zool. Soc.*, p. 45 (non *affinis*, Gmel., 1789, non *affinis*, Mathéron, 1842)."

*Pitaria (Lamelliconcha) acuticostata* Gabb, Li, *Bull. Geol. Soc. China*, Vol. 9, No. 3, October, 1930, p. 261, pl. 4, fig. 28. Dredged in Panama Bay. Referred to the Miocene. Li's record was referred to *Pitar (Lamelliconcha) concinna* Sowerby by Pilsbry (*Proc. Acad. Nat. Sci. Philadelphia*, Vol. 83, 1931, p. 430).

Not *Callista acuticostata* Gabb, 1873. [Now considered to be referable to the genus *Pitar*].

*Pitaria (Lamelliconcha) labreana* Maury, Li, *Bull. Geol. Soc. China*, Vol. 9, No. 3, 1930, p. 261, pl. 4, fig. 29. Dredged in Panama Bay. Referred to the Miocene. Li's record was referred to *Pitar (Lamelliconcha) concinnus* Sowerby by Pilsbry (*Proc. Acad. Nat. Sci. Philadelphia*, Vol. 83, 1931, p. 430).

Not *Pitaria (Lamelliconcha) labreana* Maury, 1912.

*Type Locality*: Panama, in 10 fathoms, fine sand.

*Range*: Magdalena Bay, Lower California, to the Gulf of California and south to Paita, Peru.

*Collecting Stations*: Mexico: Chamela Bay (182-D-1), 8 fathoms, sand, algae; Guatemala: 7 miles west of Champerico (197-D-1-2), 14 fathoms, mud; El Salvador: La Libertad (198-D-1,2), 13-14 fathoms, mud; Meanguera Island, Gulf of Fonseca (199-D-1), 16 fathoms, sand, mud, crushed shell; Nicaragua: Potosi and Monvenny Point; Corinto (200-D-11,17,19), 7-13 fathoms, sand, mangrove leaves, also on shore and at La Cardon; Costa Rica: Golfito; Panama: Gulf of Chiriqui (221-D-1-5), 35-40 fathoms, sandy mud.

*Description*: Shell oblong, heart-shaped, rather compressed, chestnut-red or white, rayed with purple rows, concentrically

ridged, ridges slightly reflected, here and there wrinkled, posterior side a little flexuous (Reeve).

The shell of *Pitar concinnus* is somewhat rostrate posteriorly and by this character is readily separable from *P. circumatus alter-natus*. It attains a length of at least 51.5 mm. On some specimens there is a shallow, radial depression just anterior to the posterior umbonal angulation.

Pilsbry & Lowe stated that "*Cytherea tortuosa*" Broderip is quite distinct from *P. concinnus*. The series of specimens of *P. concinnus* available to us leads us to agree with Dall's (1902) conclusion that *tortuosa* "is a white specimen with the ribs more irregular than usual."

*Pitar (Lamelliconcha) salangus* Pilsbry & Olsson, 1941, described from the Pliocene of Ecuador, is a very similar species. It is said to be constantly higher in proportion to the length and less produced posteriorly. *Pitar (Lamelliconcha) labreanus* Maury from the Pliocene of Trinidad is another similar species.

**Distribution:** This species was taken from west Mexico to Panama, on the shore and dredged at depths of 7 to 40 fathoms. It was dredged abundantly in the Gulf of Fonseca in 16 fathoms. It also has been cited as occurring in the Pleistocene of Maria Madre Island, Mexico, by Hertlein, in the Pliocene of Costa Rica by Olsson, and in the Pliocene of Ecuador as *Pitar (Lamelliconcha) affinis* by Pilsbry & Olsson.

***Pitar (Lamelliconcha) frizzelli* Hertlein & Strong, sp. nov.**

Plate I, Figures 1, 5 and 7; Plate II, Figure 11.

Shell oblong, somewhat compressed, beaks low; surface sculptured by close, concentric ridges, the whole exterior colored by light brown with darker brown blotches and tent-shaped lines; anterior dorsal margin concave with an impressed, elongately cordate lunule; posterior dorsal margin sloping and slightly arched, ends and basal margin rounded; a faint shallow radial depression occurs just anterior to the posterior umbonal curve; hinge and ligament normal for the genus, hinge teeth rather delicate; pallial sinus fairly wide, ascending, rounded at the end, and projecting forward to nearly the center of the shell; interior yellow in the center shading to purple under the beaks and over the muscle scars, white toward the basal margin; margins smooth. The type measures: length, 46 mm.; height, 33.5 mm.; convexity (both valves together), 24 mm.; pallial sinus projects anteriorly 23.5 mm. from the posterior margin.

Holotype dredged at Station 136-D-22, Lat. 23° 28' 30" N., Long. 109° 25' W., Arena Bank, Gulf of California, in 45 fathoms (82 meters), mud. Five valves were dredged in the same general vicinity at Station 136-D-26, Lat. 23° 27' N., Long. 109° 24' W., in 45 fathoms, sand, crushed shell. Two valves

were dredged at Station 150-D-6, Lat. 23° 02' N., Long. 109° 31' W., Gorda Banks, in 60 fathoms, muddy sand, rocks, and two valves were dredged in the same general vicinity at Station 150-D-10, Lat. 23° 06' N., Long. 109° 25' W., in 50 fathoms, rock, crushed shell.

The concentric sculpture on this species is similar to that on *Pitar concinnus* Sowerby but the posterior end is much less pointed and the coloration is of an entirely different pattern.

This species is named for Dr. Don L. Frizzell in recognition of his contribution to the classification of the Veneridae.

**Distribution:** Specimens of this species were dredged only in the south end of the Gulf of California at depths of 40-60 fathoms.

Subgenus ***Tinctora*** Jukes-Browne.

*Callizona* Jukes-Browne, *Proc. Malacol. Soc. London*, Vol. 10, Pt. 6, September, 1913, p. 346. "Type, *Callista vulnerata*, Brod."

Not *Callizona* Doubleday, 1848. *Lepid. Not Callizona* Greef, 1875. *Verm. (Polych.)*.

*Tinctora* Jukes-Browne, *Proc. Malacol. Soc. London*, Vol. 11, Pt. 1, March, 1914, p. 62. "Type, *Cytherea vulnerata*, Brod." New name for *Callizona* Jukes-Browne, 1913, not *Callizona* Doubleday, 1848.

*Callizonata* Strand, *Arch. f. Naturgesch.*, Jahrg. 92, 1926, Abt. A, Heft 8, p. 40. New name for *Callizona* Jukes-Browne not *Callizona* Doubleday.

**Type** (by original designation): *Cytherea vulnerata* Broderip.

Shell thick, sub-orbicular, glossy; valve-margins crenulated; left posterior cardinal long and partly free from nymph; median very thick; pallial sinus short and rounded. Pedal scar as in *Callista* (Jukes-Browne, 1914).

Only one species of *Tinctora* is known.

*Nanopitar* Rehder<sup>30</sup> is said to be somewhat similar to *Tinctora* but lacks the irregular crenulations on the inner margin.

***Pitar (Tinctora) vulneratus* Broderip.**

*Cytherea vulnerata* Broderip, *Proc. Zool. Soc. London*, June 1, 1835, p. 46. "Hab. in America Centrali. (Real Llejos)." "It was dredged up from sandy mud at a depth of six fathoms."—Sowerby, *Thes. Conch.*, Vol. 2, 1851, p. 632, pl. 131, figs. 95, 96 (as *Cytheraea vulnerata*). Original locality cited.

*Dione vulnerata* Broderip, *Reeve, Conch. Icon.*, Vol. 14, *Dione*, 1863, species 16, pl. 5, figs. 16a, 16b. Original locality cited.

*Pitaria vulnerata* Broderip, *Dall, Proc. U. S. Nat. Mus.*, Vol. 26, 1902, p. 388. Magdalena Bay, Lower California, to the Gulf of California and south to the Bay of Panama.

**Type Locality:** Real Llejos [near Corinto], Nicaragua, in 6 fathoms, sandy mud.

**Range:** Magdalena Bay, west coast of

<sup>30</sup> *Nanopitar* Rehder, *Proc. U. S. Nat. Mus.*, Vol. 93, No. 3161, January 20, 1943, p. 188. "Genotype: *Pitar (Nanopitar) pilula*, new species," p. 188, pl. 19, figs. 5-10. Collected "in Lake Worth, Fla."

Lower California, to the Gulf of California and south to the Bay of Panama.

*Collecting Stations:* Mexico: Santa Inez Point, east coast of Lower California; Arena Point area, Lower California; Cerralbo Island, Gulf of California; Chamela Bay (182-D-1), 8 fathoms, sand, algae, also on beach; Tenacatita Bay.

*Description:* Shell suborbicular, moderately convex, finely concentrically ridged; cream color, the umbonal region often finely rayed or mottled with brown, irregularly spaced violet rings or zones of color usually occur more strongly developed toward the ventral margin; pallial sinus rather wide and projecting slightly upward and forward nearly half the length of the shell; inner margins irregularly crenulated. A fairly large specimen measures approximately: length, 45 mm.; height, 40 mm.; convexity (both valves), 27.5 mm.

*Distribution:* A few specimens of this species were taken by the expedition in the Gulf of California region. It has also been recorded as occurring in the Pleistocene of Oaxaca, Mexico.

#### Genus *Callocardia* A. Adams.

##### Key to the subgenera of *Callocardia*.

- A. Left anterior lateral very small and distant from cardinals (in type species); pallial sinus well developed ..... *Agriopoma*  
 B. Left anterior lateral and pallial sinus lacking (in type) ..... *Callocardia* s.s.<sup>31</sup>

#### Subgenus *Agriopoma* Dall.

##### *Callocardia (Agriopoma) catharia* Dall.

Plate II, Figures 14 and 15.

*Callocardia (Agriopoma) catharia* Dall, *Proc. U. S. Nat. Mus.*, Vol. 26, No. 1312, December, 1902, pp. 387, 402, pl. 14, fig. 3 (as *Callocardia catharia* on p. 402). "Bay of Panama in 30 fathoms, mud."

*Type Locality:* Panama Bay, in 30 fathoms, mud.

*Range:* Ballenas Bay, west coast of Lower California, to the Gulf of California and south to Panama, in 7 to 66 fathoms (Dall).

*Collecting Station:* Panama: Gulf of Chiriqui (221-D-1-5), 25-40 fathoms, sandy mud.

*Description:* Shell trigonally ovate, broadly rounded posteriorly, dull white, earthy, ornamented by fine concentric threads; lunule cordate, defined by an impressed line; pallial sinus wide, shallow, ascending.

One left valve 22.8 mm. long and 20.5 mm. high appears to be referable to the species described by Dall as *Callocardia catharia*. The hinge has a well developed anterior lateral tooth which is well separated from the anterior cardinal. The anterior and middle cardinal teeth are formed by a thin folded lamina (the middle tooth the longer) which at the apex of the fold bears two or three minute cusps; on the ventral side there are two triangular pits formed by shelly folds,

the anterior one deeper and lower and forming a depression in the hinge plate; the posterior cardinal is thin and separated from the middle cardinal by a flat-bottomed interspace, the posterior part of the hinge plate is roundly truncated; the pallial sinus is broad and shallow.

K. V. W. Palmer<sup>32</sup> gave a discussion of the genus *Callocardia* and published illustrations of *C. guttata* A. Adams, the type of the genus, of which only a left valve is known. The anterior and middle cardinal teeth are formed of a folded lamina with 4 cusps and with a triangular pit on each side. Adams stated that it lacked a left anterior lateral and that the pallial line is simple. Later authors state that the pallial line on the type cannot be discerned clearly and that the degree of sinuosity cannot be definitely stated. Palmer concluded from the curvature of the hinge of the type that a slight elevated area might occur in the region anterior to the cardinals. The general characters described for the shell are similar to those of the present species except that *C. catharia* has a well developed left anterior lateral and a short but well developed pallial sinus.

Dall placed *Callocardia catharia* in the subgenus *Agriopoma* Dall, the type of which is *Callocardia (Agriopoma) texasiana* Dall. As pointed out by Palmer, the characters of the hinge of that species are intermediate between *Callocardia* and *Pitar*. It has a very small left anterior lateral which is situated near the extreme anterior end of the hinge plate and there is a well developed pallial sinus. She considered both *Callocardia* and *Agriopoma* to be subgenera of *Pitar*. She also stated that several east American species originally assigned to *Callocardia* are now referable to other genera or subgenera.

No illustration of the hinge of the type specimen of *Callocardia catharia* has been published but Dall stated: "hinge well developed, normal." The present specimen shows many features said to characterize *Callocardia* as well as *Agriopoma* although it is not typical of the latter. We have therefore retained Dall's nomenclature for the present shell, at least until the characters of the type of *Callocardia* as well as those of the present species are better known.

*Distribution:* The specimen assigned to this species was taken by the expedition in the Gulf of Chiriqui, Panama, in 35-40 fathoms. According to Dall it occurs commonly as far north as Ballenas Bay, Lower California. A species with a somewhat similar shell which we have found occurring commonly in this same region is *Pitar (Pitar-ella) mexicanus* [= *P. lenis* Pilsbry & Lowe].

#### Genus *Antigona* Schumacher.

##### Key to the subgenera of *Antigona*.

- A. Pallial sinus moderately long, wide, and rounded at the end; escutcheon with a longitudinal furrow ..... *Periglypta*

<sup>32</sup> See discussion of *Callocardia* by Palmer, *Palaeontogr. Amer.*, Vol. 1, No. 5, pp. 246-248 (38-40), 1927, pl. 38 (7), figs. 1, 4, 11, 1929, and *Agriopoma*, pp. 241-242 (33-34), text fig. 3, 1927, pl. 38 (7), figs. 5, 12, 13, 14, 1929.

<sup>31</sup> Not represented in the present collection.

B. Pallial sinus short and acutely angular; escutcheon without a longitudinal furrow

a. Interspaces between major lamellae bearing concentric threads or lamellae  
*Ventricola*

aa. Interspaces between major lamellae lacking concentric sculpture  
*Antigona* s.s.<sup>33</sup>

Subgenus *Periglypta* Jukes-Browne.

*Periglypta* Jukes-Browne, *Proc. Malacol. Soc. London*, Vol. 11, Pt. 1, March, 1914, p. 72. "Type, *Venus puerpera*, Linn."

Type (by original designation): *Venus puerpera* Linnaeus.

Shell cancelled by strong concentric ridges crossed by radial riblets which crenulate the ridges. Escutcheon narrow, and the right half overlapping the left. Ligament deeply sunk. Nymphs usually having a fine rugose area. Anterior lateral very small and close to the anterior cardinal. Pallial sinus usually wide and rounded (Jukes-Browne).

The right posterior and middle cardinal teeth of each valve are cleft. A narrow longitudinal furrow occurs on the escutcheon.

*Periglypta* is known to occur from Miocene to Recent. It is represented in the lower Miocene of California by *Antigona vaquerosensis* Loel & Corey, 1932.

*Ameghinomya* von Ihering,<sup>34</sup> founded on a fossil form from Argentina, appears to differ from *Periglypta* chiefly in lacking a longitudinal furrow along the escutcheon.

*Antigona (Periglypta) multicostata* Sowerby.

*Venus multicostata* Sowerby, *Proc. Zool. Soc. London*, April 16, 1835, p. 22. "Hab. in Sinu Panamae." "Found in coarse sand at low water."—Sowerby, *Thes. Conch.*, Vol. 2, *Venus*, 1853, p. 706, pl. 152, fig. 10. Original locality cited.—Reeve, *Conch. Icon.*, Vol. 14, *Venus*, 1863, species 9, pl. 3, fig. 9. Original locality cited.

*Antigona multicostata* Sowerby, Van Winkle Palmer, *Palaeontogr. Amer.*, Vol. 1, No. 5, p. 336 (128) (in text), 1927, pl. 61 (30), fig. 11, 1929. West coast of Panama.

Type Locality: Bay of Panama, at low water, sand.

Range: Gulf of California to Punta Verde, Peru, and the Galápagos Islands.

Collecting Stations: Mexico: Banderas Bay; Costa Rica: Port Parker; Culebra Bay; Colombia: Gorgona Island.

Description: Shell large, roundly quadrate, moderately inflated, very thick, anterior end rounded, posterior end roundly truncated; ornamented by thick concentric ribs reflected at the anterior end, undulated, in the middle crenulated, posteriorly irregular, alternately interrupted and slightly crenulated; evenly spaced low radial ribs cross both ribs and interspaces; lunule elongately cordate, pro-

jecting medially; a longitudinal furrow occurs on the escutcheon; hinge with three stout cardinal teeth in each valve and a small denticle near the base of the anterior cardinal of the left valve, the middle cardinal of both valves and the posterior cardinal of the right valve cleft; pallial sinus short, rounded, slightly ascending, projecting anteriorly not quite a third of the distance between the two muscle impressions; inner margin very finely crenulated; interior white, often pinkish or violet under the hinge and umbonal region.

A large specimen collected at Port Parker, Costa Rica, measures approximately: length, 118 mm.; height, 115 mm.; convexity (both valves), 78 mm.; pallial sinus extends anteriorly 54 mm. from the posterior margin.

The shell of this species is quite similar to that of *Antigona listeri* Gray, an east American species. The west American shell is ornamented by coarser concentric lamellae and by more widely spaced radial sculpture.

*Antigona dominica* Palmer [= *Antigona caribbeana* Anderson], described from the Miocene of Santo Domingo, is a similar species.

Distribution: A few specimens of this species were collected by the expedition off west Mexico, Costa Rica, and Gorgona Island, Colombia. It also occurs in the Pliocene and Pleistocene of the Gulf of California region, and in the Pleistocene of Ecuador and the Galápagos Islands. Trechmann, 1933, cited a species under the name of "*Chione*" *multicostata* as occurring fossil on Barbados Island. We have not seen specimens from that region.

Subgenus *Ventricola* Römer.

Key to the species of *Ventricola*.

- A. Shell suborbicular; large ..... *isocardia*  
B. Shell more elongated; smaller; primary concentric lamellae finer and more closely spaced ..... *magdalenae*

*Antigona (Ventricola) isocardia* Verrill.

Plate II, Figures 2 and 3.

*Venus isocardia* Verrill, *Amer. Jour. Sci.*, Vol. 49, No. 146, March, 1870, p. 221. "Near La Paz,—Capt. J. Pedersen."

*Cytherea (Ventricola) rigida* Dillwyn, Dall, *Proc. U. S. Nat. Mus.*, Vol. 26, 1902, p. 390. Near La Paz, Lower California, in 9½ fathoms.

Not *Venus rigida* Dillwyn, *Descript. Cat.*, Vol. 1, 1817, p. 164. "Inhabits the coast of Jamaica. *Lister*. Brazils. *Solander*. West Indies. *Humphreys*."

Type Locality: Near La Paz, Lower California.

Range: Gulf of California, to Gorgona Island, Colombia.

Collecting Stations: Mexico: Arena Bank in the Gulf of California (136-D-2, 16, 26, 30), 35-40 fathoms, mud, *Arca* conglomerate, muddy sand, sand, weed, crushed shell; 3 miles off Pyramid Rock, Clarion Island (163-D-2), 55 fathoms, rock, coral; Costa Rica: Culebra Bay; 14 miles S. × E. of Judas Point

<sup>33</sup> Not represented in the present collection.

<sup>34</sup> *Ameghinomya* von Ihering, *An. Mus. Nac. de Buenos Aires*, Vol. 14, (Ser. 3, Vol. 7), 1907, p. 71. "Je propose le nouveau sous-genre *Ameghinomya* pour ces espèces éteintes de *Chione* avec *Ch. argentina* Ih. comme type." Illustrated by von Ihering, *Rev. Mus. Paulista*, Vol. 2, 1897, p. 252, pl. 7, fig. 45. Upper Patagonian formation.

(214-D-1-4), 42-61 fathoms, mud, shell, rocks; Panama: Hannibal Bank (224), 35-40 fathoms, rock, mud, dead coral, sand, shells, algae; Colombia: Gorgona Island.

*Description*: Shell large, suborbicular, very convex, ornamented by strong concentric, slightly recurved lamellae which are crowded anteriorly and posteriorly, between these are several (about 6) crowded, slightly elevated lamellae, all lamellae faintly radially striated; lunule broad, cordate, impressed; a narrow smooth area present above and extending beyond the ligament on the left valve but not present on the right valve; right valve with 3 strong cardinal teeth, the middle one somewhat bifid, left valve with 3 cardinals and one short anterior lateral; pallial sinus short, pointed, extending toward the anterior adductor muscle impression a few millimeters beyond the anterior margin of the posterior impression; inner margin crenulated; colored exteriorly with brownish blotches arranged radially, interior white, pinkish or orange under the umbos. The largest specimen in the collection, from Costa Rica, measures approximately; length, 87 mm.; height, 81 mm.; convexity (one valve), 32 mm.; pallial sinus projects anteriorly about 30.5 mm. from the posterior margin.

The shell of this species is very similar to that of the Atlantic *Antigona rigida* Dillwyn and has at times been recorded from west American waters under that name. The posterior teeth of the west American shell are generally larger and longer and in the left valve the posterior tooth is separated from the ligament plate by a shallower groove than on the Atlantic shell. The hinge plate of *A. isocardia* is less flaring in front of the beak than that on the east coast species. *Antigona orientalis* Cox, described from the Pliocene of Mombasa, Africa, is said to be very similar to *A. rigida*.

*Description*: This interesting large bivalve was collected on beaches and was dredged at depths of 35-61 fathoms, in the southern end of the Gulf of California, off Clarion Island, off Costa Rica, and Gorgona Island, Colombia. It has been recorded as occurring in the Pleistocene of the Galápagos Islands.

***Antigona (Ventricola) isocardia magdalanae*  
Dall.**

*Cytherea (Ventricola) magdalanae* Dall, *Proc. U. S. Nat. Mus.*, Vol. 26, No. 1312, December, 1902, pp. 390, 403, pl. 15, fig. 6. Dredged "off Magdalena Bay on the west shore of Lower California, at station 2989, in 36 fathoms."

*Type Locality*: Off Magdalena Bay, Lower California, Mexico, in 36 fathoms.

*Range*: Magdalena Bay, Lower California, to Arena Bank, Gulf of California.

*Collecting Station*: Mexico: Arena Bank (136-D-2), 45 fathoms, mud, *Arca* conglomerate.

*Description*: Four single valves, about 35-40 mm. in length, in the collection dredged on Arena Bank in the Gulf of California, are

here referred to *Antigona isocardia magdalanae*. These shells agree well with Dall's description and illustration of that form. The specimens appear to differ from young shells of *A. isocardia* Verrill in possessing a more elongated form and finer and more closely spaced concentric sculpture. The similarity to *A. isocardia* is so great that we consider *magdalanae* to be a subspecies of Verrill's species. Dall stated that this form is similar to the east American *A. strigillina* Dall.

*Distribution*: The specimens here referred to *Antigona isocardia magdalanae* were dredged on Arena Bank in the Gulf of California in 45 fathoms. Previously it has been recorded only from the type locality, off Magdalena Bay, Lower California.

**Genus *Cyclinella* Dall.**

Key to the species of *Cyclinella*.

- A. Shell inflated, lunule broadly cordate; sinus sharply angular at end and projecting nearly to center of shell *singleyi*<sup>35</sup>
- B. Shell less inflated, lunule lanceolate
  - a. Shell subquadrate and elongated ventrally; compressed and rather thin; sinus often pointed at end  
*subquadrate*
  - aa. Shell orbicular, dosinoid; moderately inflated and thick; sinus short, rounded at end and more anteriorly directed
    - b. Shell not exceeding 30 mm. in height ..... *kröyeri*<sup>35</sup>
    - bb. Shell exceeding 30 mm. in height  
*ulloana*

***Cyclinella kröyeri ulloana* Hertlein & Strong,  
subsp. nov.**

Plate II, Figures 5, 6 and 7.

Shell orbicular, dosinoid, white, moderately inflated, moderately thick; sculptured by fine but well developed concentric lines of growth; pallial sinus fairly broad, short, rounded at the end, projecting about 33 mm. from posterior margin toward the anterior muscle impression; margin smooth. Dimensions: length, 75.5 mm.; height, 76.5 mm., convexity (one valve), 19 mm.

Holotype, left valve, from Station 143-D-4, Santa Inez Bay, Gulf of California, Lat. 26° 55' N., Long. 111° 54' W., dredged in 25 fathoms (46 meters), sand. Another large and two small valves were also found at this same locality. A few other valves, apparently referable to this subspecies, were taken at Station 136-D-2, Arena Bank, at the south end of the Gulf of California, in 45 fathoms, mud, *Arca* conglomerates.

*Cyclinella kröyeri* Philippi<sup>36</sup> was originally described from South America, and two localities, "Patria: Chile, Peru," were cited. The dimensions were given as "Long. 2"; alt. 11½"; crass. 6". These measurements

<sup>35</sup> Not represented in the present collection.

<sup>36</sup> *Venus (Artemis) kröyeri* Philippi, Zeit. f. Malakozool., Jahrg. 4, June, 1847, p. 87. "Patria: Chile, Peru; legit cl. Kröyer."—Philippi, Abhild. u. Beschreib. Conchyl., Bd. 3, Heft 3, *Venus*, 1848, p. 78 (26), Taf. 7, fig. 9. Original locality cited.

in lines<sup>37</sup> would be equivalent, in the metric system, to length, 26.16 mm., height, 20.39 mm., convexity, 13.08 mm. The figures of the species given by Philippi in 1848 appear to represent nearly the natural size of the shell. Römer<sup>38</sup>, 1862, stated regarding Philippi's species . . . "ist eine ächte *Cyclina*."

Dall<sup>39</sup>, 1902, stated regarding this species: "It is smaller, more orbicular, and proportionately flatter than *C. subquadrata*." He also stated that *Artemis macilentata* Reeve<sup>40</sup> might be referable to Philippi's species. Reeve's illustration does not agree with the original illustration of *Cyclinella kröyeri* nor with our specimens but appears to resemble more nearly some forms of *C. subquadrata*. Sowerby<sup>41</sup> suggested that it might be the young of *C. subquadrata*. In a later paper Dall<sup>42</sup> gave the range of *C. kröyeri* as the Gulf of California to Valparaiso, Chile.

Specimens in the present collection vary in size from a small valve 23 mm. in length to a huge left valve 75.4 mm. in length. The huge size of these larger specimens, so far as we know, is much greater than that of any specimens which have been referred to *Cyclinella kröyeri*. The shells in the present collection were dredged only in the southern portion of the Gulf of California. We therefore have proposed the subspecific name *ulloana* for these large shells. This subspecies is named for Francisco de Ulloa, Spanish explorer, who in 1540 discovered that the Gulf of California was land-locked at the north end, thus revealing that Lower California was a peninsula, not an island as formerly believed.

The larger, more orbicular dosinoid form, more polished shell, broader, shorter, usually less pointed and more anteriorly directed pallial sinus, as well as the lack of elongation ventrally, are characters which serve to separate the present subspecies from *Cyclinella subquadrata* Hanley.

*Cyclinella beteyensis* Olsson<sup>43</sup>, described from the Miocene of Costa Rica, was compared by its author to *C. kröyeri*.

#### ***Cyclinella subquadrata* Hanley.**

*Artemis subquadrata* Hanley, *Proc. Zool. Soc. London*, April, 1845, p. 11. "Hab. St. Elena, West Columbia. Mus. Cuming, Hanley." Ref. to "Ind. Test., sup. t. 15, f. 39."—Hanley, *Cat. Rec. Bivalve Shells*, p. 357, 1856?, pl. 15, fig. 39, 1844. "W. Columbia."—Reeve, *Conch. Icon.*, Vol. 6, *Artemis*, Febru-

<sup>37</sup> For the metric equivalents of European "lines" see H. A. Rehder, *Mollusca* (Tavares, Florida), Vol. 1, No. 6, August 10, 1945, p. 73.

<sup>38</sup> Römer, E., *Monogr. Molluskengattung Dosinia*, Scopoli, (Cassel), 1862, p. 84.

<sup>39</sup> Dall, W. H., *Proc. U. S. Nat. Mus.*, Vol. 26, 1902, p. 391.

<sup>40</sup> *Artemis macilentata* Reeve, *Conch. Icon.*, Vol. 6, *Artemis*, March, 1850, species 51, pl. 9, fig. 51. "Hab. Salango, West Columbia (in sandy mud at a depth of nine fathoms); Cuming."

<sup>41</sup> Sowerby, G. B., *Thes. Conch.*, Vol. 2, 1846, p. 662.

<sup>42</sup> Dall, W. H., *Proc. U. S. Nat. Mus.*, Vol. 37, 1909, p. 267.

<sup>43</sup> *Cyclinella beteyensis* Olsson, *Bull. Amer. Paleo.*, Vol. 9, No. 39, January 21, 1922, p. 414 (242), pl. 34 (31), fig. 2. "Gatun Stage: Rio Betey." Costa Rica, Miocene.

ary, 1850, species 15, pl. 3, fig. 15. "Hab. St. Elena, West Columbia (in sandy mud at low water), and Lobos Island, Peru (in sandy mud at a depth of from six to seventeen fathoms); Cuming."

*Arthemis saccata* Gould, *Proc. Boston Soc. Nat. Hist.*, Vol. 4, November, 1851, p. 91. "Inhabits Mazatlan?"—Gould, *Boston Jour. Nat. Hist.*, Vol. 6, October, 1853, p. 396, pl. 15, fig. 2. "Inhabits Mazatlan."

*Type Locality*: Santa Elena, Ecuador.

*Range*: Guaymas, Mexico, in the Gulf of California, to Paita, Peru, in 4 to 40 fathoms.

*Collecting Stations*: Mexico: Port Guatulco (195-D-19), 17 fathoms, gr. mud, crushed shell; Guatemala: 7 miles west of Champerico (197-D-2), 14 fathoms, mud; El Salvador: La Libertad (198-D-2), 14 fathoms, mud; Meanguera Island, Gulf of Fonseca (199-D-1), 16 fathoms, sand, mud, crushed shell; Costa Rica: Port Parker (203-D-1,2,3), 10-15 fathoms, sandy mud, crushed shell, shelly mud, algae; Port Culebra (206-D-1,2,3), 14 fathoms, mud; Cedro Island, Gulf of Nicoya (213-D-1-10), 4-10 fathoms, mud, sand, crushed shell; Gulf of Dulce; Panama: Gulf of Chiriqui (221-D-1-5), 35-40 fathoms, sandy mud; Bahia Honda (222).

*Description*: Suborbicular-subquadrate, broader than long, compressed, a little pellucid, very inequilateral, whitish both within and without, concentrically substriated; ventral edge arcuated in front; convex and rising behind; dorsal edge straightish and decidedly sloping in front, convex and not sloping behind; anterior end very broad, posterior end narrow; lunule large, nearly obsolete (Hanley, *Cat. Rec. Biv. Shells*, p. 357). The measurement was given as 1 $\frac{3}{4}$  [inches]. The pallial sinus is rather narrow, pointed, and directed toward the umbos, margin smooth.

The compressed, suborbicular-subquadrate and somewhat ventrally attenuated form of this species are characters which separate it from other west American species of the genus. *Cyclinella singleyi* Dall, 1902, which ranges from Scammon Lagoon, Lower California, to the Gulf of California and south to Panama, possesses a more tumid shell. *Cyclinella galera* Pilsbry and Olsson, 1941, described from the Pliocene of Ecuador, is similar to *C. singleyi* but the pallial sinus is said to differ in shape and direction. *Cyclinella kröyeri* Philippi is more orbicular and dosinoid in outline. We have not observed any specimens which could be referred to the species described as *Cyclina producta*<sup>44</sup> by Carpenter, which species was referred to the genus *Cyclinella* by Dall.

A subspecies, *Cyclinella subquadrata quitana* Olsson<sup>45</sup>, has been described from the Miocene of Costa Rica and Trechmann<sup>46</sup> has

<sup>44</sup> *Cyclina producta* Carpenter, *Proc. Zool. Soc. London*, November 11, 1856, p. 161. "Hab. In Sinu Panamensi; legit T. Bridges."

<sup>45</sup> *Cyclinella subquadrata quitana* Olsson, *Bull. Amer. Paleo.*, Vol. 9, No. 39, June 21, 1922, p. 415 (243), pl. 34 (31), fig. 8. "Gatun Stage; Quitana Creek." Costa Rica.

<sup>46</sup> Trechmann, C. T., *Geol. Mag.*, Vol. 70 (No. 823), 1933, p. 36, pl. 4, fig. 4.

cited a species as "*Cyclinella* near *C. subquadrata* Hanley" which occurs as a fossil on Barbados Island.

*Distribution*: Specimens of *Cyclinella subquadrata* were taken by the expedition from Port Guatulco, Mexico, to Bahia Honda, Panama, in 4 to 40 fathoms. This species has also been reported as occurring in the Pliocene of Ecuador and in the Quaternary of Peru.

### Genus *Chione* Megerle von Mühlfeld.

Key to the subgenera of *Chione*.

- A. Concentric sculpture predominant
- a. Concentric lamellae of broad thickened rolls sometimes coalescent medially  
*Lirophora*
  - aa. Concentric lamellae thin, sharp, serrated
  - b. Pallial sinus well developed; one or more cardinal teeth in each valve bifid or strongly grooved  
*Chionopsis*
  - bb. Pallial sinus very small; one or more teeth in each valve faintly grooved or all smooth ... *chione* s.s.
- B. Radial sculpture predominant (often coarse) anteriorly or over entire shell
- a. Escutcheon present on left valve
  - b. Left anterior cardinal tooth elongated anteriorly and rather thin and high; radial ribs coarse anteriorly ..... *Nioche*
  - bb. Left anterior cardinal tooth short and thick; radial ribs coarse, flat-topped, over entire shell  
*Notochione*
  - aa. Escutcheon lacking ..... *Timoclea*<sup>47</sup>

### Subgenus *Chione* s.s.

Key to the species of *Chione* s.s.

- A. Concentric lamellae few and widely spaced; pallial line distant from margin  
*compta*
- B. Concentric lamellae numerous, closer, often recurved
- a. Shell rostrate or subrostrate posteriorly
  - b. Concentric lamellae strongly expanded posteriorly; interior rose and white ..... *gatulcoensis*
  - bb. Concentric lamellae very low over entire shell; a radial shallow depressed area usually present anterior to dorsal margin  
*crenifera*<sup>48</sup>
  - aa. Shell usually rounded or subtruncated posteriorly; larger
  - c. Concentric lamellae on lower half of shell flattened forming a smooth surface  
*californiensis*
  - cc. Concentric lamellae not flattened on lower half of shell, and

finer and more closely spaced  
*undatella*

### *Chione (Chione) californiensis* Broderip.

*Venus succincta* Valenciennes in Humboldt & Bonpland, Rec. d'Observ. sur Zool., 1827, p. 219, pl. 48, figs. 1a, 1b, 1c. "Habitat ad litus Oceani Pacifici, prope Acapulco Mexicanorum."

Not *Venus succincta* Linnaeus, Syst. Nat., ed. 12, Mantissa, 1771, p. 546. "Habitat . . ."

*Venus californiensis* Broderip, Proc. Zool. Soc. London, June 1, 1835, p. 43. "Hab. in sinu Californiae. (Guaymas.)" "Found in sandy mud at low water."—Reeve, Conch. Icon., Vol. 14, *Venus*, 1863, species 35, pl. 11, fig. 35. Original locality cited.

*Chione succincta* Valenciennes, Weymouth, State of Calif. Fish and Game Comm., Fish Bull. 4, 1920, p. 37, pl. 9, figs. 3, 4. Anaheim Slough, California. Also San Pedro, California, to Mexico.

*Type Locality*: Guaymas, Mexico, in the Gulf of California, at low water, sandy mud.

*Range*: Point Mugu, California, to Panama.

*Collecting Stations*: Mexico: East of Cedros Island (126-D-2), 38 fathoms, mud; Cape San Lucas; Monument Station, Santa Inez Bay, east coast of Lower California.

*Description*: Shell subcordiform, thick; ornamented by rather widely spaced (3 to 5 mm.), nearly equidistant, slightly reflexed concentric lamellae which at about the middle of the valve, and increasingly so toward the base, become crowded, flattened, thickened and nearly cover the interspaces; rounded radial ribs are present and increase by intercalation; lunule ornamented by incremental laminae and radiating riblets; 3 cardinal teeth in each valve, the right anterior and left posterior ones weaker than the others; pallial sinus very short and angular; margin crenulated.

Large specimens from the Gulf of California attain a length of approximately 68 mm., height, 65 mm., convexity (both valves), 38 mm.

As pointed out by Dall, this species can be separated from *C. undatella* Sowerby by the coarser and more widely spaced concentric sculpture, and by the fact that in adult forms the concentric lamellae on the ventral half of the disk are generally flattened and thickened, showing a smooth polished surface which nearly covers the interspaces.

A specimen 48 mm. in height may possess from 18 to 23 concentric lamellae while a large specimen 60 mm. in height may possess 30 to 40 such lamellae.

This species has also been recorded in the earlier literature under the names of *Venus leucodon* Sowerby, *Venus californiana* Conrad, and *Venus crassa* Sloat MS. in Carpenter.

*Chione cancellata christopheri* Trechmann, described from the Pliocene of St. Kitts Island in the Caribbean, is said to be a similar form.

<sup>47</sup> Not represented in the present collection.

<sup>48</sup> Not represented in the present collection.

*Distribution:* Specimens of this species were taken by the expedition at a few localities along western Mexico. It is often taken with *Chione undatella* Sowerby in bays and inlets just under the surface in firm sand or sandy mud. It also occurs in the Pleistocene of southern California and in the Pliocene and Pleistocene of the Gulf of California region.

***Chione (Chione) compta* Broderip.**

*Venus compta* Broderip, *Proc. Zool. Soc. London*, June 1, 1835, p. 43. "Hab. ad Peruviam. (Bay of Sechura.)" "It was dredged up in coarse sand and mud at a depth of seven fathoms."—Sowerby, *Thes. Conch.*, Vol. 2, 1853, p. 710, pl. 154, figs. 32, 33, 34. Original locality cited.—Reeve, *Conch. Icon.*, Vol. 14, *Venus*, 1863, species 48, pl. 13, fig. 48. Original locality cited.

*Chione meridionalis* I. S. Oldroyd, *Nauticus*, Vol. 34, No. 3, January, 1921, p. 93, pl. 4, figs. 3 and 4. "Type locality, Peru."

Not *Venus meridionalis* Sowerby, 1846. [Referred to the genus *Chione* by von Ihering, 1907].

*Type Locality:* Bay of Sechura, Peru, in 7 fathoms, sand and mud.

*Range:* Gulf of California to Bayovar, Peru.

*Collecting Station:* Costa Rica: Port Parker (203-D-1,2,3), 12-15 fathoms, sandy mud, crushed shell, shelly mud.

*Description:* Shell triangularly rounded, compressed, ornamented by widely spaced concentric ribs which posteriorly develop into broad, raised, gently reflexed lamellae; radial sculpture consists of well developed ribs and, in each interspace, a tiny riblet, anteriorly and posteriorly the ribs become fine and divaricate; pallial line unusually distant from the ventral margin; pallial sinus only slightly indented; margin crenulated.

The specimens of this species in the present collection are all small; the largest, a right valve, measures approximately: length, 33 mm.; height, 31 mm.; convexity (one valve), 10 mm.

The illustrations of *Chione compta* given by Sowerby do not reveal the most characteristic features shown on our specimens. However, the descriptions given by Broderip, Sowerby, and Dall, all exactly apply to our specimens. The species described by I. S. Oldroyd as *Chione meridionalis* appears to be identical with *C. compta*. Both were described from Peru and the characters described for the two are the same. The few, flattened and slightly up-turned concentric lamellae, flattened shell, fine divaricating ribs anteriorly and posteriorly, and pallial line distant from the margin, are all characteristic features of this species.

*Distribution:* Specimens of this species were dredged at Port Parker, Costa Rica, in 12-15 fathoms. It ranges south to Peru where it has also been recorded as occurring in the Pleistocene. It ranges north to the Gulf of California.

***Chione (Chione) guatulcoensis* Hertlein & Strong, sp. nov.**

Plate I, Figures 2, 4, 6 and 10;

Plate II, Figures 1, 8, 12 and 13.

Shell small, subrostrate, only moderately inflated; with low distant concentric lamellae which become expanded posteriorly; radial sculpture of low rather flattened ribs which are separated by subequal, smooth, narrower, interspaces, in the anterior medial area the ribs become obsolete toward the base especially on large specimens and anterior to this the ribs become faintly divaricate toward the base and a few interstitial threads appear; lunule elongated, ornamented by concentric and radial striations; escutcheon well developed, forming nearly a right angle with the dorsal margin, ornamented by fine concentric imbricating lamellae, the right valve slightly overlapping the left posteriorly; exterior white with brown or rose colored radial bands, or brown blotches and fine V-shaped brown lines and dots; interior white and rose, the latter predominant on large specimens; the right posterior and sometimes the left middle cardinal slightly grooved; pallial sinus shallow, broad, rather blunt, nearly vertical; inner margins crenulated except posteriorly. Dimensions (type): length, 11.2 mm.; height, 9.4 mm.; convexity (both valves together), 6 mm. The largest specimen, a paratype, measures 14 mm. in length.

Holotype and paratypes (Calif. Acad. Sci. Paleo. Type Coll.), dredged at Station 195-D-9, in Latitude 15° 44' 28" N., Longitude 96° 07' 51" W., off Port Guatulco, Mexico, in 7 fathoms (12.6 meters), in gr. sand and crushed shell.

This species is similar to *Chione mazyckii* Dall<sup>49</sup> described from North Carolina. It differs from the east American species in the narrower interspaces, the obsolete radial sculpture in the medial anterior ventral area and anterior to this the presence of only a few faintly divaricate ribs and interstitial threads. In *C. mazyckii* the anterior half of the ribs appear to divaricate and many interstitial threads make their appearance.

*Chione crenifera* Sowerby<sup>50</sup>, described from Ecuador and Peru, has very low concentric lamellae over the entire shell and a radial, shallow, depressed area is present just anterior to the posterior dorsal margin.

***Chione (Chione) undatella* Sowerby.**

*Venus undatella* Sowerby, *Proc. Zool. Soc. London*, April 16, 1835, p. 22. "Hab. in Sinu Californiensi (Island of Tres Marias.)"—Sowerby, *Thes. Conch.*, Vol. 2, 1853, p. 711, pl. 153, fig. 22. Original locality cited.

*Venus neglecta* Sowerby, *Zool. Beechey's*

<sup>49</sup> *Chione mazyckii* Dall, *Proc. U. S. Nat. Mus.*, Vol. 26, No. 1312, December, 1902, pp. 373, 382, pl. 13, fig. 2. Dredged "off Cape Fear, North Carolina, in 17 fathoms, sand."

<sup>50</sup> *Venus crenifera* Sowerby, *Proc. Zool. Soc. London*, June 1, 1835, p. 43. "Hab. ad Sanctam Elenam." Variety, "Hab. ad Paytam, Peruviae." "Found in the sand at low water."—Sowerby, *Thes. Conch.*, Vol. 2, 1853, p. 715, pl. 156, figs. 73, 74. "... found in sand at low water at Payti, Peru."

Voy., 1839, p. 151, pl. 41, fig. 8. "Inhabits sandy mud on the coast of Central America."

*Venus simillima* Sowerby, Thes. Conch., Vol. 2, 1853, p. 708, pl. 153, figs. 17, 18. "California."—Reeve, Conch. Icon., Vol. 14, *Venus*, 1863, species 44, pl. 13, fig. 44. "Hab. San Diego, California."

*Chione undatella* Sowerby, Weymouth, State of Calif. Fish and Game Comm., *Fish Bull.* No. 4, 1920, p. 37, pl. 9, fig. 2. Anaheim Slough, California. Also San Pedro, California, to Mexico.

*Type Locality*: Tres Marias Islands, Mexico.

*Range*: Mugu Point, California, to Paita, Peru.

*Collecting Stations*: Mexico: Arena Bank (136-D-27), 50 fathoms, sand, calcareous algae, rock; Port Angeles, beach; Port Guatulco (195-D-1,2,5,10), 2-4 fathoms, sand, algae, crushed shell, also on beach; Tangola-Tangola Bay.

*Description*: Shell similar to that of *Chione californiensis* Broderip but slightly more inflated and ornamented with more numerous and more closely spaced thinner and sharper concentric lamellae. Often, but not always, the anterior cardinal tooth is more nearly parallel to the margin than that of *C. californiensis*. A specimen about 46 mm. in altitude may possess from 33 to 40 concentric lamellae.

This species has received many names in the literature, including *Venus bilineata* Reeve, *V. excavata* Carpenter, *V. entobapta* Jonas, *V. neglecta* Sowerby, *V. nuttalli* Conrad, *V. perdis* Valenciennes, *V. simillima* Sowerby and *V. sugillata* Reeve. Coarsely lamellose shells marked with brown and white are referable to the form named *Venus neglecta* Sowerby but there is so much variation in a series of specimens that we have followed Dall in referring them all to *C. undatella*.

*Distribution*: This species occurs commonly from southern California to Peru. It was taken by the expedition at a few localities off west Mexico. It also is known to occur in the Pleistocene of southern California, Lower California and the Galápagos Islands and in the Pliocene of the Gulf of California region.

#### Subgenus *Chionopsis* Olsson.

*Chionopsis* Olsson, *Bull. Amer. Paleo.*, Vol. 19, No. 68, June 30, 1932, p. 111. "Type.—*Chione amathusia* Philippi."

*Type* (by original designation): *Chione amathusia* Philippi.

Shell of moderate size to large; right posterior and middle left cardinal teeth bifid or grooved, sometimes the others; resilium very narrow with the ligament not deeply inserted and separated by a narrow, linear nymph; shell usually thinner than amongst the true Chiones; pallial sinus well developed; lunule equal or discrepant in size, its margin strongly crenate (Olsson).

Key to the species of *Chionopsis*.

- A. Coarsely serrated concentric lamellae
  - a. Concentric lamellae high; lunule elongately cordate. .... *gnidia*
  - aa. Concentric lamellae lower; lunule broadly cordate; finer radial ribbing; adductor impressions larger ..... *amathusia*
- B. Concentric lamellae thin and very finely serrated
  - a. Posterior end obliquely truncated or rounded ..... *purpurissata*
  - aa. Posterior end forming nearly a right angle or subrostrate ..... *pulcaria*

#### *Chione (Chionopsis) amathusia* Philippi.

*Venus amathusia* Philippi, *Abbild. u. Beschreib. Conchyl.*, Bd. 1, Helt 5, *Venus*, April, 1844, p. 129 (7), pl. 2, fig. 4. "Patria? . . ."

*Type Locality*: Panama Bay (here designated as type locality). No locality cited originally.

*Range*: Gulf of California to Mancora, Peru.

*Collecting Stations*: Mexico: 17 mi. SE. × E. of Acapulco (189-D-1,2,3), 13-20 fathoms, sandy mud, mud, algae; Guatemala: 7 miles west of Champerico (197-D-1,2), 14 fathoms, mud; El Salvador: La Libertad (198-D-1,2), 13-14 fathoms, mud; Costa Rica: 14 miles S. × E. of Judas Point (214-D-1-4), 42-61 fathoms, mud, shell, rocks; Gulf of Dulce; Gofito, Gulf of Dulce; Panama: Gulf of Chiriqui (221-D-1-5), 35-40 fathoms, sandy mud.

*Description*: Shell triangularly ovate, rather inflated, posteriorly somewhat attenuated; ornamented by pairs of fine, radial ribs between which there is an interrib, and by concentric lamellae which are crenulated and give rise to prickly scales, the lamellae are radially marked on the ventral side; hinge with three cardinal teeth in each valve, the right posterior tooth and the left middle one cleft; pallial sinus well developed, short, rounded; margin crenulated.

The shell of this species is smaller than that of *Chione gnidia* Broderip & Sowerby. It often attains a length of about 40 mm. although it may reach a greater length. Compared to *Chione gnidia* the umbos of the present species are more highly rounded, giving a more cordate cross-section and more rounded lunule, the form is less elongate, the radial sculpture is finer and the concentric lamellae are lower. The adductor impressions of *C. amathusia* are a little larger than those on shells of *C. gnidia* of the same size.

*Chione rowleyi* Olsson, described from the Miocene of Costa Rica, is a similar species.

Sowerby's figures of *Venus amathusia* (1853, pl. 154, figs. 26, 27) were referred by Römer to *Venus darwini* Dunker<sup>51</sup>. Lamy<sup>52</sup>

<sup>51</sup> *Venus darwini* Dunker in Römer, *Krit. Untersuch. Moll. Venus* (Cassel), 1857, p. 25 [No locality cited].—Römer, *Malakozool. Blätter*, Bd. 14, February, 1867, p. 51 (as *Chione darwini*.) "Panama, Mazatlan."—Pfeiffer, *Conchyl.-Cab. von Martini-Chemnitz*, Bd. 11, Abt. 1, Veneracea, 1869, p. 204, Taf. 33, figs. 3 and 4.

<sup>52</sup> Lamy, E., *Journ. de Conchyl.*, Vol. 57, No. 3, 1909, pp. 243-244.

likewise referred Sowerby's figures as well as those of Reeve (1863, pl. XI, figs. 36a, 36b) to Dunker's species. Deshayes, 1853, considered Dunker's species to be a variety of *Chione amathusia* but Carpenter, 1857, regarded it as a variety of *C. gnidia*. Dall, 1902, regarded it "as a doubtfully distinct form and perhaps a variety of *C. subrostrata*." We have not seen specimens which we could refer with certainty to *Chione darwinii*.

*Distribution*: Specimens of this species were collected by the expedition from west Mexico to Costa Rica but nowhere abundantly. The largest number from any one locality was dredged in 14 fathoms west of Champerico, Guatemala. This species has been cited as occurring in the Quaternary of Manta, Ecuador, the Pliocene of Panama, and a similar or identical form in the Pliocene of Costa Rica.

***Chione (Chionopsis) gnidia* Broderip & Sowerby.**

*Venus gnidia* Broderip & Sowerby, *Zool. Jour.*, Vol. 4, No. 15, January, 1829, p. 364. "Hab. ad littora Oceani Pacifici." Dredged "near St. Blas."—Sowerby Genera Rec. and Foss. Shells, No. 41, 1834, pl. 251, fig. 7. [No locality cited].—Sowerby, *Thes. Conch.*, Vol. 2, 1853, p. 709, pl. 154, fig. 25. Pacific Ocean.—Reeve, *Conch. Icon.*, Vol. 14, *Venus*, 1863, species 37, plate 11, fig. 37. San Blas, Mexico.

*Venus (Chione) gnidia* Sowerby, Grant & Gale, *Mem. San Diego Soc. Nat. Hist.*, Vol. 1, 1931, p. 318, pl. 16, figs. 5a, 5b. Earlier records cited. Pleistocene and Recent.

*Type Locality*: San Blas, Mexico, dredged.

*Range*: Cedros Island, Lower California, to Paita, Peru.

*Collecting Station*: Mexico: Santa Inez Bay, east coast of Lower California.

*Description*: Shell roundly trigonal, convex, ornamented by prominent concentric lamellae which are rather coarsely scalloped and develop erect prickly scales, the under surface of the lamellae are radially sculptured; interspaces ornamented by well developed, nearly evenly spaced, obscurely paired ribs which are separated from the next pair by a smaller rib; hinge normal for the subgenus; pallial sinus well developed, short, the end rather rounded; exterior colored light drab brown or white, interior white; margin crenulated.

The shell of this species attains a large size. A large specimen collected at San Ignacio Lagoon, Lower California, by Henry Hemphill measures approximately: length, 101 mm.; height, 94.5 mm.; convexity (both valves), 68 mm.

This species attains a larger size, possesses a more elongated form, more prominent lamellation, more elongated lunule and coarser ribs than *C. amathusia*.

*Venus ornatissima* Broderip, 1835, is now considered referable to *C. gnidia*. *Chione jamaniana*, *C. manabia* and *C. traftoni*, described by Pilsbry & Olsson, 1941, from the Pliocene of Ecuador, are all quite similar to

*C. gnidia*. *Chione temblorensis* Anderson & Martin from the Miocene of California and *C. richthofeni* Hertlein & Jordan from the Miocene of Lower California are other species belonging to the *Chione gnidia* group.

*Distribution*: A couple of specimens of this species were collected by the expedition in Santa Inez Bay in the Gulf of California. It often occurs in the quiet waters of bays along the tropical west American coast. It also is known to occur in the Pleistocene of southern California, in the Gulf of California region, and has been cited as occurring in the Quaternary of Ecuador.

***Chione (Chionopsis) pulicaria* Broderip.**

*Venus pulicaria* Broderip, *Proc. Zool. Soc. London*, June 1, 1835, p. 44. "Hab. ad Columbianam Occidentalem. (Chiriqui and Tumaco.)" "Dredged up from sandy mud at a depth of three fathoms."

*Venus cingulata* Lamarck, Sowerby, *Thes. Conch.*, Vol. 2, 1853, p. 729, pl. 161, fig. 191. "West Columbia. Cuming."

Not *Venus cingulata* Lamarck, 1818.

*Chione montezuma* Pilsbry & Lowe, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 84, May 21, 1932, p. 101, pl. 15, figs. 12, 13, 14. "Costa Rica: Puntarenas."

*Chione pulicaria* Broderip, E. K. Jordan, *Contrib. Dept. Geol. Stanford Univ.*, Vol. 1, No. 4, 1936, p. 139. Magdalena Bay, Lower California, Pleistocene. Gulf of California to Colombia, Recent.

*Type Locality*: Chiriqui, Panama, in 3 fathoms, sandy mud (here designated as type locality). Tumaco, Colombia, also cited originally.

*Range*: Gulf of California, to Tumaco, Colombia.

*Collecting Station*: Nicaragua: Corinto (200-D-11-13,17,19), 3-10 fathoms, sand, mangrove leaves.

*Description*: Shell roundly triangular, in the adult somewhat acuminate at anterior and posterior ends, moderately convex, a broad shallow radial depression occurs parallel and anterior to the posterior dorsal margin; lunule cordate, brown, sculptured only by incremental lines of growth; escutcheon fairly large and elongate; concentric sculpture of numerous, rather fine, generally equally spaced, low, concentric lamellae, stronger and closer anteriorly and posteriorly and finely serrated by the radial sculpture which occurs on the ventral sides and in the interspaces; on large specimens the concentric sculpture is coalescent and subobsolete medially toward the ventral margin; colored exteriorly by white or cream ground mass with brown dots often arranged in a ^-shaped pattern; middle left and right posterior teeth bifid; pallial sinus well developed, ascending, rounded at end, directed toward the anterior adductor impression and attaining a height of about one half the height of the posterior adductor impression; color of interior white or cream and with purple often just below but sometimes also above the pallial line; margin crenulated.

Specimens of this species in the present collection are small, not over 22 mm. in length, but a large specimen from Kino Bay, Sonora, Mexico, collected by H. N. Lowe, measures: length, 47.3 mm.; height, 39 mm.; convexity (both valves), 30.5 mm.

Specimens of this species from various localities agree exactly with the description of the species given by Broderip, Sowerby, and Hanley, and with the illustration given by Sowerby. The illustration given by Reeve (*Venus*, pl. 8, fig. 26) does not show the acuminate form which develops with large shells, especially posteriorly.

We have been unable to detect any constant difference between this species and the shell described as *Chione montezuma* by Pilsbry & Lowe. There is variation in the amount of rostration and in the development of stronger and more obtuse lamellae posteriorly. After a consideration of these facts we have concluded that the species described by Pilsbry & Lowe belongs in the synonymy of *C. pulicaria*.

The ornamentation of *Chione oulotricha* Gardner, 1936, described from the Alum Bluff Miocene of Florida, appears to be similar to that of *C. pulicaria* but the posterior end of the Floridan fossil is obliquely truncated similar to that of *C. purpurissata*.

*Distribution*: Specimens of this species were taken only at Corinto, Nicaragua, in 3 to 10 fathoms. It occurs as far south as Colombia and is also known to occur in the Pleistocene of Magdalena Bay, Lower California.

#### *Chione (Chionopsis) purpurissata* Dall.

*Venus crenulata* var., Reeve, Conch. Icon., Vol. 14, *Venus*, June, 1863, species 46, pl. 13, fig. 46. "From the Gulf of California."

[*Venus crenulata*] "?var. *lilacina*" Carpenter, *Rept. Brit. Assoc. Adv. Sci.* for 1863 (issued August, 1864), p. 570. Ref. to fig. 46 of Reeve. Reprint in *Smithson. Miscell. Coll.*, No. 252, 1872, p. 56. "Cape St. Lucas, Xantus."

Not *Chione lilacina* Gray, 1838.

*Chione (Chione) purpurissata* Dall, *Proc. U. S. Nat. Mus.*, Vol. 26, No. 1312, December, 1902, p. 393. "Cape St. Lucas and the Gulf of California."

*Type Locality*: Cape San Lucas, Lower California, Mexico.

*Range*: Gulf of California to Guatemala.

*Collecting Stations*: Mexico: Santa Inez Point, east coast of Lower California; Chamela Bay (183-D-4), 16 fathoms, sand, algae, crushed shell.

*Description*: Shell roundly trigonal, rather tumid, posterior end rounded; ornamented by rather fine radial and concentric sculpture; lunule large, ornamented only by lines of growth; a shallow and rather narrow radial depression occurs posteriorly just above the escutcheon which is large and smooth; a strong raised ridge just above the ligament occurs on the left valve; mottled with brown externally, lunule brown; hinge normal for

the subgenus; pallial sinus ascending and projecting to a point about level with the middle of the posterior adductor impression; margin crenulated except posteriorly; interior colored rose purple.

A large specimen in the collection of the California Academy of Sciences, collected by Fred Baker at Carmen Island in the Gulf of California, measures approximately: length, 64.5 mm.; 57 mm.; convexity (both valves), 42.6 mm.

This shell is much like *Chione pubera* Valenciennes, an east American species, but is rounder in outline and it has less prominent lamellation.

*Distribution*: Only a couple of specimens of this species were collected by the expedition, one in the Gulf of California and one in Chamela Bay, Mexico. De Long<sup>53</sup> has cited this species as occurring in the Palos Verdes Sands, Pleistocene of Signal Hill, Long Beach, California, but we have not seen fossil specimens.

#### Subgenus *Lirophora* Conrad.

Key to the species of *Lirophora*.

- A. Concentric ribs of uniform strength across entire shell ..... *mariae*
- B. Concentric ribs flattened and nearly coallescent medially
  - a. Ribs bifid on posterior dorsal slope; posterior end rather rostrate and pointed ..... *obliterata*<sup>54</sup>
  - aa. Ribs not bifid on posterior dorsal slope; ribs develop prominent lamellae along anterior and posterior ends; posterior end more broadly rounded ..... *kellestii*

#### *Chione (Lirophora) kellestii* Hinds.

*Venus kellestii* Hinds, *Zool. Voy. Sulphur*, Vol. 2, Moll., Pt. 3, 1844 [January, 1845, on cover of Pt. 3], p. 65, pl. 19, fig. 5. "Inhab. Island of Quibo, West coast of Veragua. In adhesive mud of a low temperature, in between thirty and thirty-four fathoms."—Sowerby, *Thes. Conch.*, Vol. 2, 1853, p. 721, pl. 155, fig. 64. Original locality cited.—Reeve, *Conch. Icon.*, Vol. 14, *Venus*, 1863, species 82, pl. 18, fig. 82. "West coast of Veragua, Central America."

*Chione (Lirophora) kellestii* Hinds, Pilsbry & Olsson, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 93, 1941, p. 64, pl. 16, fig. 2. Canoa formation, Punta Blanca, Ecuador, Pliocene.

*Type Locality*: Island of Quibo [= Coiba], west coast of Veragua, Panama, in 30-34 fathoms, mud.

*Range*: Gulf of California to the Bay of Panama.

*Collecting Stations*: Mexico: Santa Inez Bay, east coast of Lower California (143-D-2,3,4), 25-30 fathoms, mud, crushed shell, sand; Tangola-Tangola Bay (196-D-19), 30 fathoms, mud; Costa Rica: 14 miles S. × E. of Judas Point (214-D-1-4), 42-61 fathoms,

<sup>53</sup> De Long, Jr., J. H., *Trans. San Diego Soc. Nat. Hist.*, Vol. 9, No. 25, April 30, 1941, p. 243, and table opp. p. 244.

<sup>54</sup> Not represented in the present collection.

mud, rocks; Panama: Gulf of Chiriqui (221-D-1-5), 35-40 fathoms, sandy mud.

*Description*: Shell elongately oval, slightly produced at the ends; ornamented by yellowish-brown concentric ribs which are smooth and coalescent over most of the shell but develop into prominent white lamellae along the anterior and posterior ends; radially striated strongest on the upper portions of the umbos; pallial line very short, angular; margin finely crenulated.

A valve from Santa Inez Bay measures approximately: length, 65 mm.; height, 52.5 mm.; convexity (one valve), 18 mm.

Occasionally, small, thick shells of this species bear a slight resemblance to *Chione* (*Lirophora*) *obliterata* Dall<sup>55</sup> which was described from the Gulf of Panama. Dall's species, however, is narrower, more rostrate and more acutely pointed posteriorly, the lunule is shorter and the exterior of the shell is said to be "sculptured with heavy, tumid, concentric waves which in the adult become somewhat irregular and sometimes coalescent on the disk, more or less angular and bifid on the posterior dorsal slope." It is similar to *C. latilirata* Conrad which occurs in the Caribbean region.

*Chione* (*Lirophora*) *trimeris* Gardner, from the Miocene of Florida, is somewhat similar to *C. kelletii*.

*Distribution*: Specimens of this species were taken from Santa Inez Bay in the Gulf of California to the Gulf of Chiriqui, Panama, at depths of 25-61 fathoms. It has been cited as occurring in the Pliocene and Pleistocene of Costa Rica and in the Pliocene of Panama.

E. K. Jordan<sup>56</sup> has cited *Chione kelletii* as occurring north to Todos Santos Bay, Lower California, but we have not seen specimens from the west side of the Peninsula.

#### *Chione* (*Lirophora*) *mariae* d'Orbigny.

*Venus cypria* Sowerby, *Proc. Zool. Soc. London*, June 1, 1835, p. 43. "Hab. ad Insulam Platae, Columbiae Occidentalis." "Found among coral sand in seventeen fathoms."—Sowerby, *Thes. Conch.*, Vol. 2, 1853, p. 722, pl. 157, fig. 113. Original locality cited.—Reeve, *Conch. Icon.*, Vol. 14, *Venus*, 1863, species 116, pl. 23, figs. 116a, 116b. Original locality cited.

Not *Venus cypria* Brocchi, 1814; not *Venus cypria* Risso, 1826.

*Venus mariae* d'Orbigny, *Voy. Amér. Mérid.*, Vol. 5, 1846, p. 563. "M. Cuming l'a pêchée à l'île de la Plata, sur les côtes de la république de l'Equateur." New name for *Venus cypria* Sowerby, not *V. cypria* Brocchi, 1814, not *V. cypria* Risso, 1826.

*Type Locality*: Island of Plata, Ecuador, in 17 fathoms, coral sand.

*Range*: Cedros Island, Lower California,

to the Gulf of California and south to Guayaquil, Ecuador.

*Collecting Stations*: Mexico: East of Cedros Island (126-D-12), 45 fathoms, crushed shell, mud; Arena Bank (136-D-13, 14, 15, 18), 40-45 fathoms, mud, *Arca* conglomerates, crushed shell; Santa Inez Bay (142-D-3, 4; 143-D-3; 145-D-1, 3; 146-D-1; 147-D-2), 4-60 fathoms, sand, weed, mud, crushed shell; Costa Rica: Port Parker (203-D-1, 3), 12-15 fathoms, sandy mud, crushed shell, shelly mud.

*Description*: Shell roundly triangular, somewhat attenuated posteriorly, dorsal margins nearly straight, only slightly arched posteriorly, slightly concave anteriorly; lunule rather narrow; escutcheon narrow, long, flat, at right angles to the posterior umbonal area and ornamented by concentric lines of growth; sculptured with strong, high, recurved, concentric ribs which cross the shell and are radially striated on the ventral side and slightly flattened posteriorly, interspaces ornamented only with lines of growth; exteriorly light brownish or yellow with a few broad and many fine radial chestnut brown stripes; pallial sinus very short, narrow, subangulate; lunular and ventral margins finely crenulated.

A large valve collected in Santa Inez Bay, in the Gulf of California, measures approximately: length, 34 mm.; height, 26.3 mm.; convexity (one valve), 9 mm.

The shell of this species may be easily separated from that of *Chione kelletii* in that strong raised concentric lamellae cross the shell without any trace of coalescence or obscuration medially.

*Chione* (*Lirophora*) *gorgona* Pilsbry & Olsson,<sup>57</sup> described from the Pliocene of Ecuador, is very similar to large specimens of *C. mariae* and there are related forms in the Caribbean region.

*Distribution*: Specimens of *Chione mariae* were collected from the Gulf of California to Costa Rica. A few small specimens dredged off Cedros Island furnish an extension north of the known range of the species. It also is known to occur in the Pleistocene of the Gulf of California region and Panama, and in the Pliocene of Costa Rica and Ecuador.

#### Subgenus *Nioche* Hertlein & Strong, subgen. nov.

*Type*: *Venus asperrima* Sowerby. Illustrated by Sowerby in *Thes. Conch.*, Vol. 2, 1853, p. 714, pl. 155, figs. 57, 58.

*Description*: Shell with well developed radial ribs but with reduced concentric sculpture, possessing a radially sculptured lunule which is delimited by an incised line and with a beveled escutcheon on the left valve; hinge similar to that of *Chione* s.s. but with the left anterior cardinal somewhat elongated, approaching parallelism with the dorsal margin and, in the type species, thin and very high, the right posterior and left central (and

<sup>55</sup> *Chione* (*Lirophora*) *obliterata* Dall, *Proc. U. S. Nat. Mus.*, Vol. 26, No. 1312, December, 1902, pp. 394, 405, pl. 16, fig. 2. "Humboldt Bay, Gulf of Panama."

<sup>56</sup> Jordan, E. K., *Bull. South. Calif. Acad. Sci.*, Vol. 23, Pt. 5, September-October (issued October 25), 1924, p. 153.

<sup>57</sup> *Chione* (*Lirophora*) *gorgona* Pilsbry & Olsson, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 93, September 9, 1941, p. 65, pl. 19, fig. 2. "Jama formation, Puerto Jama." Ecuador, Pliocene.

sometimes right central) cardinals bifid; inner margin crenulated; pallial sinus well developed.

This subgenus possesses characters apparently intermediate between *Chione* and *Protothaca*. It differs from the subgenus *Timochea* in possessing an escutcheon on the left valve and in that the left anterior cardinal is elongated and high. The well developed escutcheon on the left valve, finer radial sculpture, broader hinge plate and the position of the elongate thin high left anterior cardinal which is more nearly parallel to the dorsal margin are features which serve to separate *Nioche*<sup>68</sup> from *Protothaca*.

Key to the species of *Nioche*.

- A. Shell exceeding 10 mm. in length  
 a. Radial sculpture predominant (and rasp-like) over entire shell; rather compressed ..... *asperima*  
 aa. Radial sculpture predominant anteriorly and posteriorly; rather inflated ..... *metodon*  
 B. Shell not exceeding 10 mm. in length; ovately oblong ..... *picta*

*Chione (Nioche) asperima* Sowerby.

*Venus asperima* Sowerby, *Proc. Zool. Soc. London*, June 1, 1835, p. 42. "Hab. ad Insulam Lobos dictam." "Found in fine sand at low water."—Sowerby, *Thes. Conch.*, Vol. 2, 1853, p. 714, pl. 155, figs. 57, 58. Original locality cited.—Reeve, *Conch. Icon.*, Vol. 14, *Venus*, 1863, species 19, pl. 6, figs. 19a, 19b. "Hab. Guacamayo, Central America (in sandy mud, at a depth of thirteen fathoms); Cuming."

*Type Locality*: Island of Lobos, Peru, at low water, in fine sand.

*Range*: Magdalena Bay, Lower California, to the Gulf of California and south to Paita, Peru.

*Collecting Station*: Costa Rica: Port Parker.

*Description*: Shell ovately oblong, rather compressed, sculptured with alternating large and small radial ribs which are crossed by fine close-set imbricating lamellae which give a rasp-like surface to the ribs; escutcheon on left valve smooth, beveled; the ribbing continues over the lunule which is elongated and delimited only by an incised line; exteriorly sometimes colored by radial violet-brown blotches; right middle and posterior teeth and left middle tooth often grooved, left anterior cardinal high; pallial sinus projecting toward middle of anterior adductor impression and reaching a point nearly midway between the two impressions, the end pointed; margin except posteriorly, crenulated.

A large valve collected at Port Parker, Costa Rica, measures approximately: length, 48.3 mm.; height, 39.8 mm.; convexity (one valve), 12.5 mm.

The rasp-like ornamentation of the ribs, larger lunule, well beveled escutcheon, broader hinge plate and high anterior cardinal on

the left valve are features which serve to separate shells of this species from those of *Protothaca grata* Say.

The species described as *Venus pectorina* by Lamarck, 1818, which occurs in the Caribbean region, is similar to *C. asperima*.

*Distribution*: Three valves of this species, somewhat worn, were collected by the expedition on the beach at Port Parker, Costa Rica.

*Chione (Nioche) metodon* Pilsbry & Lowe.

*Chione metodon* Pilsbry & Lowe, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 84, May 21, 1932, p. 100, pl. 15, figs. 7, 8, 9, 10, 11. "Montijo Bay, Rep. Panama (Lowe)."

*Type Locality*: Montijo Bay, Panama.

*Range*: Banderas Bay, Mexico, to Montijo Bay, Panama.

*Collecting Station*: Mexico: Banderas Bay.  
*Description*: Shell rotundly triangular, inflated, rather thin, colored buff with radially arranged violet-brown markings; lunule delimited by an incised line; sculpture of many low, rather evenly spaced concentric threads which are stronger and slightly lamellose anteriorly and posteriorly; radial sculpture of many fine, low riblets which also occur on the lunule but not on the escutcheon and several coarser radial ribs occur anteriorly; the left anterior cardinal tooth is thin and high; pallial sinus short, but well developed, rounded or subangulate; interior margin finely crenulated; interior white with purple posteriorly.

The largest specimen collected, a right valve, measures approximately: length, 34 mm.; height, 31 mm.; convexity (one valve), 11 mm.; pallial sinus extends forward 14 mm. from the posterior margin.

This species bears some resemblance to specimens of *Chione purpurissata* Dall but is easily separated by the presence of 6 to 8 coarse grooves anteriorly, the radially sculptured lunule and the high left anterior cardinal.

*Distribution*: A few specimens of this species were collected by the expedition in Banderas Bay, Mexico. The record of the occurrence at this locality is an extension northward of the known range of the species.

*Chione (Nioche) picta* Dall in Willett.

*Chione picta* Dall in Willett, *Bull. South. Calif. Acad. Sci.*, Vol. 43, Pt. 1, January-April (issued May 31), 1944, p. 21, pl. 8, figs. A, B. Type "collected by C. R. Orcutt in Magdalena Bay, Lower California, Mexico." Also cited from various localities in the Gulf of California region and in the Pleistocene in Los Angeles County, California.—Woodring, U. S. Geol. Surv., *Prof. Paper* 207, 1946, pp. 84, 88, pl. 37, figs. 3 and 4. San Pedro region, southern California, Pleistocene. Magdalena Bay, Lower California, to Panama, Recent.

*Type Locality*: Magdalena Bay, Lower California.

*Range*: Magdalena Bay, Lower California, to the head of the Gulf of California and south to Panama.

<sup>68</sup> *Nioche*, an anagram of *Chione*.

*Collecting Stations:* Mexico: Port Guatulco (195-D-8, 9), 6-7 fathoms, sand, gr. sand, algae, crushed shell.

*Description:* Shell small (not exceeding 10 mm. in length), ovately oblong, posterior dorsal margin long and nearly straight, an escutcheon present on left valve, the right valve overlaps the left along the posterior dorsal margin; sculptured with flattish radial ribs and concentric lamellae which become stronger and laminate on the posterior area; hinge with 3 teeth in each valve, the anterior cardinals slanting strongly forward, the right posterior and left middle cardinals grooved; pallial sinus short but well developed, blunt; inner margin of shell crenulated; exterior white with purple spots, occasionally purple spots over entire shell, interior white with purple beneath hinge and the posterior area.

A valve from Port Guatulco, Mexico, measures: length, 7.2 mm.; height, 5 mm.; convexity (one valve), 2 mm. The largest specimen in the collection measures 8.5 mm. in length.

*Chione springvalensis* Vokes<sup>59</sup> described from the upper Miocene of Trinidad, appears to be quite similar to *C. picta*.

*Distribution:* About 75 specimens of this species were dredged at Port Guatulco, Mexico, in 6-7 fathoms. It has been recorded as occurring north to the head of the Gulf of California and to Magdalena Bay on the west coast of Lower California. It has also been recorded as occurring in the Pleistocene of Los Angeles County, California, and it is known to occur in the Pleistocene at Magdalena Bay, Lower California.

***Notochione* Hertlein & Strong, subgen. nov.**

*Type:* *Venus columbiensis* Sowerby. Illustrated by Reeve, *Conch. Icon.*, Vol. 14, *Venus*, 1863, species 61, pl. 15, figs. 61a, 61b.

Shell ovately oblong, thick, moderately inflated, ornamented by fairly broad, heavy, flat-topped ribs which are separated by narrower grooves and crossed by rather fine closely spaced concentric lamellae, subobsolete on medial portions of valves; lunule cordate, delimited by an incised line and ornamented by concentric lines of growth and weak radial riblets; escutcheon beveled, smooth, and well developed on left valve, on the right valve the corresponding area is rounded; three cardinal teeth in each valve, the posterior teeth and the left middle (and sometimes the right middle) tooth grooved; adductor impressions large; pallial sinus well developed, narrow, slightly ascending; ventral margin crenulated, lunular margin only faintly so, posterior margin smooth.

*Venus columbiensis* Sowerby possesses characters some of which seem referable to *Chione* and others to *Protothaca*. The well developed, beveled escutcheon on the left valve is similar to *Chione* s.s. and the well developed pallial sinus is similar to that of

*Chionopsis*. The moderate inflation, ovate, elongate shape and strong predominant radial ribbing is suggestive of *Protothaca*. It hardly seems referable to any supraspecific group with which we are familiar and we therefore propose a new subgenus *Notochione* with *Venus columbiensis* Sowerby as type.

***Chione (Notochione) columbiensis* Sowerby.**

*Venus columbiensis* Sowerby, *Proc. Zool. Soc. London*, April 16, 1835, p. 21. "Hab. ad Sanctam Elenam Columbiae Occidentalis." "Found in coarse sand at low water."—Sowerby, *Thes. Conch.*, Vol. 2, 1853, p. 713, pl. 155, figs. 53, 54. Original locality cited.—Reeve, *Conch. Icon.*, Vol. 14, *Venus*, 1863, species 61, pl. 15, figs. 61a, 61b. Original locality cited.

*Type Locality:* Santa Elena, Ecuador, at low water, in coarse sand.

*Range:* Mazatlan, Mexico, to Pacasmayo, Peru.

*Collecting Stations:* Mexico: Banderas Bay; Nicaragua: Potosi and Monypenny Point, Gulf of Fonseca; Fumarole, Gulf of Fonseca.

*Description:* Shell ovately oblong, thick; sculptured with rather broad, heavy, flat-topped radial ribs which are separated by narrower interspaces; ribs and interspaces crossed by fine, rather closely spaced concentric lamellae which are almost or wholly obsolete on the medial portions of the valves but are crowded anteriorly, giving a nodose appearance to the ribs; lunule cordate, rather small for the size of the shell, ornamented by concentric lines of growth and weak radial riblets; escutcheon beveled, smooth, well developed on the left valve, the corresponding portion of the right valve is rounded and posteriorly overlaps the left; colored by yellowish-gray and brown in general radial arrangement and mottled with larger blotches of ash-brown; hinge typical for the subgenus; pallial sinus well developed, narrow, slightly ascending, rounded or bluntly subangulate, projecting about a third the distance between the adductor impressions; margin crenulated, except posteriorly; interior white tinged with a streak of purple.

The largest specimen in the collection, from Potosi and Monypenny Point, Nicaragua, measures approximately: length, 52 mm.; height, 48 mm.; convexity (both valves), 31.5 mm.

The shell from Japan described as *Venus hirasei* by Pilsbry<sup>60</sup> was compared to *Chione columbiensis* and appears to be another member of the same group.

*Distribution:* A few specimens of this species were taken in Banderas Bay, Mexico, and off Nicaragua, in the Gulf of Fonseca. It has been cited occurring as a fossil in Peru.

<sup>59</sup> *Chione (Chione) springvalensis* Vokes, *Amer. Mus. Novitat.*, No. 988, May 16, 1938, p. 14, fig. 6 (on p. 13). Springvale, Trinidad, Upper Miocene.

<sup>60</sup> *Venus hirasei* Pilsbry, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 53, May 2, 1901, p. 205. "Hirado, Hizen." Japan. Also p. 400, pl. 19, fig. 1, pl. 20, fig. 20, August 16, 1901.

*Protothaca jodoensis hirasei* Pilsbry, *Hirase, Coll. Jap. Shells*, (Matsumura Sanshodo: Tokyo, Japan), 1934, p. 22, pl. 41, fig. 3.

Genus *Anomalocardia* Schumacher.

*Anomalocardia* Schumacher, Essai nouv. Syst. Vers Test., 1817, pp. 44, 134, pl. 20, fig. 4. Sole Species, "*Venus flexuosa* Lin. Chemn. 6. pag. 332. Tab. 31. fig. 335."—Prashad, Siboga Exped., Monogr. 53c, 1932, Lamell., p. 260. Genotype: *Anomalocardia fluctuosa* Linnaeus.

*Type* (by virtual monotypy): *Venus flexuosa* Linnaeus. Illustrated by Chemnitz, Neues Syst. Conchyl.-Cab., Bd. 6, 1782, p. 332, pl. 31, fig. 335. "Es wohnet diese seltene Muschel in den ostindischen Meeren."

*Anomalocardia* appears to be closely related to *Chione*. The teeth are not bifid and diverge widely from a common center. The shells are usually rather thick and somewhat rostrate posteriorly. The sculpture consists of concentric ridges and subdued radial ribs. The lunule and escutcheon are impressed. The inner margins are crenulated and the pallial sinus is small, often angular and sometimes almost obsolete.

The three west American species in the present collection assigned to *Anomalocardia* differ somewhat in details of shape and sculpture as compared to the type of the genus, *A. flexuosa* Linnaeus. However, there are also similarities and we have therefore followed Dall and Jukes-Browne<sup>61</sup> in placing these species under *Anomalocardia*.

This genus occurs from Pliocene to Recent in Lower California and from Miocene to Recent in Peru and in the Caribbean region. It also occurs both fossil and Recent in the East Indies.

Key to the species of *Anomalocardia*.

- A. Shell with radial furrow anterior to posterior dorsal fold
  - a. Concentric sculpture usually strong over entire shell; posterior dorsal fold strong from beak to base ..... *subrugosa*
  - aa. Concentric sculpture well developed near the beak and anterior submargins only; posterior dorsal fold well developed near beak only ..... *broggi*<sup>62</sup>
- B. Shell without radial furrow anterior to posterior margin; with bifurcate radial ribs
  - a. Shell with 20-25 concentric ridges ..... *subimbricata*
  - aa. Shell with 6-8 concentric step-like ridges; tumid ..... *tumens*

*Anomalocardia subimbricata* Sowerby.

*Venus subimbricata* Sowerby, Proc. Zool. Soc. London, April 16, 1835, p. 21. "Hab. ad Portam Portreram Americae Centralis." "Found in fine sand in thirteen fathoms." Variety from "Acapulco."—Sowerby, Thes. Conch., Vol. 2, 1853, p. 711, pl. 154, figs. 35-38. Puerto Portrero, Central America. Fig. 38 from [Lower] "California."—Reeve, Conch. Icon., Vol. 14, *Venus*, 1863, species 85,

pl. 19, figs. 85a, 85b, 85c. Original locality cited.

*Type Locality*: Puerto Portrero, Costa Rica, in 13 fathoms, sand.

*Range*: La Paz, Lower California, to Paita, Peru.

*Collecting Stations*: Mexico: Banderas Bay; Chamela Bay; Passavera Island; Chamela Bay; Tenacatita Bay; Port Guatulco (195-D-2, 6, 7, 11, 14, 15), 1.5-5 fathoms, sand, algae, crushed shell, gr. sand, coral; Santa Cruz Bay; Tangola-Tangola Bay; Costa Rica: Port Parker; Port Culebra; Culebra Bay; Panama: Isla Parida, Gulf of Chiriqui, Panama.

*Description*: Shell subtrigonal, ornamented by strong concentric ridges which in large specimens may number about 20-25; radial ribs are present, these are single in the early stages of growth but soon bifurcate due to deepening of a shallow medial incised line, a low radial riblet occurs in the major interspaces; lunule cordate, bordered by an incised line, lunule and escutcheon ornamented only by lines of growth; exteriorly colored by brown radial bands and sometimes by small irregular, V-shaped or zigzag markings on a whitish background; hinge with three teeth, the anterior one narrow and close against the margin; pallial sinus very small or almost obsolete; margin crenulated but often smooth posteriorly; interior white.

A large specimen from Culebra Bay, Costa Rica, measures approximately 50 mm. in length and 45.5 mm. in height.

The shell of this species is less tumid and has many more concentric ridges than that of *Anomalocardia subimbricata tumens* Verrill. Both *Anomalocardia subimbricata* and the subspecies *tumens* differ from *A. subrugosa* Wood in lacking a decided posterior rostration and posterior dorsal groove and in possessing bifurcated radial ribs and a low radial riblet in the major interspaces.

*Anomalocardia subrugosa* Manger,<sup>63</sup> de—"Type Locality: San Quintin Bay, Lower California." described from the Pleistocene of San Quintin Bay, Lower California, was said to differ from *A. subimbricata* in the possession of concentric lamellae between the major ridges. *Venus subrugosa* Wood, 1828, is now placed in the genus *Anomalocardia*; therefore the species described by Manger, 1934, as *Anomalocardia subrugosa* requires a new name. The name *Anomalocardia mangeri* is here proposed for Manger's species.

Pilsbry & Olsson have referred the species here cited as *Anomalocardia subimbricata* to the genus *Chione*. It is not a typical form of *Anomalocardia* but on the other hand it seems as well placed here as in *Chione*.

*Distribution*: Specimens of *Anomalocardia subimbricata* were collected on beaches and dredged at depths of 1.5 to 5 fathoms, from Banderas Bay, Mexico, to the Gulf of Chiriqui, Panama. This species has a generally more southern distribution than that of the subspecies *A. subimbricata tumens*

<sup>61</sup> Jukes-Browne, A. J., Proc. Malacol. Soc. London, Vol. 11, Pt. 2, June, 1914, p. 80.

<sup>62</sup> Not represented in the present collection.

<sup>63</sup> *Anomalocardia subrugosa* Manger, Johns Hopkins Studies in Geol., No. 11, 1934, p. 299, pl. 21, figs. 3 and 4.

and occurs chiefly south of the Gulf of California. It also has been recorded as occurring from Pliocene to Recent in the Gulf of California region, in the Quaternary of Ecuador and in the Pleistocene of Peru.

Specimens from the West Falkland Islands in the south Atlantic Ocean were identified as "*Cryptogramma subimbricata*" by Melvill & Standen<sup>64</sup> who stated that the occurrence was adventitious. If correctly identified that no doubt would be the right interpretation because that locality is far beyond the range of the present species, which inhabits warm water.

***Anomalocardia subimbricata tumens* Verrill.**

*Chione tumens* Verrill, *Amer. Jour. Sci.*, Vol. 49, No. 146, March, 1870, p. 222. "La Paz,—Capt. J. Pedersen."

*Type Locality*: La Paz, Lower California, Mexico.

*Range*: Magdalena Bay, Lower California, to the Gulf of California.

*Collecting Stations*: Mexico: Cerralbo Island, Gulf of California; Cape San Lucas, Lower California.

*Description*: Shell rather tumid; ornamentation similar to that of *Anomalocardia subimbricata* except that there are only about 6-8 heavy, concentric, step-like ridges.

Judging from the illustration and the description there appear to be but slight differences between *Chione* (*Chione*) *vaca* Olsson,<sup>65</sup> described from the Pliocene of Panama, and *Anomalocardia subimbricata tumens*.

*Distribution*: *Anomalocardia subimbricata tumens* appears to be confined to the Gulf of California and the southern part of the west coast of Lower California. There is overlapping in the ranges of this subspecies and *A. subimbricata* but the two forms, for the most part, appear to be readily separable.

***Anomalocardia subrugosa* Wood.**

*Venus subrugosa* W. Wood, *Index, Test.*, Suppl., *Venus*, 1828, p. 5, pl. 2, fig. 6. "Panama."—Sowerby, *Gen. Rec. and Foss. Shells*, No. 41, 1834, pl. 250, fig. 2, pl. 251, fig. 5.—Reeve, *Conch. Icon.*, Vol. 14, *Venus*, 1863, species 86, pl. 19, fig. 86. West Colombia (Cuming).

Not *Venus subrugosa* Bronn, *Ergeb. Nat. Reisen*, Vol. 2, 1831, p. 607.

*Anomalocardia subrugosa* Sowerby, *Dall, Proc. U. S. Nat. Mus.*, Vol. 37, 1909, pp. 158, 269, pl. 26, fig. 3. Gulf of California to Valparaiso, Chile.—Pilsbry & Lowe, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 84, 1932, p. 134. Localities cited from Guaymas, Mexico, to Santa Elena Bay, Costa Rica.

Not *Anomalocardia subrugosa* Manger, 1934. [= *Anomalocardia mangeri* nom. nov.].

*Type Locality*: Magdalena Bay to the Gulf

<sup>64</sup> Melvill, J. C., and Standen, R., *Ann. & Mag. Nat. Hist.*, Ser. 8, Vol. 13, 1914, p. 133.

<sup>65</sup> *Chione* (*Chione*) *vaca* Olsson, *Bull. Amer. Paleol.*, Vol. 27, Bull. No. 106, December 25, 1942, p. 192 (40), pl. 18 (6), fig. 7. "Rio La Vaca. Quebrada Melissa." Panama. Pliocene.

of California and south to Boca Pan near Zorritos, Peru. To Valparaiso, Chile (Dall).

*Collecting Stations*: Mexico: Cape San Lucas, Lower California; Chamela Bay; Tenacatita Bay; Nicaragua: Potosi and Monypenny Point; Corinto (200-D-19), 3 fathoms, mud, mangrove leaves, also beach, Castanones peninsular lagoon and Isla Encantada; Costa Rica: Port Parker; Culebra Bay; Port Culebra; Jasper Island; Panama: Bahia Honda; Colombia: Gorgona Island.

*Description*: Shell triangularly ovate, somewhat rostrate posteriorly; ornamented by numerous concentric ridges which are crossed by fine incised radial lines; a shallow radial groove from the beak to the ventral margin is present just anterior to the posterior margin; the lunule which is cordate and bounded by a fine incised line and the escutcheon which is elongate are both ornamented only by lines of growth; exteriorly a white or cream colored background is nearly always crossed by 3 (occasionally 4) dark radial rays; hinge with three cardinal teeth in each valve; pallial sinus very short; margin finely crenulated; interior dorsal area purplish-black, the remainder white or with purple areas.

A large specimen from Port Parker, Costa Rica, measures approximately 46 mm. in length.

The presence of a well developed posterior dorsal radial groove easily serves to separate this species from *Anomalocardia subimbricata*. Some of the large nearly smooth specimens collected at Port Parker, Costa Rica, are very similar to *A. broggi* Pilsbry & Olsson<sup>66</sup> which was described from Peru. A well developed posterior dorsal fold and groove is present from beak to base on the present specimens. According to Pilsbry & Olsson a corresponding fold is well developed only near the beaks on *A. broggi* but is otherwise absent or feebly developed. Their species was described as possessing well developed concentric sculpture only near the beaks and on the anterior submargins.

*Anomalocardia paziana* Fischer<sup>67</sup> was described from Panama but it was not stated whether from the east or west coast of that country. The other species described in the same article are from east American waters. The illustration is that of a small elongated posteriorly rostrate form with concentric ridges and a posterior radial depression. We have not seen any west American specimens that could be referred to it but it bears some resemblance to *A. cuneiformis* Conrad, an east American species. Two species occurring fossil in western South America have been described, *Anomalocardia anomiana* Olsson from the Miocene of Peru, and *A. callistoides* Pilsbry & Olsson from the Pliocene of Ecuador.

<sup>66</sup> *Anomalocardia broggi* Pilsbry & Olsson, *Nautilus*, Vol. 56, No. 3, January, 1943, p. 78, pl. 8, fig. 7. Type "from Bayovar, Sechura, north Peru." Also, Zaramilla, Peru.

<sup>67</sup> *Anomalocardia paziana* Fischer, *Journ. de Conchyl.*, Vol. 7, 1858, p. 186, pl. 7, figs. 9, 10. "Hab. Panama (Paz). Coll. du Journal."

*Distribution:* *Anomalocardia subrugosa* was collected on beaches and in shallow water from Cape San Lucas to Colombia. It has been recorded as occurring in the Pleistocene of Lower California and in the Quaternary of Peru.

### Genus *Compsomyax* Stewart.

#### *Compsomyax subdiaphana* Carpenter.

*Clementia subdiaphana* Carpenter, *Rept. Brit. Assoc. Adv. Sci.* for 1863 (issued August, 1864), pp. 602, 607, 640. "Vancouver]. Is." Reprint in *Smithson. Miscell. Coll.*, No. 252, 1872, pp. 88, 93, 126.—Dall, *Proc. U. S. Nat. Mus.*, Vol. 14, 1891, p. 185, pl. 7, figs. 5 and 6. Cited from Port Etches, Alaska, in 14-60 fathoms, to off Drake's Bay, California, in 24 fathoms.

*Marcia subdiaphana* Carpenter, I. S. Oldroyd, *Stanford Univ. Publ. Univ. Ser. Geol. Sci.*, Vol. 1, 1924, p. 155, pl. 33, fig. 3; pl. 38, fig. 1. Range, Sannakh Islands, Alaska, to Santa Barbara Islands and San Pedro, California.

*Clementia (Compsomyax) subdiaphana* Carpenter, Grant & Gale, *Mem. San Diego Soc. Nat. Hist.*, Vol. 1, 1931, p. 334, pl. 17, figs. 10a, 10b, ?15. Earlier records cited. Miocene to Recent.

*Type Locality:* Vancouver Island, British Columbia.

*Range:* Sannakh Islands, Alaska, to Cedros Island, Lower California.

*Collecting Station:* Mexico: East of Cedros Island (126-D-3, 4), 40 fathoms, mud.

*Description:* Shell elongately ovate, varying in outline and ventricosity, beaks anterior and pointing forward; sculpture consisting of fine concentric lines of growth; lunule broad, faintly defined; hinge with three cardinal teeth in each valve, the right posterior cardinal deeply bifid; pallial sinus ascending and extending forward less than one-half the length of the shell; interior margins smooth.

A very large specimen from Port Ludlow, Washington, in Puget Sound, in the Hemphill collection of the California Academy of Sciences, measures, 68.8 mm. in length, 58 mm. in height, and 40.3 mm. in convexity (both valves).

*Distribution:* Four specimens of this species were dredged by the expedition east of Cedros Island in 40 fathoms. The occurrence of the species at this locality is an extension south of the known range. It is known to occur from Pliocene to Recent in western America and perhaps also in the Miocene.

### Genus *Protothaca* Dall.

Key to the subgenera of *Protothaca*.

- A. Escutcheon well developed on left valve  
*Protothaca s.s.*<sup>68</sup>  
 B. Escutcheon lacking or nearly so on left valve ..... *Callithaca*

### Subgenus *Callithaca* Dall.

Key to the species of *Callithaca*.

- A. Pallial sinus extends forward more than ½ the length of the shell ..... *staminea*  
 B. Pallial sinus extends forward less than ½ the length of the shell ..... *grata*

#### *Protothaca (Callithaca) grata* Say.

*Venus grata* Say, *Amer. Conch.*, No. 3, September, 1830, [pages of text not numbered] pl. 26, [three figures] . . . "West coast of Mexico."—Reeve, *Conch. Icon.*, Vol. 14, *Venus*, 1863, species 8, pl. 3, figs. 8a, 8b. [Not the locality "Gulf of Mexico"].

*Venus histrionica* Sowerby, *Proc. Zool. Soc. London*, June 1, 1835, p. 41. "Hab. apud Real Llejos, Americae Centralis, et ad Sanctam Elenam." "Found in muddy sand at low water."—Sowerby, *Thes. Conch.*, Vol. 2, 1853, p. 714, pl. 155, fig. 52. "Found in sandy mud at a depth of thirteen fathoms, Guacomo, Central America. Cuming."

*Venerupis (Protothaca) grata* Say, Grant & Gale, *Mem. San Diego Soc. Nat. Hist.*, Vol. 1, 1931, p. 323. Earlier references cited. Pleistocene and Recent.

*Type Locality:* West coast of Mexico.

*Range:* Cape Colnett, west coast of Lower California (Lowe), to the Gulf of California and south to Antofogasta, Chile.

*Collecting Stations:* Mexico: Banderas Bay; Tangola-Tangola Bay; Nicaragua: Potosi and Monypenny Point; Isla Encantada and Isla Cardon, Corinto; San Juan del Sur; Costa Rica: Port Parker; Culebra Bay; Ballenas Bay; Golfito Bay; Panama: Isla Parida; Colombia: Gorgona Island.

*Description:* Shell elongately ovate, often 30-50 mm. in length, moderately inflated, ornamented by many flattish radial ribs which are coarser anteriorly, separated by narrow interspaces and both crossed by usually weaker concentric imbrications and irregularities due to growth; lunule cordate or elongated, ornamented by fine, radial ribs; escutcheon absent or only slightly developed, ligament deeply sunken; the color pattern varies greatly from blackish-brown to striped or checked brown and white to almost wholly white; the middle cardinals and usually the right posterior cardinal grooved; pallial sinus ascending, end rounded or roundly pointed, directed toward center of anterior adductor impression, projecting about one-third the distance between the two impressions; margin crenulated; color of interior white and purple or often wholly purple.

Specimens of this species are usually about 40 mm. in length but a large specimen in the collection of the California Academy of Sciences is 50 mm. in length. In this specimen the pallial sinus projects anteriorly 21 mm. from the posterior margin.

The shell of *Protothaca grata* differs from that of *P. staminea* Conrad in the shorter pallial sinus, brighter color patterns and in the generally smaller size. This species has received many different names in the literature due in great part to the variable color

<sup>68</sup> Not represented in the present collection.

pattern. Grant & Gale (1931) have cited many of the names now placed in the synonymy of this species.

The almost complete absence of an escutcheon, smaller lunule, less rasp-like sculpture of the ribs, usually more inflated shell and narrower hinge plate are features which serve to separate *Protothaca grata* from *Chione asperrima* Sowerby.

Some specimens of this species bearing a small escutcheon on the left valve are strongly suggestive of the subgenus *Nioche* but on most of these shells the left anterior cardinal is less elongate and the hinge plate is narrower than it is in typical species of that subgenus.

*Distribution*: This species was collected at many localities, usually between tides, from west Mexico to Colombia. It has been reported as occurring in the Pleistocene of Magdalena Bay, Lower California, and in the Pliocene of the Galápagos Islands.

***Protothaca (Callithaca) staminea* Conrad.**

*Venus staminea* Conrad, *Jour. Acad. Nat. Sci. Philadelphia*, Vol. 7, 1837, p. 250, pl. 19, fig. 15. "Inhabits the coast of California, with the above" [that is, *Venus nuttalli* from "Sta. Barbara, and Sta. Diego"].

*Paphia staminea* Conrad, I. S. Oldroyd, *Stanford Univ. Publ. Univ. Ser. Geol. Sci.*, Vol. 1, 1924, p. 156, pl. 35, figs. 1a, 1b. Range, Commander and Aleutian Islands to Puget Sound and Socorro Island, Japan. Also Miocene to Recent.

*Venerupis (Protothaca) staminea* Conrad, Grant & Gale, *Mem. San Diego Soc. Nat. Hist.*, Vol. 1, 1931, p. 329, pl. 18, figs. 1a, 1b, 2a, 2b. Earlier records cited. Miocene to Recent.

*Type Locality*: San Diego, California (here designated as type locality). Santa Barbara and San Diego, California, indicated at the time of original description.

*Range*: Aleutian Islands to Cape San Lucas, Lower California. Socorro Island (Dall).

*Collecting Station*: Mexico: Cape San Lucas, Lower California.

*Description*: Shell elongately ovate, often 40 to 65 mm. in length, moderately inflated, ornamented by radial and concentric sculpture, the radial usually the stronger; lunule lanceolately cordate, sometimes only faintly defined; color yellowish-gray with varying amounts of wavy brown concentric lines or spots; ligament sunken, escutcheon absent or only faintly indicated; right posterior and middle teeth of both valves grooved; pallial sinus long, rather narrow, rounded at the end or blunt, projecting anteriorly more than one-half the distance between the two adductor impressions; margin crenulated; color of interior usually white but some southern specimens are partly purple and white.

A large specimen of this species in the collection of the California Academy of Sciences collected by Henry Hemphill at Turtle

Bay, Lower California, measures: length, 75.5 mm.; height, 64 mm.; convexity (both valves) 44.5 mm.; pallial sinus projects anteriorly 44 mm. from the posterior margin.

The longer pallial sinus, less brilliant and less variable color pattern and the generally larger size all serve to separate *Protothaca staminea* from *P. grata* Say.

Smith<sup>69</sup> has discussed the ecology and growth of *Protothaca staminea*.

*Distribution*: A single specimen of this species was collected on the beach at Cape San Lucas, Lower California. In California the species has been recorded from upper Miocene to Recent. It has been pointed out by Keen<sup>70</sup> that the species recorded from Japan under the name of *P. staminea* can be referred to *P. euglypta* Sowerby. Bales<sup>71</sup> cited *P. staminea* from Acapulco but we have not seen specimens from south of Cape San Lucas. Eyerdam<sup>72</sup> cited it from Arica, Peru, but it seems probable that the South American record can be referred to *P. thaca* Molina or some other species.

Genus *Irus* Oken.

Key to the subgenera of *Irus*.

- A. Lunule bounded by an incised line; margin crenulated ..... *Paphonotia*
- B. Lunule not bounded by an incised line; margin smooth ..... *Irus* s.s.<sup>73</sup>

Subgenus *Paphonotia* Hertlein & Strong, subgen. nov.

*Type*: *Petricola elliptica* Sowerby, 1834.

Shell variable in shape but usually elliptically oblong, beaks anteriorly situated, rather compressed; sculptured with rather distantly spaced concentric lamellae and fine radial riblets which are usually reduced or lacking on the posterior area; lunule defined by an incised line; escutcheon usually well defined on the left valve; teeth small, hinge of left valve with a posterior cardinal moderately strong and fused to the margin, middle cardinal shorter and strongly grooved, anterior cardinal longer than middle tooth and slanting strongly forward; hinge of right valve with posterior and median cardinals about the same length, the median one grooved, and an anterior cardinal almost parallel to the lunular margin; pallial sinus ascending, angular, usually not extending quite to the middle of the shell; exterior usually whitish, interior white, posteriorly brown and often the anterior adductor impression and hinge brown, and sometimes the interior of the shell is wholly brown.

Compared to *Irus* s.s., which has as type *Donax irus* Linnaeus, the shell of *Paphonotia* has the lunule delimited by a well marked in-

<sup>69</sup> Smith, G. M., *Trans. Roy. Soc. Canada*, Sect. 5, Vol. 27, 1933, pp. 229-245.

<sup>70</sup> Keen, A. M., *Sixth Pac. Sci. Congress*, Vol. 3, 1941, p. 480.

<sup>71</sup> Bales, B. R., *Nautilus*, Vol. 52, No. 2, 1938, p. 45.

<sup>72</sup> Eyerdam, W. J., *Nautilus*, Vol. 53, No. 3, 1940, p. 108.

<sup>73</sup> Not represented in the present collection.

cised line, the teeth are more diverging, the inner margin is crenulated and the pallial sinus is angular. Grant & Gale, 1931, pointed out that some west American shells referred to the genus *Venerupis* Lamarck, which has as type *Venus perforans* Montagu, bear considerable resemblance to some species referred to *Irus*.

The species described as *Petricola elliptica* by Sowerby has been referred by some writers to *Petricola* and by others to *Venerupis*. It does not seem to be exactly referable to either of those genera. Some of the specimens in the present collection possess features in common with *Venerupis elegans* Deshayes, the type of *Notopaphia* Oliver<sup>74</sup> as illustrated by Marwick. The west American species possesses different sculpture and appears to differ in some other details and therefore we have thought it desirable to propose a new subgeneric name *Paphonotia*<sup>75</sup> with *Petricola elliptica* Sowerby as type.

The similarity of *Paphonotia* to *Notopaphia* of New Zealand is not surprising when it is recalled that *Protothaca* is present in New Zealand (Marwick, 1927, p. 623). Furthermore it appears that the west American species *Chione fluctifraga* Sowerby is very similar to the New Zealand species, *Venus stutchburyi* Gray, and may perhaps be referable to the same subgenus, *Austrovenus* Marwick<sup>76</sup>.

#### *Irus (Paphonotia) ellipticus* Sowerby.

*Petricola elliptica* Sowerby, *Proc. Zool. Soc. London*, September 26, 1834, p. 46. "Hab. ad Paytam." "Found in hard mud at low water."—Sowerby, *Thes. Conch.*, Vol. 2, 1854, p. 774, pl. 164, fig. 3; pl. 166, fig. 10. Original locality cited.—Sowerby, *Conch. Icon.*, Vol. 19, *Petricola*, 1874, species 12, pl. 2, fig. 10. Original locality cited.

*Venerupis elliptica* Sowerby, *Lamy, Journ. de Conchyl.*, Vol. 67, No. 4, 1923, p. 306, two figs. p. 307. Peru.

*Petricola solida* Sowerby, *Proc. Zool. Soc. London*, September 26, 1834, p. 46. "Hab ad oras Peruviae. (Lambeyeque)." "Found in hard clay and stones at low water."—Sowerby, *Thes. Conch.*, Vol. 2, 1854, p. 774, pl. 166, fig. 9. Original locality cited.—Sowerby, *Conch. Icon.*, Vol. 19, *Petricola*, 1874, species 15, pl. 2, fig. 15. Original locality cited.

*Petricola solidula* Sowerby, *Thes. Conch.*, Vol. 2, 1854, p. 770, pl. 164, fig. 17.

*Type Locality*: Paita, Peru, at low water, in hard mud.

*Range*: Tangola-Tangola Bay, Mexico, to Arica, Chile.

<sup>74</sup> *Notopaphia* Oliver, *Proc. Malacol. Soc. London*, Vol. 15, Pt. 4, March, 1923, p. 185. Type: *Venerupis elegans* Deshayes, fig. p. 185. [Originally described in *Proc. Zool. Soc. London* for 1853 (issued June 27, 1854), p. 5, pl. 18, figs. 2a, 2b, 2c. "Hab. New Zealand. Coll. Cuming].—Marwick, *Trans. New Zealand Inst.*, Vol. 57, February 12, 1927, p. 662. Type: *Venerupis elegans* Deshayes. Illustrated on pl. 49, figs. 174, 176, 177. New Zealand.

<sup>75</sup> *Paphonotia*, an anagram of *Notopaphia*.

<sup>76</sup> *Austrovenus* Marwick, *Trans. New Zealand Inst.*, Vol. 57, February 12, 1927, p. 620. "Type: *Venus stutchburyi* Gray." Illustrated on pl. 47, figs. 158, 159, 160. Recent, also fossil in New Zealand.

*Collecting Station*: Nicaragua: Corinto (200-D-19), 12-13 fathoms, mangrove leaves.

*Description*: Shell elliptically oblong, beaks in front of the middle, rather compressed; ornamented by rather distantly spaced concentric lamellae and by moderately fine, closely spaced radial ribs which however, are usually much reduced or lacking on the posterior area; lunule defined by an impressed line; right posterior and middle tooth and left middle tooth are medially grooved; pallial sinus angular, ascending, not reaching quite the middle of the shell; interior brown and white or almost wholly brown; margin crenulated.

The specimens of this species in the present collection are small, not over 10 mm. in length, but large specimens attain a length of 26 mm. or more.

The shell of this species is variable in shape due to the fact that it lives in holes in rocks. Some young specimens that are elliptical in shape later develop into forms vertically truncated posteriorly. The strongly frilled and squarely truncated form was named *Venerupis foliacea* by Deshayes<sup>77</sup>. It appears to be of not more than subspecific value. Dall, 1902, stated that synonyms of this form include *Tapes squamosa* Carpenter, 1857, *Venus troglodytes* Mörch, 1861, and perhaps *Venerupis paupercula* Deshayes, 1853.

The species described as *Venerupis oblonga* Sowerby<sup>78</sup> appears to be a very similar form but may differ in possessing stronger radial ornamentation on the posterior portion of the valves.

*Distribution*: Specimens of this species were dredged by the expedition at Corinto, Nicaragua, in 12-13 fathoms. It has been reported as ranging south to Chile. The subspecies *foliaceus* has been recorded as occurring north to Mazatlan, Mexico.

#### Genus *Psephidia* Dall.

##### *Psephidia cymata* Dall.

*Psephidia cymata* Dall, *Proc. U. S. Nat. Mus.*, Vol. 45, No. 2002, June 11, 1913, p. 593. "Near Cerros Island, Lower California, in shallow water."—Dall, *U. S. Nat. Mus., Bull.* 112, 1921, p. 44, pl. 3, fig. 2. Santa Barbara Islands, California, to the Gulf of California.

*Type Locality*: Near Cedros Island, Lower California, in shallow water.

*Range*: Santa Barbara Islands, California, to the Gulf of California.

<sup>77</sup> *Venerupis foliacea* Deshayes, *Proc. Zool. Soc. London* for 1853 (issued June 27, 1854), pl. 18, figs. 5a, 5b. [Without description].—Sowerby, *Thes. Conch.*, Vol. 2, 1854, p. 764, pl. 164, figs. 8, 9. "Mazatlan." Not *Venus foliacea* Philippi, 1846.

<sup>78</sup> *Petricola oblonga* Sowerby, *Proc. Zool. Soc. London*, September 26, 1834, p. 46. "Hab ad oras Peruviae. (Pacos-mayo)." "Found in hard mud at low water."—Sowerby, *Thes. Conch.*, Vol. 2, 1854, p. 765, pl. 165, fig. 21 (as *Venerupis oblonga*). Original locality cited.

*Venerupis fernandesiana* Stenpell (*Zool. Jahrb., Suppl. Bd. 5, Fauna Chilensis. Bd. 2, Heft 1, December 20, 1898, p. 237, pl. 12, figs. 22, 23.* "Fundort: Zahlreiche Exemplare aus Juan Fernandez (Bahia Cumberland)"), was questionably referred to *V. oblonga* by Dall.

*Collecting Station:* Mexico: East of Cedros Island (126-D-12), 45 fathoms, crushed shell, mud.

*Description:* Shell small, about 6 mm. in length and 5.5 mm. in height; white, rounded triangular, somewhat anterior beaks; lunule and escutcheon feebly indicated; ornamented by fine concentric low thread-like sculpture; interior polished; three cardinals in each valve; pallial sinus small, ascending, inner extreme bluntly rounded; inner margin smooth; periostracum yellowish, rather coarse (adapted from Dall).

*Distribution:* A few somewhat worn specimens dredged east of Cedros Island in 45 fathoms appear to be referable to this species. It also has been recorded as occurring in the Pleistocene of Lower California.

#### FAMILY PETRICOLIDAE.

Genus *Petricola* Lamareck.

Key to the subgenera of *Petricola*.

- A. Radial sculpture nearly uniform over shell ..... *Petricola* s.s.  
 B. Radial sculpture much coarser anteriorly; subcylindrical ..... *Petricolaria*

Subgenus *Petricola* s.s.

Key to the species of *Petricola* s.s.

- A. Shell usually attenuated posteriorly; radial sculpture strong ..... *robusta*  
 B. Shell usually subquadrate or subrounded; radial sculpture fine  
 a. Length usually not exceeding 12 mm. .... *tellimyalis*<sup>79</sup>  
 aa. Length exceeding 12 mm.  
 b. Interior white ..... *carditoides*<sup>79</sup>  
 bb. Interior blackish-brown *lucasana*

*Petricola (Petricola) lucasana* Hertlein & Strong, sp. nov.

Plate II, Figures 4 and 9.

Shell oblong, subquadrate or subrounded, thick; ornamented by fine radial riblets; exterior white with bluish tinged concentric areas and reddish or brown near the beaks; interior blackish-brown, sometimes whitish under the umbos; pallial sinus short, broad, rounded; margin smooth; hinged normal for the genus. Dimensions: length, 24.6 mm.; height, 25 mm.; convexity (both valves), 16.6 mm.

Holotype, (Calif. Acad. Sci. Paleo. Type Coll.), from Cape San Lucas, Lower California, Mexico.

This species, in some cases, has been referred to *Petricola robusta* Sowerby but it differs from that species in the oblong or subquadrate shape of the shell which does not taper posteriorly and is less inflated anteriorly, the thicker shell, and in the much finer and nearly uniform radial sculpture. Specimens of *Petricola robusta* dredged by G. D. Hanna and E. K. Jordan in 10 fathoms at Maria Madre Island, Tres Marias group, agree exactly with Sowerby's illustrations

of that species and show it to be quite different from the present species.

This new species resembles *Petricola carditoides* Conrad<sup>80</sup> which has been reported as ranging from Vancouver Island, British Columbia, to Magdalena Bay, Lower California, but differs in the slightly coarser sculpture, blackish-brown interior and whitish and dark orange brown exterior.

This species occurs in the Gulf of California, at least as far north as Punta Penasco, Sonora, Mexico, where it was collected by H. N. Lowe.

*Petricola (Petricola) robusta* Sowerby.

*Petricola robusta* Sowerby, *Proc. Zool. Soc. London*, September 26, 1834, p. 47. "Hab. ad Panamam et ad Insulam Muerte dictam." "Found in rocks at the depth of from six to eleven fathoms."—Sowerby, *Thes. Conch.*, Vol. 2, 1854, p. 775, pl. 166, figs. 16, 17. "In rocks, six to eleven fathoms, at Panama. Cuming."—Sowerby, *Conch. Icon.*, Vol. 19, *Petricola*, 1874, species 20, pl. 3, figs. 20a, 20b. Panama.—Lamy, *Journ. de Conchyl.*, Vol. 67, No. 4, 1923, p. 330. Gulf of California and Panama.

*Type Locality:* Panama (here designated as type locality). Island of Muerte also cited originally.

*Range:* Gulf of California to Guayaquil, Ecuador.

*Collecting Stations:* Mexico: Tangola-Tangola Bay; Nicaragua: Corinto (200-D-19), 12-13 fathoms, mangrove leaves.

*Description:* Of a dull orange tint, with purple at the apices and blackish inside, rather thick, very globose in front, tapering behind, where the valves are unequal, the right valve slightly overwrapping. The radiating striae are distant, numerous, and close in front, but towards the back become separated, strong, acute; the hinder ones of all are a little smaller, serrated, and their ends form a denticulated edge (Sowerby, *Thes. Conch.*).

The pallial sinus is short, broad, rounded at the end; hinge normal for the genus.

*Petricola sinuosa* Conrad, 1849. *P. bulbosa* Gould, 1851, and *P. venusta* De Folin, 1867, are names now relegated to the synonymy of *P. robusta*.

*Petricola typica* Jonas, a Caribbean species, has a similar shell but the interior is white. *Petricola riocanensis* Maury, 1917, described from the Miocene of Santo Domingo, is also a similar species.

*Distribution:* A few specimens, mostly young, referred to this species, were taken off west Mexico and Nicaragua. This species has been recorded from South Africa but as pointed out by Bartsch<sup>81</sup> it does not occur in that region.

<sup>80</sup> *Soxycava carditoides* Conrad, *Jour. Acad. Nat. Sci. Philadelphia*, Vol. 7, 1837, p. 255, pl. 20, fig. 8. "Inhabits California near Sta. Barbara, where a single valve was collected."

*Petricola carditoides* Conrad, I. S. Oldroyd, *Stanford Univ. Publ. Univ. Ser. Geol. Sci.*, Vol. 1, 1924, p. 163, pl. 34, figs. 6a, 6b. Range, Vancouver Island to Lower California.

<sup>81</sup> Bartsch, P., *U. S. Nat. Mus., Bull.* 91, 1915, p. 247.

<sup>79</sup> Not represented in the present collection.

Subgenus *Petricolaria* Stoliczka.Key<sup>82</sup> to the species of *Petricolaria*.

- A. A flattened lunule-like area present
- a. Height nearly one-half the length
    - b. Teeth in right valve massive; shell fairly thick ..... *cognata*<sup>83</sup>
    - bb. Teeth in right valve moderately fine; lunule-like area and nymphs narrower ..... *pholadiformis*<sup>83</sup>
  - aa. Height about one-third the length or less ..... *parallela*
- B. Lunule-like area lacking
- a. Anterior end evenly rounded; pallial sinus rounded at end; shell thin ..... *californiensis*<sup>83</sup>
  - aa. Anterior end tapering to a narrow point; pallial sinus angular, tapering to a point; shell fairly thick, partly purplish-brown ..... *denticulata*<sup>83</sup>

*Petricola (Petricolaria) parallela*

Pilsbry &amp; Lowe.

*Petricola gracilis parallela* Pilsbry & Lowe, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 84, May 21, 1932, p. 99, pl. 13, figs. 4, 5, 5a, 6. "Nicaragua: Corinto (Lowe)." Type.

*Type Locality*: Corinto, Nicaragua.

*Range*: Scammon Lagoon, Lower California, to the Gulf of California and south to Corinto, Nicaragua.

*Collecting Station*: Nicaragua: Corinto (200-D-11), 8 fathoms, sand.

*Description*: Shell very elongated, dorsal and ventral margins nearly parallel; sculptured with 11-13 coarse, nodulous ribs on the anterior half, posteriorly the ribs diminish to radial striae; lunular region somewhat excavated and ornamented by fine growth lamellae; pallial sinus long, of equal width throughout, rounded at end.

The specimen in the present collection is only about 24 mm. long but agrees exactly with larger shells of this species.

*Petricola parallela* is very similar to *Petricola gracilis* Deshayes<sup>84</sup>, a species originally described without information as to the locality from which it came. As pointed out by Pilsbry & Lowe there are differences in the shape, ribbing and apparently in the pallial sinus of the two forms.

Compared to *Petricola pholadiformis* Lamarck, an east American species, the shell of the present species is more elongated and the dorsal and ventral margins are more nearly parallel.

Some of the records of *Petricola cognata*

C. B. Adams cited<sup>85</sup> from the Gulf of California region undoubtedly can be referred to *P. parallela*. *Petricola cognata* C. B. Adams<sup>86</sup> was described from Panama. Pilsbry & Lowe illustrated the type and stated that it resembles *P. pholadiformis* Lamarck but differs in possessing more massive teeth in the right valve, broader nymphs and in the wider lunule-like area free of radiating sculpture.

*Distribution*: A single small specimen of this species was dredged in 8 fathoms at Corinto, Nicaragua. It also has been cited<sup>87</sup> as occurring in the Pleistocene of the Newport Bay region in southern California.

## FAMILY COOPERELLIDAE.

Genus *Cooperella* Carpenter.

*Oedalia* Carpenter, Rept. Brit. Assoc. Adv. Sci. for 1863, issued August, 1864, pp. 611, 639. "*Oedalia (Cooperella) scintillaeformis*, n. subgen., n.s." (p. 611) [No description]; "*Oedalia subdiaphana*, n. g., n.s." (p. 639) [Description]. Reprint in *Smithson. Miscell. Coll.*, No. 252, 1872, pp. 97, 125.—Carpenter, *Journ. de Conchyl.*, Vol. 12 (Ser. 3, Vol. 5), April, 1865, p. 134. "*Oedalia*, n.g." [*Oedalia subdiaphana* described]. Reprint in *Smithson. Miscell. Coll.*, No. 252, 1872, p. 134.

Not *Oedalia* Meigen, 1820. Dipt.

*Cooperella* Carpenter, Rept. Brit. Assoc. Adv. Sci. for 1863 issued August, 1864, pp. 611, 639. "*Oedalia (Cooperella) scintillaeformis*, n. subgen., n. s." (p. 611) [no description]; "*Cooperella scintillaeformis*, n. s. New subgenus of *Oedalia*" (p. 639) [no description]. Reprint in *Smithson. Miscell. Coll.* No. 252, 1872, pp. 97, 125.—Dall, *Trans. Wagner Free Inst. Sci.*, Vol. 3, Pt. 5, December, 1900, p. 1061. "The type *Cooperella subdiaphana* (+ *scintillaeformis*) Cpr."

Not *Cooperella* Gunnell, *Jour. Paleo.*, Vol. 7, No. 3, 1933, p. 291. Pisces.

*Oedalina* Carpenter, *Proc. Calif. Acad. Nat. Sci.*, Vol. 3, February, 1865, p. 208. New name for *Oedalia* Carpenter, preoccupied.—Lamy, *Journ. de Conchyl.*, Vol. 61, No. 3, 1914, p. 301.

*Type* (by monotypy): *Cooperella scintillaeformis* Carpenter.

Shell small, very thin, white, ovately rectangular, moderately inflated, beaks a little anterior, smooth or concentrically striated; resilium narrow, depressed, behind and separated from the teeth by a thin plate; hinge of right valve with 2 cardinals, left valve with 3 cardinal teeth, the left middle and usually the right posterior, and frequently the other teeth, bifid; pallial sinus deep, wide, broadly rounded at the end; margins smooth.

<sup>85</sup> *Petricola cognata* C. B. Adams, E. K. Jordan, *Bull. South. Calif. Acad. Sci.*, Vol. 23, Pt. 5, September-October (issued October 25), 1924, p. 163. The record "Scammon's Lagoon," Lower California, can be referred to *P. parallela*.

<sup>86</sup> *Petricola cognata* C. B. Adams, *Ann. Lyceum Nat. Hist. New York*, Vol. 5, July, 1852, pp. 510, 546 (separate pp. 286, 322). "Habitat.—Panama."—Pilsbry & Lowe, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 84, 1932, p. 99, pl. 13, figs. 10, 11. Figure of type, Panama.

<sup>87</sup> See Bruff, S. C., *Univ. Calif. Publ., Bull. Dept. Geol. Sci.*, Vol. 27, No. 6, 1946, p. 232.

<sup>82</sup> Adapted from Pilsbry & Lowe.

<sup>83</sup> Not represented in the present collection.

<sup>84</sup> *Petricola gracilis* Deshayes, *Cat. Conchif. or Bivalve Shells in Coll. Brit. Mus.*, Pt. 1, 1853, p. 214. "Hab. —? Coll. Cuming."—Deshayes, *Proc. Zool. Soc. London* for 1853 (issued June 27, 1854), pl. 18, figs. 9, 9a. [No description].—Sowerby, *Thes. Conch.*, Vol. 2, 1854, p. 772, pl. 166, fig. 12. "Hab. —? Cuming's collection."—Lamy, *Journ. de Conchyl.*, Vol. 67, No. 4, 1923, p. 344.

This genus has been recorded as occurring from Miocene to Recent in the Caribbean region and Pleistocene and Recent in the eastern Pacific. One species, "*Oedalina asiatica*" Melvill, 1899, doubtfully referred to the genus, was described from the Arabian Sea.

A subgenus, *Cooperellopsis* Woodring<sup>88</sup>, 1925, described from the Miocene of Bowden, Jamaica, possesses a subequilateral, strongly inflated shell in which the left middle cardinal is only obscurely bifid rather than strongly so as in *Cooperella* s.s.

***Cooperella subdiaphana* Carpenter.**

*Oedalia subdiaphana* Carpenter, Rept. Brit. Assoc. Adv. Sci. for 1863 (issued August, 1864), p. 639. Region between San Diego and San Pedro, California. Also Santa Barbara Islands, California. Reprint in *Smithson. Miscell. Coll.*, No. 252, 1872, p. 125.—Carpenter, *Journ. de Conchyl.*, Vol. 12 (Ser. 3, Vol. 5), April, 1865, p. 134. "Hab. San Diego, Cassidy."

*Oedalia (Cooperella) scintillaeformis* Carpenter, Rept. Brit. Assoc. Adv. Sci. for 1863 (issued August, 1864), p. 611. [No description]. San Diego. Santa Barbara Islands. Reprint in *Smithson. Miscell. Coll.*, No. 252, 1872, p. 97.

*Cooperella scintillaeformis* Carpenter, Rept. Brit. Assoc. Adv. Sci. for 1863 (issued August, 1864), p. 639. Region between San Pedro and San Diego, California. Also Santa Barbara Islands. Reprint in *Smithson. Miscell. Coll.*, No. 252, 1872, p. 125.—Carpenter, *Proc. Calif. Acad. Nat. Sci.*, Vol. 3, February, 1865, p. 208. "Hab. San Diego; San Pedro, 2 dredged in 8-20 fms. Cooper."

*Cooperella subdiaphana* Carpenter, Arnold, *Mem. Calif. Acad. Sci.*, Vol. 3, 1903, p. 153, pl. 13, fig. 1. Vancouver Island to Todos Santos Bay (Dall). Also San Pedro and San Diego, California, Pleistocene. — Lamy, *Journ. de Conchyl.*, Vol. 67, No. 4, 1923, pp. 313, 314, (two figs. of hinge, p. 314).

*Oedalina subdiaphana* Carpenter, Lamy, *Journ. de Conchyl.*, Vol. 61, No. 3, 1914, p. 303, (two figs. of hinge, p. 302). California.

*Type Locality*: San Diego, California

<sup>88</sup> *Cooperellopsis* Woodring, *Carnegie Institution of Washington*, Publ. 366, May 25, 1925, p. 165. "Type.—*Cooperella (Cooperellopsis) thaumastra*, new species." P. 165, pl. 22, figs. 13, 14, 15. Bowden, Jamaica, Miocene.

(cited by Carpenter, 1865, and here designated as type locality). Region between San Diego and San Pedro, California, also Santa Barbara Islands, cited originally.

*Range*: Queen Charlotte Islands, British Columbia, to San Felipe, east coast of Lower California in the Gulf of California.

*Collecting Station*: Mexico: Santa Inez Bay, Gulf of California (145-D-1-3), 4-13 fathoms, sand.

*Description*: Shell small and fragile, nearly equilateral, moderately inflated, smooth or concentrically striated; hinge typical for the genus; margins smooth; pallial sinus deep and rounded at the end.

Specimens in the present collection are about 4-6 mm. in length. A large specimen from San Diego, California, in the collections of the California Academy of Sciences, measures: length, 14.6 mm.; height, 11.6 mm.; convexity (both valves), 7.3 mm.

Dall<sup>89</sup>, 1903, gave a careful description of this species. He stated that the types of Carpenter's species "*Oedalia subdiaphana*" and *Cooperella scintillaeformis* are in the United States National Museum. He considered them to represent the same species<sup>90</sup>.

Haas<sup>91</sup> described the "nest" which this species sometimes builds.

*Cooperella atlantica* Rehder<sup>92</sup>, recently described from Florida, is said to be smaller, more translucent and more equilateral than *C. subdiaphana*. *Cooperella carpenteri* Dall, 1903, described from the Miocene of Florida, is another similar species.

*Distribution*: Three small somewhat worn single valves of this species were dredged by the expedition in Santa Inez Bay in the Gulf of California, in 4-13 fathoms. It also has been recorded as occurring in the Pleistocene of San Pedro, Playa del Rey and San Diego, southern California, and at San Quintin, Lower California.

<sup>89</sup> Dall, W. H., *Trans. Wagner Free Inst. Sci.*, Vol. 3, Pt. 5, December, 1900, p. 1062.

<sup>90</sup> Orcutt, 1919, credited Dall for the identification, and cited *Cooperella scintillaeformis* as occurring at Magdalena Bay, Lower California (*West Amer. Sci.*, Vol. 21, No. 5 (1919), 1919, p. 39).

<sup>91</sup> Haas, F., *Nautilus*, Vol. 55, No. 4, 1942, p. 113.—Haas, *Field Mus. Nat. Hist., Zool. Ser.*, Vol. 29, No. 1, 1943, p. 12 fig. 7 (a, b). Alamitos Bay, San Pedro, California.

<sup>92</sup> *Cooperella atlantica* Rehder, *Proc. U. S. Nat. Mus.*, Vol. 93, No. 3161, January 20, 1943, p. 187, pl. 19, figs. 3, 4. "dredged off Peanut Island, northern Lake Worth, Fla."

## EXPLANATION OF THE PLATES.

## PLATE I.

- FIG. 1. *Pitar (Lamelliconcha) frizzelli* Hertlein & Strong, sp. nov. Holotype, right valve, from Station 136-D-22, Lat. 23° 28' 30" N., Long. 109° 25' W., Arena Bank, Gulf of California, dredged in 45 fathoms (82 meters). Length, 46 mm., height, 33.5 mm. P. 176.
- FIG. 2. *Chione (Chione) guatulcoensis* Hertlein & Strong, sp. nov. Holotype, left valve, from Station 195-D-9, Lat. 15° 44' 28" N., Long. 96° 07' 51" W., off Port Guatulco, Mexico, dredged in 7 fathoms (12.6 meters). Length, 11.2 mm., height, 9.4 mm. P. 182.
- FIG. 3. *Pitar (Pitarella) mexicanus* Hertlein & Strong, sp. nov. Holotype, left valve, from Station 192-D-1, Lat. 16° 16' 30" N., Long. 98° 37' W., 4 miles south-southwest of Maldonado Point, Mexico, dredged in 26 fathoms (47 meters). Length, 42.3 mm., height, 33.3 mm. View of the interior. P. 171.
- FIG. 4. *Chione (Chione) guatulcoensis* Hertlein & Strong, sp. nov. Holotype. View of the interior of the right valve of the specimen shown in Fig. 2.
- FIG. 5. *Pitar (Lamelliconcha) frizzelli* Hertlein & Strong, sp. nov. Holotype. View of the exterior of the left valve of the specimen shown in Fig. 1.
- FIG. 6. *Chione (Chione) guatulcoensis* Hertlein & Strong, sp. nov. Holotype. View of the exterior of the specimen shown in Fig. 2.
- FIG. 7. *Pitar (Lamelliconcha) frizzelli* Hertlein & Strong, sp. nov. Holotype. View of the interior of the specimen shown in Fig. 5.
- FIG. 8. *Pitar (Pitarella) mexicanus* Hertlein & Strong, sp. nov. Holotype. View of the exterior of the right valve of the specimen shown in Fig. 3.
- FIG. 9. *Pitar (Hyphantosoma) aletes* Hertlein & Strong, sp. nov. Holotype, right valve, from Station 136-D-13, Lat. 23° 29' N., Long. 109° 24' W., Arena Bank, Gulf of California, in 45 fathoms (82 meters). Length, 53.8 mm., height, 46 mm. View of the interior. P. 172.
- FIG. 10. *Chione (Chione) guatulcoensis* Hertlein & Strong, sp. nov. Holotype. View of the exterior of the specimen shown in Fig. 4.
- FIG. 11. *Pitar (Hyphantosoma) aletes* Hertlein & Strong, sp. nov. Holotype. View of the interior of the left valve of the specimen shown in Fig. 9.

FIG. 12. *Pitar (Hyphantosoma) aletes* Hertlein & Strong, sp. nov. Holotype. View of the exterior of the specimen shown in Fig. 9.

FIG. 13. *Pitar (Hyphantosoma) aletes* Hertlein & Strong, sp. nov. Holotype. View of the exterior of the specimen shown in Fig. 11.

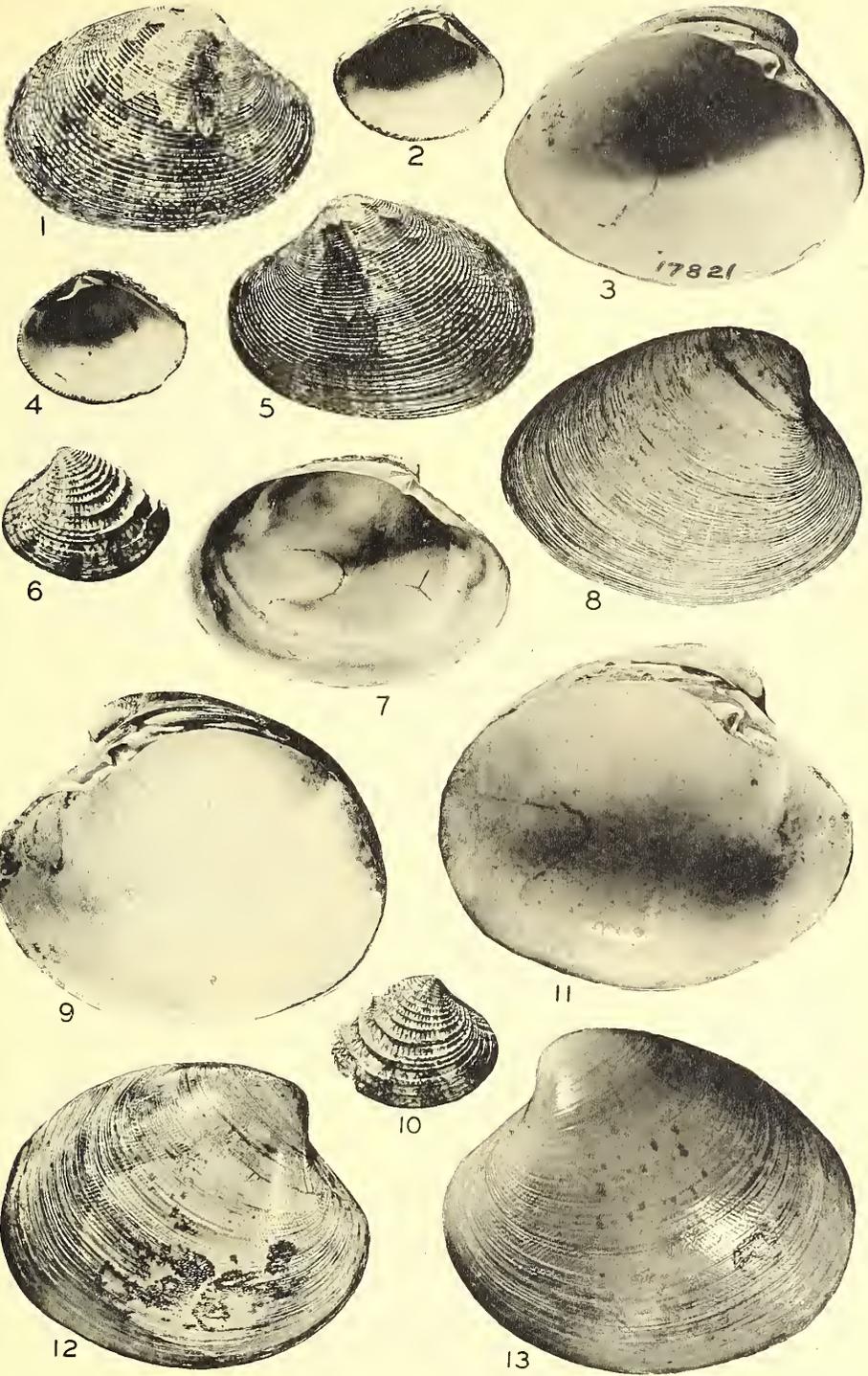
All the specimens illustrated on this plate are in the type collection of the Department of Paleontology of the California Academy of Sciences.

## PLATE II.

- FIG. 1. *Chione (Chione) guatulcoensis* Hertlein & Strong, sp. nov. Paratype, left valve, from Station 195-D-9, dredged in Lat. 15° 44' 28" N., Long. 96° 07' 51" W., Port Guatulco, Mexico, dredged in 7 fathoms (12.6 meters). Length, 14.6 mm., height, 11.1 mm. P. 182.
- FIG. 2. *Antigona (Ventricola) isocardia* Verrill. Hypotype, left valve, from Gorgona Island, Colombia. Length, 63.5 mm., height, 57.3 mm. P. 178.
- FIG. 3. *Antigona (Ventricola) isocardia* Verrill. Hypotype, left valve, from Station 136-D-26, dredged in Lat. 23° 27' N., Long. 109° 24' W., Arena Bank, Gulf of California, in 45 fathoms (82 meters). Length, 48.2 mm., height, 44.5 mm.
- FIG. 4. *Petricola (Petricola) lucasana* Hertlein & Strong, sp. nov. Holotype, left valve, from Cape San Lucas, Lower California, Mexico. Length, 24.6 mm., height, 25 mm. P. 194.
- FIG. 5. *Cyclinella kröyeri ulloana* Hertlein & Strong, subsp. nov. Holotype, left valve, from Station 143-D-4, Lat. 26° 55' N., Long. 111° 54' W., Santa Inez Bay, Lower California, in the Gulf of California, dredged in 25 fathoms (46 meters). Length, 75.5 mm., height, 76.5 mm. P. 179.
- FIG. 6. *Cyclinella kröyeri ulloana* Hertlein & Strong, subsp. nov. Holotype. View of the interior of the specimen shown in Fig. 5.
- FIG. 7. *Cyclinella kröyeri ulloana* Hertlein & Strong, subsp. nov. Paratype, left valve, from the same locality as the holotype shown in Fig. 5. Length, 65.3 mm., height, 63 mm.
- FIG. 8. *Chione (Chione) guatulcoensis* Hertlein & Strong, sp. nov. Paratype. View of the interior of the right valve of the specimen shown in Fig. 1.

- FIG. 9. *Petricola (Petricola) lucasana* Hertlein & Strong, sp. nov. Holotype. View of the interior of the right valve of the specimen shown in Fig. 4.
- FIG. 10. *Tivela delessertii* Deshayes in Sowerby. Hypotype, left valve, from Santa Inez Bay, Lower California, in the Gulf of California, on beach. Length, 30.9 mm., height, 23.5 mm.
- FIG. 11. *Pitar (Lamelliconcha) jrizzelli* Hertlein & Strong, sp. nov. Holotype, right valve from Station 136-D-22, Lat. 23° 28' 30" N., Long. 109° 25' W., Arena Bank, Gulf of California, dredged in 45 fathoms (82 meters). Length, 46 mm., height, 33.5 mm. P. 176.
- FIG. 12. *Chione (Chione) guatulcoensis* Hertlein & Strong, sp. nov. Paratype. View of the exterior of the specimen shown in Fig. 1.
- FIG. 13. *Chione (Chione) guatulcoensis* Hertlein & Strong, sp. nov. Paratype. View of the interior of the specimen shown in Fig. 8.
- FIG. 14. *Callocardia (Agriopoma) catharia* Dall. Hypotype, left valve, from Station 221-D-1-5, Lat. 7° 54' 45" to 7° 52' 30" N., Long. 82° 04' 32" to 82° 01' W., Gulf of Chiriqui, Panama, in 35-40 fathoms (64-73 meters). Length, 22.8 mm., height, 20.5 mm. View showing the hinge. P. 177.
- FIG. 15. *Callocardia (Agriopoma) catharia* Dall. View of the exterior of the specimen shown in Fig. 14.

All the specimens illustrated on this plate are in the type collection of the Department of Paleontology of the California Academy of Sciences.



MOLLUSKS FROM THE WEST COAST OF MEXICO AND CENTRAL AMERICA.





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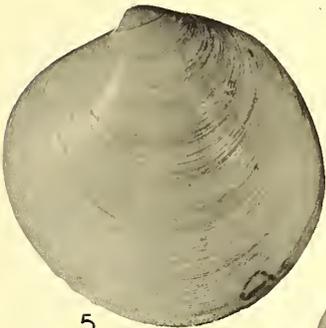
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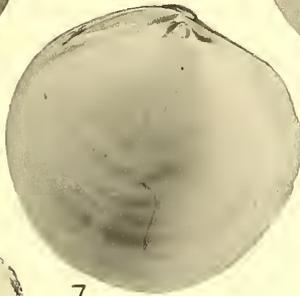
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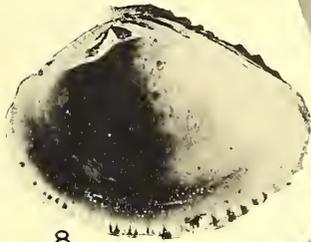
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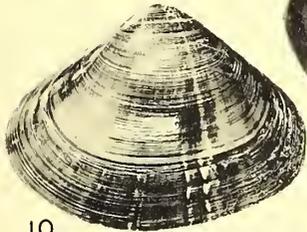
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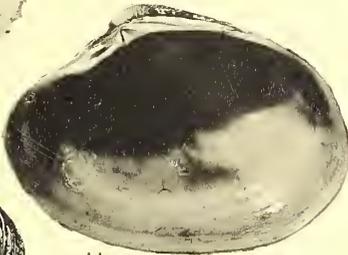
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MOLLUSKS FROM THE WEST COAST OF MEXICO AND CENTRAL AMERICA.



## 14.

Notes on Indian Birds. II.  
The Species *Glaucidium cuculoides*.

S. DILLON RIPLEY.

*Peabody Museum of Natural History.*

The collection of a number of specimens of barred owlets in India recently and discussions with my friend H. G. Deignan, have prompted me to review this species and to attempt to clear up some of the anomalous specimens and the ranges of the races.

## HISTORY OF THE SUPER-SPECIES.

1. *radiatum*.

*Glaucidium cuculoides* and *G. radiatum* apparently form a super-species, for such evidence as exists of their distribution indicates that they are allopatric. The species *radiatum* is found at low altitudes in the Himalayas, lower than *cuculoides*, and apparently replaces it. From the Himalayan foothills, *radiatum* spreads south throughout the Indian Peninsula as far as Khandesh, the eastern drier part of the Nilghiri plateau and south through Madras Presidency. In the wetter area of the west side of the lower peninsula, Coorg, Cochin and Travancore, *radiatum* is replaced by the darker subspecies, *r. malabaricum*.

In relatively recent times, *r. radiatum* has apparently invaded Ceylon, where it occurs in the drier zones of the Island, east, south and eastern part of the central "massif," only to be replaced in the wet zones of the central Hills, on their western side, and in the low country of the southwest by the strongly differentiated race, *castanonotum*. This race, characterized by having the feathers of the back, wing coverts, scapulars and rump suffused with light chestnut with greatly reduced barring, has been termed a race of *cuculoides* by Peters (Check List Birds World, 1940, IV, p. 133.), and so followed by me (*Spolia Zeylanica*, 1945, 24, pt. 3, p. 209.). In fact *castanonotum* is a small bird (wing 126-138.5 mm.), with fine close barring and obviously belongs with *radiatum*. However, in its high degree of differentiation as compared to the Peninsula race, *malabaricum*, I believe it represents an early wave of invasion which has become localized in the heavy rainfall area in the face of the advance of the later typical *radiatum* stock. The occurrence of typical *radiatum* in Ceylon and in southern India where it impinges closely on the present ranges of its two related races implies a secondary degree of adaptation by the typical race which has allowed it to spread south through drier, more lightly wooded

areas, from its potential land of origin along the base of the Himalayas. Presumably this spread is correlated with geologically recent postpluvial conditions.

2. *cuculoides*.

This species is found along the Himalayan chain from Murree in the west to Assam, the Indo-chinese, Malayan and Chinese subregions. It occurs at higher altitudes in the Himalayas than *radiatum* until the range of that species ceases in Bengal and Arakan. In Bengal *cuculoides* is found at lower altitudes and becomes a lowland and submontane as well as montane bird throughout the rest of its range. Thus it replaces *radiatum* ecologically east of the latter's range. An interesting correlation with the range of *cuculoides* is that it seems to be confined to areas with an annual rainfall of more than 60 inches. In addition the darkest race of the species, most saturated in tone of plumage, occurs in the area where the annual rainfall is more than 120 inches.

One anomaly in the range of *cuculoides* is that there is a discontinuous distribution of the species in the Malayan subregion. A race of *cuculoides* occurs in Tenasserim and Peninsular Siam, and then the species is absent from Malaya, Sumatra and Borneo, but occurs as a very well-marked race, *castanonotum*, in Java and Bali. Like *G. r. castanonotum* of Ceylon, this subspecies is marked by a rufous suffusion on the back, wing coverts, scapulars and rump, but in this case the larger size (wing 142-148.5 mm.) and the wider, coarser barring identify it closely with *cuculoides*. The similar plumage pattern in Ceylon and Java, however, is an interesting case of parallelism in response by the two species.

No valid explanation for this case of discontinuous distribution seems to exist. The original invasion of the Greater Sunda Islands by *cuculoides* stock was presumably pre-pluvial, but no outstanding environmental conditions occur to explain the absence of the species from Malaya or the other Greater Sundas. The only potential competitor would appear to be the smaller species, *Glaucidium brodei*, which, however, occurs not only in the gap area, but throughout a large part of the range of *cuculoides* from the western Himalayas to the Indo-chinese subregion.

## SPECIATION TRENDS.

There are two main trends of differentiation in *Glaucidium cuculoides* which act independently. One is size, which follows the degrees of latitude or montane altitude in the traditional way expressed by Bergmann's hypothesis. The second is color which varies from brown to rufous in a random way without obvious correlation except in one case. There is apparently no selective advantage in shades of dark color in these semi-diurnal owls. Dimorphism is not marked as it is in *G. brodei*. In the case of *Glaucidium radiatum* there is some dimorphism, i.e., a more gray plumage, vide Whistler and Kinnear (*Journ. Bomb. Nat. Hist. Soc.*, 1935, 38, p. 238). In *cuculoides* some specimens seem more brownish or more rufescent than others, but I have not seen any specimens in which this is so marked as to prevent their identification.

## RACES.

Peters (tom. cit., p. 133.), lists seven races of the species, but as Mayr notes (*Ibis*, 1938, p. 314.), there are several populations of varying color included in one or more of the existing forms, particularly *rufescens*. I would list, therefore, the following:

1. *Glaucidium cuculoides cuculoides* (Vigors).

This is a race lacking in rufescence; blackish-brown above and closely barred with fulvous, the bars on the upper back and nape rather broad and whitish. The wings are rufous-brown with rufous-fulvous bars, the scapulars and outer median wing coverts with white outer edges to the feathers, giving the appearance of spots (not shown in Gould's Plate 4, Century Birds, 1832.). The lower parts are whitish with dark brown and fulvous bars on the breast. The abdomen and vent areas tend to be streaked, more than barred, with light rufous brown.

## Measurements:

N. Punjab and Nepal 11 ♂♂ and ♀♀

Wing	Tail	Culmen (from cere)
141-157 (149.5)	75-90 (83.5)	14-16 (15.4)

Range: western Himalayas from Murree and Musoorie through Nepal. Foothills to 6,000 ft.

2. *Glaucidium cuculoides austerum* subsp. nov.

Type: ♂ ad. (U.S.N.M. No. 390166.), collected Jan. 11, 1947, at Tezu, Mishmi Hills, N.E. Assam, by S. Dillon Ripley.

Description: above this race is dark rufous brown with rufous-buff bars. The tone of the wings is darker, richer rufous than in the other races of the species. The tail is blackish, the barring fulvous. Below the amount of basal white on the underparts is much reduced as the barring is heavy and complete on the breast and the bars are rufous buff rather than whitish or fulvous. The abdomen and vent areas are heavily streaked or barred or streaky-barred with dark rufous brown, darker than in any other race of the species.

There is an average size increase over *cuculoides*.

## Measurements:

Sikkim to N. Assam, 16 ♂♂ and ♀♀

Wing	Tail	Culmen
148-156.5 (153.1)	81-94 (87.6)	15-16.5 (15.7)

Range: Sikkim, Bengal Duars, Bhutan, Assam north of the Brahmaputra, Mishmi Hills, and south in north Lakhimpur Division, Dibrugarh to Margherita, and into the upper Hukawng Valley of northwest Burma.

Remarks: birds from the Mishmi Hills are the most blackish in tone, but not sufficiently so as to distinguish them from the population of the rest of the range outlined above.

3. *Glaucidium cuculoides rufescens*

Stuart Baker.

This race is more pure brown, far less rufous than *austerum*, and with pure fulvous, less rufous fulvous, bars on the upper and lower parts. The population is, however, distinctly more rufous in tone than typical *cuculoides*. Below *rufescens* is barred and streaked with cinnamon brown, paler than *austerum*, but darker and with far less white showing than *cuculoides*.

## Measurements:

Cachar, Burma, 8 ♂♂ and ♀♀

Wing	Tail	Culmen
148-156.5 (153)	85-91 (87.6)	15-16 (15.6)

Range: southeast Bengal, Assam in Cachar, Manipur north to the Patkoi, Burma in the Hukawng Valley (where it may intergrade with *austerum*, the Chin Hills, Myitkina, and south to Pegu and the Shan States.

4. *Glaucidium cuculoides brüggeli* (Parrot).

In color there is no real character to separate this race from the preceding one. It is supposed to be less dark above and less rufous below, but I can find no real consistency in this claim. In series it might be asserted that *brüggeli* is a trace more rufous on the under parts. There is however, a distinction in size. This race is smaller than *rufescens*.

## Measurements:

Siam, 10 ♂♂ and ♀♀

Wing	Tail	Culmen
138-148.5 (144)	76.5-81 (78.7)	14.5-16.5 (15.6)

Range: Burma in Tenasserim; Siam except the southeast; and possibly (?) northern Cambodia, Indo-china.

Remarks: the type of *brüggeli* is in Munich. Apparently it came from near Bangkok. However, the type locality has been fixed by Deignan (*Bull. 186 U. S. Nat. Mus.*, 1945, p. 179.), at the Sam Khok district, half-way between Bangkok and Ayutthaya. In this area birds represent the type described above.

5. *Glaucidium cuculoides deignani* subsp. nov.

Type: ♀ ad. (U.S.N.M. No. 308542.), col-

lected Feb. 12, 1927, at Nongkhor, Southeast Siam, by Hugh M. Smith.

Description: This race is more rufescent on the upper parts than *brügeli* or *rufescens*, but it is a paler type of rufescence. The wing feathers and wing coverts are ferruginous-cinnamon. On the under parts the barring and streaking tends to be more extensive than in *brügeli* and *rufescens* and much more rufescent, but of a ferruginous-cinnamon type, less saturated with fulvous. There is no difference in size between this race and *brügeli*.

In color and in smaller size this race differs greatly from *cuculoides*, being ferruginous-cinnamon in tone and more barred and streaked below. From *austerum* it differs in size and in the cinnamon rather than dark fulvous-rufous coloration of the plumage.

Measurements:

S.E. Siam, S.W. Indo-china 8 ♂♂ and ♀♀

Wing	Tail	Culmen
145-151(148.1)	74-80.5(78.3)	14-16(14.7)

Range: southeast Siam, Nongkhor, Hoopon, Ban Sadet, Sriracha; southwest Indo-china, Da Ban, Dalat, Trang Bom, south Annam, and Bienhoa in Cochin China.

Remarks: a single bird from the forests of Banteai Srei in northern Cambodia, taken in January, belongs to *brügeli*, although it is rather dark in tone. It may well be a winter wanderer from east Siam.

This race is named for my friend, Herbert G. Deignan.

6. *Glaucidium cuculoides delacouri* subsp. nov.

Type: ♀ ad. (U.S.N.M. No. 304182.), collected May 5, 1924, at Baetan Tray, 36 km. N.N.E. of Lai Chau, Tonkin, Indo-china, by F. R. Wulsin.

Description: this race is the most pure rufescent of all races of the species, darker and more rufous on the upper parts than any other except *austerum*, which is more saturated with dark fulvous, more blackish in tone. Below this race is heavily barred and streaked, more so than any race except *austerum*, in which the barring descends farther onto the abdomen. The general effect is of a suffusion of dark rufescence, richer rufous than in any other race. The rufous tone appears richer than in *austerum* because it is less infused with melanin, more truly "reddish." The bill is longer in *delacouri* than in the preceding races.

Measurements:

N. Indo-china 4 ♂♂ and ♀♀

Wing	Tail	Culmen
150-157.5(154)	86.5-92.5(89.4)	16-16(16.4)

Range: Indo-china in Tonkin, except the northern valley of the Red River (Chapa area), and the extreme east (Tunghing); northern Laos at Xiengkhouang; north Annam at Hoi-Xuan.

This race is named for my friend, Jean Delacour.

7. *Glaucidium cuculoides whitelyi* (Blyth).

This is the largest race of the species and lives in the northernmost part of the range. It is composed of more than one phenotypic population, but I have been unable to separate them on any satisfactory basis. Birds from the western and southern part of the range are darker, more rufous fulvous than birds from the northern and eastern segments of the range. In these latter the barring on the plumage seems paler fulvous in tone. However, lighter birds appear in the west in a declining ratio moving from east to west, just as dark individuals appear in the east.

Beneath, the underparts of this race show more white basally with less of an overlay of brown than any other race except typical *cuculoides*. The general tone of the barring and streaking on the underparts is dark brown.

Measurements:

China, N. Burma, N. Tonkin, 9 ♂♂ and ♀♀

Wing	Tail	Culmen
155-170(162.1)	87-107(96.3)	15-17.2(15.9)

Range: extreme northeast Burma on the Yunnan border (Nan Ling R.); China in Yunnan, southern Szechuan and east, south of the Yangtse River, to Kiangsu; Indo-China in northern Tonkin (upper Red River Valley), and the extreme east, Tunghing.

Remarks: the difference in color between individuals of *whitelyi* had been noted by Sharpe in 1875 (Cat. Birds, II, p. 222), who wrote that Fukien birds in the British Museum collection were more rufous than typical *whitelyi*. As the other specimens listed are from Ningpo, I think it advisable to restrict the type locality of *whitelyi* to Chekiang Prov., eastern China. There is, of course, a possibility that dimorphism in color is developing in this subspecies as it has not apparently developed in other members of the species. However, the general appearance of the series from any one locality, their basic uniformity, tends to discount this possibility.

Many of the previous authors have relied on the number of tail bars in this species as a racial character. There does seem to be a tendency for birds from China to have one less bar on the tail than birds from India (6-7 versus 7-8). This is an uncertain character, however, for birds from intermediate areas like Burma and Assam vary from 6 to 9!

8. *Glaucidium cuculoides persimile* Hartert.

In color this race is more brownish, less rufous above and below than *delacouri*, and smaller and more rufous than *whitelyi*. In general appearance it is very similar but very slightly more rufous than *rufescens*. The culmen, however, is somewhat longer.

Measurements:

Hainan 9 ♂♂ and ♀♀

Wing	Tail	Culmen
148-156(153.3)	85-90(88.1)	16.5-18

Range: Hainan Island.

9. *Glaucidium cuculoides castanopterum*  
(Horsfield).

A dark brownish-rufous form with a strong rich rufous suffusion on the back, upper wing coverts, scapulars and rump. In these areas the barring has become obsolete. A distinctive isolated race.

Measurements:

Bali, 2 ♂♂

Wing	Tail	Culmen
142,148.5	70,77	14.5

Range: Islands of Java and Bali.

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## 1.

*Paradilepis simoni* n. sp., a Cestode Parasitic in the Osprey.  
(Cestoda: Dilepididae).<sup>1</sup>ROBERT RAUSCH<sup>2</sup>.*Department of Veterinary Science, University of Wisconsin, Madison*<sup>3</sup>

(Text-figure 1).

The knowledge of helminths parasitic in North American birds is very incomplete, especially for the region west of the Mississippi. Not only is this true in regard to parasite-host ecology, but a little work with almost any group of birds discloses undescribed forms or species unreported from North America, as well. In fact, anyone wishing to carry out host-parasite studies must devote considerable time to describing species—time which could be more profitably spent otherwise. The osprey might be mentioned to illustrate this situation. Of this bird the writer has examined but three specimens, one each from Ohio, Wisconsin and Wyoming. From this small series of birds, four species of helminths were collected; of these, two species were undescribed and two had never been recorded from North America. While it is true that a comparable situation is not to be expected in every case, it soon becomes obvious from work with a given host-group that much remains to be done before the helminths encountered in birds can be readily identified.

The cestodes with which this paper is concerned were obtained from the small intestine of an osprey, *Pandion haliaetus carolinensis* (Gmelin), collected on June 3, 1948, near Moran, Wyoming. This osprey was one of 267 birds collected by the writer for helminthological study from the Jackson Hole region of Wyoming.

A total of more than 75 worms was obtained. Whole-mounts were prepared of specimens stained with Semichon's acetic carmine and Delafield's haematoxylin. Serial sections, cut at 15 $\mu$ , were also studied.

This cestode is named in honor of Mr. James Simon, Director of the Jackson Hole Wildlife Park, whose generous cooperation contributed much to the success of the field work in Jackson Hole.

<sup>1</sup> Contribution of the 1948 Research Program of the New York Zoological Society at Jackson Hole Wildlife Park.

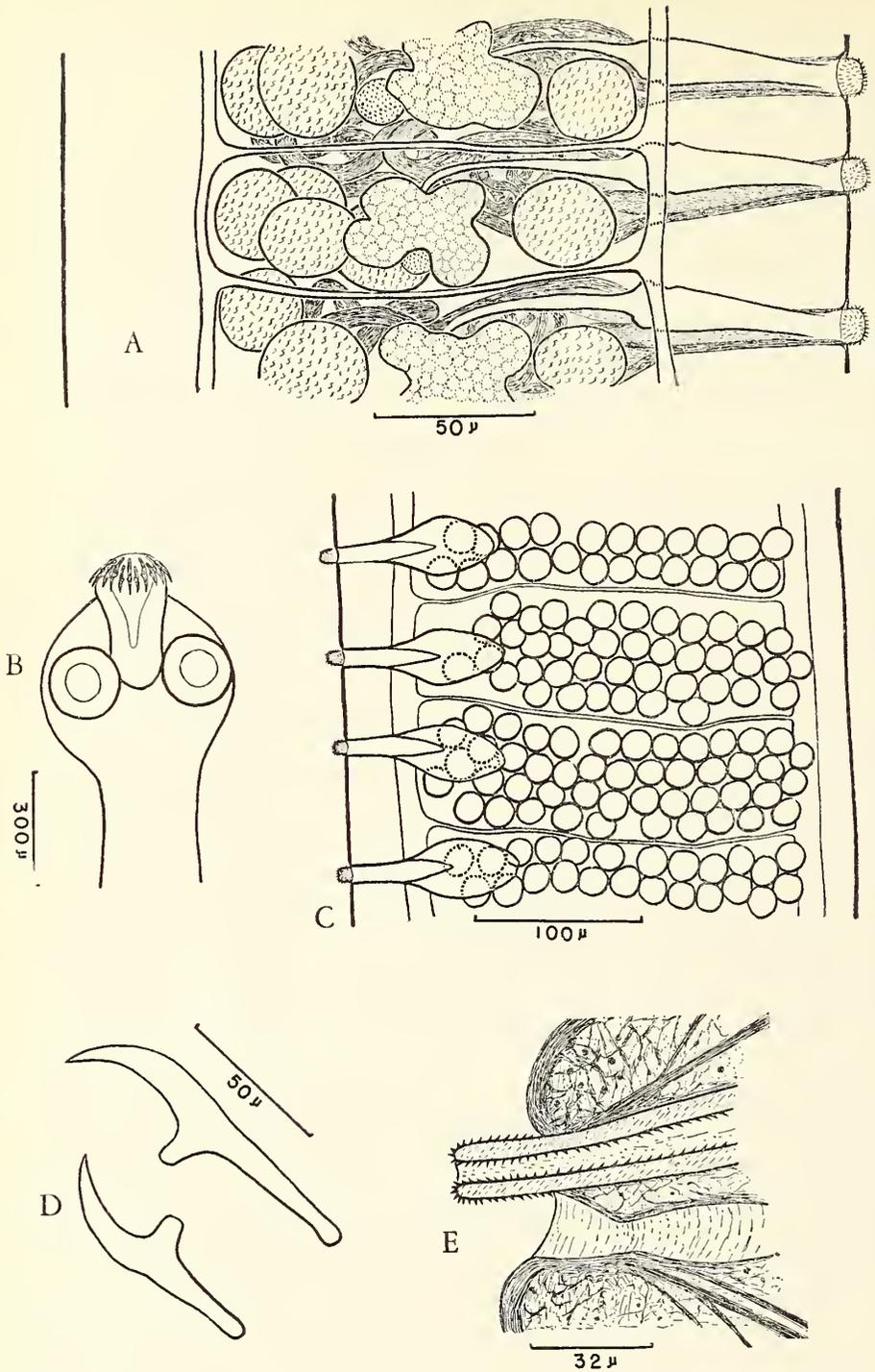
<sup>2</sup> Now with U. S. Public Health Service, Anchorage, Alaska.

<sup>3</sup> Section on Parasitology, B. B. Morgan, Project Leader.

*Paradilepis simoni* n. sp.

(Text-fig. 1 A-E).

*Diagnosis:* Strobila from 50 to 90 mm. long; greatest width, up to 450  $\mu$ , attained in terminal gravid segments. External segmentation absent; strobila very delicate and translucent in the living worm. Scolex large and distinct from neck; from 470 to 596  $\mu$  in diameter. Suckers from 180 to 220  $\mu$  in diameter. Well-developed rostellum slightly over 100  $\mu$  long; armed with about 36 hooks arranged in a double row. Large hooks from 98 to 102  $\mu$  long; small hooks 68 to 72  $\mu$  long. Hook shape typical for genus. Neck from 250 to 270  $\mu$  wide, narrowing gradually to a distance of about 2 mm. posterior to scolex; from this point the strobila widens to reach greatest width at posterior end. Musculature consists of two layers; the first layer, of longitudinal fibers, is from 1 to 3 bundles deep; directly beneath it is a layer of transverse fibers. Excretory canals typical in arrangement; the ventral longitudinal canal measures from 6 to 20  $\mu$  in diameter; the dorsal and transverse canals about 3  $\mu$  in diameter. Internal segmentation best recognized by the arrangement of the transverse excretory canals, which divide the strobila into about 30 "segments" per mm. of length in the mature region. Genital organs not confined entirely to space between transverse canals, but overlap into adjacent segments. Genital *Anlagen* appear about 2 mm. posterior to scolex. Genital pores unilateral and sinistral; genital atrium about 16  $\mu$  deep. Genital canals pass dorsal to longitudinal excretory canals. Five spherical to ellipsoidal testes, not all in same plane, in each segment; testes measure from 26 to 33  $\mu$  in diameter in mature segments. Usually 4 testes are aporal, and one is poral of female organs; at times 2 may be poral. Flask-shaped cirrus sac extends to middle of mature segments, or beyond, dorsal to testes; it measures from 100 to 132  $\mu$  long by 30 to 40  $\mu$  wide. Cirrus heavily spined. Internal and external seminal vesicles absent; ductus ejaculatorius coiled within bulb of cirrus sac.



TEXT-FIG. 1. The morphology of *Paradilepis simoni* n. sp. The drawings were made in part with the aid of a projector. **A.** Ventral view of a typical mature segment. **B.** Typical scolex. **C.** Dorsal view of a section of gravid segments. **D.** Hooks from rostellum. **E.** Cross-section of genital atrium region, showing relation of cirrus to vagina.

Well-developed vas deferens with numerous convolutions situated in dorsal part of segment. Cirrus sac provided with strongly-developed retractor muscles. Thin-walled vagina opens ventral to cirrus sac; it enlarges gradually, attaining greatest diameter near place where longitudinal excretory canals are crossed; it narrows after this point and runs medially to join small seminal receptacle dorsal to ovary. Ovary rather variable in shape and position; usually 4-lobed, situated near middle of segment. Spherical to ellipsoidal vitelline gland dorsal to posterior part of ovary; it increases in size toward posterior end of strobila, attaining a maximum diameter of about 40  $\mu$ . Uterus develops as two lateral, spherical sacs situated ventral to ovary, and connected by a narrow neck. Gravid uterus fills entire segment; unlobed and sac-like when completely gravid. Cirrus sac and vagina persist into terminal gravid segments. Eggs, from 27 to 33  $\mu$  in diameter, are arranged in 3 to 4 rows across the segments. Embryonic hooks about 6  $\mu$  in length.

*Host*: *Pandion haliaetus carolinensis* (Gmelin) (Osprey).

*Habitat*: Small intestine.

*Locality*: Moran, Wyoming.

*Type*: Three slides of cotype material have been deposited in the Helminthological Collection of the U. S. National Museum, No. 46403.

#### DISCUSSION.

As far as could be determined, the genus *Paradilepis* Hsü, 1935, has not been previously recorded from North America. Neither has the writer discovered any record of cestodes parasitic in the osprey.

Cestodes of the genus *Paradilepis* are typically parasitic in pelicaniform birds, particularly in cormorants, *Phalacrocorax* spp. The genus *Paradilepis* was established (Hsü, 1935) for cestodes from a Chinese cormorant, with *P. duboisi* as type. Hsü also assigned *Dilepis scolecina* (Rudolphi, 1819) to the genus *Paradilepis*. According to Joyeux and Baer (1935), *P. duboisi* is identical with *P. scolecina*; consequently *P. scolecina* (Syn. *P. duboisi*) becomes type species. The examination of the original preparations of *Oligorchis delachauxi* Fuhrmann, 1909, led Joyeux and Baer (1935) to place it in the genus *Paradilepis*. It had been earlier assigned by the same writers (1930) to the genus *Dilepis* Weinland. Further study of their African material disclosed that they were dealing with two species, referred to as *Dilepis delachauxi* (Fuhrmann, 1909). As a result, a new name, *P. macracantha*, was proposed (Joyeux and Baer, 1935) for *Dilepis delachauxi* Joyeux and Baer, 1930 nec Fuhrmann, 1909.

Burt (1940) described *Paradilepis brevis* from a Ceylon cormorant, apparently without referring to the work of Joyeux and Baer (1935). It is possible that *P. brevis* is identical with *P. scolecina*.

Joyeux and Baer (1935) suggested that *Oligorchis longivaginosus* Mayhew, 1925, might also belong to the genus *Paradilepis*. This is of particular interest in connection with the present paper, since *O. longivaginosus* was collected from a white pelican from Yellowstone Park, Wyoming. Apparently this species has a single crown of hooks, instead of a double row as seen in *Paradilepis*; external segmentation also seems evident.

The number of species of the genus *Paradilepis* is at present indefinite, and must remain so until some of the material is studied further. Regardless of this situation, *P. simoni* is readily differentiated from any others previously assigned to the genus in that it possesses 5 testes in each segment, instead of 4.

Although the presence of 4 testes is considered a generic character by Joyeux and Baer (1935, 1936), we do not consider it justifiable to erect a new genus for *P. simoni* on the basis of this character alone. It is otherwise very similar to the other members of the genus. Since the previously known species have been described from pelicaniform birds, it is not strange that they are morphologically similar. If, in addition to *P. simoni*, cestodes of this genus are recorded from other host groups, a much better concept of morphological variation within the genus may be had.

It is possible that *P. simoni* is an "accidental" parasite of the osprey, and occurs naturally in cormorants. It would be of interest to examine cormorants from the colony north of Jackson Hole in order to determine whether they are parasitized by any species of *Paradilepis*. Since all the hosts are piscivorous, presumably species of fish might act as the intermediate hosts of cestodes of this genus. At present, there is no reason to doubt that the osprey is the natural host of *P. simoni*.

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## 2.

A Contribution to the Study of North American Cestodes  
of the Genus *Paruterina* Fuhrmann, 1906<sup>1</sup>.ROBERT RAUSCH<sup>2</sup> AND EVERETT SCHILLER.*Department of Veterinary Science, University of Wisconsin, Madison*<sup>3</sup>

(Text-figures 1-12).

Two of the 16 apparently valid species of *Paruterina* Fuhrmann, 1906, have been recorded from North American birds. *Paruterina similis* (Ransom, 1909) occurs in the yellow-billed cuckoo, *Coccyzus a. americanus* (L.), and *P. candelabraria* (Goeze, 1782) is the most frequently encountered cestode parasitic in owls. The latter occurs in Europe as well as in North America, and infects several species of owls (Wolffhügel, 1900; Rausch, 1948). Evidence to the present would indicate that a high degree of host specificity has been developed in the cestodes of this genus.

It is the purpose of this paper to describe two species of *Paruterina*, and to include some remarks concerning the two previously-recorded North American species. The undescribed species were collected by one of us (R. R.) from birds in the Jackson Hole region of Wyoming. Both were taken from hosts whose parasites probably have not been previously studied.

The Wyoming birds parasitized by cestodes of the genus *Paruterina* were a rock wren, *Salpinctes o. obsoletus* (Say), and a green-tailed towhee, *Chlorura chlorura* (Audubon), which were collected from the same area, along with numerous birds of other species. The wren was collected from the southeast slope of a hill, at an altitude of about 7,000 feet. Sandstone outcroppings were numerous here, and rock wrens were rather commonly observed among them. A marmot, *Marmota flaviventris nosophora* Howell, was the characteristic mammal of this zone. The towhees were common a few hundred feet lower, where a sage, *Artemisia tridentata* Nutt., was the characteristic plant. Brewer's sparrow, *Spizella b. breweri* Cassin, was also characteristic of this habitat.

In view of the fact that representatives of the genus *Paruterina* have not been often reported in North America, it seemed un-

usual to collect two undescribed species from so small an area. However, since the morphological differences are quite distinct, there can be no doubt as to their specific validity. As pointed out earlier (Rausch, 1948), the helminth parasites of the North American avifauna are only poorly known.

*Paruterina chlorurae* n. sp.

(Text-figs. 1-4).

*Diagnosis:* Strobila from 35 to 50 mm. long; greatest width, attained in terminal gravid segments, about 1 mm. Strobila consists of about 140 segments; margins of latter not serrate. Segments wider than long in mature segments, with a gradual increase in length as segments become older; terminal gravid segments, in well relaxed strobilae, considerably longer than wide. Scolex about 550  $\mu$  in diameter, not set off from neck. Suckers rather weakly developed, about 180  $\mu$  in diameter. Rostellum armed with a double row of hooks, from 40 to 42 in number; large hooks 20  $\mu$  long, and small hooks 16  $\mu$  long. Handle of larger hook about same length as guard and blade; guard of smaller hook relatively shorter, with blade and guard of nearly equal length.

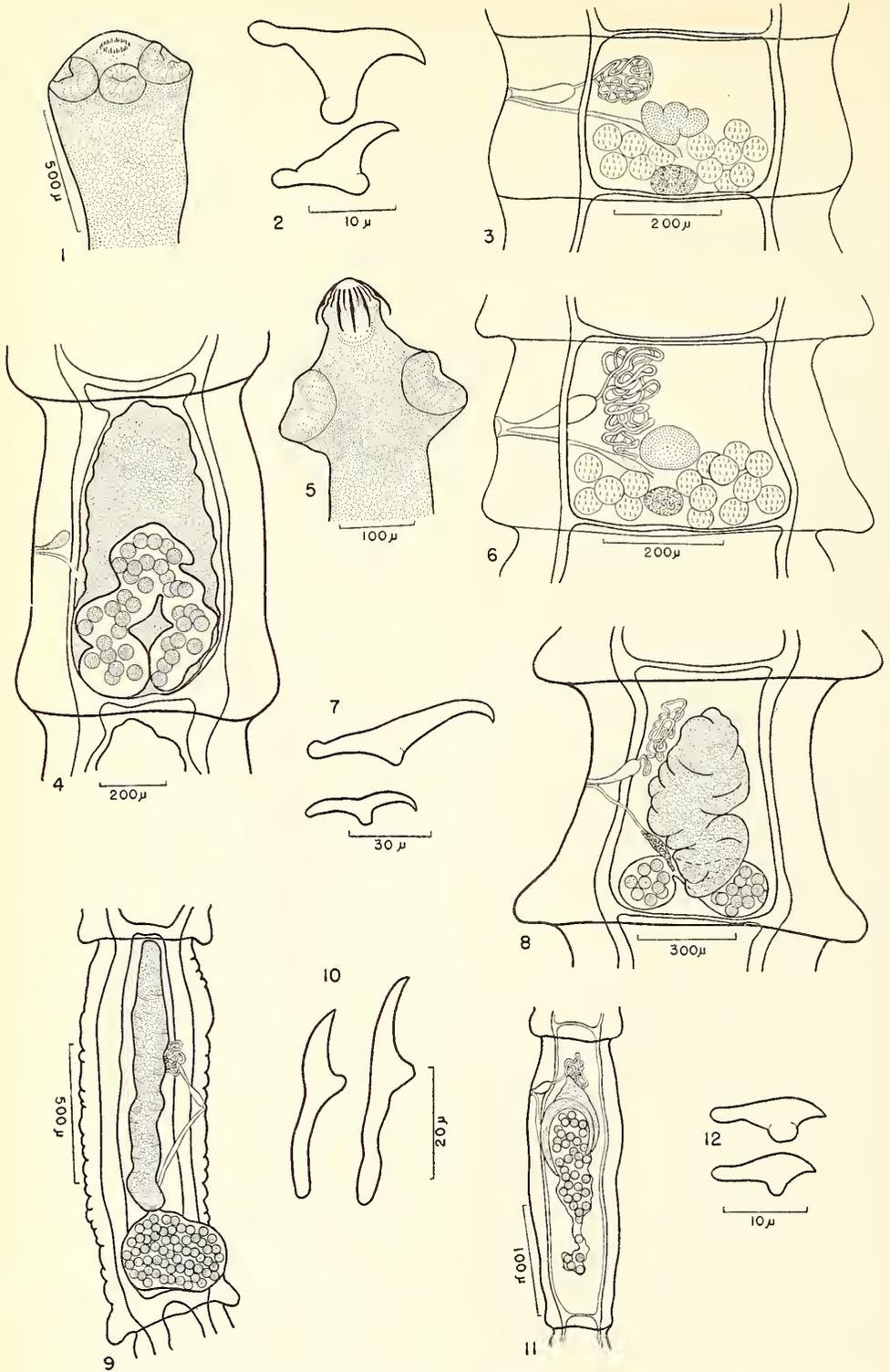
Ventral longitudinal excretory canals measure about 33  $\mu$  in diameter; dorsal canals about 10  $\mu$  in diameter, median to ventral canals. Transverse canals about 3  $\mu$  in diameter. Genital pores irregularly alternate; genital ducts pass between longitudinal excretory canals. Musculature well developed; longitudinal bundles numerous.

Cirrus sac anterior to vagina, from 105 to 119  $\mu$  long by 23 to 29  $\mu$  wide. Cirrus sac does not extend to level of ventral longitudinal excretory canal. Internal and external seminal vesicles absent. Vas deferens well developed and strongly coiled in area between poral ventral excretory canal and ovary. Testes spherical, from 10 to 12 in number; about 50  $\mu$  in diameter in mature segments. Testes lateral and posterior to female genital organs, not extending anterior to vagina on poral side, nor anterior to ovary on aporal side.

<sup>1</sup> Contribution of the 1948 Research Program of the New York Zoological Society at Jackson Hole Wildlife Park.

<sup>2</sup> Now with U. S. Public Health Service, Anchorage, Alaska.

<sup>3</sup> Parasitology Section, B. B. Morgan, Project Leader.



TEXT-FIGS. 1-12. 1. Scolex of *Paruterina chlorurae* n. sp. 2. Rostellar hooks of *P. chlorurae*. 3. Mature segment of *P. chlorurae*. 4. Gravid segment of *P. chlorurae*. 5. Scolex of *P. morgani* n. sp. 6. Mature segment of *P. morgani*. 7. Rostellar hooks of *P. morgani*. 8. Gravid segment of *P. morgani*. 9. Gravid segment of *P. candelabraria* (Goeze, 1782). 10. Rostellar hooks of *P. candelabraria*. 11. Gravid segment of *P. similis* (Ransom, 1909). 12. Rostellar hooks of *P. similis*.

Vagina runs directly from genital pore toward ovary; poral to latter it enlarges to form a well-developed seminal receptacle. Ovary slightly lobed, about 50 by 60  $\mu$  in mature segments; situated on mid-line near middle of segment. Vitelline gland spherical to ellipsoidal, about 20  $\mu$  in diameter; situated at posterior margin of segment on mid-line, directly posterior to ovary. Uterus appears as a crescent-shaped organ ventral to ovary; the arms lengthen until the organ assumes an inverted V-shape. In terminal gravid segments, arms of uterus become somewhat sinuous. Parauterine organ develops slowly from anterior margin of early uterus; it becomes elongate and finally attains anterior margin of segment. Spherical eggs, observed only in the uterus, measure from 43 to 50  $\mu$  in diameter.

*Host*: *Chlorura chlorura* (Audubon). (Green-tailed towhee).

*Locality*: Near Moran, Wyoming.

*Habitat*: Small intestine.

*Type*: Cotype material has been deposited in the Helminthological Collection of the U. S. National Museum, slide number 46421.

*Paruterina chlorurae* is differentiated from the other species of the genus by shape, size and number of rostellar hooks. Differentiation of this species is considered more fully under the discussion below.

#### *Paruterina morgani* n. sp.

(Text-figs. 5-8).

*Diagnosis*: Strobila about 40 mm. long; maximum width, attained in gravid segments, about 500  $\mu$ . Strobila consists of about 150 segments; margins of latter strongly serrate. Mature segments wider than long; they increase gradually in length as they become older, with gravid segments being slightly longer than wide. Scolex about 250  $\mu$  wide, distinctly set off from neck; suckers about 100  $\mu$  in diameter. Rostellum armed with a double row of 34 to 36 hooks; large hooks measure 66  $\mu$  long; short hooks measure 40  $\mu$  long. Blade of large hook, slightly longer than handle, curves downward abruptly at end; guard, near middle of hook, inconspicuous. Blade and handle of small hook nearly equal in length; guard, at middle hook, about  $\frac{1}{3}$  as long as blade.

Ventral longitudinal excretory canals about 13  $\mu$  in diameter; dorsal canals about 4  $\mu$ . Transverse canals about 3  $\mu$  in diameter. Genital pores irregularly alternate; genital ducts pass between longitudinal excretory canals. Musculature well developed; two rows of longitudinal and a single row of transverse fibers occur in close contact. Longitudinal muscle fiber bundles not numerous; accurate count not obtained.

Cirrus sac clavate, anterior to vagina; it extends beyond poral ventral excretory canal, and measures from 86 to 105  $\mu$  long by 16 to 20  $\mu$  wide. Internal and external seminal vesicles absent. Vas deferens well developed and strongly coiled; convolutions fill greater part of poral half of segment,

from end of cirrus sac to level of mid-line of ovary. Testes spherical, from 15 to 18 in number; about 50  $\mu$  in diameter in mature segments. Testes lateral and posterior to female genital organs; not extending anterior to vagina on poral side, nor anterior to ovary aporally.

Vagina runs directly from genital pore, without convolution, to form a well-developed seminal receptacle posterior and poral to ovary. Ovary unlobed, ellipsoidal; about 120  $\mu$  long by 80  $\mu$  wide in mature segments; situated in posterior half of segment, at mid-line. Vitelline gland ellipsoidal; about 60  $\mu$  long, situated directly behind ovary somewhat anterior to posterior margin of segment. Uterus appears as an elongate organ lying transversely in the posterior part of the segment, ventral to ovary. It enlarges gradually, and finally forms an elongate, irregular sac, situated at posterior margin or completely gravid segments. Parauterine organ grows gradually from anterior margin of uterus; it does not reach anterior margin of segment. Eggs spherical, observed only in uterus; from 36 to 43  $\mu$  in diameter.

*Host*: *Salpinctes o. obsoletus* (Say). (Rock wren).

*Locality*: Near Moran, Wyoming.

*Habitat*: Small intestine.

*Type*: Cotype material has been deposited in the Helminthological Collection of the U. S. National Museum, slide number 46422.

*Paruterina morgani* is differentiated from the other members of the genus by size, shape and number of hooks, as well as by other, less obvious details. This cestode is named in honor of Dr. B. B. Morgan, Department of Veterinary Science, University of Wisconsin.

#### DISCUSSION.

At least 18 species have been assigned to the genus *Paruterina*; of these, 2 species, *P. fuhrmanni* Baczynska, 1914, and *P. melierax* (Woodland, 1929) have been transferred to other genera. Three of the remaining species, *P. angustata* Fuhrmann, 1906, *P. guineensis* Joyeux and Baer, 1923, and *P. southwelli* Hilmy, 1936, have unilateral genital pores, and are immediately separated by this character from the species described in the present paper.

Of the North American species, *Paruterina similis* (Ransom, 1909) has been re-described by Linton (1927). This species was placed in the genus *Paruterina* by Jones (1929). Certain morphological details of this species have never been completely described; Linton (1927, page 50) stated "There is a short rostellum surmounted by a double circle of very short hooks. Their exact number was not satisfactorily made out, but there appear to be in the neighborhood of 40 . . ." Jones (1929) examined both Linton's material, and that of Ransom, but did not give further details concerning the hooks of *P. similis*. We found that *P. similis* possesses from 50 to 52 hooks, arranged in

a double row. The large hooks measure 13  $\mu$  long, while the small hooks measure 11  $\mu$  long. They are essentially the same in form, except that the larger hooks have a larger, more rounded guard (Text-fig. 12). Our observations were made under oil immersion on hooks which had been removed from the scolices, and were lying flat on the slide.

*Paruterina chloruræ* and *P. morgani* are differentiated from *P. similis* and *P. candelabraria* by hook size, shape and number (Text-figs. 2, 7, 10, 12). It is of interest to note that the North American species can also be separated by differences in the arrangement of the parauterine organ and the uterus in the fully-gravid segments (Text-figs. 4, 8, 9, 11). In fact, differences here are more obvious than are those seen in the mature segments. It might also be mentioned here that cestodes of this genus can easily be recognized as such macroscopically, at the time they are removed from the intestine of the host, by the appearance of the gravid segments.

The remaining 11 species, widely distributed geographically, are best separated by hook characters. All of these (*P. boviæ* Hübscher, 1937; *P. bucerotina* Fuhrmann, 1909; *P. cholodkowskii* Skrjabin, 1914; *P. daouensis* Joyeux, Baer, and Martin, 1936; *P. javanica* Hübscher, 1937; *P. meggitti* Johri, 1931; *P. otidis* Baczyńska, 1914; *P. parallelipida* (Rud. 1809); *P. purpurata* (Dujardin, 1845); *P. septotesticulata* Moghe and Inamdar, 1934; *P. vesiculigera* (Krabbe, 1882) all differ appreciably in hook size, shape and number.

There are also differences in testes number in most cases. Where there is overlapping of this character, hook differences serve to separate the species involved. Other taxonomic details need not be discussed here in order to separate the species described in the present paper.

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## 3.

Behavioral Interactions in a Herd of Barbary Sheep  
(*Ammotragus lervia*).<sup>1</sup>

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## INTRODUCTION.

Studies of social behavior in animals have generally been of two types, the naturalistic field investigation and the laboratory experiment. Field studies of ungulates have been made by Darling (5) on the red deer, and Mills (10), Davis (6) and Spencer (13) on the Rocky Mountain bighorn sheep. The experimental method has produced an extensive literature on dominance relationships and aggressive behavior in many species. Collias (4) has reviewed the work on aggressive behavior among vertebrates up to 1944. Studies on dominance have been too numerous even to be mentioned briefly in the present paper.

Carpenter (2) has pointed out that the development of a science of comparative social behavior requires that the results of field investigations and those of the laboratory should be systematically co-related. He also has stated that the standards of scientific research which apply in the laboratory can and should be applied in the field. Recognizing the research potentialities of an integrated approach to animal behavior, Scott (11) recently combined systematic observation and experimentation in a study of a small flock of domestic sheep living under semi-natural conditions.

The methods and aims of the following study of a herd of Barbary sheep were suggested in large part by the work of Scott and the theoretical discussions of Carpenter (2, 3). Carpenter (2) has listed 11 types of behavioral interactions found in primate societies. It was hoped that the first six of these might be studied in the Barbary sheep. They are: 1, Interactions among adult males of organized groups; 2, among adult females of organized groups; 3, between adult males and adult females; 4, between adult males and young; 5, between adult females and

young; and 6, among the young. The data were to be compared with information on the domestic sheep and the Rocky Mountain bighorn. In addition, the investigator sought to obtain data relevant to the hypothesis that deprivation is an effective instigator of aggressive behavior.

## THE HERD.

The Barbary sheep, or aoudad (*Ammotragus lervia*) is very distinct in appearance from all other wild sheep, its most unique features being a mane of long hairs over the fore-quarters, the length of tail and the large size of the female's horns. Its color is uniform rufous tawny. The habitat of the Barbary sheep is the arid southern slopes and foothills of the mountains of North Africa, extending from near the Atlantic seaboard to Egypt. Lydekker (8) quotes reports that the animals go about in groups of four or five and may drink as seldom as once in four or five days.

The herd at the New York Zoological Park is descended from stock brought to the Park during the years 1901-1906. No new stock has been introduced since then. During the summer of 1947 the herd consisted of four rams, four ewes and four lambs. One of the lambs was a yearling, while the others were first-season. The sheep lived on an enclosed field of about two acres. They shared the field with two elands and a zebra. Human regulation of the activity of the sheep has been kept at a minimum by the Park authorities. Under normal circumstances the herd is fed about one and one-half buckets of grain, which is spread out on a large, flat rock at about 9:30 every morning. The elands and the zebra usually feed from a box some distance away, although they sometimes wander over to the rock and feed with the sheep. The grain ration is supplemented occasionally with hay, which is placed in one corner of the field. Vending machines in the Park provide special food pellets which visitors may throw through the fence. During the warm months the sheep regularly gather at the north fence in the afternoon to receive these pellets. The sheep tend generally to avoid the two elands and the zebra. In recent years a newborn lamb was killed by the male eland, and another by the zebra.

<sup>1</sup> A report submitted to the New York Zoological Society on research performed as a Summer Research Fellow of the Society during July, August and September, 1947.

The writer is indebted to his colleagues, Dr. N. E. Collias and Dr. B. F. Riess, who made many valuable suggestions and participated in the observation and experimentation from time to time. Special gratitude is due a third associate, Mr. D. Lehrman, who did most of the work with the Bristol Recorder, and who shared equally in some of the experiments. The Summer Research Fellows worked under the general direction of Professor C. R. Carpenter.

## METHODS.

Casual observations were made almost daily from mid-July until mid-September, and during all hours of the day, so that a complete picture of the daily routine could be obtained. Colored dyes were used to mark the individual animals until the observer could recognize them easily by differences in appearance and behavior. The following experiments were performed repeatedly: (1) tossing of bread between pairs to ascertain relationships of dominance-subordination; (2) placing of daily grain ration in a small box to study dominance-subordination relationships in a complex herd situation, as well as to provide observations on food sharing, fighting, and related phenomena; (3) frightening of the herd to elicit leadership and timidity. These experiments were carried out from July 22 to September 13. In addition, on two days a Bristol multi-pen recorder was employed in connection with the feed box experiment to ascertain the amount of time each animal actually fed from the box. Motion pictures were taken of types of behavior which had been previously recognized and described.

The study of social relationships was limited by the fact that the age and percentage of adult individuals could not be established with certainty. Although the Park maintains complete records of births and deaths, there is no provision made for identifying individual members of herds. It was possible, however, to know three ewe-lamb relationships on the basis of observed behavior.

## DAILY ROUTINE.

The daily pattern of behavior of the herd was marked by fairly regular periods of alternating activity and rest. But this was greatly modified by changes in the weather, experimentation and marked variations in the supply of food from visitors. Usually in the early morning the sheep wandered about the field. Grazing was desultory, since other food was available. At about 9:00 A.M. the sheep generally gathered on an outcropping of broad, flat rocks situated on a hillock in the center of the field, and there they rested until 9:30 A.M., when grain was scattered on a nearby rock by the keeper. The sheep ate the grain peacefully, with very little butting or shoving. By 10:15 A.M. the sheep were either back at their earlier places on the rocks or were under a tree, where they remained until after the noon hour.

Shortly afterwards children and adults would usually begin to gather along the north fence. The movement of the sheep to the fence seemed to be associated with the size of the gathering of people rather than the hour. On days when very few people visited the Park the sheep might remain entirely away from the fence throughout the afternoon. Once at the fence, the herd remained there as long as pellets were given to them, usually until about 5:30 P.M. On hot after-

noons the males made occasional trips to a nearby water hole. Here they cooled themselves by sinking down into the shallow water and rolling in the mud.

In the evening the sheep wandered and rested until dark. The lambs played actively at this time by running and leaping on the rocks. During late August and September fighting and attempted breeding occurred among the males, and most frequently in the evening. At dusk the herd gathered inside or near a shed and bedded down for the night. Sometimes the sheep moved as a group, but consistent leadership was not apparent. In general, there was much independent movement among the ewes, rams and lambs.

## MATCHING TESTS.

The matching tests were conducted every few days from July 22 until September 13 to determine dominance-subordination interactions between individual animals. Usually the tests were made in the afternoon, when the sheep were gathered at the north fence. By supplying several willing children with bread, and placing them along the fence, it was possible to disperse the sheep so that all or most of the possible pairings could be made among the rams, the ewes and the lambs. The matching of adults and lambs, or of rams and ewes, was not attempted after the first day because of practical difficulties.

The matching test was simple. The experimenter stood at the fence and held a small piece of bread in his extended hand. When two sheep, which were not more than ten feet apart, looked in the direction of the experimenter, the bread was tossed so that it landed approximately equidistant between them. No score was recorded unless both animals moved toward the bread. The one which obtained possession of the bread by causing the other to withdraw was considered dominant. The behavior elicited in this situation was clear and unambiguous; if both sheep advanced toward the food, one *always* threatened or butted and the other *always* withdrew. Sometimes the bread landed much closer to the animal known to be subordinate. In such a case the subordinate sheep might obtain the bread, but this was usually followed by vigorous butts from the dominant animal. Often, however, a quick dash by the dominant sheep caused the other to retreat, even when the bread lay directly at its feet.

On three occasions the sheep appeared to be uniformly unmotivated with regard to the bread. Two of these days were extremely hot, and the third was marked by a morning of heavy feeding. At all other times competition was keen and sustained. The method of scoring is somewhat defective in that no scores were recorded for those tests in which only one animal moved toward the food. The assumption here is that of "no contest" and this is, of course, questionable, since the animal's lack of a positive overt response to the food might be due to the presence of the dominant animal. However, the almost per-

fect consistency of the results presented in Table I, and the agreement between these results and behavior observed in other situations strongly suggest that the method is highly valid.

In the majority of contests, dominance was decided by a sudden *twisting movement* of the dominant sheep's head in the direction of the other sheep. At this "signal" (or sign) the subordinate sheep stopped advancing. Sometimes a token butt was delivered, but seldom was a more forceful attack necessary to effect retreat. Counter attacks by subordinates occurred rarely and were *never* successful. Among the rams, the ewes and the lambs straight line dominance orders were revealed on the first day and remained almost stable during the 53-day period of testing. Only two instances of reversals occurred during a total of 272 matching tests. Although interactions between rams and ewes, and between adults and lambs, were not formally tested, it was apparent that *all rams were dominant over all ewes, and all adults over all lambs.*

The results of the matching tests are presented in Table I. The dominance order is as follows: Ram 1 > Ram 2 > Ram 3 > Ram 4 > Ewe 1 > Ewe 2 > Ewe 3 > Ewe 4 > Lamb 1 > Lamb 2 > Lamb 3 > Lamb 4 >. The attempt was to test at least twice a week every possible combination of individuals within each of the three subgroups. But this could not always be done because of the difficulty of bringing certain of the sheep together. For example, matchings between lambs were often disrupted by the sudden approach of one or more adults.

#### FEED BOX EXPERIMENTS.

The feed box experiments were intended to furnish information on social behavior in a competitive group situation. The matching tests had indicated the existence of a clear, stable relationship between any two animals which were made to compete for a small food object while in relative isolation from the other members of the herd. But it could not be assumed that these relationships would hold in all types of competitive situations, especially in those where more than two animals are interactive. Maslow (9) found that stable dominance-submission relationships which were established between monkeys by the method of paired matching tests broke down when three or more individuals were placed together.

The food incentive box was heavy and made of wood, typical of those used in the Park for the feeding of large animals. Its sides were about two feet long and about one and one-half feet high. The box was modified so that the interior sides measured 15" by 12", with the depth remaining unaltered. The interior was large enough to hold more than a bucket of grain without spilling by the feeding animals. The size of the opening was such that two adults could not feed simultaneously without frequent contact, while simultaneous feeding by three

TABLE I.  
Results of the Matching Tests.

	Number of matchings
<i>Rams*</i>	
1-2	25
1-3	20
1-4	22
2-3	22
2-4	21
3-4	12
4-2†	1
2-1†	1
<i>Ewes*</i>	
1-2	22
1-3	18
1-4	15
2-3	15
2-4	13
3-4	9
<i>Lambs*</i>	
1-2	7
1-3	6
1-4	5
2-3	12
2-4	10
3-4	14
<i>Groups</i>	<i>Total</i>
Rams	124
Ewes	94
Lambs	54

\* Numbers indicate sheep according to position in dominance order. Number of dominant animal precedes that of subordinate.

† Reversal.

adults would result in almost constant contacts. It was hoped that food sharing, and the conditions surrounding this behavior might result as well as competition for food.

The feed box experiment was conducted 12 times. On mornings when the experiments were performed, the experimenter moved the elands and the zebra from the field to adjacent pastures. At about 9:30 or 10:00 the box was placed on the rock where grain normally was scattered by the keeper. Then the experimenter emptied one bucket of grain into the box and withdrew behind a gate about 20 yards away. The sheep were observed by means of binoculars and their behavior was recorded immediately in a note book. Usually at the end of an hour it was necessary to place more grain in the box.

The general pattern of social interaction at the feed box was similar throughout the entire series of experiments. During the series of group tests an order of dominance was formed which conformed closely to that observed during the matching tests. Rams 1 and 2 always dominated the other animals at the box during the first 15 or 20 minutes of feeding. The other sheep milled around the feed box but were not permitted to eat. *The two dominant rams ate alternately.* Whenever Ram 1 raised his head to chew or rest, Ram 2 ate from the box. As Ram 1 again lowered his head, Ram 2 usually withdrew his head. A high degree of orderliness usually characterized the feeding of these two sheep. Often Ram 2 did not withdraw until

he was threatened or mildly butted by Ram 1. In the main, Ram 1 butted and shoved Ram 2, and the latter in turn kept the other sheep from the box. Upon being forced from the box by the more dominant animal, Ram 2 might circle the box and butt all the sheep in his path.<sup>2</sup> After the first few minutes the other animals ceased to crowd around the box. Some of them moved to a nearby tree and others formed a wide circle about the feeding place.

When he had completed his first feeding, Ram 1 left the feeding area. Ram 2 would either leave at the same time, or continue feeding. Then Ram 3, or Rams 3 and 4 together, moved up to the box, and interactions very similar to the previous ones were exhibited. During the first 30 or 40 minutes the box was controlled constantly by a pair of rams. But after the initial feeding of Rams 1 and 2 the pairings shifted frequently due to the movements to and from the box of dominant rams. From time to time ewes and lambs attempted to feed, usually with little success. The subordinate ram of a pair did most of the butting and chasing of the other members of the herd.

During the second hour the rams spent less time at the box, and when there manifested *increasing tolerance* toward the lambs and ewes. The order of feeding among the ewes was also determined mainly by dominance status, while a lamb's ability to feed depended on the tolerance of its own ewe. Often Ewe 4 and Lamb 1 (the yearling) obtained little or no food during an entire experiment. Being of low dominance status, the ewe was excluded, and the lamb likewise because it lacked high dominance maternal protection. The experiment usually ended shortly after the noon hour, when the sheep began to move toward the north fence for pellets offered by visitors.

*Dominance.* In Table II are presented the butts and threats given and received by each sheep during the series of 12 feed box experiments.<sup>3</sup> Except for two instances, threats were always directed by dominant animals against subordinate ones. The butt more frequently was directed by a subordinate sheep against a dominant one. Nineteen butts, of a total of 198, fall in this category.

The data on rams in Table II indicate that the dominance-subordination relationships among these animals were somewhat less rigid and involved more behavioral interaction among individuals than in the matching tests. However, it must not be assumed that relationships at the feed box were less stable. Stability cannot be inferred from the ratio of butts given and received. Nor would

a mere tabulation of instances of food sharing and food hoarding provide a valid basis for inferring dominance status. For example, Rams 1 and 2 usually ate together with little overt indication of dominance-subordination. Often they fed alternately for three or four minutes without observable conflict. But upon closer examination it could be seen that Ram 1 *permitted* Ram 2 to eat with him, and even to shove him occasionally. Over-vigorous shoving or persistent crowding on the part of Ram 2 always elicited a sharp attack from Ram 1. Exchanges of butts might be equal in number but they always ended with Ram 1 in control of the box.

Wide variations in the "social distance" between different rams are apparent. Reciprocity of aggression was relatively high between Rams 1 and 2 and between Rams 2 and 4, but Ram 3 never aggressed against Ram 1 or Ram 2, and was almost never aggressed against by Ram 4.<sup>4</sup> The meaning of these differences in "social distance" will become clearer at a later point in the discussion. Among the sheep included in Table II, frequencies of butts and threats decrease in almost perfect rank order. The data on ewes and lambs has not been analyzed in detail because of the low frequency of aggressions. Lambs 2, 3 and 4 are not included in the Table only because their scores on both items were zero.

*Feeding time.* Scores for feeding time were computed from the Bristol recordings of an experiment on August 11 according to the method described in the first footnote to Table III. The time score for each sheep is the number of 10-second periods during which the animal had its head in the box for two seconds or longer. In Table III individual scores are given for each of nine consecutive periods. The periods are 16.6 minutes in length. Individual totals for the whole experiment indicate a lack of positive relationship between dominance status and feeding time, although the differences between rams and ewes, and adults and lambs, are on the whole substantial. The lack of relation between feeding time and dominance status may be due to wide individual differences both in rate of food intake and nutritional needs.

For most of the sheep there is a single period during which much more feeding occurred than during other periods. This would seem to justify a comparison of the periods in which individuals made their highest scores. Such scores have been indicated in the Table by a small circle. The circles follow a line which gradually descends from left to right, indicating that time-of-maximum-feeding is closely related to the dominance order. The near-zero scores of Ewe 4 and Lamb 1 have already been discussed.

*Coordinate-feeding.* An important type of social interaction among the sheep was that of coordinate-feeding, or food sharing. The concept and the unit of measurement employed are described in the first footnote to

<sup>2</sup> These attacks by Ram 2 against subordinate sheep appeared to be clear instances of *displaced aggression*, and will be discussed later on in this paper.

<sup>3</sup> A threat is defined as an aggressive movement or pattern of movements which one sheep directs at another, but which does not end in physical contact. The typical threat consisted of a sudden lowering of the head and slight movement toward the other animal. But sometimes a mere lowering and twisting of the head composed the pattern. The object of a threat usually withdrew immediately or modified his behavior in some observable way.

<sup>4</sup> See footnote to Table II.

TABLE II.  
Total Butts and Threats for 12 Feed Box Experiments\*.

	Threats						Butts					
	Recipients						Recipients					
	Ram #1	Ram #2	Ram #3	Ram #4	Ewes & Lambs	Total	Ram #1	Ram #2	Ram #3	Ram #4	Ewes & Lambs	Total
Ram #1	x	21	1	2	21	45	x	42	5	5	15	67
Ram #2	0	x	4	2	16	22	9	x	2	13	16	40
Ram #3	0	1	x	8	11	20	0	0	x	14	19	33
Ram #4	0	0	1	x	18	19	0	8	2	x	15	25
Ewe #1	0	0	0	0	5	5	0	0	0	0	17	17
Ewe #2	0	0	0	0	6	6	0	0	0	0	12	12
Ewe #3	0	0	0	0	0	0	0	0	0	0	8	8
Ewe #4	0	0	0	0	0	0	0	0	0	0	3	3
Lamb #1	0	0	0	0	0	0	0	0	0	0	4	4

\* Intermittent fighting was observed between Ram 2 and Ram 4, and between Ram 3 and Ram 4, during the second week in September. Butts exchanged during these fights have not been included in the table because on the two days that these fights occurred the experimenter was occupied with taking motion pictures. However, only one

fight might be said to have ended in favor of Ram 4. This fight was between Ram 4 and Ram 2. Since these fights were associated with sexual excitement in Ram 4 the table as presented is representative of social relations before the onset of rutting behavior. Fighting and rutting behavior will be discussed in a later section.

Table IV. The unit of measurement is, of course, arbitrary, but it has the merits of being easily computed from the raw data and of yielding quantitative relationships which are in close agreement with observations made during 12 experiments. Table IV contains data on coordinate-feeding among the rams. Both absolute frequencies and coordinate-feeding ratios indicate that among those pairings in which the possibility of coordinate-feeding existed relatively often its frequency varied widely. The ratios are high for Rams 1 and 2 and Rams 2 and 4, and low for Rams 2 and 3 and Rams 3 and 4. Parallel differences among pairs have already been noted with regard to butts and threats. *Aggressive interactions and food sharing vary together.* But although they are associated, it would be wrong to assume that one is a primary cause of the other. Rather, both are directly related to the amount of social distance between individuals. Social distance is psychological rather than spatial, and is de-

termined by the willingness-for-contact, or tolerance, of the dominant sheep with regard to the subordinate. Lack of unilateral or bilateral aggression between two sheep may be an indication of very low tolerance on the part of the dominant animal. Thus, on the day for which coordinate-feeding data is presented, Rams 3 and 4 were the only rams together at the box for a longer time than Rams 1 and 2 were present together, yet the only aggression between the former individuals was a single threat by Ram 3, and the coordinate-feeding ratio was 4/25. In contrast, Ram 1 threatened or butted Ram 2 sixteen times and received three butts from the latter, while the coordinate-feeding ratio was 16/21.

Quantitative data on coordinate-feeding among the ewes was not obtained because during the experiment on August 11 one or more rams were almost always present at the box. The recorded observations of all 12 experiments show that when no ram was pres-

TABLE III.  
Feeding Time Scores of Sheep in Experiment Lasting Two and One-half Hours.\*

Periods†	Ram #1	Ram #2	Ram #3	Ram #4	Ewe #1	Ewe #2	Ewe #3	Ewe #4	Lamb #1	Lamb #2	Lamb #3	Lamb #4
I	87°	82°	2	3	1	5	0	3	0	0	0	0
II	27	18	54°	8	6	3	0	0	0	0	0	0
III	0	13	28	18	26°	15	14	3	0	9	5	8
IV	10	26	6	39°	7	0	11	0	0	18	0	0
V	0	0	15	12	0	7	7	0	0	11	0	0
VI	9	9	28	25	14	22°	13	0	0	21	4	0
VII	12	0	5	15	12	0	35°	0	0	36°	0	11
VIII	0	28	1	28	0	16	0	0	0	8	11°	0
IX	0	43	19	19	15	7	3	0	2	1	6	14°
Totals	145	219	158	167	81	75	83	6	2	104	26	33

\* This was the only occasion upon which a Bristol recording was made for an entire experiment. The experiment was conducted on August 11, and was the sixth in the series of 12. Time scores were computed from the recorded data by counting for each sheep the number of 10-second periods during which the animal had its head in the box for two seconds or longer. This method of

scoring, while less accurate than the very laborious procedure of counting actual time in seconds, does not introduce a serious bias, in the opinion of the experimenter.

† The total time of two and one-half hours was divided into nine periods of 16.6 minutes each.

° Maximum score for a single period.

TABLE IV.

Incidence of Coordinate-feeding Between Rams During Experiment Lasting Two and One-half Hours.\*

Pairings	Frequency of coord-feeding	Highest frequency possible†	Coord-feeding ratio
Rams 1 and 2	16	21	16/21
Rams 1 and 3	1	5	1/5
Rams 1 and 4	1	4	1/4
Rams 2 and 3	3	14	3/14
Rams 2 and 4	8	11	8/11
Rams 3 and 4	4	25	4/25

\* Coordinate-feeding between two rams is said to occur when both of these rams obtain feeding scores of 3 or more during a 100-second period, while the other two rams obtain scores of zero (c.f. first footnote to Table III for unit of scoring). The coordinate-feeding data were obtained from the Bristol recordings and synchronized field notes of the feed box experiment on August 11.

† The highest frequency possible is the total number of 100-second periods during which a given ram could have engaged in coordinate-feeding with the dominant ram by virtue of the fact that the dominant ram was (a) the only other ram at the box, or (b) accompanied at the box by a ram subordinate to the ram in question.

ent Ewes 1 and 2 dominated other animals at the box. Food sharing was common among Ewes 1, 2 and 3. The lambs almost never had exclusive possession of the box, and when at the box they showed no overt aggression.<sup>5</sup> The amount of time that they fed depended on the tolerance of the lambs by the ewes. Hence, differences in the ability of individual lambs to feed are related to differences in ewe-lamb relationships. Field observations furnished ample evidence of the following mother-young relationships: Ewe 3 and Lamb 2, Ewe 1 and Lamb 3, and Ewe 2 and Lamb 4.<sup>6</sup> The yearling was not associated with a ewe in any observable way, either at the box or in the field.

There is reason to believe that the very high feeding score of Lamb 2 was due to an especially close and permissive relationship with its mother. Lamb 2 usually stood very close to its own ewe at the box, and fed whenever she did. Ewe 3 never butted her lamb, although she did not tolerate other lambs. Lambs 3 and 4, on the other hand, did not stay close to their ewes, and often were not at the box when their ewes were feeding. It will be seen in Table III that the feeding scores of Ewe 3 and Lamb 2 are very similar from period to period. The average difference in scores for the same period is only 2.8. Analysis of the Bristol recordings reveals that, of a total of 20 100-second periods during which Ewe 3 fed, her lamb also fed during 17 periods. In contrast with this, Ewe 1 and Ewe 2 fed about as frequently as Ewe 3, but Ewe 1 shared with her lamb only twice, and Ewe 2 never shared with hers.

The lack of agreement between the dominance status of ewes and their lambs may have been noted. Dominance order among the first-season lambs shows no relation to dominance order among the mothers. Of course the number of sheep is much too small to warrant generalizing, but there are two possible correlates of dominance order among first-season lambs that might be mentioned. First,

<sup>5</sup> The lambs often shoved each other, but never threatened or butted when at the box.

<sup>6</sup> Sucking and following were the principal behavioral indications of mother-young relationships during July, August, and September.

it is possible that dominance among these lambs is related to order of birth, so that lambs born in February tend to be dominant over those born in March or later. There is no way of checking this hypothesis in the present study, since the birth dates of individuals are not known. Stewart and Scott (14) have found that age is favorable to dominance in a herd of goats.

A second hypothesis is that the amount of social distance between a ewe and her lamb will have a direct bearing on the dominance status of the lamb. In the case of Ewe 3 and Lamb 2 extreme social closeness is associated with dominance of this lamb over two other lambs born in the same season. On the other hand, the relationship between Ewe 2 and Lamb 4 (the lamb of lowest dominance status) was the weakest of the three mother-young relationships. Ewe 2 was the least willing to share food with her lamb or to be sucked. Further credence is given to this suggestion by Scott's (11) observations of two orphan lambs which were placed with a flock of domestic sheep. He noted that, "Both orphans appeared to show less fighting than the other sheep . . . and the ram was not aggressive toward other males even in the breeding season." The hypothesis could be tested in a large herd by testing dominance interactions among the ewes and among the lambs over a period of time beginning shortly after the birth of the lambs, and making frequent observations of each ewe with her lamb in isolation from the other sheep.

#### LEADERSHIP

Recent studies indicate that leadership may be a behavioral characteristic quite unrelated to dominance status maintained by fighting. The reports of Darling (5) on red deer, Mills (10) and Davis (6) on Rocky Mountain bighorn sheep, and Scott (11) on domestic sheep, all mention that the usual leader in a herd is an old female. Lack of correlation between leadership and dominance interactions has been noted by Allee et al (1) in a flock of ducks, and Stewart and Scott (14) in a herd of goats.

In the present study, clear instances of

leadership occurred only when the sheep were in a conflict situation involving both a source of attraction and a source of danger in close proximity to each other. The source of attraction was the feed box; danger usually was represented by the presence of a strange person, such as the experimenter. The experimenter discovered that if he stood a few yards behind the box after filling it, the sheep would flock into the center of the field and not advance to feed for several minutes. Finally, Ewe 1 slowly moved forward about ten yards and then halted. Her lamb immediately ran to her. Then the other ewes and lambs, and finally the rams, moved up to her advanced position. If the experimenter withdrew further from the box the process of advancing and halting under the leadership of Ewe 1 might be repeated several times, until the herd finally reached the box. The pattern of advance might vary from day to day, but Ewe 1 always led the others. Sometimes she advanced 15 or 20 yards in front of the herd before they followed her. Sometimes the entire herd moved in single file, with Ewe 1 in the lead and the rams bringing up the rear. The rams rarely came up to the box until Ewe 1 had begun to eat.

Leadership was observed 15 times, always in connection with the feed box experiments. Once the rams dashed ahead of Ewe 1 when she was about five yards from the box, and on two occasions Ewe 2 took the lead after Ewe 1 had led most of the way. But at all other times Ewe 1 moved in advance of the others. There is ample evidence that the sheep were following Ewe 1, rather than just moving toward the feed box. Seven times Ewe 1 did not take the most direct path to the box, but turned and walked at right angles to it for several yards. When she did this, the other sheep continued to follow her just as as though she were approaching the box. When no person was in the field, the sheep moved toward the box more or less independently of each other, but the rams still tended to stay behind the ewes.

On general grounds it would be expected that boldness and leadership were related. In the present study there were no opportunities for observing differences in boldness among the ewes. However, the rams did appear to be more timid than the ewes. A lone ram rarely stayed at the box for more than a few seconds. In all likelihood, when he raised his head from the box and saw that the others had left he would quickly run to where they were. On the other hand, a single ewe might continue feeding alone indefinitely. When the zebra, which had been placed in an adjacent enclosure, suddenly galloped toward the fence, the rams were the first to run from the box and the last to return. This was also true when the experimenter intentionally frightened the herd. The zebra frightened the sheep away from the box about eight times, and each time Ewe 1 led them back. Thus there is considerable evidence that the role of Ewe 1 as leader was

not due merely to a greater familiarity with humans.

In the field studies cited above, leadership usually was an important factor in the normal moving about of the sheep and deer. But among the Barbary sheep, instances of leadership were quite rare outside of the special conflict situations described. In wandering and grazing the herd often was scattered widely over most of the field. The rams, ewes and lambs often formed into separate and dispersed sub-groups, yet no consistent leadership was apparent in any one of the subgroupings. What little leading and following there was occurred between lambs and ewes, and between rams and ewes with the onset of sexual activity.

*Ewes and lambs.* During approximately 80 hours of observation from mid-July to mid-September, each first-season lamb attempted to suck its ewe about 20 or 30 times. The usual duration of sucking was only a few seconds, and often the attempt consisted of a single, brief thrust at the udder. Generally the ewe was passive while the attempt was made. Lamb 4, however, often was rejected by its ewe, even though it tried to suck less often than the others. For a while, in fact, its maternal origin was not clear. The lamb alternated between following Ewe 2 and Ewe 4, and twice tried to suck from Ewe 4. Repeated observations confirmed its relationship with Ewe 2. Sucking was accompanied by a certain amount of following of ewes by their lambs. When the herd rested a lamb often lay beside its ewe. The yearling associated with the other lambs and joined in the general movements of the herd, but did not favor a particular ewe.

*Rams and ewes.* As the rams began to manifest sexual interest in the ewes they gradually spent more time in the company of the ewes and tended to follow them closely during early morning and evening. Before August 15 relatively little following occurred. Perhaps the following of the ewes by the rams in the conflict situations is, in part, the result of conditioning which develops during the rutting season.

#### FIGHTING.

The Barbary sheep would seem to fall about half way between the domestic sheep and the bighorn with regard to amount of fighting. Scott (11) mentioned pushing and shoving among domestic sheep competing for food in winter, and some butting between rams following the same ewe in heat. In contrast, Mills (10) stated that fights between big-horn rams in rut might result in "bleeding noses, splintered horn tips, limping, and skull fractures." No complete comparison can be made with the bighorn because the Barbary sheep were not observed during the height of rutting. There were no observable injuries, and it is probable that the fighting witnessed was far less serious than that associated with breeding.

Two main types of fighting occurred

among the Barbary sheep. One type consisted of a series of head-on charges, usually between rams. The sheep walked away 10 or 15 yards, turned, and walked rapidly toward each other, gradually picking up speed and breaking into a run shortly before they collided. Just before impact their heads were lowered and turned slightly to opposite sides. They attempted to meet squarely with their noses crossed. At the beginning of the charge, the sheep got in step and then tried to keep in step until they struck. If one got out of step they broke off the charge and walked away to charge again. Spencer (13) described bouts between bighorn rams which were very similar in detail. He termed such fights "playful" because one ram would not attack if the other was off balance or not prepared. A fight of this type between Ram 1 and Ram 2 continued intermittently for 25 minutes on August 25. Before that time fights had never lasted more than five minutes.

The second type of fighting consisted of close butting, and locking and twisting of horns. Usually the sheep stood head to head, facing in the same or in opposite directions, and engaged their horn tips. Each tried to twist the head of the other by pulling downward and away. Also, attempts were made to hook the belly or the flank. Fighting of this sort might continue for several minutes. It sometimes started at the feed box as a kind of maneuvering for position.

Until mid-August fighting was almost as common among the ewes as among the rams. The usual fight between ewes consisted of a brief exchange of butts, perhaps with locking of horns and twisting. Charges were very rare. Ewes did not fight with rams.

From mid-August until the termination of the study fighting among the rams increased in frequency, duration and vigor, and was connected with sexual excitement. Rams 2 and 4 were the first to show increased pugnacity and sexual behavior. These rams fought with each other and with the other two rams. Sometimes the penis of a fighting ram emerged briefly from its sheath. By September 10 all four rams had reached a high level of sexual arousal and aggressiveness. Most of the fighting took place in the early morning and in the evening, with relatively little aggressive interaction at the feed box or during the matching tests. Even when Ram 4 was beginning rut and displayed strong aggression toward Rams 2 and 3, he remained rather submissive at the feed box. During the final two days at the box, Ram 4 started fights with Rams 2 and 3. He fought with each male about three times, the average duration of fighting being about two or three minutes. But only once, in a contest with Ram 2, did it appear that he had achieved temporary dominance over his opponent.<sup>7</sup> And only once did Ram 4 achieve dominance

in a paired matching test. His opponent in this test was Ram 2. Possibly in the two experimental situations Ram 4 was inhibited by previous experiences of defeat and subordination. Seward (12) with rats, and Ginsburg and Allee (7) with mice, have shown that an animal could be conditioned to defeat much more readily than to victory. Although they did not study the factor of physical environment, it seems reasonable to expect that aggression would be most strongly inhibited in the place where subordination had been experienced most frequently.

Play fighting was frequent among the lambs. Often in the evening they scrambled about, pushing and butting each other, in order to gain a position on top of the rocky hillock in the center of the field. This activity was similar to the children's game, "king-of-the-hill," and has been reported by Darling (5) as occurring among red deer fawns. Sometimes fighting in lambs had a more serious appearance. Two lambs might butt head-on forcefully and in rapid succession until both seemed quite exhausted. There was one instance of a lamb fighting with an adult. Late in August Ewe 4 butted Lamb 3 and the lamb immediately butted back. A short fight ensued, ending with the lamb's retreating and then attacking Lamb 4.

#### SEXUAL BEHAVIOR OF THE RAMS.

The first witnessed attempt to mount a female was by Ram 2 on August 10. The ram reared on his hind legs and his penis emerged about three inches from its sheath for a few seconds. The ewe ran off. The ram then tried to mount another ram. Toward the end of August attempted mountings by rams of both rams and ewes were common. This behavior was not observed to occur in the ewes or lambs. Female urine had an excitatory effect upon the rams. The ram sniffed the urines, then curled the upper lip, extended the neck, and tilted the nose in the air. This pattern, according to Spencer (13) is found in bighorns, as well as in other ungulates. Rams sometimes lay on their backs and sucked their penises for short periods. Ejaculation of semen was not observed to occur. Often in the evening, sexual activity and fighting occupied the rams continuously until dark. At no time during observation was a ewe receptive. A ram did not persist in attempting to mount the same ewe. Two tries were usually enough to discourage him. There was no chasing about the field. A ewe had only to walk or run a few yards to get rid of a ram.

#### DISPLACED AGGRESSION.

One of the most striking behavior patterns observed in the course of this study was that in which a sheep responded to a butt, threat or attack from a dominant sheep by delivering in kind to the nearest subordinate. Such "displaced aggression" might continue chain-wise through three or four

<sup>7</sup> The butts exchanged have not been included in the data because the experimenter was engaged in taking motion pictures, and so could not take notes.

individuals, each successive one being lower in dominance. Thus a ram might butt a subordinate ram away from a piece of bread, the latter might butt a ewe nearby, and the ewe in turn a lamb. At the feed box Ram 2 often responded to a sharp butt from Ram 1 by circling the box and butting all the sheep in his path. The examples of displaced aggression are too numerous to be listed. The pattern appeared in rams, ewes and lambs with great frequency. There seemed to be only two factors determining which sheep was to receive a displaced attack, physical proximity and lower dominance status. No special relationships between individuals were apparent, other than the usual ones of dominance-subordination. Winslow (15) found displaced aggression in cats made to compete for food.

#### SUMMARY AND CONCLUSIONS.

1. This study represents an attempt to analyze social behavior and group organization in a small herd of Barbary sheep.

2. Observations and experiments were made on the herd of four rams, four ewes, and four lambs at the New York Zoological Park during the summer of 1947, under conditions with a minimum of human care and interference.

3. In two types of tests it was found that stable relationships of dominance-subordination existed between all individuals, and that the dominance order of all eight sheep was one of straight descent through rams, ewes and lambs.

4. When grain was placed in a small feed box it was found that individual differences in total feeding time at the box were not related to the dominance order. These individual variations probably were due to different rates of food intake and differences in nutritional needs.

5. In the feed box experiments it was found that there was an order of time-of-maximum-feeding which was very similar to the order of dominance.

6. Differences were found in the "social distance" between any two rams when at the feed box. These differences were reflected in the amount of food sharing that occurred and in amount and reciprocity of aggression. Food sharing and aggressive interaction were positively related, and both appeared to be manifestations of the dominant animal's tolerance, or willingness-for-contact with regard to the subordinate.

7. There were individual differences in amount of food sharing and amount of suckling among three ewe-lamb pairs. The dominance status of the lamb seemed to be associated with the social distance between the lamb and its mother. But there appeared to be no relation between the dominance status of the ewe and the dominance status of her lamb.

8. Consistent leadership appeared only in conflict situations characterized by a locus

of attraction and a locus of danger in close proximity to each other. In conflict situations a ewe always led, and with only two exceptions it was always the same ewe. The rams were more timid than the ewes in strange and potentially "dangerous" situations.

9. Fighting occurred between rams, ewes and lambs. With one exception, there were no fights between ewes and rams, or between adults and lambs. Ewes fought less than rams, while among lambs play-fighting often was observed.

10. As sexual activity appeared in the rams, fighting became more frequent and vigorous.

11. Dominance relationships between rams remained stable throughout the study and from the time of the first appearance of sexual interest until the study terminated five weeks later.

12. Sexual activity in the rams consisted of attempted mounting of ewes and rams and sometimes of incomplete masturbation. Ewes were not receptive up to September 14, when the study ended.

13. Instances of displaced aggression were very numerous. The recipient was usually the nearest subordinate animal.

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## 4.

The *Pericopidae* (Moths) of Kartabo, British Guiana, and Caripito, Venezuela.<sup>1</sup>

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[This contribution is the result of various expeditions of the Department of Tropical Research of the New York Zoological Society to British Guiana and to Venezuela, all under the direction of Dr. William Beebe. The Guiana expeditions were made during the years 1917, 1919, 1920, 1921 and 1924. The expeditions were arranged so that each month of the year is represented in the collections. The Venezuelan expedition, in 1942, during which field work was carried on from February 19 to September 2, was sponsored by grants from the Committee for Inter-American Artistic and Intellectual Relations and from four trustees of the Zoological Society, George C. Clark, Childs Frick, Laurance S. Rockefeller and the late Herbert L. Satterlee, and by invaluable assistance from the Standard Oil Companies of New Jersey and Venezuela.]

A total of eight species of *Pericopidae* were collected at Kartabo and four at Caripito. One species from British Guiana and two species from Caripito are new locality records for their respective countries. One species common to both British Guiana and Venezuela is represented by a new race in Venezuela.

*Eucyane bicolora* (Sulzer).

Sulzer, *Gesch. Ins.*, t. 22, f. 6 (Expl. Tab.) (1776) (Noctua).

Three specimens taken at Kartabo, two on October 11 and one on December 2. The species has been reported from the Guianas, South Brazil and Peru.

*Eucyane temperata* Walker.

Walker, *List. Lep. Ins. Brit. Mus.*, 7, p. 1656 (1856).

One specimen taken at Caripito on July 11. The species has been reported from South Brazil, Guianas and Colombia, so this is a new record for Venezuela.

*Pericopis catilina catilina* (Cramer),  
new status.

Cramer, *Pap. Exot.*, 1, t. 79, f. E. F. (1775) (Attacus).

In my opinion *Dysschema brotes* (Druce) *Ann. Mag. Nat. Hist.*, 15 s. 6, p. 48 1895 (*Anthomyza*) is only the male form and thus a synonym of *Pericopis catilina catilina*. The males in collections are usually named *brotes*

and the females *catilina*. The male specimens match Druce's description better since the males are usually blackish-brown rather than the cinnamon brown typical of the females. Furthermore, the character given in the literature to separate the genus *Dysschema* from *Pericopis* is not valid. This character, the length of the pinnæ of the antennæ double the width of the shaft, is a male sexual character typical of many of the species of *Pericopis*. I am not synonymizing the genus *Dysschema* since the genotype *tiresias* is not available, but the present generic character does not justify the genus. Thus, on the basis of this character the male specimens of *catilina* are assignable to *Dysschema*, hence *brotes*, and the females to *Pericopis*, hence *catilina*.

One male captured at Kartabo on May 24. Recorded from Brazil, Guianas and Colombia.

*Pericopis catilina angustilineata*, new  
sub-species.

Specimen	Sex	Date	Length of forewing	Type
42487	male	March 15	35 mm.	Holotype
42488	female	March 16	38 mm.	Allotype
4239	male	March 11	38 mm.	Paratype
42489	male	April 15	35 mm.	Paratype
42490	male	March 15	37 mm.	Paratype
42491	male	June 5	35 mm.	Paratype
42492	female	April 8	38 mm.	Paratype

Head as in *c. catilina*. In the male the length of the pinnæ of the antennæ is twice the width of the antennal shaft, while in the female the pinnæ are barely as wide as the antennal shaft.

Ground color of both the fore and hindwings blackish-brown to cinnamon brown with bands of greenish-yellow.

The forewing with two semi-hyaline greenish-yellow bands, one median and the other apical as in *c. catilina* with brown or brownish-black veins crossing the bands. The bands differ from those of *c. catilina* in being much reduced; little more or not more than half the width of the bands of *c. catilina*. If one assumes the nomenclatural type to be ancestral, the reduction of the bands has been caused by the encroachment of the brown or blackish-brown scales on both sides of the bands. This is most easily discerned in the median band. The inner side of the band in *c. catilina* crosses the wing nearer to the

<sup>1</sup> Contribution No. 827, Department of Tropical Research, New York Zoological Society.

point where vein  $Cu_2$  forks from the cubital stem than it does in *c. angustilineata*. Similar results are obtained if one measures basally from the point where vein  $Cu_1$  forks from the cubital stem. In both *c. catilina* and *c. angustilineata*, but particularly in the latter, the encroachment of the ground color on the yellow bands may be seen. The brown scales on the margins of the bands are duller and lighter than the surrounding ground color. This is variable, being more evident in some specimens than others and occurring indiscriminately along the length of the bands. It is most noticeable and frequent on the median bands. The white spots along the outer margin of the forewing are evident to varying degrees. Their place is taken by the brown or blackish-brown scales making up the background. However, all specimens have a streak of white scales on the outer side of the yellow spot which terminates the apical band in cell  $M_3$ . The spots in cells  $M_1$  and  $M_2$  appear to vanish first since they are faintly discernible in only one specimen.

The hindwings of *angustilineata*, as in *catilina*, are yellow hyaline for half the length of the wings from the base with a large yellow spot beyond in cells  $M_1$  and  $M_2$ . *Pericopis c. angustilineata* differs in that this large yellow spot is separated from the basal patch by a distance approximately twice that of *catilina*. The part of the basal facies that extends into the proximal part of cell  $Cu_1$  is much smaller in *angustilineata* than in *catilina*. The ground color along the inner margins of the hindwings encroaches more on the yellow basal area in *angustilineata* than in *catilina*.

The specimens were all collected during the day while flying. No specimens of Danaidae or Heliconiinae were captured or seen in the same area, though the general appearance and flight of *angustilineata* is suggestive of various members of either of the above groups. The specimens were captured in an area of about one hundred meters' diameter near the end of an unmaintained road going to an abandoned oil well "No. 1". The locality is approximately ten miles west of Caripito, State of Monagas, eastern Venezuela. The area the specimens came from is parched during the dry season, flooded during the wet and characterized by numerous palms and small to very moderate-sized seasonal trees.

***Pericopis tricolora tricolora* (Sulzer).**

Sulzer, Gesch. Ins., t. 22, f. 5 (1776) (Noctua).

Three specimens taken at Kartabo; two females on March 22 and one male on November 24. Recorded from eastern Peru, Amazonas and Guiana.

***Dysschema heliconides* (Swainson).**

Swainson, Zool. 111. (2), 3, t. 124, f. 2 (1833) (Anthomyza).

One specimen collected at Kartabo in 1920. Recorded from the Amazons, Guianas, Colombia and Peru.

***Hyalurga fenestra* (Linnaeus).**

Linnaeus, Syst. Ent. (ed. 10), 1, p. 505, n. 41 (1758) (Phalaena).

One specimen collected at Kartabo which represents a new record since the species has only been reported from Brazil and Peru.

***Hyalurga sixola* Schaus.**

Schaus, Ann. Mag. Nat. Hist., (8), 6, p. 206 (1910).

A total of seven specimens was taken at Caripito; the males on March 20 (two specimens), April 5, May 12, and May 16 and the females on April 15 and July 2. Recorded from Venezuela and Colombia.

***Hyalurga mysis* (Erichson).**

Erichson in Schoenburgk, Brit. Guiana, 3, p. 606 (1848) (Glaucopis).

A female from Kartabo on May 25. Has only been found in British Guiana.

***Hyalurga modesta* Moschler.**

Verh. Zool.-bot. Ges. Wien, 27, p. 663, t. 9, f. 29 (1877).

One female at Kartabo on August 19. Recorded from Guiana and Colombia.

***Hyalurga pariita* (Walker).**

Walker, List. Lep. Ins. Brit. Mus., Het. 2, p. 335, n. 27 (1854) (Dioptis).

Four female specimens at Kartabo; two with no date and the remaining two specimens on November 21 and December 21. One female at Caripito on March 21. Recorded from Brazil, Guianas, Venezuela and Peru.

## 5.

Report on a Collection of Phalangids from Rancho Grande, Venezuela.<sup>1</sup>

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(Text-figures 1-4.)

[This is one of a series of papers resulting from the 45th and 46th Expeditions of the Department of Tropical Research of the New York Zoological Society, made during 1945 and 1946 under the direction of Dr. William Beebe, with headquarters at Rancho Grande in the National Park of Aragua, Venezuela. The expeditions were made possible through the generous cooperation of the National Government of Venezuela and of the Creole Petroleum Corporation.]

[The characteristics of the research area are in brief as follows: Rancho Grande is located in north-central Venezuela (10° 21' N. Lat., 67° 41' W. Long.), 80 kilometers west of Caracas, at an elevation of 1,100 meters in the undisturbed montane rain forest which covers this part of the Caribbean range of the Andes. Adjacent ecological zones include seasonal forest, savanna, thorn woodland, cactus scrub, the fresh-water lake of Valencia and various marine littoral zones. The Rancho Grande area is generally subtropical, being uniformly cool and damp throughout the year because of the prevalence of the mountain cloud cap. The dry season extends from January into April. The average humidity during the expeditions, including parts of both wet and dry seasons, was 92.4%; the average temperature during the same period was 18° C; the average annual rainfall over a five-year period was 174 cm. The flora is marked by an abundance of mosses, ferns and epiphytes of many kinds, as well as a few gigantic trees. For further details, see Beebe and Crane, *Zoologica*, Vol. 32, No. 5, 1947. Unless otherwise stated, the specimens discussed in the present paper were taken in the montane cloud forest zone, within a radius of one kilometer of Rancho Grande.]

This paper is a report on the phalangids collected during the 45th and 46th Expeditions of the Department of Tropical Research.

The species showed relationships to those of Trinidad (Goodnight and Goodnight, 1947), many of the specimens representing the same species. The Cosmetidae, one of the most typical of neotropical families, is here represented by two species, one of which is new.

Among the Phalangodidae, the Stygnommatinae are represented by the wide-ranging *Zygobunus rufus* (Petrunkevitch). This was formerly known only from Panama. The subfamily Phalangodinae is represented by *Kalina tuberculata* Goodnight and Goodnight

known formerly only from Trinidad. The Triacommatae are represented by one new species, *Vima plana*.

Among the family Gonyleptidae, three species are represented, one of which is new.

The writers wish to express their appreciation to Dr. Beebe and Mr. H. Fleming for making this material available for their study. Types are deposited in the collections of the Department of Tropical Research, New York Zoological Society, New York 60, New York.

## SUBORDER LANIATORES THORELL.

## PHALANGODIDAE Simon.

## Phalangodinae Roewer.

*Kalina tuberculata* Goodnight and Goodnight.

Reference: *Kalina tuberculata* Goodnight and Goodnight, 1947, p. 1, fig. 4.

Record: Zone 28, Rancho Grande, Venezuela, 1945.

## Stygnommatinae Roewer.

*Zygobunus rufus* (Petrunkevitch).

References: *Stygnomma rufum* Petrunkevitch, 1925, p. 62.

*Zygobunus barronus* Chamberlin, 1925, p. 245; Roewer, 1928, p. 546.

*Stygnommatiplus rufus* Roewer, 1928, p. 544.

*Zygobunus barronus* Goodnight and Goodnight, 1942, p. 4, figs. 10, 11, 12.

Record: Rancho Grande, Venezuela, March 4, 1945.

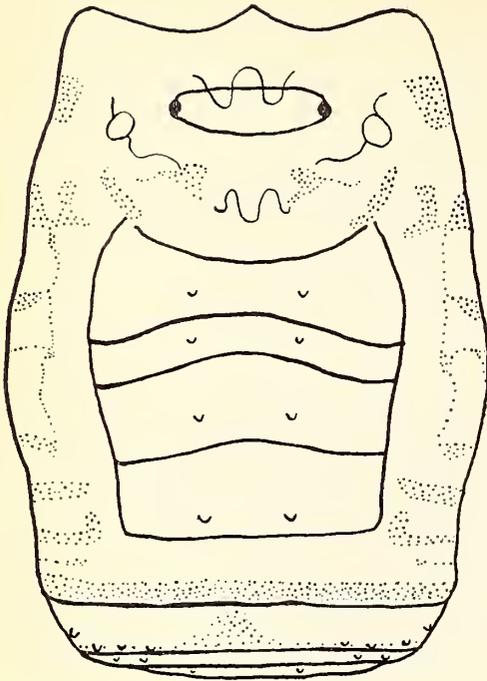
## Tricommatae Roewer.

*Vima plana* sp. nov.

(Text-figs. 1 &amp; 2).

Male: Dorsum with five areas, very small paired tubercles on the 1st, 2nd, 3rd and 4th areas. These tubercles are very small and vary in size in different individuals. Cephalothorax smooth, with a low tubercle at the posterior lateral portion. Eye tubercle wider than long, with low tuberculations across the median portion. First area of the abdomen without a median line. Boundaries of areas indistinct, not parallel. Lateral margin of abdominal scute smooth, without median armature. 5th area and free tergites each with a few small granulations. Anal operculum smooth, free sternites each with a transverse

<sup>1</sup> Contribution No. 828, Department of Tropical Research, New York Zoological Society.



TEXT-FIG. 1. *Vima plana* sp. nov. Dorsal view of male holotype.

row of minute tubercles. Spiracle visible. Coxae with a few small granulations; 1st coxa with a transverse row of spines.

First leg slender, unarmed; 2nd to 4th legs heavier, a few scattered tuberculations on the trochanters. Femora with longitudinal rows of spines, remainder of legs only with scattered hairs. 4th patella with a few apical tubercles. Double claws smooth, without scopula or false claw. Tarsal segments: 9-18-8-9. Distitarsus of 1st tarsus with 3 segments, 2nd with 3 also.

LENGTH OF LEGS.

	I.	II.	III.	IV.
	mm.	mm.	mm.	mm.
Trochanter	0.3	0.7	0.8	0.8
Femur	6.3	14.4	11.5	16.2
Patella	0.7	1.2	1.4	1.5
Tibia	4.0	10.8	6.1	8.5
Metatarsus	8.5	17.4	12.4	20.5
Tarsus	1.5	4.5	2.9	3.2
Total	21.3	49.0	35.1	50.7

Palpus with the trochanter 0.8 mm. long, femur 1.1, patella 0.7, tibia 0.6, and tarsus 0.7. Total length, 3.9 mm. Femur armed retrolaterally as in figure. Prolaterally femur and patella each with a median apical spine. Tibia and tarsus armed as on retrolateral margin.

Proximal segment of chelicera with a dorsal elevation on which are scattered tubercles. Distal segment greatly enlarged.

Body, chelicerae, and palpi light yellowish with scattered black mottlings. First leg uniformly colored; second leg with a white mark at the distal end of the femur; patella black,

a white patch at the distal portion of the tibia; third leg with a darker patella but no white markings; fourth leg with a white band following a black band on the distal portion of the tibia. Legs otherwise uniformly dark brown to dusky.

Female: Similar in appearance to male.

Measurements in mm.: Male, total length 3.7; cephalothorax 1.5; width at widest portion 2.6. Female, total length 7.2; cephalothorax 1.7; width at widest portion 4.2.

Record: Male holotype from Rancho Grande, Venezuela, July 22, 1945; paratypes from same locality, March 22, 1945, and July 22, 1945.

Remarks: *Vima plana* is related to *Vima insignis* Hirst. It differs from this latter species by lacking the raised area of the dorsum and the paired low tubercles over the eye.

COSMETIDAE Simon.

Cosmetinae Cambridge.

*Cynorta estebana* Roewer.

Reference: *Cynorta estebana* Roewer, 1947, p. 18, pl. 18, fig. 66.

Record: Rancho Grande, Venezuela, August 9, 1945.

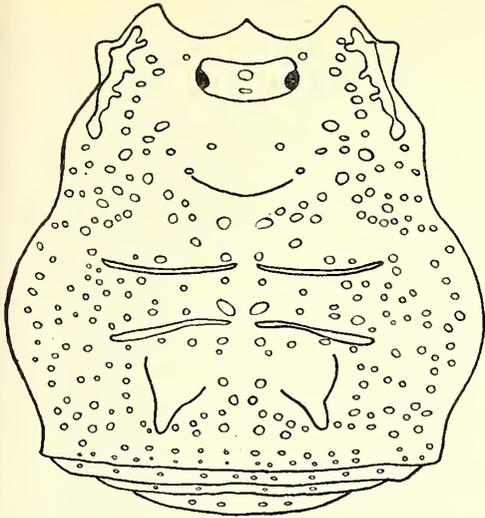
*Cynorta bromeliaca* sp. nov.

(Text-fig. 3).

Male: Eye tubercle wider than long. 1st area with a pair of enlarged tubercles, 3rd area with a pair of robust spines which are short and heavy at the base. Remaining areas and free tergites without median armature. Entire dorsum covered with small white elevations. These are more numerous on the lateral posterior portions of the scute. Each free tergite with a transverse row of these same tuberculations. Anal operculum with only a few granulations, free sternites each with a transverse row of hair-tipped granulations. Coxae and genital operculum smooth except for scattered hairs. A few teeth on the anterior margins of the 3rd and 4th coxae, and a transverse row of granulations across the 1st coxa.



TEXT-FIG. 2. *Vima plana* sp. nov. Retrolateral view of palpus of male holotype.



TEXT-FIG. 3. *Cynorta bromeliaca* sp. nov. Dorsal view of male holotype.

Legs clothed only with hairs except for a few tuberculations at the apical portion of the 4th patella; femora straight. Tarsal segments: 6-14-11-12. Distitarsus of both 1st and 2nd tarsi with 3 segments. Proximal portion of 1st tarsus enlarged.

LENGTH OF LEGS.

	I. mm.	II. mm.	III. mm.	IV. mm.
Trochanter	0.6	0.8	0.8	0.8
Femur	4.4	6.6	6.6	9.3
Patella	1.0	1.6	1.6	1.6
Tibia	2.8	8.3	3.8	5.3
Metatarsus	4.3	10.3	5.5	9.4
Tarsus	2.6	5.2	3.6	4.4
Total	15.7	32.8	21.9	29.8

Palpus with the trochanter 0.8 mm. long, femur 1.4, patella 0.9, tibia 1.5, and tarsus 0.8. Total length, 5.4 mm. Palpus characteristically flattened with a ventral row of teeth on the femur.

Proximal segment of chelicera with a dorsal elevation on which are a few granulations. Distal segment somewhat enlarged.

Dorsum reddish-brown, thickly covered with white spots which are more numerous on the lateral and posterior portions of the scute. These form an irregular band of white spots, with a few scattered ones in the median area. Several white spots on the eye tubercle. A transverse row of white spots across each free tergite. Anal operculum without markings. Venter, coxae, and chelicerae reddish-brown with darker markings. Legs yellowish, trochanters, and bases of femora, patellae, and tibiae reddish-brown. Metatarsi white.

Measurements in mm.: Male, total length 6; cephalothorax 1.9; width of body at widest portion 4.1.

Record: Male holotype from bromeliads, Rancho Grande, Venezuela, August 8, 1946.

Remarks: This species is most nearly related to *Cynorta catenulata* Roewer. It differs from this latter species by having an entirely different pattern of white on the dorsal scute.

GONYLEPTIDAE SUNDEVALL.

Cranainae Roewer.

*Poecilocranaus graciosus* Roewer.

Reference: *Poecilocranaus graciosus* Roewer, 1943, p. 54, pl. 7, fig. 63.

Record: Rancho Grande, March 22, 1945.

*Santinezia albilineata* Roewer.

Reference: *Santinezia albilineata* Roewer, 1932, p. 290, fig. 7.

Record: Rancho Grande, Venezuela, August 1, 1945.

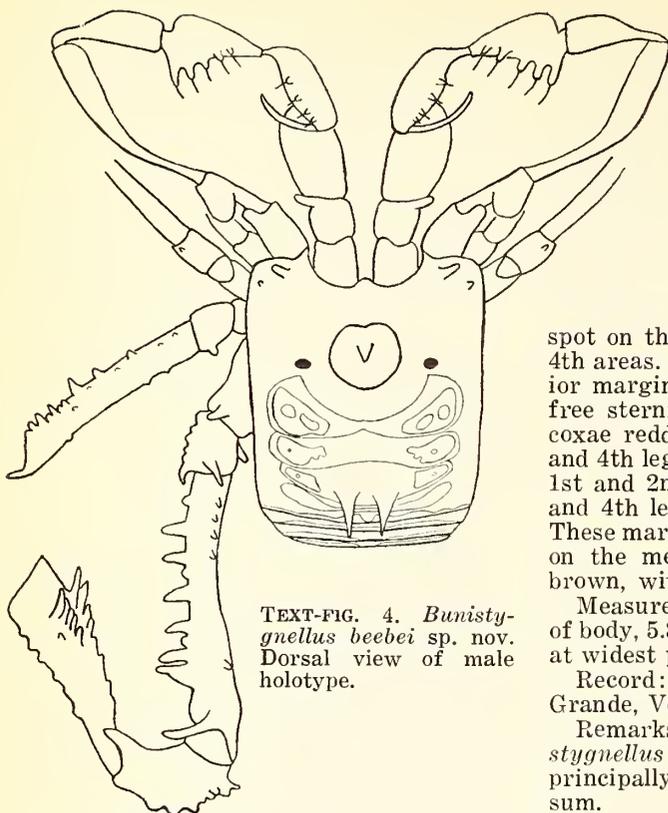
Stenostyginae Roewer.

*Bunistygnellus beebii* sp. nov.

(Text-fig. 4).

Male: Dorsum smooth, cephalothorax without a median eye tubercle. Eyes widely separated near the posterior portion of the cephalothorax. Between the eyes a large rounded elevation with a short apical spine. Elevation granular. Anterior margin of the cephalothorax with a short anterior projection between the chelicerae and palpi. A large vertical spine at the anterior margin near the coxa of the palpus. A small tubercle at the anterior lateral margin. Abdomen with five areas. 1st area constricted in the middle, 2nd area narrow, 3rd area with a pair of large spines, 4th and 5th areas unarmed. Free tergites smooth, unarmed. Lateral margins of scute smooth, anal operculum smooth. Free sternites each with a transverse row of hair-tipped tubercles which are enlarged into spines at the lateral margin: Spiracles widely open. Coxae covered with hair-tipped tubercles. A transverse row of spines across the 1st coxa. 3rd coxa with anterior and posterior teeth. 4th coxa only slightly projecting and with a large dorsal apical spine.

Trochanters globular. 2nd and 3rd trochanters tuberculate, 2nd with two small dorsal apical spines, 3rd with a posterior apical spine. 4th trochanter very heavy, with a large dorsal apical spine and a lateral spine on each side; covered with smaller tubercles. 1st and 2nd femora clothed only with hairs. 3rd femur covered with hairs and tubercles, ventrally with 2 long rows of spines and with 2 dorsal apical spines. 4th femur tuberculate, ventrally with 2 rows of very large spines, dorsal-apically with 2 large spines. Remaining segments of 1st and 2nd legs clothed only with hairs. Patella of 3rd leg tuberculate with a large ventral apical spine. 3rd tibia with 2 ventral rows of tubercles at the distal third, remainder of 3rd leg unarmed. 4th patella heavily tuberculate and with large apical spines. 4th tibia clavate, with 2 ventral rows of spines at the apical third. Remainder of leg clothed only with hairs. 3rd and 4th tarsi with heavy scopulae, double claws toothed. Tarsal segments: 7-



TEXT-FIG. 4. *Bunistygneus beebey* sp. nov. Dorsal view of male holotype.

16-8-9. Distitarsi of both 1st and 2nd tarsi with 3 segments.

LENGTH OF LEGS.

	I. mm.	II. mm.	III. mm.	IV. mm.
Trochanter	0.7	0.8	1.0	1.0
Femur	3.0	4.8	3.8	4.1
Patella	0.9	1.3	1.8	2.0
Tibia	2.0	4.3	2.6	3.3
Metatarsus	3.2	5.0	4.0	5.0
Tarsus	1.4	4.8	2.7	3.1
Total	11.2	21.0	15.9	18.5

Palpus with the trochanter 1.2 mm. long, femur 3.6, patella 1.6, tibia 1.9, and tarsus 1.9. Total length, 10.2 mm. Coxa with scattered granulations. Trochanter globular with a dorsal elevation, with a small dorsal and a small ventral spine. Femur curved, unarmed except for a small basal ventral tubercle. No dorsal apical or median apical spine. Patella unarmed, tibia and tarsus each with 5 hair-tipped spines on either side. Tarsal claw long and curved back against the tarsus.

Chelicera greatly enlarged, proximal segment with a dorsal elevation, with several small tubercles dorsal and ventral. A large retrolateral spine at the apical portion. Distal segment huge, elevated considerably over the proximal segment. Distal segment smooth.

Dorsum reddish-brown. Spines and elevation of the cephalothorax likewise reddish-brown. Eyes black. Lateral portions of 1st

to 3rd segments with a large white blotch. Within these white areas 1 or 2 circles of reddish-brown. 4th area with a transverse line of white, ending in a wider area at the lateral edge. 4th area with a posterior margin of white. A narrow line of white at the lateral margin of the scute, extending from the anterior portion of the cephalothorax to the 2nd area. A large white

spot on the lateral margins of the 3rd and 4th areas. Each free tergite with the posterior margin irregularly lined in white. Last free sternite lined with white. Venter and coxae reddish-brown, basal portions of 3rd and 4th legs likewise reddish-brown. Palpus, 1st and 2nd legs, and distal portion of 3rd and 4th legs yellowish, penciled with gray. These markings give an annulate appearance on the metatarsi. Chelicera dark reddish-brown, with netted dark markings.

Measurements in mm.: Male, total length of body, 5.8; cephalothorax, 3; width of body at widest portion, 4.

Record: Male holotype from Rancho Grande, Venezuela, 1945.

Remarks: This species is related to *Bunistygneus macrochelis* Roewer, differing principally in the color markings on the dorsum.

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## 6.

Fresh-water Crabs of the Genus *Pseudothelphusa* from Rancho Grande, Venezuela.<sup>1</sup>

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New York Zoological Society.*

(Text-figures 1-3).

[This is one of a series of papers resulting from the 45th, 46th and 47th Expeditions of the Department of Tropical Research of the New York Zoological Society, made during 1945, 1946 and 1948 under the direction of Dr. William Beebe with headquarters at Rancho Grande in the National Park of Aragua, Venezuela. The expeditions were made possible through the generous cooperation of the National Government of Venezuela and of the Creole Petroleum Corporation.

[The characteristics of the research area are in brief as follows: Rancho Grande is located in north central Venezuela (10° 21' N. Lat., 67° 41' W. Long.), 80 kilometers west of Caracas, at an elevation of 1,100 meters in the undisturbed montane cloud forest which covers this part of the Caribbean range of the Andes. Adjacent ecological zones include seasonal forest, savanna, thorn woodland, cactus scrub, the fresh water Lake Valencia, and various marine littoral zones. The Rancho Grande area is generally subtropical, being uniformly cool and damp throughout the year because of the prevalence of the mountain cloud cap. The dry season extends from January into April. The average humidity during the expeditions, including parts of both wet and dry seasons, was 92.4%; the average temperature during the same period was 18° C.; the average annual rainfall over a 5-year period was 174 cm. The flora is marked by an abundance of mosses, ferns and epiphytes of many kinds, as well as a few gigantic trees. For further details, see Beebe & Crane, *Zoologica*, Vol. 32, No. 5, 1947. Unless otherwise stated, the specimens discussed in the present paper were taken in the montane cloud forest, within a radius of 1 kilometer of Rancho Grande.]

## GENERAL ACCOUNT.

Two species of Potamonidae, both belonging to the genus *Pseudothelphusa*, live within the Rancho Grande area and are common near the laboratory at an altitude of about 3,500 feet. One, *P. garmani*, occurs also farther down, near stream-beds in semi-evergreen seasonal forest, at least to 2,000 feet. The other, the apparently new *P. chacei*, is confined to the cloud forest. Each occurs on both the Caribbean and Valencia sides of the Cordillera.

The general habits are similar in both. Each is occasionally found walking along the damp forest floor, at considerable distances from the small mountain torrents. More rarely the crabs are seen submerged in the streams themselves, clinging tightly to the rocks and moss with their spiny feet. In both species the young are carried principally during the dry season, in March and early April, three females with young having been taken during that season, as well as all of the very small free-living young in the collection. In contrast only one female taken during the rains, in June, carried young. The single female with spermatophores was captured in September; by inference the eggs are laid between October and February, the season during which we have not visited the laboratory.

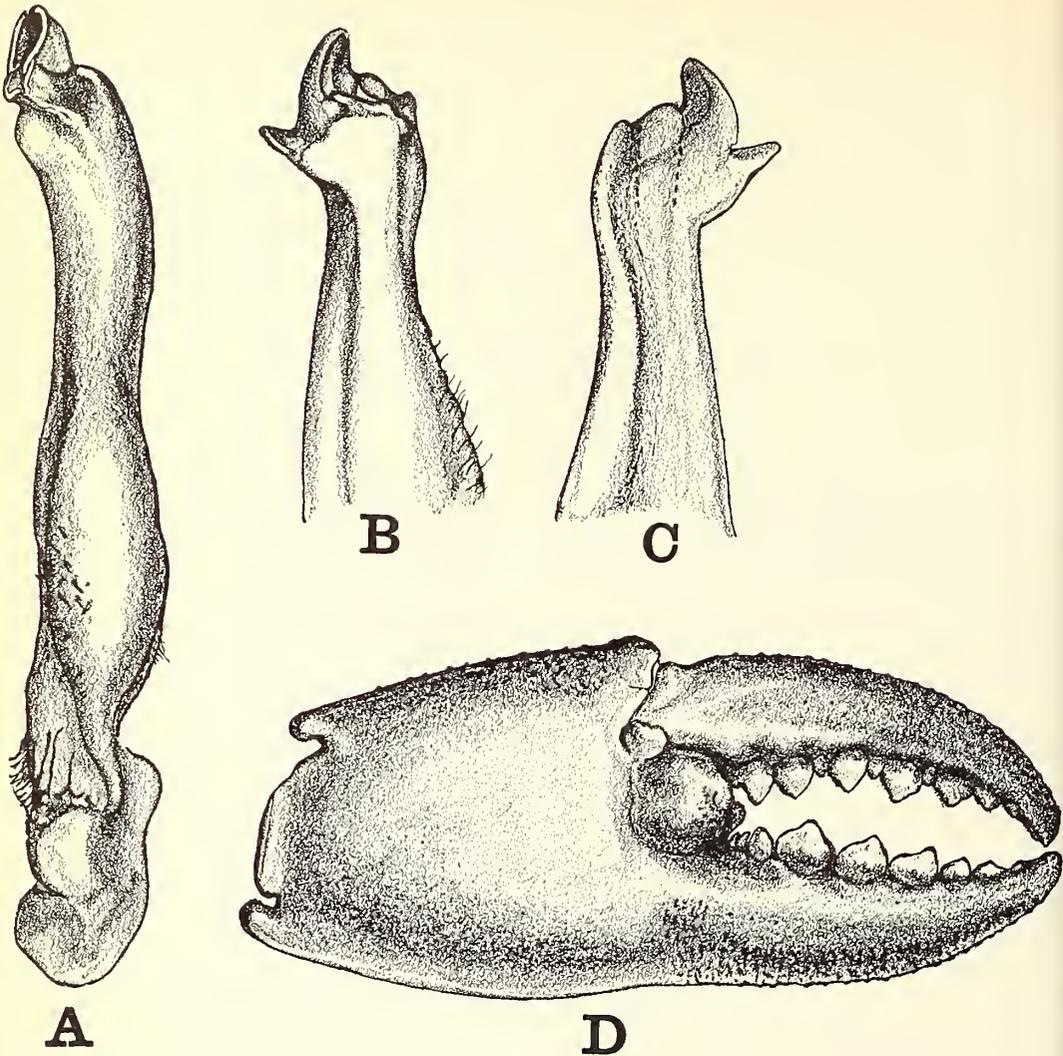
The food of both species consists largely of insects, especially beetles. The remains of eaten crabs are found frequently, and it seems certain that these crustaceans form an important food item in the diet of such local animals as tayras and opossums.

My sincere appreciation goes to Dr. Fenner A. Chace of the United States National Museum for his kindness in determining the identity of *P. garmani* and the systematic status of *P. chacei*. The specimens are in the collections of the Department of Tropical Research of the N. Y. Zoological Society, except for two examples of each species which have been deposited in the United States National Museum. Text-figs. 3A and 3B are the work of Miss Pamela Marmont; the remainder are by Miss Louise Moore.

Field Key to the Rancho Grande Species of *Pseudothelphusa*.

- A. Manus of cheliped with a large tubercle at base of fingers; anterior part of carapace slightly rough to touch; adults large, measuring at least three inches across, females 2¾ inches across still having narrow abdomens; marsupial young numbering between 200 and 300, their front distinctly bilobed and convex; semi-evergreen seasonal and cloud forests ..... *garmani*

<sup>1</sup> Contribution No. 829, Department of Tropical Research, New York Zoological Society.



TEXT-FIG. 1. *Pseudothelphusa garmani*. Adult male, length 47 mm. **A**, right first abdominal appendage, extero-posterior view; **B**, same, extero-anterior view; **C**, same, postero-internal view; **D**, major cheliped, external view.

AA. Manus of cheliped without tubercle at base of fingers; anterior part of carapace smooth to touch; adults small, mature females measuring about  $1\frac{1}{2}$  inches across, males less; marsupial young numbering between 20 and 40, their front scarcely lobed, truncate; cloud forest only ..... *chacei*, sp. nov.

*Pseudothelphusa garmani* Rathbun, 1898.

(Text-fig. 1, 2A).

*Reference.* *Pseudothelphusa garmani* Rathbun, 1898, p. 522, text-fig. 14.

*Color in life.* Adults of both sexes: variable shades of dark brown; color of carapace uniformly distributed, the chelipeds, ambulatories and abdomen slightly lighter. Marsupial young: carapace dark brown anteriorly, paler behind; chelipeds apricot buff (Ridgway), deepest on upper merus, carpus and upper half of manus; chelae creamy or white;

sides of carapace light brown to buff; sternum and abdomen white; ischium and trochanter of ambulatories buff, other segments dark brown.

*Development.* Two females carried 258 and 260 young, respectively. An example, illustrated in Text-fig. 2A, measures 3.5 mm. in length, 4.7 in breadth. The general form is closely similar to that of the adult, but the front has each of the two distinct lobes more convex and there is no trace of a tubercle outside the manus at the base of the fingers; manus not swollen. No very small free-living examples of this species were taken, but a young female 29 mm. long has the tubercle distinct.

*Food.* Three large examples all contained comminuted black chitin, showing in one case unmistakable beetle elytra; in addition one stomach held soft animal matter, probably worm tissue.

*Habitat and Range.* Taken at Rancho Grande from semi-evergreen seasonal and cloud forests, between 2,000 and 3,800 feet. Previously known also from near Caracas, Venezuela, and from Trinidad.

*Material.* A total of six specimens, not counting marsupial young, have been preserved. Department of Tropical Research Cat. Nos. 4635, male, length 47 mm.; cloud forest, Mar. 28, 1946; 4626, female, 55 mm., Rancho Grande verandah, June 24, 1946, with 260 marsupial young, No. 4626a; No. 45449, 2 immature females, 29, 42.5 mm., cloud forest, April 1, 1945. U. S. Nat. Mus. Nos. 82379, male, length 38.5, cloud forest, Mar. 18, 1946; 82380, female, with spermatophores, length 42.5, semi-evergreen seasonal forest (2000 feet), Sept. 6, 1946.

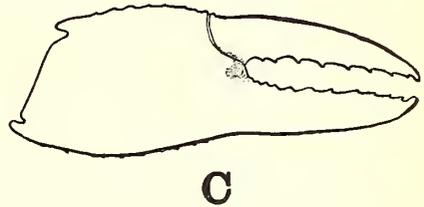
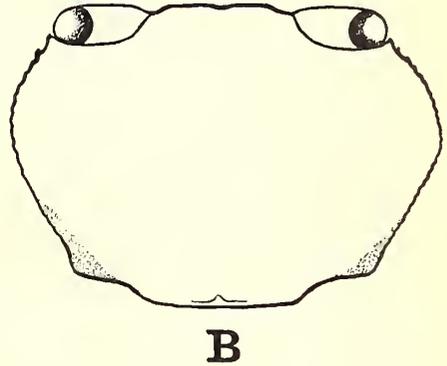
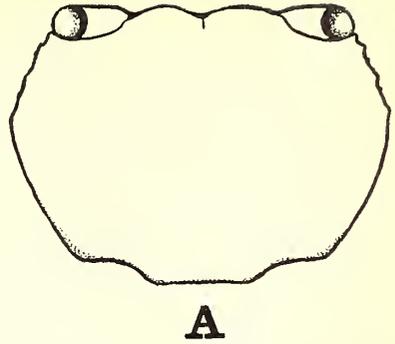
*Pseudothelphusa chacei* sp. nov.

(Text-figs. 2B, 2C, 3).

*Diagnosis:* Superior margin of front distinct and tuberculate but not carinate; bilobed, with median suture present; cervical suture nearly straight; carapace scarcely convex, smooth; exognath of maxillipeds reduced to a stump; manus somewhat swollen; no tubercle at base of fingers; front low; male matures at length of 17 mm., female at about 23.

*Description.* Carapace slightly convex, regions scarcely elevated; gastric region slightly less elevated than branchial; anterior margins of protogastric lobes distinct but not prominent; depressions defining anterior part of mesogastric region scarcely indicated; median furrow less well defined than in *garmani*; cervical groove nearly straight, deep, continued practically to lateral margin. Carapace almost completely smooth to the touch, with only a hint of microscopically fine granules in antero-lateral regions. Antero-lateral margins with a small orbital tooth followed by a slight gap; behind this are about 23 to 25 fine teeth, similar and close-set. Front low; superior margin distinct but not carinate, almost truncate, bilobed, finely tuberculate, scarcely or not at all projecting over the vertical surface; in front view slightly depressed in middle; lower margin sinuous, the tubercles tending to be obsolete. Orbits nearly filled by eyes, margins almost smooth, the superior slightly sinuous. Maxillipeds substantially as in *garmani* and *simoni*.

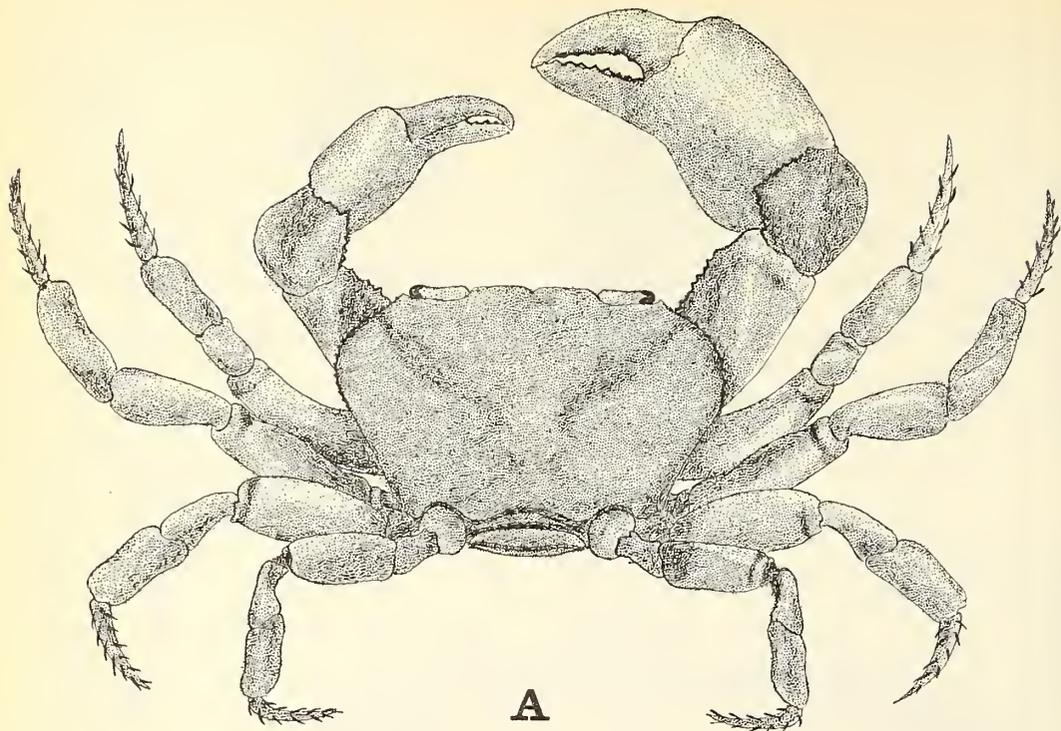
Merus of chelipeds finely rugose above, the inner margin armed with a single line of stout, graduated teeth, the lower and ventro-distal margins by beaded granules. Carpus smooth except for dorso-inner surface which is armed by a crest of small, distinct teeth, of which the usual large tooth is only one exaggerated element. Major and minor manus smooth in both sexes, save for scattered microscopic granules and punctations on outer surface and faint rugosities dorsally. Major manus, especially in male, definitely swollen; upper and lower margins in all slightly convex; sinus at base of pollex



TEXT-FIG. 2. Young crabs taken from abdominal pouches of female *Pseudothelphusa*. A, *P. garmani*, carapace, length 3.5 mm.; B, *P. chacei*, carapace, length 3.65 mm. (drawn to same scale as A); C, same, right cheliped, outer view, length 2.9 mm.

practically lacking; no tubercle at base of fingers, although there may be a very slight swelling of the margin at that point; fingers moderately broad, slightly and irregularly punctate, and near dorsal surface of dactyl, tuberculate; prehensile edges practically in contact, the teeth broad, irregular and variable. Merus of all ambulatories flattened, with upper margins convex and finely denticulate; superior margin of carpus and both margins of manus microscopically spinulose; dactyli slender and spined. Male abdominal appendage illustrated (Text-fig. 3).

*Color in Life.* Adults variable and capable to a certain extent of color change, the carapace ranging from a dull red to dark brown. A female with marsupial young had the cara-



TEXT-FIG. 3 [Part]. *Pseudothelphusa chacei* male holotype, length 17.5 mm. **A**, dorsal view; **B**, major cheliped, external view; **C**, right first abdominal appendage, extero-posterior view; **D**, same, extero-anterior view; **E**, same postero-internal view.

pace snuff brown (Ridgway), slightly lighter posteriorly. Chelipeds chiefly cinnamon buff to clay color with snuff brown on dorsal ridge; fingers pale buff; ambulatories snuff brown with darker segment markings. Her young were apricot buff in general coloring; front much darker, almost black; ambulatories cinnamon rufous; dorsal ridges of chelipeds apricot buff; underparts pale buff.

*Measurements.* Holotype male, No. 461197: Length of carapace 17.5 mm.; breadth 28.5; depth 11.5; width of front, lower margin, 7 mm.; major manus (measured along lower margin) plus pollex 26. Paratype female, No. 45105: Length of carapace 23 mm.; breadth 38.5; depth 15; width of front, lower margin, 8.4; major manus (measured along lower margin) plus pollex 30.

*Development.* Two females carried 22 and 40 marsupial young, respectively. An example, illustrated in Text-fig. 2B, measures 3.65 mm. long by 5.0 mm. broad. Compared with the corresponding stage of *P. garmani* the front is scarcely lobed and strongly truncate, the eyes are larger and the cheliped manus is distinctly swollen; the latter difference is carried through into the adult.

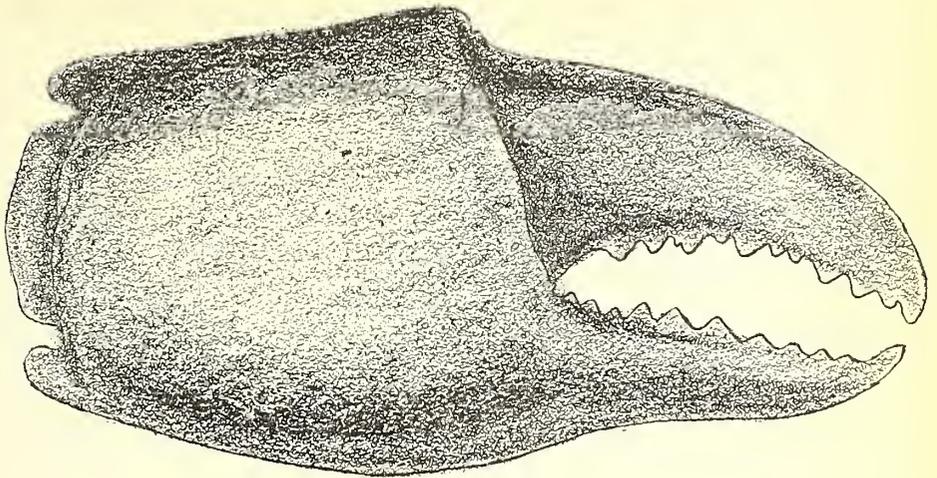
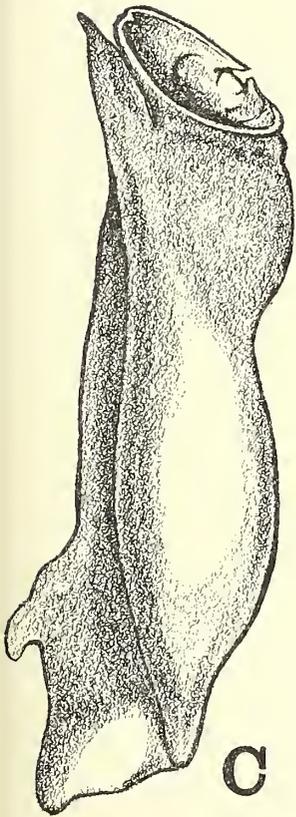
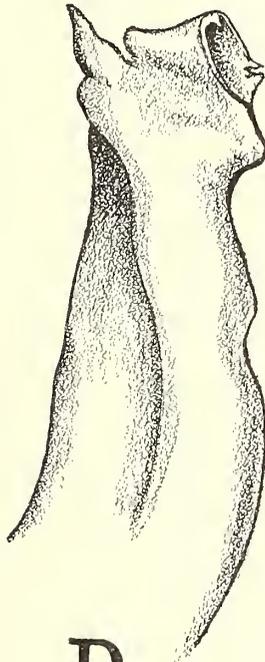
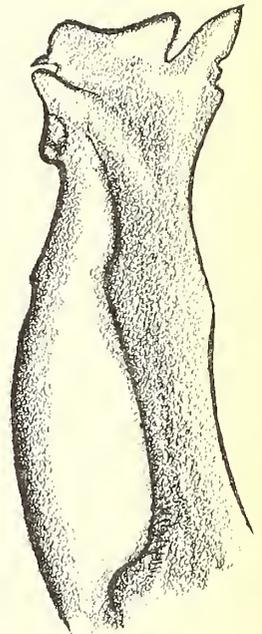
*Behavior of Young.* Samples of the young, when removed from one of the mothers and placed close to her, were almost helpless; they could move feebly, but did not try to climb back into the pouch; one, however, attempted to grip one of her legs as she moved slowly past.

*Food.* A female with young, when captured in an open patio of Rancho Grande, was holding a large, black tenebrionid beetle (D.T.R. No. 45,107) in her major chela, and pulling off the legs with her left. The beetle was uncrushed, being strong and active when liberated. Two of three stomachs examined contained black chitin, including small beetle elytra, in addition to indeterminate soft animal matter; the third was empty.

*Habitat and Range.* Known only from Rancho Grande, in the National Park of Aragua, Venezuela, in the montane cloud forest, between about 3,000 and 3,800 feet.

*Affinities.* Dr. Chace writes as follows regarding this species: "It is very close to Miss Rathbun's *P. simoni*. The male abdominal appendages agree very well with her figure of that species, but your specimens have a somewhat less convex carapace and a sharply carinate upper frontal margin which is completely lacking in *P. simoni*. The general appearance of your material would indicate full specific distinction from *P. simoni*, but the similarity in the male appendages suggests that possibly it deserves only subspecific rank." *P. simoni* is known only from the types, taken from Colonia Tovar and Caracas, Venezuela, and from the "Antilles" (Claudius).

*Material.* A total of 13 specimens was taken, not including marsupial young. The following have been designated as types: Holotype male, Department of Tropical Re-

**B****C****D****E**

TEXT-FIG. 3 [Part]. *Pseudothelphusa chacei* male holotype, length 17.5 mm. **A**, dorsal view; **B**, major cheliped, external view; **C**, right first abdominal appendage, extero-posterior view; **D**, same, extero-anterior view; **E**, same postero-internal view.

search Cat. No. 461197, length 17.5 mm., Rancho Grande court, March 5, 1946; paratype female, D.T.R. No. 45105, 23 mm., with 21 young, Rancho Grande court, March 29, 1945; paratype male, United States National Museum No. 87067, 17 mm., Water Trail, March 15, 1945; paratype female, U.S.N.M. No. 87067, 24 mm., Water Trail, March 7, 1945. In addition, the following were taken, all retained in the collections of the Department of Tropical Research: No. 45106, 1 female, length 22 mm., and 3 young, 7-16 mm., cloud forest, March 20-April 20, 1945; No. 4636, 1 female, length 22 mm., with 40 young, cloud forest, March 14, 1946; No. 461198, 4

young, 7-9 mm., cloud forest, March 1-15, 1946.

It gives me great pleasure to name this species for Dr. Fenner A. Chace, Jr.

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## 7.

# Comparative Biology of Salticid Spiders at Rancho Grande, Venezuela.

## Part III. Systematics and Behavior in Representative New Species.<sup>1</sup>

JOCELYN CRANE.

Research Zoologist, Department of Tropical Research,  
New York Zoological Society.

(Text-figures 1-8).

[This is one of a series of papers resulting from the 45th, 46th and 47th Expeditions of the Department of Tropical Research of the New York Zoological Society, made during 1945, 1946 and 1948, under the direction of Dr. William Beebe, with headquarters at Rancho Grande in the National Park of Aragua, Venezuela. The expeditions were made possible through the generous cooperation of the National Government of Venezuela and of the Creole Petroleum Corporation.

[The characteristics of the research area are in brief as follows: Rancho Grande is located in north-central Venezuela (10° 21' N. Lat., 67° 41' W. Long.), 80 kilometers west of Caracas, at an elevation of 1,100 meters in the undisturbed montane cloud forest which covers this part of the Caribbean range of the Andes. Adjacent ecological zones include seasonal forest, savanna, thorn woodland, cactus scrub, the fresh water Lake Valencia, and various marine littoral zones. The Rancho Grande area is generally subtropical, being uniformly cool and damp throughout the year because of the prevalence of the mountain cloud cap. The dry season extends from January into April. The average humidity during the expeditions, including parts of both wet and dry seasons was 92.4%; the average temperature during the same period was 18° C.; the average annual rainfall over a 5-year period was 174 cm. The flora is marked by an abundance of mosses, ferns and epiphytes of many kinds, as well as a few gigantic trees. For further details, see Beebe & Crane, *Zoologica*, Vol. 32, No. 5, 1947. Unless otherwise stated, the specimens discussed in the present paper were taken in the montane cloud forest zone, within a radius of 1 kilometer of Rancho Grande.]

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<sup>1</sup> Contribution No. 840, Department of Tropical Research, New York Zoological Society.

### INTRODUCTION.

The eight species described in the present paper have been selected from among other Rancho Grande salticids for two reasons. First, they represent a number of different stages and directions in salticid evolution; and, second, special experimental display data and/or examples of the earliest instars have been assembled in each. Part I of this series (Crane, 1948.1) dealt monographically with several species of *Corythalia*, while Part II (1948.2) described the methods of study. In the succeeding parts, which will be based largely on *Corythalia* and the present group of species, it is proposed to discuss the releasing mechanisms of display, to compare post-embryological development and, finally, to evaluate evolutionary trends.

With the exception of Text-figure 8F, which was drawn from life at Rancho Grande by Mr. Kenneth Gosner, all the illustrations are the work of Miss Louise A. Moore.

The types are deposited in the collections of the Department of Tropical Research, New York Zoological Society, New York 60, N. Y.

### *Lyssomanes bradyspilus* sp. nov.

(Text-fig. 1)

*Diagnosis:* Retromargin of fang groove with 6 teeth, the 2 proximal minute, none crowded toward fang base; basal segment of chelicera in male with cluster of 3 to 7 dorsal distal spines; fang toothless; no fringes on first metatarsi, which are straight; no cluster of dorsal tibial spines on palp, its distal apophysis very small, blunt; bulb with three strong, spinous, distal processes; epigynum with two pairs of large rounded bodies distinct, the anterior pair the smaller and practically contiguous. Abdominal black spots present or absent.

### COLOR.

*Color in Life:* Adult male. Cephalothorax: Integument of carapace translucent green, without dark pigment, varying from a yellowish-green, especially in recently molted

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examples, to apple green (Ridgway). Ocular quadrangle including black eye tubercles with varying amounts and proportions of yellowish- or silvery white and orange-red scale hairs, the latter usually placed anteriorly. AME rimmed with silvery-white; the eyes themselves clear apple green, shifting to black (see under BEHAVIOR); other eyes black. A narrow submarginal clypeal band of orange-red scale hairs, directed downward. Chelicerae fangs brown. Palpal bulbs pinkish to orange. Integument of legs translucent apple green, without dark pigment except for black tarsal pads. Abdomen: Integument translucent green, sparsely covered with short hairs, ranging from apple green to dull green-yellow, usually with a short, median basal stripe of darker green. Hairs short, rather sparse, of same color as integument. Paired, subdermal black spots on posterior half of abdomen present or absent, strong or weak, rarely appearing—if at all—until three or four days after final molt; any number up to four pairs may develop. A patch of white hairs often present at distal end of dorsum.

Adult female. Differs from male as follows: Scale hairs of ocular quadrangle, including eye tubercles, tend to be more uniformly yellowish- or silvery white, with the orange-red reduced or absent, except for a variable, sometimes conspicuous, crest behind AME; subdermal clypeal band of orange-red absent, replaced by a band of scant white hairs; palps completely green; legs usually with some dark subdermal pigment concentrated near joints; this often is confined to a single spot in antero-distal part of first tibia. As in the case of the abdominal spots, it develops, if at all, after the final molt. No female seen with more than two pairs of abdominal spots; as in the male, they develop slowly or not at all.

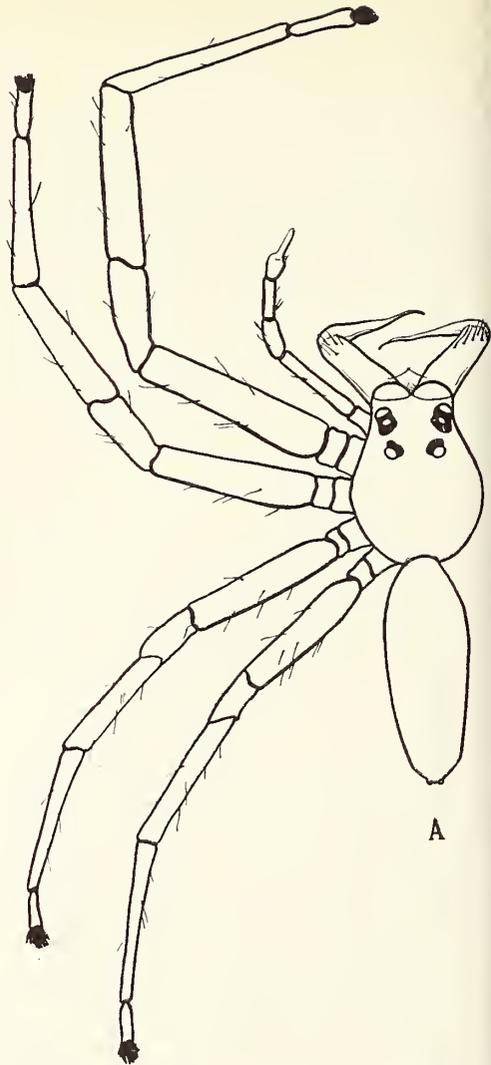
*Color in Alcohol:* All green fades promptly, as usual in the genus, to yellowish-white; no black leg or abdominal pigment remains; on the other hand, the orange-red clypeal band of males and the crest of females are strongly persistent and even intensified.

#### STRUCTURE.

Characteristics below apply to both males and females unless otherwise specified; percentages approximated; measurements of types given on p. 34.

*Carapace:* Height, including tubercle of PLE, scarcely more than half length; short anterior part of thoracic slope almost level, descent of posterior part moderate; width greatest midway between PLE and pedicel, wider in male (1.5 times height, 79% of length), narrower in female (1.35 times height, 71% of length); longitudinal thoracic groove well developed, lying midway between PLE and pedicel.

*Eyes:* Eight eyes in four distinct rows; all except AME elevated on low black tubercles, the PME on same tubercle as ALE. First row 87% as wide as second; length of

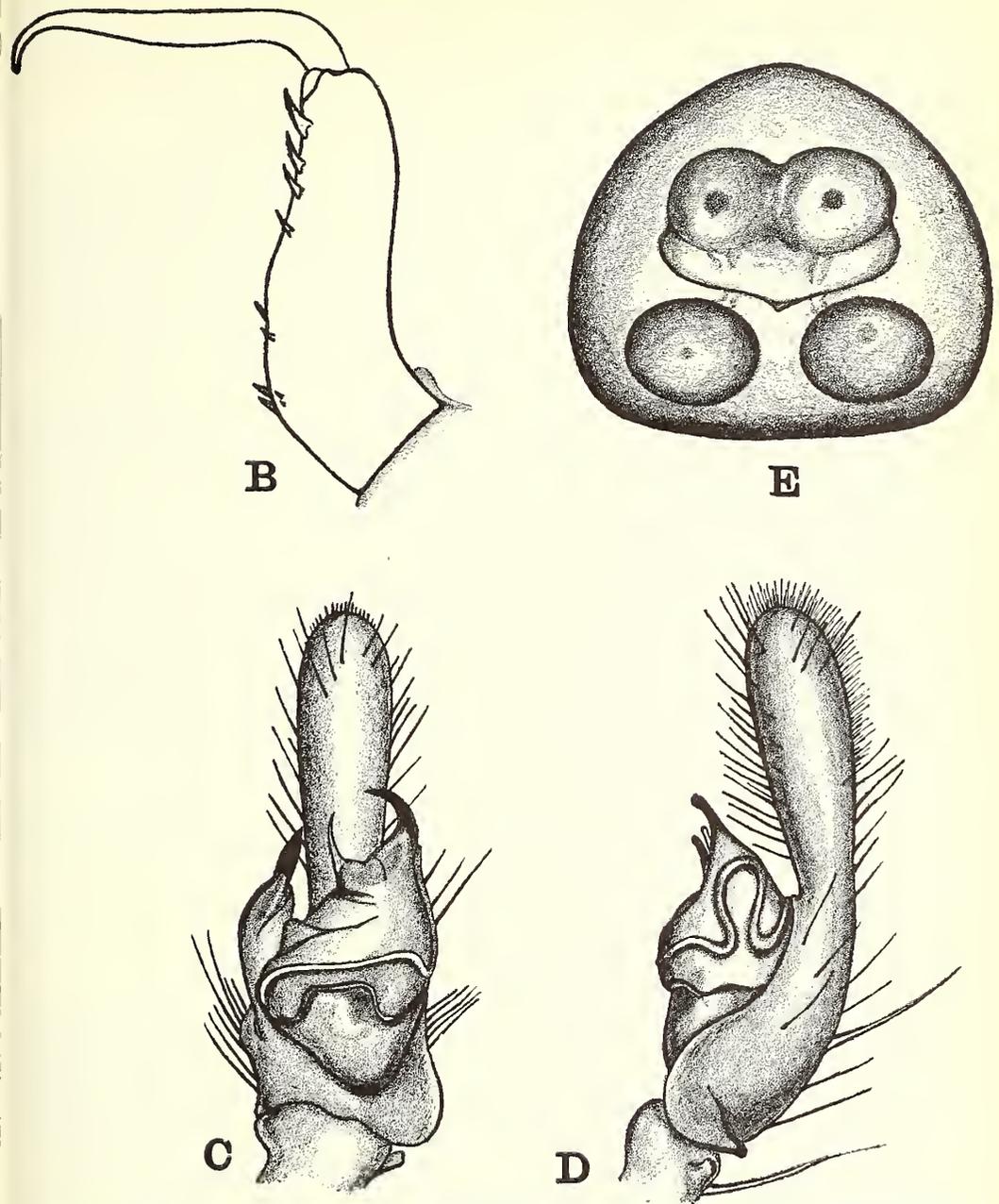


TEXT-FIG. 1. (Part). *Lyssomanes bradyspilus*. A-D holotype ♂: A, dorsal view; B, chelicera, ventral view; C, left palp, ventral view; D, same, ectal view. E, paratype ♀: epigynum.

ocular quadrangle including AME 42% of carapace length, length from ALE to PLE 27%; breadth at ALE much wider than at PLE, 46% and 34% of length respectively; ocular quadrangle length from ALE to PLE only 66% of its breadth at ALE. Diameter of AME 21% of carapace length; ratio of eyes: AME: ALE: PME: PLE: :100: 42: 11. 5: 35. AME practically contiguous, separated from ALE by about a tenth of their diameter; PME slightly closer to ALE than to PLE.

*Clypeus:* Height in males 38% of AME diameter; 54% in females.

*Chelicerae:* In males, strongly produced but of variable length, porrect, robust, divergent. Length of basal segment in best developed more than half carapace length, in least developed about half. Each with 1-2 prs. of overlapping spines near base on medial front



TEXT-FIG. 1. (Part). *Lyssomanes bradyspilus*. A-D, holotype ♂: **A**, dorsal view; **B**, chelicera, ventral view; **C**, left palp, ventral view; **D**, same, ectal view. **E**, paratype ♀: epigynum.

margin, and a group of 3 to 7 strong distal spines, the number and arrangement varying even on two sides of same individual. Fang slender and sinuous, toothless; groove weak; promargin with three small teeth near base, the smallest proximal, it and the next closer together than second and third; no tooth at base of fang; inferior margin typically with 6 teeth in a straight row, increasing in size distally, along entire edge of groove. The basal one or two, however, although apparently constant, are minute, delicate and easily destroyed; they are separated consid-

erably from each other and the distal 4, which are quite evenly spaced. In females the chelicerae are, of course, much shorter; distal spine group absent; teeth closer together, tending to be evenly spaced throughout and of more nearly equal size.

*Maxillae*: Parallel; width 60% of length; distal dilation slight; external angle evenly rounded without tubercle.

*Lip*: Breadth 90% of length; basal excavation extending 25% of length; distal end reaching slightly beyond middle of maxillae; sternal suture straight.

*Sternum*: Broadly scutiform; width 85% of length in males, slightly less in females; equally wide between second and third coxae; base of lip 60% as wide as anterior border in males, 50% in females; posterior end a bluntly rounded lobe extending about halfway between fourth coxae, which are separated by two-thirds of their diameter.

*Legs*: Tibial indices: Holotype male, first leg 12, fourth leg 11; paratype female, first and fourth legs, 13. First legs of male considerably elongated and enlarged. See Table I for formula.

TABLE I.

*Lyssomanes bradyaspilus*: Leg Formula.

	1	2	4	3
Male holotype	3.8	3.0	3.0	2.9
	1	4	2	3
Female paratype	3.2	2.9	2.7	2.6

All legs with little hair; hairs on metatarsi arranged clearly in dorsal and ventral rows, but in no sense profusely enough to be called fringes.

*Spines*: (Male holotype and female paratype). First and second legs: Femur dorsal 1-1-1; prolateral and retrolateral 0-1-1. Patella 0 but with a long, slender dorsal distal bristle. Tibia: Prolateral 1-1; retrolateral 1-1 in male, and on second female leg, 0-1 on first female leg; ventral 2-0-2-2, not opposite, the distal ones not terminal. Metatarsus ventral only 2-2-2, not terminal. Third leg: Femur as in first and second. Patella dorsal distal only 1. Tibia, dorsal 1-0-0-1; pro- and retrolateral, as in first and second male; ventral 0-0-2-0. Metatarsus, prolateral and retrolateral 1-1-0; ventral, male, 2-0-0, female none. Fourth leg: Femur dorsal 1-1-1; pro- and retrolateral male 0-0-1, female none. Patella as in third. Tibia dorsal as in third; pro- and retrolateral as in first and second male, except fourth female prolateral is 0-1; ventral none. Metatarsus ventral only 1 (retro) -0-0. In addition, there are rudiments on third and fourth legs of distal metatarsal spines, 2 prolaterals, 2 retrolaterals and 2 ventrals, all minute and very weak. Palpal spines: Femur dorsal 0-1-1; pro- and retrolateral distal 1; patella, dorsal distal 1; tibia, prolateral male, 0-1, female, 1-1; metatarsus female, dorsal 1-0; pro and retrolateral 1-1.

*Abdomen*: About 3 times longer than broad in males and young females, tapering from level of genital groove; anal tubercle not pronounced; vestigial colulus not indicated.

*Palp*: Femur slightly curved; patella and tibia nearly equal; tibia without dorsal spine cluster; tibial apophysis scarcely more than a truncate tubercle opposing basal ridge of tarsus; bulb with three pointed distal processes, variously shaped, and a distal tubercle (see Text-fig. 1), the whole complex structure differing only in proportions and details from Chickering's description of the palp in *L. banksi* (1946, p. 12).

*Epigynum*: No median notch. Two pairs of large, rounded bodies; members of anterior pair smaller, apparently contiguous; posterior pair separated by less than half their own diameter.

## MEASUREMENTS.

Male holotype. Total length in alcohol 4.7 mm.; carapace length 2.1; carapace breadth 1.6; carapace height 1.1; ocular quadrangle length, AME to PLE .89, ALE to PLE .58; ocular quadrangle breadth, at ALE .96, at PLE .72; diameter AME .45, ALE .19, MLE .05, PLE .15; clypeus height .17; basal segment chelicera 1.1; patella breadth, 1st leg .38, 4th .24.

## Leg Measurements, Male.

Leg	Femur	Pat.	Tib.	Metat.	Tarsus	Total
1st	2.3	.96	2.1	2.0	.55	7.9
2nd	1.9	.75	1.6	1.7	.41	6.4
3rd	1.8	.68	1.4	1.7	.41	6.0
4th	1.7	.65	1.5	1.9	.44	6.2
Palp	1.0	.44	.41	—	.58	2.4

Female paratype. Total length in alcohol 4.7 mm.; carapace length 2.1; carapace breadth 1.5; carapace height 1.1; ocular quadrangle length, AME to PLE .89, ALE to PLE .65; ocular quadrangle breadth, at ALE .99, at PLE .72; diameter AME .45, ALE .19, AME .05, PLE .15; clypeus height .24; basal segment chelicera .75; patella breadth 1st leg .34, 4th .24.

## Leg Measurements, Female.

Leg	Femur	Pat.	Tib.	Metat.	Tarsus	Total
1st	2.0	.79	1.8	1.7	.41	6.7
2nd	1.7	.75	1.4	1.5	.38	5.7
3rd	1.6	.68	1.2	1.5	.38	5.4
4th	1.9	.55	1.4	1.8	.41	6.1
Palp	.82	.44	.44	—	.68	2.4

## BEHAVIOR.

*Locomotion*: This species is a typical runner; I have never seen it jump, except in a final short pounce upon prey. The spider runs in brief spurts, during which the palps hang down practically touching the ground; during the pause they palpate the surface. No special use is made of the first legs, which take an active part in running.

*Courtship Display*: In Stage I, the carapace is held high, the first three pairs of legs braced somewhat forward, obliquely, and the fourth pair back; the palps hang over chelicerae, now and then tapping ground, while the abdomen hangs straight down. To superficial observation, the display consists only of posing in this position, varied with occasional bobbing of the carapace and twitching of the abdomen during rising excitement. Not until Stage II is reached, within touching distance of the female, are the first legs raised; they are then extended to the front, while the carapace sinks low and the abdomen is swung back in the horizontal position.

When the spiders are observed from their own level, however, in a straight front view, it is obvious that during display the rate of

activity of the muscles controlling the antero-median eyes is considerably increased; this gives rise to a much accelerated color "change" of the eyes, from green to black to green again. Similar eye color shifts have been known for many years in a few other salticids (e.g. Bristowe 1941, p. 419 ff. and referencés). It is apparently caused by slight motions of the long, cone-shaped optic "cups," possibly concerned with a change in focus, or in the lateral range of vision, although the exact mechanism does not seem to have been worked out. In *Lyssomanes* the shifts take place slowly but continuously during ordinary daily activity, and may be observed at close range under a binocular microscope. The mechanism works independently in the two eyes, and at a given instant either or both eyes show any proportion of green or black. To human beings, at least, the asymmetrically rolling effect is startling. In a dorsal view, the slight motions of the elongate "cups" may be simultaneously viewed through the translucent cuticle of the carapace.

Bristowe suggests the possibility that the color shifts may be useful in enticing prey. However that may be, after the Rancho Grande observations it seems to me highly probable that acceleration of muscular activity during display should be considered as a definite part of the behavior pattern, probably with an adaptive significance; its relative value among the various sign stimuli has not yet been established. This entire subject will be further considered in subsequent papers.

Once her attention has been attracted, the female usually sits quietly, sagging to one side on several folded legs; during the male's display, the rate of her ocular muscular activity also is increased.

*Threat Display:* Males usually took no notice of one another, and were induced to display only three times. During these periods, eye color shift was not especially noted. No differences were observed between threat position and activity from those of courtship, except that the carapace and abdomen were neither bobbed nor twitched. I never saw the long chelicerae unsheathed, although twice there was a brief, butting skirmish before one opponent retreated.

*Habitat:* Known only from the cloud forest near Rancho Grande. Shaken from green herbs, shrubs and low trees; one example taken from an epiphytic bromeliad growing twenty feet from the ground.

*Affinities:* This species holds its chief characteristics in common with a number of *Lyssomanes*, although their combination seems quite distinct. *L. quadrinotatus* Simon, (1900), from nearby mountains, has only three teeth on inferior margin of fang groove.

*Material:* A total of 7 adult males and 4 females have been preserved in addition to a number of young. The following have been designated as types:

**HOLOTYPE:** Male. Cat. No. 461199, Department of Tropical Research, New York Zoological Society; Portachuelo, Rancho Grande, near Maracay, National Park of Aragua, Venezuela; 1136 meters; cloud forest; March 20, 1946.

**PARATYPE:** Female. Cat. No. 45450, Department of Tropical Research, New York Zoological Society; same locality as holotype; July 9, 1945.

The name *bradyopilus* is proposed in reference to the delayed development of the black markings after the final molt.

***Semorina brachychelyne* sp. nov.**

(Text-fig. 2).

*Diagnosis:* Small, brown, scale-less salticids, carapace low, abdomen long and narrow with a very slight constriction near middle, first legs greatly elongated and enlarged, extended forward and scarcely used in walking, while the abdomen is frequently elevated. Chelicerae in male scarcely a fourth length of carapace; tibial apophyses of palp both curved.

**COLOR.**

*Color in Life:* Adult male. Carapace integument dark brown, without scales and almost without hairs, except around eyes. AME clear ochraceous brown shifting to black. Palps dark. First legs brown, the femur and tibia almost black, the tarsi and sometimes the metatarsi translucent horn-color. Other legs translucent horn. Abdomen covered with fine dark brown hairs with a pair of small spots of white hairs (not scales and not shiny or iridescent) three-fifths of distance from base to tip. In one male there was a pair of faint pale spots near tip of abdomen in addition to the distinct more anterior pair.

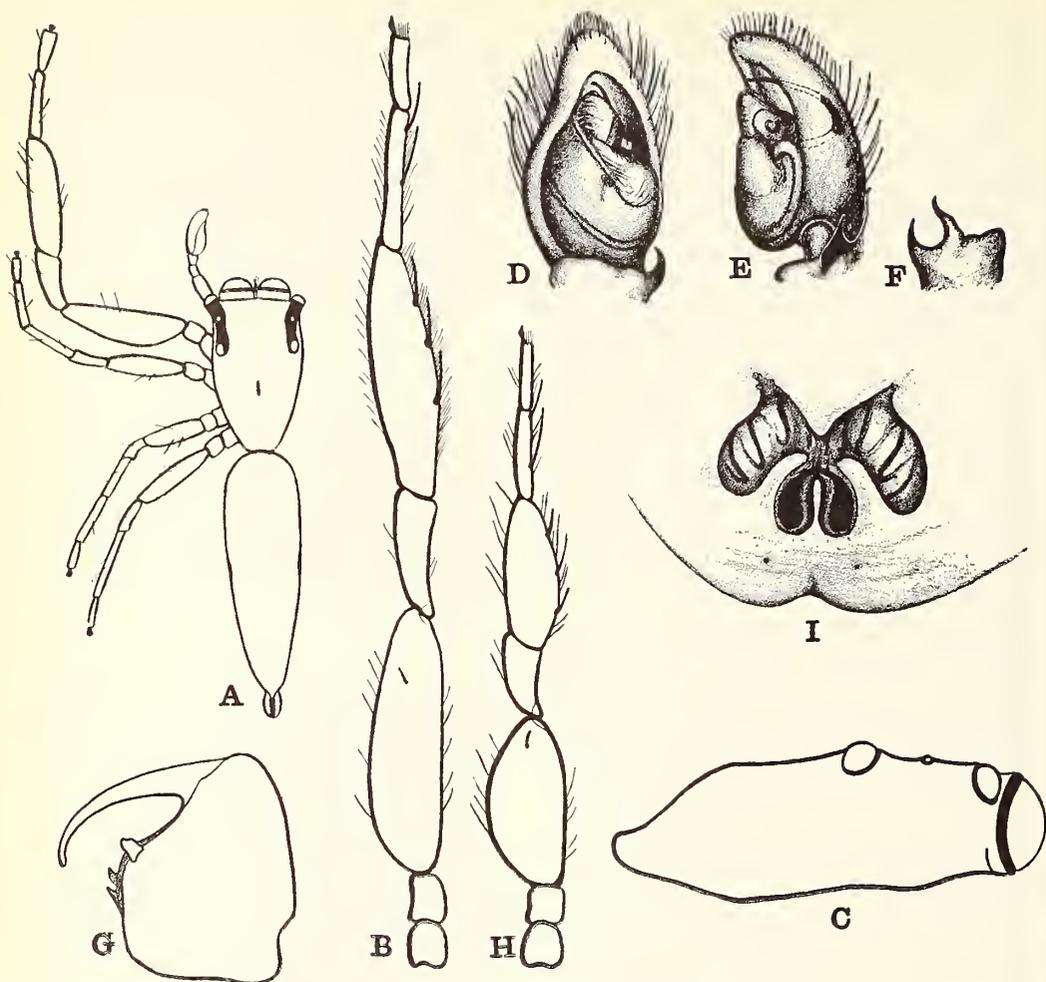
Adult female. Carapace integument yellowish-brown except sternum which is faintly pinkish. Eyes surrounded by a few yellowish hairs. Eyes themselves as in male. Tibia and tarsus of palps shiny silvery white, very conspicuous when vibrated. Swollen tibia of first legs with a ventral dark spot extending laterally; entire first leg darker than the others, which are pale translucent yellow-brown. Abdomen with a median, slightly darker stripe giving off three pairs of dark cross bars reaching middle of side. A median dark spot immediately before tip of abdomen.

*Color in Alcohol:* The white spot(s) of the male abdomen are practically invisible, the pattern now resembling closely that of the female, which is little altered from life.

**STRUCTURE.**

The characteristics below apply to both males and females unless otherwise specified; percentages approximated; measurements of types given on p. 37.

*Carapace:* Height only 30% of carapace length; postocular plateau long; thoracic



TEXT-FIG. 2. *Semorina brachychelyne*. A-G, holotype ♂: A, dorsal view; B, first leg, anterior view; C, carapace, lateral view; D, palp, ventral view; E, same, ectal view; F, same, tibial apophysis; G, chelicera, ventral view. H-I, paratype ♀: H, first leg, anterior view; drawn to same scale as B; I, epigynum.

slope slightly concave; width of carapace greatest at level of PLE, about twice height, and 60% of carapace length. Longitudinal groove well defined, in middle of postocular plateau.

**Eyes:** Eyes occupying slightly less than one-half length of carapace. Ocular quadrangle only a third as long as broad, the sides practically parallel but with PLE very slightly closer together than ALE. Carapace extending moderately beyond PLE at their level; PME median, or slightly nearer ALE than PLE. Diameter of AME about 21% of carapace length; ratio of eyes, holotype: AME : ALE : PME : PLE :: 100 : 41 : 7 : 3 : 41. AME practically contiguous, separated from ALE, which are recurved, by about one-third diameter of ALE.

**Clypeus:** Height in male only 5 to 6% of AME diameter, in female 11 to 12%.

**Chelicerae:** Short, divergent, 25% of carapace length in male, slightly shorter in fe-

male. Two small teeth on superior, one larger on inferior margin.

**Maxillae:** Length 54% of width in male, 64% in female; outer distal margin a blunted, obtuse angle, not produced.

**Lip:** Width 55% of length in male, 78% in female. Sternal suture straight.

**Sternum:** Width 56% of length in males, 53% in females. Anterior margin straight, a little narrower than lip base, greatest width between posterior margins of first legs; posterior end tapering, blunt-tipped extending between fourth coxae; the latter separated by less than a quarter of their thickness.

**Legs:** Tibial indices: Holotype male, first leg 17, fourth leg 14; paratype female, first leg 23, fourth leg 12. First leg in both sexes much elongated and enlarged with the femur and tibia especially deep (tibia depth of first leg in male 30% of its length, in female 45%). See Table II for formula. Hair scanty

except as follows. In male, first tibia and metatarsus with a short, moderately dense ventral fringe of dark hairs, and a scantier dorsal one of pale hairs; second tibia with a very scant pale fringe, dorsally and ventrally, metatarsus with a similar, slightly longer one ventrally only; third and fourth legs with very scanty ventral metatarsal fringes only. Fringes of negligible development in female.

TABLE II.

	1	4	2	3
Male holotype	2.5	1.8	1.6	1.3
	1	4	2	3
Female paratype	1.6	1.6	1.3	1.1

*Spines:* (From male holotype and female paratype). Femur, dorsal 0-1-1-1 throughout, the proximal two weak, bristle-like, especially in female. Patella spineless throughout. Spines otherwise as follows: First leg: Tibia, ventral only 0-2-2-2, the latter not terminal; metatarsus, ventral only 0-2-2. Second leg: Tibia, retro-ventral only 1-1-0; metatarsus, male 0, female 0-2. Third leg: Tibia and metatarsus 0. Fourth leg: Femur, retrolateral distal in male 1, in female 0; tibia and metatarsus 0.

*Abdomen:* Very elongate and tapering in both sexes, the breadth about a third of length, a very slight constriction near middle.

*Palp:* Femur practically straight; tibia more than one-half length of patella; two lateral tibial apophyses, the more dorsal longer, tapering, recurved at tip, the more ventral shorter, strongly curved antero-inwardly. Embolus slender and tapering. Distal part of bulb with a conspicuous, chitinized, knob-like protuberance directed outward.

*Epigynum:* An anterior pair of kidney-shaped bodies, diverging posteriorly; a posterior pair, smaller and closer together, followed by a pair of conspicuous small dark spots; a broad and shallow marginal notch.

## MEASUREMENTS.

Male holotype. Total length in alcohol 5.3 mm.; carapace length 2.2, breadth 1.3, height .68; ocular quadrangle length .79, breadth 1.2; diameter AME .46, ALE .19, PME .03, PLE .19; clypeus height .02; basal segment of chelicera .55; sternum length .86, breadth .48; patella breadth, 1st leg, .38, 4th .21; abdomen length 3.2, breadth .99.

## Leg Measurements, Male.

Leg	Femur	Pat.	Tib.	Metat.	Tarsus	Total
1	1.7	.89	1.5	.96	.48	5.5
2	1.1	.51	.79	.65	.31	3.4
3	.82	.38	.58	.68	.31	2.8
4	1.1	.51	1.0	.89	.38	3.9
Palp	.72	.24	.14	—	.62	1.7

Female paratype. Total length in alcohol 5.3 mm.; carapace length 2.2; carapace breadth 1.3; carapace height .65; ocular

quadrangle length .79; ocular quadrangle breadth 1.2; diameter AME .45; ALE .19, PME .03, PLE .19; clypeus height .05; basal segment of chelicera .50; sternum length .96, breadth .50; patella breadth, 1st leg, .32, 4th .15; abdomen, length 3.2, breadth 1.1.

## Leg Measurements, Female.

Leg	Femur	Pat.	Tib.	Metat.	Tarsus	Total
1	1.1	5.8	.92	.65	.38	3.6
2	.82	.48	.62	.51	.44	2.9
3	.79	.34	.44	.55	.34	2.5
4	1.0	.48	.79	.75	.48	3.5
Palp	.65	.27	.24	—	.44	1.6

## BEHAVIOR.

*Locomotion:* The movements of this spider in the field are absurdly reminiscent of those of scorpions or pseudoscorpions, and bear little resemblance to ant behavior. Their small size, however, makes the existence of an adaptive mimetic function extremely questionable. They are to be counted among the runners in the family, their progress being a rapid sort of scurry, with short jumps reserved for crossing gaps in the terrain, or, of course, for the final stage in catching prey. During running the palps are vibrated continually up and down, while the first legs are held straight out in front, the metatarsi and tarsi curved inward; these legs are often vibrated, scarcely or not at all touching the ground, almost as rapidly as the palps. Meanwhile the abdomen is frequently elevated and waved slightly, also in the vertical plane. Immature specimens show all these characteristics in progress, and they are typical of locomotion whether or not another individual is present. Both abdomen and first legs are invariably raised whenever any obstacle is encountered.

*Courtship Display:* Indistinguishable from ordinary locomotion except that the first legs are extended at a wide angle (more than 90°) and slightly more elevated, the tarsi usually bent down; often the palps are held still; there is the usual pursuit with sidling, and the abdomen, with increasing excitement, tends to remain elevated. Motionless posing with abdomen up and first legs extended at the usual angle, also occurs with excitement. In Stage II the first legs are brought close together in front, about as in simple locomotion. During courtship the female vibrates her white palps rapidly, once her attention has been gained.

*Threat Display:* No threat displays were seen, although a number of attempts were made to induce them.

*Habitat:* Known only from the montane cloud forest (about 3,600 feet) around Rancho Grande. Always shaken from shrubs and low trees.

*Affinities:* This species differs from Simon's Venezuelan species, known only from females (*S. seminuda* and *S. iris*, 1901), in the complete lack of shining abdominal scales in any specimens. It likewise appears distinct from Mello-Leitao's *S. lineata* (1945)

from the Argentine. No other species seem to have been referred to this genus. It differs clearly from the other Rancho Grande species (see below) in details of the chelicerae, palp and epigynum.

*Material*: A total of 5 adult males and 4 adult females have been preserved, in addition to a number of young. The following have been designated as types:

**HOLOTYPE**: Male. Cat. No. 481558, Department of Tropical Research, New York Zoological Society; Portachuelo, Rancho Grande, near Maracay, National Park of Aragua, Venezuela; 1136 meters; cloud forest; July 15, 1948.

**PARATYPE**: Female. Cat. No. 461200, Department of Tropical Research, New York Zoological Society; Limon Gorge, Rancho Grande, near Maracay, National Park of Aragua, Venezuela; 1100 meters; lower edge of cloud forest; April 20, 1946.

The name *brachychelyne* is proposed in reference to the relatively short chelicerae.

***Semorina megachelyne* sp. nov.**

(Text-fig. 3).

*Diagnosis*: Very similar to *S. brachychelyne* in general appearance. Chelicerae elongated, about half carapace length in male; tibial apophyses of palp slender and straight.

**COLOR.**

*Color in Alcohol*: Both sexes scaleless, brown except for pale second, third and fourth legs; no distinct and unvarying spots or other markings.

**STRUCTURE.**

Does not differ significantly from *S. brachychelyne* except as follows: Height of carapace slightly more in male (33% of length, instead of 30%); thoracic groove less distinct, transverse rather than longitudinal; ALE and PLE slightly larger, almost one-half diameter of AME. Ratio of eyes, holotype: AME:ALE:PME:PLE::100:48:8:48. Clypeus even narrower, in both sexes, about 4% of AME in male, 5.4% in female. Maxillae and sternum both narrower with little sexual difference in breadth.

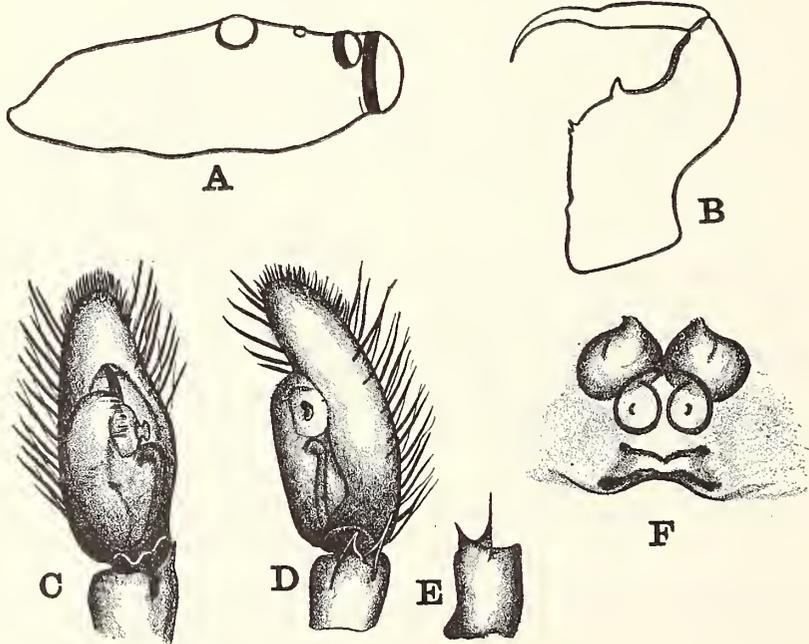
*Chelicerae*: These form a major specific difference, being long in males, the length of the basal segment 50% of carapace length; in females it is only 30%. They are held almost horizontally in both sexes, but are more divergent in males than in females. Tooth on inferior margin relatively larger in males of present species than in *brachychelyne*.

*Legs*: Tibial indices: Holotype male, first leg 12, fourth leg 12; paratype female, first leg 20, fourth leg 15. General form, proportions and fringes similar to those in *brachychelyne*. The leg formula is given in Table III.

TABLE III.

*Semorina megachelyne*: Leg Formula.

	1	4	2	3
Male holotype	2.3	1.7	1.5	1.2
Female paratype	1.5	1.4	1.1	1.1



TEXT-FIG. 3. *Semorina megachelyne*. A-E, holotype ♂: A, carapace, lateral view; B, chelicera, ventral view; C, palp, ventral view; D, same, ectal view; E, same, tibial apophysis. F, paratype female: epigynum.

*Spines*: (From male holotype and female paratype). As in *brachychelyne*, except for second leg, as follows: In male, metatarsus retroventral 1-0, not 0; female, as in *brachychelyne* male, except metatarsus is 1r-2.

*Palp*: Differs from *brachychelyne* as follows: Both tibial apophyses are straight, the tarsus along with its bulb is more slender, and the coiling of the tubule within the bulb is different.

*Epigynum*: The structure differs distinctly in the two species, as shown in the figure; the more nearly spherical shape of the four bodies is especially noticeable.

#### MEASUREMENTS.

Male holotype. Total length in alcohol 4.7 mm.; carapace length 2.2, breadth 1.3, height .75; ocular quadrangle length .79, breadth 1.2; diameter AME .43, ALE .21, PME .03, PLE .21; clypeus height .02; basal segment of chelicerae 1.1; sternum length .96, breadth .46; patella breadth, 1st leg .27, 4th .17; abdomen, length 2.5, breadth .82.

#### Leg Measurements, Male.

Leg	Femur	Pat.	Tib.	Metat.	Tarsus	Total
1	1.5	.82	1.4	.96	.41	5.1
2	.96	.51	.75	.62	.34	3.2
3	.82	.38	.55	.68	.27	2.7
4	1.1	.48	.92	.85	.38	3.7
Palp	.72	.31	.17	—	.58	1.8

Female paratype. Total length in alcohol 4.0 mm.; carapace length 1.7, breadth 1.0, height .55; ocular quadrangle length .75, breadth .96; diameter AME .36, ALE .16, PME .03, PLE .17; clypeus height .09; chelicera, basal segment .52; sternum length .79, breadth .36; patella breadth 1st leg .21, 4th leg .14; abdomen, length 2.3, breadth .79.

#### Leg Measurements, Female.

Leg	Femur	Pat.	Tib.	Metat.	Tarsus	Total
1	.79	.48	.58	.44	.27	2.6
2	.62	.34	.41	.31	.24	1.9
3	.55	.31	.34	.41	.27	1.9
4	.79	.31	.62	.55	.27	2.5
Palp	.44	.17	.14	—	.34	1.1

*Behavior*: Locomotion as in *brachychelyne*. No displays observed.

*Habitat*: Known only from lower edge of montane cloud forest, about 3,500 feet, near Rancho Grande. Collected from tree trunks and shrubs.

*Affinities*: See remarks under *brachychelyne*.

*Material*: A total of 2 adult males and 5 adult females were taken, along with a number of young. The following have been designated as types:

**HOLOTYPE**: Male Cat. No. 461201, Department of Tropical Research, New York Zoological Society; Water Trail, Rancho Grande, near Maracay, National Park of Aragua, Venezuela; 1100 meters; lower edge of cloud forest; May 5, 1946.

**PARATYPE**: Female. Cat. No. 461202. Same data as holotype.

The name *megachelyne* is proposed in reference to the long chelicerae of the male.

#### *Ashtabula furcillata* sp. nov.

(Text-fig. 4).

*Diagnosis*: Color in life above entirely iridescent green with white dorso-lateral band encircling carapace and abdomen; dorsal abdominal spots lacking, although sometimes faintly indicated in alcohol; carapace low; abdomen elongate; tibial apophysis of male forked.

#### COLOR.

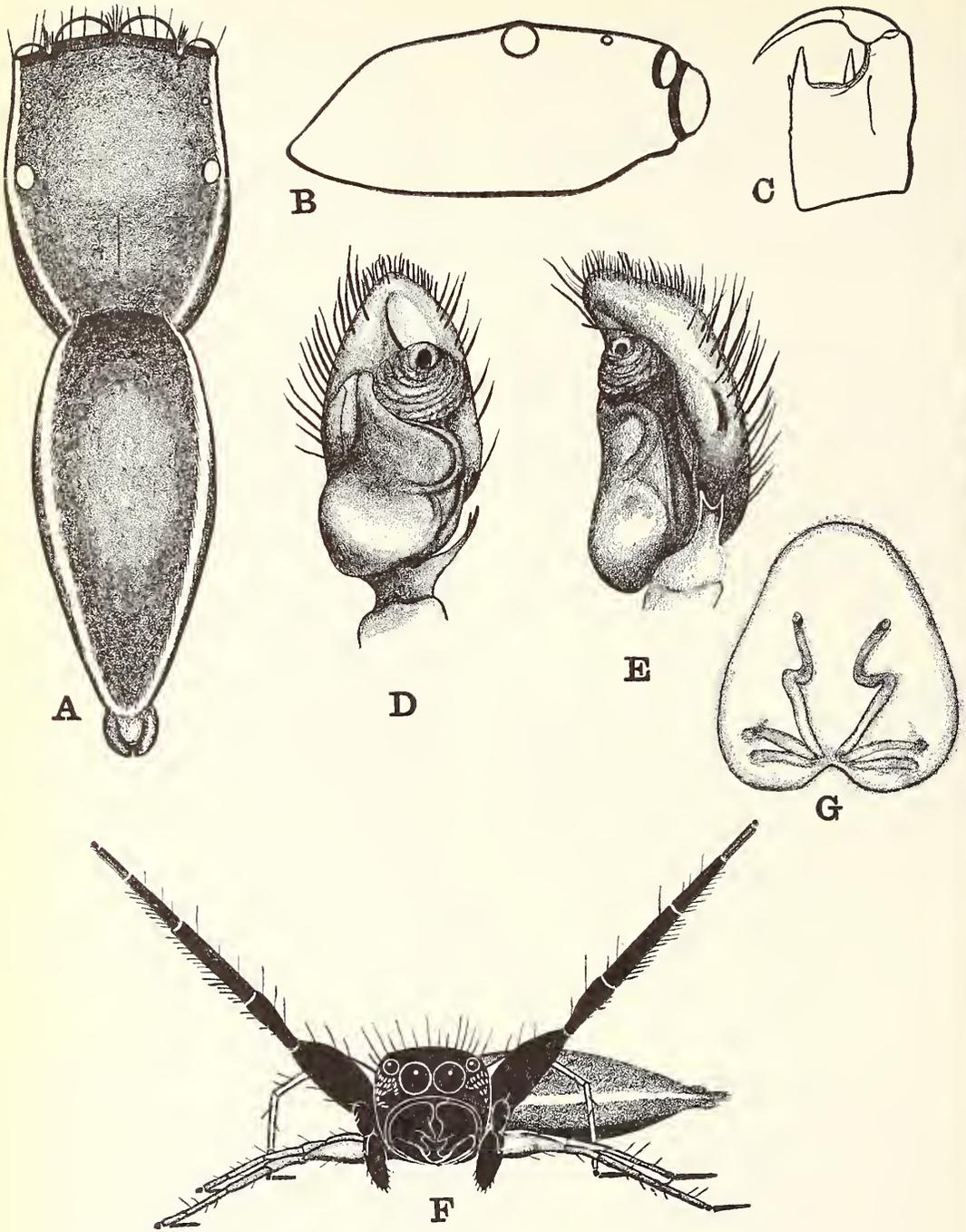
*In Life*: Adult male. Carapace above entirely covered with iridescent scales, rich green with bronze reflections. A white stripe starting behind ALE, bordered narrowly on ventral margin with black, passing immediately below PME and PLE, and extending along thorax almost to pedicel. Sides of carapace naked, black with a narrow white submarginal border of scales. AME narrowly rimmed with yellowish. Clypeus black, naked. Palps and first legs black (except pale 1st tarsi), other legs translucent buff. Sternum black. Abdomen covered with green scales like those of carapace, outlined dorso-laterally with white, which either continues to tip of abdomen or stops short of the tip; a white distal median spot present or absent. Moderate green iridescence on lower abdominal sides, below white stripe; venter black.

Adult female. Like male, except sides of carapace brown, not black; palps light green-yellow, not black; first legs dark brown, not black, the distal metatarsus and entire tarsus paler; other legs pale as in male, but with greenish tinge.

*In Alcohol*: The green iridescence is almost or completely lacking, and the scales may be largely missing, especially on the abdomen, where there may be faint traces of median spots or other markings. The white dorso-lateral bands, however, are very persistent.

#### STRUCTURE.

Essentially as in Chickering's description of *A. dentata* Cambridge, 1901 (Chickering, 1946, p. 248). The only significant differences are as follows: *Chelicerae*: Large prolateral tooth of basal segment of chelicera straight, not curved; enlargement at base of fang less distinct, a tubercle rather than a tooth. *Fringe* on first leg continues onto metatarsus. *Spines*: Very similar in the two species; the femoral prolateral distal spines tend to be more numerous than in *dentata* (first leg 2, not 1; 4th leg, male, 1 not 0, but 0 in female); metatarsal prolaterals tend to be fewer than in *dentata* (second leg 0, not 1; third leg 1, not 2); a weak fourth metatarsal ventral distal is present in *furcillata*, absent in *dentata*. Female *furcillata* as in male, except that femoral distal spines are reduced, about as in male *dentata*, and tibials are completely absent. *Palp*: Tibial apophysis differs radically from that of all pre-



TEXT-FIG. 4. *Ashtabula furcillata*. A-E, holotype ♂: A, carapace and abdomen, dorsal view; B, carapace, lateral view; C, chelicera, ventral view; D, palp, ventral view; E, same, ectal view; F, courtship display. G, paratype ♀: epigynum.

viously known males—*zonura* Peckham, 1894, *dentata* Cambridge, 1901, and of *denticheleis*, *sexgutta* and *glauca*, all of Simon, 1902; in *furcillata* alone it is not simple, but distally forked.

#### MEASUREMENTS.

Male holotype. Total length in alcohol 4.2 mm.; carapace length 1.9, breadth 1.4, height .75; ocular quadrangle length .82, breadth 1.2; diameter AME .34; ALE .17; PME .04; PLE .17; clypeus height .05; basal segment of chelicera 2.4; patella breadth, 1st leg, .19, 4th .21; length of abdomen 2.3, breadth 1.1.

#### Leg Measurements, Male.

Leg	Femur	Pat.	Tib.	Metat.	Tarsus	Total
1	.12	.79	.99	.79	.41	4.2
2	.82	.44	.55	.48	.31	2.6
3	.79	.38	.51	.51	.31	2.5
4	.99	.51	.72	.58	.34	3.1
Palp	.68	.14	.10	—	.62	1.5

Female paratype. Total length in alcohol 3.7 mm.; carapace length 1.7; carapace breadth 1.1; carapace height .68; ocular quadrangle .79; ocular quadrangle breadth 1.1; diameter AME .33; ALE .17; PME .04; PLE 17; clypeus height .03; basal segment of chelicera .36; patella breadth, 1st leg .26, 4th .21; length of abdomen 2.0, breadth 1.0.

#### Leg Measurements, Female.

Leg	Femur	Pat.	Tib.	Metat.	Tarsus	Total
1	.82	.55	.62	.48	.31	2.8
2	.68	.38	.44	.38	.27	2.2
3	.68	.38	.38	.41	.31	2.2
4	.85	.44	.65	.51	.31	2.8
Palp	.44	.21	.41	—	.38	1.4

Tibial indices: Holotype male, first leg 11, fourth leg 17; paratype female, first leg 22, fourth leg 19. See Table IV for formula.

TABLE IV.

#### *A. furcillata*: Leg formula.

	1	4	2	3
Male holotype	2.2	1.6	1.4	1.3
	1	4	2	3
Female paratype	1.6	1.6	1.3	1.3

#### BEHAVIOR.

*Locomotion*: A scurrying run, the first legs held flat and low, straight in front of body; both they and the palps palpate the surface almost constantly during progress. During pauses the first legs are usually elevated, and they and the palps jerked rapidly up and down. Both *Ashtabula* and *Sassacus* are masters of backward running, and both can jump well, although they never resort to it except in crossing gaps and in the final stage of prey capture.

*Courtship Display*: *Stage I*. Male carapace well elevated, abdomen swung to one side (usually the left), where it is held low, practically resting on ground; the spider sidles back and forth, raising the front legs at a wide angle and waving them up and down

in unison. The palps occasionally jerk up and down, but hang quietly during height of display. The white abdominal stripe and its bounding iridescence show clearly, little impeded by the short, pale, posterior legs. When the attention of a female has been gained, her pale, greenish-yellow palps jerk up and down rapidly and almost continuously, being conspicuous against her dark brown clypeus and mouthparts. *Stage II*. Not seen.

*Threat Display*: Inter-male display seems feebly developed in this species; three different pairs of males at various times, all in display condition, judging by their behavior toward females, paid little or no attention to each other, except for some brief elevation of the forelegs, which frequently takes place in any situation and appears to be of an exploratory nature.

*Habitat*: Known only from the montane cloud forest (about 3,600 feet) around Rancho Grande. Always taken on herbs, shrubs and low trees.

*Affinities*: Close to *A. dentata*; see remarks under *Structure*. It seems likely that *dentata*, *denticheleis* and *furcillata* will prove to be no more than subspecies of *zonata*.

*Material*: A total of 5 adult males and 1 adult female have been preserved. The following have been designated as types:

**HOLOTYPE**: Male. Cat. No. 461203, Department of Tropical Research, New York Zoological Society; Portachuelo, Rancho Grande, near Maracay, National Park of Aragua, Venezuela; 1,136 meters; cloud forest; June 15, 1946.

**PARATYPE**: Female. Cat. No. 481559, Department of Tropical Research, New York Zoological Society; same locality as holotype; July 21, 1948.

The name *furcillata* is proposed in reference to the characteristic forked tip of the palp's tibial spine.

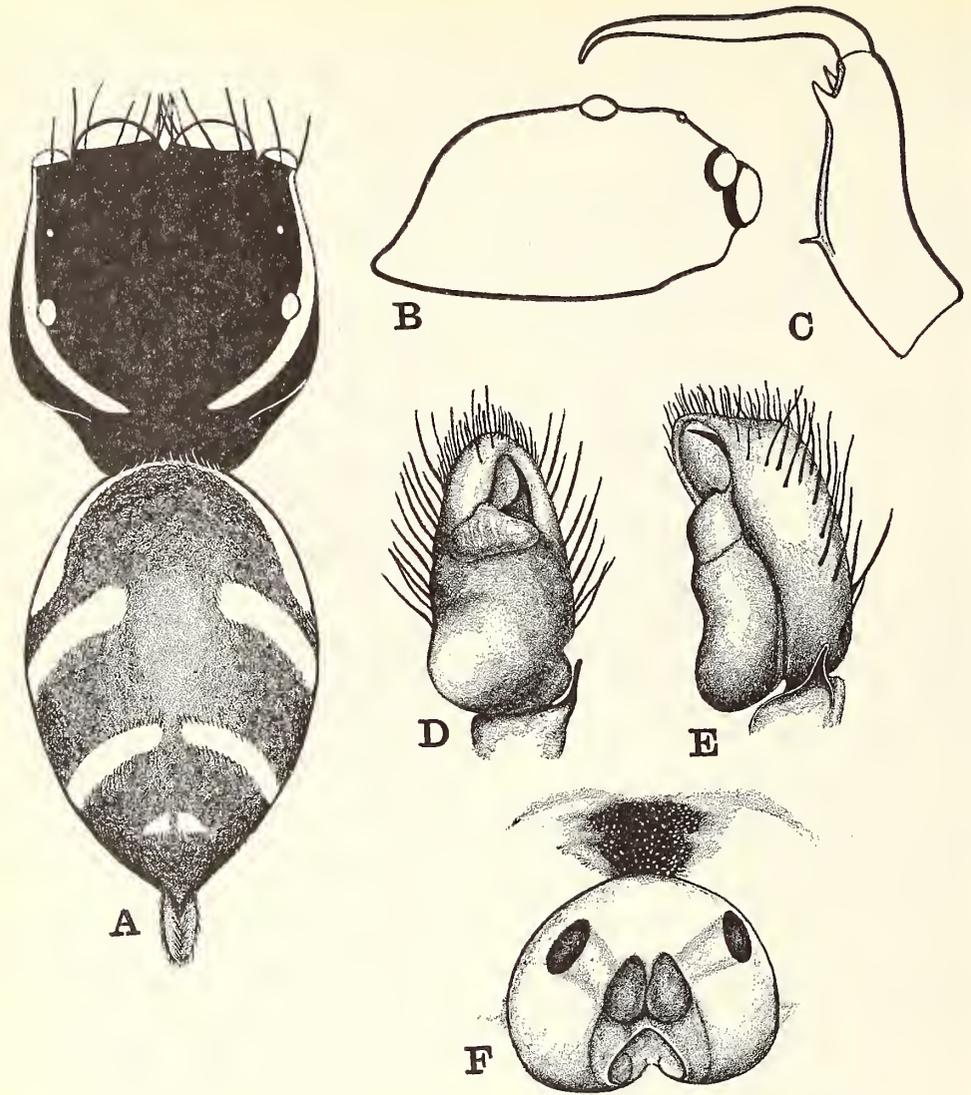
#### *Sassacus flavicinctus* sp. nov.

(Text-fig. 5).

*Diagnosis*: Male black with yellow on clypeus, in paired stripes and a submarginal band on carapace, and in transverse markings on abdomen. Female brown with obscure ochraceous markings. Chelicera of male strongly produced, the promargin with two teeth, far separated, the retromargin with a single strong tooth near distal end. Tibial apophysis of palp strong, simple, tapering, tip slightly recurved; embolus curved.

#### COLOR.

*Color in Life*: Adult male. Cephalothorax: Integument of carapace black, with a moderate number of long bristles in ocular region, and with lemon yellow (Ridgway) scales arranged in dense bands as follows: A pair on carapace just below dorsal eyes, converging slightly behind them and ending, without meeting, halfway down thoracic slope; a narrow submarginal band; a well-developed band of scales and scale-hairs



TEXT-FIG. 5. *Sassacus flavicinctus*. A-E, holotype ♂: A, carapace and abdomen, dorsal view; B, carapace, lateral view; C, chelicera, ventral view; D, palp, ventral view; E, same, ectal view. F, paratype ♀: epigynum.

completely covering and slightly pendent from the narrow clypeus. Mouthparts and legs black except as noted below; all tarsi brown; tibia and metatarsi of all except first legs banded brown and black in varying proportions; all legs with small anterior patches of yellow and white hairs and scales on some or all of the following segments: Femur, patella and tibia; these markings are highly variable. Sternum black with white hairs, which occur also on underside of coxae. Abdomen: A basal semi-circular band of lemon yellow scales continuing backward a third of abdominal length; behind this two pairs of short, curved bars, concave posteriorly, of which the posterior pair may join in the midline; at tip of abdomen a tiny round spot, or a short bar concave posteriorly, may be

present or absent. Center black with a triangular patch of white hair, the apex posterior.

Adult Female. Cephalothorax: Carapace black with rather weak markings of ochraceous brown scale-hairs as follows: Across clypeus and completely encircling sides of carapace and thoracic slope, absent only in middle of ocular quadrangle. Palps dark with yellowish hairs. Legs banded light and dark brown. Sternum black.

Abdomen: Dorsum with an indistinct, interrupted reticulated pattern which consists basically of an anterior basal band, followed by several pairs of hollow bands; the latter do not meet in midline, but join with the preceding band by a narrow stripe just before the center; tip of abdomen covered with

ochraceous hairs. Venter black with a few scattered light hairs.

All scale-hairs easily removed, and frequently absent in preserved specimens.

#### STRUCTURE.

The characteristics below apply to both males and females unless otherwise specified; percentages approximated; measurements of types given below.

*Carapace*: Height about half (female) or slightly less than half (male) of carapace length; anterior part of thorax flat, with a very gentle slope, rounding into rounded sides of cephalic part; descent of posterior part (less than half postocular length) abrupt, slightly concave; width of carapace greatest a little behind PLE, 1.5 times height, 67% (male) to 75% (female) of carapace length; thoracic groove scarcely indicated.

*Eyes*: Length of ocular quadrangle about 58% as long as broad, its sides almost parallel, though very slightly wider at ALE than at PLE; carapace extending slightly beyond PLE at their level, PME slightly nearer ALE than PLE. Diameter of AME about 20% of carapace length; ratio of eyes, holotype: AME: ALE: PME: PLE:: 100:48:8:44. AME practically contiguous, separated from ALE, which are slightly recurved, by about an eighth of their diameter.

*Clypeus*: Height 12% of AME diameter.

*Chelicerae*: In males strongly produced, held almost parallel to ground, divergent; length of basal segment about three-fifths of carapace length. Promargin with one slender tooth at proximal end of groove and one, long, robust, triangular, far removed, near base of fang; slightly proximal to this on retromargin a single large tooth. Fang slender, slightly sinuous. Chelicerae of females much shorter with a very short groove flanked on promargin by two teeth close together, the proximal the smaller, and one large tooth on retromargin.

*Maxillae*: Width about 75% of length; outer distal edge in male more dilated and obtusely angled than in female.

*Lip*: Breadth more than 90% of length; distal end reaching slightly beyond middle of maxillae; sternal suture curved, especially in male.

*Sternum*: Width 62% of length in males; wider, about 73%, in females. Anterior margin concave, narrower than base of lip; greatest width between first and second legs; posterior end bluntly pointed, extending slightly between fourth coxae; the latter separated by less than half their diameter.

*Legs*: Tibial indices: Holotype male, first leg 16, fourth leg 17.5; paratype female, first leg 26, fourth leg 23. First femur in both sexes enlarged, and entire first leg somewhat thickened and elongated in male. See Table V for formula. All legs with little hair.

*Spines*: (From male holotype and female paratype). Patella without spines throughout. First leg: Femur, dorsal 3 in distal half; prolateral distal 1 in male, 2 in female; tibia ventral only 1r-2-2, the two distal pairs close together, the proximal at beginning of second quarter of segment; metatarsus, ventral only, 0-2-2. Second leg differs from first in having tibia ventral 1r-1r-2, (male) or 1r-0-2 (female); tibia prolateral, male only, 1-1 (both small); metatarsus, female only, with 1 prolateral distal. Third leg, femur, dorsal 0-1-1-1, prolateral distal 2 (male), or 1 (female); tibia prolateral 0-1 (male) or none (female); retrolateral 0-1; ventral 0-0-2 (male) or 1p-1p-2 (female); metatarsus prolateral distal 2, retrolateral distal 2, ventral distal 2. Fourth leg, femur as in third; tibia prolateral none (male), or 0-1 (female); retrolateral 0-1 or none (variable on two sides); ventral 1p-0-2 or 1r-1r-2 or 0-0-2 (variable on two sides); metatarsus prolateral distal 0-1, sometimes in female only 0-2, the second weak; ventral distal only 2, on one side of female 0-2-2.

*Abdomen*: Ovate in both sexes, the breadth about 70-75% of length, widest near middle.

*Palp*: Femur strongly curved; tibia more than one-half length of patella; tibia with a retrolateral apophysis which tapers to a blunt, slightly recurved point. Embolus tapering from a broad base to a curved and slender tip.

*Epigynum*: An anterior pair of bodies well separated, a posterior pair contiguous; marginal notch deep and narrow.

#### MEASUREMENTS.

Male holotype. Total length in alcohol 4.51 mm.; carapace length 2.4, breadth 1.6, height 1.0; ocular quadrangle length .79, breadth 1.4; diameter AME .43, ALE .21, PME .03, PLE .19; clypeus height .05; basal segment of chelicera 1.37; patella breadth, 1st leg, .31, 4th .24.

#### Leg Measurements, Male.

Leg	Femur	Pat.	Tib.	Metat.	Tarsus	Total
1	1.3	.85	1.0	.72	.44	4.3
2	1.1	.58	.62	.62	.41	3.3
3	1.1	.48	.55	.68	.34	3.2
4	1.2	.55	.82	.75	.34	3.7
Palp	.79	.27	.17	—	.58	1.8

Female paratype. Total length in alcohol 4.68 mm.; carapace length 2.05, breadth 1.54, height 1.03; ocular quadrangle length .83, breadth 1.4; diameter AME .43, ALE .21, PME .03, PLE .19; clypeus height .05; basal segment of chelicera .72; patella breadth, 1st leg, .34, 4th .26.

TABLE V.

#### *S. flavicinctus*: Leg Formula.

	1	4	2	3
Male holotype	1.8	1.5	1.4	1.35
Female paratype	2	1	3	4
	1.8	1.65	1.7	1.4

## Leg Measurements, Female.

Leg	Femur	Pat.	Tib.	Metat.	Tarsus	Total
1	1.1	.65	.68	.55	.38	3.4
2	1.2	.51	.85	.72	.38	3.7
3	1.2	.51	.79	.68	.34	3.5
4	.92	.55	.55	.48	.34	2.8
Palp	.55	.24	.24	—	.38	1.4

## BEHAVIOR.

*Locomotion*: Compared with *Ashtabula*, this *Sassacus* is somewhat more a jumper and walker, less a scurrier; also it palpates the ground far less with the first legs and palps. Compared to the spiders of the *Plexippus* group, however, it is a poor and reluctant jumper.

*Courtship Display: Stage I.* Male follows female about, the carapace moderately elevated and the first legs raised at a wide angle to each other; frequently lowered; the abdomen hangs down and is trailed inconspicuously from side to side with sideling. Display tends to be in a wide semi-circle around female, once her attention has been attracted. The long chelicerae are folded but held out laterally (when not displaying they are held at right angles to each other), and the palps extend straight out also, in contrast to their usual resting position when they hang over chelicerae. With increasing stimulation, zig-zagging becomes more pronounced and a slow rocking is involved, the carapace and abdomen held stiffly and rocking as a unit. Stage II is usually attained within three to five minutes by couples of low threshold to display stimuli, and consists of the first legs thrust out in front, clear of the ground.

*Threat Display: Stage I.* Indistinguishable from Stage I of courtship, except that no rocking is involved. *Stage II.* It is only in the rare occurrence of this stage that the chelicerae blades are unsheathed; when two opponents are practically touching the first legs are brought upright, from the obliquely outward display position, and simultaneously the chelicerae blades are extended straight out in front, at right angles to the basal segment, which is maintained in the horizontal position typical of display. In each of the dozen or so observed encounters that reached this stage, one or the other male usually backed off promptly at this point; more rarely there was a brief tangle which ended without apparent injury. Usually one or both males retreated before reaching Stage II.

*Habitat*: Known only from the montane cloud forest (about 3,600 feet) around Rancho Grande. Always shaken from herbs, shrubs and low trees.

*Affinities*: This species appears exceedingly close to *S. arcuatus* Simon, 1902, from Tefte, in the Amazon region. From the brief description, the only apparent differences are slight distinctions in the abdominal markings and the absence, in the present form, of a yellow spot on the palp femur.

*Material*: A total of 5 adult males and 5 adult females have been preserved in addi-

tion to a number of young. The following have been designated as types:

**HOLOTYPE**: Male. Cat. No. 45451. Department of Tropical Research, New York Zoological Society; Portachuelo, Rancho Grande, near Maracay, National Park of Aragua, Venezuela; 1,136 meters; cloud forest; June 1, 1945.

**PARATYPE**: Female. Cat. No. 45452 Department of Tropical Research, New York Zoological Society; same locality as holotype (with which she mated); July 1, 1945.

The name *flavieinctus* is proposed in reference to the yellow bands characterizing the male.

***Sassacus ocellatus* sp. nov.**

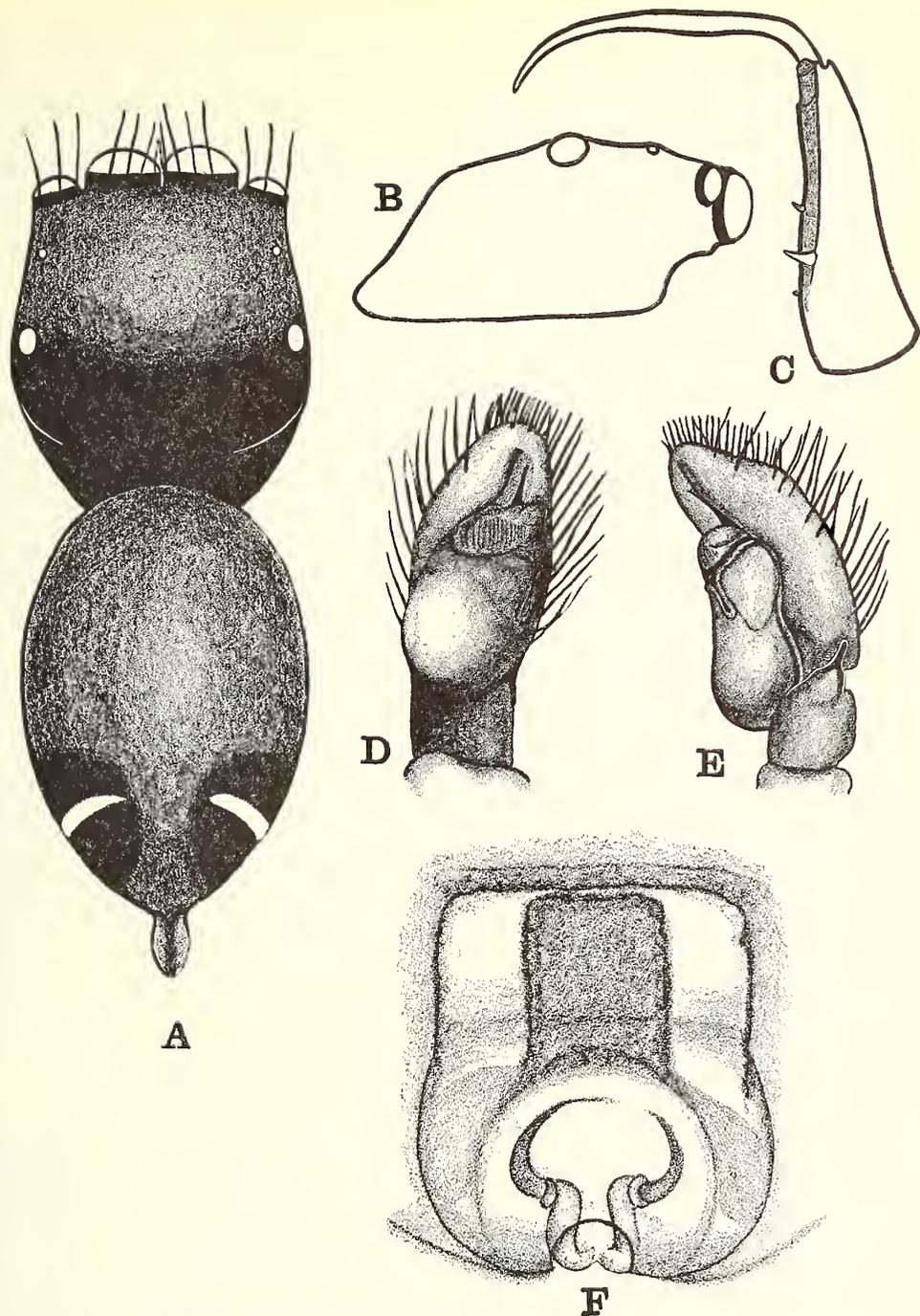
(Text-fig. 6).

*Diagnosis*: Both sexes iridescent green above, with a pair of black spots, each crossed by a white bar, near tip of abdomen. Chelicera of male strongly produced, the promargin with two well-separated teeth in proximal half, opposed by a single large tooth on retromargin. Spines of first tibia 2-2-2. Tibial apophysis of palp strong, simple, tapering, tip straight; embolus tip straight.

## COLOR.

*Color in Life*: Adult male. Cephalothorax: Integument of carapace black; ocular region with a number of long bristles and completely covered with iridescent green scales which extend a little below it on sides and thoracic region. A broad band of white hairs, starting below PME on side of carapace, extends forward across clypeus. Palps, mouthparts and first legs jet black; other legs brown; two narrow, conspicuous stripes of white scales extend along anterior and posterior sides of first patella, tibia and base of metatarsus. These scales, although progressively fewer posteriorly, are present on anterior sides of all other legs, as well as on posterior sides of second legs. Sternum black. Abdomen entirely covered above, except as hereafter noted, with iridescent green scales, larger than those on carapace. On dorso-lateral surface on each side of posterior third is a large spot of velvety black scales, each with a narrow cross-bar of white scales from one-third to two-thirds of the way to its posterior edge. Around the entire abdomen laterally is a narrow band of iridescent green, confluent except in region of spot, with the dorsal green. Venter black.

Adult female. Cephalothorax: carapace as in male, with the addition of a narrow sub-marginal border of white scales continuing almost as far as pedicel. Entire face, around eyes, with more white scales and hairs than in male. Chelicerae black with a few white hairs basally; palps translucent brown barred narrowly with darker on joints, and with a few white hairs on patellae. All legs translucent brown except first femora, which are almost black. Sternum black. Abdomen as in male, except that there is a faint an-



TEXT-FIG. 6. *Sassacus ocellatus*. A-E, holotype ♂: **A**, carapace and abdomen, dorsal view; **B**, carapace, lateral view; **C**, chelicera, ventral view; **D**, palp, ventral view; **E**, same, ectal view. **F**, paratype ♀: epigynum.

terior band of white scales, dying out laterally in variable faint spots, while the white cross-bars on the posterior black spots tend to be on the latter's anterior margin.

In alcohol the iridescent green completely vanishes, the scales appearing dull yellowish or brownish; the abdominal black spots with white cross-bars are discernible, but far less

distinct than in life, the anterior part of the spot tending to disappear altogether. As usual, the black integumentary areas fade to brown.

#### STRUCTURE.

Essentially as in *S. flavicincta* except in the following respects: carapace lower, its height less than half carapace length in both

sexes, lower in male than in female. *Chelicera* of male even longer in some specimens, but varying in individuals; basal segment in holotype is 5/6 of carapace length; promargin with two small teeth well separated, along proximal half of groove; opposite their interspace, on retromargin, is a single, much larger, conical tooth. *Tibial indices*: Holotype male, first leg 21, fourth leg 19; paratype female, first leg 25, fourth leg 19. See Table VI for formula.

TABLE VI.

*S. ocellatus*: Leg Formula.

	1	4	2	3
Male holotype	1.9	1.5	1.4	1.2
	1	4	2	3
Female paratype	1.7	1.7	1.3	1.3

*Spines*: As in *flavicinctus*, but with first tibial ventral 2-2-2, not 1r-2-2, and with spines on posterior legs somewhat fewer, viz.: Second leg: Male, tibia prolateral 0, not 1-1; female as in *flavicinctus*. Third leg: Male, femur prolateral distal 1, not 2; female, prolateral 0, retrolateral 1; tibia 0 in both sexes, not with a few pro- and retrolaterals and ventrals; metatarsus (both sexes) pro- and retrolateral distals each 1, not 2. Fourth leg (both sexes): Femur prolateral 1 not 2; tibia, ventral distal only 1p in male, 0 in female; metatarsus, as in third leg, but with traces of another lateral distal pair (very weak), similar to those in *flavicinctus*; especially noticeable in female.

*Palp*: Tibial apophysis and embolus both straight, not curved. *Epigynum*: Radically different from that of *S. flavicinctus* (see figure); marginal notch broad and shallow.

## MEASUREMENTS.

Male holotype. Total length in alcohol 3.3 mm.; carapace length 2.1, breadth 1.5, height .79; clypeus height .07; basal segment of chelicera 1.8; patella breadth, 1st leg .34, 4th leg .22; length of abdomen 2.2, breadth 1.4.

## Leg Measurements, Male.

Leg	Femur	Pat.	Tib.	Metat.	Tarsus	Total
1	1.2	.72	.92	.65	.44	3.9
2	.89	.55	.62	.58	.38	3.0
3	.82	.44	.51	.48	.38	2.6
4	.99	.51	.68	.65	.38	3.2
Palp	.82	.55	.14	—	.58	2.1

Female paratype. Total length in alcohol 5.0 mm.; carapace length 1.7, breadth 1.3, height .72; clypeus height .10; basal segment of chelicera .58; patella breadth, 1st leg .31, 4th leg .21; length of abdomen 3.3, breadth 2.1.

## Leg Measurements, Female.

Leg	Femur	Pat.	Tib.	Metat.	Tarsus	Total
1	.85	.62	.62	.48	.34	2.9
2	.68	.48	.41	.38	.31	2.3
3	.68	.41	.41	.44	.31	2.3
4	.89	.48	.65	.55	.37	2.9
Palp	.44	.21	.21	—	.34	1.2

## BEHAVIOR.

*Locomotion*: About midway between *Ash-tabula* and *S. flavicinctus*. Its usual progress is a rapid scurry, jumping only when necessary, the first legs held forward, usually scarcely touching the ground, the palps held just clear of it. During the infrequent pauses, the first legs and palps are raised in the air and waved up and down; after which both sets of appendages sometimes palpate the ground itself.

*Courtship Display: Stage I.* Carapace scarcely elevated, first legs held up at about right angles to each other, and brought to ground again during the jerking, zig-zag approach to female. The long chelicerae are sheathed, the palps hanging quietly over them in the normal resting position, except for occasional vibration. Approach to the female is often quick and direct after the preliminary zig-zags. The most interesting phase may or may not be included; it consists of posing for a few moments, motionless, the legs elevated, and the abdomen twisted slightly to one side or the other; once the female was seen to perform the same motion, although that courtship was not completed. The relatively short abdomen was never swung far to the side as in the elongate *Ash-tabula*, and the black, white-barred terminal spot could not have been in full view. In the single courtship which ended in actual mating, this phase was altogether omitted. *Stage II.* This was often reached within three minutes; in one case mating followed five minutes after display began. It did not differ from that of *flavicinctus*.

*Threat Display*: True fighting frequently takes place in this species and even when inter-male display ends in mere threat, the chelicerae are always more or less unsheathed, which never happens in courtship. The behavior otherwise is similar except that I observed little or no trace of the side-swinging of the abdomen. During actual battle the first legs are raised directly overhead, and the palps extended laterally, widespread, out of the way; the wide-open chelicerae are opposed to those of the opponent. The two may then push back and forth for seconds, until one of the pair retreats or is bitten.

*Habitat*: Known only from the montane cloud forest (about 3,600 feet) around Rancho Grande. Always shaken from herbs, shrubs and low trees.

*Affinities*: The abdominal markings are somewhat similar to those of *S. aurantiacus* Simon, 1902, from Para, Brazil, known only from the briefly described female. The present species has a full set of 2-2-2 spines on the first tibia, instead of 1p-2-2, in both sexes.

*Material*: A total of 11 adult males and 9 adult females have been preserved in addition to a number of young. The following have been designated as types:

HOLOTYPE: Male. Cat. No. 461204, Department of Tropical Research, New York

Zoological Society; Portachuelo, Rancho Grande, near Maracay, National Park of Aragua, Venezuela; 1,136 meters; cloud forest; March 27, 1946.

PARATYPE: Female. Cat. No. 481560, Department of Tropical Research, New York Zoological Society; same locality as holotype; July 17, 1948.

The name *ocellatus* is proposed in reference to the eye-like abdominal markings.

*Phiale flammea* sp. nov.

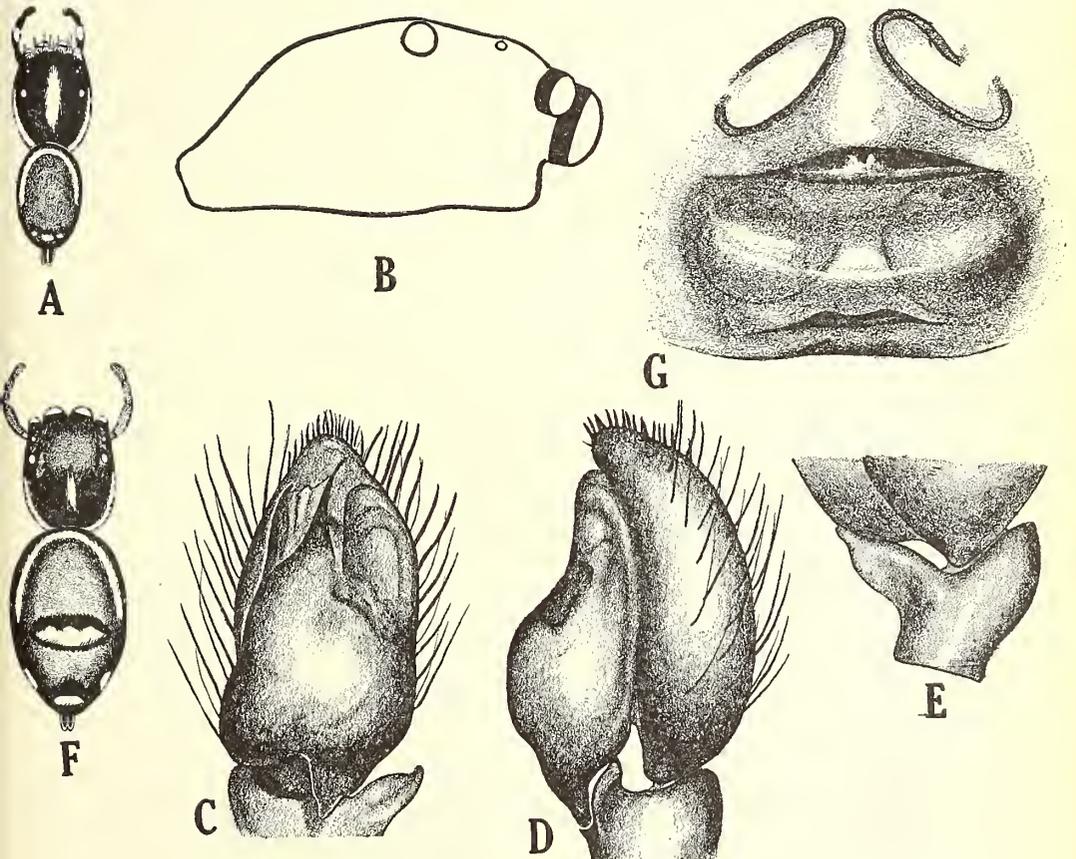
(Text-fig. 7).

*Diagnosis:* All carapace bands in both sexes creamy yellow. Male: Carapace markings broad, including submarginal and clypeal bands and mid-dorsal stripe; no spots near PME. Abdomen above bright rufous with white markings; median spot absent, although a faint cross-bar may be present or absent beneath rufous scales; no terminal hook on antero-lateral band; three terminal spots. Palp with tibial apophysis stout, truncate; bulb strongly bilobed; lateral process of embolus shorter than and widely separated from embolus proper. Female: Carapace markings less extensive than in male. Abdomen with reddish scales ranging almost to black; anterior abdominal band as in

male; strong, post-median cross-bar and terminal spots present. Epigynum with two strongly chitinized, external cross-bars.

COLOR.

*Color in Life:* Adult male. As in Chickering's description of *P. aliciae* in alcohol (1946, p. 207), except as follows: Cephalothorax: Integument of carapace, mouthparts, palps and first legs (except metatarsus and tarsus) black, not dark brown; integument of other legs translucent, medium brown. All carapace scale-hair bands distinctly buffy yellow; anterior eyes rimmed with rust; clypeus with a strong band of creamy yellow scale-hairs, instead of only "a fringe of yellowish bristles;" palp femur with dorsal scale-hair patch as in *aliciae*; a patch of white-scale hairs on proximal anterior face of first metatarsus and tarsus; variable numbers and arrangements of similar scales, diminishing posteriorly, on other segments of other legs. Abdomen: Dorsum in full sunlight often matches the flame scarlet of Ridgway; other individuals tend to orange rufous. As in *aliciae*, white markings consist of a simple anterior band extending dorso-laterally more than halfway to spinnerets, and ending without a hook-shaped inward curve



TEXT-FIG. 7. *Phiale flammea*. A-E, holotype ♂: A, carapace and abdomen, dorsal view; B, carapace, lateral view; C, palp, ventral view; D, same, ectal view; E, same, tibial apophysis. F, G, paratype ♀: F, carapace and abdomen, dorsal view; G, epigynum.

(as is characteristic of *P. dybowskii*, for example); usually it ends abruptly; sometimes there is a very slight inward curve. The "narrow, light-colored central bar" of *aliceae* is invisible in live specimens though it sometimes shows in preserved examples, beneath the rufous scales. Three small white terminal markings, in the form of spots or short bars, as in *aliceae*; carapace stripe easily rubbed, often small in preservative.

Adult female. Exceedingly variable, both in the pattern of white and dark scales, and in the vividness of the reddish abdominal markings; the individuals are separated with difficulty in pattern from at least two other species occurring typically on the lower slopes of the same mountain range. They differ from the male as follows: Cephalothorax: buff stripe and bands of carapace—median, submarginal and clypeal—much less extensive; sparse rusty hairs usually present on and around ocular quadrangle; anterior eyes rimmed with yellowish-white, not rust; some buff hairs on face below ALE; palps translucent buffy yellow, not black, and lacking buff scales; first legs black only on femur and patella; white hairs and scales of all legs reduced or absent. Abdomen: Red of dorsum exceedingly variable, practically always less bright than in male, sometimes almost black. A strong post-median, black-bordered cross-bar of white scales always present, but of variable length and breadth, sometimes confluent with ends of anterior dorso-lateral band, which is as in male; posterior spots present as in male, but of more variable size and shape, sometimes partly confluent.

#### STRUCTURE.

This species is so close to *P. aliceae* (known only from holotype male) that no significant structural differences emerge from a comparison of Chickering's description with our species, except for minor spine and palp differences as given below. The females are closely similar to the males in structure, except for the usual leg differences, and for the absence of the small hooked maxillary process.

*Spines* (both sexes): Differ from *aliceae* as follows: First leg, Female: Patella prolateral 0, not 1. Second leg, both sexes: Tibia prolateral as in first (1-0-1, not 1-1-1), ventral apparently consistently 1r-2-2, not variable; metatarsus male, prolateral distal 0, not 1, but this spine present in female. Third leg (female only): Femur prolateral distal only 2, not 1-2, retrolateral 1, not 2; tibia dorsal 0, not 1; metatarsus with slight irregularities on one side of paratype female only, retrolateral 0-1-2, not 1-1-2, ventral 1p-1p-2, not 0-2-2. Fourth leg: Femur (both sexes) prolateral and retrolateral distal respectively 0 and 1, not each 2; male tibia as on right side of *aliceae* holotype, female dorsal 0, not 1.

*Palp*: Differs from that of *aliceae* in its relatively greater breadth and in the char-

acter of lateral process of embolus; in *flammea* the two parts are much farther apart, though connected by a thin, horny plate; also, the lateral process is much shorter than embolus proper, and scarcely curved distally.

*Epigynum*: Confusing, as usual in this genus, on account of the frequent secretion of gummy matter which obscures and distorts the structure. Always distinct, however, are two strongly chitinized transverse, lip-like structures, one between the two pairs of subdermal bodies and one near posterior border.

#### MEASUREMENTS.

Male holotype. Total length in alcohol 4.6 mm.; carapace length 2.7, breadth 1.9, height 1.1; clypeus height .19; basal segment of chelicera .89; patella breadth. 1st leg, .41, 4th .28; length of abdomen 1.9, breadth 1.4.

#### Leg Measurements, Male.

Leg	Femur	Pat.	Tib.	Metat.	Tarsus	Total
1	1.8	1.1	1.7	1.1	.68	6.4
2	1.3	.75	.89	.79	.48	4.2
3	1.5	.79	.85	1.1	.55	4.8
4	1.6	.75	1.2	1.3	.55	5.4
Palp	.85	.24	.24	—	.82	2.2

Female paratype. Total length in alcohol 5.1 mm.; carapace length 2.5, breadth 1.7, height 1.1; clypeus height .07; basal segment of chelicera .85; patella breadth, 1st leg .40, 4th .31; length of abdomen 2.6, breadth 1.7.

#### Leg Measurements, Female.

Leg	Femur	Pat.	Tib.	Metat.	Tarsus	Total
1	1.2	.85	.89	.65	.51	4.1
2	1.1	.65	.65	.62	.48	3.5
3	1.3	.72	.79	.82	.55	4.2
4	1.4	.72	.99	1.1	.62	4.8
Palp	.65	.27	.31	—	.55	1.8

Tibial indices: Holotype male first leg 15, fourth leg 14; paratype female, first leg 23, fourth leg 18. See Table VII for formula.

TABLE VII.

#### *P. flammea*: Leg Formula.

	1	4	3	2
Male holotype	2.4	2.0	1.8	1.5
	4	1	3	2
Female paratype	1.9	1.6	1.7	1.4

*Locomotion*: Primarily a runner, although jumps are undertaken over gaps without hesitation. The first legs take little part in locomotion and are habitually waved up and down during the pauses.

*Courtship Display: Stage I.* Carapace elevated high; abdomen hangs down, usually touching ground and leaving a silk thread. First legs raised at 45° angle with each other and the ground. Female approached in zig-zag spurts, as the carapace is rocked from side to side, sinking alternating almost to the ground, from right to left. Palps irregularly vibrated up and down. Pursuit of female plays an important part in early stages,

but once female's attention is gained, she usually watches with first legs elevated and palps vibrating rapidly.

*Stage II.* Male abruptly crouches almost on ground, when two inches or less from female; his legs far outstretched in front, almost parallel, he approaches her directly with crawling motion, the palps vibrating in unison and entire body quivering. The remarkable point about Stage II in this species is that it begins at such a relatively long distance from the female.

*Threat Display:* As in Stage I of courtship, except that the palps are held quiet most of the time, the creamy yellow patch of the curved femur continuing that of the clypeus in an unbroken line. When approach is very close the chelicerae are opened and the first legs spread more widely, often actually touching those of the opponent. The bouts are always brief and I have never seen damage inflicted.

*Habitat:* Known only from the montane cloud forest (about 3,600 feet) around Rancho Grande. Always taken on herbs, shrubs or small trees.

*Affinities:* The closeness of this species to *P. aliciae* has already been noted. When adequate material is taken from intermediate localities, it seems likely that the distinctions will prove to be of only subspecific importance.

*Material:* A total of 14 adult males and 20 adult females have been preserved. The following have been designated as types:

**HOLOTYPE:** Male. Cat. No. 481561, Department of Tropical Research, New York Zoological Society; Portachuelo, Rancho Grande, near Maracay, National Park of Aragua, Venezuela; 1,136 meters, cloud forest; July 25, 1948.

**PARATYPE:** Female. Cat. No. 45453, Department of Tropical Research, New York Zoological Society; same locality as holotype; July 26, 1945.

The proposed name *flammea* refers to the color of the male dorsum.

***Mago denticelis* sp. nov.**

(Text-fig. 8).

*Diagnosis:* Carapace of unrubbed individuals with a median white stripe enclosing a central black spot. Male chelicera with tooth on external border; four or five teeth on inferior margin; two or three teeth, plus a series of denticles, on superior margin; tibia of palp with three unequal apophyses; epigynum with a median, rounded, superficial, pale anterior body.

**COLOR.**

*Color in Life:* Adult male. Cephalothorax: Carapace integument black, practically naked except for a conspicuous median stripe of white scales enclosing, behind level of PLE, a central black spot. The stripe begins behind AME, or near level of PME, widens to encompass the spot, then narrows once

more, ending at or behind middle of thorax. White of spot region sometimes extending laterally as a short cross-bar. Sparse chestnut and black hairs scattered on ocular quadrangle near dorsal eyes, and around AME. The wide clypeus is black and completely naked; palps, mouthparts and first pairs of legs black, except for leg tarsi. These and entire third and fourth legs translucent brown, variably and faintly banded with darker near ends of segments. Palps and all legs, especially first two, with inconspicuous white scale-hairs on antero-dorsal surfaces near joints. Sternum black. Abdomen: Pattern of dorsum very variable, formed chiefly of short hairs or scale hairs, brown mixed with gray and white areas. Usually a white lyre-shaped anterior marking—a strongly curved band with a short median basal stripe—is distinct; this is followed by several pairs of faint chevrons and some white lateral streaks and spots. The most constant markings are a pair of white terminal spots. Venter black with a pair of pale faint longitudinal stripes in middle; buff hairs rather thickly scattered over entire surface.

Adult female. Dorsal markings very similar to those of male, but posterior abdominal spots less distinct and more variable. Palps pale, translucent horn; first and second legs banded, not black; white scale-hairs on appendages almost or completely absent, though short yellowish hairs sometimes present near joints.

*In alcohol,* the distinctive markings usually disappear from both sexes.

**STRUCTURE.**

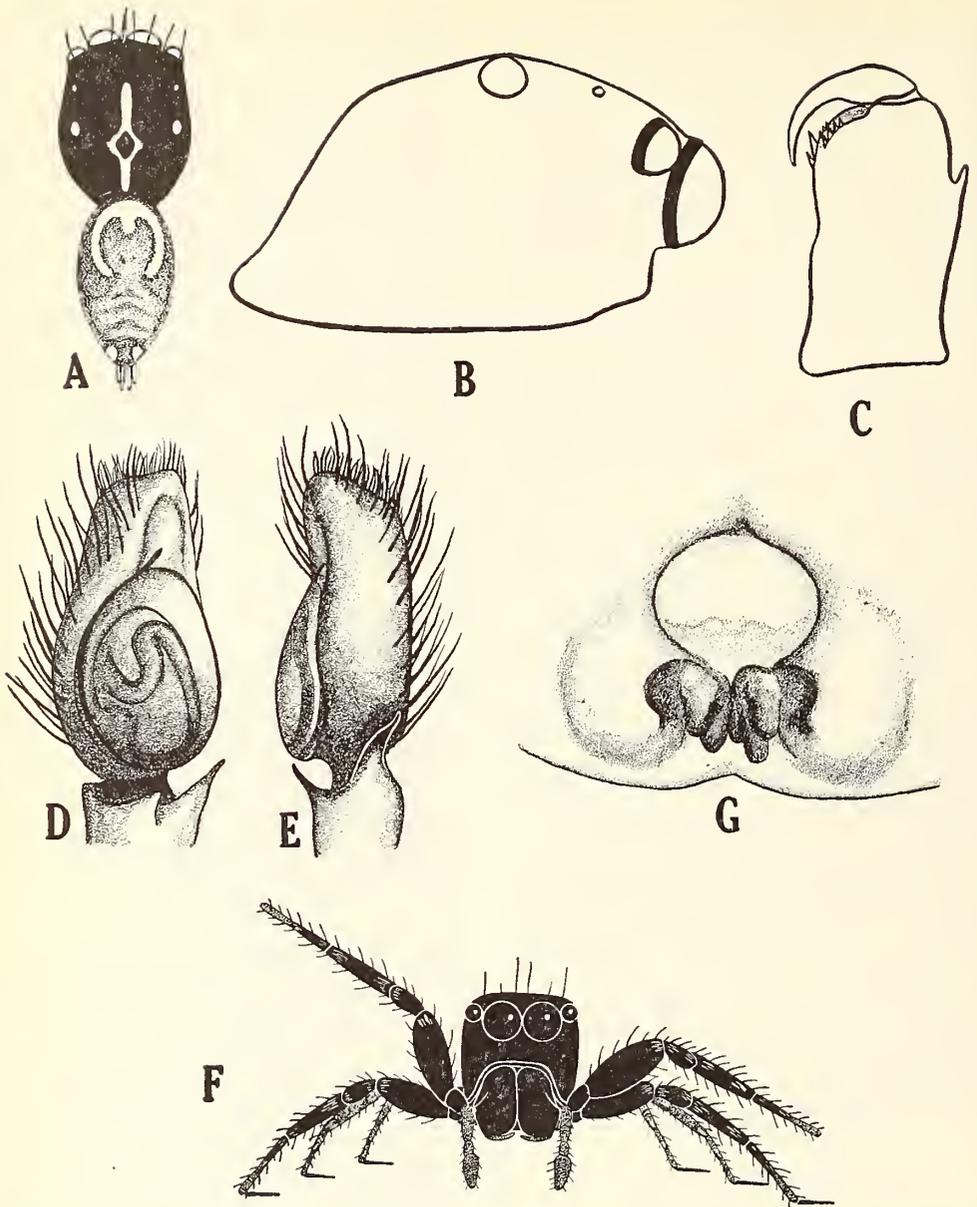
The characteristics below apply to both males and females unless otherwise specified; percentages approximated; measurements of types given on p. 51.

*Carapace:* Height 57% of carapace length; profile rises behind AME, gently convex, to PLE; anterior half of thorax descends very gently, posterior half abruptly; widest at level of PLE, 1.3 times height, 73% of length; total length of eye group slightly more than half carapace length. A distinct longitudinal thoracic groove, centering at level of posterior margin of PLE.

*Eyes:* Length of ocular quadrangle about two-thirds of breadth, its sides almost parallel but width at ALE slightly greater than at PLE; carapace extending well beyond PLE at their level; PME slightly closer to ALE than to PLE. Diameter of AME 23% of carapace length; ratio of eyes, holotype: AME : ALE : PME : PLE :: 100:46:14:40. AME practically contiguous, separated from ALE, which are slightly recurved, by about a tenth of their diameter.

*Clypeus:* Height 52% of AME diameter in male, 28% in female.

*Chelicerae:* Not produced, vertical, parallel. Length of basal segment less than 30% of carapace length. Male with a strong tooth about middle of external border. Promargin



TEXT-FIG. 8. *Mago dentichelis*: A-E, holotype ♂: A, carapace and abdomen, dorsal view; B, carapace, lateral view; C, chelicera, ventral view; D, palp, ventral view; E, same, ectal view; F, threat display. G, paratype ♀: epigynum.

with two (rarely three) moderate-sized teeth at proximal angle, the distal the larger; distal to these is a series of minute granular teeth, numbering three or more. Inferior margin usually with four, sometimes five, contiguous, well developed teeth.

*Maxillae*: Less than twice as long as wide, outer distal angle little dilated.

*Lip*: Length and breadth similar; posterior margin slightly convex, about equal in breadth to anterior margin of sternum.

*Sternum*: Breadth three-fourths of length

in male, two-thirds in female, widest at anterior margin of third leg. Anterior border concave, posterior broad and convex, ending before anterior half of fourth coxae; posterior half of latter separated by about an eighth of their diameter.

*Legs*: Tibial indices: Holotype male, first leg 17, fourth 29; paratype female, first leg 23, fourth 16. First femur, patella and tibia moderately enlarged, less so in second leg. See Table VIII for formula. All legs with little hair.

TABLE VIII.

*M. dentichelis*: Leg Formula.

	1	4	3	2
Male holotype	2.1	2.0	1.9	1.9
	4	3	1	2
Female paratype	1.9	1.8	1.7	1.6

*Spines*: First leg: Femur dorsal 0-1-1-1, prolateral distal only 2; patella prolateral only 1 or 0; tibial prolateral 1-0-1 (both weak), or 0-0-0; retrolateral 0; ventral, 1r-1r-2, or 2-2-2; metatarsus ventral only 2-2. Second leg: Femur dorsal 0-1-1-1, prolateral distal only 2, retrolateral female only 1; patella prolateral 1 or 0; tibia prolateral 1-1-1 or 1-0-1, retrolateral 0, ventral 1r-2-2; metatarsus ventral only 2-2. Third leg: Femur dorsal 0-1-1-1, prolateral 1 or 2, retrolateral 1 or 0; patella prolateral 1, retrolateral 1; tibia prolateral 1-1, retrolateral 1-1-1; ventral 1p-0-2; metatarsus prolateral 1-1, retrolateral 1-2, ventral 2-2. Fourth leg: Femur dorsal 0-1-1-1, prolateral 1, retrolateral 1; patella prolateral 1, retrolateral 1; tibia prolateral 1-1-1 or 1-1, retrolateral 1-1-1, ventral 1p-2; metatarsus prolateral 1-1, retrolateral 1-1-2, ventral 1p-2.

*Abdomen*: Rather narrowly ovate, widest near middle.

*Palp*: Femur slightly curved, tibia about 70% length of patella; tibia with three apophyses, one small and ventral, one long and tapering, external to the first, and the third still larger, sinuously tapering, dorso-lateral. Embolus short and simple.

*Epigynum*: A large, rounded, median, whitish anterior area, followed by a variable arrangement of four or five subdermal, near-median tubules, related to two less distinct, well separated oval bodies.

## MEASUREMENTS.

Male holotype: Total length in alcohol 5.2 mm.; carapace length 2.6, breadth 1.9, height 1.5; total length of eye group 1.4; ocular quadrangle length 1.1, breadth 1.7; diameter AME .60, ALE .28, PME .09, PLE .24; clypeus height .31; basal segment of chelicera .99; sternum length .99, breadth .75; abdomen length 2.6, breadth 1.5; patella breadth, 1st leg, .41, 4th .39.

## Leg Measurements, Male.

Leg	Femur	Pat.	Tib.	Metat.	Tarsus	Total
1	1.6	.96	1.4	.99	.58	5.5
2	1.4	.89	1.1	.92	.58	4.9
3	1.6	.75	1.1	1.1	.48	5.0
4	1.5	.68	1.2	1.2	.62	5.2
Palp	.89	.38	.27	—	.68	2.2

Female paratype: Total length in alcohol 5.3 mm.; carapace length 2.5, breadth 1.8, height 1.4; total length of eye group 1.4; ocular quadrangle length 1.1, breadth 1.6; diameter AME .55, ALE .26, PME .09, PLE .24; clypeus height .15; basal segment of chelicera .79; sternum length .96, breadth

.65; abdomen length 2.8, breadth 2.0; patella breadth, 1st leg .40, 4th .28.

## Leg Measurements, Female.

Leg	Femur	Pat.	Tib.	Metat.	Tarsus	Total
1	1.3	.79	.96	.72	.38	4.2
2	1.3	.79	.85	.65	.44	4.0
3	1.4	.79	.92	.89	.51	4.5
4	1.5	.65	1.1	1.1	.58	4.9
Palp	.68	.41	.34	—	.38	1.8

## BEHAVIOR.

*Locomotion*: Not specially observed in this species; however, another *Mago* (undescribed) as well as *Hypaeus* sp. are both excellent jumpers. In these the repeated pattern of ordinary progress is a deliberate walk for two or three centimeters followed by a series of short jumps; the first legs take active part in the walking and jumping, and are never raised except during display.

*Courtship Display: Stage I.* Carapace elevated only enough so that the motionless, hanging palps clear the ground; first legs raised at a wide angle to each other (about 135°), the other legs extending far sideways, the second pair slightly forward. Posing in this attitude is extended, but at intervals the first legs wave alternately up and down. Meanwhile the abdomen, which is held horizontally clear of the ground, is occasionally vibrated briefly up and down.

*Stage II.* First legs extend to front, usually not before female thrusts her first legs momentarily forward. Carapace and legs of male, in addition to the abdomen, twitch and jerk before he touches her.

*Threat Display*: Much more active than courtship, and in several respects quite distinct. *Stage I*: Carapace held moderately low, the abdomen either straight out as in courtship, or relaxed downward for silk attachment. First legs held with femur bent obliquely up, the other segments out; from that joint the two legs are waved up and down, usually in unison with each other, sometimes alternately. The palps hang down outside the closed chelicerae, as in courtship.

*Stage II.* The tempo and span of waving increases, the first legs almost meeting overhead at peak of display. Series of waves are punctuated by the rapid rubbing together of the first and second tarsi of each side, the second legs are braced somewhat forward, as in courtship, and are occasionally lifted briefly from the ground during waving.

*Stage III.* The two males oppose each other closely, the first legs straight overhead, practically or completely touching, the palps swung obliquely out, and the chelicerae opened wide and knocking against each other for seconds at a time. I have seen this stage reached only twice, no injury being inflicted either time. Only when one was retreating did the abdomen twitch very briefly, as in courtship.

*Habitat*: Known only from the montane cloud forest (about 3,600 feet) around

Rancho Grande, taken from vines on tree trunks, herbs and shrubs. Several specimens collected on upper Rancho Grande verandah, many yards from vegetation.

*Affinities*: Apparently related to Simon's briefly described *longidens* and *acutidens* from Brazil, although distinct in details of white markings, distal dentition of chelicerae and presence of three apophyses on palpal tibia.

*Material*: A total of 6 adult males and 11 adult females have been preserved in addition to a number of young. The following have been designated as types:

**HOLOTYPE**: Male. Cat. No. 45454, Department of Tropical Research, New York Zoological Society; Portachuelo, Rancho Grande, near Maracay, National Park of Aragua, Venezuela; 1,136 meters; cloud forest; June 6, 1945.

**PARATYPE**: Female. Cat. No. 45455. Taken near holotype, same locality and date.

The name *denticheles* is proposed in reference to the large outer tooth of the chelicera.

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## 8.

The Swifts of Rancho Grande, North-central Venezuela,  
with Special Reference to Migration.<sup>1</sup>

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(Plate I; Text-figures 1-3).

[This is one of a series of papers resulting from the 45th, 46th and 47th Expeditions of the Department of Tropical Research of the New York Zoological Society, made during 1945, 1946 and 1948, under the direction of Dr. William Beebe, with headquarters at Rancho Grande in the National Park of Aragua, Venezuela. The expeditions were made possible through the generous cooperation of the National Government of Venezuela and of the Creole Petroleum Corporation.

[The characteristics of the research area are in brief as follows: Rancho Grande is located in north-central Venezuela (10° 21' N. Lat., 67° 41' W. Long.), 80 kilometers west of Caracas, at an elevation of 1,100 meters in the undisturbed montane cloud forest which covers this part of the Caribbean range of the Andes. Adjacent ecological zones include seasonal forest, savanna, thorn woodland, cactus scrub, the fresh water lake of Valencia, and various marine littoral zones. The Rancho Grande area is generally subtropical, being uniformly cool and damp throughout the year because of the prevalence of the mountain cloud cap. The dry season extends from January into April. The average humidity during the expeditions, including parts of both wet and dry seasons, was 92.4%; the average temperature during the same period was 18° C.; the average annual rainfall over a 5-year period was 174 cm. The flora is marked by an abundance of mosses, ferns and epiphytes of many kinds, as well as a few gigantic trees. For further details, see Beebe & Crane, *Zoologica*, Vol. 32, No. 5, 1947. Unless otherwise stated, the specimens discussed in the present paper were observed or taken in or over the montane cloud forest zone, within a radius of 1 kilometer of Rancho Grande.]

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<sup>1</sup> Contribution No. 841, Department of Tropical Research, New York Zoological Society.

## INTRODUCTION.

In all of South America there have been recorded (Peters, 1940) nine genera of swifts, divided into twenty species and a total of thirty-three kinds, including subspecies. In Venezuela Mr. William H. Phelps informs me there are six genera, of thirteen species of twenty kinds, if we include subspecies. Of these Venezuelan birds, within an area of less than one square kilometer with its center at Rancho Grande, I have recorded eight species of five genera; roughly eighty per cent. of the genera and sixty per cent. of the total Venezuelan species of swifts.

Late in the year 1937 Dr. Alexander Wetmore (Wetmore, 1939) spent some time collecting birds near Rancho Grande, and I quote the following notes concerning the swifts.

"In Tropical America swifts are tantalizing birds usually seen out of range . . . On November 4 at Rancho Grande several (*Chaetura brachyura*) circled out of range. This species appears very black as it flies overhead, so that at first glance it suggests the black swift (*Nephoecetes niger*), but a second look distinguishes it by the shorter, light-colored tail. The specimen taken, a male, measures as follows: Wing 118.7, tail 29.0, culmen from base 5.8, tarsus 11.8 mm."

Concerning *Streptoprocne zonaris albicincta*, he writes, "While I was collecting in Portachuelo above Rancho Grande on November 3, 6 and 10, groups of these large swifts dashed at intervals through the pass at lightning speed with a great rushing of wings. Occasionally I observed them circling in air."

These are, I believe, the only published notes on swifts in this restricted area.

My thanks go to Mr. William H. Phelps for the loan of skins of rare swifts, to Dr. Neal Weber for names of ants in the food of birds taken in 1948, and to Dr. J. Bequaert for the name of the feather fly found on *Aëronautes*. The three text-figures are the work of Miss Louise A. Moore. The photographs were taken by Miss Jocelyn Crane.

***Streptoprocne zonaris albicincta***

(Cabanis, 1862).

## Giant White-collared Swift.

*Species Range:* Southern Mexico and the Greater Antilles, south over northern South America to British Guiana, north Matto Grosso and Peru; vertically to more than ten thousand feet in the Andes.

*Subspecies Range:* Five subspecies are recognized, of which *albicincta* occurs at Rancho Grande. Its range is extensive, from Honduras south to British Guiana, northern Matto Grosso and Peru, together with the islands of Granada and Trinidad. In Venezuela, Mr. Phelps records it as inhabiting the northern mountains.

*Field Characters for Sight Identification:* The most unmistakable species, distinguished by great size and white nuchal collar. It measures eight to nine inches in length, as compared to the five-inch average of the seven other species. *Panyptila* is the only other Rancho Grande swift with a white collar, but is about half the size of *albicincta*, and has a deeply forked tail. In young giant swifts the collar is reduced and indistinct in flying birds.

*Occurrence:* February 22 and September 9 are the earliest and the latest dates of our occupancy of Rancho Grande throughout three years. On both dates I recorded giant swifts within sight of the laboratory. Seldom did a day pass between these extremes when one or more did not come into view. Soon after we opened the station I ceased keeping detailed notes on these birds, as their visits seemed governed by no regularity.

They commanded attention under four separate conditions: (1) Almost daily either singly, but usually in small flocks, they hawked in the sky after insects, or (2) they flew headlong through Portachuelo Pass, low over the trees. (3) They entered rarely into the diet of a pair of resident bat falcons, *Falco albigularis*, and (4) on nights of storm, rain or neblina they occasionally struck against the windows of our lighted laboratory. Throughout the seven months during which we carried on our observations, there was no marked period of absence or extreme scarcity of these swifts. The breeding period must have occurred throughout part of this time but it was not noticeable in the rarity or abundance of individuals or flocks.

When it became evident that Portachuelo Pass was used as a migrating flyway on an unprecedented scale by other birds and by insects, I watched and noted these passing swifts for a period of several weeks, to see if there was any definite factor or sequence in their numbers or movements.

The daily, circling, feeding birds whose general direction was indefinite, varied their elevation, high or low, according to the volant stratification of edible insects. This proved to be definitely associated with the southward migration of insects of many orders through the pass. The swifts often joined flocks of

swallows and even of large dragonflies where, on clear days, the migrants offered rich feeding in the area of the pass. At times of dense fog, high winds or lowering of temperature, the lessening or cessation of migration was correlated with a total absence of giant swifts. At Kilometer 15, a few kilometers south of the pass, I frequently saw flocks of these birds feeding high in air as I passed in the car; and to the north at Kilometer 30, six or eight pairs of the swifts were occasionally seen hawking about. Beyond these limits I saw no swifts.

Giant swifts are supposed to be normal inhabitants of strictly tropical regions. At Kartabo, British Guiana, at practically sea-level, I found them commonly in good-sized flocks, feeding on flying insects, especially in June, July and early August. During this season, mating flights of ants and termites were frequent.

From March 14 to July 17 I noted the following groups of giant swifts passing on twenty-three days at full speed south through the pass, all between 7 and 8:30 A.M. 1, 16, 6, 2, 11, 4 and 16, 3 and 7, 21, 12, 8, 16, 4, 1, 3, 1, 2, 14, 5, 4, 22, 19, 7, 5. All were in a terrific hurry, flying headlong, mostly low, their whistling wings just clearing the upper branches of bushes and trees. Throughout this period there were only five records of birds going north in early morning and few in numbers, 2, 6, 1, 9, 1. On June 24 at 3 P.M. 64 swifts rushed past over my head, headed full speed northward through the pass, just ahead of the onrolling fog.

On June 6, at five in the afternoon, a compact flock of 200 to 210 birds, at a moderate height, circled northward, giving the impression of a leisurely, non-feeding migration. On August 1, closely intermingling with about five thousand Argentine martins, *Phaeoprocne tapera fusca*, about 300 giant swifts accompanied the other birds, all at high speed. On August 8, 24 swifts passed low, going north through the pass.

The assumption of the northward return every afternoon and evening of these swifts through Portachuelo Pass seems justified because of the number of birds which long after dark on nights of storm or fog struck against the windows of our laboratory. These accidents occurred from 7:20 to 10:45 P.M. Fourteen birds struck in this way on eleven nights, April 9, 12, 18, May 4, 16, 23, June 10, 27, July 3, 4 and 6. On three nights two birds appeared. Four of the swifts which crashed the windows were skinned, three others were sexed, and the remaining seven escaped. All examined were males, and, of those examined, only the two birds which struck on April 9 were in full breeding condition.

Reviewing the records through the pass, it seems reasonable to assume a daily migration from some more northerly sleeping or breeding place, south to a feeding area, with the return very late in the afternoon or in the evening.

On May 4, four of these swifts fearlessly attacked a bat falcon, the male of the pair whose nesting we were watching. In connection with the attacking and repulsing of this hawk by the the swifts, we were interested to see the same individual falcon on three separate occasions return to his lofty perch with a dead swift. This is a remarkable feat when we realize that the latter is only about one-quarter less in size than the hawk. In an active flight dive the falcon could strike and capture any small bird it selected, but on a level the swifts were superior.

In the Santa Marta mountains of Colombia, about 575 kilometers west of Rancho Grande and at an altitude of 1,500 meters, this giant swift has been found nesting (Todd and Carriker, 1922). The account is as follows (p. 245): At the coffee plantation of Cincinnati, "on March 19, 1917, a colony of this large swift was discovered nesting in a shallow cavern behind a waterfall. The place was absolutely inaccessible, so that no idea of the number of nests could be had. Only one nest, which happened to be near the top, was secured, together with the occupants, . . . which had been stunned by the blasting, and proved to be an adult female and two recently hatched young. The nest resembled very closely that of the Chimney Swift, being composed of twigs fastened together with saliva. The birds entered and left the cavern by dashing through the curtain of water falling over the front of it. The altitude of the site was about 4,300 feet."

#### DATA ON COLLECTED SPECIMENS.

For comparison I have included data concerning a female of this species taken many years ago at Kartabo, British Guiana.

		Lgth.	Wing	Tail	Grams Weight	Extent	Date	
30447	male	205	194	64	105.8	501	July	3, 1945
30452	male	196	188	61	96	482	July	3, 1945
31135	male	202	195	67	68.5	500	April	9, 1948
31188	male	210	200	70	109.5		July	6, 1948
529	female	190	190	60	77.2		July	10, 1919

The relative discrepancies between length and weight are accounted for by the food. The stomach, with contents, of No. 31188 weighed 22.6 grams. Gross food content may be expressed as follows: 30447, crammed with ants; 30452, moderately filled; 31135, empty, after a day in cage; 31188, crammed with ants; 529, only about one-fourth filled with insects. Without exception, all the ants in the food were winged females.

#### Detailed Food.

30447: At least 800 ants of an undetermined species of *Azteca*.

30452: Several hundred females of *Dolichoderus (Monacis) debilis* Emery, and *Crematogaster (Orthocrema) sp.* A single female *Solenopsis geminata edwardi* Forel.

31135: Five female *Atta sp.* More than four

hundred winged females of small ants.

31188: Stomach crammed with ants. (Weber).

Homoptera: Cicadellidae.

Diptera: fly fragments.

Hymenoptera: parasitic sp.

Hymenoptera: *Pheidole sp.*

Hymenoptera: *Atta sexdens* Linn.

Four gasters and a hind wing fragment. A species known from Ciudad Bolivar, Venezuela, and south. Found in Eastern British Guiana, but apparently not in Venezuelan Guiana, the Orinoco Delta, N. W. District (B.G.); in these places replaced by *A. cephalotes* Linn.

*Azteca?*: wings.

*Camponotus (Myrmobrachys) sp.* Same as I took at 1,020 meters in Rio Porce, Colombia.

*Camponotus (Tanaemyrmex) substituta* Emery. Distribution: Central America to Paraguay. I have the same form from Kartabo, B. G.

*Camponotus (Myrmobrachys) crassus* Mayr. Distribution: South America.

529: Three beetles, three wasps, one hemipteron, three membracids, one tipulid, and upwards of two hundred female ants of six species.

It is significant that although swifts 30447 and 30452 struck the laboratory within six minutes of each other, yet their food was quite distinct, indicating very different feeding territories. Yet they were headed for the pass, focusing upon a sixty-foot-wide bottleneck.

#### INDIVIDUAL CHARACTERS.

I find the following recorded concerning the Kartabo female, No. 529:

*Parasites*: Only a few bête rouge on the head feathers.

*Colors*: Bill black, face pale medici blue, iris light brownish-olive, legs and feet vinaceous slate.

*Eyelid*: Quite bare above. Below, a line of fifteen small feathers along rim. At posterior end of eye a small group of a dozen feathers, arranged in several rows.

*Oilgland*: Elongated, blunt, tapering, bare.

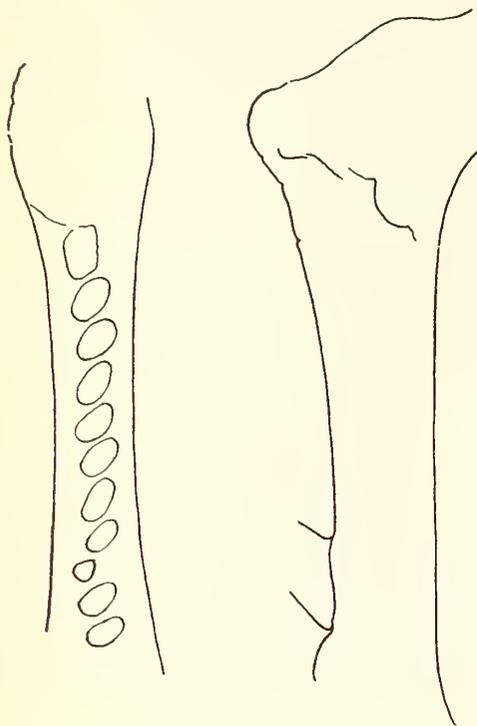
*Wing Graph*: Primaries

10th—152 mm.	5th—111 mm.
9th—155 "	4th—98 "
8th—149 "	3rd—86 "
7th—139 "	2nd—75 "
6th—126 "	1st—62 "

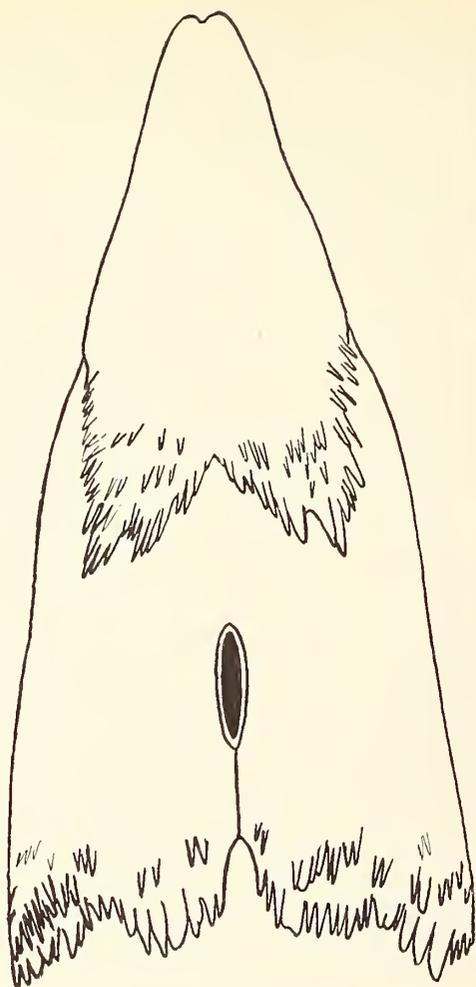
## Secondaries

1st—49 mm.	5th—53 mm.
2nd—50 “	6th—53 “
3rd—52 “	7th—49 “
4th—54 “	8th—42 “

*Scalation*: Front of tarsus with an indistinct irregular line of ten, fleshy scales down the inner aspect. Inner, rear and outer sides of tarsus, bare, wrinkled skin, with no trace of scales.



TEXT-FIG. 1. *Streptoprocne zonaris albicincta* (Cabanis). Scalation of tarsus, front and side views.



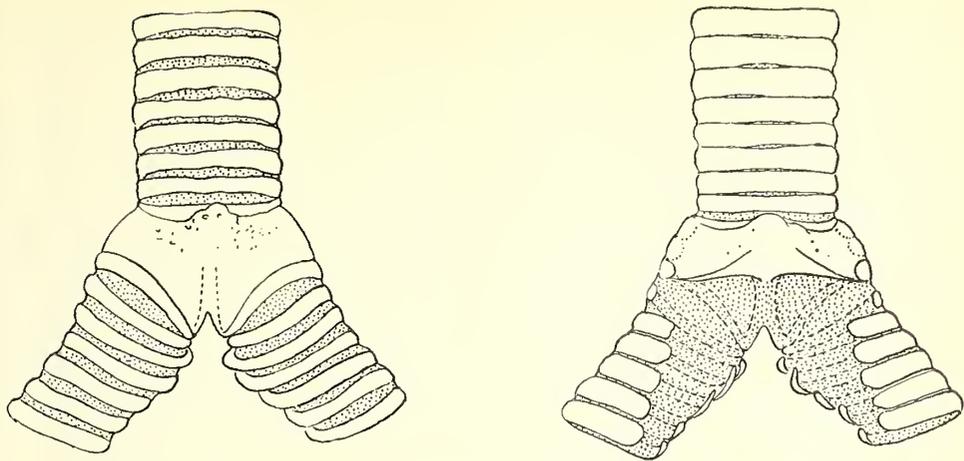
TEXT-FIG. 2. *Streptoprocne zonaris albicincta* (Cabanis). Tongue.

*Palate*: The palatine fissure begins well toward the front of the roof of the mouth, and divides in front. It is rather long (12.5 mm.) and is guarded by about a dozen pairs of teeth. Four-fifths of the way back there is a double-curved or angular transverse row of teeth, extending out at right angles on each side, with about twenty teeth on each side. The guardian, denticulated flaps end openly posteriorly, and just beyond is the very small tubal fissure. At the extreme posterior of the roof of the mouth is a transverse row of about twenty weak teeth.

*Tongue*: Narrow for a swift, and small for the size of the mandibular area. Greatest width of tongue 5.7 mm., length 10; greatest width of mandible 20 mm., length 26. Tongue fleshy, channelled toward the tip, sides somewhat sinuate, tapering slowly to two blunt tips. The two cornua are lined along the edge, both on inner and outer sides, with strong teeth. Smaller ones are scattered over the posterior surface of the tongue itself.

*Glottis*: A narrow ellipse on a low flat area, with inconspicuous unarmed rim. Posteriorly, there is an irregular transverse row of teeth, all large, flattened, sub-equal in size and numbering about fifteen on each side. Beyond these there arises a second irregular row. Most of the teeth, in a cleared condition, show stout, parallel-sided bases, and slender tips.

*Syrinx*: Swift No. 31135 (KOH No. 2589). Male. April 9, 1948. There is little change in the posterior tracheal rings except that the last eight are slightly narrowed with more even edges. The syrinx is a wide tracheo-bronchial collar of bone. Anteriorly the upper margin is level except in the center where an irregular, rounded projection overlies a segment of the last tracheal ring. This, like the rest of the syringeal collar is ossified and coarsely fenestrated. The anterior vertical width of the collar is 1.6 mm., its lateral, front to back, length is 3.3 mm. The lower border of the collar is formed by the closely-applied, strongly arched, upper bronchial



TEXT-FIG. 3. *Streptoprocne zonaris albicincta* (Cabanis). Syrinx, front and side views.

semiring. This semiring dips far down in front, forming an acute angle with the pessalus. The triangular space within this angle, as far anterior as the collar, is ossified, but without fenestration.

Posteriorly the tracheal rings are appreciably wider, with little more intervening membrane showing than the median, open notches. Two of the rings anastomose. The two lowermost rings are narrow and even as to outline.

Posteriorly, the syringeal collar is similar to its anterior half, with the difference that this aspect is flat and the median anterior projection is less pronounced. There is a faint but distinct indication that the present ossified syringeal collar was originally composed of two rings. The entire ventral syringeal aspect, bounded by the lower border of the collar, the pessalus and the first semiring is of course membranous. The free ends of the anterior semirings, joined by the tympaniform membrane, narrow rapidly posteriorly, until the ninth onwards become almost complete rings, thus forming the end of the membrane. There are about twenty-three bronchial rings, the second, third and fourth being somewhat longer, projecting slightly into the inner profile of the bronchi. From the eighteenth bronchial ring onwards there is a gradually increasing disintegration of the rings within the lung tissue, a thinning and irregular anastomosing of adjoining rings.

A drawing and description of the syrinx of the female No. 529, made thirty years ago, are similar to that of the present male except that posteriorly, the median protuberance is considerably larger, and extends forward over the last three tracheal rings.

***Chaetura brachyura brachyura***

(Jardine, 1846).

Short-tailed Swift.

*Species Range:* Same as that of the sub-

species below, with the addition of the Lesser Antilles.

*Subspecies Range:* Northern Venezuela and the Guianas to Trinidad and Tobago, south through eastern Ecuador and Peru to Matto Grosso and Pará.

*Field Characters for Sight Identification:* This is the smallest of the Rancho Grande swifts (length 100 mm.). On the wing it appears totally black, with conspicuous pale brownish-gray rump, tail-coverts and tail. The absence of gray on the underparts distinguishes it from the slightly larger *cinereiventris*.

*Occurrence:* By far the commonest swift at Rancho Grande, becoming really abundant after the rains began.

On clear days numbers were often seen feeding with swallows and other swifts, especially when migration of various orders of insects was in full swing. On partly cloudy days or when fog drifted up the lower valleys, these short-tailed swifts would swing through the pass in small or larger numbers.

There was none of the rather regular, southward, morning shift of the giant swifts. We saw this species every month from March to August, and on almost every clear day. It often flew in twos and threes, or again in flocks of considerable size. For three consecutive days, we were able to identify an individual trio. Two of the birds had recognizable gaps in their primaries due to molt, and these marked birds hawked on the north side of the pass, low in the gorge, throughout a three-day flight of termites, *Coptotermes testaceus*. On the third day an onrushing mass of dense fog drove these swifts away in the wake of eight turkey vultures hastening toward the upper zone of clear sunshine. The swifts did not return, and the next day the insect flight had ceased.

On July 9, 1948, we observed an unusual flocking, a migration of sorts; a fairly compact mass of considerably more than four

hundred of these swifts, circling, not feeding. As they approached the pass from the south, the flight changed to a more direct movement, and when siphoning through, all circling ceased, and the rush of wings was like a loud wind as the birds passed low and at great speed. The northern valley was partly filled with fog and the birds rose slowly above it, and before they passed from view, were again circling high in air as before. The general effect was of a maze of inorganic units, without volition, sucked by a wind through the narrow notch, and then sprayed out in a slower movement as the draught lessened. As a matter of fact, there was little or no breeze in the pass itself.

A spectacular coincidental sight of the same type of flocking of the same species is recorded in my notes on an identical July 9, but thirty-two years before, at Kalacoon, British Guiana. The note reads as follows: "An enormous flock of short-tailed swifts appeared over the forest at 9:30 this morning. There were certainly more than a thousand birds, all flying in a great circle, gradually attaining higher and higher altitude. They were massed so closely together that there seemed hardly room for any movement of the outspread, crescentic wings. The relative slowness of movement and the frequent effortless gliding indicated an upward surge of air. Through the glasses a scattering of equally small white-rumped swifts, *Chaetura spinicauda*, was clearly seen. The whole company vanished very high up and drifting southward."

Although these swifts showed little fear of the pair of bat falcons nesting near the laboratory, yet at least seven individuals fell victims to these hawks, and an eighth mangled swift found in the road near the nesting tree indicated an additional dropped item of diet. In this, as in other species, the swifts were able to evade the raptors when on the same aerial level. It was only when the hawks could go into a vertical dive that their speed made them almost unavoidable.

Two short-tailed swifts crashed against the laboratory windows on successive evenings, May 16 and 17, but one was able to fly away. The other was a male, breeding, with the stomach quite empty.

*Chaetura cinereiventris lawrencei*

Ridgway, 1893.

Gray-breasted Swift.

*Species Range:* The range of the eight recognized subspecies extends from Nicaragua, Grenada, Tobago and Trinidad south to Venezuela, Colombia, Ecuador, Peru, central Brazil and Bolivia.

*Subspecies Range:* *lawrencei* occurs in Grenada, Tobago, Trinidad and the mountains of northern Venezuela.

*Field Characters for Sight Identification:* A small swift. Black, except for rump and all underparts, which are pale gray. When associated with *brachyura* and seen from above at a distance, the birds are much alike, the

brownish shade of the rump of *brachyura* being hardly distinguishable. From below, the gray of *cinereiventris* instantly sets it apart.

*Occurrence:* This is not common at Rancho Grande, but was observed occasionally throughout May, June and July. Only once, on June 9, did an individual come to the laboratory windows. It clung for five minutes to the sill but evaded all efforts at capture.

On May 9, the male bat falcon caught a gray-breasted swift and plucked it. The female then gave it to her nestlings who tore it apart and ate it. As they pulled it apart I could distinctly see the mass of small ants which filled the stomach, together with two large abdomens of *Atta* queens which were eaten by the young birds.

*Chaeturella rufila brunneitorques*

Lafresnaye, 1844.

Chestnut-collared Swift.

*Species Range:* Central Mexico, south through northern South America to Peru, the Guianas and Trinidad.

*Subspecies Range:* Southeastern Mexico, south to Colombia, Venezuela, Ecuador and Peru.

*Field Characters for Sight Identification:* A medium-sized swift, about five inches in length. It is the only species marked with chestnut; throat, breast and collar. This color is especially distinct when the birds are silhouetted against the foliage of the mountain jungle, but with glasses is conspicuous even when they are high in the sky.

*Occurrence:* The chestnut-collared swift was third in order of abundance at Rancho Grande, surpassed only by *Streptoprocne* and *Chaetura brachyura*. It was frequently seen shuttling back and forth through the pass, or hawking about on days of insect migration, associating with giant swifts or with swallows, mostly single birds or in small flocks. Occasionally they would race back and forth through the pass, yet the diurnal observations I was able to make showed no certain regularity of north or southward shift.

On the other hand sixteen birds struck against the laboratory windows and on three occasions, when no swifts actually flew against the glass, individuals were seen fluttering about among the bats within the area of illumination. This would indicate a daily, crepuscular northward migration, as in *Streptoprocne*, also perhaps to some roosting or breeding colony.

Support of the probability of such a migration is furnished by a chestnut-collared swift (31129) taken eight kilometers east of Rancho Grande. A reliable assistant, Pedro Infante, shot this bird January 8, before my arrival, on the Choroni road which parallels that from Maracay to Ocumare. He reported this swift as shot from a group of thirty to forty which, throughout October, November and December assembled every evening and spent the night clinging in a

compact mass to the vertical side of a rocky cliff near the road. All left at dawn. Thus we have evidence of a roosting colony at the same elevation as the pass, and, from the point of view of a volant swift, only a short distance away.

At Rancho Grande the meteorological conditions which induced the appearance of the swifts at the lighted windows were, high but dense clouds; low neblina fog with or without wind; precipitation, whether drizzle or pelting rain and with or without lightning. No birds ever came on clear nights, whether moon or starlighted, and no bird after 10 P. M.

There was considerable variation in the amount of chestnut on the plumage of these swifts, but the typical pattern was rich chestnut throat and breast with a wide collar extending over nape and hind neck. Two adult males had the chestnut reduced to a pectoral tinge, and several swifts on the wing were intermediate between these extremes. The only female examined (31143), an adult, showed no pigmental difference from a full-plumaged male, except that the under tail coverts were strongly edged with white.

Coleoptera spp., including a cerambycid.

Hymenoptera: *Camponotus* sp., fragmentary remains of several hundred.

31132: Half the meal composed of ants (Weber).

Coleoptera spp.

Hymenoptera: *Camponotus* sp., fragmentary.

31143: Dominant food, hundreds of small flying ants (Weber).

Hemiptera spp.

Coleoptera: cucurliionid.

Hymenoptera: *Pheidole* sp.

Hymenoptera: Very small dolichoderine fragments.

#### *Cypseloides cherriei* Ridgway, 1893.

White-spotted Swift.

*Former Records and Species Range:* Two swifts taken on Volcan de Irazu, central Costa Rica, were described by Ridgway in 1893. The type was thought to be a male; the second bird was uncertainly sexed as a female. The most noticeable character was "a large, sharply defined spot of silky white

#### DATA ON CHESTNUT-COLLARED SWIFTS

		Lgth.	Wing	Tail	Grams Weight	Extent	Date
30382	male	126	123	45	25		May 14, 1945
30382a	male						May 14, 1945
30448	male	133	128	43	22.9	320	July 3, 1945
	Four swifts escaped						July 3, 1945
31128	male	115	120	36		292	Mar. 23, 1948
	One swift escaped						Mar. 23, 1948
31131	male	130	120	43	21.5	295	April 3, 1948
31132	male	128	120	45	21.5	302	April 3, 1948
	Four swifts escaped						April 3, 1948
31143	female	122	125	43	19.5	305	April 24, 1948

#### DETAILED FOOD.

30382: Many winged females of *Camponotus (Tanaemyrmex) coruscus* F. Smith; and *Solenopsis geminata edwardi* Forel.

30448: A series of winged females of *Cre-matogaster (Orthocrema)* sp.

31128: Stomach crammed with a mass of winged ants and small beetles. (Weber).

Homoptera: Cicadellidae.

Coleoptera spp., including a carabid.

Hymenoptera: parasitic sp.

Hymenoptera: *Cre-matogaster* ? wing.

Hymenoptera: *Solenopsis geminata* Fabr., widespread in the northern neotropics and replaced in the south by *saevissima* F. Smith, from the interior of British Guiana (Courantyne) and Brazil.

*Camponotus* sp.

31131: Food dominantly flying ants (Weber).

Hemiptera: wing.

on each side of the forehead, immediately over the lores, and a short streak of the same color immediately behind the eye." A third specimen was reported (Zimmer, 1945) in a collection of birds from Colombia. This was taken at San Gil, Santander, and was also questionably sexed as a female.

This then, on February 26, 1948, was the summation of our knowledge of the white-spotted swift. The Costa Rican birds came from the same 10th degree of north latitude as Rancho Grande, but 1,800 kilometers west; whereas the Colombian swift, from 6 degrees, 33 minutes north latitude, was 750 kilometers to the southwest of our laboratory.

*Field Characters for Sight Identification:* The white-spot is a five-inch swift, appearing uniformly black, with a conspicuous, round, white spot between beak and eye. These spots stand out strongly whenever these birds are seen head-on in flight or from the side, giving a rather fantastic impression of a slightly misplaced pair of brilliant eyes.

*Occurrence:* At 9.30 o'clock in the evening

of February 26, 1948, a white-spotted swift came to the windows of Rancho Grande and was caught. From this time until June 13 we captured or recorded eight others, making a total known of this unusual species of twelve individuals. The details of the nine Rancho Grande birds are as follows.

31125: Female not breeding. February 26, 1948. Length 132, wing 123, tail 132, extent 308 mm. Black above, sooty brown below; supra-ocular spot and small post-ocular patch white; small feathers along edge of wrist and front of wing white-edged; trace of white on chin. Ovary small but distinct.

At 10 P.M. this bird fluttered against a bedroom window. It was later found and captured on the Rancho Grande porch, fluttering confusedly around the electric light. The evening was one of dense fog, with a strong breeze blowing from the southwest.

*Food*: A mass of rather comminuted flying ants. (Weber).

Coleoptera spp.

Hymenoptera: Highly fragmentary *Camponotus* sp., forming most of the contents.

31133: Male, not breeding, April 4, 1948. Length 120, wing 120, tail 39, extent 305 mm. Weight 22.5 grams.

Frontal spots large and pure white, beginning on lores with only a few feathers between them and nostrils, and extending back over eye frame, and on a narrow line to midway over eyes, thus approaching the post-ocular spot. This latter forms the posterior border of the feather circle around the bare area on the lower lid. When the eye is closed and this lid drawn up, the spot is directly behind the eye. When the eye is open it is behind and below eye. Wrist edge of wing and rim featherlets all have distinct white edges. The chin is grayish-white.

The bird was caught at 8:30 P.M. as it clung to the vertical electric light wire depending from the ceiling of the porch outside the laboratory. There was sufficient fog to hide the stars and the recent wind had died down. The air was cool, 62 degrees Fahrenheit, sufficient to keep all moths away.

*Food*: Flying ants. (Weber).

Coleoptera spp.

Hymenoptera: *Camponotus* sp.

*Syrinx*: *C. cherriei*, No. 31133 (KOH No. 2588) differs from *Streptoprocne zonaris albicincta* in there being three, instead of two, rows of post-glottid teeth. The syrinx proper, although completely ossified, shows distinctly its composition of three rings. The median anterior protuberance is directly connected with a slight, posterior, cartilaginous projection of the lowermost free tracheal ring.

31134: Female, not breeding. April 5, 1948. Length 137, wing 127, tail 51, extent 310 mm. Weight 25.5 grams.

Large white preocular spots almost join white chin. Postocular and white wing edges well developed. Flew against laboratory windows at 7:30 P.M. in dense cold fog.

*Food*: Stomach crammed with insects, one-half of which were ants (Weber).

Hemiptera spp.

Coleoptera spp.

Hymenoptera: parasitic sp.

Hymenoptera: *Camponotus* sp. fragmentary.

Hymenoptera: dolichoderine wings.

April 5. At 7:45 two more white-spots came to the porch but both escaped. At 8:10 another bird came and went. In all, the mental white was almost absent.

April 11. In dense, drenching fog a white-spot came to my bedroom window at 9:30 P.M. and clung out of reach to the rough surface of a cement pillar. Eye-white as usual, with more on the chin than in any bird hitherto seen.

May 10. Male bat falcon caught a white-spot, held it for three minutes, with the dangling head in full view. Hardly any mental white, but very large and fluffed out eye spots. After plucking it he gave it to the female who fed her young.

June 13. Female bat falcon brought a swift to her perch, and had begun plucking it when the young male flew up, took it and ate it.

#### *Cypseloides cryptus* Zimmer, 1945.

Tropical Black Swift.

*Former Records and Species Range*: In 1945 a new species of swift was described (Zimmer, 1945). The type came from the Rio Tavera, Peru. Only four other specimens were known, taken at the following localities: British Guiana (Kaieteur Falls), Venezuela (Mt. Auyan-tepui, and Saroropan-tepui), and Costa Rica (San Pedro).

Only a single individual of this species was seen at Rancho Grande in 1948. The two which were taken in 1946 have already been reported by me (Beebe, 1947), and I here repeat several paragraphs.

*Field Characters for Sight Identification*: This five-inch black swift would show no definite characters in flight except the general black coloration. The grizzled and variable dull whitish of the lores and chin could hardly be detected.

*Occurrence*: On April 20, 1946, a female of this swift crashed against the laboratory windows at Rancho Grande at 8:30 o'clock in the evening and was stunned. It is No. 30,634, female, not breeding, fairly fat, weight 40.2 grams. Length 120, wing 137, tail 48, extent 355 mm. The stomach was filled with winged female *Azteca* ants.

On April 21, the following evening, at the same time, a second bird killed itself against the identical window. This is No. 30,640, female, not breeding, considerable fat, weight 35.8 grams. Length 138, wing 130, tail 50 mm. First primary in each wing half grown.

*Food*: A great quantity of *Crematogaster* and *Azteca* flying ants.

April 12, 1948. At 10:15 A.M. the male bat falcon swung up to his perch in the top of the candelo tree, with a swift. Through the

20-power glasses I could see every detail and in every respect of the cephalic pale color it seemed to be this species. There was no trace of the supraloral white spots of *cherriei*, and the area around the base of the beak showed the pale grizzled appearance so apparent in both of the specimens taken in 1946. I could have had no more certain evidence if the bird had been in my hand. It was slowly and thoroughly plucked and as the female did not appear, the male proceeded to eat the eighth known individual of *Cypseloides cryptus*.

***Aëronautes montivagus montivagus***

(d'Orbigny and Lafresnaye, 1837).

White-breasted Swift.

*Species and Subspecies Range:* Mountains of northern Venezuela, Peru and Bolivia.

*Field Characters for Sight Identification:* A small five-inch swift. Easily distinguished by great extent of ventral white, no nuchal collar, and almost square tail.

*Occurrence:* Known at Rancho Grande laboratory from a single specimen which flew into the porch in dense neblina, and at about 9:15 P.M. was caught as it crouched in a corner.

31142: Adult male, breeding, testes 8.5 mm. April 23, 1948. Length 120, wing 110, tail 40, extent 266 mm. Weight 20 grams.

*Food:* Many flying ants and small cucurlioid beetles (Weber).

Hymenoptera: ponerine and *Camponotus* ant fragments.

*Parasites:* This swift was strongly infested with parasites, one of which (48375) was a giant feather fly with bright green abdomen. In addition, there were several *Mallophaga*, and a number of *bête rouge*.

Dr. J. Bequaert has kindly identified the large feather fly, and sends me the following note:

"The fly is *Brachypteromyia neotropica* J. Bequaert. This was described from a single male, taken from the same host species, at Galipan, close to Pico Avila, Estado Miranda, 2,000 meters elevation, Venezuela.<sup>2</sup> Yours is the second specimen known, also a male. The description, with figure, is in *Psyche*, 49. (1942) published in 1943, p. 113. The only other species of the genus, *Brachypteromyia fimbriata* (Waterhouse), is North American, on the swifts *Aëronautes saxatilis* and *Nephoecetes niger*."

In addition to the single captured specimen of this swift, we have three other records.

June 19, 1948. Six white-breasted swifts flew, one after the other, through the pass at 10 A.M. They were headed south and not flying very fast. While still in sight two of the birds veered aside from their direct flight and caught insects.

June 21, 1948. A compact flock of twelve of these swifts swung south through the pass at 8:05 in the morning. They flew very low, just skimming the trees.

Three of this species were caught by the male bat falcon; on April 4, June 10 and 19, 1948.

***Panyptila cayennensis* (Gmelin, 1789).**

Fork-tailed White-collared Swift.

*Species Range:* Southeastern Nicaragua, south over Colombia, Ecuador, Venezuela, Tobago, Trinidad and the Guianas to Bahia and São Paulo.

*Field Characters for Sight Identification:* A five-inch swift, unmistakably fork-tailed, black except for white eye-spots and flank-spots, chin, throat and collar.

*Occurrence:* 30439: A male flew against the windows of the laboratory and was badly injured. July 1, 1945. Length 123, wing 125, tail 57 mm.

*Food:* Small species of flying ants.

(This specimen was overlooked in the paper on Avian Migration at Rancho Grande, Beebe, 1947).

June 8, 1948. Six fork-tailed swifts hawking about early in the morning with three blue and white swallows, over the compound of Rancho Grande.

June 12, 1948. A swift of this species caught and eaten by male bat falcon.

**SUMMARY.**

At Rancho Grande a total of eight species of swifts were collected or observed, out of the thirteen species recorded from Venezuela as a whole. The types of observation resolve into: flocks feeding at various altitudes, others migrating through Portachuelo Pass usually low down, or striking against the lighted windows of the laboratory on nights of fog or rain. Finally a number of the birds were caught by a male bat falcon.

Throughout twenty months of residence during three years no swift was seen to alight, nor was there at Rancho Grande first-hand proof of breeding or roosting colonies, although the latter were indicated as a result of various activities.

Observations in adjoining areas, both higher up the surrounding mountains, and down to four hundred and forty-five meters on the Maracay plain, showed a relative dearth or absence in comparison with their numbers in the square kilometer whose center was Rancho Grande and the pass. The obvious explanation of this concentration of swifts, by day and night, must be the same as that of many other organisms, both vertebrates and invertebrates; viz., the continual procession on migration of countless numbers of insects representative of almost every order, traversing the sixty-foot-wide pass, from north to south, on every clear day throughout the rainy season. This abundant and ever renewed source of food was obviously a focusing factor of prime importance.

A second reason for the abnormal numbers of species and individuals was the use of the pass by several of the species on daily migration from a presumed breeding or roost-

<sup>2</sup> Pico Avila is in the immediate neighborhood of Caracas, about 100 kilometers due east of Rancho Grande.

ing place to a trans-pass feeding-area. It is difficult otherwise to account for the forty-four specimens of all eight species taken or observed on black nights of poor visibility. Of twenty-two specimens sexed, seventeen were males, five females.

The presence throughout their breeding season of a pair of bat falcons, close to Rancho Grande, revealed an interesting relationship between these birds and the swifts. The latter showed little fear of the small falcons when these were perched, and giant swifts did not hesitate to attack and drive off the male hawk. Yet I recorded nineteen individuals and seven out of the eight species of swifts as entering into the diet of the hawks. When high in the sky, a power dive attack of the male falcon rendered escape impossible on the part of the swifts, but when the birds met at horizontal levels, the speed and dodging ability of the small birds rendered them safe.

The flocking habits of these Venezuelan swifts are, in some ways, suggestive. Single birds were very rare, and pairs were not often seen. But, especially in mid rainy season months, trios were common. Even in flocks of twenty to fifty, feeding in midair, subdivision into trios was often evident. If the same rule of a single surviving young holds in tropical swifts as in many other tropical birds, these trios probably represented the season's families. Larger flocks in rapid movement were too infrequent to warrant definite classification or object.

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## EXPLANATION OF THE PLATE.

## PLATE I.

Two migrant swifts which came to the electric lights of Rancho Grande on nights of rain or fog.

Fig. 1. Giant White-collared Swift. *Streptoprocne zonaris albicincta* (Cabanis).

Fig. 2. Chestnut-collared Swift. *Chaeturella rutila brunneitorques* Lafresnaye.



FIG. 1.



FIG. 2.

THE SWIFTS OF RANCHO GRANDE, NORTH-CENTRAL VENEZUELA, WITH  
SPECIAL REFERENCE TO MIGRATION.



## 9.

## Eastern Pacific Expeditions of the New York Zoological Society. XL.

Mollusks from the West Coast of Mexico and Central America. Part VII.<sup>1</sup>

LEO GEORGE HERTLEIN &amp; A. M. STRONG.

California Academy of Sciences.

(Plate I).

[This is the fortieth of a series of papers dealing with the collections of the Eastern Pacific Expeditions of the New York Zoological Society made under the direction of William Beebe. The present paper is concerned with specimens taken on the Templeton Crocker Expedition (1936) and the Eastern Pacific Zaca Expedition (1937-1938). For data on localities, dates, dredges, etc., refer to *Zoologica*, Vol. XXII, No. 2, pp. 33-46, and Vol. XXIII, No. 14, pp. 287-298.]

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## INTRODUCTION.

This is the seventh of a series of papers dealing with collections of mollusks taken on the Templeton Crocker Expedition (1936) and the Eastern Pacific Zaca Expedition (1937-1938). The general plan of presentation followed in the present contribution is that mentioned in Part II of this series of papers<sup>2</sup>. Formal headings and keys are given for 51 species and subspecies of the Tellinidae collected by the expeditions of 1936 and 1937-1938. Occasionally additional species are included in the keys for convenience but in such cases it is indicated which species do not occur in the present collection.

Acknowledgment is due Dr. G. Dallas Hanna, Curator, Department of Paleontology of the California Academy of Sciences, Mr. A. G. Smith, Research Associate of the same institution, and Dr. A. Myra Keen, Stanford University, California, for assistance and suggestions. Acknowledgment is also due Miss Viola Bristol, Curator of Mollusks, San Diego Society of Natural History, for the loan of specimens. The photographs used for illustrations on the plate were prepared by Mr. Frank L. Rogers.

<sup>2</sup>Hertlein, L. G., and Strong, A. M. Eastern Pacific Expeditions of the New York Zoological Society. XXIII. Mollusks from the West Coast of Mexico and Central America. Part II. *Zoologica*, New York Zool. Soc., Vol. 28, Pt. 3, December 6, 1943, pp. 149-168, pl. 1. See especially pp. 149-150.

<sup>1</sup>Contribution No. 842, Department of Tropical Research, New York Zoological Society.

Superfamily Tellinacea.

FAMILY TELLINIDAE.

Papers by Dall<sup>3</sup> and Salisbury<sup>4</sup> dealing with the Tellinidae are very useful in a study of West American members of this family.

KEY TO THE GENERA OF THE FAMILY TELLINIDAE.

- A. Shell with lateral teeth in one or both valves
  - a. Exterior with oblique, flexuous, divaricating striae; orbicular.....*Strigilla*
  - aa. Exterior usually without, sometimes with, oblique but not flexuous, divaricating striae
    - b. Dorsal margins serrate; trigonal; very inequivalve and compressed  
*Tellidora*
    - bb. Dorsal margins not serrate or occasionally so only posteriorly; usually elongate .....*Tellina*
- B. Shell without lateral teeth
  - a. Suborbicular to subtrigonal; subequilateral; moderately inflated; broad submedian concavity in right valve  
*Apolymetis*
  - aa. Subtrigonal or elongate; posterior end produced and narrowed; moderately compressed; sometimes inequivalve  
*Macoma*

Genus *Tellina* Linnaeus.

The present collection from the tropical eastern Pacific contains a good representation of the species of *Tellina* which occur in that region. Many of these shells are conspicuous because of their beautiful red color, especially when observed upon the beach. Mörch long ago mentioned that red *Tellinas* are characteristic of tropical American waters.

KEY TO THE SUBGENERA OF *Tellina*.

- A. Posterior area with simple concentric lamellae or smooth
  - a. Surface obliquely grooved.....*Scissula*
  - aa. Surface not obliquely grooved
    - b. Beaks anteriorly directed  
*Macaliopsis*
    - bb. Beaks not anteriorly directed
      - c. Right anterior lateral distant from the beak
        - d. Smooth, polished  
*Tellina s.s.*<sup>5</sup>
        - dd. Strong concentric sculpture  
*Tellinella*

- cc. Right anterior lateral extends close beneath or near beak
  - e. Shell usually exceeding 25 mm. in length
  - f. Resilium external; shell elongate  
*Eurytellina*
  - g. Thick; right posterior lateral strong  
*Tellinidella*
  - gg. Thin; right posterior lateral weak; fine reticulate sculpture  
*Tellinidella*
  - ff. Resilium internal; shell thin, high  
*Scrobiculina*
  - ee. Shell not exceeding 25 mm. in length (usually not exceeding 20 mm.)
    - h. Sculpture chiefly of concentric lines of growth (except on posterior area)  
*Moerella*
    - hh. Sculpture chiefly of concentric lamellae (over entire shell); trigonal; strong; very narrow posterior flexure .....*Merisca*

- B. Posterior area with plate-like foliations or posterior end with strong radial sculpture
  - a. Pallial sinus free or confluent with pallial line for not more than one-third its length  
*Phyllodina*
  - b. Posterior area with plate-like foliations .....*Phyllodina*
  - bb. Posterior end of shell with strong radial sculpture; very small  
*Elliplotellina*
  - aa. Pallial sinus confluent with pallial line for entire length.....*Phyllodella*

Subgenus *Tellinella* Mörch.

*Tellinella* Gray, Mörch, Cat. Conch. Yoldi, Fasc. 2, 1853, p. 13. [Species originally cited under *Tellinella* include *antoni* Philippi, *interrupta* Solander, *pulchella* Lamarck, *rostrata* Linnaeus, *virgata* Linnaeus, and several others]. —Dall, Bartsch & Rehder, Bernice P. Bishop Mus., *Bull.* 153, July 25, 1938, p. 187. Type: *Tellina virgata* Linnaeus. Type (designated by Stoliczka, *Mem. Geol. Surv. India, Palaeont. Indica*, Ser. 6, Vol. 3, 1870, pp. XVII, 116): *Tellina virgata* Linnaeus [*Syst. Nat.*, ed. 10, 1758, p. 674. "Habitat in O. Indico." Illustrated by Hanley,

<sup>3</sup> Dall, W. H. Synopsis of the Family Tellinidae and of the North American species. *Proc. U. S. Nat. Mus.*, Vol. 23, [No. 1210], November, 1900, pp. 285-326, pls. 2-4.

<sup>4</sup> Salisbury, A. E. On the Nomenclature of Tellinidae, with Descriptions of new species and some remarks on Distribution. *Proc. Malacol. Soc. London*, Vol. 21, Pt. 2, July, 1934, pp. 74-91, pls. 9-14.

<sup>5</sup> Not represented in the present collection.

Thes. Conch., Vol. 1, 1846, p. 228, pl. 63, fig. 212. Indian Ocean].

KEY TO THE SPECIES OF *Tellinella*.

- A. Ornamented by radial stripes or spots of chocolate or purple; distance separating pallial sinus from anterior adductor impression 5 mm. or more ..... *cumingii*  
 B. Ornamented by radial stripes or bands of golden-orange; distance separating pallial sinus from anterior adductor impression not exceeding 2 mm. .... *zacae*

*Tellina (Tellinella) cumingii* Hanley.

*Tellina cumingii* Hanley, *Proc. Zool. Soc. London*, September, 1844, p. 59. "Hab. Guacomayo, Central America; in coral sand."  
 —Hanley, *Thes. Conch.*, Vol. 1, 1847, p. 223, pl. 58, fig. 72. "Guacomayo and America."  
 —M. Smith, *Panamic Mar. Shells* (Tropical Photogr. Lab., Winter Park, Florida), 1944, p. 64, fig. 847. Lower California to Panama. [Not the record "Red Sea?"].

*Type Locality*: Guacomayo, Central America.

*Range*: Magdalena Bay, Lower California, to the Gulf of California and south to Gorgona Island, Colombia.

*Collecting Stations*: Mexico: Tangola-Tangola Bay (196-D-14, 15), 5 fathoms, crushed shell; Costa Rica: Culebra Bay; Cedro Island (213-D-4), 5 fathoms, mud; off Ballena Bay, Gulf of Nicoya (213-D-15), 40 fathoms, mud.

*Description*: Shell elongate, narrow, rather compressed, subrostrate, somewhat biangulated and bent to the right posteriorly; yellowish-white with radiating brown or chocolate or purplish streaks or spots; sculptured with moderately fine, close, concentric lamellae which become coarser and elevated on the posterior portion of the shell; hinge with two cardinal teeth in each valve, the right posterior and left anterior cardinals grooved, and two equidistant laterals in each valve; pallial sinus rather wide (in young shells rounded but in the adult obliquely pointed at the end), projecting forward about two-thirds the distance between the two adductor impressions and for about two-thirds its length confluent with the pallial line; interior white or pale yellow or a combination of the two.

Large specimens of this species attain a length of 55 mm. or more.

*Tellina interrupta* Wood<sup>6</sup>, which ranges from North Carolina to Brazil, is a similar species. *Tellina strophia* Dall, in the Miocene of Florida, also is somewhat similar to *T. cumingii*.

<sup>6</sup> *Tellina interrupta* Wood, *General Conch.*, 1815, p. 146, pl. 36, fig. 3. "Inhabits the Indian and American Seas." Also edit. 1835. [Regarding the dates of issue of this book see Pritchard & Gatliff, *Proc. Roy. Soc. Victoria*, Vol. 16 (N.S.), Pt. 1, September, 1903, p. 114; Iredale, *Proc. Malacol. Soc. London*, Vol. 15, Pts. 2 and 3, December, 1922, p. 911.

Not *Tellina interrupta* Solander, *Portland Cat.*, 1786, pp. 31, 72, 105. *Nomen nudum*.

*Distribution*: A few specimens of this species were taken by the expedition off western Mexico and Costa Rica. The species also is known to occur in the Pleistocene of Magdalena Bay, Lower California.

*Tellina (Tellinella) zacae* Hertlein & Strong, sp. nov.

Plate I, Figs. 12, 13, 17.

Shell of moderate size, elongately ovate, umbos a little posterior to the center, white, with golden-orange radiating bands of varying width; anterior end elliptically rounded, posterior end rather pointed (but acutely rounded at the extremity) and slightly bent toward the right, the ventral margin is broadly curved; right valve with an elevated, rounded, curved ridge radiating from the posterior side of the umbo to the posterior ventral margin and there is a corresponding depression in the left valve; posterior to the ridge the shell is depressed and anterior to the ridge there is a slight sinus; the early part of the shell is ornamented with fine, rounded, concentric threads, these on the adult shell become stronger and slightly irregular and somewhat lamellated posteriorly; ribs separated by interspaces of about the same width or in some instances slightly narrower, very fine concentric threads are present in the interspaces; a short but rather stout ligament on a narrow nymph is present posterior to the umbos; hinge with two cardinals in each valve, the right posterior and the left anterior ones grooved, the other two are more slender, there are two laterals in each valve, those on the right valve are strong, those on the left low and fused with the margin; pallial sinus long, rounded at the end and extending about three-fourths the length of the shell; interior whitish, the external rays showing through the shell. Dimensions of the holotype: length, 33.4 mm.; height, 15.2 mm.; convexity (both valves together), 7.8 mm.; pallial sinus extends anteriorly 25 mm. from the posterior end of the shell.

Holotype (California Acad. Sci. Paleo. Type Coll.), from Station 136-D-1, Arena Bank in the Gulf of California, Lat. 23° 29' N., Long. 109° 25' W., dredged in 45 fathoms (82 meters), mud. Paratypes were dredged in the same general region at Station 136-D-31-32, Lat. 23° 24' 30" to 23° 28' N., Long. 109° 24' to 109° 23' 30" W., in 35-42 fathoms, in sand, calcareous algae and weeds. Other specimens were dredged at Station 150-D-12, Gorda Banks in the Gulf of California, Lat. 23° 02' N., Long. 109° 28' W., in 80-90 fathoms, sand.

The shell of this new species is in general features similar to that of *Tellina cumingii* but it differs in several details. In the present species the posterior area on the left valve possesses a deep well-developed groove corresponding to a ridge in the opposite valve, while in *T. cumingii* the corresponding area on the left valve is somewhat flat-



angularly or bluntly rounded and then joins the pallial line; a large sunken ligament is situated upon a nymph; hinge with two cardinals in each valve, the right posterior and left anterior ones grooved; right valve with two well-developed laterals, left valve with a weak anterior lateral and the posterior lateral very slight or obsolete; interior white with blotches of greenish-yellow, especially toward the dorsal portion of the shell.

A specimen from the Gulf of California in the Henry Hemphill collection of the California Academy of Sciences, measures: length, 62 mm.; height, 44 mm.; convexity (both valves together), 14.5 mm.; pallial sinus extends anteriorly 46 mm. from the posterior end of the shell. The species attains a greater size than this.

As mentioned by Dall, about the only difference between *Tellina viridotincta* and *T. ochracea* is in color.

*Distribution*: One rather worn pair of valves of this species was dredged in 3 fathoms at Port Guatulco, Mexico.

#### Subgenus *Moerella* Fischer.

*Moerella* Fischer, Man. de Conchyl., Fasc. 11, June 15, 1887, p. 1147. Sole species, *Tellina donacina* Linnaeus.

*Type* (by monotypy): *Tellina donacina* Linnaeus. Recent, seas of Europe. Illustrated by Bucquoy, Dautzenberg & Dollfus, Moll. Mar. Roussillon, Vol. 2, Fasc. 25, March, 1898, p. 648, pl. 91, figs. 13, 14, and vars. 15-19. Mediterranean. Also other localities cited.

In the present paper nine species and subspecies have been referred to the subgenus *Moerella*. Some of these, in earlier publications, have been referred to *Angulus* Megerle von Mühlfeld. The type of *Angulus* designated by Gray, 1847, is *Tellina lanceolata* Linnaeus, a species in which the hinge is said to possess a right anterior lateral but lacking all other laterals. Salisbury, 1934, stated that only two Recent species, *T. lanceolata*, the type, and *T. armata* Sowerby, were referable to *Angulus*. However, in the explanation to his plates five species are referred to *Angulus*. It is unfortunate that this well known supraspecific group name should be applicable to so few species.

All the species in the present paper which have been referred to *Moerella*, although varying somewhat in shape, possess a right posterior lateral tooth of varying strength. This lateral occurs just below a socket which is present just below the ventral end of the nymph upon which the ligament is situated.

The results of our studies which have led us to place the following group of species under the subgenus *Moerella*, are in agreement with the conclusions reached by Gardner<sup>9</sup> with regard to the east American Miocene and Pliocene species formerly referred to *Angulus*.

#### KEY TO THE SPECIES OF *Moerella*.

- A. Posterior end triangular or bluntly pointed
- a. Posterior end the longer, tapering, pointed; white, yellowish or pinkish  
*suffusa*
- aa. Anterior end the longer
- b. Posterior dorsal margin sinuous; ivory white ..... *tabogensis*
- bb. Posterior dorsal margin straight or slightly curved
- c. Ventral margin strongly curved; posterior end blunt; white  
*paziana*
- cc. Ventral margin very gently curved
- d. Length more than twice the height; white, occasionally yellowish ..... *amianta*
- dd. Length less than twice the height
- e. Area anterior to posterior umbonal angulation strongly depressed; usually pink on dorsal margins ..... *erythronotus*
- ee. Area anterior to posterior umbonal angulation not depressed or only faintly so; red or pink zoned with white
- f. Umbos moderately inflated; posterior end very short  
*macneilii*
- ff. Umbos rather compressed; posterior end more attenuated; rose red ..... *felix*
- B. Posterior end broad, obliquely truncated
- a. Pale rose color ..... *arenica*
- aa. White; posterior end more abruptly truncated ..... *recurvata*

#### *Tellina (Moerella) amianta* Dall.

*Tellina (Moerella) amianta* Dall, Proc. U. S. Nat. Mus., Vol. 23, No. 1210, November, 1900, pp. 303, 317, pl. 3, fig. 12. "Dredged in 14 fathoms, sand, off Cape Tepoca, Lower California, near the head of the Gulf, by the U. S. Fish Commission at station 3019."

*Type Locality*: Off Cape Tepoca, Lower California, near the head of the Gulf of California, in 14 fathoms, sand.

*Range*: Gulf of California to Colombia.

*Collecting Station*: Mexico: Santa Inez Bay, Gulf of California (145-D-1, 3), 4-13 fathoms, sand; Nicaragua: Corinto (200-D-19), 12-13 fathoms, mangrove leaves, sand, also on shore in beach drift; Costa Rica: Port Parker (203-D-1, 3), 12-15 fathoms, sandy mud, shelly mud, crushed shell.

*Description*: Shell small, elongated, anteriorly produced and rounded, the posterior end shorter, obliquely truncated and rather

<sup>9</sup> Gardner, J., U. S. Geol. Surv., Prof. Paper 142-B, 1928, p. 195; U. S. Geol. Surv., Prof. Paper 199-A, 1943, p. 94.

pointed at the extremity; sculptured with fine, close, concentric threads which toward the posterior angulation become somewhat irregular, sharper, and in the adult shell two or three ribs coalesce to form low raised lamellae on the posterior area; hinge with two cardinals in each valve, the right posterior and left anterior ones grooved, right valve with a strong fairly close anterior lateral and a small posterior lateral; pallial sinus extends near to, but does not touch, the anterior adductor impression, confluent with the pallial line below; color white or partly salmon yellow.

A large right valve dredged in Santa Inez Bay in the Gulf of California in 4-13 fathoms, measures: length, 14 mm.; height, 6.8 mm.; convexity (one valve), 2.2 mm.

The small size, elongate form which is much produced anteriorly, and fine, close, concentric sculpture are characteristic features of this species.

Specimens dredged by the expedition in Santa Inez Bay in the Gulf of California are typical of the species. Specimens collected at Corinto, Nicaragua, in beach drift, and dredged in 12-13 fathoms agree in general characters with *T. amianta* except that they are thinner. Many small specimens dredged in 12-13 fathoms off Port Parker, Costa Rica, in which the hinge, concentric sculpture and other general characters agree well with *T. amianta*, appear to represent the young of that species. Some are less elongate in proportion to the height as compared to typical *T. amianta* but this appears to be somewhat variable among these young shells.

Many small specimens in the collections of the California Academy of Sciences, dredged in the Gulf of California, are similar to *T. amianta*. Some are white, some white with pink radial streaks or dots, others yellowish-white. These bear a similarity to one of the illustrations given by Sowerby<sup>10</sup> (pl. 47, fig. 278d) under the name of *Tellina silicula* Deshayes. That species was originally described by Deshayes<sup>11</sup> with the type locality "W. Columbia." Salisbury<sup>12</sup> stated that the type specimen of *T. silicula* Deshayes is referable to *Tellina rhomboides* Quoy & Gaimard, a species which occurs in the western Pacific region. According to Iredale<sup>13</sup> *Tellina clathrata* Deshayes is the correct name for that species. Sowerby's figures 278a, b, c, appear to be referable to it but it seems possible that his figure 278d might be referable to a young *T. amianta*.

**Distribution:** This species was dredged in Santa Inez Bay, Gulf of California, in 4-13 fathoms, at Corinto, Nicaragua, in 12-13

fathoms, also in beach drift on shore, and at Port Parker, Costa Rica, in 12-15 fathoms. It also has been recorded as occurring in the Pleistocene at Magdalena Bay, Lower California.

***Tellina (Moerella) arenica* Hertlein & Strong, sp. nov.**

Plate I, Figs. 5, 11.

*Tellina carpenteri* Dall, Packard, *Univ. Calif. Publ. Zool.*, Vol. 14, No. 2, September 12, 1918, p. 276, pl. 25, figs. 10a, 10b. . . . "in 68 fathoms just south of the Farallon Islands."—I. S. Oldroyd, *Publ. Puget Sound Biol. Sta.*, Vol. 4, 1924, pl. 41, figs. 10a, 10b. (Copies of Packard's figures). —I. S. Oldroyd, *Stanford Univ. Publ. Univ. Ser. Geol. Sci.*, Vol. 1, 1924, pl. 44, figs. 10a, 10b. (Copies of Packard's figures).

Not *Tellina carpenteri* Dall, 1903.

**Description:** Shell of moderate size, transversely ovate, thin, compressed, the anterior end slightly the longer, color creamy white, salmon pink and rose in concentric zones of irregular width; anterior dorsal margin sloping gently convexly from the beaks, anterior end rounded, ventral margin broadly rounded, posterior dorsal margin gently sloping, slightly concave, posterior end obliquely truncated; posterior area defined only by a rounded umbonal angulation; sculptured with concentric lines of growth and by somewhat irregularly spaced fine, shallow, concentric grooves which on the posterior area become deeper and give rise to sublamellate sculpture; hinge of right valve with two cardinal teeth, the posterior one bifid, an anterior lateral is fairly close to the cardinals and there is a distant posterior lateral below a socket; left valve (paratype) with a bifid anterior cardinal and traces of a posterior cardinal (some valves with a thin posterior cardinal lamella); pallial sinus highly triangular back of the beak then sloping somewhat irregularly to a position below and well separated from the anterior adductor impression, the end rounded then bending posteriorly for a very short distance where it becomes confluent with the pallial line; interior white and pink. Dimensions of the holotype: length, 24.5 mm.; height, 15 mm.; convexity (one valve), 2.5 mm.; pallial sinus extends anteriorly 19 mm. from the posterior end of the valve.

Holotype, a right valve (Calif. Acad. Sci. Paleo. Type Coll.), dredged at Station 136-D-20 in Lat. 23° 30' N., Long. 109° 26' W., in 43 fathoms, mud, on Arena Bank, at the south end of the Gulf of California. One additional specimen, a paratype, was dredged at the same locality. Three small single valves were dredged in the channel east of Cedros Island at Station 126-D-17, in 40 fathoms. Paratypes were dredged by the Templeton Crocker Expedition in 1932, near Puntarenas, Costa Rica.

**Range:** Farallon Islands, California, to Panama.

<sup>10</sup> Sowerby, G. B., *Conch. Icon.*, Vol. 17, *Tellina*, October, 1868, species 278, pl. 47, fig. 278d. "Hab. W. Columbia." [Not figs. 278a, b, c.]

<sup>11</sup> *Tellina silicula* Deshayes, *Proc. Zool. Soc. London* for 1854, (issued May 16, 1855), p. 363. "Hab. Columbia. Coll. Cuming."

<sup>12</sup> Salisbury, A. E., *Proc. Malacol. Soc. London*, Vol. 21, Pt. 2, 1934, p. 89. See also Lamy, E., *Bull. Mus. Nat. Hist. Nat. (Paris)*, Vol. 24, No. 2, 1918, p. 116.

<sup>13</sup> Iredale, T., *Mem. Queensland Mus.*, Vol. 9, Pt. 3, June 29, 1929, p. 266.

This beautiful species has often been referred to *Tellina carpenteri* Dall<sup>14</sup>, a distinct species, which has a smaller shell and a generally more northern distribution. Dall<sup>15</sup> cited *T. carpenteri* as occurring in the Gulf of Panama at a depth of 182 fathoms. It seems probable that that record may be referable to the present species.

The form illustrated under the name of *T. carpenteri* by Packard, 1918, which was dredged in 68 fathoms just south of the Farallon Islands, the illustrations of which were reproduced by I. S. Oldroyd, appears to be identical with the present specimens. This new species differs from *T. carpenteri* in the much greater size, irregular concentric zones of color and in the stronger concentric grooves. It differs from *Tellina recurvata* Hertlein & Strong [= *T. recurva* Dall, 1900, not of Deshayes, 1844], in the much more obliquely truncated posterior end and in the pink coloration. The shell of *Tellina arenica* differs from that of *T. tabogensis* in the larger size, pink color and in that the posterior dorsal margin is slightly concave or nearly straight rather than flexuous.

*Tellina (Moerella) erythronotus* Pilsbry & Lowe.

*Tellina (Angulus) erythronotus* Pilsbry & Lowe, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 84, May 21, 1932, p. 94, pl. 12, fig. 7. "Panama, east of the city" (type). Also from Montijo Bay, Panama.

*Type Locality*: Panama, east of the city.

*Range*: Magdalena Bay, Lower California, to the Bay of Panama.

*Collecting Stations*: El Salvador: Meanguera Island, Gulf of Fonseca (199-D-1), 16 fathoms, sand, mud, crushed shell; La Union, Gulf of Fonseca (199-D-8-16, 19-25), 3-16 fathoms, mud, mangrove leaves; Nicaragua: Monypenny Point, Gulf of Fonseca (199-D-2-6), 4-7 fathoms, mud.

*Description*: Shell donaciform, moderately thin, somewhat compressed, creamy white often tinged with pink around the margins, opalescent; anteriorly elongated and rounded, ventrally gently rounded and posteriorly slightly embayed due to the presence of a shallow depressed area which occurs anterior

to the posterior umbonal ridge; posteriorly triangular and somewhat bluntly pointed, with nearly straight dorsal margin; pallial sinus long not quite touching the anterior adductor impression, along the base wholly confluent with the pallial line; hinge of right valve with a grooved anterior and a bifid posterior cardinal, the anterior lateral strong and close to the cardinals, the posterior lateral farther removed but not distant; left valve with a grooved anterior and a thin posterior cardinal lamina, anterior lateral represented by a triangular projection of the margin, a similar posterior projection faintly developed or absent.

One of the largest specimens in the present collection measures: length, 25 mm.; height, 14.5 mm.; convexity (both valves together), 7 mm.

The specimens in the present collection show all the characters of *Tellina erythronotus* mentioned by Pilsbry & Lowe.

The shell of this species appears to be very similar to that of *Tellina hiberna* Hanley<sup>16</sup> which also has been cited as occurring at Panama. However, the shell of *T. erythronotus* appears to be somewhat more elongate in comparison to the figures of *T. hiberna* given by Hanley and Salisbury. The posterior dorsal margin of Hanley's species is said to be first convex then concave, but there is no marked convexity on the margin of *T. erythronotus*. Furthermore there is nothing in Hanley's description regarding pink or prismatic colors such as often can be observed on *T. erythronotus*.

*Tellina puellula* Salisbury<sup>17</sup> (= *T. puella* C. B. Adams, not Hanley), is another closely related species. According to Pilsbry & Lowe it is larger, relatively higher and thicker than *T. erythronotus*.

*Tellina hiberna* was described in 1844 and it seems possible that either *T. erythronotus* or *T. puellula*, both described later, may be referable to it, but we have not the type specimens available to enable us to make any definite decision on this question.

*Tellina panamensis* Philippi<sup>18</sup>, from Panama, was described as white with the umbos red both exteriorly and interiorly but it was said to lack lateral teeth.

*Distribution*: *Tellina erythronotus* was dredged quite abundantly in the Gulf of Fonseca at a depth of 3 to 16 fathoms on a bottom of mud and mangrove leaves. The present

<sup>14</sup> *Angulus variegatus* Carpenter, *Rept. Brit. Assoc. Adv. Sci.* for 1863 (issued August, 1864), p. 611. "Mont., Cat. Is., 20-60 fm.; rare (Neeah Bay, Swan)." Also pp. 627, 639. Reprint in *Smithson. Miscell. Coll.*, No. 252, 1872, pp. 97, 113, 125. —Carpenter, *Ann. & Mag. Nat. Hist.*, Ser. 3, Vol. 14, December, 1864, p. 423. "Hab. Neeah Bay (Swan); Monterey and Catalina Island, 20-60 fathoms, rare (Cooper)." Reprint in *Smithson. Miscell. Coll.*, No. 252, 1872, p. 235.

Not *Tellina variegata* Gmelin, *Syst. Nat.*, ed. 13, 1790, p. 3237.

*Tellina (Angulus) carpenteri* Dall, *Proc. U. S. Nat. Mus.*, Vol. 23, No. 1210, November, 1903, pp. 303, 320. New name for *Angulus variegatus* Carpenter, 1864, not *Tellina variegata* Gmelin, 1790. "Strait of Juan de Fuca to Lower California." Illustrated by I. S. Oldroyd, *Publ. Puget Sound Biol. Sta.*, Vol. 4, 1924, p. 51, pl. 10, fig. 4. —I. S. Oldroyd, *Stanford Univ. Publ. Univ. Ser. Geol. Sci.*, Vol. 1, 1924, p. 166, pl. 29, fig. 2. San Pedro, California.

<sup>15</sup> *Tellina (Angulus) carpenteri* Dall, *Bull. Mus. Comp. Zool.*, Vol. 43, No. 6, October, 1908, p. 421. "U. S. S. 'Albatross', station 3355, Gulf of Panama, in 182 fathoms, mud, bottom temperature, 54° F. U. S. N. Mus. 122, 934."

<sup>16</sup> *Tellina hiberna* Hanley, *Proc. Zool. Soc. London*, December, 1844, p. 148. "Hab. Panama and Bay of Quayaquil; six to eleven fathoms, in sandy mud; Cuming." —Hanley, *Thes. Conch.*, Vol. 1, 1846, p. 282, pl. 57, fig. 53. Original localities cited.

*Tellina (Angulus) hiberna* Hanley, Salisbury, *Proc. Malacol. Soc. London*, Vol. 21, Pt. 2, 1934, p. 91, pl. 13, figs. 7, 8, 9. [Illustrations of holotype and paratypes].

<sup>17</sup> *Tellina puellula* Salisbury, *Proc. Malacol. Soc. London*, Vol. 21, Pt. 2, July, 1934, p. 86. A new name for *Tellina puella* C. B. Adams, *Ann. & Lycum Nat. Hist. New York*, Vol. 5, July 1852, pp. 507, 546 (separate, pp. 283, 322). "Panama." Not *Tellina puella* Hanley, *Proc. Zool. Soc. London*, February, 1845, p. 165. "Hab. Senegal. Cuming, Metcalfe."

<sup>18</sup> *Tellina panamensis* Philippi, *Zeit. f. Malakozool.*, Jahrg. 5, No. 11, 1848, p. 175. "Ad Panama legit frater E. B. Philippi."

records of occurrence furnish a long extension north of the known range of the species. The northernmost occurrence of this species known to us is that based upon a specimen in the collections of the California Academy of Sciences which was collected by C. R. Orcutt at Magdalena Bay, Lower California.

*Tellina (Moerella) felix* Hanley.

Plate I, Fig. 1.

*Tellina felix* Hanley, *Proc. Zool. Soc. London*, September, 1844, p. 71. "Hab. Panama; sandy mud, six to ten fathoms." — Hanley, *Thes. Conch.*, Vol. 1, 1846, p. 281, pl. 57, fig. 52. "Panama."

*Type Locality*: Panama, in 6 to 10 fathoms, sandy mud.

*Range*: Mazatlan, Mexico, to Zorritos, Peru.

*Collecting Station*: Nicaragua: Potosi and Monypenny Point, Gulf of Fonseca; Corinto (200-D-8, 9, 17, 19), 6-13 fathoms, sand, mangrove leaves, also beach drift.

*Description*: Shell small, elongate, anterior end much the longer, rounded, the posterior end very short and obtusely obliquely subtruncated, anterior dorsal and ventral margins nearly parallel, exterior and interior of a glossy rose red color; a posterior area is set off by an umbonal angulation; valves ornamented with fine, regular, concentric striae; hinge of right valve with two cardinals, the posterior one grooved, a strong, high, elongate anterior lateral extends almost to the beak and a small posterior lateral is present just beyond and below the posterior end of the ligamentary area; left valve with a well-developed anterior cardinal, a thin posterior cardinal lamella is almost fused to the posterior margin and a pointed projection of the nymph represents an anterior lateral; pallial sinus not quite reaching the anterior adductor impression and along the base, except for a short distance, it is confluent with the pallial line.

A specimen from the Gulf of Fonseca in the Henry Hemphill collection in the California Academy of Sciences measures approximately: length 17.2 mm.; height, 9.4 mm.; convexity (both valves together), 4.3 mm.

The shell of this little species is characterized by the beautiful glossy rose red color, weakly inflated valves, nearly parallel anterior dorsal and ventral margins, strong right anterior lateral, and by the short, obliquely subtruncated posterior end.

The shorter posterior end, more gently sloping anterior dorsal margin and deep red color are features which serve to separate *Tellina felix* from *T. tabogensis* Salisbury.

The longer, stronger, right anterior lateral and more steeply sloping posterior dorsal area just below the beaks are features separating *T. felix* from *T. carpenteri* Dall.

Carpenter<sup>19</sup> mentioned that *Tellina puella*

C. B. Adams<sup>20</sup> [= *T. puellula* Salisbury] is "not unlike *T. felix*." The remarks of Pilsbry & Lowe seem to indicate that the species described by Adams possesses a higher, heavier shell than *T. felix*.

*Distribution*: Specimens of this species were dredged off Nicaragua in 6-13 fathoms and also were taken in the beach drift. It has been recorded with doubt, as occurring in the Miocene<sup>21</sup> of Peru, and definitely in the Pliocene of Ecuador. This species has been cited as occurring in the Red Sea but, as mentioned by Lamy<sup>22</sup>, it does not occur in that region.

*Tellina (Moerella) macneilii* Dall.

*Tellina (Angulus) macneilii* Dall, *Proc. U. S. Nat. Mus.*, Vol. 23, No. 1210, November, 1900, pp. 303, 318, pl. 3, fig. 7. "Obtained at Guaymas, Mexico, by W. H. Dall."

*Type Locality*: Guaymas, Mexico.

*Range*: Guaymas, Mexico, to the Gulf of Nicoya, Costa Rica.

*Collecting Station*: Costa Rica: Cedro Island to off Ballena Bay, Gulf of Nicoya (213-D-11-17), 35-40 fathoms, mud.

*Description*: Shell small, solid, inequilateral, the anterior end longer, rounded, the posterior end quite short, depressed, bluntly pointed; color deep rosy, slightly zoned, and paler toward the basal margin; surface closely, sharply concentrically striated, the posterior dorsal area feebly imbricate, with a little obscure radial striulation; valves moderately full, flattish toward the middle of the disk; hinge strong, normal; internal ray obscure; pallial sinus long, nearly reaching the anterior adductor scar, wholly confluent below. Lon. 12.5, alt. 7.6, diam. 3.5 mm. (Original description).

One pair and two single valves dredged in the Gulf of Nicoya agree well with Dall's description and illustration. The largest specimen measures approximately: length 11.5 mm.; height, 7.3 mm.; convexity (both valves together), 4.2 mm. These are identical with specimens identified as *T. macneilii* in the Lowe collection in the San Diego Society of Natural History.

The hinge of this species is similar to that of *T. felix* Hanley.

Compared to *T. felix*, the valves of *T. macneilii* are more inflated in proportion to their size, less elongate, the posterior end is more abruptly truncated and the anterior dorsal margin slopes more steeply. These same characters (except the slope of the anterior dorsal margin) as well as the pink color likewise serve to separate this species from *T. tabogensis*.

*Tellina guaymasensis* Pilsbry & Lowe<sup>23</sup> is

<sup>20</sup> See footnote No. 17, p. 69.

<sup>21</sup> *Tellina (Eurytellina)* cf. *felix* Hanley, Olsson, *Bull. Amer. Paleol.*, Vol. 19, No. 68, June 30, 1932, p. 123, pl. 14, fig. 8. "Tumbez formation, Que Tucillal at Zorritos." Peru. Miocene.

<sup>22</sup> Lamy, E., *Bull. Mus. Nat. Hist. Nat. (Paris)*, Vol. 24, No. 2, 1918, p. 119 (footnote).

<sup>23</sup> *Tellina (Angulus) guaymasensis* Pilsbry & Lowe, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 84, May 21, 1932, p. 94, pl. 16, fig. 7. "Guaymas." Mexico.

<sup>19</sup> Carpenter, P. P., *Proc. Zool. Soc. London*, 1863, p. 366. Reprint in *Smithson. Miscell. Coll.*, No. 252, 1872, p. 202.

quite similar to *T. macneilii* but the shell appears to be a little more depressed medially and is in greater part white with streaks of pink.

The present specimens agree well with the brief description of *Tellina deshayesii* Carpenter<sup>24</sup> from the Bay of Panama. It was said to resemble *Tellina similis* Sowerby but much more inequilateral. However the specific name proposed by Carpenter is untenable in any case because of the prior use of that combination of names, *Tellina deshayesii*, by Hanley<sup>25</sup>.

**Distribution:** Specimens of *Tellina macneilii* were taken by the expedition in the Gulf of Nicoya in 35-40 fathoms. This record represents an extension south of the known range of this species.

#### *Tellina (Moerella) paziana* Dall.

*Tellina (Moerella) paziana* Dall, *Proc. U. S. Nat. Mus.*, Vol. 23, No. 1210, November, 1900, pp. 303, 318, pl. 3, fig. 8. "Dredged in 26½ fathoms, near La Paz, Lower California, by the U. S. Fish Commission, at station 2823."

**Type Locality:** Near La Paz, Lower California, Mexico, in 26½ fathoms.

**Range:** Gulf of California to Cedro Island, Costa Rica.

**Collecting Stations:** Mexico: Port Guatulco (195-D-2, 7, 10, 11), 3-5 fathoms, sand, gr. sand, crushed shell, dead coral; Tangola-Tangola Bay (196-D-6, 7, 13, 14, 15), 5-12.8 fathoms, sand, crushed shell; Nicaragua: Corinto (200-D-8, 9, 19), 6-13 fathoms, mangrove leaves, also on the beach; Costa Rica: Cedro Island, Gulf of Nicoya (213-D-1-10), 4-10 fathoms, mud, sand, crushed shell.

**Description:** Shell small, thin, white, convex, the anterior end slightly longer, rounded, the posterior end bluntly pointed; surface finely concentrically sculptured by the incremental lines, covered with a very delicate dehiscent pale straw-colored epidermis; hinge well-developed, a minute but distinct anterior or left lateral present; interior polished, only about half the lower portion of the pallial sinus confluent, the anterior part not reaching the adductor. Lon. 10.2, alt. 7, diam. 3.5 mm. (Original description).

The shell of this species is usually small, about 10-15 mm. in length. A large right valve in the present collection from Corinto, Nicaragua, measures approximately: length, 17.5 mm.; height 14 mm., convexity (one valve), 3.3 mm.; pallial sinus extends forward 12.8 mm. from the posterior margin.

The pallial sinus in this species ascends to a high rounded point slightly posterior to a line vertical with the beaks, then descends obliquely. The end is rounded and well separated from the anterior adductor impression.

<sup>24</sup> *Tellina deshayesii* Carpenter, *Proc. Zool. Soc. London*, November 11, 1856, p. 160. "Hab. in Sinu Panamensi; legit T. Bridges. Sp. un. in Mus. Cuming."

<sup>25</sup> *Tellina deshayesii* Hanley, *Proc. Zool. Soc. London*, December, 1844, p. 148. "Hab. Red Sea? Mus. Cuming, Deshayes."

*Tellina paziana* somewhat resembles *T. meropsis* Dall. It differs from that species in the more elongate outline, the anterior end is longer in proportion to the length, the posterior end is much more bluntly pointed and the pallial sinus is separated from the anterior adductor impression by a much wider space. According to Dall, "This differs from the young of *Scrobiculina viridotincta* Carpenter, which in outline it resembles, by being less polished, more inflated, and without the deep-set resilium."

**Distribution:** This species was taken by the expedition from off western Mexico to the Gulf of Nicoya, Costa Rica, in 3-13 fathoms, also on the beach. This is an extension south of the known range of this species.

#### *Tellina (Moerella) recurvata* Hertlein & Strong, sp. nov.

Plate I, Figs. 2, 3, 4, 8.

*Tellina (Angulus) recurva* Dall, *Proc. U. S. Nat. Mus.*, Vol. 23, No. 1210, November, 1900, pp. 304, 320, pl. 3, fig. 4. "Dredged near the head of the Gulf of California in 24 fathoms, mud, off Point Fermin."

Not *Tellina recurva* Deshayes, *Proc. Zool. Soc. London* for 1854 (issued May 16, 1855), p. 361. "Hab. Australia."—Hedley, *Proc. Linn. Soc. New South Wales*, Vol. 38, Pt. 2, 1913, p. 272. Hedley stated: "I failed to find this unfigured Australian species in the British Museum. It is recommended that the name be treated as lost and unrecognizable."

**Description:** Shell small, translucent white, polished, rather compressed, beaks very low, the anterior end the longer; anterior or dorsal margin gently curved, ventral margin gently rounded, posterior dorsal margin depressed below the beak, sloping gently along the ligamentary area (about 2 mm. on the type), the end obliquely sloping and roundly truncated; a weak posterior umbonal angulation present; surface of valves with concentric, chiefly incremental sculpture, the posterior area with low lamellae; hinge plate arched anterior to the beaks; right valve with two cardinals, the posterior one grooved, anterior lateral strong and fairly close to the cardinals, a posterior lateral occurs below a socket at about the end of the ligamental area; left valve with two cardinals, the posterior one sloping posteriorly, a faint projection of the margin represents an anterior lateral; pallial sinus subtriangular, extending forward about three-fourths the length of the shell but well separated from the anterior adductor impression, along the base confluent with the pallial line. Dimensions of the type: length, 12 mm.; height, 7.5 mm.; convexity (both valves together), 2.9 mm.

Holotype (Calif. Acad. Sci. Paleo. Type Coll.), from Loc. 23802 (C.A.S.), San Luis Gonzaga Bay, Gulf of California. Paratypes from the same locality. Dredged by the expedition at the following stations: Mexico: 4 miles SSW. of Maldonado Point (192-D-

1), 26 fathoms, mud; Port Guatulco (195-D-20), 23 fathoms, mud; Costa Rica: Port Parker (203-D-1), 15 fathoms, sandy mud, crushed shell.

*Range*: Point Firmin, Lower California, near the head of the Gulf of California, to Port Parker, Costa Rica.

Some of the shells of this species are iridescent. Dall pointed out that the shell of this species somewhat resembles that of young *Macoma yoldiformis* but is more blunt posteriorly and the hinge of course is different. The more abruptly truncated posterior end and white color are features separating the present species from *T. arenica*. Compared to *T. tabogensis* the outline of *T. recurvata* is less elongate, the anterior dorsal margin is more arcuate and the posterior dorsal margin is not flexuous. Compared to *T. buttoni* Dall, the shell of the present species is less attenuated both anteriorly and posteriorly, the posterior dorsal margin just below the beaks slopes more gently and it lacks the strong anterior ray internally which is so conspicuous in Dall's species.

*Distribution*: A few specimens of this species were dredged by the expedition off western Mexico in 23-26 fathoms and off Port Parker, Costa Rica, in 15 fathoms. The present record of the occurrence of this shell off Costa Rica is an extension south of the known range of the species.

***Tellina (Moerella) suffusa* Dall.**

*Tellina (Angulus) suffusa* Dall, *Proc. U. S. Nat. Mus.*, Vol. 23, No. 1210, November, 1900, pp. 303, 319, pl. 3, fig. 10. "Collected at San Ignacio Lagoon, Lower California, by Henry Hemphill."

*Type Locality*: San Ignacio Lagoon, west coast of Lower California.

*Range*: San Ignacio Lagoon, Lower California, to Corinto, Nicaragua.

*Collecting Station*: Nicaragua: Corinto, beach.

*Description*: Shell cuneate, very thin, convex, blunt in front, pointed behind, the posterior end slightly longer, pinkish, yellowish, or translucent white in color; surface rather strongly, closely, and irregularly concentrically striate, with an unusually large and wide lunular impression, but no escutcheon to speak of; hinge normal, delicate; interior polished; the pallial sinus high, well separated from the anterior adductor, though there seems to be no trace of a ray in the specimens examined. Lon. 13.5, alt. 9.2, diam. 4.7 mm. (Original description).

The unusually large lunular area, short, blunt anterior end and pointed posterior end are features characteristic of this little species.

Several single valves from Corinto, Nicaragua, the largest measuring 11 mm. in length, agree well with Dall's description and illustration of *Tellina suffusa*. They likewise appear to be identical with specimens of that species from Magdalena Bay in the

Hemphill collection of the California Academy of Sciences.

*Tellina pumila* Hanley,<sup>26</sup> described from Chile, is somewhat similar in outline but the posterior end is narrower.

*Distribution*: Specimens of this species were taken by the expedition only in beach drift at Corinto, Nicaragua. This is a considerable extension south of the known range of this species.

***Tellina (Moerella) tabogensis* Salisbury.**

*Tellina (Angulus) panamensis* Dall, *Proc. U. S. Nat. Mus.*, Vol. 23, No. 1210, November, 1900, p. 319, pl. 3, fig. 3. "Types.—No. 108557, U.S.N.M., dredged in 30 fathoms in Panama Bay by the U. S. Fish Commission, at station 2799."

Not *Tellina panamensis* Philippi, *Zeit. f. Malakozool.*, Jahrg. 5, No. 11, 1848, p. 175. "Ad Panama legit frater E. B. Philippi."

*Tellina tabogensis* Salisbury, *Proc. Malacol. Soc. London*, Vol. 21, Pt. 2, July, 1934, p. 86. A new name for *Tellina (Angulus) panamensis* Dall, 1900, not *Tellina panamensis* Philippi, 1848.

*Type Locality*: Panama Bay, in 30 fathoms.

*Range*: Gulf of California to Santa Elena Bay, Ecuador.

*Collecting Stations*: El Salvador: Meanguera Island, Gulf of Fonseca (199-D-1), 16 fathoms, sand, mud, crushed shell; La Union (199-D-13), 6 fathoms, mud; Nicaragua: Corinto (200-D-19), 12-13 fathoms, mangrove leaves; Costa Rica: Cedro Island, Gulf of Nicoya (213-D-1-10), 4-10 fathoms, mud, sand, crushed shell.

Shell small, thin, ivory white, polished, rather compressed, flexuous behind, the anterior end much the longer, produced and rounded, posterior end with the ligament rather deeply inset, margin obliquely descending to a rather blunt point; surface smooth or marked only by incremental lines, except near the basal margin, where there are a few incised lines with wider interspaces, not quite in harmony with the lines of growth; posterior dorsal area minutely concentrically rippled; hinge normal, delicate; pallial sinus large, not reaching the adductor, mostly confluent below; the elevated ray absent or obsolete. Lon. 9, alt. 5.25, diam. 2.5 mm. (Original description of *Tellina panamensis* Dall).

Fresh specimens exhibit on the surface a lovely iridescent glow (Dall).

A large series of specimens of this species dredged off El Salvador by the expedition have been compared with a series dredged at Acapulco, Mexico, in the H. N. Lowe Collection in the Museum of the San Diego Society of Natural History and with specimens

<sup>26</sup> *Tellina pumila* Hanley, *Proc. Zool. Soc. London*, September, 1844, p. 69. "Hab. Valparaiso; sandy mud, from seven to thirty fathoms." —Hanley, *Thes. Conch.*, Vol. 1, 1846, p. 279, pl. 57, fig. 41. "Valparaiso."  
*Tellina (Angulus) pumila* Hanley, Salisbury, *Proc. Malacol. Soc. London*, Vol. 21, Pt. 2, July, 1934, p. 91, pl. 13, figs. 3 and 4. (Illustrations of holotype and paratype).

in the California Academy of Sciences. It appears from this study that Dall's type, 9 mm. in length, is a juvenile shell and that the species reaches a much larger size. A large right valve in the present collection dredged off El Salvador, measures: length, 18.3 mm.; height, 10 mm.; convexity (one valve), 2.6 mm.

The most striking features of this species are the ivory white color, iridescence in fresh shells and the flexuous posterior dorsal margin. This flexuosity is caused by the convexity of an area on the posterior dorsal margin just posterior to the ligamentary area. Some specimens are faintly tinted with pink on the umbonal area. Variation in the thickness and in the flexuosity of the posterior dorsal margin can be observed in a series of specimens. These features are most pronounced in the larger shells. The present specimens as well as a series in the Collections of the California Academy of Sciences from Panama Bay, a series in the same collection from Santa Elena Bay, Ecuador, collected by Woodbridge Williams, and a series in the H. N. Lowe collection from Acapulco, Mexico, show gradation from small, thin shells with a slightly flexuous posterior dorsal margin to fairly thick shells with strong flexuous posterior margins.

The hinge of this species is similar to that of *Tellina felix* except that the right anterior lateral is shorter and in the left valve the inner margin back of the beak is slightly thickened and some large specimens show traces of a left posterior lateral. The ivory color, longer posterior end and more convex posterior dorsal margin easily serve to separate this species from *T. felix*.

*Tellina hiberna* Hanley<sup>27</sup> appears to be a very similar shell. The illustrations of that species published by Hanley and Salisbury indicate that the shell is more abruptly sloping posteriorly, that there is a constricted area just anterior to the posterior umbonal ridge and anterior to this the shell is more expanded than in *T. tabogensis*.

*Distribution*: This species was dredged by the expedition off Meanguera Island, El Salvador, in the Gulf of Fonseca, where it occurred abundantly in 6 to 16 fathoms, off Corinto, Nicaragua, in 12-13 fathoms, and in the Gulf of Nicoya, Costa Rica, in 4-10 fathoms. It occurs north to the Gulf of California and south to Ecuador.

Subgenus *Eurytellina* Fischer.

KEY TO THE SPECIES OF *Eurytellina*.

- A. Shell white or brownish
  - a. Pallial sinus touching the anterior adductor impression
  - b. Very elongate; adult valves with a median depressed area ventrally  
*planulata*

- bb. Shell high; without a median depressed area ventrally... *laceridens*
- aa. Pallial sinus not touching anterior adductor impression
  - c. Sculpture coarse, about 1 rib per millimeter... *panamanensis*
  - cc. Sculpture fine, about 3 ribs per millimeter... *eburnea*
- B. Shell entirely or partly some shade of pink or red
  - a. Concentric sculpture of even strength over shell
  - b. Pallial sinus confluent with a portion of the posterior margin of the anterior adductor impression  
*rubescens*
  - bb. Pallial sinus not touching anterior adductor impression
    - c. Concentric sculpture decussated by radial striae... *princeps*<sup>28</sup>
    - cc. Concentric sculpture not decussated, radial striae very fine or absent
    - d. About 10 concentric grooves per millimeter... *prora*
    - dd. About 2 or 3 concentric grooves per millimeter
    - e. Right valve with depressed area anterior to posterior umbonal angulation... *simulans*
    - ee. Right valve without depressed area anterior to posterior umbonal angulation
      - f. Posterior dorsal area with strong concentric sculpture  
*mantaensis*
      - ff. Posterior dorsal area with weak concentric sculpture or of growth lines only  
*ecuadoriana*<sup>28</sup>

- aa. Concentric sculpture of unequal strength over shell
  - g. Posterior third of shell with coarse concentric lamellae giving way to fine striae anteriorly  
*inaequistriata*
  - gg. Posterior third of shell smooth or nearly so in one or both valves, anteriorly sculptured with distant concentric grooves... *regia*

*Tellina (Eurytellina) eburnea* Hanley.

*Tellina eburnea* Hanley, *Proc. Zool. Soc. London*, September, 1844 p. 61, "Hab. Tumbuz, Peru; in soft sandy mud, five fathoms." —Hanley, *Thes. Conch.*, Vol. 1, 1846, p. 241, pl. 58, fig. 91. Tumbuz, Peru. —Sowerby, *Conch. Icon.*, Vol. 17, *Tellina*, 1867, species 60, pl. 13, fig. 60. Original locality cited.

<sup>27</sup> See *Tellina hiberna* Hanley, *Thes. Conch.*, Vol. 1, 1846, p. 282, pl. 57, fig. 53. "Panama; Bay of Guayaquil." —Salisbury, *Proc. Malacol. Soc. London*, Vol. 21, Pt. 2, 1934, p. 91, pl. 13, figs. 7, 8, 9. [Illustrations of holotype and paratypes].

<sup>28</sup> Not represented in the present collection.

*Tellina (Peronaeoderma) eburnea* Hanley, Mörch, *Malakozool. Blätter*, Bd. 7, 1860, p. 186. Sonsonate, El Salvador.

*Type Locality*: Tumbes, Peru, in 5 fathoms, sandy mud.

*Range*: Gulf of California to Tumbes, Peru.

*Collecting Stations*: Guatemala: 7 miles west of Champerico (197-D-1, 2), 14 fathoms, mud; El Salvador: La Libertad (198-D-1, 2), 13-14 fathoms, mud; Nicaragua: Corinto, beach; Panama: Gulf of Chiriqui (221-D-1-5), 35-40 fathoms, sandy mud.

*Description*: Oblong, solid, opaque, rather inequivalve, convex, whitish, glossy, clearly inequilateral, with strong deep concentric sulci, which usually become obsolete in one of the valves, and which diverge and become elevated on passing the flattened space at the upper edge of the more convex valve; ventral edge very slightly convex, curving obliquely upward anteriorly; posterior side much the shorter, subcuneiform; the ligamental edge straight, and abruptly sloping; ligament short and prominent; fold and umbonal ridge almost obsolete; inside pure white, teeth as in *punicea*. (Hanley, *Thes. Conch.*, 1846).

The largest specimen in the present collection measures: length 28.3 mm.; height, 17.8 mm. The present specimens agree well with the younger stages of a specimen of *T. eburnea* in the collection at Stanford University which was collected in Ecuador by Stanley Herold, which measures: length, 47.5 mm.; height, 29.8 mm.; convexity (both valves together), 12.6 mm.

The concentric sculpture on the posterior dorsal areas becomes stronger and raised after crossing the umbonal ridge. This feature is emphasized by Hanley and Sowerby but it is not very pronounced on the present specimens.

*Tellina eburnea* is very similar to *T. alternata* Say, an east American species.

*Tellina laplata* Pilsbry & Olsson<sup>29</sup>, described from the Pliocene of Peru, is also very similar to *T. eburnea*. Compared to *T. laplata* the present specimens do not show such strong raised sculpture on the posterior dorsal areas nor is the sculpture as strong on the left anterior dorsal area as that shown in the illustrations by Pilsbry & Olsson.

The shell of *Tellina eburnea* is higher in proportion to the length as compared to that of *T. simulans*, furthermore the color is pure white both exteriorly and interiorly. The general character of the pallial sinus is similar to that of *T. simulans*. It is somewhat higher behind and extends forward almost to but does not quite touch the anterior adductor impression and is confluent with the pallial line below. The hinge is similar to that of *T. simulans* except that the right posterior lateral is less distant from the cardinals. The sculpture is much finer and the pallial sinus

extends nearer the anterior adductor impression than that of *T. panamanensis* Li.

*Distribution*: Specimens here referred to *Tellina eburnea* were dredged by the expedition in 13-40 fathoms, from off Guatemala and El Salvador, in the Gulf of Chiriqui, Panama, and were taken on the beach at Corinto, Nicaragua.

*Tellina (Eurytellina) inaequistriata* Donovan.

Plate I, Fig. 18.

*Tellina inaequistriata* Donovan, *Nat. Hist. Brit. Shells*, Vol. 4, 1802, pl. 123 [two figs.]. "A very rare species of *Tellina* communicated to Da Costa after his *Conchology* was published, and therefore not noticed in that work. It has been found by the late Dr. Pulteney we believe on the coast of Dorsetshire." — Chenu, *Bibl. Conchyl.*, Ser. 1, Vol. 1, 1845, p. 82, pl. 32, figs. 7, 8. [French translation of Donovan's work on Shells]. — Hanley, *Thes. Conch.*, Vol. 1, 1846, p. 238, pl. 57, fig. 58; pl. 58, fig. 80. "Bay of Guayaquil; (Cuming)." — Forbes & Hanley, *Hist. Brit. Moll.*, Vol. 1, 1853 (issued August 1, 1848), p. 314. "Inhabits the Bay of Guayaquil; was introduced by Donovan, who only surmised that it had been taken by Dr. Pulteney on the Dorset coast."

*Tellina sanguinea* Wood, *Gen. Conch.*, 1815, p. 159, pl. 44, fig. 2. "This shell is in the cabinet of Dr. Coombe." [No locality cited]. — Wood, *Index Test.*, 1825, p. 18, pl. 4, fig. 27. Also ed. 1828. Locality unknown. Also ed. by Hanley, 1842-1856, p. 23, pl. 4, fig. 27. "Guayaquil." [States that fig. 80 in *Thes. Conch.* represents *T. sanguinea*]. — Hanley, *Cat. Rec. Riv. Shells*, 1843, p. 67.

*Tellina (Eurytellina) leucogonia* Dall, *Proc. U. S. Nat. Mus.*, Vol. 23, No. 1210, November, 1900, p. 317, pl. 4, fig. 5. "Type. — No. 102182, U.S.N.M., from the Gulf of California, Stearns collection."

*Type Locality*: Bay of Guayaquil, Ecuador (according to Hanley and Forbes & Hanley). [Erroneously cited from the coast of Dorsetshire, England, by Donovan].

*Range*: Gulf of California to the Bay of Guayaquil, Ecuador. Caribbean (Dautzenberg).

*Collecting Stations*: Mexico: Santa Cruz Bay (195-D-19-21), 17-18 fathoms, mud, gr. mud, crushed shell; Tangola-Tangola Bay (196-D-13), 10 fathoms, gr. sand, crushed shell; Costa Rica: Port Parker (203-D-3), 12 fathoms, shelly mud.

*Description*: Shell ovate, compressed and rather flattish, rosy, very finely striated transversely: the striae fewer and larger at the anterior [posterior] end (Donovan).

Shell elongate, moderately thick, somewhat compressed, glossy, subequilateral, red or orange-red; a well-defined fairly broad posterior area is set off by a rounded post-umbonal ridge; posterior dorsal margin slightly rounded, sloping downward and slightly expanded along the ventral half; the ornamentation consists of concentric striae which, especially on the right valve, are very

<sup>29</sup> *Tellina (Eurytellina) laplata* Pilsbry & Olsson, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 93, September 9, 1941, p. 67, pl. 15, figs. 1-5. "Canoa formation, Punta Blanca." Ecuador. Pliocene.

strongly developed and widely spaced on about the posterior third of the shell then change abruptly to fine striae anteriorly; hinge normal for the subgenus; the pallial sinus does not quite touch the anterior adductor impression but is separated by a narrow area, wholly confluent with the pallial line below and, in general features, similar to that of *T. simulans* and *T. prora*.

A right valve in the present collection from Santa Cruz Bay, Mexico, measures: length, 23 mm.; height, 12.5 mm. It agrees well with Hanley's plate 50, figure 80. Other specimens in the collection are similar but show the strong sculpture only slightly developed anterior to the angulation.

Some of the small shells, especially left valves, almost lack strong concentric sculpture anterior to the posterior area; in such cases they may be ornamented only by faint grooves slightly out of harmony with the incremental lines.

A series of specimens in the H. N. Lowe collection of the San Diego Society of Natural History, varying in length from approximately 8.5 mm. to 26.2 mm. and identified by Lowe as *Tellina leucogonia* Dall, are identical with the present specimens. The present series together with Lowe's specimens show all variations from young smooth shells up to a large right valve with the typical sculpture of *T. inaequistriata*. We are therefore inclined to consider Dall's species as identical with *T. inaequistriata*.

The very distinct concentric sculpture, changing from coarse to fine at about the posterior third of the shell, serves to separate this form from similar west American species of the genus.

*Tellina waylandvaughani* Maury<sup>30</sup>, described from the Miocene of Santo Domingo, is a similar species.

*Distribution*: Specimens of this species were dredged by the expedition in 10 to 18 fathoms from off western Mexico and Costa Rica. The present records of occurrence show the range of this species to extend from the Bay of Guayaquil north to the Gulf of California. Dautzenberg<sup>31</sup> cited *Tellina inaequistriata* as occurring in the Caribbean region at the Island of Martinique and in Venezuela. He stated that he could detect no differences which would serve as a basis for separating the Caribbean shells from those illustrated under that name from the Bay of Guayaquil.

#### *Tellina (Eurytellina) laceridens* Hanley.

*Tellina laceridens* Hanley, *Proc. Zool. Soc. London*, September, 1844, p. 61. "Hab. Tumbez, Peru; soft sandy mud, five fathoms." "Var. testa, magis trigona . . ." "Hab. Chiriqui, West Columbia; sandy mud, three fathoms." —Hanley, *Thes. Conch.*, Vol. 1, 1846, p. 243, pl. 61, figs. 168, 176. [Not. pl. 66,

fig. 258.]. Original localities cited. —Sowerby, *Conch. Incon.*, Vol. 17, *Tellina*, 1867, species 104, pl. 20, fig. 104. Tumbez, Peru.

*Type Locality*: Tumbez, Peru, in 5 fathoms, soft, sandy mud.

*Range*: Realejo [near Corinto], Nicaragua, to Tumbez, Peru.

*Collecting Stations*: Nicaragua: Corinto, beach; Costa Rica: Port Culebra; Colombia: Gorgona Island.

*Description*: Shell elongately trigonal, beaks nearly central but slightly anteriorly placed, posterior end obliquely truncated; sculpture of fine, concentric grooves which in places are irregular, the umbonal region, and often the posterior area, relatively smooth; white, sometimes with a pinkish spot on the umbonal region; ligament large, exterior; hinge with cardinals grooved, especially the right posterior cardinal which appears ragged due to 7 to 10 grooves; the pallial sinus touches the anterior adductor impression just above the base; interior white and yellow and in large specimens with somewhat granular areas and salmon pink spots.

A specimen collected at Gorgona Island, Colombia, measures: length, 53 mm.; height, 34.8 mm.; convexity (both valves together), 11.6 mm.

Some of the characters in which this species differs from *Tellina panamanensis* Li are: the finer concentric sculpture, larger smooth umbonal area, regular sculpture along the posterior dorsal margin and in that the pallial sinus touches the anterior adductor impression.

*Distribution*: A few specimens of this species were collected by the expedition in the beach drift at Corinto, Nicaragua, one at Port Culebra, Costa Rica, and one at Gorgona Island, Colombia. It also has been recorded as occurring in beds of Pliocene age in Panama.

#### *Tellina (Eurytellina) mantaensis* Pilsbry & Olsson.

*Tellina (Eurytellina) mantaensis* Pilsbry & Olsson, *Nautilus*, Vol. 56, No. 3, January, 1943, p. 80, pl. 8, figs. 1-4. "Manta, Ecuador."

*Type Locality*: Manta, Ecuador.

*Range*: Gulf of Chiriqui, Panama, to Manta, Ecuador.

*Collecting Station*: Panama: Gulf of Chiriqui (221-D-1-5), 35-40 fathoms, sandy mud.

*Description*: Shell elongated, rather compressed, the anterior end slightly the longer, posterior end obliquely subtruncated; sculpture of flat concentric ridges which are separated by narrower grooves; the posterior area is usually ornamented by wavy raised threads and with faint radial lines on one or the other valve; hinge of right valve with a strong anterior lateral adjacent to the cardinals and a more distant posterior lateral, the laterals are smaller in the left valve; the pallial sinus reaches almost to the anterior adductor impression and in this character is similar to *T. simulans*,

<sup>30</sup> *Tellina waylandvaughani* Maury, *Bull. Amer. Paleontol.*, Vol. 5, No. 29, 1917, p. 386 (222), pl. 64 (38), figs. 7 and 8. "Zone G. Rio Gurabo at Los Quemados." Santo Domingo, Miocene.

<sup>31</sup> Dautzenberg, P., *Mem. Zool. Soc. France*, Vol. 13, 1900, p. 260.

and is confluent with the pallial line below; fresh specimens are rose colored, more deeply on the umbos, and somewhat brownish colored ventrally.

Two valves in the present collection agree well with the illustrations of *T. mantaensis* Pilsbry & Olsson. The larger specimen measures approximately 21 mm. in length and 15 mm. in height.

The shell of this species differs from that of *Tellina simulans* in that it is more elongated and the dorsal margins slope more gently, especially posteriorly where the area is somewhat flattened. There also are differences in the details of the hinges of the two species. The right posterior cardinal of *T. mantaensis* reaches almost to the ventral margin of the hinge plate which beneath that tooth is strongly indented. In *T. simulans* the corresponding tooth reaches little more than halfway to the ventral margin of the hinge plate which at that point is gently rounded.

The strong concentric sculpture on the posterior dorsal area and more gently sloping anterior dorsal margin are features which serve to separate this species from *T. ecuadoriana* Pilsbry & Olsson.

*Distribution*: Two single valves of this species were taken by the expedition in 30-40 fathoms on a bottom of sandy mud in the Gulf of Chiriqui, Panama. This is an extension north of the known range of the species.

#### *Tellina (Eurytellina) panamanensis* Li.

*Tellina panamanensis* Li, *Bull. Geol. Soc. China*, Vol. 9, No. 3, October, 1930, p. 262, pl. 5, fig. 32. "Brought up by marine dredge from depths varying from 10. ft. to 40. ft. in the mud at the mouth of the Rio Grande near La Boca about one mile from the mainland in Panama Bay." "Horizon: Gatun formation."—Pilsbry, *Nautilus*, Vol. 58, No. 4, April, 1945, p. 145.

*Tellina (Eurytellina) panamanensis* Li, Pilsbry, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 83, November 13, 1931, p. 436, pl. 41, figs. 4, 5, 6. A Recent shell from Panama Bay.

*Tellina liana* Hertlein & Strong, *Nautilus*, Vol. 58, No. 3, January, 1945, p. 105. "Dredged off Meanguera Island, El Salvador, in the Gulf of Fonseca, in 16 fathoms."

*Type Locality*: Mouth of Rio Grande near La Boca about 1 mile from the mainland in Panama Bay, 10-40 feet, mud.

*Range*: Tenacatita Bay, Mexico, to the Bay of Panama.

*Collecting Stations*: Mexico: Tenacatita Bay (183-D-2), 30 fathoms, muddy sand; Port Guatulco (195-D-20, 21), 18-23 fathoms, mud; Tangola-Tangola Bay (196-D-17, 18), 23-30 fathoms, mud; El Salvador: Meanguera Island, Gulf of Fonseca (199-D-1), 16 fathoms, sand, mud, crushed shell.

*Description*: Shell similar in general outline to that of *Tellina laceridens* but more steeply truncated posteriorly; the left valve is more convex and overlaps the right along

the right anterior dorsal margin; a faint broad median concavity is present toward the ventral margin of the valves; color grayish-white covered by a thin ochraceous periostracum; the concentric sculpture consists of ridges (about 1 per millimeter) which on their upper portions are flat, on the lower sloping, crossed by fine weak radial striae; on the right valve a ridge or angulation occurs from beak to base posteriorly; on the posterior dorsal area the concentric sculpture is usually sinuated, sometimes bent back, due to the presence (although sometimes absent) of a median radial convexity; hinge with two cardinals and two laterals in each valve, the right anterior cardinal grooved, the posterior with about four sulcations, the anterior lateral close to the cardinals, the posterior lateral distant about one-third the length of the posterior dorsal margin; left valve with the anterior cardinal grooved, the posterior cardinal a thin lamella, laterals weak; pallial sinus highest beneath the beaks, descending to a broadly rounded or blunt point which is well separated from and lower than but posterior to the anterior adductor impression, along the base confluent with the pallial line. Dimensions of a typical specimen: length, 44.9; height, 29 mm.; convexity (both valves together), 13 mm.; pallial sinus extends anteriorly 34.5 mm. from posterior end of shell.

The shell of this species differs from that of *Tellina laceridens* in the more steeply sloping posterior dorsal margin, more convex valves, much coarser sculpture which, especially on the left valve, is sinuated on the posterior dorsal area, in the smaller smooth area at the beaks, less crenated cardinal teeth and in that the pallial sinus does not touch the anterior adductor impression but is separated from it by a considerable distance. The much coarser sculpture and the much greater distance between the pallial sinus and the anterior adductor impression are features separating it from *T. eburnea*.

*Distribution*: Specimens of *Tellina panamanensis* were dredged by the expedition from Tenacatita Bay, Mexico, to Meanguera Island, El Salvador, in 16-30 fathoms. This record of Tenacatita Bay, Mexico, is an extension north of the known range of the species. It also has been recorded as occurring in the Pliocene of Ecuador.

#### *Tellina (Eurytellina) planulata* Sowerby.

Plate I, Fig. 22.

*Tellina planulata* Sowerby, *Conch. Icon.*, Vol. 17, *Tellina*, June, 1867, species 186, pl. 33, fig. 186. "Hab. —?"

*Type Locality*: Gulf of Dulce, Costa Rica (here designated as type locality). No locality originally cited.

*Range*: La Libertad, El Salvador, to the Gulf of Dulce, Costa Rica.

*Collecting Stations*: El Salvador: La Libertad (198-D-2), 14 fathoms, mud; Costa

Rica: Gulf of Dulce; Golfito Bay, Gulf of Dulce.

*Description:* Shell elongate, the posterior end the longer, fairly thick, white, similar to *Tellina laceridens* in general features but longer in proportion to the height; sometimes with a low broad medial depression toward the ventral margin; posterior dorsal area set off by a slight angulation; sculpture consisting of very fine, shallow, somewhat irregularly spaced concentric grooves; right valve with two grooved cardinals, anterior lateral close to the cardinals but the posterior lateral distant about half the length of the posterior dorsal margin; left valve with a grooved anterior cardinal and posterior to this two small, thin, laminae, laterals small; the pallial sinus projects anteriorly and barely touches the base of the anterior adductor impression, along the base it is confluent with the pallial line.

A left valve measures: length, 59.2 mm.; height, 33 mm.; convexity (one valve), 6 mm.

Several single valves from the Gulf of Dulce agree so closely with Sowerby's description and figure of *Tellina planulata* that we have assigned our specimens to that species. This species was originally described without information as to the locality from which it came. Paetel<sup>32</sup> cited the species as occurring at "Sitka," Alaska, but we have not seen any specimens from that region which appear to be referable to it. Other than Paetel's record the species apparently has not been recognized as occurring elsewhere. We therefore have designated the Gulf of Dulce as type locality. Sowerby stated that it is "A much larger and flatter shell than *Tellina eburnea*, with closer grooves and no transverse ridges on the dorsal margin of the overlapping valve." Those differences are true with regard to the present specimens. The pallial sinus in the present specimens touches the anterior adductor impression whereas in *T. eburnea* it is separated from the corresponding impression by a narrow space. Sowerby stated with regard to the posterior end: "terminal margin notched." This latter feature is not pronounced on our specimens but they are not perfectly preserved.

The present specimens closely resemble *Tellina ecuadoriana* Pilsbry & Olsson<sup>32a</sup> described from Ecuador. A single valve of that species collected by the senior author at Corinto, Nicaragua, is in the collections of the California Academy of Sciences.

Compared to *Tellina ecuadoriana* the posterior dorsal margin of *T. planulata* slopes a little more steeply and the posterior area, especially on the right valve, appears to be a little narrower than the corresponding

area on the species described by Pilsbry & Olsson. The shell of the present species is white rather than rose red with whitish zones. Furthermore the pallial sinus in the present specimens touches the anterior adductor impression while in *T. ecuadoriana* the two are separated by a narrow space.

*Distribution:* Several valves of this species were collected by the expedition on the beach in the Gulf of Dulce, Costa Rica. One small specimen with both valves was dredged in 14 fathoms off La Libertad, El Salvador.

#### *Tellina (Eurytellina) prora* Hanley.

*Tellina prora* Hanley, *Proc. Zool. Soc. London*, September, 1844, p. 61. "Hab Porto St. Elena, West Columbia; sandy mud, six fathoms; and Salango, West Columbia, sandy mud, nine fathoms."—Hanley, *Thes. Conch.*, Vol. 1, 1846, p. 243, pl. 60, fig. 152. Original localities cited. — Sowerby, *Conch. Icon.*, Vol. 17, *Tellina*, 1866, species 90, pl. 18, fig. 90. Original localities cited. — Salisbury, *Proc. Malacol. Soc. London*, Vol. 21, Pt. 2, July, 1934, p. 86. "The shell ranges through the south of the Panamic and north of the Peruvian areas."

*Tellina cibaoica* Maury, Li, *Bull. Geol. Soc. China*, Vol. 9, No. 3, 1930, p. 261, pl. 4, fig. 30. Dredged in Panama Bay. Referred to the Gatun formation, Miocene. According to Pilsbry (*Proc. Acad. Nat. Sci. Philadelphia*, Vol. 83, 1931, p. 430), Li's record was based upon "A left valve of *Tellina prora* Hanley"...

Not *Tellina cibaoica* Maury, 1917. Santo Domingo, Miocene.

*Type Locality:* Santa Elena, Ecuador, in 6 fathoms, sandy mud (here designated as type locality). Salango, Ecuador, in 9 fathoms, sandy mud, also originally cited by Hanley.

*Range:* Mazatlan, Mexico, to the Bay of Guayaquil, Ecuador.

*Collecting Stations:* Mexico: Tangola-Tangola Bay (196-D-17), 23 fathoms, mud; Guatemala: 7 miles west of Champerico (197-D-1, 2), 14 fathoms, mud; El Salvador: La Libertad (198-D-2), 14 fathoms, mud; Meanguera Island, Gulf of Fonseca (199-D-1), 16 fathoms, sand, mud, crushed shell; La Union, Gulf of Fonseca (199-D-15), 6 fathoms, mud; Nicaragua: Potosi and Mompenny Point; Costa Rica: Port Parker (203-D-3), 12 fathoms, shelly mud; Panama: Bahía Honda (222-D-5), 11 fathoms, mud, shells, leaves.

*Description:* Shell ovately trigonal, smooth, polished, a posterior area set off by an angulation, colored rose pink with whitish concentric bands; sculpture of very fine closely spaced (about 10 per millimeter) incised concentric striae; hinge with two grooved cardinals in each valve, the left posterior one very narrow, two laterals in each valve, those in the left valve much the smaller; pallial sinus highest in middle part of shell, usually separated from the anterior adductor impression by about a millimeter

<sup>32</sup> Paetel, Fr., *Cat. Conchyl.*—Samml., Vierte Neubearbeitung (Berlin: Verlag von Gebrüder Paetel), Abt. 3, 1890, p. 49.

<sup>32a</sup> *Tellina (Eurytellina) ecuadoriana* Pilsbry & Olsson, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 93, September 9, 1941, p. 67, pl. 15, figs. 6, 7, 8. Canoa formation, Punta Blanca, Ecuador, Pliocene. Also Recent, Santa Elena, Ecuador (type), also at Canoa and Callo, the port of Jipijapa.

but sometimes almost, but not quite, touching, the end blunt and almost in line vertically below the posterior side of the adductor impression, along the base confluent with the pallial line.

A large specimen dredged off Guatemala measures approximately: length, 46.4 mm.; height, 17.5 mm.; convexity (both valves together), 12 mm.

The shell of this species differs from that of *Tellina rubescens* Hanley in that the posterior slope is more gently inclined, the concentric incised striae are much finer and much more closely spaced and the pallial sinus does not touch the anterior adductor impression. The very much finer and more closely spaced concentric sculpture easily serves to separate the species from *T. simulans* C. B. Adams.

The record of *Tellina prora* from the Cape Verde Islands in the Atlantic cited by Rochebrune<sup>33</sup> can be referred to some other species. *Tellina (Eurytellina) trinitatis* Tomlin<sup>34</sup>, described from Colon Harbor on the east side of the isthmus of Panama, is said to be similar to *T. prora*.

**Distribution:** This species was collected by the expedition off western Guatemala, El Salvador and Nicaragua, in 6-14 fathoms on a muddy bottom. It also has been recorded as occurring in the Pliocene of Ecuador.

#### *Tellina (Eurytellina) regia* Hanley.

*Tellina regia* Hanley, *Proc. Zool. Soc. London*, September, 1844, p. 61. "Hab. Real Lleos, Central America; in coarse sandy mud, seven fathoms." —Hanley, *Thes. Conch.*, Vol. 1, 1846, p. 240, pl. 60, fig. 140. Original locality cited.

**Type locality:** Real Lleos [near Corinto], Nicaragua, in 7 fathoms, coarse, sandy mud.

**Range:** Known only from the type locality and vicinity.

**Collecting Station:** Nicaragua: Corinto, beach drift.

**Description:** Oblong, thin, rather compressed, almost inequivalve, subequilateral; extremely glossy, both externally and internally of a deep subpellucid purplish crimson; the surface marked with distant concentric grooves, which posteriorly become obsolete in one or both of the valves; the ventral edge nearly straight, subretuse in the middle; anterior side slightly shorter, its extremity obtusely rounded; posterior extremity almost biangulated; dorsal moderately and almost equally sloping on either side of the beaks, nearly straight posteriorly; umbonal ridge and flexure nearly obsolete; the ligament rather prominent; teeth as in *punicea*. (Hanley, *Thes. Conch.*, 1846).

<sup>33</sup> *Peronaeoderma prora* Hanley, Rochebrune. *Nouv. Arch. Mus. d'Hist. Nat.* (Paris), Ser. 2, Vol. 4, 1881, p. 258. "Hab.—Rade de Saint-Vincent." Cape Verde Islands.

<sup>34</sup> *Eurytellina trinitatis* Tomlin, *Jour. Conch.*, Vol. 18, No. 11, July, 1929, p. 310. "Hab. Colon Harbour, not uncommon, dead but very fresh in 5 f."

A left valve from Corinto, Nicaragua, measures approximately: length, 17 mm.; height, 10 mm.; convexity (one valve), 1.8 mm.

The outline as well as the other features of the present specimen are similar to those described for *Tellina regia* which came from the same general vicinity. The concentric ornamentation of the shell is like that described for *T. regia*, namely, distant concentric grooves which become obsolete posteriorly.

*Tellina regia* differs from *Tellina rubescens* in that the concentric grooves become obsolete posteriorly, the dorsal margins do not slope so steeply, and the pallial sinus does not touch the anterior adductor impression. It differs from *Tellina princeps* in lacking radial striae.

**Distribution:** Only one valve referred to this species was found in the beach drift at Corinto, Nicaragua.

#### *Tellina (Eurytellina) rubescens* Hanley.

*Tellina rubescens* Hanley, *Proc. Zool. Soc. London*, September, 1844, p. 60. "Hab. Panama and Tumbez; in sandy mud."—Hanley, *Thes. Conch.*, Vol. 1, 1846, p. 242, pl. 60, fig. 153. Tumbez, and Panama (Cuming). —Sowerby, *Conch. Icon.*, Vol. 17, *Tellina*, 1866, species 93, pl. 18, fig. 93. "Hab. Tumbez and Panama, Peru."

**Type Locality:** Panama in sandy mud (here designated as type locality). Tumbez, Peru, in sandy mud, also originally cited.

**Range:** Tenacatita Bay, Mexico, to Tumbez, Peru.

**Collecting Stations:** Mexico: Tenacatita Bay; El Salvador: La Union, Gulf of Fonseca (199-D-12), 5 fathoms, mud; Nicaragua: Potosi and Monypenny Point, Gulf of Fonseca; Costa Rica: Port Parker.

**Description:** Shell trigonally ovate, smooth, polished, colored exteriorly and interiorly by light and darker concentric bands of rose pink; posterior dorsal margin sloping steeply, the area set off by an angulation; sculpture consists of fine concentric grooves (about 2 per millimeter) and between these finer concentric striae, the whole crossed by very fine submicroscopic radial striae; hinge with two cardinals and two laterals in each valve, the right anterior cardinal usually grooved, the posterior bifid, left anterior grooved, the posterior one thin, laterals in left valve weak; anterior end of pallial sinus confluent with the lower posterior margin of the anterior adductor impression from a point just above the base to approximately the middle of the base of the impression, confluent with the pallial line below.

A large specimen from the Gulf of Fonseca measures: length, 43 mm.; height, 37 mm.; convexity (both valves together), 9.3 mm.

The shell of *Tellina rubescens* differs from that of *T. prora* Hanley in that it is higher

in proportion to the length, the posterior dorsal margin slopes more steeply, the incised concentric sculpture is more widely spaced and the pallial sinus is confluent with a portion of the posterior side of the anterior adductor impression. These same characters of proportionate height to length and that of the pallial sinus serve to separate *T. rubescens* from *T. simulans* C. B. Adams, a species in which the concentric sculpture is much more strongly developed.

*Distribution:* This species was taken by the expedition along the west coast of Mexico and Central America but at no place abundantly. It also has been recorded by Arnold, 1903, as occurring in the upper Pleistocene of San Pedro, California. Some of the records of the occurrence of this species at San Ignacio Lagoon and at Magdalena Bay, Lower California, are referable to *T. simulans*.

***Tellina (Eurytellina) simulans* C. B. Adams.**

*Tellina simulans* C. B. Adams, *Ann. Lycceum Nat. Hist. New York*, Vol. 5, July, 1852, pp. 508, 546 (separate pp. 284, 322). "Panama." Also cited from Xipixapi, Ecuador, in sandy mud at 10 fathoms. —Römer, *Neues Syst. Conchyl.-Cab. Martini-Chemnitz*, Bd. 10, Abt. 4, *Tellina*, 1872, p. 99, pl. 25, figs. 4, 5.

*Tellina punicea* Born, Carpenter, *Cat. Mazatlan Shells*, August, 1855, p. 35. Mazatlan, Mexico. Also earlier records cited. —Sowerby, *Conch. Icon.*, Vol. 17, *Tellina*, 1866, species 53, pl. 12, fig. 53. "Hab. Xipixapi, W. Columbia; in sandy mud, ten fathoms; H. Cuming."

Not *Tellina punicea* Born, *Test. Mus. Caes. Vind.*, 1780, p. 33, pl. 2, fig. 8. "Patria ignota." [Now believed to be a Caribbean species. See Gardner, *U. S. Geol. Surv., Prof. Paper 142-E*, 1928, p. 193].

*Tellina costaricana* Olsson, Li, *Bull. Geol. Soc. China*, Vol. 9, No. 3, October, 1930 p. 262, pl. 4, fig. 31. Dredged in Panama Bay at mouth of Rio Grande River in 10-40 ft. "Occurrence: Gatun Stage, Banana River, Costa Rica." "Horizon: Gatun formation." This record is based upon "Two valves of *Tellina simulans* C. B. Ad." Panama, Recent, according to Pilsbry (*Proc. Acad. Nat. Sci. Philadelphia*, Vol. 83, 1931, p. 430).

*Type Locality:* Panama.

*Range:* Scammon Lagoon, Lower California, to the Gulf of California and south to Tumbez, Peru.

*Collecting Stations:* Mexico: Santa Inez Bay, Gulf of California; Tenacatita Bay; 17 miles SE. × E. of Acapulco (189-D-3), 13 fathoms, mud; Nicaragua: Corinto (200-D-11, 19), 8-13 fathoms, sand, mangrove leaves; Costa Rica: Culebra Bay; 1 mile south of Golfito.

*Description:* Shell elongately oval, posterior dorsal margin obliquely sloping, the end obliquely truncated and slightly bent to the right, rose pink with whitish concentric bands; posterior area set off by an angula-

tion anterior to which is a shallow broad depressed area on the right valve, the posterior area bears a narrow, shallow, radial furrow which is especially noticeable on the left valve; sculpture of regular, deep, concentric grooves (about 2 or 3 per millimeter) and very fine submicroscopic radial striae; hinge with anterior laterals close to the cardinals, posterior laterals distant, weaker in left valve; the pallial sinus does not quite touch the anterior adductor impression, the end is blunt and almost in line vertically below the posterior margin of the adductor impression, along the base it is confluent with the pallial line.

A large specimen of this species in the Henry Hemphill Collection of the California Academy of Sciences from Magdalena Bay, Lower California, measures: length, 48.8 mm.; height, 29 mm.; convexity (both valves together), 11 mm.

This species, in some instances, has been cited in the earlier literature under the names of *Tellina punicea* Born and *T. rubescens* Hanley.

The shell of this species differs from that of *T. rubescens* in the greater length in proportion to the height, in the much deeper, stronger and more widely spaced concentric sculpture and in that the pallial sinus does not touch the anterior adductor impression.

*Tellina simulans* is similar to *T. angulosa* Gmelin (*T. punicea* of some authors), an east American species; in fact Carpenter and others considered the two to be identical. According to Adams *T. simulans* differs from the east American species in that "its furrows are deeper and are continued over the flexure, without change of depth; the interspaces are less flattened, and the lateral teeth are nearly obsolete." A comparison of specimens of *T. simulans* with a series of *T. angulosa* collected by F. M. Anderson at Cartagena Bay, Colombia, shows differences between the two. The west coast shells are more pointed posteriorly, there is a low depressed area anterior to the posterior angulation on the right valve, and the concentric grooves along the posterior dorsal margin bend more acutely upward than on the east coast shells.

*Tellina princeps* Hanley, described from Tumbez, Peru, is a distinct species possessing a large, red, subequilateral shell with a gently sloping posterior dorsal margin and the concentric sculpture is crossed by strong radial striae.

*Distribution:* This species was taken by the expeditions although not abundantly, from Santa Inez Bay, in the Gulf of California to Culebra Bay, Costa Rica. It ranges south to Peru. It also is known to occur in the Pleistocene at San Ignacio Lagoon and at Magdalena Bay, Lower California.

Subgenus ***Tellinidella*** Hertlein & Strong, subgen. nov.

Type: *Tellinides purpureus* Broderip & Sowerby.

Shell elongate, compressed, very thin,

with a strong posterior angulation; ornamented with fine concentric granulated ridges which are crossed by impressed radial striae forming reticulate sculpture; hinge as in *Eurytellina* but with a very small right anterior lateral and a weak posterior lateral, in the left valve the laterals are faint or obsolete.

The general outline and hinge of this new subgenus are similar to those of *Eurytellina*. The weak distant right posterior lateral and the very thin shell, which is ornamented by both concentric and radial sculpture, are characteristic features of the type species of *Tellinidella*.

Dall, 1900, placed *Tellina purpureus* Broderip & Sowerby in the subgenus *Tellinides* Lamarck<sup>35</sup>. That name was proposed by Lamarck for a genus of *Tellina* with the sole species *T. timorensis* as type. No illustrations accompanied that work. Dubois<sup>36</sup> discussed Lamarck's genera but he did not illustrate the type species of *Tellinides*. Neither did Delessert, 1841, include *T. timorensis* among his illustrations of the types of Lamarck's shells. Hanley<sup>37</sup> later gave illustrations showing two views of the exterior of right valves of *T. timorensis*. Philippi<sup>38</sup> also illustrated a species under that name and gave views of both the exterior and interior of the right valve and an umbonal view of both valves. His illustrations agree well with Lamarck's description of the species. Bertin<sup>39</sup>, 1878, stated that 4 type specimens of Lamarck's species were present in the collections of the Museum of Natural History in Paris. In his synonymy of the species he included references to Hanley's figures 158 and 172, Philippi's figure 3, as well as illustrations of Römer's, 1812, plate 34, figures 4-6.

It appears then that these figures may be considered to represent authentic specimens of *T. timorensis*. The right valve has two diverging cardinal teeth, a close anterior lateral and a weak close posterior lateral. The left valve is said to lack laterals. The valves are not flexed posteriorly and the posterior umbonal fold or ridge is broadly rounded and nearly obsolete.

The hinge of the right valve of *Tellina purpureus* has two diverging cardinal teeth, the posterior one strong and bifid or grooved. The posterior lateral is distant from the cardinals. A small lamina sometimes occurs near the margin above the small anterior lateral and sometimes the margin is some-

what projecting just over the posterior lateral. Furthermore the shell has a strong, angular posterior umbonal fold exteriorly and the concentric sculpture on the shell is decussated by radial grooves giving it a finely granulose character. These characters on the present shell are so different from those of *T. timorensis* that we propose a new subgenus *Tellinidella* with *Tellina purpureus* Broderip & Sowerby as type.

*Tellina (Tellinidella) purpureus* Broderip & Sowerby.

*Tellinides purpureus* Broderip & Sowerby, *Zool. Jour.*, Vol. 4, No. 15, January, 1829, p. 363. "Hab. ad littora Oceani Pacifici." — Sowerby, *Zool. Beechey's Voy.*, 1839, p. 153, pl. 42, fig. 2. "Inhabits the sandy shores of the Pacific Ocean."

*Tellina (Tellinides) purpurascens* Broderip & Sowerby, Hanley, *Thes. Conch.*, Vol. 1, 1846, p. 295, pl. 62, fig. 194. "Real Leijos [Llejos] Central America (Cuming)."

Not *Tellina purpurascens* Gmelin, *Linn. Syst. Nat.*, ed 13, Vol. 1, Pt. 6, 1790, p. 3237. Habitat not cited. Ref. to Lister, *Conch.*, pl. 391, fig. 230. Also "B" and "Y," ref. to Gualtieri, *Test.*, pl. 77, figs. L? and M? *Tellina purpurata* is described on p. 3243. Hab. not cited. Ref. to Gualtieri, *Test.*, pl. 77, fig. L.

*Tellina broderipii* "Desh. ms. (teste Cum.)" Carpenter, *Cat. Mazatlan Shells*, August, 1855, p. 32. "Mazatlan."

*Tellina purpurascens* Broderip & Sowerby, Sowerby, *Conch. Icon.*, Vol. 17, *Tellina*, 1867, species 103, pl. 20, fig. 103. Same locality as given by Hanley.

*Type Locality*: Real Llejos [near Corinto], Nicaragua (here designated as type locality). Shores of Pacific Ocean originally cited.

*Range*: Altata, Mexico, in the Gulf of California, to Colombia.

*Collecting Stations*: Mexico: Tenacatita Bay; Sihuatanejo Bay; Nicaragua: Corinto, beach drift.

*Description*: Shell ovately oblong, subequilateral, thin, compressed, colored a beautiful purplish-rose with the dorsal margins white; sculpture of close, decussating concentric and radial striae; posteriorly a low radial furrow is present near the dorsal margin which anteriorly is bounded by a low carina; right valve with two cardinals, the posterior one the larger and bifid, and a very close, small, anterior lateral above which there is sometimes a small lamina near the margin, and a posterior lateral distant nearly half the length of the posterior dorsal margin, above this tooth the margin is sometimes somewhat projecting; left valve with laterals obsolete; the end of the pallial sinus is considerably lower than and posterior to the anterior adductor impression, the base is confluent with the pallial line.

A right valve from Tenacatita Bay, Mexico, measures: length, 49.4 mm.; height, 26.4 mm.; convexity (one valve), 4 mm.; pallial

<sup>35</sup> *Tellinides* Lamarck, *Hist. Nat. Anim. s. Vert.*, Vol. 5, July, 1818, p. 535. Type, *Tellina timorensis*, p. 536. "Habite l'océan des grandes Indes ou austral, près de Timor."

<sup>36</sup> Dubois, C., *Epit. Lamarck's Arrang. Test.*, 1824, p. 58.

<sup>37</sup> *Tellina (Tellinides) timorensis* Lamarck, Hanley, *Thes. Conch.*, Vol. 1, 1846, p. 292, pl. 61, figs. 158 and 172. Isle of Negros, Philippines, etc.

<sup>38</sup> *Tellina timorensis (Tellinides)* Lamarck, Philippi, *Abbild. u. Beschreib. Conchyl.*, Bd. 2, Heft 4, *Tellina*, August, 1846, p. 90 (22), pl. 4, fig. 3. Timor, Philippine Islands, Sumatra, etc.

<sup>39</sup> Bertin, V., *Nouv. Arch. Mus. Hist. Nat. (Paris)*, Ser. 2, Vol. 1, 1878, p. 283. [He mentioned that *T. timorensis* is represented in the collection by specimens including "par 4 individus ordinaires de Timor (types de Lamarck)."]

sinus extends forward 36 mm. from the posterior end of the valve. The species attains a greater size than this specimen.

The original name for this species, given by Broderip & Sowerby in 1829, was *Tellinides purpureus*. Dall<sup>40</sup> apparently considered that combination of names preoccupied due to the fact that *Tellinides* is now considered to be a subgenus of *Tellina*, also the fact that Dillwyn<sup>41</sup> had referred to a *Tellina purpurea*.

However, Dillwyn in a footnote, in remarking on certain of Gmelin's species, referred to Gmelin, page 3243, and on that page of Gmelin's work the species was cited as *Tellina purpurata*. It thus appears that Dillwyn's spelling of "purpurea" was a misprint and not a renaming of Gmelin's species. If this view is accepted, there then appears to be no valid reason for rejecting the original name given the west American species by Broderip & Sowerby. The name *Tellina purpurascens* which Hanley used for this species is preoccupied by *Tellina purpurascens* Gmelin, 1790. The name *Tellina broderipii* attributed to Deshayes was applied to the west American form by Carpenter.

The shell of this species bears a resemblance to that of *Tellina princeps* Hanley<sup>42</sup> but is thinner, narrower, the posterior dorsal margin slopes more gently, the radial striae are stronger and the right posterior lateral is weaker.

*Distribution*: A few specimens of this species, nearly all right valves, were taken by the expedition along the coast of west Mexico and in the beach drift at Corinto, Nicaragua.

Subgenus *Macaliopsis* Cossmann.

#### KEY TO THE SPECIES OF *Macaliopsis*.

- A. Beaks directed strongly anteriorly; concentric lamellae about 1 per mm. .... *lyra*  
 B. Beaks directed only slightly anteriorly; concentric lamellae, lower, fewer, usually about 3 per mm. .... *lyrica*

*Tellina (Macaliopsis) lyra* Hanley.

*Tellina lyra* Hanley, *Proc. Zool. Soc. London*, September, 1844, p. 68. "Hab. Tumbes, Peru."—Hanley, *Thes. Conch.*, Vol. 1, 1846, p. 271, pl. 62, fig. 187. Tumbes, Peru.—Sowerby, *Conch. Icon.*, Vol. 17, *Tellina*, September, 1867, species 203, pl. 36, fig. 203. Tumbes, Peru.

*Type Locality*: Tumbes, Peru.

*Range*: Lower California to Tumbes, Peru (Dall).

<sup>40</sup> Dall, W. H., *Proc. U. S. Nat. Mus.*, Vol. 23, 1900, p. 302.  
<sup>41</sup> Dillwyn, L. W., *Descript. Cat. Rec. Shells*, Vol. 1, 1817, p. 72, footnote.

<sup>42</sup> *Tellina princeps* Hanley, *Proc. Zool. Soc. London*, September, 1844, p. 62. "Hab. Tumbes, Peru; soft sandy mud, five fathoms."—Hanley, *Thes. Conch.*, Vol. 1, 1846, p. 238, pl. 63, fig. 206. "Tumbes, Peru; (Cuming)." —Sowerby, *Conch. Icon.*, Vol. 17, *Tellina*, 1867, species 135, pl. 25, fig. 135. Tumbes, Peru.—Salisbury, *Proc. Malacol. Soc. London*, Vol. 21, Pt. 2, 1934, p. 91, pl. 9, fig. 4. [Illustration of type].

*Collecting Stations*: Guatemala: 7 miles west of Champerico (197-D-1, 2), 14 fathoms, mud; El Salvador: La Libertad (198-D-2), 14 fathoms, mud,

*Description*: Shell elliptic, thin, compressed, slightly longer anteriorly, dull white exteriorly and interiorly, beaks curved forward; anterior dorsal margin excavated below the beaks, anterior end rounded, ventral margin broadly rounded, the posterior dorsal margin nearly straight or very broadly curved and sloping posteriorly directly from the beaks; a deep smooth lunule and escutcheon present; the sculpture consists of regular, thin, sharp, raised, concentric ribs which are separated by much wider interspaces (about 1 mm. wide) but which become narrower toward the ventral margin, a narrow posterior area is set off by an umbonal carina; hinge of right valve with a strong grooved triangular posterior and a thin anterior cardinal near the margin, a strong anterior and posterior lateral present; left valve with a grooved anterior and a thin posterior cardinal tooth and lateral triangular projections of the nymph; the pallial sinus extends for about three-fifths the length of the shell, sub-trigonal above and highest just posterior to a line vertical with the beaks, then descending and narrowly elliptically rounded anteriorly then bending posteriorly and for about two-thirds of its length confluent with the pallial line.

The largest specimen in the present collection, a left valve, measures: length, 50 mm. height, 35 mm.; convexity (one valve), 6 mm.; pallial sinus extends anteriorly 29 mm. from the posterior end of the valve.

The strongly anteriorly directed beaks, more convex anterior dorsal margin which is excavated beneath the beaks, higher and more widely spaced concentric sculpture and shorter and more trigonal pallial sinus are features separating this species from *Tellina lyrica* Pilsbry & Lowe.

*Tellina protolyra* Anderson<sup>43</sup> is a similar species but it is smaller, less elongate, more inflated and the posterior dorsal margin is straighter than in the present species.

*Tellina (Macaliopsis) aequizonata* Pilsbry & Olsson<sup>44</sup>, described from the Pliocene of Ecuador, is said to be much larger, more strongly sculptured and more circular in outline than *T. lyra*.

*Distribution*: A few specimens, mostly single valves, of this interesting species were dredged in 14 fathoms off Guatemala and El Salvador on a mud bottom.

*Tellina (Macaliopsis) lyrica* Pilsbry & Lowe.

*Tellina (Macaliopsis) lyrica* Pilsbry & Lowe, *Proc. Acad. Nat. Sci. Philadelphia*,

<sup>43</sup> *Tellina protolyra* F. M. Anderson, *Proc. Calif. Acad. Sci.*, Ser. 4, Vol. 18, No. 4, March 29, 1929, p. 174, pl. 21, figs. 2, 3. "From Loc. 267-B, C. A. S., horizon M-N, of the Tubera group, Colombia; Miocene."

<sup>44</sup> *Tellina (Macaliopsis) aequizonata* Pilsbry & Olsson, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 93, September 9, 1941, p. 68, pl. 14, fig. 7. "Jama formation, Puerto Jama." Ecuador, Pliocene.

Vol. 84, May 21, 1932, p. 94, pl. 10, figs. 4, 4a. "Guaymas in about 20 fathoms."

*Type Locality*: Guaymas, Mexico, in about 20 fathoms.

*Range*: Gulf of California to the Gulf of Chiriqui, Panama.

*Collecting Stations*: Mexico: Santa Inez Bay in the Gulf of California (143-D-3, 4), 25-35 fathoms, mud, crushed shell, sand; El Salvador: La Libertad (198-D-2), 14 fathoms, mud; Panama: Gulf of Chiriqui (221-D-1-5), 35-40 fathoms, sandy mud.

*Description*: Shell transversely oval, beaks turned slightly forward, anterior end broadly rounded, posterior dorsal margin broadly curved and rather steeply sloping; a slight angulation sets off a narrow posterior area; lunule smooth, slightly sunken; escutcheon deeply sunken and bounded by a high keel; sculpture consists of fine, close, concentric ribs (about 3 per millimeter) which are narrower than the interspaces; right valve with a simple anterior and grooved posterior cardinal and well-developed laterals, the posterior one more distant; left valve with a grooved anterior and thin posterior lamella-like cardinal, anterior lateral weak, posterior lateral represented by a triangular projection of the margin; the pallial sinus is highest posteriorly, rounded at the end and extends forward about four-fifths the length of the shell and is separated from the anterior adductor impression by a considerable distance, for over half its length along the base it is confluent with the pallial line.

A large right valve from Santa Inez Bay in the Gulf of California measures: length, 40.2 mm.; height, 29.6 mm.; convexity (one valve), 6.5 mm.; pallial sinus extends forward 31 mm. from the posterior end of the valve.

The exterior of fresh valves shows a brilliant iridescence of spectral colors due to the fine growth lines between the concentric ridges acting as a diffraction grating.

The specimens in the present collection show the differences pointed out by Pilsbry & Lowe between this species and *Tellina lyra*. They stated: "Related to *T. lyra* Hanley, but relatively longer, with the beaks less, only very slightly, turned forward, the dorsal margin in front of them less convex, and the concavity running to the posterior basal extremity wider." The concentric ribbing on *T. lyricea* is much finer and more closely spaced than that on *T. lyra*.

*Distribution*: This species was dredged in Santa Inez Bay in the Gulf of California, in 25-35 fathoms, off La Libertad, El Salvador, in 14 fathoms and in the Gulf of Chiriqui, Panama, in 35-40 fathoms, in mud and sandy mud. It also has been recorded as occurring in the Pliocene of Ecuador.

#### Subgenus *Merisca* Dall.

#### KEY TO THE SPECIES OF *Merisca*.

A. Interspaces with minute radial striae

a. Rostrum attenuated posteriorly; concentric lamellae about 1 per mm.

*crystallina*

aa. Rostrum not attenuated posteriorly; concentric lamellae about 5 per mm.

*reclusa*

B. Interspaces without radial striae

*proclivis*

#### *Tellina (Merisca) crystallina* Spengler.

*Tellina crystallina* Chemnitz, Neues Syst. Conchyl.-Cab. von Martini-Chemnitz, Bd. 11, 1795, p. 210, pl. 199, figs. 1947, 1948. "Es ist diese Muschel an der Nordamerikanischen Küste bey Newport auf Rhode-Island gefunden worden." (Spengler). —Spengler, *Skr. Nat. Selsk.* (Copenhagen), Vol. 4, No. 2, 1798, p. 113. "Fra Newport Long-Island." Ref. to Chemnitz, pl. 199, figs. 1947, 1948.—Wood, *General Conch.*, 1815, p. 149. [No locality cited]. Ref. to Chemnitz, pl. 199, figs. 1947, 1948.—Hanley, *Thes. Conch.*, Vol. 1, 1846, p. 270, pl. 57, fig. 43. "St. Elena, West Columbia."—Olsson, *Bull. Amer. Paleo.*, Vol. 9, No. 39, 1922, p. 421 (249), pl. 29 (26), fig. 10. Banana River, Costa Rica. Miocene. Also Recent.

*Tellina (Merisca) crystallina* Wood, Dall, *Proc. U. S. Nat. Mus.*, Vol. 23, 1900, pp. 293, 302, 311, pl. 2, fig. 10. Sullivan's Island, South Carolina, to Cartagena, Colombia. Lower California to Panama.—M. Smith, *Panamic Mar. Shells* (Tropical Photogr. Lab., Winter Park, Florida), p. 64, fig. 834. Lower California to Guayaquil, Ecuador. Also West Indies.

*Tellina schrammi* Recluz, *Journ. de Conchyl.*, Vol. 4, December, 1853, p. 152, pl. 6, figs. 7, 8. . . "habite la rade de la Pointe-à-Pitre (Guadeloupe); elle a été draguée sur un fond vaseux au fond de cette rade."

*Type Locality*: Newport, Rhode Island.

*Range*: Scammon Lagoon, Lower California, to the Gulf of California and south to Guayaquil, Ecuador. Also Atlantic, from Charleston, South Carolina, to Cartagena Bay, Colombia.

*Collecting Stations*: Mexico: Tangola-Tangola Bay, on beach; Nicaragua: Corinto (200-D-19), 12-13 fathoms, mangrove leaves, also on beach.

*Description*: Shell rather small, roundly trigonal, posteriorly rostrate, somewhat attenuated and with a sharp flexure, thin, white; sculpture of strong, raised distant, concentric ribs separated by much wider interspaces (about 1 mm. wide) although the spacing varies with various specimens, and where the lamellae cross the flexure they are V-shaped; the interspaces contain fine concentric striae (sometimes about 8) and faint radial striae; right posterior and left anterior cardinals grooved, lateral teeth in right valve well developed, in the left obsolete or nearly so; pallial sinus high behind then descending and sometimes touching the base of the anterior adductor impression, wholly confluent with the pallial line below.

The specimens in the present collection are

small but a large valve in the collections of the California Academy of Sciences, from Mazatlan, Mexico, measures: length, 23 mm.; height, 17.4 mm.; convexity (one valve), 3.4 mm.

Chemnitz originally described and illustrated *Tellina crystallina* and cited Spengler as the authority for the locality, Newport, Rhode Island. The International Committee on Zoological Nomenclature has recently ruled against acceptance of the specific names proposed by Chemnitz. Spengler next described the species. He referred to Chemnitz's description and illustrations and gave the same locality as Chemnitz. However, the species is not known with certainty to occur north of Charleston, South Carolina. One might venture the opinion that since Spengler was a citizen of Denmark, the type specimens secured by him originally might have come from the Danish West Indies.

Salisbury<sup>45</sup> recently stated that the east and west American shells referred to this species should be considered as separate species. So far as we have been able to determine, there is no reason to differ from Dall's<sup>46</sup> conclusion that "The specimens from the two oceans are absolutely similar, and differ no more than individuals from either sea among themselves." *Tellina schrammi* Recluz, described from the island of Guadeloupe in the West Indies, appears to be identical with *T. crystallina*.

*Tellina errati* Pilsbry & Johnson<sup>47</sup>, described from the Miocene of Santo Domingo, is identical or a very similar form. Maury,<sup>48</sup> 1917, stated that fossils from Santo Domingo were identical with Recent shells found on the beach on that island.

*Tellina (Merisca) sancti-dominici* Maury,<sup>49</sup> also described from the Miocene of Santo Domingo, is a similar species. *Tellina martensi* Lynge,<sup>50</sup> described from the East Indies, was compared to *T. crystallina*, but the west American species is longer with a more rostrate form.

**Distribution:** A few specimens of this species were collected by the expedition on the beach at Tangola-Tangola, Mexico, and others were dredged in 12-13 fathoms at Corinto, Nicaragua. It also occurs from Miocene to Recent in the Caribbean region and has been recorded as occurring in the Plio-

cene of Ecuador and Pleistocene of Magdalena Bay, Lower California.

***Tellina (Merisca) proclivis* Hertlein & Strong, sp. nov.**

Plate I, Figs. 6, 7, 14.

*Tellina declivis* Sowerby, *Conch. Icon.*, Vol. 17, *Tellina*, March, 1868, species 261, pl. 44, fig. 261. "Hab.—?"—I. S. Oldroyd, *Stanford Univ. Publ. Univ. Ser. Geol. Sci.*, Vol. 1, 1924, p. 165 (under section *Merisca*). Catalina Island, California, to Panama.—Strong & Hertlein, *Allan Hancock Pac. Exped.*, Vol. 2, No. 12, 1939, p. 184. Bahia Honda, and off Taboga Island, Panama.

Not *Tellina declivis* Conrad, *Jour. Acad. Nat. Sci. Philadelphia*, Ser. 1, Vol. 7, 1834, p. 131. "Locality, Yorktown, Va." Tertiary. [Miocene].

*Tellina (Merisca) declivis* Sowerby, Dall, *Proc. U. S. Nat. Mus.*, Vol. 23, 1900, p. 301. "Cerro Island, Lower California, to the Gulf of California."

**Type Locality:** Magdalena Bay, Lower California, Mexico.

**Range:** Cedros Island, Lower California, to Panama.

**Collecting Stations:** Mexico: 4 miles SSW. of Maldonado Point (192-D-1), 26 fathoms, mud; Port Guatulco (195-D-20), 23 fathoms, mud; Tangola-Tangola Bay (196-D-17), 23 fathoms, mud; Costa Rica: Port Parker (203-D-1, 3), 12-15 fathoms, sandy mud, crushed shell, shelly mud.

**Description:** Shell small, subtrigonal, white, beaks subcentral and elevated; anterior dorsal margin sloping, anteriorly rounded and inflated, posterior dorsal margin steeply sloping, the end pointed, wedge-shaped, subcompressed; a well-developed and sunken lunular area and long escutcheon present; right valve with a broad flexure, the left with a shallow radial depression followed by an angulation; sculpture of fine, regular, concentric lamellae, about 3 or 4 per millimeter on adult shells; hinge of right valve with two strong cardinals, the posterior one grooved, and two laterals, left valve with a strong grooved anterior and weaker posterior cardinal, the latter close to the margin, the posterior cardinal in each valve grooved, pallial sinus high in the middle then descending near to but not touching the anterior adductor impression, then bending posteriorly and for about half its length confluent with the pallial line. Dimensions of the type: length, 9 mm.; height, 7.8 mm.; convexity (both valves together), 4.8 mm.

**Holotype** (Calif. Acad. Sci. Paleo. Type Coll.), from Loc. 20299 (C.A.S.), Magdalena Bay, Lower California, Mexico; Charles R. Orcutt collector. **Paratype**, from station 196-D-17, Lat. 15°45' N., Long. 96°05'34" W., Tangola-Tangola Bay, Mexico, dredged in 23 fathoms, mud.

One of the largest valves in the present collection measures 9.3 mm. in length. A large right valve dredged about 5 miles west of Mazatlan, Mexico, by the Templeton

<sup>45</sup> Salisbury, A. E., *Proc. Malacol. Soc. London*, Vol. 21, Pt. 2, July, 1934, p. 83.

<sup>46</sup> Dall, W. H., *Proc. U. S. Nat. Mus.*, Vol. 23, 1900, p. 302.

<sup>47</sup> *Tellina (Merisca) errati* Pilsbry & Johnson, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 69, May 5, 1917, p. 201. Santo Domingo, Oligocene [Miocene].—Pilsbry, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 73, Pt. 2, 1922, p. 425, pl. 41, fig. 7. [Figure of type].

<sup>48</sup> Maury, C. J., *Bull. Amer. Paleol.*, Vol. 5, No. 29, 1917, pp. 387 (223)-388 (224), pl. 64 (38), fig. 4.

<sup>49</sup> *Tellina (Merisca) sancti-dominici* Maury, *Bull. Amer. Paleol.*, Vol. 5, No. 29, Pt. 1, April 7, 1917, p. 388 (244), pl. 64 (38), fig. 11. "Bluff 3, Cerco de Mao." Santo Domingo, Miocene.

<sup>50</sup> *Tellina (Merisca) martensi* Lynge, *Kgl. Dansk. Vidensk. Skr.*, Ser. 7, Nat. og Math., Bd. 5, 1909, p. 195, pl. 3, figs. 40-42. "South of Koh Kut, 17-20 fathoms, mud (½)." Gulf of Siam. Singapore, 2-3 fathoms, coral reef; 5/2."

Crocker Expedition of the California Academy of Sciences in 1932, measures: length, 11.4 mm.; height, 9.8 mm.; convexity (one valve, 3 mm.

The use of the combination of names, *Tellina declivis* by Conrad, 1834, makes it necessary to propose a new name which is based on a new type specimen for the west American shell described under that name by Sowerby in 1868 which is here named *Tellina proclivis*.

The shell of *Tellina proclivis* differs from that of *T. reclusa* in the more steeply sloping dorsal margins, in lacking radial sculpture, in that the pallial sinus does not touch the anterior adductor impression and along the base it is confluent with the pallial line for only about one-half its length. It differs from *T. meropsis* in the more steeply sloping dorsal margins, more pointed posterior end and in the narrower, radially depressed area posteriorly.

**Distribution:** Specimens of this species, mostly single valves, were dredged by the expedition off western Mexico and Costa Rica in 12-26 fathoms, mostly on a mud bottom. Dall<sup>51</sup> cited this species as occurring north to Catalina Island, California, but Burch<sup>52</sup> indicated that it is questionable whether it is a member of the fauna of California.

#### *Tellina (Merisca) reclusa* Dall.

*Tellina (Merisca) reclusa* Dall, *Proc. U. S. Nat. Mus.*, Vol. 23, No. 1210, November, 1900, pp. 301, 315, pl. 3, fig. 2. "Types.—No. 105513, U. S. N. M., from San Ignacio Lagoon, Lower California, Hemphill. Also off Lower California, in lat. 30° 28', by the U. S. Fish Commission, at Station 3019, in 14 fathoms, Gulf of California."

*Tellina reclusa* Dall, E. K. Jordan, *Contrib. Dept. Geol. Stanford Univ.*, Vol. 1, No. 4, 1936, p. 145. Magdalena Bay and San Ignacio Lagoon, Lower California, Pleistocene. Recent from San Ignacio Lagoon to the Gulf of California.

**Type Locality:** San Ignacio Lagoon, Lower California.

**Range:** San Ignacio Lagoon, Lower California, to the Gulf of California and south to Bahia Honda, Panama.

**Collecting Stations:** Mexico: Arena Bank, Gulf of California (136-D-18, 21, 22), 40-45 fathoms, mud; Santa Inez Bay, Gulf of California (142-D-3; 145-D-1, 3), 4-40 fathoms, sand, weed; Port Guatulco (195-D-2, 3), 3-3.5 fathoms, sand, crushed shell, Tangola-Tangola Bay (196-D-14-15), 5 fathoms, crushed shell; Nicaragua: Corinto (200-D-8, 9), 6-6.6 fathoms, mangrove leaves, also on beach.

**Description:** Shell small, moderately convex, subtrigonal, posteriorly wedge-shaped and flexed, the posterior end keeled dorsally;

sculpture of fine, close (about 5 per mm.), little elevated, sharp, concentric lamellae which are separated by wider interspaces which are faintly, radiately striated; lunular area smooth, escutcheon long, narrow, deep; hinge normal for the subgenus; pallial sinus high behind then descending and usually, although not always, touching the base of the anterior adductor impression and wholly confluent with the pallial line below.

A specimen from Tangola-Tangola Bay, Mexico, measures: length, 20 mm.; height, 15.5 mm.; convexity (one valve), 3.6 mm.

Dall stated that "this species is notable for the rasp-like quality of its surface to the touch."

Compared to *Tellina proclivis* the shell of *T. reclusa* is longer in proportion to the height, the dorsal margins slope less steeply and the interspaces are ornamented by fine radial sculpture. The shell of *T. reclusa* is more elongate in outline but the posterior end is less attenuated and flexed and the concentric sculpture is more closely spaced than that of *T. crystallina*. The coarser sculpture and the fact that the pallial sinus usually touches the anterior adductor impression are features separating *T. reclusa* from *T. meropsis* Dall<sup>53</sup>.

*Tellina (Merisca) linteata* Turton, which occurs in the Caribbean region from Florida to Brazil, is very similar to *T. reclusa*. *Pristipagia gemonia* Iredale,<sup>54</sup> an Australian species, also is a somewhat similar shell.

**Distribution:** This species was collected by the expeditions from Santa Inez Bay in the Gulf of California, to Corinto, Nicaragua, on the beach and dredged at depths of 3-45 fathoms. It is also known to occur in the Pleistocene of Lower California.

#### Subgenus *Scissula* Dall.

##### KEY TO THE SPECIES OF *Scissula*.

- A. Shell large, length exceeding 25 mm.
  - a. Posterior end obliquely truncated; white or tinged with brown... *cognata*
  - aa. Posterior end tapering and roundly pointed; pale rose color..... *nicoyana*
- B. Shell small, length not exceeding 25 mm.; very thin, glassy
  - a. Oblique striae widely spaced, coarse, very oblique..... *virgo*
  - aa. Oblique striae closer, finer, less oblique and approaching lines of growth..... *varilineata*<sup>55</sup>

<sup>55</sup> Not represented in the present collection.

#### *Tellina (Scissula) cognata* C. B. Adams.

*Tellina cognata* C. B. Adams, *Ann. Lyceum Nat. Hist. New York*, Vol. 5, July, 1852, pp. 503, 545 (separate pp. 279, 321). "Habitat.—Panama."

<sup>53</sup> *Tellina (Moerella) meropsis* Dall, *Proc. U. S. Nat. Mus.*, Vol. 23, No. 1210, November, 1900, p. 317, pl. 3, fig. 1. "San Diego, California."

<sup>54</sup> *Pristipagia gemonia* Iredale, *Rec. Australian Mus.*, Vol. 19, No. 5, April 7, 1936, p. 281, pl. 21, fig. 6. "Habitat.—New South Wales. Type from Sydney Harbour."

<sup>51</sup> *Arcopagia declivis* Sowerby, Dall, *U. S. Nat. Mus. Bull.* 112, 1921, p. 45 (under section *Merisca*). Catalina Island, California, to Panama.

<sup>52</sup> Burch, J. Q., *Min. Conch. Club South Calif.*, No. 45, 1945, p. 16.

*Psammobia casta* Reeve, Conch. Icon., Vol. 10, *Psammobia*, June, 1857, species 55, pl. 8, fig. 55. "Hab. Guatemala."

Not *Tellina casta* Hanley, Proc. Zool. Soc. London, September, 1844, p. 63. "Hab. Singapore; sandy mud."

*Tellina tenuilineatus* Li, Bull. Geol. Soc. China, Vol. 9, No. 3, October, 1930, p. 262, pl. 5, fig. 33. "Brought up by marine dredge from depths varying from 10. ft. to 40. ft. in the mud at the mouth of the Rio Grande near La Boca about one mile from the mainland in Panama Bay." "Horizon: Probably Gatun formation." According to Pilsbry this record is based upon "Two pieces of a left valve of '*Tellina cognata* C. B. Ad. Compared with Adams' type" (Proc. Acad. Nat. Sci. Philadelphia, Vol. 83, 1931, p. 431).

Type Locality: Panama.

Range: Mazatlan, Mexico, to Panama.

Collecting Stations: Guatemala: 7 miles west of Champerico (197-D-1, 2), 14 fathoms, mud; El Salvador: La Libertad (198-D-1, 2), 13-14 fathoms, mud; Meanguera Island, Gulf of Fonseca (199-D-1), 16 fathoms, sand, mud, crushed shell; Nicaragua: Monypenny Point, Gulf of Fonseca (199-D-4, 5, 6), 4-7 fathoms, mud; Costa Rica: 13 miles S. × E. of Judas Point (214-D-1), 42 fathoms, mud, shell; Panama: Gulf of Chiriqui (221-D-1-5), 35-40 fathoms, sandy mud.

Description: Shell oblong, anterior end obliquely rounded, posterior end obliquely truncated, gaping, a depressed posterior area is delimited by a rounded umbonal angulation, white or with a reddish or pale brownish tinge; sculpture consists of minute unequal radiating striae and concentric grooved striae which cross the lines of growth obliquely and become weak or absent on the posterior third of the shell; lateral teeth obsolete; pallial sinus highest posteriorly then descending gently and extending anteriorly for a little more than three-fourths the length of the shell but well separated from the anterior adductor impression; basally, for about one-half its length, it is confluent with the pallial line.

A specimen from the Gulf of Fonseca, in the present collection, measures: length, 45.3 mm.; height, 30 mm.; convexity (both valves together), 13.5 mm.; pallial sinus extends forward 36.4 mm. from the posterior end of the shell. A large left valve dredged in the Gulf of Chiriqui, Panama, measures: length, 49.5 mm.; height, 32 mm.; convexity (one valve), 7.5 mm.

This species is unlike any other along the Pacific Coast of the Americas. It bears only a general resemblance to the east American species *T. similis* Sowerby.

The present species appears to be referable to the subgenus *Scissula* Dall, 1900, type *Tellina decora* Say, rather than to other supraspecific groups in which the shell bears oblique striations such as *Scissulina* Dall, 1924, type, *T. dispar* Conrad; *Tactellina* Iredale, 1929, type, *T. obliquaria* Deshayes; *Obtellina* Iredale, 1929, type, *T. bougei*

Sowerby; and *Loxoglypta* Dall, Bartsch & Rehder, 1938, type, *T. obliquilineata* Conrad.

Distribution: This species was dredged by the expedition from Guatemala to Panama in 4-42 fathoms. It occurred rather abundantly off Champerico, Guatemala, in 14 fathoms, and in the Gulf of Chiriqui, Panama, in 35-40 fathoms, mostly on a muddy bottom. It also has been recorded as occurring in the Pliocene of Ecuador.

*Tellina (Scissula) nicoyana* Hertlein & Strong, sp. nov.

Plate I, Figs. 23, 24, 25, 26.

Shell elongately ovate, thin, gently inflated, nearly equilateral, color, pale rose; anterior dorsal margin slightly rounded, gently sloping anteriorly then rounding abruptly to the elliptically rounded anterior end which merges into the broadly rounded ventral margin; posterior end tapering, roundly pointed; the posterior dorsal margin slopes gently from the beaks with a convexity in the middle portion; the ornamentation consists of fine concentric lines of growth; these are crossed by oblique striae which begin on the anterior end and continue for about two-thirds the length of the shell but are absent on the posterior end where there are a few vague submicroscopic radiating striae; hinge of right valve with two grooved cardinals and, close by, an anterior lateral, and distally a posterior socket below which is a weak lateral; left valve with a grooved anterior cardinal and a thin lamella-like posterior cardinal, also a short anterior lateral or projection of the nymph and a faint posterior lateral; pallial sinus extending about four-fifths the length of the shell and separated from the anterior adductor impression by a considerable distance, high and rounded beneath the beaks then sloping and broadly undulating downward then turning abruptly downward to the pallial line with which it is confluent below; interior beautifully pale yellowish-rose and with faint submicroscopic radiating striae. Length, 34.4 mm.; height, 19 mm.; convexity (both valves together), 7.8 mm.; pallial sinus extends forward about 27 mm. from the posterior end of the shell.

Holotype and paratypes (Calif. Acad. Sci. Paleo. Type Coll.), dredged in Ballena Bay, Gulf of Nicoya, Costa Rica; also dredged in the same vicinity at Station 213-D-11, 17, in Lat. 9° 44' 52" to 9° 42' 00" N., Long. 84° 51' 25" to 84° 56' 00" W., in 35 fathoms, mud.

This beautiful species appears to be distinct from any described shell. It apparently has some characters in common with *Tellina delicatula* Deshayes<sup>56</sup>, the type of which has never been illustrated, but differs in that the shell is nearly equilateral, rather than strongly inequilateral, and the hinge is quite different from that described by Deshayes. It also lacks the dark irregular lines crossing the oblique striae on that species mentioned

<sup>56</sup> *Tellina delicatula* Deshayes, Proc. Zool. Soc. London for 1854 (issued May 16, 1855), p. 363. "Hab. Mazatlan. Coll. Cuming."—Bertin, Nouv. Arch. Mus. Hist. Nat. (Paris), Ser. 2, Vol. 1, 1878, p. 290. Coast of Mazatlan.

by Carpenter<sup>57</sup>. It is interesting to note that Maury has described *Tellina* (*Scissula*) *cercadica*<sup>58</sup> from the Miocene of Santo Domingo, which species, she stated, is very similar to a Recent shell from Panama Bay in the Newcomb collection which was labeled *Tellina delicatula* Deshayes. The Miocene shell illustrated by Maury is not at all similar to the present species but is more similar to *Tellina* (*Scissula*) *cognata* C. B. Adams from Panama.

*Tellina* (*Scissula*) *virgo* Hanley.

*Tellina virgo* Hanley, *Proc. Zool. Soc. London*, December, 1844, p. 143. "Hab. —? Mus. Cuming." "Allied to the *Iris* of Say, but much larger." —Hanley, *Thes. Conch.*, Vol. 1, 1846, p. 284, pl. 57, fig. 42. "Chiriqui, West Columbia." —Sowerby, *Conch. Icon.*, Vol. 17, *Tellina*, 1867, species 207, pl. 37, fig. 207. "Hab. Chiriqui, West Indies." —Pilsbry & Olsson, *Nautilus*, Vol. 56, No. 3, January, 1943, p. 79 (in text), pl. 8, fig. 5. Panama and west coast of northern South America to Puerto Pizarro, Peru.

*Tellina* (*Fabulina*) *virgo* Hanley, *Salisbury, Proc. Malacol. Soc. London*, Vol. 21, Pt. 2, July, 1934, p. 91, pl. 13, figs. 5 and 6. [Illustrations of holotype and paratype].

*Type Locality*: Chiriqui, west Panama (here designated as type locality). No locality cited originally.

*Range*: Magdalena Bay to the Gulf of California and south to Puerto Pizarro, Peru.

*Collecting Stations*: Nicaragua: Corinto (200-D-11-13, 15), 1-8 fathoms, mangrove leaves, also on beach.

*Description*: Shell small, ovately elongate, very thin, glassy, transparent, obtusely angulated posteriorly, colored pink or white; sculpture consists of fine striae which cross the shell obliquely but are absent on the posterior area; the pallial sinus projects anteriorly about four-fifths the length of the shell but does not quite touch the anterior adductor impression, along the base it is confluent with the pallial line.

One of the largest valves collected on the beach at Corinto, Nicaragua, measures: length, 20.2 mm.; height, 12 mm.; convexity (one valve), 2 mm.

The spacing of the oblique lines on this shell seems to vary somewhat but on the specimens which we have observed these lines are always more widely spaced and cross the shell at a greater inclination than those of the similar *Tellina* (*Scissula*) *varilineata* Pilsbry & Olsson<sup>59</sup>.

*Distribution*: This species was collected by the expedition only at Corinto, Nicaragua, on the beach and dredged in 1 to 8 fathoms.

<sup>57</sup> Carpenter, P. P., *Cat. Mazatlan Shells*, September, 1855, p. 37.

<sup>58</sup> *Tellina* (*Scissula*) *cercadica* Maury, *Bull. Amer. Paleontol.*, Vol. 5, No. 29, Pt. 1, April 7, 1917, p. 388 (224), pl. 64 (38), fig. 9. "Bluff 3, Cercado de Mao." Santo Domingo, Miocene.

<sup>59</sup> *Tellina* (*Scissula*) *varilineata* Pilsbry & Olsson, *Nautilus*, Vol. 56, No. 3, January, 1943, p. 79, pl. 8, fig. 6. Type, "from Puerto Bucaro, Province of Los Santos, Panama." Also ranges south to Puerto Pizarro, Province of Tumbes, Peru.

Subgenus *Phyllodina* Dall.

*Tellina* (*Phyllodina*) *pristiphora* Dall.

*Tellina* (*Phyllodina*) *pristiphora* Dall, *Proc. U. S. Nat. Mus.*, Vol. 23, No. 1210, November, 1900, pp. 302, 316, pl. 4, fig. 14. "Dredged near La Paz, Lower California, in 26½ fathoms."

*Tellina pristiphora* Dall, Pilsbry & Lowe, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 84, 1932, p. 132. Dredged in 20 fathoms, Manzanillo; Acapulco, Mexico.

*Type Locality*: Near La Paz, Lower California, in 26½ fathoms.

*Range*: Santa Inez Bay, Gulf of California, to Puntarenas, Costa Rica.

*Collecting Stations*: Mexico: Arena Bank, Gulf of California (136-D-4, 7, 9, 15, 18, 20-22, 28, 32), 40-85 fathoms, mud, crushed shell, muddy sand, sand; Santa Inez Bay (146-D-1), 35 fathoms, mud, crushed shell; Manzanillo (184-D-2), 30 fathoms, gravelly sand; Port Guatulco (195-D-21), 18 fathoms, mud; Costa Rica: Port Parker (203-D-3), 12 fathoms, shelly sand.

*Description*: Shell of medium size, ovate, compressed, nearly equilateral, beaks low, anterior end rounded, posterior dorsal margin sloping, the end blunt, surface yellowish-white, somewhat chalky; sculpture consists of evenly spaced concentric lamellae which are separated by wider and finely concentrically striated interspaces, the lamellae are somewhat obsolete medially; on the posterior area, which on the right valve is set off by an angulation and on the left valve by a groove, the lamellae develop small squarish or rounded elevated foliations, along the anterior dorsal margin similar foliations present a serrated character; lunule and escutcheon elongate; two cardinal teeth in each valve, the right posterior and left anterior ones grooved, two large laterals in the right valve and two small ones in the left, the anterior ones closest to the cardinals; pallial sinus highest behind, then tapering, the end pointed, extending toward the anterior adductor impression for more than one-half the length of the shell, free and ascending from the pallial line except for a short distance posteriorly; interior white and in large specimens yellowish which becomes pale salmon in the anterior dorsal area.

A large specimen dredged on Arena Bank in the southern portion of the Gulf of California measures: length, 35.8 mm.; height, 23 mm.; convexity (both valves together), 10.2 mm.; pallial sinus extends forward 21.5 mm. from the posterior end of the shell.

*Tellina fluctigera* Dall<sup>60</sup>, described from the Gulf of Panama, the type of which has not been illustrated, appears to be a very similar form.

*Tellina dodona* Dall and *T. leptalea* Gardner are representative of the subgenus *Phyllodina* in the Miocene of Florida.

<sup>60</sup> *Tellina* (*Phyllodina*) *fluctigera* Dall, *Bull. Mus. Comp. Zool.*, Vol. 43, No. 6, October, 1908, p. 419. Dredged "in the Gulf of Panama, in 182 fathoms, mud, bottom temperature 54° 1 F."

*Distribution*: Specimens of *Tellina pristi-phora* were dredged from Santa Inez Bay, in the Gulf of California, to Port Parker, Costa Rica, in 12-85 fathoms. The present record of occurrence at Costa Rica is an extension south of the known range of this species.

Subgenus *Phyllodella* Hertlein & Strong,  
subgen. nov.

Shell elongate, compressed, moderately thin, equilateral, both sides sloping nearly equally, anterior end rounded, posterior end roundly obliquely truncated, a posterior area is set off by a weak posterior umbonal angulation; sculpture consists of fine close concentric threads which are crossed by fine radial striae; on the posterior area the concentric sculpture becomes squamose with fine plate-like scales; right valve with two grooved cardinals, a close anterior lateral and a small distant posterior lateral; left valve with a grooved anterior cardinal, a thin posterior cardinal and a weak anterior lateral, no posterior lateral; pallial sinus long, almost touching the anterior adductor impression, along the base wholly confluent with the pallial line.

The character of the hinge, the pallial sinus, and concentric sculpture anterior to the posterior angulation in this subgenus are similar to those of *Eurytellina*. The character of the posterior area, ornamented with squamose foliations, resembles that of *Phyllodina* Dall.

*Tellina* (*Phyllodella*) *insculpta* Hanley.

*Tellina insculpta* Hanley, *Proc. Zool. Soc. London*, September, 1844, p. 70. "Hab. Chiriqui, West Columbia; sandy mud, three fathoms." —Hanley, *Thes. Conch.* Vol. 1, 1846, p. 289, pl. 60, fig. 136. "Chiriqui, W. Columbia." —Sowerby, *Conch. Icon.*, Vol. 17, *Tellina*, 1867, species 208, pl. 37, fig. 208. "Hab. Chiriqui, West Columbia."

*Type Locality*: Chiriqui, west Panama, in three fathoms, sandy mud.

*Range*: Champerico, Guatemala, to Santa Elena Bay, Ecuador.

*Collecting Stations*: Guatemala: 7 miles west of Champerico (197-D-2), 14 fathoms, mud; El Salvador: La Libertad (198-D-1, 2), 13-14 fathoms, mud.

*Description*: Shell elongate, compressed, thin, white, equilateral, dorsal margins sloping, anterior end rounded, posterior end angulated; sculpture of fine, close, equidistant, concentric ribs (about 4 per mm.), both ribs and interspaces are crossed by fine submicroscopic radiating striae; posterior area set off by a weak angulation and on this area the surface is roughened by small scales or interrupted delicate lamellae; right valve with two grooved cardinals and an anterior lateral so closely situated near the beaks as to resemble a cardinal, and a small posterior lateral; left valve with a grooved anterior cardinal, a thin posterior cardinal and a faint anterior lateral; pallial sinus rather high

behind then descending, end blunt and almost, but not quite, touching the posterior basal margin of the anterior adductor impression, along the base it is confluent with the pallial line.

The largest specimen in the collection measures: length, 33.6 mm.; height, 18.3 mm.; convexity (both valves together), 5.8 mm.

The only other shell described from west American waters that bears much resemblance to this species appears to be *Tellina* (*Phyllodina*) *fluctigera* Dall, the type of which has not been illustrated. According to Dall's description the concentric sculpture of his species is more widely spaced (about 2 lamellae per mm. whereas there are about 4 per mm. in the present species) and the pallial sinus is entirely free from the pallial line rather than confluent with it.

*Distribution*: Specimens of *Tellina insculpta* were dredged by the expedition west of Champerico, Guatemala, in 14 fathoms, and at La Libertad, El Salvador, in 13 fathoms, on a muddy bottom. A small specimen of this species in the collections of the California Academy of Sciences was collected by Woodbridge Williams in Santa Elena Bay, Ecuador. These records extend the known range of the species both to the north and to the south.

Subgenus *Elliptotellina* Cossmann.

*Tellina* (*Elliptotellina*) *pacifica* Dall.

*Tellina* (*Elliptotellina*) *pacifica* Dall, *Proc. U. S. Nat. Mus.*, Vol. 23, No. 1210, November, 1900, pp. 302, 316, pl. 3, fig. 9. . . "dredged in Panama Bay, in 18 fathoms, sand."

*Type Locality*: Panama Bay, in 18 fathoms, sand.

*Range*: Santa Inez Bay, in the Gulf of California, to the Bay of Panama.

*Collecting Stations*: Mexico: Santa Inez Bay, Lower California, in the Gulf of California (145-D-1-3), 4-13 fathoms, sand; Manzanillo (184-D-2), 30 fathoms, gravelly sand; Port Guatulco (195-D-9, 19), 7-17 fathoms, gr. mud, gr. sand, crushed shell; Tangola-Tangola Bay (196-D-6, 7), 6-7 fathoms, sand, crushed shell.

*Description*: Shell small, oval, both ends rounded, the anterior the longer, moderately convex, yellowish-white with a rose colored spot near each end of the hinge margin; sculpture of fine concentric grooves separated by wider interspaces, these on the posterior half (and sometimes faintly to the anterior third) of the shell are crossed by deep, angular, radial grooves which serrate the posterior ventral margin and between which are narrow interspaces; hinge of right valve with two cardinals, the anterior one a large subtriangular mass and the posterior one smaller and faintly grooved, two laterals present; left valve with two cardinals, the anterior one grooved, the laterals obsolete; pallial sinus ascending, extending anteriorly about one-half or more the length of the shell, rounded at the end and, except for a short

distance posteriorly, free from the pallial line.

A specimen from Tangola-Tangola Bay, Mexico, measures approximately: length, 7.8 mm.; height, 4.4 mm.; convexity (both valves together), 2.5 mm. A left valve from Port Guatulco, Mexico, measures 8.2 mm. in length.

This species differs from *Tellina americana* Dall, 1900, a similar east American species, in that the radial sculpture is stronger and is present farther anteriorly, the pallial sinus is longer and the color is said to be somewhat brighter.

*Tellina cymobia* Woodring<sup>61</sup>, described from the Miocene of Jamaica, is a very similar species.

*Distribution*: The discovery of the occurrence of *Tellina pacifica* in Santa Inez Bay in the Gulf of California is a long extension north of the known range of the species.

Genus *Tellidora* Mörch in H. & A. Adams.

*Tellidora burneti* Broderip & Sowerby.

*Tellina burneti* Broderip & Sowerby, *Zool. Jour.*, Vol. 4, No. 15, January, 1829, p. 362, pl. 9, fig. 2. "Hab. ad Mazatlan, in Aestuário." "Found in the Estuary of Mazatlan, among the shoals of large Pinnae which are left dry at low water." —Hanley, *Thes. Conch.*, Vol. 1, 1846, p. 271, pl. 58, fig. 99. "Salango, W. Columbia." —Sowerby, *Conch. Icon.*, Vol. 17, *Tellina*, 1867, species 199, pl. 35, figs. 199a, 199b. West Colombia. —M. Smith, *Panamic Shells* (Trop. Photogr. Lab., Winter Park, Florida), 1944, p. 65, fig. 843. Lower California to Ecuador.

*Type Locality*: Mazatlan, Mexico, in the estuary among shoals of large Pinnae at low water.

*Range*: Soledad, Lower California, to the Gulf of California and south to Salango, Ecuador.

*Collecting Stations*: Mexico: Port Guatulco (195-D-17), 6 fathoms, sand; El Salvador: Meanguera Island, Gulf of Fonseca (199-D-1), 16 fathoms, sand, mud, crushed shell; Nicaragua: Corinto, beach.

*Description*: Triangular, rather thin, inequivalve, subequilateral, compressed, subnacreous, white; the convex valve with obsolete distant dilated concentric grooves, which are most visible in front and towards the elevated acute and curving beaks (one of which projects over the other); the flat valve with the elevated fine rather irregular and close concentric striae, which become obsolete posteriorly; ventral edge arcuated; dorsal edges strongly sloping on either side, and armed with large tooth-like projections, the front one greatly incurved, the hinder nearly straight; ligament minute; dorsal slopes excavated; fold and flexure distinct; lateral teeth distinct, rather remote, and subequidistant. (Hanley, *Thes. Conch.*, Vol. 1, 1846, p. 271).

<sup>61</sup> *Tellina* (*Elliptotellina*) *cymobia* Woodring, *Carnegie Inst. Washington, Publ.* 366, May 20, 1925, p. 174, pl. 24, figs. 14-16. Bowden, Jamaica, Miocene.

The pallial sinus is rather high and projects anteriorly more than half the length of the shell.

A large valve in the present collection from the Gulf of Fonseca, measures: length, 49 mm.; height, 40.5 mm.; convexity (one valve), approximately 3.4 mm.

There is some variation in the concentric sculpture of this species but the shape and ornamentation are so characteristic that it cannot be confused with any other west American shell.

*Tellidora cristata* Récluz<sup>62</sup> is a similar species which occurs from Miocene to Recent in the Caribbean region. *Tellidora* (*Tellipiura*) *peruana* Olsson, 1944, has been described from the Cretaceous of Peru.

*Distribution*: This species was collected by the expedition off west Mexico, in the Gulf of Fonseca off El Salvador and at Corinto, Nicaragua. It also has been recorded as occurring in the Pleistocene at Magdalena Bay, Lower California, and Panama.

Genus *Macoma* Leach.

KEY TO THE SUBGENERA OF *Macoma*.

- A. Shell subtrigonal, beaks subcentral
  - a. Shell ornamented with slightly oblique corrugations; small; thin. *Cymatoica*
  - aa. Shell ornamented with concentric striae only ..... *Macoma* s.s.
- B. Shell elongate, beaks posteriorly situated; posterior end much the shorter
  - a. Resilium internal and shorter than the ligament ..... *Psammotreta*
  - aa. Resilium external and about as long as the ligament
    - b. Posterior area granulated ..... *Macoploma*
    - bb. Posterior area not granulated ..... *Psammacoma*

Subgenus *Macoma* s.s.

*Macoma* (*Macoma*) *nasuta* Conrad.

*Tellina nasuta* Conrad, *Jour. Acad. Nat. Sci. Philadelphia*, Ser. 1, Vol. 7, 1837, p. 258. "Inhabits coast of California near Sta. Diego."

*Macoma nasuta* Conrad, I. S. Oldroyd, *Stanford Univ. Publ. Univ. Ser. Geol. Sci.*, Vol. 1, 1924, p. 174, pl. 45, figs. 1a, 1b, 1c, 1d. Kodiak Island and Cook Inlet, Alaska, to Scammon Lagoon, Lower California. Also Miocene, Pliocene and Pleistocene of California. —Grant & Gale, *Mem. San Diego Soc. Nat. Hist.*, Vol. 1, 1931, p. 365, pl. 20, figs. 11a, 11b. Earlier records cited. ? Oligocene and Miocene to Recent.

<sup>62</sup> *Lucina cristata* Récluz, *Rev. Zool., Soc. Cuvierienne*, 1842, p. 270. "Hab.: —Trouvée sur le banc de Campeche par M. Cosmao, commandant la station navale du Mexique." —Récluz, *Mag. de Zool.* (par Guérin-Méneville), 1843, Moll., pl. 60, p. 1, figs. 1-5. Original locality cited.

*Tellina cristata* Récluz, Sowerby, *Conch. Icon.*, Vol. 17, *Tellina*, 1868, species 291, pl. 49, figs. 291a, 291b. "Hab. —?" —M. Smith, *East Coast Mar. Shells* (Edwards Bros., Ann Arbor, Michigan), 1937, p. 60, pl. 54, figs. 6a, 6b. West Florida to Trinidad, West Indies.

*Type Locality*: Coast near San Diego, California.

*Range*: Kodiak Island and Cook's Inlet, Alaska, to Cape San Lucas, Lower California.

*Collecting Station*: Mexico: Cape San Lucas, Lower California.

*Description*: A single right valve of this well known strongly flexed shell, measuring 81 mm. in length and 42.8 mm. in height, was taken by the expedition at Cape San Lucas, Lower California.

The present specimen might be referable to *Macoma kelseyi* but it appears to be intermediate in characters between that form and *M. nasuta*. Dall described *Macoma kelseyi*<sup>63</sup> from the "Pleistocene" of San Diego, California.

It was said to differ from *M. nasuta* by its greater size, thicker, flatter shell and in that the pallial sinus in the right valve bends posteriorly before coalescing with the pallial line rather than joining it at a right angle. Study of a series of specimens of *Macoma nasuta* and of *M. kelseyi* reveals that there is some variation in the pallial sinus and it may be open to question whether *Macoma kelseyi* is a distinct species, subspecies, or merely a very large *M. nasuta*.

*Distribution*: The discovery of the occurrence of *Macoma nasuta* at Cape San Lucas, Lower California, is an extension south of the known range of the species. It also is known to occur as a fossil in California from Oligocene or Miocene to Recent.

#### Subgenus *Cymatoica* Dall.

##### *Macoma (Cymatoica) undulata* Hanley.

*Tellina undulata* Hanley, *Proc. Zool. Soc. London*, September, 1844, p. 72. "Hab. St. Elena, West Columbia; sandy mud, six fathoms."—Hanley, *Thes. Conch.*, Vol. 1, 1846, p. 310, pl. 59, figs. 107, 107\*. "St. Elena, West Columbia."—Sowerby, *Conch. Icon.*, Vol. 17, *Tellina*, 1867, species 119, pl. 23, figs. 119a, 119b. "St. Elena, West Columbia."

*Cymatoica occidentalis* Dall, *Proc. U. S. Nat. Mus.*, Vol. 12, No. 773, 1889 (issued March 7, 1890), p. 272, pl. 10, fig. 11. Dredged "... in latitude 24° 18' N., longitude 110° 22' W., off the coast of Lower California, in 26½ fathoms, fine sandy mud."

*Tellina (Cymatoica) undulata* Hanley, Dall, *Proc. U. S. Nat. Mus.*, Vol. 23, No. 1210, 1900, p. 309. "Gulf of California, south to St. Elena, West Columbia."

*Type Locality*: Santa Elena, Ecuador, in 6 fathoms, sandy mud.

*Range*: Off the west coast of Lower California in Lat. 24° 18' N., Long. 110° 22' W., to the Gulf of California and south to Santa Elena, Ecuador.

*Collecting Stations*: Mexico: Santa Inez Bay, Gulf of California (145-D-1, 3), 4-13 fathoms, sand; Port Guatulco (195-D-19,

20), 17-21 fathoms, gr. mud, crushed shell, mud; Santa Cruz Bay (195-D-21), 18 fathoms, mud; Tangola-Tangola Bay (196-D-6, 7), 6-7 fathoms, sand, crushed shell; El Salvador: Meanguera Island, Gulf of Fonseca (199-D-1), 16 fathoms, sand, mud, crushed shell; Costa Rica: Port Parker (203-D-3), 12 fathoms, shelly mud.

*Description*: Shell small, thin, oblong, beaks subcentral, bluntly pointed and flexed to the right posteriorly, ornamented with small, rounded, undulating riblets which do not coincide with the incremental lines of growth except partially so on the posterior fold.

A right valve from the Gulf of Fonseca, measures: length, 16.4 mm.; height, 9 mm.; convexity (one valve), 2.6 mm.

*Macoma orientalis* Dall<sup>64</sup>, described from the Antilles, is a very similar species.

*Distribution*: Specimens of this species were dredged from the Gulf of California to Costa Rica, in 4 to 21 fathoms.

#### Subgenus *Psammacoma* Dall.

##### KEY TO THE SPECIES OF *Psammacoma*.

- A. Shell moderately thick; telliniform  
*lamproleuca*
- B. Shell thin; sometimes iridescent
  - a. Posterior end narrow; length usually not exceeding 35 mm.
  - b. Very narrow and thin *panamensis*
    - bb. Higher and thicker ..... *spectri*
    - aa. Posterior end wide; length usually exceeding 35 mm. .... *elongata*

##### *Macoma (Psammacoma) elongata* Hanley.

*Tellina elongata* Hanley, *Proc. Zool. Soc. London*, December, 1844, p. 144. "Hab. Chiriqui [Chiriqui], West Columbia; in sand at three fathoms."—Hanley, *Thes. Conch.*, Vol. 1, 1846, p. 302, pl. 62, fig. 199. "Chiriqui, West Columbia."—Sowerby, *Conch. Icon.*, Vol. 17, *Tellina*, 1867, species 137, pl. 25, fig. 137. "Hab. Chiriqui, West Columbia."

*Type Locality*: Chiriqui, Panama, in 3 fathoms, sand.

*Range*: Lower California (Lat. 30° 36' N.) to Panama (Dall). Caribbean region (Dautzenberg).

*Collecting Stations*: Mexico: Santa Cruz Bay (195-D-21), 18 fathoms, mud; Acapulco (189-D-4), 28 fathoms, mud; El Salvador: Meanguera Island, Gulf of Fonseca (199-D-1), 16 fathoms, sand, mud, crushed shell; La Union (199-D-8-10, 12-14, 22), 3-6 fathoms, mud, mangrove leaves; Nicaragua: Monypenny Point (199-D-2-6), 4-7 fathoms, mud; Costa Rica: Cedro Island, Gulf of Nicoya (213-D-1, 10), 8-10 fathoms, mud; 14 miles S. × E. of Judas Point (214-D-1, 4), 42-61 fathoms, mud, shell, rocks.

*Description*: Shell elongate, thin, smooth,

<sup>63</sup> *Macoma kelseyi* Dall, *Trans. Wagner Free Inst. Sci.*, Vol. 3, Pt. 5, December, 1900, p. 1052, pl. 49, fig. 7. "Pleistocene of San Diego, California, obtained in the City Park by Dr. R. E. C. Stearns." According to Dr. W. P. Woodring (oral communication), the type of this species came from Pliocene beds.

<sup>64</sup> *Cymatoica orientalis* Dall, *Proc. U. S. Nat. Mus.*, Vol. 12, 1889, No. 773, (issued March 7, 1890), p. 273, pl. 10, fig. 12. "Hab.—Samana Bay, Santo Domingo, in 16 fathoms, mud". . . . Also found at the same depth at Cardenas, Cuba.

white, sometimes iridescent outside, white within; anterior end rounded, posterior end produced and bluntly truncated; a submedian radial, depressed area present on the ventral half of the shell; ornamented with fine concentric lines of growth which are coarser along the posterior dorsal area, and along the posterior umbonal ridge there are faint irregular oblique striations that do not coincide with the lines of growth; hinge with two cardinals in each valve (on a large specimen the right anterior one sometimes somewhat roughened anteriorly), the posterior tooth slightly cleft, the left anterior cardinal slightly cleft, sometimes slightly indented at the base, on some specimens there are grooves along the margin back of the posterior tooth; pallial sinus higher behind and rounded in front, projecting forward about two-thirds the length of the shell and along the base for about half its length confluent with the pallial line.

A specimen dredged southwest of Maldonado Point, Mexico, measures approximately: length, 47.4 mm.; height, 25.5 mm.; convexity (both valves together), 13 mm.; pallial sinus extends forward 30 mm. from the posterior end of shell.

*Tellina lamproleuca* Pilsbry & Lowe is a somewhat similar species but the median depressed area is less developed, the shell is thicker and more telliniform and the posterior end is generally narrower.

*Macoma gatunensis* Toula, 1908, described from the Miocene Gatun beds at Panama, is very similar but is more excavated beneath the beaks. The shell illustrated by Olsson<sup>65</sup> under the name of *Macoma guatunensis* Toula appears to be very similar to the present species; in fact Olsson mentioned that he could detect no differences between the fossil form and Recent specimens of *M. elongata*. *Macoma falconensis* H. K. Hodson, described from the Miocene of Venezuela, also is a somewhat similar form as is *Macoma hosfordensis* Mansfield<sup>66</sup> which was described from the upper Miocene of Florida.

The posterior area of *Macoma elongata* is smooth in comparison to somewhat similar species assigned to *Macoploma* Pilsbry & Olsson in which the posterior area is ornamented with granules.

*Distribution*: Specimens of *Macoma elongata* were dredged by the expedition from off western Mexico to Costa Rica, in 3 to 61 fathoms, mostly on a muddy bottom. Dautenberg<sup>67</sup> cited this species as occurring at the island of St. Lucie in the West Indies and in the Gulf of Paria and Gulf of Maracaibo, Venezuela. We have not seen specimens from east American waters.

*Macoma (Psammacoma) lamproleuca* Pilsbry & Lowe.

*Tellina lamproleuca* Pilsbry & Lowe, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 84, May 21, 1932, p. 93, pl. 11, figs. 6 and 7. "Corinto, Nicaragua." Also Panama.

*Macoma parthenopa* Pilsbry & Lowe, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 84, May 21, 1932, p. 144, pl. 11, figs. 6 and 7. "Corinto," type. Also Panama.

*Macoma lamproleuca* Pilsbry & Lowe, Pilsbry & Olsson, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 93, 1941, p. 69. Jama formation, Puerto Jama, and Canoa formation, Punta Blanca, Ecuador, Pliocene. Also Recent from Panama to Zorritos, Peru.

*Type Locality*: Corinto, Nicaragua.

*Range*: Santa Inez Bay, Gulf of California, to Zorritos, Peru.

*Collecting Stations*: Mexico: Santa Inez Bay, Gulf of California (142-D-4), 40-50 fathoms, sand; Guatemala: 7 miles west of Champerico (197-D-1, 2), 14 fathoms, mud; El Salvador: La Libertad (198-D-1, 2), 13-14 fathoms, mud; Meanguera Island (199-D-1), 16 fathoms, sand, mud, crushed shell.

*Description*: Shell elongate, telliniform, fairly thick, white under a buff periostracum, somewhat inequilateral, the anterior end the longer, dorsal margins sloping and nearly straight, anterior end broadly rounded, posterior end bluntly truncated; surface ornamented with irregular lines of growth and wrinkles, stronger on the posterior area; sometimes in the right sometimes in the left valve the posterior area bears a median radial depression; a medial flattening from the umbos to the ventral margin often present; lunular area lanceolate and concave; hinge with two cardinals in each valve, the right posterior and left anterior ones bifid, no laterals present; the pallial sinus extends about four-sevenths the length of the shell, it is usually higher in the middle, rounded at the end and joins the pallial line at an acute angle and for a little over half its length is confluent with the pallial line.

The largest specimen in the present collection, a left valve, measures: length, 72.8 mm.; height, 40.5 mm.; convexity (one valve), 10.5 mm.; pallial sinus extends forward 41 mm. from posterior end of shell.

The shell of this species is similar to that of *Macoma elongata* but the dorsal margins slope more steeply, especially anteriorly, the posterior extremity is usually narrower, the shell is thicker and the hinge is heavier.

*Macoma falconensis* H. K. Hodson<sup>68</sup>, described from the Miocene of Venezuela, is a similar species.

*Distribution*: This species was taken off Guatemala and El Salvador in 13 to 16 fathoms, usually on a muddy bottom. It also has

<sup>65</sup> Olsson, A. A., *Bull. Amer. Paleol.*, Vol. 5, No. 39, Pt. 2, June 21, 1922, pl. 29 (26), fig. 13. Banana River, Costa Rica. Miocene.

<sup>66</sup> *Macoma (Psammacoma) hosfordensis* Mansfield, *Florida Geol. Surv., Bull.* 8, 1932, p. 142, pl. 30, figs. 6, 10, 12, 13. "Type locality: Station 3671, 2 miles north of Hosford, Liberty County, Fla." Choctawhatchee, upper Miocene.

<sup>67</sup> Dautenberg P., *Mem. Zool. Soc. France*, Vol 13, 1900, p. 263.

<sup>68</sup> *Macoma (Psammacoma) falconensis* H. K. Hodson, *Bull. Amer. Paleol.*, Vol. 16, No. 59, October 1, 1931, p. 16, pl. 6, figs. 1, 6, 7. "Holotype Locality—5 kilometers north and 350 meters west of Urumaco, in Rio Codore, District of Democracia, Falcón." Venezuela. Miocene. Also other localities.

been recorded as occurring in the Pliocene of Ecuador.

***Macoma (Psammacoma) panamensis* Dall.**

*Macoma (Psammacoma) extenuata* var. ? *panamensis* Dall, *Proc. U. S. Nat. Mus.*, Vol. 23, No. 1210, November, 1900, p. 310. "Panama."

*Macoma (Psammacoma) panamensis* Dall, *Proc. U. S. Nat. Mus.*, Vol. 23, No. 1210, November, 1900, p. 324, pl. 4, fig. 3. . . . "dredged in 33 fathoms, sand, in Panama Bay."

**Type Locality:** Panama Bay, in 33 fathoms, sand.

**Range:** Gulf of California to Panama.

**Collecting Stations:** Mexico: Tenacatita Bay (183-D-3), 40 fathoms, sandy mud; 4 miles SSW. of Maldonado Point (192-D-3), 38 fathoms, mud; Tangola-Tangola Bay (196-D-18), 30 fathoms, mud; Costa Rica: Port Parker (203-D-3), 12 fathoms, shelly mud; 14 miles S. × E. of Judas Point (214-D-1, 4), 42-61 fathoms, mud, shell, rocks; Panama: Gulf of Chiriqui (221-D-1, 5), 35-40 fathoms, sandy mud.

**Description:** Shell very elongated, slender, thin, moderately convex, right valve slightly flattened posterior to the center, inequilateral, the anterior end the longer, posterior end produced and subrostrate, yellowish-white; ornamented with fine concentric striae which are heavier on the posterior area; hinge with two teeth in each valve, the right posterior and left anterior ones cleft; pallial sinus rounded at the anterior end which projects forward about five-eighths the length of the shell, and for about one-half its length confluent with the pallial line; interior of valves sometimes show obscure striations near the margins.

A right valve from the Gulf of Chiriqui, Panama, measures: length, 31 mm.; height, 14.4 mm.; convexity (one valve), 3.5 mm.; pallial sinus extends forward 20 mm. from the posterior end of the valve.

*Macoma extenuata* Dall,<sup>69</sup> described from the Gulf of Mexico, is a very similar species. *Macoma panamensis canalis* Olsson, described from the Miocene of the Canal Zone, is higher in proportion to the length.

Compared to *Macoma elongata* Hanley, the shell of *M. panamensis* is generally narrower and more elongate and the posterior end is narrower.

**Distribution:** This species was dredged by the expedition from off Mexico to the Gulf of Chiriqui, Panama, in 12-61 fathoms, mostly on a muddy or sandy mud bottom.

***Macoma (Psammacoma) panamensis spectri***

Hertlein & Strong subsp. nov.

Plate I, Figs. 9, 10, 16.

Shell elongate, fairly thick, white, some-

what flexed posteriorly; left valve moderately inflated, the right flattened a little posterior to the middle; posterior dorsal margin sloping, anterior end the longer, the dorsal margin slightly convex and gently sloping, that of the right overlapping the left for about a third of its length; anterior end well rounded, ventral margin only slightly curved, posterior end produced, roundly truncated, on each valve a distinct angulation extending from near the beaks to the lower end of the truncation; exterior surface showing distinct resting stages between which there are many very fine concentric striations and microscopic radial striae most distinct just anterior to the posterior angulation; fresh specimens are often iridescent; interior shining white; two cardinal teeth in each valve, the right posterior and left anterior ones bifid, lateral teeth lacking; pallial sinus subangulate above, highest at a point nearly vertically below the beaks, end elliptically rounded and extending forward about two-thirds the length of the shell and along the base for more than half its length confluent with the pallial line. Holotype, a left valve, measures: length, 34.4 mm.; height, 18.5 mm.; convexity, 5.3 mm.; pallial sinus extends anteriorly 21.5 mm. from the posterior end of the shell.

Holotype, left valve, and paratype, a right valve (Calif. Acad. Sci. Paleo. Type Coll.), dredged in Santa Inez Bay, Gulf of California, Station 143-D-3, Lat. 26° 57' N., Long. 111° 56' W., in 35 fathoms (64 meters), mud, crushed shell.

Three additional specimens were dredged at the same locality. Other specimens were dredged in the same general area in Santa Inez Bay at Station 143-D-1, 4, in 25-29 fathoms, mud, crushed shell, weed, sand; specimens were dredged on Arena Bank, Gulf of California, at Station 136-D-2, 45 fathoms, mud, *Area* conglomerates. About a dozen single valves, probably from the Gulf of California, are without information as to locality. One valve from the Gulf of Chiriqui, Panama, Station 221-D-1-5, 35-40 fathoms, sandy mud, appears to belong to this subspecies.

The growth lines of these specimens are so fine that when fresh specimens are examined at an angle they act as a grating and produce beautiful iridescent spectral colors.

The shell here described as a new subspecies is similar to that of *Macoma panamensis*, but it is higher in proportion to the length and so far as known it is generally restricted to a more northern range. Some young specimens are very similar to Dall's species and perhaps additional specimens may show the form here described as new to be without significance, but the greater height, iridescent color and generally more northern distribution appear, at the present time, to be sufficient reasons for separating it as a distinct subspecies.

This new subspecies is very similar to

<sup>69</sup> *Macoma (Psammacoma) extenuata* Dall, *Proc. U. S. Nat. Mus.*, Vol. 23, No. 1210, November, 1900, p. 314, pl. 2, fig. 7. Dredged "between the delta of the Mississippi and Cedar Keys, Florida, in 32 fathoms, sand." Cited on p. 300 as "*Macoma (Cydippina) extenuata*."

*Macoma panamensis canalis* Olsson,<sup>70</sup> described from the Miocene Gatun beds of Panama, which also is higher in proportion to the length as compared to *M. panamensis*. The shell of the present subspecies is higher and a little less elongate than Olsson's subspecies. Furthermore adult shells are moderately thick whereas those of Olsson's subspecies were described as very thin and fragile.

Subgenus *Psammotreta* Dall.

KEY TO THE SPECIES OF *Psammotreta*.

- A. Umbos orange-red; shell subrectangular, narrow ..... *aurora*  
 B. Umbos white shading to ochraceous; shell proportionately larger and higher ..... *pacis*

*Macoma (Psammotreta) aurora* Hanley.

*Tellina aurora* Hanley, *Proc. Zool. Soc. London*, December, 1844, p. 147. "Hab. Panama; soft sandy mud, ten fathoms: Cuming."—Hanley, *Thes. Conch.*, Vol. 1, 1846, p. 301, pl. 58, fig. 76. Panama.

*Macoma (Psammacoma) aurora* Hanley, Salisbury, *Proc. Malacol. Soc. London*, Vol. 21, Pt. 2, July, 1934, p. 91, pl. 11, fig. 4. Figure of lectotype.

*Type Locality*: Panama, in 10 fathoms, soft sandy mud.

*Range*: Gulf of California to Boca de Pan, Peru.

*Collecting Stations*: Mexico: Santa Cruz Bay (195-D-21), 18 fathoms, mud; Tangola-Tangola Bay (196-D-14, 15), 5 fathoms, crushed shell; Nicaragua: Corinto (200-D-8, 9), 6-6.6 fathoms, mangrove leaves.

*Description*: Shell elongate, longer anteriorly, the end rounded, posterior end bluntly truncated, posterior area set off by an umbonal angulation; resilium internal and partly separated from the ligament; shell white or yellowish-white with the umbonal area both exteriorly and interiorly ornamented with orange red which grades into yellow anteriorly; two cardinals in each valve, the right posterior and left anterior ones faintly cleft; on some large right valves there is a small denticle-like projection of the nymph at the ventral end of the resilium; the pallial sinus extends forward about two-thirds the length of the shell to the anterior edge of the orange red area but is separated from the anterior adductor impression by considerable space; along the base for about half its length it is confluent with the pallial line.

A left valve of this species from Tangola-Tangola Bay, Mexico, in the present collection, measures 28 mm. in length. A specimen from Panama in the collections of the California Academy of Sciences, measures: length, 27.5 mm.; height, 17.3 mm.; convexity (both valves together), 8.2 mm.; pallial

sinus extends forward 19 mm. from the posterior end of the shell.

The elongate, subrectangular form and orange red radial area on the umbonal region are characteristic features of this *Macoma*.

*Macoma hesperus* Dall,<sup>71</sup> an unfigured species described from the Gulf of Panama, was said to bear a resemblance to *M. aurora* but with a narrower shell and a different hinge.

*Distribution*: A few specimens of this species were dredged in 5-18 fathoms off west Mexico and Corinto, Nicaragua.

*Macoma (Psammotreta) pacis* Pilsbry & Lowe.

*Macoma pacis* Pilsbry & Lowe, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 84, May 21, 1932, p. 95, pl. 10, figs. 1, 1a, 2, 3. "La Paz, Lower California."

*Type Locality*: La Paz, Lower California. *Range*: Gulf of California to Golfito, Gulf of Dulce, Costa Rica.

*Collecting Stations*: Mexico: Port Gualtulo; Guatemala: 7 miles west of Champerico (197-D-2), 14 fathoms, mud; Costa Rica: Cedro Island, Gulf of Nicoya; Golfito.

*Description*: Shell resembling that of *Macoma aurora* but larger and higher in proportion to the length, usually whiter and tinted with yellow and on some specimens the umbonal area is of an ochraceous salmon color. Two cardinal teeth in each valve, the right posterior and left anterior ones bifid, the left posterior cardinal narrow and near the posterior margin; pallial sinus high beneath the beaks then descending to a bluntly rounded end and for about half its length confluent with the pallial line.

A specimen in the present collection from Golfito, Costa Rica, measures: length, 34.6 mm.; height, 21.8 mm.; convexity (both valves together), 9.9 mm. A large right valve from Cedro Island in the Gulf of Nicoya, measures: length, 52.6 mm.; height, 34 mm.; convexity (one valve), 6.6 mm.; pallial sinus extends forward 35 mm. from the posterior end of the shell.

Small specimens of this species are very similar to those of *Macoma aurora* but seem to differ constantly in the particular mentioned above. As pointed out by Pilsbry & Lowe the relation of height to length varies considerably in different specimens.

Illustrations of *Macoma plebeia* Hanley<sup>72</sup> indicate a shell which is more roundly oval with a more rounded ventral margin posteriorly. According to the illustration of that species given by Pilsbry & Lowe the pallial sinus is more broadly rounded at the end and is confluent with the pallial line for a shorter distance than that of *Macoma pacis*.

<sup>71</sup> *Macoma (Psammacoma) hesperus* Dall, *Bull. Mus. Comp. Zool.*, Vol. 43, No. 6, October, 1908, p. 421. Dredged in the "Gulf of Panama, in 182 fathoms, mud, bottom temperature 54° 1 F."

<sup>72</sup> *Tellina plebeia* Hanley, *Proc. Zool. Soc. London*, December, 1844, p. 147. "Hab. Real Ilejos, Central America; sandy mud, seven fathoms."—Hanley, *Thes. Conch.*, Vol. 1, 1846, p. 299, pl. 60, fig. 151. Original locality cited. [Not pl. 59, fig. 129, "Senegal"].

*Macoma plebeia* Hanley, Pilsbry & Lowe, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 84, 1932, p. 95 (in text), pl. 10, fig. 5. "Real Ilejos (=Corinto)."

<sup>70</sup> *Macoma panamensis* Dall var. *canalis* Olsson, *Bull. Amer. Paleol.*, Vol. 9, No. 39, Pt. 2, June 21, 1922, p. 429 (257), pl. 29 (26), fig. 11. "Gatun Stage; Mt. Hope, C. Z."

*Macoma mazatlanica* Deshayes<sup>73</sup> is very similar to *M. pacis* but is more tapering posteriorly.

*Distribution*: Specimens of *Macoma pacis* were taken by the expedition off west Mexico, Guatemala and Costa Rica. This is an extension south of the known range of the species.

Subgenus *Macoploma* Pilsbry & Olsson.

*Macoma (Macoploma) medioamericana* Olsson.

*Macoma (Macoploma) medioamericana* Olsson, *Bull. Amer. Paleol.*, Vol. 27, No. 106, December 25, 1942, p. 196 (44), pl. 17 (4), fig. 8. "Pliocene. Quebrada Peñitas, Costa Rica."

*Type Locality*: Quebrada Peñitas, Costa Rica. Pliocene.

*Range*: Arena Bank, Gulf of California, to Panama.

*Collecting Stations*: Arena Bank, Gulf of California (136-D-21), 45 fathoms, mud; El Salvador: La Libertad (198-D-2), 16 fathoms, mud; Costa Rica: off Ballena Bay, Gulf of Nicoya (213-D-11-17), 35-40 fathoms, mud.

*Description*: Shell elongate, moderately thin, general characters much like those of *Macoma elongata* but with the anterior dorsal margin more steeply sloping and with the posterior area ornamented with strong concentric laminae and earthy granules.

The largest specimen in the collection from the Gulf of Nicoya, measures approximately: length, 101 mm.; height, 54 mm.; convexity (both valves together), 24 mm.

Some of the specimens in this collection agree so closely with Olsson's description and illustration of *Macoma medioamericana* that we have referred them to his species. There is variation in the specimens and some might be equally well referred to *Macoma (Macoploma) ecuadoriana* Pilsbry & Olsson<sup>74</sup> described from the Pliocene of Ecuador. According to Olsson, *M. medioamericana* is proportionately longer and has coarser and more earthy granulations on the posterior submargins in comparison to *M. ecuadoriana*.

It is obvious from a study of a series of specimens that there are several very closely related variable species, including *Macoma elongata*, *M. panamensis*, *M. lamproleuca*, *M. ecuadoriana* and *M. medioamericana*. The presence of granulation on the posterior areas appears to be the only certain criterion separating the species of *Macoploma* from some of the others. The granules are present on specimens in the present collection after they have attained a length of about 20 to 25 mm. It is very difficult to separate specimens of a smaller size from those of *M. elongata* or *M. lamproleuca*.

<sup>73</sup> *Tellina mazatlanica* Deshayes, *Proc. Zool. Soc. London* for 1854 (issued May 16, 1855), p. 359. "Hab. Mazatlan. Coll. Cuming." —Sowerby, *Conch. Icon.*, Vol. 17, *Tellina*, October, 1868, species 320, pl. 54, fig. 320. "Hab. Mazatlan. Coll. Cuming."

<sup>74</sup> *Macoma (Macoploma) ecuadoriana* Pilsbry & Olsson, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 93, September 9, 1941, p. 69, pl. 19, fig. 5. "Canoa formation, Punta Blanca." Ecuador, Pliocene.

*Distribution*: Specimens of this species were dredged by the expedition at depths of 16 to 45 fathoms from Arena Bank, Gulf of California, La Libertad, El Salvador, and off Costa Rica in the Gulf of Nicoya, mostly on a muddy bottom. The species also is known to occur in the Pliocene of Costa Rica. The present records of occurrence reveal for the first time that this species is living at the present time in west American waters.

Genus *Apolymetis* Salisbury.

KEY TO THE SPECIES OF *Apolymetis*.

- A. Posterior end broadly rounded  
 a. Shell thick, hinge broad...*biangulata*<sup>75</sup>  
 aa. Shell thin, hinge narrow .....*cognata*  
 B. Posterior end tapering, truncated  
 a. Hinge fairly broad; anterior adductor impression elongately oval; pallial sinus for a little less than half its length confluent with pallial line .....*dombei*  
 aa. Hinge very narrow; anterior adductor impression very long and narrow; pallial sinus confluent with pallial line for only a very short distance  
*asthenodon*<sup>75</sup>

*Apolymetis cognata* Pilsbry & Vanatta.

*Lutricola cognata* Pilsbry & Vanatta, *Proc. Washington Acad. Sci.*, Vol. 4, September 30, 1902, p. 556, pl. 35, fig. 5. "From Tagus Cove, Albemarle." Galápagos Islands.

*Apolymetis cognata* Pilsbry & Vanatta, Pilsbry & Lowe, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 84, 1932, pp. 96 (in text), 133. Galápagos Islands, also Taboga Island, Panama, and Corinto, Nicaragua.

*Type Locality*: Tagus Cove, Albemarle Island, Galápagos Islands.

*Range*: Magdalena Bay, Lower California, to Paita, Peru.

*Collecting Station*: Nicaragua: Corinto (200-D-19), 12-13 fathoms, mangrove leaves.

*Description*: Shell rounded-quadrate, moderately compressed, bent to the right posteriorly, rather thin, gray white. Sculptured with irregular growth wrinkles and low radial striae, covered with an extremely minute secondary radial striation. Beaks median, worn at the tip. Anterior margin rounded; posterior margin subtruncate, the basal margin straightened, sinuous; pallial sinus ample. Length of left valve, 41 mm., alt. 34 mm., diameter 8 mm. (Original description).

Closely related to *L. alta* Conr., but higher, shorter, of a more quadrate shape. The anterior end of the pallial sinus is more rounded, and its upper margin is not sinuous. *L. excavata* Sowb. is a more wedge-shaped shell (Pilsbry & Vanatta).

This species differs from the generally more northern *A. biangulata* Carpenter in the much narrower, weaker hinge, in the more flaring and less steeply sloping posterior area, and in the generally thinner shell.

<sup>75</sup> Not represented in the present collection.

Specimens referable to the present species from the Gulf of California and southward have in some instances, formerly been referred to "*Tellina excavata* Sowerby<sup>76</sup> which was originally described without information as to locality. As pointed out by Pilsbry & Vanatta the illustration given by Sowerby indicates a shell with the posterior end wedge-shaped. Pilsbry & Lowe later pointed out that there seemed to be no characters by which "*Tellina excavata* could be separated from *Apolymetis dombei* Hanley. They recognized only four west American species of the genus, *Apolymetis alta* Conrad [= *biangulata* Carpenter], *A. asthenodon* Pilsbry & Lowe, *A. cognata* Pilsbry & Vanatta and *A. dombei* Hanley. However for some unexplained reason, probably an oversight, they cited (p. 195) *A. excavata* Sowerby from Mazatlan, Mexico. In later publications, Lowe<sup>77</sup> cited "*Metis excavata* Sowerby" as occurring at Punta Penasco, Mexico, in the Gulf of California, and Pilsbry & Olsson<sup>78</sup> recorded "*Apolymetis excavatus* Sowerby" from the Pliocene of Ecuador. No illustrations were given of the shells representing those records so we are uncertain which species was represented. Specimens from the coast of the mainland appear to be identical with those from the Galápagos Islands, the type locality of *A. cognata*.

*Distribution*: A single small right valve of this species, measuring about 20 mm. in length, was taken by the expedition at Corinto, Nicaragua, in 12-13 fathoms.

#### *Apolymetis dombei* Hanley.

*Tellina dombei* Hanley, *Proc. Zool. Soc. London*, December, 1844, p. 144. "Hab. Panama; twelve fathoms, sandy mud."—Hanley, *Thes. Conch.*, Vol. 1, 1846, p. 323, pl. 62, fig. 182. Panama. Variety, pl. 64, fig. 222. Tumbez, Peru.

*Tellina dombeyi* Hanley, *Proc. Zool. Soc. London* for 1844 (issued February, 1845), p. 195 (index).—Sowerby, *Conch. Icon.*, Vol. 17, *Tellina*, 1867, species 169, pl. 30, fig. 169. "Hab. Panama, Tumbez, Peru."—Römer, *Syst. Conchyl.-Cab. von Martini und Chemnitz*, Bd. 10, Abt. 4, *Tellina*, 1871, p. 205, pl. 39, figs. 7-9. Various localities cited from the Gulf of California to Tumbez, Peru.

*Psammobia* sp., Li, *Bull. Geol. Soc. China*, Vol. 9, No. 3, 1930, p. 262, pl. 5, fig. 32. Dredged in Panama Bay in 10-40 ft. "Probably Gatun formation." Pilsbry (*Proc. Acad. Nat. Sci. Philadelphia*, Vol. 83, 1931, p. 431) stated that Li's record was based on "A good but bleached valve of *Apolymetis dombei* (Hanley)."

*Type Locality*: Panama, in 12 fathoms, sandy mud.

*Range*: Gulf of Fonseca to Tumbez, Peru.  
*Collecting Stations*: Nicaragua: Potosi

and 5 miles SSW. of Monypenny Point, Gulf of Fonseca, beach; Costa Rica: 1 mile S. of entrance to Golfito Bay, Gulf of Dulce, beach.

*Description*: Shell ovately subtriangular, moderately thick, rather smooth, white but often with umbonal area reddish-orange exteriorly and sometimes interiorly; the anterior end the longer, rounded and somewhat obliquely produced; a flexure or depressed radial area is present anterior to the posterior umbonal ridge; posterior end sloping, subtriangular and subtruncated, area set off by an umbonal angulation; hinge with two cardinals, the right posterior bifid, the left anterior grooved, no laterals present; the pallial sinus is high and subangulate in the middle then sloping down even with but well separated from the anterior adductor impression and for a little less than one-half its length confluent with the pallial line.

The shell of this species is somewhat variable in outline. Some specimens agree almost exactly with Hanley's original figure, others are more trigonal. A large right valve from the Bay of Panama in the collections of the California Academy of Sciences, measures: length, 66 mm.; height, 51 mm.; convexity (one valve), 14 mm.

Römer, 1871, and Stearns, 1891, pointed out the resemblance between "*Tellina dombei* and "*Tellina excavata* Sowerby<sup>79</sup> which was described without information as to the locality from which it came. Later Pilsbry & Lowe, 1932, stated that they knew of no difference separating these two species.

Compared to *Apolymetis dombei*, *A. asthenodon* Pilsbry & Lowe<sup>80</sup> was described as possessing a more elongate shell with a very narrow hinge, a narrower, longer anterior adductor impression. Judging from the illustrations, the pallial sinus is confluent with the pallial line for a very short distance if at all.

The shell of *Apolymetis dombei* differs from that of *Macoma grandis* Hanley<sup>81</sup> which was originally described from Tumbez, Peru, and was taken at Corinto, Nicaragua, by the Templeton Crocker Expedition, 1932, in the stronger, broader, posterior umbonal fold and much longer pallial sinus. Judging from the illustration of *Macoma gubernaculum* Hanley,<sup>82</sup> originally described from Real

<sup>79</sup> *Tellina excavata* Sowerby, *Conch. Icon.*, Vol. 17, *Tellina*, March, 1867, species 138, pl. 26, fig. 138. "Hab. —?"

Soot-Ryen (*Nyt. Mag. for Naturvid.*, Bd. 70 (Meddel. Zool. Mus. Oslo, No. 27), 1932, p. 321, pl. 2, fig. 10) illustrated a shell under the name of *Apolymetis excavata* Sowerby from Floreana (Charles) Island, Galápagos group. He remarked on the variability of the outer form revealed by different specimens, some of which were elongated, other shorter and higher.

<sup>80</sup> *Apolymetis asthenodon* Pilsbry & Lowe, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 84, May 21, 1932, p. 96, pl. 11, figs. 1-3. "Panama, on the beach (D. E. Harrower, J. Zetek)." Type. Also at La Union, Gulf of Fonseca, El Salvador.

<sup>81</sup> *Tellina grandis* Hanley, *Proc. Zool. Soc. London*, December, 1844, p. 141. "Hab. Tumbez, Peru."—Hanley, *Thes. Conch.*, Vol. 1, 1846, p. 327, pl. 65, fig. 247. Tumbez, Peru.

<sup>82</sup> *Tellina gubernaculum* Hanley, *Proc. Zool. Soc. London*, December, 1844, p. 142. "Hab. Real Lejos, Central America; in sandy mud, seven fathoms."—Hanley, *Thes. Conch.*, Vol. 1, 1846, p. 325, pl. 62, fig. 186. "Real Lejos, Central America (Cuming)."

<sup>76</sup> *Tellina excavata* Sowerby, *Conch. Icon.*, Vol. 17, *Tellina*, March, 1867, species 138, pl. 26, fig. 138. "Hab. —?"

<sup>77</sup> Lowe, H. N., *Trans. San Diego Soc. Nat. Hist.*, Vol. 8, No. 6, 1935, p. 28.

<sup>78</sup> Pilsbry, H. A., and Olsson, A. A., *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 93, 1941, p. 70.

Llejos, Nicaragua, the anterior dorsal margins slope more abruptly than those of *A. dombei*.

*Distribution*: Specimens of *Apolymetis dombei* were taken by the expedition on the beaches in the Gulf of Fonseca, Nicaragua, and Gulf of Dulce, Costa Rica. We have not seen specimens from north of Nicaragua. It has been reported as ranging south to Peru. It also has been recorded as occurring in beds of upper Pliocene age in the Galápagos Islands. "*Apolymetis* cf. *A. dombei* (Hanley)" has been cited by Stewart<sup>83</sup> as occurring in upper Pliocene beds in the Kettleman Hills, San Joaquin Valley, California.

### Genus *Strigilla* Turton.

#### KEY TO THE SPECIES OF *Strigilla*.

- A. Shell equilateral; small, white.....*lenticula*  
 B. Shell inequilateral, elongated posteriorly  
 a. Striae much more widely spaced anteriorly .....*cicercula*  
 aa. Striae equally or more closely spaced anteriorly  
 b. Shell thick; convex; roundly truncated anteriorly .....*costulifera*  
 bb. Shell thin; flatter; expanded anteriorly .....*disjuncta*

#### *Strigilla cicercula* Philippi.

Plate I, Fig. 19.

*Tellina cicercula* Philippi, *Zeit. f. Malakozool.*, Jahrg. 3, February, 1846, p. 19. "Patria: Mazatlan."

*Tellina dichotoma* Philippi, *Zeit. f. Malakozool.*, Jahrg. 3, February, 1846, p. 20. "Patria: Mazatlan."

*Tellina ervilia* Philippi, *Zeit. f. Malakozool.*, Jahrg. 3, February, 1846, p. 20. "Patria: Mazatlan."

*Strigilla maga* Mörch, *Malakozool. Blätter*, Bd. 7, December, 1860, p. 189. "Sonsonate." El Salvador.

*Strigilla interrupta* Mörch, *Malakozool. Blätter*, Bd. 7, December, 1860, p. 190. "Sonsonate." El Salvador.

*Strigilla circercula* Philippi, Dall, *Proc. U. S. Nat. Mus.*, Vol. 23, No. 1210, 1900, p. 305. Gulf of California to Panama.

*Type Locality*: Mazatlan, Mexico.

*Range*: Gulf of California to Ecuador.

*Collecting Station*: Nicaragua: Corinto (200-D-11, 19, also beach), 8-13 fathoms, sand, mangrove leaves.

*Description*: Shell small, usually less than 1 cm. in length, rounded, elongated posteriorly, polished, white, with pink color usually confined to the umbonal region; sculptured with fine radial striae which on the anterior area are curved and very much more widely spaced.

A large right valve of this beautiful little

species, dredged off Corinto, Nicaragua, in 13 fathoms, measures: length, 9.5 mm.; height, 8.5 mm.; convexity (one valve), 2.5 mm.

The smaller size, pink colored umbonal area, and much wider spaced sculpture on the anterior area, are characters which serve to separate the shell of *Strigilla cicercula* from that of the young of *S. costulifera* Mörch.

*Strigilla pisiformis* Linnaeus, which occurs in the Caribbean region, is a very similar species.

*Distribution*: This species was collected by the expedition at Corinto, Nicaragua, on the beach and dredged at depths of 8 to 13 fathoms.

#### *Strigilla costulifera* Mörch.

Plate I, Fig. 15.

*Tellina carnaria* Linnaeus, Hanley, *Thes. Conch.*, Vol. 1, 1846, p. 260 (in part), pl. 56, fig. 38 [West Colombia record only].

Not *Tellina carnaria* Linnaeus. Caribbean region.

*Tellina (Strigilla) fucata* Gould, *Proc. Boston Soc. Nat. Hist.*, Vol. 4, November, 1851, p. 91. Pacific coast [No exact locality cited].—Gould, *Boston Jour. Nat. Hist.*, Vol. 6, October, 1853, p. 399, pl. 16, fig. 4. "Inhabits Mazatlan."

Not *Tellina fucata* Hinds, *Zool. Voy. Sulphur, Moll.*, Pt. 3, 1844, p. 67, pl. 21, fig. 4.

*Strigilla costulifera* Mörch, *Malakozool. Blätter*, Bd. 7, December, 1860, p. 189. "Sonsonate." El Salvador.

*Tellina chroma* Salisbury, *Proc. Malacol. Soc. London*, Vol. 21, Pt. 2, July, 1934, p. 84. New name for *Tellina (Strigilla) fucata* Gould, 1851, not *Tellina fucata* Hinds, 1844.

*Type Locality*: Sonsonate, El Salvador.

*Range*: Magdalena Bay, Lower California, to the Gulf of California and south to Ecuador.

*Collecting Stations*: Mexico: Tenacatita Bay, beach; Sihuatanejo Bay, beach; Nicaragua: Corinto (200-D-16), 4-7 fathoms, mangrove leaves.

*Description*: Shell suborbicular, the anterior side much the shorter, moderately thick, glossy, pink, rose or white ringed with pink or carmine; umbos smooth; the ornamentation consists of striae, anteriorly flexuous, forming an angle with those on the central area, which usually radiate obliquely posteriorly; on the posterior slope the striae are fine and usually meet at an acute angle; a lunule present; hinge with a bifid cardinal and two laterals in each valve; one or two thickened rays often present interiorly; the pallial sinus touches the anterior adductor impression and is confluent with the pallial line below; the interior is often of a beautiful deep red or carmine color.

Dall pointed out that the shell of this species is very inconstant in details of sculpture, color, and in the presence or absence of a smooth radial streak on each valve.

A very large specimen of this species from Magdalena Bay, Lower California, in the

<sup>83</sup> *Apolymetis* cf. *A. dombei* (Hanley), Stewart, *U. S. Geol. Surv., Prof. Paper* 195, 1940 (issued June 7, 1941), p. 93, pl. 32, fig. 2. *Siphonalia* zone in North Dome, Kettleman Hills, San Joaquin Valley, California. Etchegoin formation, upper Pliocene.

Henry Hemphill collection of the California Academy of Sciences, measures approximately: length, 25 mm.; height, 23 mm.; convexity (both valves together), 10.3 mm. The specimens in the present collection are smaller.

*Strigilla costulifera* is very similar to the east American *S. carnaria* Linnaeus. The west American shell is often somewhat more rounded and the striae appear to be less numerous.

*Distribution*: Specimens of *Strigilla costulifera* were taken by the expedition on the beaches along western Mexico and dredged in 4 to 7 fathoms at Corinto, Nicaragua.

***Strigilla disjuncta* Carpenter.**

Plate I, Fig. 20.

*Strigilla disjuncta* Carpenter, *Proc. Zool. Soc. London*, November 11, 1856, p. 160. "Hab. In Sinu Panamensi; legit. T. Bridges."

*Type Locality*: Bay of Panama.

*Range*: Corinto, Nicaragua, to Panama.

*Collecting Station*: Nicaragua: Corinto (200-D-11), 8 fathoms, sand.

*Description*: S. testa satis magna, alba, tenui, planata; inaequaliter, postice producta; marginibus dorsalibus subrectis, ad angulam 120°, aliis bene arcuatis; lineis incrementi vix monstrantibus; lineis undulatis exillimis, antice concentricis, umbones versus ascendentes, sinu angustiore; dein ad marginem ventralem rapide descendentes; dein subito, angulo acuto, circiter 20° postice rursus ascendentes; lineis angularum in valva utraque haud convenientibus; margine postico sinuato, sculptura postea fortiore; margine antico quoque sinuato; lunula distincta, sinuata; ligamento subelongato; dent. card. valva altera uno parvo et uno magno bifido; altera uno parvo bifido; dent. lat. acutioribus, haud distantibus. Long. 1.35, lat. 1.54, alt. .54 poll. (Original description).

"Allied to *S. sincera* Hanl.; remarkable for its large size and very fine markings, and named from the lines of markings in the two valves not agreeing at the edges." (Carpenter).

Compared to *Strigilla costulifera* Mörch, the shell of *S. disjuncta* is usually larger and the shell is thinner, flatter, more produced anteriorly, the beaks are more projecting and beneath them the dorsal margin is more concave. It is generally white or white tinged with pink.

A large specimen collected at Panama by James Zetek measures: length, 36 mm.; height, 31 mm.; convexity (both valves together), 13.8 mm.

This species has been cited from west American waters under the name of *Strigilla sincera* Hanley<sup>84</sup> which, according to Hedley<sup>85</sup>, is an Australian species. Salisbury<sup>86</sup> in 1934 stated that *Strigilla sincera* occurs in the Panamic area but he did not mention Hedley's remarks on that species.

*Distribution*: Two single valves of this species were dredged by the expedition at Corinto, Nicaragua, in 8 fathoms, and one valve was taken on shore. This is an extension north of the known range of the species.

***Strigilla lenticula* Philippi.**

Plate I, Fig. 21.

*Tellina lenticula* Philippi, *Zeit. f. Malakozool.*, Jahrg. 3, February, 1846, p. 19. "Patria: Mazatlan."

*Strigilla serrata* Mörch, *Malakozool. Blätter*, Bd. 7, December, 1860, p. 189. Central America.

*Strigilla lenticula* Philippi, Dall, *Proc. U. S. Nat. Mus.*, Vol. 23, No. 1210, 1900, p. 305. Cape San Lucas to Central America.

*Type Locality*: Mazatlan, Mexico.

*Range*: Cape San Lucas, Lower California, to Corinto, Nicaragua.

*Collecting Stations*: Nicaragua: Corinto (200-D-11, 17, 19, also on beach), 7-13 fathoms, sand, mangrove leaves.

*Description*: Shell small, about 8 mm. in length, rounded, inflated, white, sculptured with well-developed, oblique, incised striae which posteriorly develop small chevron-shaped situations.

A large right valve of this species, dredged off Corinto, Nicaragua, in 13 fathoms, measures approximately: length 8 mm.; height, 7 mm.; convexity (one valve), 2.7 mm.

The rounded form, white color, and slight development of V-shaped situations in the sculpture posteriorly are characters which easily serve to separate this species from others of the genus in west American waters.

*Strigilla flexuosa* Say, an east American species, is a very similar form.

*Distribution*: This little species was taken by the expedition only at Corinto, Nicaragua, on the beach and at depths of 7-13 fathoms.

<sup>84</sup> *Tellina sincera* Hanley, *Proc. Zool. Soc. London*, April, 1844, p. 68. "Hab.—? Mus. Cuming, Metcalfe." —Hanley, *Thes. Conch.*, Vol. 1, 1846, p. 261, pl. 60, fig. 144. [Not the record "N. W. Coast of America, (Dr. Sinclair)," according to Hedley].

<sup>85</sup> *Strigilla sincera* Hanley, Hedley, *Proc. Linn. Soc. New South Wales*, Vol. 38, Pt. 2, 1913, p. 272. *Strigilla grossiana* Hedley, 1908, was considered by Hedley to be a synonym of *S. sincera* Hanley.

<sup>86</sup> Salisbury, A. E., *Proc. Malacol. Soc. London*, Vol. 21, Pt. 2, July, 1934, p. 89.

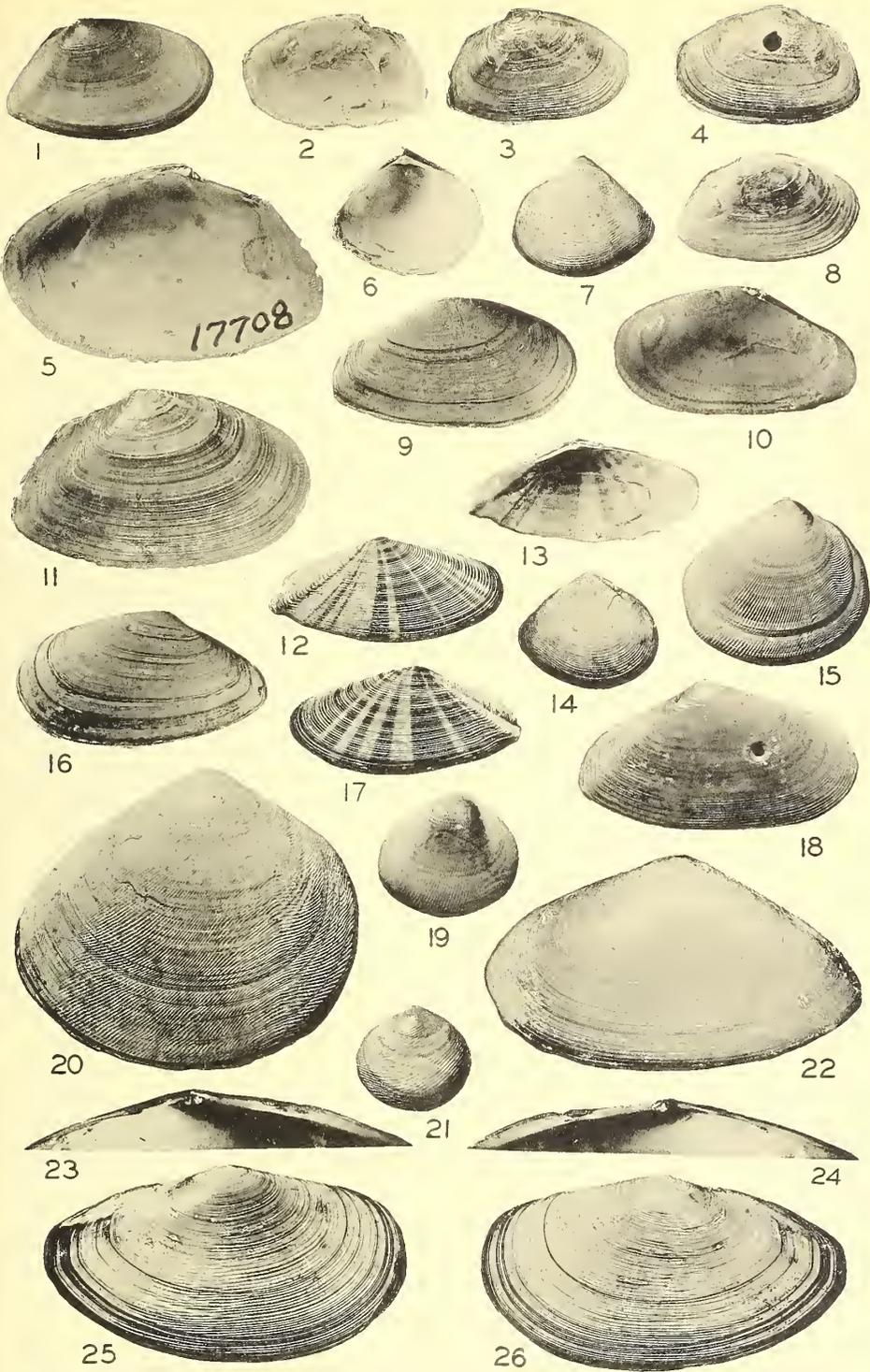
## EXPLANATION OF THE PLATE.

## PLATE I.

- FIG. 1. *Tellina (Moerella) felix* Hanley. Hypotype, right valve, from Monypenny Point, Gulf of Fonseca, Nicaragua. Length, 17 mm.; height, 10 mm. View of exterior. P. 70.
- FIG. 2. *Tellina (Moerella) recurvata* Hertlein & Strong, sp. nov. Holotype, right valve, from Loc. 23802 (C.A.S.), San Luis Gonzaga Bay, Lower California, in the Gulf of California. Length, 12 mm., height, 7.5 mm. P. 71
- FIG. 3. *Tellina (Moerella) recurvata* Hertlein & Strong, sp. nov. Holotype. View of the exterior of the specimen shown in Fig. 2.
- FIG. 4. *Tellina (Moerella) recurvata* Hertlein & Strong, sp. nov. Holotype, left valve. View of the exterior of the left valve of the specimen shown in Figs. 2 and 3.
- FIG. 5. *Tellina (Moerella) arenica* Hertlein & Strong, sp. nov. Holotype, right valve, from Station 136-D-20, Lat. 23° 30' N., Long. 109° 26' W., Arena Bank, Gulf of California, dredged in 43 fathoms (78 meters), mud. View of interior. P. 68.
- FIG. 6. *Tellina (Merisca) proclivis* Hertlein & Strong, sp. nov. Holotype, left valve, from Loc. 20299 (C.A.S.), Magdalena Bay, Lower California, Mexico. Length, 9 mm.; height, 7.8 mm. View of interior. P. 83.
- FIG. 7. *Tellina (Merisca) proclivis* Hertlein & Strong, sp. nov. Holotype. View of the exterior of the specimen shown in Fig. 6.
- FIG. 8. *Tellina (Moerella) recurvata* Hertlein & Strong, sp. nov. Paratype, right valve, from the same locality as the holotype shown in Figs. 2, 3 and 4. Length, 11.5 mm.; height, 7 mm.
- FIG. 9. *Macoma (Psammacoma) panamensis spectri* Hertlein & Strong, subsp. nov. Paratype, right valve, from Station 143-D-3, Lat. 26° 57' N., Long. 111° 56' W., Santa Inez Bay, Lower California, in the Gulf of California, dredged in 35 fathoms (64 meters), mud, crushed shell. Length, 33.8 mm.; height, 18 mm. P. 91.
- FIG. 10. *Macoma (Psammacoma) panamensis spectri* Hertlein & Strong, subsp. nov. Paratype. View of the interior of the specimen shown in Fig. 9.
- FIG. 11. *Tellina (Moerella) arenica* Hertlein & Strong, sp. nov. Holotype. View of the exterior of the specimen shown in Fig. 5.
- FIG. 12. *Tellina (Tellinella) zacae* Hertlein & Strong, sp. nov. Holotype, right valve, from Station 136-D-1, Lat. 23° 29' N., Long. 109° 25' W., Arena Bank, Gulf of California, dredged in 45 fathoms (82 meters), mud. Length, 33.4 mm.; height, 15.2 mm. P. 65.
- FIG. 13. *Tellina (Tellinella) zacae* Hertlein & Strong, sp. nov. Holotype, left valve. View of the interior of the left valve of the specimen shown in Fig. 12.
- FIG. 14. *Tellina (Merisca) proclivis* Hertlein & Strong, sp. nov. Holotype, Right valve of the specimen shown in Figs. 6 and 7.
- FIG. 15. *Strigilla costulifera* Mörch. Hypotype, right valve, from Loc. 4798 (C.A.S.), Lower California; Henry Hemphill Coll. Length, 25 mm.; height, 22 mm. P. 95.
- FIG. 16. *Macoma (Psammacoma) panamensis spectri* Hertlein & Strong, subsp. nov. Holotype, left valve, from the same locality as the paratype shown in Figs. 9 and 10. Length, 34.4 mm.; height, 18.4 mm. P. 91.
- FIG. 17. *Tellina (Tellinella) zacae* Hertlein & Strong, sp. nov. Holotype. View of the exterior of the specimen shown in Fig. 13. P. 65.
- FIG. 18. *Tellina (Eurytellina) inaequistriata* Donovan. Hypotype, right valve, from Station 195-D-21, Lat. 15° 44' 45" N., Long. 96° 06' 55" W., Santa Cruz Bay, Mexico, dredged in 18 fathoms (33 meters), mud, crushed shell. Length, 23 mm.; height, 12.5 mm. P. 74.
- FIG. 19. *Strigilla cicercula* Philippi. Hypotype, right valve, from Station 200-D-19, Lat. 12° 28' 03" N., Long. 87° 12' 39" W., Corinto, Nicaragua, dredged in 12-13 fathoms (22-24 meters), mangrove leaves. Length, 9.6 mm.; height, 8.5 mm. P. 95.
- FIG. 20. *Strigilla disjuncta* Carpenter. Hypotype, right valve, from Panama; James Zetek Coll. Length, 36 mm.; height, 31.3 mm. P. 96.
- FIG. 21. *Strigilla lenticula* Philippi. Hypotype, right valve, from the same locality as the specimen shown in Fig. 19. Length, 7.9 mm.; height, 7.0 mm. P. 96.
- FIG. 22. *Tellina (Eurytellina) planulata* Sowerby. Hypotype, left valve, from 1 mile south of entrance to Golfito Bay, Costa Rica. Length, 51.8 mm.; height, 29.5 mm. P. 76.
- FIG. 23. *Tellina (Scissula) nicoyana* Hertlein & Strong, sp. nov. Holotype, right valve, from Ballena Bay, Costa Rica. Length, 34.4 mm.; height, 19 mm. View of hinge. P. 85.
- FIG. 24. *Tellina (Scissula) nicoyana* Hertlein & Strong, sp. nov. Holotype, left valve. View of hinge.
- FIG. 25. *Tellina (Scissula) nicoyana* Hertlein & Strong, sp. nov. Holotype, right valve. View of the exterior of the specimen shown in Fig. 23. P. 85.
- FIG. 26. *Tellina (Scissula) nicoyana* Hertlein & Strong, sp. nov. Holotype, left valve. View of the exterior of the specimen shown in Fig. 24. P. 85.

All the specimens illustrated on this plate are in the type collection of the Department of Paleontology of the California Academy of Sciences.





MOLLUSKS FROM THE WEST COAST OF MEXICO AND CENTRAL AMERICA.



## 10.

## Fishes That Rank Themselves Like Soldiers on Parade.

E. W. GUDGER.

*American Museum of Natural History.*

(Plate I; Text-figures 1 &amp; 2).

## INTRODUCTION.

I have read that some mammals, such as the American bison and the antelopes of South Africa, advance, wheel and deploy in something like military order. But it is doubtful if they form in ranks with heads in a real military formation. We all know that migrating birds fly in fair formation and some writers have alleged that some aquatic birds will fish in synchronous order. But so far as known, no one seems to have produced photographic evidence of this latter alleged behavior.

For reptiles we apparently have no photographic evidence, but there are at least two written accounts that surely establish the matter of ranked formation. The first of these is from the pen of the old naturalist, William Bartram. In 1774 (*Travels through North and South Carolina, Georgia, and . . . Florida, etc.* London, 1792, p. 118), while ascending the St. Johns River in eastern Florida, he found great numbers of huge and very aggressive alligators. Some of these threatened attacks on his little boat, when he sought to go into a lagoon off the river to catch some fish for his supper. He says—"I . . . made good my entrance into the lagoon, though not without opposition from the alligators who formed a line across the entrance but did not pursue me into it." Here the alligators were ranked in a line, apparently waiting for the fishes to try to get out into the main stream, when the alligators too would get their supper.

This account is counterbalanced by a parallel description of what C. R. S. Pitman (*A Game Warden Among his Charges*, London, 1931, p. 248) saw just below Murchison Falls on the Nile River in East Central Africa, where crocodiles are found in incredible numbers. "Looking from above on a still evening, one will be struck by the regular formation taken up by row after row of crocodiles, like ships of war, with intervals of about 50 feet between each crocodile [and those on either side] and 300 feet between the rows, which extend from bank to bank and for about two miles down stream." But let a fish come down and all is wild confusion

and struggle of the neighboring crocodiles to get it or at least a portion of it.

The more we know about animals, the more we find them doing unusual and unexpected things. It is not safe offhandedly to contradict accounts by non-scientific observers of unusual behavior not otherwise physically impossible—in fishes, as well as in other animals. No article has been found in this search describing regimented fishes and bearing such a title as that at the head of this report. However, there is widely scattered evidence that fishes do "fall in and form ranks." Unfortunately, I have never had the opportunity to see fishes take on a military formation but various reputable observers have, and their cumulative evidence will now be set forth chronologically.

## FISHES RANKED LIKE SOLDIERS ON PARADE.

The earliest account of ranked fishes found in this search is by a writer in *The New Monthly Magazine*, 1820, part II, p. 137, who signs himself "Amateur." This account is also found in Thomas Boosey's "Anecdotes of Fish and Fishing," London, 1887, p. 123.

"Amateur", in writing of the exploits of one Darcey of Oxford, an expert swimmer and diver, who caught fishes with his hands in a deep hole well-known to Oxonians, makes the following statement:—

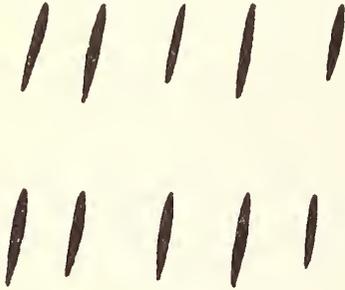
The report that Darcey made, was that many of these fish [barbel] lay with their heads against the bank, in parallel line, like horses in their stalls. They were not disturbed at his approach, but allowed him to come close and select the finest.

In talking over this unusual matter with my long-time friend, the late Dr. John L. Peters, an upstate New York man, he told me that in his boyhood he had seen this very thing in a stream in Ulster County. At my request he prepared a statement of his observations, which is the earliest American evidence that has come to hand.

In 1907 or 1908, while trout-fishing in the headwaters of Woodland Stream in Ulster Co., New York, my attention was called to the

peculiar formation of some brook trout after a disturbed pool had quieted down. They seemed to line up in a formation as if some military officer among them had got them ready for a parade. This I saw more than once since I used to go out of my way to watch the trout in this pool. When disturbed, they would scatter, but when things quieted down, they would again take on their military formation.

This pool was just below a little rapid in a narrow stream. It was about 8 feet wide, 3 feet deep at its head and about 6 or 8 inches at its shallow end. Dr. Peters drew a little diagram (Text-fig. 1) to show how the fishes were ranked.



TEXT-FIG. 1. Diagram of trout on parade, in Woodland Stream, Ulster County, New York, 1907 or 1908. Sketch by Dr. John L. Peters.

Chronologically our next evidence is in a personal communication from Mr. Joshua W. Atlee of Riverton, New Jersey. He wrote that in October, 1911, he saw ranked fishes in a pool in a rivulet flowing into the Bay of Chaleur, Gulf of St. Lawrence. Carefully pushing aside the shrubbery on the bank of the pool, he had a clear view of it and its piscine inhabitants, which he thought were getting ready for spawning. Of these fishes he noted that:

An interesting feature of the sight was the fact that in the slowly moving water, due to the [small] volume of the pool, the fish lay in "sardine fashion" closely packed with heads upstream, stemming the current so as to retain a similar relative position by the slight movement of their tails and fins.

Finally on being disturbed, some left the pool in various directions, mostly upstream; but my guide, detouring and getting into the stream above them, actually drove many of the trout back into the pool, where they finally settled down again as we had first found them.

My next evidence is from Mr. Howard B. MacDonald of Yonkers, N. Y., a traveler and lecturer of wide experience. A photograph taken by him at Rotorua, New Zealand, in 1925, is reproduced as Plate I, Fig. 1. Of it he wrote (personal communication) as follows:

Unfortunately, the photograph does not show the fish in quite such straight lines as the other picture you have. However, these fish I saw did act in the same manner as the ones you are studying. Each fish had a certain definite position in relation to the others of this company;

and if the fish were disturbed by throwing a stone into the water near them (as we all did) then they would scatter, but each would return almost immediately to his same position in the group. This was checked and verified by observation many times and there is no doubt but that each fish knew his correct position and always went to it.

Here is the word of another reliable observer, backed by photographic evidence. As Mr. MacDonald says, this is not such as may be seen in Plate I, Fig. 2, but discounting shadows, the fish are in pairs and they are lined up fairly well in ranked rows.

And now follows an excerpt from a personal communication from Dr. Louise M. Perry, long a winter resident of Sanibel Island off Fort Myers, southwest coast of Florida. Dr. Perry, an acute observer for many years of the habits of marine fishes in that region, writes as follows under date of July 26, 1926:

Naples, Florida [below Fort Myers], has a fine pier for still fishing, and while waiting for bites, I have repeatedly watched small schools of snook (rovalle) 8 or 12 in a group, lying on the sandy bottom, close together and parallel with each other, all heading the same way and all their tails gently moving to right and left in perfect unison. Suddenly with a rush they would dart into a school of minnows and play havoc for a moment, then each would gently settle down in its former place and position. This performance would be repeated at fairly regular intervals for a long time, and always made me wonder how separate individual actions could be so perfectly synchronized. How do they do it? What is the stimulus that keeps all the tails waving to marching time and starts the snook off in a simultaneous dash after the little fish?

Specific attention is called to the fact that all the tails of these marine fishes moved to right and left in perfect unison. And so did the tails of the freshwater fishes observed by Mr. Atlee in 1911 in the rivulet flowing into the Bay of Chaleur, Gulf of St. Lawrence. Presumably the same purpose activated both lots of fishes—to maintain position.

And now, also in 1926, come three accounts of this behavior of other marine fishes at the Galápagos Islands, from the pen of that veteran observer, William Beebe, in his "Arc-turus Adventure" (New York, 1926). On p. 54 he states that they paid out strings with pieces of bait and enticed three sharks alongside their boat. Here follows his description of the behavior of a large shark and its attendants.

... by pulling in the tempting morsel two feet in front of the eager blunt snouts, we brought them to the surface directly under our feet, so that we could watch the movements of the brilliant blue pilotfish, that . . . anticipated every movement of their huge patrons. One of the big fellows had three of these little satellites that unflinchingly held their formation, one just above his head, the other two in perfect alignment a few inches in front of his jaws. So exactly synchronized are the movements . . . that

it is impossible to tell whether the shark follows the pilotfish or the pilotfish the shark.

Again Beebe (1926, p. 183) notes that:

Two mighty schools of *Xesurus laticlavus* [the yellow-tailed surgeonfish] passed me grazing slowly. When within six feet, they left off their eternal feeding and formed up into more or less orderly ranks which flowed like some enormously long sea-serpent around the identical corners of rocks where had passed the leaders, yards and yards in advance. Invariably the formation of an irregular line led very close to me, the closing up of ranks evidently being connected with the presence of danger or at least something suspicious or strange.

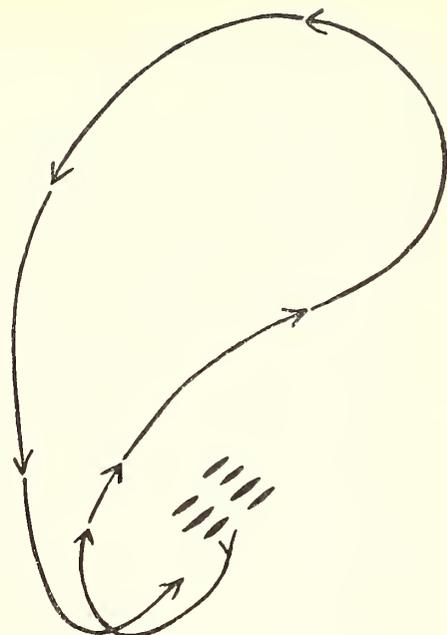
Further, Beebe (1926, pp. 290-291) makes note of another synchronous action of the yellow-tailed surgeonfish: "Several hundred approached swimming slowly along, when, as if at a signal, all would stop, and over a rather flat bottom would up-end like ducks and begin to graze ["on the plant and animal fodder which covers the rocks," p. 290].

On February 27, 1929, the late Prof. M. M. Metcalf wrote—"I am sending you some quotations [copied] from an old letter. These . . . aroused my interest at the time the observations were made some years ago." These observations were by another man, and lacking a name and date, will be entered under date (1929) of the covering letter. The pertinent quotation reads as follows:

. . . I saw in the clear pool below Trick Falls in the Two Medicine River in Glacier National Park seven trout behaving in a way that seemed interesting. They were headed into the current and were lying motionless in two perfectly straight rows, four in the front row and three in the back row, aligned as accurately as a squad of well drilled soldiers. A moth came flipping over the pool, touching the water now and then. All the trout remained quiet, except that the right trout in the rear row turned to the right and backed around the left end of the squad, caught the moth, returned around the left end of the squad to his place at the right end of the rear row again, and they all remained in perfect formation for the several minutes I watched them.

On the margin of the typed sheet is a pencil sketch of the movements of the trout at the right hand end of the second rank. This is reproduced herein as Text-fig. 2, and is a graphic presentation of the interesting action of this particular fish.

The well-known sports magazine, *Field and Stream*, for November, 1929, p. 104, has reproduced the splendid photograph shown in Plate I, Fig. 2. It is also reproduced (in larger size) in the same journal for June, 1935, p. 44. But in neither issue is there any account of the phenomenon, marvellous as it is. The 1929 figure has this caption: "A most extraordinary photograph of resting trout in the Brule River, 40 miles from Duluth, Minnesota. Note the very unusual formation—like soldiers on parade." The 1935 issue has a caption which remarks that "When great schools of fish lie in still water, it takes a



TEXT-FIG. 2. Trout in two ranks in Two Medicine River, Glacier National Park. The right trout in row two, backed out and followed the course indicated to catch a moth dipping in the water, and then returned to his position. Sketch furnished by Prof. M. M. Metcalf, 1929.

skillful angler to interest them" — and nothing about military formation in the article in which the figure is set.

Here is a priceless photograph showing eight rows of "trout on parade." It is apparently the only one ever published of this unique, indeed phenomenal, behavior of fishes, and there is no word of comment beyond the caption. It seems incredible, but such is the fact. However, the figure splendidly illustrates the accounts quoted above. But before going further, the present writer submits the following remarks.

Trout at rest in running water always face upstream. In pools, especially small ones, they are likely to do the same. In "trout water," such a pool always has a riffle or rapid at its head, and just below this the water is cooler and has more oxygen than ordinary. Gill-breathing is much easier in fishes facing upstream. Also, in such position, the fish can readily snap up any edibles coming down with the current. These would seem to explain, in part at least, the heads-upstream of this regiment of trout.

At first glance, in Plate I, Fig. 2, we see scores of trout in right-left ranks—fishes on parade—and the ranks separated by right-left stretches of gravel swept clean of fine detritus. Now let us recall that Mr. Atlee found ranked trout in the stream leading into the Bay of Chaleur, Gulf of St. Lawrence, maintaining their positions by moving their tails right and left in unison. Also Dr. Perry saw marine fishes at Naples, southwest coast

of Florida, acting in similar fashion. So we must conclude that the trout in Plate I, Fig. 2, were doing this very thing. Any given rank of trout fans out the fine detritus under the tails of its members. This is checked and some of it precipitated by the bodies of the rank of fishes just behind it—and so all the way from the foremost rank to the hindmost. Probably these rows of trout lie on gently backward sloping ridges of the detritus. This cleaning action holds best for the center of the stream but fades out somewhat on the edges where the current is weaker.

The collecting of data for an article on military fishes was begun more than 20 years ago. But the work went slowly and presently press of other work—particularly the editing of the Bashford Dean Memorial Volume—led to the filing away of all material till a more convenient time—which has just come. During this period of inactivity in this study; letters came in from a few persons who had heard of my interest in this problem. But their statements were in very general terms, and quite unclear. Had I taken the time to ask for more specific accounts of what they saw, I might have gotten additional valuable data. Now it is too late.

However, abundant evidence is to be found in the written accounts and in the sketches and photographs herein to establish the fact that various fishes, but especially trout, do rank themselves in parade order. These data certainly justify the title of this article. For

trout in running water, some tenable explanation has been advanced. But for trout and all other fishes, where behavior has been described, there must be a more fundamental universal reason. This no one has attempted—the explanation must be left to the animal behaviorists.

Finally, it may be said that, from the comments of several friends, who know of the work on this article, I am satisfied that this curious behavior of ranked fishes, "fishes on parade," is not at all uncommon. In fact, it is probably far better known than the present writer realizes. However, it is a curious thing that in this study there has not been found a single article with such an indicative title as this paper bears and it is hoped that others, who have witnessed this curious behavior, will publish their observations and thus establish this parade behavior as a normal procedure.

## EXPLANATION OF THE PLATE.

### PLATE I.

- Fig. 1. Ranked trout in a pool at Rotorua, New Zealand. Discounting the shadows, the trout are seen to be roughly ranked in pairs. Photograph by Howard B. MacDonald.
- Fig. 2. Resting trout in eight ranks, like soldiers on parade, photographed in the Brule River, 40 miles from Duluth, Minnesota. From *Field & Stream*, 1929.

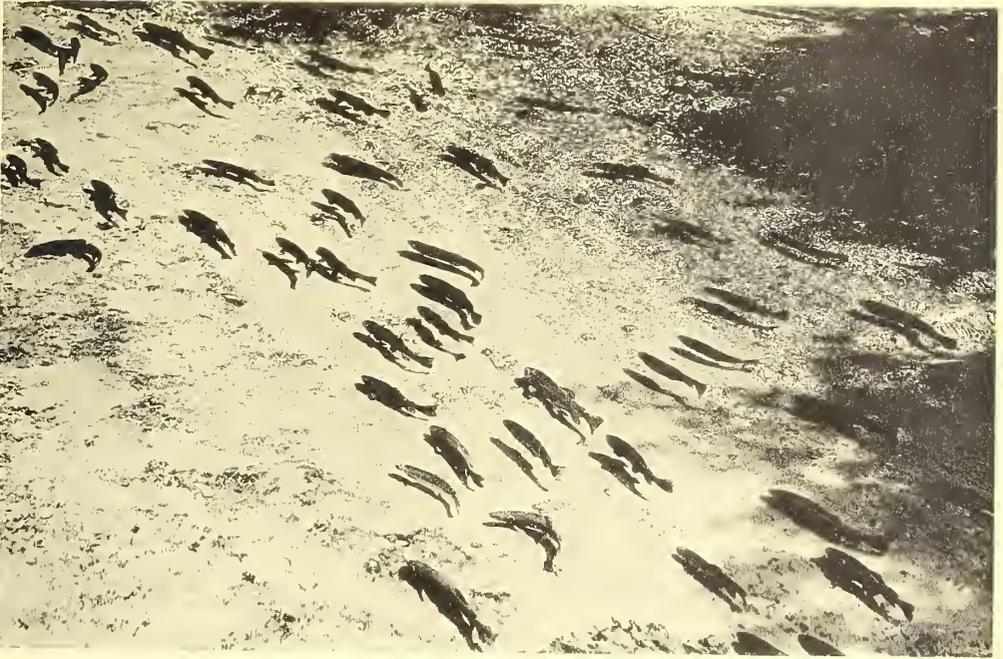


FIG. 1.

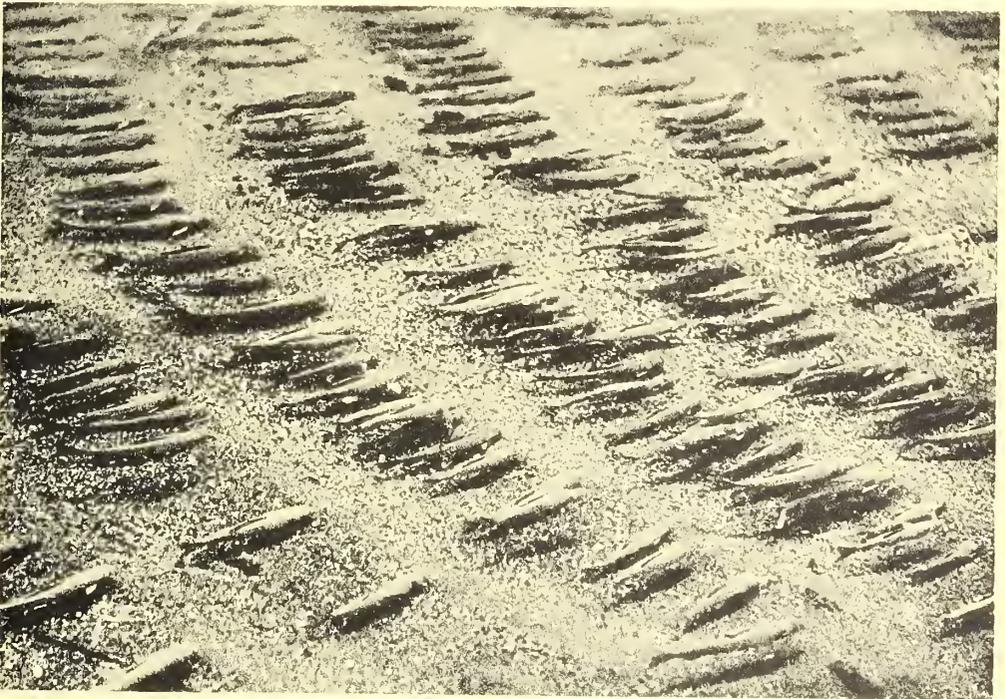


FIG. 2.

FISHES THAT RANK THEMSELVES LIKE SOLDIERS ON PARADE.



## 11.

Notes on Seasonal Changes in *Creatophora cinerea*, the Wattled Starling.

LEE S. CRANDALL.

(Plate I).

The Wattled Starling (*Creatophora cinerea*), is an African member of the family Sturnidae. It has a rather wide distribution, extending from southwestern Arabia through East Africa to the Cape. An investigation of seasonal changes in males of this species is outlined in the following notes.

## SEQUENCE 1.

A young specimen of the Wattled Starling (*Creatophora cinerea*) of undetermined sex, and unknown locality, was received at the New York Zoological Park on October 17, 1927.

During the entire period of observation this bird, as well as the others noted, was kept in an indoor, heated aviary from October to May, with access to an outdoor cage during the intervening months.

At the time of arrival, the head and throat were completely feathered and only the usual narrow, bare malar streaks were visible.

In the spring of 1928, the bird showed itself to be a male by an enlargement of the throat wattle, although there was no evidence of crown wattles and no loss of plumage of the head.

In the spring of 1929, the throat wattle again became enlarged, a small area of the forehead became bare and the crown wattles appeared, reaching an upright maximum of about  $\frac{1}{8}$ ".

On April 19, 1930, the feathers of the forehead were dropping out. By May 9, the crown and face were black and entirely bare, except for a small tuft behind each nostril. The occipital region was bare and yellow.

The crown wattles, completely sessile, had no power of erection. The posterior wattle, attached longitudinally, measured 9 mm. at the base, expanding to a width of 11 mm. and reaching a length of 20 mm. The anterior wattle, set at an approximate right angle to the longitudinal center line, overhung the base of the bill and was overhung, in turn, by the posterior wattle. Its width at the base was 7 mm., its greatest width was 15 mm. and its greatest length 11.5 mm.

The throat wattle, along the anterior margin, measured 40 mm. when drawn out with the fingers. (As this wattle is slightly re-

tractile, an accurate measurement could not be made.) It is bifurcated at the tip, the right division measuring 9 mm., the left 12 mm.

At this time, the bird indulged in mild courtship maneuvers, tossing his head so that the crown wattles might fall on one side or other, and singing a broken and guttural song.

On August 25, the wattles were seen to be shrinking and feathers of head and face growing. This process continued until, on September 14, the wattles were entirely withdrawn and feathering was complete. However, the nodular crown wattles, normally invisible, remained discernible when the plumage was tightly compressed. Also, the malar streaks, from which the throat wattle had sprung, remained slightly more pronounced than in an immature male or a female.

During the following years, changes took place as follows:

- 1931. April 11. Feathers dropping.  
May 2. Change complete.  
September 26. Feathers growing.  
October 17. Change complete.
- 1932. March 1. Feathers dropping.  
March 22. Change complete.  
September 19. Head feathering, wattles shrinking.  
October 10. Change complete.
- 1933. January 4. Feathers dropping.  
January 25. Change complete.  
August 18. Head feathering.  
September 12. Change complete.  
December 1. Feathers dropping.  
December 26. Change complete.
- 1934. September 12. Head feathering.  
October 1. Change complete.
- 1935. February 27. Feathers dropping.  
March 22. Change complete.  
September 30. Head feathering.  
October 22. Change complete.  
December 30. Feathers dropping.
- 1936. January 13. Change complete.  
January 20. Feathers re-growing, wattles shrinking.

- February 3. Head entirely re-feathered, wattles partly retracted.  
 February 10. Feathers dropping again, wattles enlarging.  
 February 24. Change complete, wattles fully extended, bird singing.  
 September 21. Feathers growing.  
 October 14. Change complete.  
 December 21. Feathers dropping.
1937. January 8. Change complete.  
 September 20. Feathers growing.  
 October 7. Change complete.  
 December 20. Feathers dropping.
1938. January 3. Change complete, wattles fully enlarged.  
 February 7. Feathers re-growing, wattles shrinking.  
 February 21. Feathering complete.  
 March 7. Feathers dropping again, wattles enlarging.  
 March 28. Change complete.  
 September 12. Feathers growing.  
 October 1. Change complete.  
 December 19. Feathers dropping.
1939. January 6. Change complete.  
 March 5. Observations ended by death of subject.
- #2. April 12. Feathers dropping.  
 April 29. Change complete, crown wattles minute, throat wattle deeply pendant.  
 October 25. Feathers growing.  
 November 14. Change complete.
1938. #1. February 28. Feathers dropping.  
 March 16. Change complete.  
 October 31. Feathers growing.  
 November 18. Change complete.  
 #2. March 28. Feathers dropping.  
 April 18. Change complete, crown wattles minute.  
 October 2. Feathers growing.  
 October 21. Change complete.
1939. #1. March 6. Feathers dropping.  
 March 25. Change complete.  
 October 23. Feathers growing.  
 November 10. Change complete.  
 #2. March 20. Feathers dropping.  
 April 7. Change complete, crown wattles minute.  
 October 23. Feathers growing.  
 November 15. Change complete.
1940. #1. February 26. Feathers dropping.  
 March 15. Change complete.  
 September 23. Feathers growing.  
 October 9. Change complete.  
 #2. April 8. Face feathers dropping.  
 April 27. Change complete, crown wattles minute.  
 October 28. Feathers dropping.  
 November 13. Change complete.

## SEQUENCE 2.

Two Wattled Starlings which proved to be males, were received on December 14, 1934, from a dealer. The locality from which they had come was unknown. These birds were kept together, under identical conditions, during the course of the following observations. They are designated as #1 and #2. Both were fully feathered on arrival.

1935. #1. May 1. Feathers dropping.  
 May 21. Change complete, crown and throat wattles well developed.  
 October 21. Feathers growing, wattles shrinking.  
 November 13. Change complete.  
 #2. June 5. Throat wattle enlarged, feathers dropping.  
 June 24. Face and crown bare, throat wattle pendant, no evidence of crown wattles.  
 October 28. Feathers growing.  
 November 11. Change complete.
1936. #1. April 6. Feathers dropping.  
 April 26. Change complete.  
 October 26. Feathers growing.  
 November 13. Change complete.  
 #2. April 27. Feathers dropping.  
 May 16. Change complete, crown wattles minute.  
 November 2. Feathers growing.  
 November 20. Change complete.
1937. #1. March 15. Feathers dropping.  
 March 31. Change complete.  
 October 18. Feathers growing.  
 November 6. Change complete.
1941. #1. March 3. Feathers dropping.  
 March 23. Change complete.  
 October 13. Feathers growing.  
 October 29. Change complete.  
 #2. April 14. Feathers dropping.  
 May 4. Change complete, crown wattles minute.  
 October 27. Feathers growing.  
 November 14. Change complete.
1942. #1. March 9. Feathers dropping.  
 March 31. Change complete.  
 September 28. Feathers growing.  
 October 19. Change complete.  
 #2. March 30. Feathers dropping.  
 April 20. Change complete, crown wattles minute.  
 November 9. Feathers growing.  
 November 29. Change complete.
1943. #1. February 15. Feathers dropping.  
 March 8. Change complete.  
 #2. March 15. Feathers dropping.  
 April 7. Change complete.

## SEQUENCE 3.

Two Wattled Starlings which appeared to be male and female, were purchased from Christoph Schulz on August 9, 1935. They were reported by Schulz to have been collected in Kenya. The male was in breeding condition at the time of arrival, with head bare and wattles well developed.

Throughout the course of observations on this pair, the female showed no plumage change and no enlargement of the bare malar streaks, at the time the male was coming into breeding condition. During October and November of each year she went through a complete body molt.

Changes in the male were noted as follows:

1935. October 22. Feathers growing.  
November 13. Change complete.
1936. April 6. Feathers dropping.  
April 24. Change complete, wattles well developed.  
October 5. Feathers growing.  
October 27. Change complete.
1937. January 18. Feathers dropping.  
February 4. Change complete.  
March 1. Feathers re-growing.  
March 15. Face almost completely feathered, wattles shrunken.  
March 22. Feathers dropping again, wattles re-enlarging.  
April 2. Head entirely bare, wattles large.  
October 25. Feathers growing.  
November 12. Change complete.
1938. February 14. Feathers dropping.  
March 3. Change complete but wattles small.  
March 28. Face re-feathering.  
April 11. Face almost entirely re-feathered.  
April 18. Feathers dropping again.  
May 5. Change complete, wattles much enlarged.  
October 31. Face feathers growing.  
November 19. Change complete.
1939. March 27. Feathers dropping.  
April 17. Change complete.  
October 9. Feathers growing.  
October 30. Change complete.

1940. February 26. Feathers dropping.  
March 20. Change complete.  
September 23. Feathers growing.  
October 10. Change complete.
1941. March 24. Feathers dropping.  
April 12. Change complete.  
September 29. Feathers growing.  
October 18. Change complete.
1942. March 2. Feathers dropping.  
March 20. Change complete.  
October 5. Feathers growing.  
October 23. Change complete.
1943. February 15. Feathers dropping.  
March 6. Change complete.

#### SUMMARY.

Seasonal changes in four male and one female specimens of the Wattled Starling (*Creatophora cinerea*) have been tabulated and described. All of these birds were kept under identical conditions, as far as caging, food and temperatures were concerned. It is shown that in the males there is a seasonal loss of the plumage of the head, accompanied by enlargement of the crown and throat wattles. The single female showed no enlargement of the bare gular tracts and had only a single annual change of plumage, which took place at the period of regression in the accompanying male.

The males of Sequence 1 and Sequence 3 showed occasional "false starts," in which newly bared heads almost immediately re-feathered, quickly followed by a resumption of the bare condition. Neither of the two males described in the second series of observations showed this phenomenon.

Recorded dates of changes were established on a visual basis. However, standards of judgement were the same in all cases, so that periods indicated are properly comparable and variations would be small.

## EXPLANATION OF THE PLATE.

## PLATE I.

- FIG. 1. Adult ♂ Wattled Starling (Sequence 1), photographed on June 13, 1933. The head is completely bare and wattles fully developed.
- FIG. 2. The same bird, photographed on November 20, 1934. He has completed regressive changes and is in resting condition. The nodular crown wattles, not normally visible at this time, are seen because the feathers are tightly compressed. The throat wattle has receded to the lateral malar patches.



FIG. 1.



FIG. 2.

NOTES ON SEASONAL CHANGES IN *CREATOPHORA CINEREA*, THE WATTLED STARLING.



## 12.

Insect Migration at Rancho Grande in North-central Venezuela.  
General Account.<sup>1</sup>

WILLIAM BEEBE.

*Director, Department of Tropical Research,  
New York Zoological Society.*

(Plates I &amp; II; Text-figure 1).

[This is one of a series of papers resulting from the 45th, 46th and 47th Expeditions of the Department of Tropical Research of the New York Zoological Society, made during 1945, 1946 and 1948, under the direction of Dr. William Beebe, with headquarters at Rancho Grande in the National Park of Aragua, Venezuela. The expeditions were made possible through the generous cooperation of the National Government of Venezuela and of the Creole Petroleum Corporation.]

[The characteristics of the research area are in brief as follows; Rancho Grande is located in north-central Venezuela (10° 21' N. Lat., 67° 41' W. Long.), 80 kilometers west of Caracas, at an elevation of 1,100 meters in the undisturbed montane rain forest which covers this part of the Caribbean range of the Andes. The migration flyway of Portachuelo Pass, which is also the water-shed between the Caribbean and Lake Valencia, is 200 meters from Rancho Grande. Adjacent ecological zones include seasonal forest, savanna, thorn woodland, cactus scrub, the fresh-water lake of Valencia and various marine littoral zones. The Rancho Grande area is generally subtropical, being uniformly cool and damp throughout the year because of the prevalence of the mountain cloud cap. The dry season extends from January into April. The average humidity during the expeditions, including parts of both wet and dry seasons, was 92.4%; the average temperature during the same period was 18° C; the average annual rainfall over a five-year period was 174 cm. The flora is marked by an abundance of mosses, ferns and epiphytes of many kinds, as well as a few gigantic trees. For further details see Beebe and Crane, *Zoologica*, Vol. 32, No. 5, 1947. Unless otherwise stated, the specimens discussed in the present paper were taken in the montane cloud forest zone, within a radius of one kilometer of Rancho Grande.]

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<sup>1</sup>Contribution No. 843, Department of Tropical Research, New York Zoological Society.

## GENERAL ACCOUNT.

Throughout the first year of our occupation of the station at Rancho Grande in north-central Venezuela, we had no idea of the importance of Portachuelo Pass as a migration flyway for birds and insects. Even later on, when we came to compile a list of thirteen life zones within our visual radius, a fourteenth, the Aerial Zone, was added with hesitation, having in mind the inclusion of organisms such as hummingbirds, swifts and mayflies which spend the major part of their lives in midair. Almost immediately, however, the value of and need for such a niche in our phenological program became apparent.

If for no other reason, an Aerial Zone was needed to accommodate the volant organisms which passed and repassed, or occasionally were detected soaring in air, and which were never to be found resting or flying in the jungle of our immediate area of research. Many of these creatures were essentially tropical, occupying our subtropical elevation only as a temporary route of passage.

About 200 meters beyond Rancho Grande, the road leads through a narrow notch in the east-west, coastal Andean range. This is Portachuelo Pass with an elevation of 1,136 meters, about 36 meters higher than Rancho Grande. The flattened floor of the pass is only about 20 meters wide, and the shoulders on either side rise in sharp ridges, 389 meters to the summit of Pico Periquito on the west, and 764 meters on the east to the top of Pico Guacamayo.

The pass is at the 22.5 kilometer mark on the road from Maracay, and, as has been stated, is at an elevation of 1,136 meters. Kilometer 31, well to the north of the pass, is 770 meters above the sea. Kilometer 15, equally distant to the south of the pass and close to the beginning of the lowland savanna, is 760 meters above the sea. At both of these lower stations many migrants have been taken, en route to or on their way from the pass.

The pass is on the real divide, shunting the waters on its northern slope into the

Caribbean Sea, and those on the south side ultimately into Lake Valencia.

Fifteen orders of insects have already been collected or observed as they passed southward on migration, singly, in few or in enormous numbers. Of other possible migrants this leaves only three orders, Ephemera, Embiidina and Trichoptera. The four parasitic groups, Anopleura, Siphonoptera, Mallophaga and Strepsiptera, are of course absent, although the two latter doubtless hitch-hike through the pass on birds and bees respectively.

The migrating orders, arranged in three columns of relative numbers, are as follows:

Rare	Moderate	Abundant
Isoptera	Orthoptera	Coleoptera
Neuroptera	Odonata	Lepidoptera
Plecoptera	Homoptera	Diptera
Corrodontia	Hemiptera	Hymenoptera
Thysanoptera		
Dermaptera		
Mecoptera		

Up to the date of this publication, Mr. Henry Fleming has identified two hundred and forty-five species of butterflies, and fifty-two species of day-flying moths. Of the single family of nocturnal moths, Sphingidae, we have recorded seventy-six species, either directly migrating through the pass, or flying about our lights at Rancho Grande. Mr. Fleming has found only two of these which may be classed as breeding in the cloud forest surrounding the pass and our laboratory.

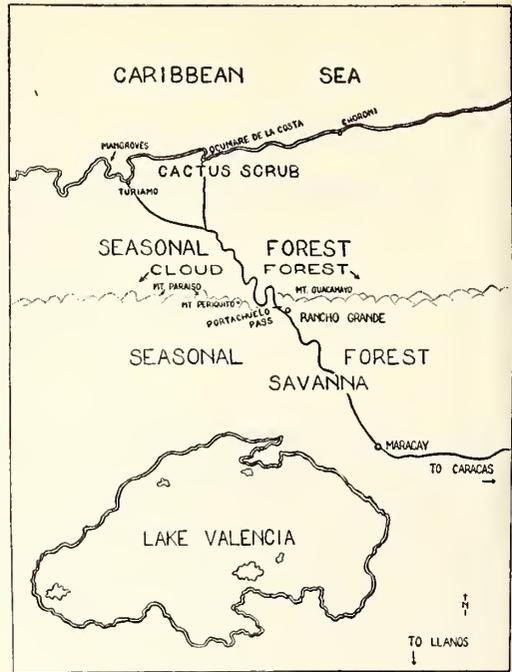
Except for a temporary, limited, northward drift of individual *Phoebis* (*Catopsilia*) in the early part of the rains, the movement of all orders of insects was invariably from north to south through the pass.

#### MIGRATING INSECTS.

Examples of extremes in migration will serve to point up succeeding papers dealing with families and species.

On April 29, 1946, I caught a solitary butterfly at the rim of the pass. Its wing spread was small, and it was an inconspicuous purplish-brown with five spots of dull white near the tip of each fore wing. It belonged to the family Nymphalidae. I gave it the reference field name of Ten-spot Brown and later found its technical name was *Eunica monima* (Cramer).

On May 4, five days later, I caught sight of several butterflies passing overhead and at the pass itself I entered a dense swarm of the Ten-spots. Mingled with them were tailed nymphalids, *Marpesia chiron chiron* (Fab.) in large numbers, and now and then a swarm of large sulphurs, *Phoebis eubule marcellina* (Cramer). In the distance I could see myriads of Ten-spots converging on the pass. One swoop of the net captured seven, five of which were tattered and torn, the remaining two freshly emerged.



TEXT-FIG. 1. Map showing location of Rancho Grande, Portachuelo Pass and surrounding territory.

Two of us climbed a mound giving a view of about half the width of the pass, and here, facing in opposite directions, at eye level, we averaged thirteen hundred butterflies in several counts of four minutes each. At intervals throughout an hour and a half this insect content of a limited time and space remained fairly constant, and when we left we knew that at the very least, two hundred and eighty-six thousand Ten-spots had passed close to us. An hour later the insects were going full strength and now I brought to bear my giant binoculars, first twelve and then twenty powers. I began about twenty-five feet overhead and then refocussed slowly upward until the limit of vision of the small insects was reached. This, judged by horizontal tests of objects of similar size would be about a half mile zenithwards, and at every fractional turn of the screw, more and more smaller-appearing butterflies fluttered into clarity.

Throughout the entire extent of verticality there was no lessening of denseness of flying insects, and it was almost a pure culture of *Eunica* and *Marpesia*. For many days this particular phase of migration continued, millions upon millions coming from some unknown source, travelling due south to an equally mysterious destination.

Three weeks later, on May 24, there was a resurgent migration of the same species, all fresh insects. Their numbers far exceeded the first wave. Four of us lined up across the entire width of the pass, with stop-watches and counters, completely failed

to keep up with fast enough estimate of numbers, but at the minimum clocked a thousand a second going past in the face of a gentle breeze. In the narrow trail above the gorge it was necessary to put on glasses, so dense were the crowds impinging upon our faces.

As the other extreme, I may mention a half hour of collecting when many species in fewer numbers were passing. Twenty successive specimens of butterflies resolved into eleven species of pierids. On another occasion thirteen individual butterflies proved to be thirteen separate species of ithomiids.

Non-recognition of the pass as a flyway accounts for the small number of observations in the year 1946, and the still more meagre and casual notes in 1945. Some time passed before we realized that all of the host of moths which came in windrows to the roof lights and laboratory windows of Rancho Grande were Portachuelo Pass migrants, deflected by confusion of fog or rain. On clear nights of star and moonlight our torches and portable ultra-violet machines revealed unbroken streams of moths of all sizes headed up and through the pass. Other indirect evidences were the wings, belonging to great numbers of species and individuals of moths, found glued in early morning to the dew-moistened leaves of shrubs and weeds in the pass; the remains of nocturnal feasts of marauding bats.

#### MIGRATION FACTORS.

One definite factor, which seems the dominant stimulus of migration, is the advent of the rainy season. For example, in 1948, there was no hint whatever of migration in February. On March 1 a single torn and bedraggled nymphalid, *Marpesia chiron chiron*, struggled up to the pass and into my net. Hardly another insect appeared for two weeks, throughout a period mostly cold and overcast. Then, on March 15, a day of warm sun after several days of heavy rain, we caught or recorded twenty species of butterflies in considerable numbers. Succeeding weeks of cold resulted in a complete dearth or mere scattering of insects, until April 15. From this date until August 1 there was no cessation of numbers pouring through, varied only by irregular fluctuations due to occasional days of cold rain or very high wind.

September 9 is the latest date of any of our three years of residence, and on that day migration was in full swing. From what I can learn, the passing insects gradually decrease throughout the succeeding two weeks. On the authority of Dr. Francisco Fernandez, Venezuelan Government Entomologist, diurnal migration at the pass ceased for the year by October 1. The annual picture thus seems clear cut.

The following applies more particularly to diurnal Lepidoptera, but in general is true of all orders:

**Inhibiting Conditions:** Very high winds, from twenty-five miles per hour upward; chilly temperatures, 62° Fahr. down; dense fog (neblina) or heavy rain; darkness.

**Favoring Conditions:** Calm, up to a twenty mile per hour following wind; 64° Fahr. plus; sun or thin neblina.

**Recurrent Waves:** These last from twenty minutes to three weeks, and usually comprise few species (two to twenty), but often large numbers of individuals. These waves are occasionally independent of favorable conditions, the hosts of insects banking up in the lee of brush, waiting for good flying weather.

**Between Waves:** At these times insects tend to fly singly, and in great variety of species.

**Wing Condition:** Worn and fresh specimens may be present in the same wave, but as a rule all are worn or all are freshly emerged.

**Models and Mimics:** Some of the more generally accepted categories of models and mimics may appear mingled together in the waves, or, very interestingly, there are not infrequently pure cultures of each, confined to waves of considerable magnitude.

**Specific Characteristics:** Normal specific characteristics of flight and of choice of habitat are maintained throughout migration. Rapid or slow flyers do not alter their relative speeds, nor change their dodging, zigzag or direct flight. The same applies as well to high or low habitual levels of flight, fast or slow flapping of wings. Species which prefer to wind their way through low, thick brush adhere to this habit en route up to and through the pass.

**Sexes and Breeding:** The general rule is the presence of both sexes, and many of the females captured alive deposit eggs within twenty-four hours. Rarely, attempts at mating on migration are observed, or pairs appear to be fighting as they circle rapidly in midair. Very few loiter to feed at blossoms. Few worn individuals stop to rest.

**Diurnal Sequence:** A few insects, belonging to various orders other than Lepidoptera, appear very early in the morning, for months on end, flying past singly, but in the aggregate in great numbers. Especially noticeable among these are two species of cockchafers (*Cyclocephala* spp.), a chrysomelid (*Diabrotica quindecimpunctata*), a small vespid (*Stalopolybia areata*), a giant hairy scoliid (*Campsomeris ianthina*), and a bee (*Euglossa fasciata*). The numbers of these solitary migrants passing on the morning of June 19, 1948, typifies the numbers on every day for the preceding two months: cockchafers, 200; chrysomelids 150; small vespids 150; giant scoliids 140; rufous bees 90.

Following these there comes, for an hour or longer, a steady procession of day-flying moths, also singly. Butterflies dominate the remainder of the day as far as relatively large insects are concerned. Throughout the

daylight hours there is a continuous passing of migration nekton, hosts upon hosts of minute winged insect life. When dusk gives way to darkness, moths and other nocturnal insects appear, and surge through the pass. If the night is fine, with clear moon or starlight, all continue down Limon Gorge. If the sky is overcast, thick with neblina or rain, the moths leave their direct southern route and detour in tens of thousands to our lighted laboratory windows or white roof walls.

Interpretation: At present, before a detailed study has been made of the mass of specimens and data, and further explorations undertaken of places of origin and destination in surrounding country, no reasonable explanation of this wholesale annual emigration is possible.

Unlike the migration of hosts of *Phoebis* males which I have observed in British Guiana and elsewhere, the Portachuelo hosts are represented by both sexes. Many of the females are ready to deposit eggs, although they are headed away from areas rich in a variety of plants, toward less luxuriant savannas.

The known distribution of many species, or especially subspecies, of butterflies such as the Papilios, shows that their place of origin cannot be very far away to the north and west, but as yet we have no hint of whence the fifteen orders are derived, or whither they are headed. From our own observations, reinforced by the reports of reliable government official entomologists, we are certain that little or no migration occurs during the dry season, and that not an insect ever returns to its natal haunts. Hence the phenomenon is really an emigration of the cross section of a considerable volant invertebrate fauna of this part of Venezuela.

Observations during three years confirm the fact that this migration is a regular annual event. It presents the inexplicable problem of a regular abstraction of an appreciable percentage of non-returning population from the area of origin. This implies the leaving behind of an adequate residual number of non-migrants to carry on the race and to sustain future migration.

Sight Identification: When there came recognition of migration on a relatively great scale, our first and indeed continued impulse was to capture as many specimens of as many different kinds as was humanly possible. On an early day of observation a butterfly was taken which, in our mind, was instantly labelled a Monarch, *Danias archippus*, or, if you prefer, *Danaus plexippus*, a familiar of our northern fields. Within an hour eighteen of the same species flapped slowly past, two of them alighting for a few seconds. Within ten minutes there passed eight smaller, darker red butterflies, two of which we took, which vividly reminded us of our northern *Danaus berenice*, commonly called the Queen. Ultimately these two resolved into *Danaus plexippus megalippe* and *Danaus eresimus*

*eresimus*, but throughout my notes, before identification, they were nostalgically recorded as Monarch and Queen. The important thing is that, being easily and accurately recognizable at a distance in flight for what they are, I am able to record, without fear of error, all the numbers that came within my purview, in all my hours of observation at the pass.

This is all by way of introducing the important question of sight identification, which, in any research such as the present, must play a dominant part. I based all my field naming first, on captured and ultimately precisely named specimens, and secondly, on characters in flying or resting insects which left no shadow of doubt. Although hundreds and tens of thousands of insects passed with only the vaguest hints of family or genus, yet day after day familiarity introduced to the perception characteristics of flight, pattern, color and shape of wings, and general facies, which materially increased range and certainty of recognition.

Viewing from a distance of ten meters, groups of species mounted in open cases, proved an excellent check on visual awareness of distinctions. A brief treatment of sight identification will be added to each paper dealing with families of insects.

This and following papers are intended only as factual presentations of notes made during three seasons of observations of migration from north to south through Portachuelo Pass. Hence no attempt has been made at correlation or even mention of migrations of the same or related species observed by entomologists elsewhere. The insects themselves will be considered group by group in successive papers, with a final summary in detail of the migration as a whole.

We hope, in future expeditions in this same field, that data will be obtained which will clarify the place of origin and ultimate destination of the insect hosts, as well as the initiating stimuli and directive factors of their migration.

An account of the bird migration through the pass has already appeared, treating of sixty species divided among ten types of migration.<sup>2</sup>

## EXPLANATION OF THE PLATES.

### PLATE I.

- Fig. 1. Looking south toward Portachuelo Pass from Kilometer 31.  
 Fig. 2. Portachuelo Pass, the notch in the distant sky-line, from farther north, near the sea.

### PLATE II.

- Fig. 3. Migrant insects alive but quieted by refrigeration.  
 Fig. 4. Migrant moths deflected in great numbers, on nights of storm, from their migration through the pass, to the electric lights on Rancho Grande roof.

<sup>2</sup> *Zoologica*, 32 (18), 1947, pp. 153-168.



FIG. 1.



FIG. 2.

INSECT MIGRATION AT RANCHO GRANDE IN NORTH-CENTRAL VENEZUELA.  
GENERAL ACCOUNT.



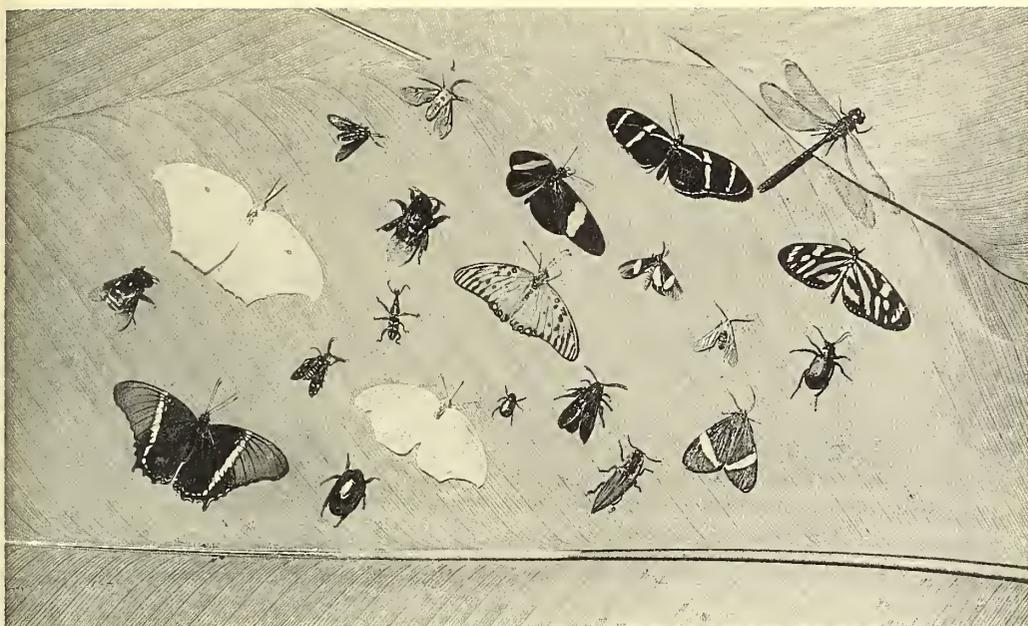


FIG. 3.



FIG. 4.

INSECT MIGRATION AT RANCHO GRANDE IN NORTH-CENTRAL VENEZUELA.  
GENERAL ACCOUNT.



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## 13.

The Behavior of Two Captive Specimens of the Lowland Gorilla,  
*Gorilla gorilla gorilla* (Savage & Wyman).<sup>1</sup>B. F. RIESS,<sup>2</sup> SHERMAN ROSS,<sup>3</sup> S. B. LYERLY,<sup>4</sup> AND H. G. BIRCH.<sup>5</sup>  
*Behavior Research Fellows* (1948), *New York Zoological Society*.

(Plates I &amp; II; Text-figures 1 &amp; 2).

## I. INTRODUCTION.

The field of comparative behavior research has long been subject to two methodological factors which have to a certain extent prevented the attainment of its goal, namely the securing of information on behavioral processes of representative species of a wide range of living organisms. The first factor has been the concentration of research workers on those animals which are adaptable to the limited conditions of laboratories. This emphasis on a few selected species has led to the second factor, the acceptance of the conventional laboratory as the prototype of habitat for the species under investigation. Both these methodological limitations have arisen in part from the same set of circumstances, the relative lack of availability of less adaptable organisms and the expense of field studies. The increasing number of investigations under naturalistic field conditions and of studies on rare specimens under favorable conditions has provided additional evidence of the fruitfulness of the extension of both laboratory and field methodology to specimens other than those generally used in comparative behavior laboratories.

It is one of the purposes of this paper to point to a source of data which can facilitate not only the collection of more information on a wider variety of animals but which can also serve as a training facility for field-workers and others. Within the reach of researchers in most large cities there exist collections of living animals in great variety of species and under varied living conditions. The reference is to the zoological parks and exhibition areas. In many of these, natural habitat conditions are approximated and even the differences can be fertile sources of comparative psycho-ecological studies.

<sup>1</sup> The success of this project was due in large part to the co-operation of the staff and keepers of the New York Zoological Park. Particular thanks are due Mr. Fairfield Osborn, Mr. John Tee-Van, Mr. Lee S. Crandall, Dr. L. J. Goss, Keepers Reilley and Quinn, and Mr. Sam Dunton, photographer.

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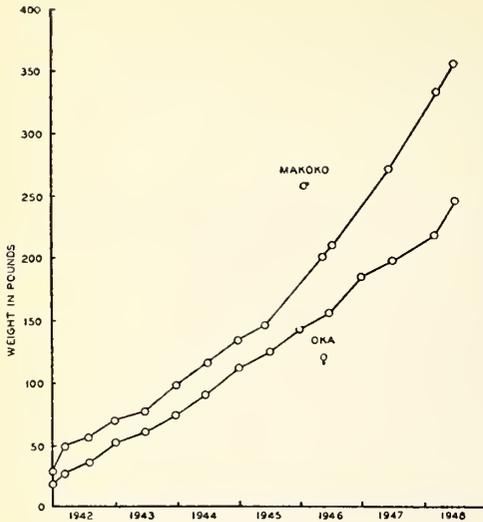
<sup>5</sup> City College of New York, N. Y. C.

In 1937, Carpenter (2) published a study of two young male mountain gorillas, *Gorilla gorilla berengei*, resident at the San Diego Zoo. In this paper he pointed to the opportunities presented by the fourteen specimens of the largest of the great apes which he listed as available in the zoological parks of the world. Gorillas offer a dramatic field for this type of research since they are, with the exception of the orang-utan, the least studied of the anthropoid apes. The present paper seeks to compare Carpenter's data with those obtained in a study of male and female pre-adolescent lowland gorillas, *Gorilla gorilla gorilla*, in the New York Zoological Park (Bronx Zoo). Such comparative data as can be assembled will be helpful to workers who seek a base line for similar investigation elsewhere. That these investigations are possible is demonstrated in Table I which lists the location and over-all biological indices of the specimens now resident in various collections. The number of gorillas in the United States is increasing. In 1937 there were only eight specimens in this country; today there are twenty-four.

Other than Carpenter's study, material on the behavior of the gorilla is found only in a limited number of papers. Yerkes' pioneer work (6) with the pre-adolescent female mountain gorilla, Congo, is known to all students of comparative psychology. Bingham's 1932 observations (1) on gorillas in their native habitat and Valker's similar study in the Gaboons (5) in 1931 are the only other relevant research. The two lowland gorillas in the New York Zoological Park are included in a report of the external genitalia published by Goss (3).

## II. SUBJECTS.

The gorillas studied at the Bronx Zoo are Oka, female, and Makoko, male. Since this study was made the Bronx Zoo has acquired a young female mountain gorilla, but no reference to it will be made in this report, except to list it in Table I. Little is known of the early history of Oka and Makoko. Both animals arrived in the Zoo on September 7, 1941, at which time they weighed 20 and 28



TEXT-FIG. 1. Rate of growth of Oka and Makoko from time of arrival at the New York Zoological Park on September 7, 1941, until summer of 1948.

pounds respectively. Ages were estimated as one and three years on the basis of weight and bone structure. Text-figure 1 gives the data on the growth of the specimens from the time of arrival until the summer of 1948. The female was weighed, up to June, 1948, while on the keeper's back, the male's weight being merely estimated. In 1948 a Toledo balance was installed, on which the animals were weighed when they voluntarily mounted a platform.

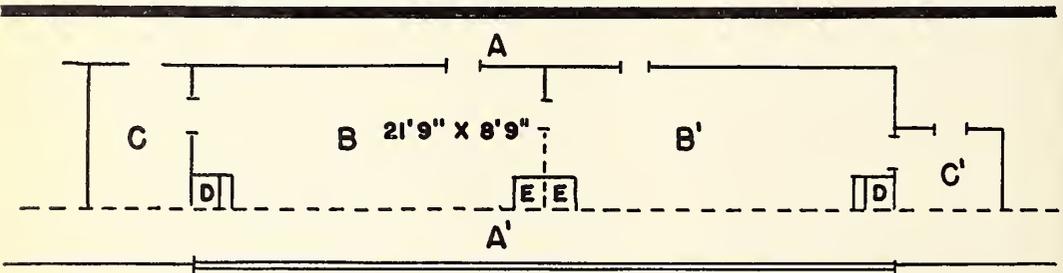
At the present time, Oka and Makoko are magnificent specimens. Makoko has a particularly brilliant coat and a notably prominent supra-orbital ridge. Oka is less impressively marked but is a splendid female example of the species. Both animals are active, healthy and strong. Indeed, Makoko's grip is so powerful that it has been necessary to replace the  $\frac{3}{4}$ -inch steel bars of the cage front, which he bent repeatedly. A steel horizontal ladder had to be removed from his cage when he tore it loose from its mooring. Oka is less destructive and retains her ladder.

### III. ENVIRONMENTAL CONDITIONS.

The gorillas are housed in individual cages separated by a partition consisting of a solid metal access door and a double grill of steel bars. At the ends of each cage are doors leading to shift cages into which the animals are chased when the exhibition compartments are cleaned or repaired. The back wall of the living space is solid masonry with a recessed access door. Between the glass partition through which the public views the animals and the metal barred cage fronts is a passageway for the keepers. The internal features of the living compartments include a platform and a three-step staircase, with the platforms raised two inches from the floor, facing each other in front of the grill between the two cages. The staircases are at the ends near the shift cages. Oka's cage contains a metal horizontal ladder slung between the rear wall and the cage front at a height of three feet.

### IV. DAILY SCHEDULE OF ANIMAL CARE.

Although the animals are on exhibition during the hours of 10:00 A.M. to 5:00 P.M. (except on Sundays when the visiting time is extended to 6:30 P.M.), the daily routine is more extensive. The overhead fluorescent lights are turned on at 8:00 A.M. when the keepers enter the building. Between 8:30 and 9:00 in the morning, the gorillas, each of whom has been in its own cage all night, are given their morning meal of skimmed milk and raw eggs. The ingredients are mixed and fed to each gorilla by tilting a can containing the mixture into the subject's mouth as the animal protrudes its lips through the bars of the cage front. Some half-hour to three-quarters of an hour later, the keepers move the gorillas to the shift cages. Separation and enclosure in the individual cages are effected by means of a stream of water. With the gorillas out of the way, the cages undergo thorough cleaning. Shortly before visiting time, the animals are released and are frequently permitted to remain together in one of the two cages for periods up to one hour. This opportunity for association occurs five



TEXT-FIG. 2. Floor plan of gorilla compartments in New York Zoological Park. **A, A'**, passageways for keepers. **B, B'**, exhibition cages for Oka (female) and Makoko (male), respectively. **C, C'**, shift cages. **D**, three-step stairs. **E**, platforms; right-hand platform used for weighing. **Thin line** indicates solid wall; **dotted line** indicates grill-front walls; **double line** indicates glass partition.

TABLE I.  
Physical Characteristics of Gorillas in the United States.\*

Name.	Location.	Form.	Sex.	Estimated age on September 1, 1949.	Known Weight.	Estimated Weight.
Oka	N. Y. Zool. Park	<i>gorilla</i>	F	9 yrs.	282 lbs.	
Makoko	N. Y. Zool. Park	<i>gorilla</i>	M	11 yrs.	408 lbs.	
Sumaili	N. Y. Zool. Park	<i>berengei</i>	F	20 mos.	20 lbs.	
Joanne	Central Park Zoo, N. Y. C.	<i>gorilla</i>	F	10 yrs.		190 lbs.
Carolyn	Central Park Zoo, N. Y. C.	<i>gorilla</i>	F	10 yrs.		190 lbs.
Bamboo	Philadelphia Z. G.	<i>gorilla</i>	M	23 yrs.		435 lbs.
Massa	Philadelphia Z. G.	<i>gorilla</i>	M	18 yrs.		400 lbs.
Bushman	Lincoln Park Zoo, Chicago	<i>gorilla</i>	M	21½ yrs.	542 lbs.	
Sinbad	Lincoln Park Zoo, Chicago	<i>gorilla</i>	M	20 mos.	38 lbs.	
Rajah	Lincoln Park Zoo, Chicago	<i>gorilla</i>	M	29 mos.		47 lbs.
Irvin Young	Lincoln Park Zoo, Chicago	<i>gorilla</i>	M	33 mos.	52 lbs.	
Lotus	Lincoln Park Zoo, Chicago	<i>gorilla</i>	F	43 mos.		75 lbs.
Miss Congo†	Chicago Z. P.	<i>gorilla</i>	F	16 yrs.		325 lbs.
Phil	St. Louis Z. P.	<i>gorilla</i>	M	10 yrs.		320 lbs.
Bobo	St. Louis Z. P.	<i>gorilla</i>	M	2 yrs.		44 lbs.
Big Boy	Cincinnati Zoo	<i>gorilla</i>	M	3 yrs.	35¼ lbs.	
Albert	San Diego Zoo	<i>gorilla</i>	M	6 mos.	9¼ lbs.	
Bouba	San Diego Zoo	<i>gorilla</i>	F	10 mos.	12½ lbs.	
Bata	San Diego Zoo	<i>gorilla</i>	F	8 mos.	10¾ lbs.	
Phil	Colorado Springs, Col.	<i>gorilla</i>	M	4 yrs.		40 lbs.
Gargantua	Ringling Bros. Circus	<i>gorilla</i>	M	17 yrs.	550 lbs.‡	
Mtoto	Ringling Bros. Circus	<i>gorilla</i>	F	16 yrs.	438 lbs.‡	

\* On October 31, 1949, three young specimens of *Gorilla g. gorilla* arrived in New York. They were a male and a female weighing 12-14 pounds, and a female weighing about 40 pounds. At the time this paper went to press they were still in the hands of Henry Trefflich, an animal dealer.

† Died Sept. 22, 1949.

‡ 1947 weight.

or six times a week and is the only occasion on which the animals are in unrestricted contact with each other. From the time of separation until the main feeding of the day at approximately 2:30 P.M., the gorillas are unattended except insofar as the keepers play with them while passing in front of the cages. The typical afternoon meal consists of carrots, celery, oranges, apples, grapes, bananas, beets, beans, sweet-potatoes, cabbage, onions, cherries and other seasonable fruits and vegetables. All food is fed raw and supplied through the front bars of the cages. Water, *ad lib.*, is available to each animal from a continuously running spigot which empties into a trough running along the back wall of each cage. At 5:30 P.M. the lights are turned out and the gorillas remain unattended until the next morning.

#### V. OBSERVATIONAL PROCEDURES.

Preliminary study of the gorillas was started at the beginning of May, 1948. One of the writers (B.F.R.) visited the Primate House at the Zoo on two days of each week and observed the gorillas for one hour. The times selected were in the early morning when the keepers placed the two gorillas in one cage, and in the late afternoon, at about 3:30 P.M. following the afternoon meal. At the later time, the animals were in separate cages.

As a result of the work during May and

early June, a list was evolved on which both quantitative and qualitative indices of behavior could be noted. The inventory consisted of 42 items divided into five categories: posture and locomotion; eating, drinking and elimination; self-oriented activity (play?); inter-individual behavior; and observer-oriented behavior. The sheets of the check list were divided into 10 columns, each of which was used for a three-minute period of observation during the total 30 minute duration of the observational session. Thus it was possible to arrive at the total amount of each of the 42 types of behavior during the 30-minute period and also to determine the sequence of behavior during the period. Additional space was provided for running comments on the activity of the gorillas and for additional notes.

The observers worked in pairs and rotated the pairing so that a measure of control over reliability of observation was possible. There was joint discussion of the meaning of each term on the check-list so that the observers would agree on how to label the activity observed. The problem of the animal's reaction to the observer was considered and it was decided to standardize the position of the observers. Since the gorillas are a very popular exhibit and attract large crowds of spectators, the public exhibition space was used as the location for the observers who sat in pairs in front of the glass partition opposite

the communicating grill between the two cages.

Because the activity of the gorillas varied considerably with the time of day, the number of visitors, the daily routine and other variables, it was decided to distribute the 30-minute observation periods over the whole working day of the animal. However, since the gorillas were allowed to be in the same cage with one another only in the early morning, there was a greater concentration of sessions between 9:00 and 10:00 A.M. The total number of observations made during these hours was 10 one-half hour periods. Sixty-eight sessions were devoted to taking notes on behavior of the animals in isolation. During these 68 periods, it was possible to get data on both Oka and Makoko so that each animal was studied an equal number of times. Every hour between 10:00 A.M. and 6:00 P.M. was covered. In addition to these systematic observations which started in July and lasted through the middle of August, 1948, each experimenter observed the gorillas several hundred times while passing through the Primate House to and from other areas in the Park. Any deviant behavior or peculiar activities were noted and added to the record.

## VI. RESULTS AND DISCUSSION.

Two factors limit the analysis of the data. In the first place, quantitative analysis affords very little insight into the problem at hand. The purpose of this study was to obtain information which would serve as a starting point for further investigation of the gorillas at the Bronx Zoo, particularly as they become physiologically more mature and show active sex and social behavior. In the second place, it was thought desirable to point to both the similarities and differences between our gorillas and those at the San Diego Zoo described by Carpenter.

In this comparison, there are many difficulties and dangers arising from two sources. In the first place, the gorillas belong to different sub-groups, ours being lowland and Carpenter's mountain specimens. Other variables in this category include age and sex differences between the two sets of observed gorillas. In the second place, it is necessary to stress the differences in the environmental setting in which the San Diego and Bronx gorillas carried out their daily activity. At San Diego, the two male gorillas were housed in outside cages equipped with tree trunks for climbing and various devices which could be manipulated by the animals, for instance logs, swings, ropes, tires, etc. In addition, the experimenter could insert objects into the gorillas' surroundings and study the effect of such introductions. At the Bronx Zoo, the separation of the gorillas from the public was much more rigorous and the cages much more bare. In interpreting the comparative findings, the obvious individual and environ-

mental differences must be kept in mind. However, despite these limitations, the comparison of the two groups should be of value, if only to emphasize the danger of generalizing from any set of observations.

With the restrictions specified above, the data in Table II represent the basic observations made upon the two gorillas at the Bronx Zoo. Where information comparable to that obtained by us was derivable from Carpenter's San Diego observations, it has been included in the Table. The discussion of the data in Table II will follow the general categories outlined above.

### A. Posture and Locomotion.

Posture and general locomotion seem fairly well established as invariant gorilla patterns. Both Carpenter's mountain and our lowland gorillas exhibited the same type and frequency of gross motor activity. Walking, running, standing and sitting were characteristically alike for Oka, Makoko and the San Diego pair. Differences were noted in the frequency of observed sleep and in swinging by the hands. Both of these differences may be the resultant of variable environmental and observational procedures. It was not feasible for us to observe night behavior, and swinging was made difficult for Oka and Makoko by the absence of a place suitable for that kind of activity. The complete absence of nest-building in the Bronx pair is also related to the lack of adequate materials. Both Carpenter and Yerkes report that it was a fairly common behavioral pattern in their subjects.

The observations on handedness in the Bronx gorillas are not comparable to other studies since this item was not listed by Carpenter. Oka was observed to make differential use of her hands on 313 occasions and Makoko 184 times. In both animals, the right hand was more frequently employed regardless of the nature of the activity. The frequency of use of this hand was 54% as compared with the report by Yerkes (6) who found that Congo used her right hand some 66% of the time. In Congo's case the left foot was preferred to the hand, whereas in our gorillas there was relatively little pedal manipulation.

### B. Eating, Drinking and Elimination.

In the presence of an abundance of food, Oka and Makoko both showed a form of behavior somewhat akin to the hoarding of rats and lower mammals. The gorillas would sweep the food into a heap with either the hands or feet. The heaped food was then examined, tossed around or eaten. This behavior is not mentioned in any other report on the gorilla and may well be the unique result of the absence of manipulatable material in the cages in the Bronx Zoo. Placing of the longer-stalked fruits and vegetables on the heads of the gorillas was a frequent aftermath of the in-gathering of the material.

An interesting aspect of the behavior of the isolated animals was a relatively infrequent passage of food from Oka to Makoko through the bars of the intercommunicating grill between the two cages. The initiation of this activity usually came from Oka and was noted particularly on the several occasions when Makoko had been deprived of his usual rations because of diarrhea or other health considerations. In such circumstances, Oka was observed forcing potatoes and cabbage through the double grill. Makoko did not seem to be particularly interested in the inserted foods. This behavior was seen on three occasions.

The drinking of water is a form of behavior common both to our animals and to those studied by Carpenter. According to Yerkes, Congo drank but little water. The manner of drinking in the Bronx animals was to bend over the fountain and suck the water into the mouth. Although there was no opportunity to study comparative satisfaction from milk and water, it is the opinion of the authors that the milk-egg liquid was preferred.

Regurgitation of the milk-egg mixture was almost invariable. Following the feeding the animals would typically squat on their haunches, lean forward, and regurgitate some if not all of the milk. The gorillas then would examine the liquid manually and eventually bend all the way and lick up the regurgitated material. The time interval after ingestion varied somewhat but was in the neighborhood of 45 seconds. Some chemical changes took place during the brief digestive stay for the milk was usually curdled. This pattern is seen not only in the gorillas at the Bronx Zoo but also in the chimpanzees. Whether or not this is a primate characteristic and analagous to the similar behavior of the pre-socialized human infant or whether it is unique to the subjects in captivity remains a matter for further research.

Voided fecal material was commonly handled both by Oka and Makoko and frequently was used to throw at the keepers, the observers or the public. Handling was casual and seemingly tactually motivated, for the feces were not examined nor used except for throwing. Since the keepers made heroic efforts to keep the cages clean, the opportunities for greater concentration on feces were limited. Carpenter makes no mention of this type of behavior. Urination was a casual affair and no localization of territory for this or for defecation was noted.

#### C. Self-oriented Activity.

Self-manipulation of parts of the body was a common form of activity in both Oka and Makoko. The parts of the body selected for handling or fingering were not consistent, with the exception of the lack of attention to or focus on the external genitalia. The major phase of activity during which handling was observed was while the gorillas were lying

on their backs or stomachs, when parts of the body such as the lips, ears, eyebrows and nose would be held. The absence of genital manipulation may well be the result of the small size of the external genitalia of the gorilla, as described by Carpenter and Goss.

Manipulation of objects in the environment is a frequent finding wherever gorillas have been studied. Carpenter and Yerkes mention this behavior pattern and it was noticeable in the animals at the Bronx Zoo. The female, Oka, showed some tendency to manipulate and examine with greater frequency than her cage mate. In the absence of a variety of objects to examine, the frequency of occurrence of this activity is all the more remarkable.

The attitude of the gorillas toward the water fountain has already been described. An observable difference was noted in the behavior toward drinking water and that emanating from the pressure hoses used in cage cleaning. As indicated above, in the discussion of daily routine, water was used to separate the gorillas and to urge them toward the shift cages. The initial reaction to the stream from the hoses was retreat and excitement. However, once wet, the animals would face into the water and jump up and down. The keepers reported that the animals would on occasion approach more closely to the nozzle of the hose when thoroughly wet. No shaking of the body after the bath was seen during the periods of observation.

Self-grooming does not seem to be a dominant activity in the lives of either the San Diego or New York gorillas. To what extent the absence of this form of self-manipulation is a function of the cleanliness of the environment and the animal is not established by our observations but, as will be noted later, grooming as a pattern of behavior is markedly less present in the gorillas under study than in other primates at the Zoo.

#### D. Inter-individual Behavior.

The data in this section were obtained during those periods when the animals were together in the same cage. To the extent that the opportunity for such interaction was limited, the enhancement of activity during the periods of joint occupancy of the cage may be a function of the limitation of time during which the two animals could interact.

Both in Carpenter's study and in ours, the major forms of inter-individual activity were running, chasing and wrestling. These behavior patterns were well marked and almost stereotypical in appearance. Chasing was especially vigorous when the cage floor was wet and the gorillas spent much time sliding in a pronograde posture from one end of the cage to the other. Initiation of this activity was fairly evenly divided between Oka and Makoko. Wrestling, too, was not started consistently by either male or female. A dominance pattern was not apparent.

The sequence of individual motor acts in

TABLE II.  
Comparative Behavior of Oka, Makoko and San Diego Gorillas.\*

Behavioral Classification	Frequency of Occurrence in		
	San Diego	Oka	Makoko
<i>A. Posture and Locomotion</i>			
Walking, pronograde	+++	+++	+++
Walking, upright	+	+	++
Running, pronograde	+++	+++	+++
Running, upright	ND	+	+
Standing, pronograde	+++	+++	+++
Standing, upright	+	+	+
Sitting	+++	+++	+++
Climbing	++	+	+
Swinging by hands	++	+	+
Hanging	+	+	+
Sliding	+++	++	++
Left-handedness	ND	46%	46%
Right-handedness	ND	54%	54%
Lying down	+++	+++	+++
Sleeping	++	+	+
Nest Building	+	NP	NP
<i>B. Eating, Drinking and Elimination</i>			
Gathering food in heaps	ND	++	+
Sharing food with cage mate	O	+	+
Drinking water	+++	++	+++
Drinking milk	+++	++	++
Regurgitation of milk	ND	++	++
Handling of feces	ND	+	+
Attention to urination	ND	+	+
<i>C. Self-oriented activity (Play?)</i>			
Self-manipulation (non-genital)	++	++	++
Manipulation of genitalia	O	O	O
Manipulation of objects	+++	++	+
Manipulation of food (non-eating)	ND	++	++
Attitude toward stream of water	positive ++	+	+
Self-grooming	++	+	+
<i>D. Inter-individual behavior</i>			
Chasing	+++	+++	+++
Wrestling	+++	+++	+++
Grooming	++	+	+
Inspection and manipulation of genitalia	O	O	+
Presenting	O	O	O
Mounting	O	O	O
Pelvic thrusts	O	O	+
Chest thumping	++	+	++
Vocalizing	++	ND	ND
Dominance	+	+	+
<i>E. Observer-oriented behavior</i>			
Throwing of feces	ND	+	++
Throwing of non-fecal material	ND	+	+
Attentional responses	positive ++	negative ++	negative ++
Vocalization	++	ND	ND

\* Key to symbols:

O—Never observed or reported  
+—Little in frequency or amount  
++—Some or fairly frequent

+++—Great deal, very frequent  
ND—No data reported  
NP—Not possible in the environment

the wrestling behavior was free of patterning and seemed to consist of random grappling at the anatomical point nearest to the initiator of the behavior. When the actions of either animal seemed to approach the point at which roughness would ensue, the animal at the moment on the receiving end would detach itself and a period of resting would follow. Of all the behavior noted in this

study, wrestling was the most dramatic and illustrative of the great strength of the gorillas. As a rule, there were few vocalizations during the bouts.

Social grooming, certainly, does not seem to be as predominant in the behavior of the gorillas as in the case of other representatives of the great apes or other primates. Carpenter likewise observed little of this sup-

posedly socially oriented activity. It is possible that in the four animals for which data are available, the age and sex differences were not sufficiently well established to facilitate the appearance of this type of social interaction. It may also be possible that there is a real species difference in such behavior.

Genital manipulation and exploration in the paired situation was not frequently observed. It was seen only three times in Oka and Makoko and was not reported for the San Diego pair. In the Bronx specimens, the initiator was always the male. This may be a reflection of the relatively greater maturity of Makoko. So, too, in our gorillas, mounting and pelvic thrusts as precursors of mating behavior were almost completely absent during the periods of observation in New York. Carpenter saw none of this at San Diego, but his animals were both males. The one instance of pelvic thrusts by Makoko occurred during a wrestling bout and was not repeated nor invited by Oka.

Chest-thumping was much more prevalent during the periods of paired activity than when the animals were in their own cages. The causal sequences leading up to the thumping could not be determined for Oka and Makoko although the observers were all of the opinion that the behavior was socially oriented and significant. Some writers have suggested that thumping of the chest is a sign of well-being and general euphoria. Yerkes states that the behavior is a sign of "impatience or other mild dissatisfaction." There was clear evidence of neither causal sequence in our observations. The range of situations during which the thumping was observed varied so widely that no specific factor can be assigned as the reason for its existence. The only statement that can be made from our data is that the male, Makoko, engaged in chest-thumping more frequently than did Oka and accompanied the beating with vocalizations more frequently than his companion.

In the absence of sound-recording devices, description of vocalization is difficult. Furthermore, the public space was somewhat soundshielded by the glass partition separating the animals from the observers. In our experience the occurrence of this activity was less than that mentioned by Carpenter.

#### E. Observer-oriented Behavior.

The types of audience-attentive behavior observed in the Bronx Zoo consisted mainly

of the throwing of feces or food at the glass plate between the cage and the visitors. The same aggressive behavior was noted during an attempt to get photographs of the animals. Visitors invariably tried to attract attention from the gorillas by tapping on the glass partition and by yelling. The effect of such devices was negligible. This difference between our data and Carpenter's may well be the result of the more restrictive conditions of the gorillas' environment in the New York Zoo.

#### VII. SUMMARY.

This report describes the behavior of two pre-adolescent lowland gorillas in the New York Zoological Park during the summer of 1948. Oka, then an eight-year-old female, and Makoko, a ten-year-old male, were observed in their regular living cages when alone and when placed together.

A check-list was prepared and regular half-hour periods of observation were systematically made. Significant behavioral items were compared for the sessions when the animals were alone and when they were together. Comparisons were also made with the data collected by Carpenter from two male mountain gorillas in the San Diego Zoo.

The descriptive material obtained during the period of observation should serve as a base line from which to note variations arising from the maturation of the two gorillas in the years to come.

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**EXPLANATION OF THE PLATES.****PLATE I.**

- FIG. 1. Makoko, the male lowland gorilla in the New York Zoological Park. Estimated age, 11 years; weight, 408 pounds.

**PLATE II.**

- FIG. 2. Oka, the female lowland gorilla in the New York Zoological Park, is still friendly and gentle with her keeper at the estimated age of 9 years. Her weight is 282 pounds.
- FIG. 3. Oka playing with her keeper.

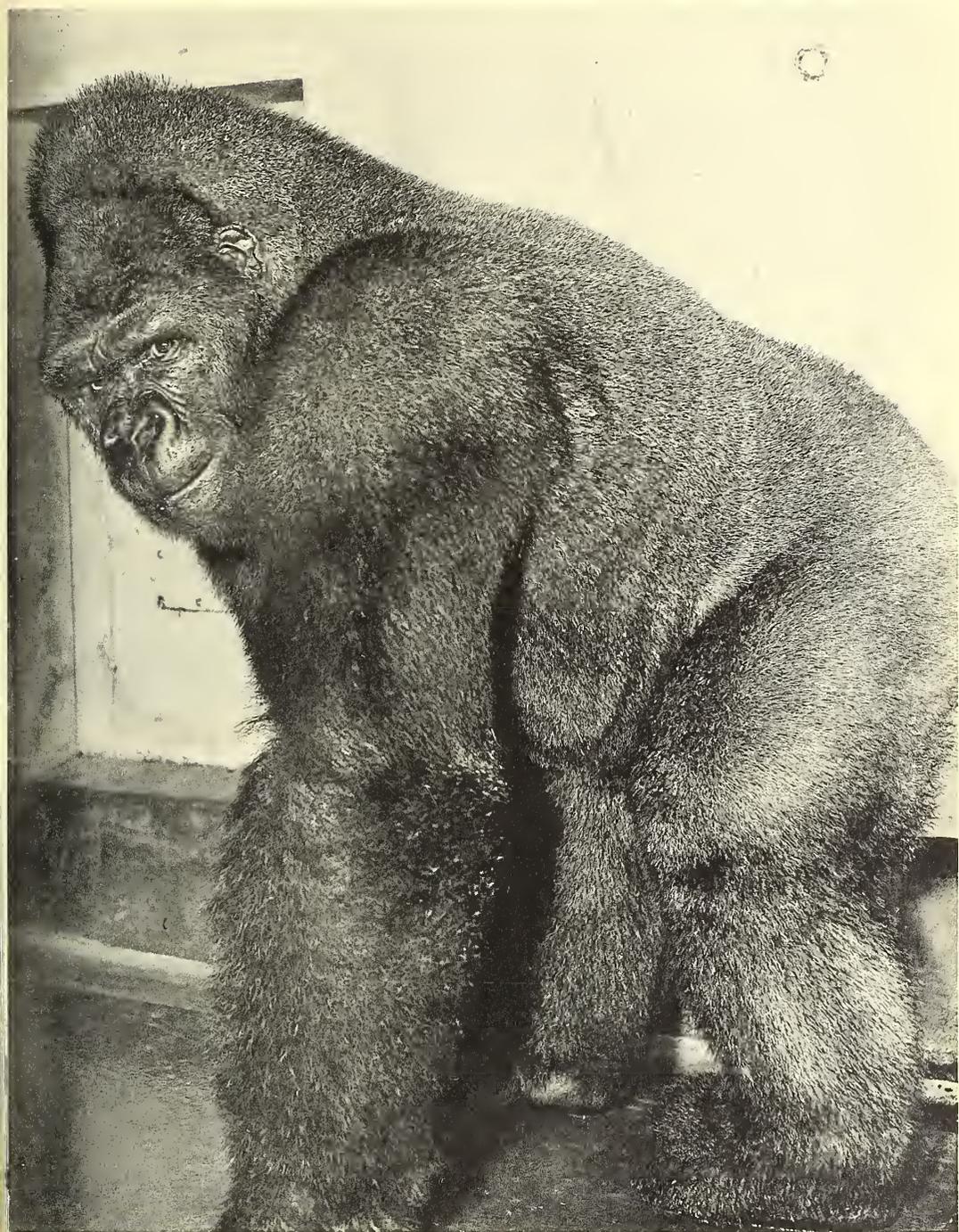


FIG. 1.

THE BEHAVIOR OF TWO CAPTIVE SPECIMENS OF THE LOWLAND GORILLA,  
GORILLA GORILLA GORILLA (SAVAGE & WYMAN).





FIG. 2.



FIG. 3.

THE BEHAVIOR OF TWO CAPTIVE SPECIMENS OF THE LOWLAND GORILLA,  
GORILLA GORILLA GORILLA (SAVAGE & WYMAN).



## 14.

Migration of Papilionidae at Rancho Grande, North-central Venezuela.<sup>1</sup>

WILLIAM BEEBE.

*Director, Department of Tropical Research, New York Zoological Society.*

(Plate I; Text-figure 1).

[This is one of a series of papers resulting from the 45th, 46th and 47th Expeditions of the Department of Tropical Research of the New York Zoological Society, made during 1945, 1946 and 1948, under the direction of Dr. William Beebe, with headquarters at Rancho Grande in the National Park of Aragua, Venezuela. The expeditions were made possible through the generous cooperation of the National Government of Venezuela and of the Creole Petroleum Corporation.]

[The characteristics of the research area are in brief as follows; Rancho Grande is located in north-central Venezuela (10° 21' N. Lat., 67° 41' W. Long.), 80 kilometers west of Caracas, at an elevation of 1,100 meters in the undisturbed montane rain forest which covers this part of the Caribbean range of the Andes. The migration flyway of Portachuelo Pass, which is also the water-shed between the Caribbean and Lake Valencia, is 200 meters from Rancho Grande. Adjacent ecological zones include seasonal forest, savanna, thorn woodland, cactus scrub, the fresh-water lake of Valencia and various marine littoral zones. The Rancho Grande area is generally subtropical, being uniformly cool and damp throughout the year because of the prevalence of the mountain cloud cap. The dry season extends from January into April. The average humidity during the expeditions, including parts of both wet and dry seasons, was 92.4%; the average temperature during the same period was 18° C; the average annual rainfall over a five-year period was 174 cm. The flora is marked by an abundance of mosses, ferns and epiphytes of many kinds, as well as a few gigantic trees. For further details see Beebe and Crane, *Zoologica*, Vol. 32, No. 5, 1947. Unless otherwise stated, the specimens discussed in the present paper were taken in the montane cloud forest zone, within a radius of one kilometer of Rancho Grande.]

For an account of Portachuelo Pass, together with a general introduction to the groups of migrating insects and migrating factors see "Insect Migration at Rancho Grande," by William Beebe, *Zoologica*, 1949, Vol. 34, No. 12, pp. 107-110.

In Volume 26 of *Novitates Zoologicae*, W. J. Kaye has a paper entitled "A Geographical Table to show the Distribution of the American Papilios." Under the heading "Venezuela, North," (pp. 352-355), the author lists thirty-one species. In a letter Dr. Rene Lichy of Caracas sends me a list of thirty-one species of this family which he

has collected in northern Venezuela. A continuation of this coincidence is that each list contains seven species not found in the other list.

Both lists contain all the species which we took migrating through Portachuelo Pass, with the single exception of *crassus* which Lichy does not mention.

In the limited width of twenty meters of Portachuelo Pass, and allowing a height of net reach of a maximum of five meters, we captured seventeen species of *Papilio*. This area may be considered, not unrealistically nor unconservatively, as, at the most, a millionth of the extent of north Venezuela. Yet within this relatively microscopic bit of Andean air, we secured almost half the papilios so far recorded from the entire northern part of the country. Thus, in the consideration of this family of butterflies, we are made to realize the wide-spread, impelling, migrational force affecting this group of insect life.

So much of this migration—its causes and extent—is at present unknown, that every verifiable fact is of value. Reviewing the known distribution of the seventeen species of *Papilio* migrants, we find that most of them extend from Mexico to Paraguay, south Brazil or Argentina. The distribution of the subspecies, however, presents a very different picture, and a very significant one in its over-all pattern. In twelve out of the seventeen, the subspecific range is confined to Colombia and Venezuela, with a few extensions to adjacent territory. Thus we may expect to find the northern point of origin of the movement of these forms a relatively short distance away.

The twelve subspecies of *Papilio* with limited distribution are as follows:

*anchises osyris*  
*anchisiades anchisiades*  
*agesilaus agesilaus*  
*arcas arcas*  
*cleotas coroebus*  
*erithalion zeuxis*  
*lycophron hippomedon*  
*paeon thrason*  
*polyxenes americanus*  
*protesilaus archesilaus*  
*sesostris tarquinius*  
*torquatus orchamus*

<sup>1</sup> Contribution No. 852, Department of Tropical Research, New York Zoological Society.

The remaining five forms of *Papilio* with wider distribution are:

*belus varus*  
*crassus*  
*phaon*  
*polydamus polydamus*  
*thoas neacles*

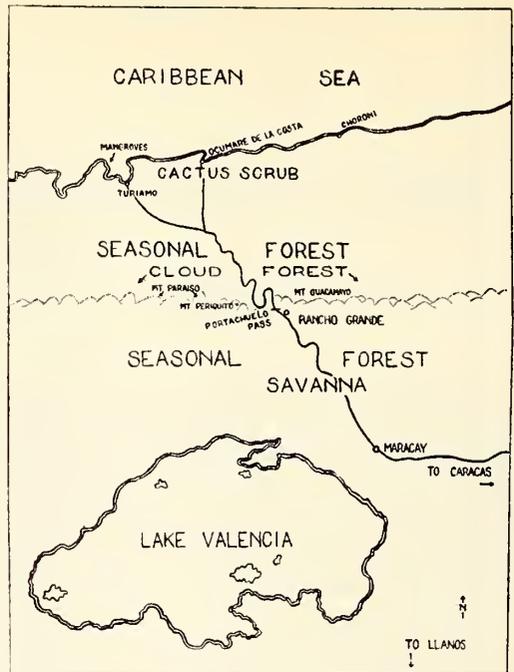
Let us take as an example *Papilio agesilaus agesilaus* or, as I called it before identification, Small Zebra Swallowtail. I recorded seven individuals captured and fifty-eight seen with certainty. Added to this number were the many papilios glimpsed too briefly, flying too high or too fast to be recognized as to species, and also those which must have passed during the hours of our absence from the pass. It was heartbreaking to realize what a minute fraction we could honestly record by sight identification, yet there is no other way, at present known, to glean definite, general knowledge of this phase of the lives of these splendid insects. Without exception, all sight-named species were subsequently confirmed or discarded by comparison with captured, definitely classified specimens.

In this as in some other species, the small number of records from the year 1946 and their entire absence from 1945 by no means indicates the absence of the species on migration, but only reflects our non-recognition of the importance of the Portachuelo Pass migration during the early years, and consequent slight attention paid to this phenomenon. An ultimate summary of the relatively few, disconnected observations made during 1945 and 1946 reveals a general movement on a scale equal in magnitude and as all-embracing of insect orders as we recorded during 1948.

The mere recording of the capture of seventeen species of *Papilio* on migration is a worth-while fact, and when more and more individuals are taken on succeeding days and weeks the phenomenon is enhanced in interest. In few or in large numbers the insects continue to fly past, slowly or circling or alighting out of reach. As in the case of many other organisms, the time has come when sight records must be used to supplement specimens in net, envelope and cabinet. Ornithologists in general and British entomologists in particular have gone far in sight identifications, while at the same time maintaining as perfect accuracy as possible with man's fallible eyesight and only too human brain.

At the end of our many months of collecting and observation at the pass, I found, in my Journal, a significant assemblage of shorthand names of papilios. They were, of course, essentially personal, stimulated by mental comparisons with swallowtails familiar to me elsewhere, or in the case of strange tropical forms, by outstanding wing shapes, size, patterns and colors.

Lepidopterists recognize three "natural groups" into which papilios may be divided.



TEXT-FIG. 1. Map showing location of Rancho Grande, Portachuelo Pass and surrounding territory.

These are based on various factors such as larvae, pupae, microscopical imaginal distinctions and/or food-plants. Our migrant species fit into these three groups as follows: ARISTOLOCHIA: *sesostris*, *erithalion*, *anchises*, *arcas*, *polydamus*, *belus* and *crassus*. FLUTED: *polyxenes*, *thoas*, *paeon*, *lycophron*, *anchisiades*, *torquatus* and *cleotas*. KITE: *phaon*, *agesilaus* and *protesilaus*.

Consideration of this arrangement shows no logical, technical or scientific agreement. This is only to be expected in sight identification, which can take no account of sexual relationships, or parallelisms, or the superficial resemblance brought about by mimicry.

After final identification of the seventeen species of *Papilio* migrants, I arranged mounted specimens of all in a large insect drawer, placed this upright on a chair in good light and studied them from a distance of ten meters. From this distance I made the following key:

A—WHITE AND BLACK

- a—Small: *agesilaus agesilaus*  
 b—Large: *protesilaus archesilaus*

B—YELLOW AND BLACK

- a—Yellow-banded  
 Broad-band-plus-spot, small: *torquatus*, *orchamus*, male  
 Broad-band, medium: *lycophron hippomedon*, male  
 Narrow-band: *paeon thrason*  
*thoas neacles*

- b—Yellow-spotted  
 Small: *polyxenes americanus*  
 Medium: *polydamus polydamus*  
 Large: *cleotas coroebus*

C—RED AND BLACK (Hindwing)

- a—Cream-spot-forewing  
*sesostris tarquinius*, female  
*erithalion zeuxis*, female  
*anchises osyris*, female  
*arcas arcas*, female  
*torquatus orchamus*, female

- b—Green-spot-forewing  
*erithalion zeuxis*, male  
*anchises osyris*, male  
*arcas arcas*, male

- c—Black-forewing  
*anchisiades anchisiades*

D—GREEN AND BLACK

- a—Green-forewing  
*sesostris tarquinius*, male

- b—Green-hindwing  
*phaon*

E—BLACK (Dominantly)

- belus varus*  
*crassus*  
*lycophron hippomedon*, female

I compared this key with the names made up on the spot in the field, and found a gratifying agreement in species recognition. The differences were chiefly substitution for patterns and colors of the names of northern species suggesting resemblances, species with which I had long been familiar in the eastern United States. For example, *agesilaus agesilaus* was "small ajax or zebra," *polyxenes americanus* was "small asterias," and *thoas neacles* was "cresphontes-like," etc.

I cite all this as in no way directly possible or in the same detail applicable for use by another observer, but merely to show a framework upon which can successfully be erected an observer's sight key. Further comments, in greater or less detail, will be found under the treatment of many of the species.

My special thanks go to Mr. Henry Fleming, entomologist of our Department of Tropical Research, for many direct observations and for frequent corroboration of my own. In addition I am beholden to him for looking up distribution data and for painstaking identification of all the species.

*Papilio anchises osyris* Felder.

Species Range: Colombia to Brazil, Bolivia and Paraguay.

Subspecies Range: Venezuela.

Field Characters: Both male and female indistinguishable in the field from *erithalion zeuxis*. Therefore all specimens observed and not taken are combined under the two species. Compared with *arcas arcas* the male lacks bright green forewing spot, and the female has a decidedly larger, 4-celled forewing cream spot.

Number and Sex: Both sexes taken; eight males, five females.

Date: April 13 to July 29.

Condition: All taken were fresh.

Record of Captures: 1945—July 15 (male), 18 (female). 1946—April 13 (male, km. 20). 1948—April 29 (male); May 1 (female), 31 (female); June 6 (male and female); July 17 (male, km. 30), 23 (male, km. 15), 29 (female at Pass, 2 males, km. 35).

Combined Sight Records: *anchises* and *erithalion*: (Total 62). 1946—May 27 (4 females); June 29 (2 females). 1948—May 26 (4 females); June 4 (11 females passed in 10 minutes), 15 (4 females resting on shrubs), 22 (5 seen); July 2 (12 females), 9 (14 males, 3 females), 29 (3 females).

*Papilio anchisiades anchisiades* Esper.

Field Name: Red-spot Black.

Species Range: Mexico to southern Brazil.

Subspecies Range: Colombia to Bolivia and Para (Brazil).

Field Characters: Black with red on hindwing. Closest in field appearance to wholly black *lycophron hippomedon*.

Number: 2 specimens taken, a male and a female.

Notes: This black-forewing-red-hindwing papilio came through the Pass with what were taken and identified as female *arcas arcas* and *anchises osyris*, all captured together.

Record of Captures: A male in frightfully worn condition collected on April 13, 1945, No. 45456. A second individual, a female, taken at the Pass May 1, 1948, No. 48474.

*Papilio agesilaus agesilaus* Guerin.

Field Name: Small Black-and-white Zebra Swallowtail.

Species Range: Mexico to Paraguay.

Subspecies Range: Magdalena Valley, Colombia, to northern Venezuela.

Field Characters: Unmistakable resemblance to our northern ajax or zebra. The only optically related species is *protesilaus archesilaus*, but the present species is much smaller (forewing 43 mm. as compared with 53 mm.). The difference easily recognizable when either species is close at hand or near other butterflies.

Number: Total recorded 58. Seven taken (48543, 48731, 481344, 481494).

Sex: Both sexes taken.

Date: From April 29 to July 26.

Frequency: Recorded on seventeen days. Moderately but markedly gregarious. Two-thirds of *agesilaus* were recorded in groups of 4 to 8, while one-third appeared singly or in twos.

Flight: Except when alarmed or fighting against a strong head wind, the flight was unhurried and wavering, always steadily south.

Condition: With one exception all that I saw hovering or resting at the Pass were in

good condition, with both long slender tails visible to the naked eye or through three-power binoculars. No. 481344, taken July 26, 1948, at kilometer 16, was badly mutilated, with one tail missing. Dissection revealed that this male had already mated.

Record: 1946—May 26 (2 seen), 27 (2 at Pass, 3 at km. 20), 30 (6 singly). 1948—April 29 (2); May 14 (1 taken), 21 (4 seen, 1 taken), 23 (1 taken), 24 (4), 26 (4), 31 (8); June 6 (1), 17 (2 taken), 19 (2); July 13 (4), 16 (2), 23 (1 taken km. 16), 24 (6), 26 (1 at Pass, 1 at km. 16).

***Papilio arcas arcas* Cramer.**

Field Name: Green-spot (male). Two-celled-cream-spot (female).

Species Range: Mexico to Colombia, Venezuela and the Guianas.

Subspecies Range: Venezuela and the Guianas.

Field Characters: Closest to *anchises* and *erithalion*, from which it differs in the bright green forewing spot in the male, and the smaller, two-cell forewing spot in the female. It is also close to the exceedingly rare *torquatus orchamus*. From the male *sesostris tarquinius* this species differs in the red on the hindwing.

Number: Total recorded 277. Twenty-one taken.

Sex: Both sexes taken. In 1946 only females were seen or taken. In 1948 females were dominant from May 1 to June 17, and males from July 6 to July 22.

Date: May 1 to July 22.

Frequency: Recorded on 20 days: 1 (15 times), 2 (4 times), 4 (once), 6 (twice), 7, 13, 14, 16, 18, 29 and 85. Decidedly gregarious, occurring singly and in twos nineteen times, comprising one-fourteenth of the total number passing in larger numbers—from 4 to 85. As mentioned above, the sexes showed a decided segregation. The flocks were usually compact waves.

Flight: Rather low and fluttering.

Condition: Most of *arcas* observed were in fresh condition, decidedly unworn.

Extent of Migration: On four separate days specimens of this species were taken both at the Pass and at kilometer 20, well to the south, and at kilometer 35, half way to the coast to the north.

Record: 1945—July 3 (3 taken), 16 (2 seen, 1 taken, Limon). 1946—May 28 (27 seen, 2 taken), 29 (7 at Pass, 6 at km. 20), June 4 (female), 22 (female); September 7 (84 in half an hour, 1 taken). 1948—May 1 (female), 4 (6 females), 5 (male), 28 (female) 29 (female); June 6 (2 males, flock of 18 females), 17 (16 females flying low), 22 (male and female), 28 (28 females); July 6 (2 males), 9 (male caught and eaten by bat falcon, 21 males seen), 14 (7 males), 15 (11 males, 3 taken), 16 (13 seen, four fighting in midair), 19 (4 males, 1 taken km. 15), 22 (2 males, 1 taken km. 35).

***Papilio belus varus* Kollar.**

Species Range: Mexico to Bolivia and Para (Brazil).

Subspecies Range: Guatemala to northern Venezuela and Ecuador.

Dichromatic Female, form *latinus* Felder.

Field Name: Greenish-hindwing-band Black.

Field Characters: Black, with a curved band of large, yellow-green spots on hind wing.

Number: Total recorded 19. Eight taken.

Sex: Females only taken.

Date: May 29 to August 4.

Frequency: Taken singly. Five once seen together.

Condition: Fresh.

Record: 1946—July 7 (1 seen km. 20). 1948—May 29 (1 seen); July 4 (4 seen at 8:30 A.M.), 14 (1 taken), 16 (3 taken), 21 (2 taken, 3 seen), 26 (1 taken, 2 seen km. 16); August 4 (1 taken).

Dichromatic Female, form *varus* Kollar.

Field Name: Cream-spot-forewing Black.

Field Characters: Irregular splash of yellow in forewing; hindwing blue-black.

Number: Total recorded 18. Three taken.

Sex: Females only taken.

Date: May 30 to July 26.

Frequency: On two occasions, five were seen together.

Condition: Fresh.

Record: 1948—April 29 (1 taken); May 30 (5 seen); July 8 (3 seen), 9 (2 seen alighted, 2 taken, 5 seen km. 31).

***Papilio cleofas corcebus* Felder, form *dione* Rothschild and Jordan.**

Field Name: Large Asterias Swallowtail.

Species Range: Costa Rica to Brazil.

Subspecies Range: North Colombia and Venezuela.

Field Characters: Rather like a very large Asterias, or *polyxenes americanus*, with forewing 67 mm. as compared with 40 mm. A very distinct species.

Number: Total recorded 19. One taken.

Sex: The single specimen taken was a female.

Date: May 26 to July 17.

Record: 1948—May 10 (4 seen), 26 (2 seen); June 6 (female taken, 2 others flying in company with three of the small *polyxenes americanus*); July 10 (2 at Pass, 2 at km. 15), 17 (3 at Pass, 3 at km. 30).

***Papilio crassus* Cramer, male form *lepidus* Felder.**

Field Name: Black Philenor.

Species Range: Costa Rica south to Brazil.

Field Characters: Wholly black except for concealed bluish-white anterior border of hindwing.

Number: Total seen 23. One taken.

Record: A single male specimen of the form *lepidus* taken on July 21, 1948, No. 481538. Twenty more, distinctly seen, passed

at the same time, all out of reach. On the following day, July 22, two more of these black papilios were seen. No other record.

***Papilio erithalion zeuxis* Lucas.**

Species Range: Costa Rica to Colombia and northern Venezuela.

Subspecies Range: North Venezuela and Colombia.

Field Characters: Both sexes indistinguishable from *anchises osyris*. Differs from *arcas arcas* in male lacking forewing green spot, and female with larger, 4-celled forewing cream spot.

Number: Total number taken 14.

Sex: Both sexes taken.

Date: June 29 to July 24.

Condition: All freshly emerged.

Record of Captures: 1945—July 3 (female taken, Limon). 1946—June 29 (female, km. 20); July 7, 8 and 10 (Each day 1 female taken, km. 20). 1948—July 9 (3 males, km. 31), 14 (male), 15 (male), 17 (2 females), 23 (female, km. 15), 24 (female).

For joint sight identification records with *anchises osyris*, see under latter species.

***Papilio lycophron hippomedon* Felder.**

Field Name: Male, Broad-band Medium Turnus. Female, Black Troilus-like Swallowtail.

Species Range: Mexico south to Argentina and Uruguay.

Subspecies Range: Colombia and northern Venezuela.

Field Characters: Male can be confused only with the very rare, smaller, yellow-spot *torquatus orchamus*; female recalling a melanistic *troilus* or *phaon* with black hindwings.

Number: Total recorded 20. Eight taken.

Sex: Both sexes taken.

Date: May 10 to July 20.

Record: 1946—May 27 (2 at Pass, 2 km. 20, all males). 1948—May 10 (3 males seen), 21 (female taken), 23 (male taken), 24 (male taken), June 6 (2 females taken), 17 (2 males taken), 29 (4 males seen); July 10 (male seen), 20 (male taken).

***Papilio paeon thrason* Felder.**

Field Name: Rare Cresphontes-like Swallowtail.

Species Range: Mexico south to Argentina and Uruguay.

Subspecies Range: North Colombia and Venezuela.

Field Characters: Indistinguishable in the field from *thoas neacles*, but as only a single specimen of *paeon thrason* was taken, compared with more than one hundred of *thoas*, I am assuming that all Cresphontes-like papilios observed were of the more abundant species.

Record of Capture: A single male taken on May 23, 1948, No. 481539, in extremely torn and worn condition. It was captured at the Pass at 12:30 P.M., the day being

warm and sunny with a Force 4 wind from the south.

***Papilio phaon* Boisduval, aberration  
*metaphaon* Butler.**

Field Name: Philenor-like Swallowtail.  
Species Range: Mexico to Ecuador and Venezuela.

Field Characters: This is the only black papilio with green on the hind wings.

Number: Total recorded 254. Seven taken.

Sex: Both sexes taken.

Date: April 13 to July 21.

Record: 1945—May 24 (1 taken). 1946—(September 9, numbers of these black papilios with large green spot on the hind wings were flying too high to catch. Several alighted and allowed detailed study with Number three glasses. Counted 228 and missed many more.) 1948—April 13 (male taken km. 20), 16 (male taken), 27 (male taken, km. 20), 29 (female taken at Pass); July 21 (2 taken, 19 seen).

***Papilio polydamus polydamus* Linnaeus.**

Field Name: Medium Asterias Swallowtail.

Species Range: South Atlantic states, West Indies and south to Argentina.

Subspecies Range: Georgia south to Buenos Aires.

Field Characters: Differs to the eye from *polyxenes americus* in the field by the single instead of double line of yellow spots across all wings. Another distinction is the larger size.

Number: Total recorded 177. Nine taken.

Sex: Both sexes taken.

Date: May 15 to July 26.

Frequency: Decidedly gregarious. One-eighth passed singly or in a scattering up to five individuals. Seven-eighths were observed in flocks of ten to forty-eight.

Record: 1946—May 27 (2 seen). 1948—May 15 (5 seen), 29 (female taken); June 6 (female taken), 22 (11), 30 (female taken, 48 passing, 2 seen at km. 21). July 9 (female taken), 10 (2 males taken, 16 seen. 2 taken km. 31), 11 (14 flurry, 1 single), 14 (1 taken, 23 seen), 17 (10 seen km. 30), 18 (3), 19 (3), 22 (3 km. 35), 26 (27 seen).

***Papilio polyxenes americus* Kollar, form  
*melasina* Rothschild and Jordan.**

Field Name: Small Asterias Swallowtail.  
Species Range: Canada south to Cuba and Peru.

Subspecies Range: Colombia, Venezuela and northern Peru.

Field Characters: Under a new name this proved to be the same species as our northern Asterias. The only other resembling migrant butterfly was the markedly larger *polydamus polydamus*.

Number: Total observed 34. Although observed on ten occasions during two seasons, only three specimens were taken.

Date: March 25 to July 20.

Frequency: 1, 1, 1, 2, 2, 2, 3, 3, 3, 6, 6.

Note: Three perfect specimens on June 5, after rain, clung to the extreme ends of large leaves. The wings were flat and expanded, with the fore edge straight across so that the transverse band and spots were continuous.

Record: 1946—March 25 (1 taken, km. 21); April 19 (1 taken, km. 21); May 28 (2 seen at Pass). 1948—April 29 (3 seen); May 4 (6 flying together), 28 (2 seen); June 5 (3 seen), 6 (3 seen); July 19 (6 seen), 20 (1 taken at Pass), 22 (6 seen at km. 35).

***Papilio protesilaus archesilaus* Felder.**

Field Name: Large Zebra Swallowtail.

Species Range: Mexico to Paraguay.

Subspecies Range: Colombia, northern Venezuela and western Ecuador.

Field Characters: Larger than (forewing 53 mm. as compared with 43 mm.) but in general similar to *agesilaus*. Size difference quite apparent when near, but not when flying high, away from other known butterflies. At least fifteen individuals were not counted because of uncertain sight identification.

Number: Total recorded 42. Three taken (48543).

Sex: Males only were taken. The female seems to be quite unknown.

Date: Recorded on migration from April 29 to July 19.

Frequency: The relative gregariousness corresponds to that in *agesilaus*. More than five-sixths were in 4 to 12 groups, and six only seen as solitary or dual migrants.

Condition: All observed in detail appeared fresh and perfect.

Additional Notes: The flurry of 12 large zebras on May 30, were in a compact body, and at a time when neblina and rain, while light, were continuous enough to discourage all other migrants. Yet these great swallow-tails flew steadily at a height of about 12 feet, up to and through the Pass and down into the fog on the south slope.

The actions of six which passed on May 26 were typical. All flew slowly and with slightly wavering flight at 10 feet, until I swooped futilely at them with the net when all swerved sharply out and down, two penetrating the underbrush and working their way separately through the Pass before rising into the free air again. Three were followed with the glasses far down the south slope.

Record: 1946—May 27 (1 seen, 1 at km. 20), 29 (4 seen, 1 taken). 1948—April 29 (4); May 1 (3), 4 (1 taken), 10 (1), 21 (5 seen, 1 taken), 26 (6), 30 (12); July 19 (1 at Pass, 1 at km. 15).

***Papilio sesostris tarquinius* Boisduval.**

Field Name: Male, Green-spot Black.

Species Range: Mexico to Bolivia and central Brazil.

Subspecies Range: Panama, Ecuador, northern Venezuela.

Field Characters: Male to be confused only with male *arcas arcas*, but wholly lacks the hindwing red.

Number: Total recorded 39. Three taken.

Sex: Males only taken.

Date: April 30 to July 20.

Frequency: 1, 4, 5, 6, 23.

Condition: All freshly emerged.

Record: 1948—April 30 (1 taken); June 10 (4 seen), 17 (6 seen), 22 (22 seen, 1 taken); July 20 (4 seen, 1 taken).

***Papilio thoas neacles* Rothschild and Jordan.**

Field Name: Common Cresphontes-like Swallowtail.

Species Range: Texas to Buenos Aires.

Subspecies Range: Nicaragua to Ecuador, Venezuela, Trinidad and the lower Orinoco.

Field Characters: Cresphontes-like. Unidentifiable, even at close range, from *paeon thrason*, but only a single specimen of the latter was taken in two years of collecting.

Number: Total recorded 105. Nine taken.

Sex: Both sexes taken.

Date: May 4 to September 8.

Frequency: Usually seen passing in small groups, five to eight, maximum sixteen. Strong flyers, difficult to capture, but occasionally alighting, affording opportunity for a good look.

Record: 1946—May 4 (male taken, km. 20), 27 (16 seen); July 7 (female taken, km. 20); September 8 (3 seen). 1948—April 29 (3 seen), 30 (3, km. 26, headed for Pass); May 1 (4), 10 (2), 11 (2), 15 (4 seen, 1 taken), 23 (8 seen, male taken), 26 (6), 31 (1 seen); June 6 (3 taken, male, 2 females. Eggs protruding from females), 10 (5), 18 (8), 22 (6), 29 (4), 30 (5); July 2 (5 seen), 9 (2 at Pass, 6 km. 31), 13 (male taken), 19 (3 seen, 1 taken km. 18).

***Papilio torquatus orchamus* Boisduval.**

Field Name: Male, Small Yellow-Band-and-Spot. Female, mimic of *arcas*.

Species Range: Mexico to Bolivia, Brazil and Paraguay.

Subspecies Range: Colombia and northern Venezuela.

Field Characters: Male somewhat similar to but smaller than male *lycophron hippomedon*; female very close to female of *arcas arcas*. The large, separate, anterior yellow spot on forewing of the male distinguishes it from the solid band of *lycophron*.

Number: Two males were seen, and two females taken.

Sex: Both sexes seen, female only taken.

Dates: May 1 to July 2.

Record: On May 1, 1948, I watched two new papilios fighting in the Pass. One flew down and alighted just out of reach, and the other soon followed. I made a detailed description of them, recording them as yellow-

banded-with-spot, tailless papilio. Not until our return north were we able to identify the insects by comparison with a male *torguatus* taken at Caripito.

On May 26 and again on July 2, 1948, a female was taken. These were badly rubbed and torn, whereas the males I saw were freshly emerged.

## EXPLANATION OF THE PLATE.

## PLATE I.

Seventeen species of butterflies of the genus *Papilio* taken as migrants at Portachuelo Pass, Rancho Grande, north-central Venezuela.

- Fig. 1. *sesostris tarquinius* (male).  
 Fig. 2. *sesostris tarquinius* (female).  
 Fig. 3. *erithalion zeuxis* (male).  
 Fig. 4. *erithalion zeuxis* (female).  
 Fig. 5. *anchises osyris* (male).  
 Fig. 6. *anchises osyris* (female).  
 Fig. 7. *arcas arcas* (male).  
 Fig. 8. *arcas arcas* (female).  
 Fig. 9. *polydamus polydamus*.  
 Fig. 10. *belus varus* form *latinus*.  
 Fig. 11. *belus varus* form *varus*.  
 Fig. 12. *crassus* form *lepidus*.  
 Fig. 13. *polyxenes americanus* form *melasina* (male).  
 Fig. 14. *polyxenes americanus* form *melasina* (female).  
 Fig. 15. *thoas neacles*.  
 Fig. 16. *paeon thrason*.  
 Fig. 17. *lycophron hippomedon* (male).  
 Fig. 18. *lycophron hippomedon* (female).  
 Fig. 19. *anchisiades anchisiades*.  
 Fig. 20. *torquatus orchamus* (male).  
 Fig. 21. *torquatus orchamus* (female).  
 Fig. 22. *cleotas coroebus* form *dione*.  
 Fig. 23. *phaon* aberration *metaphaon*.  
 Fig. 24. *agesilaus agesilaus*.  
 Fig. 25. *protesilaus archesilaus*.



MIGRATION OF PAPILIONIDAE AT RANCHO GRANDE, NORTH-CENTRAL VENEZUELA.



## 15.

Notes on *Ergasilus* Parasites from the New Brunswick, New Jersey, Area, with a Check List of All Species and Hosts East of the Mississippi River.

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## INTRODUCTION.

The members of the genus *Ergasilus* represent the most undifferentiated of all the copepod parasites and clearly show a possible line of evolution from the free-living forms to the very specialized parasites that are to be found in other families and genera.

Even in the genus itself one finds the transition taking place, and *E. chautauquaënsis* (which has never been found as a parasite) to *E. elegans*, which is parasitic only after the eggs begin to develop, and on to the other forms where the females are parasitic after they have become sexually mature.

The main characteristics of the genus are its cyclops-like appearance; 2nd pair of antennae enlarged and prehensile, 1st antennae six-jointed; first thoracic segment and head fused to form a large carapace; five pairs of swimming legs; the first four biramous, the fifth pair very degenerate and uniramous. Egg sacs are similar to those in *Cyclops*. The genus is typically fresh-water, though some ergasilids are to be found in brackish and marine waters. The type species of the genus is a very common European species, *E. sieboldi*, established by Nordmann in 1832.

These parasites are generally found clinging to the gill filaments, but one species, *E. megaceros*, has been found in the nasal fossae of the Fulton cat, *Ictalurus anguilla*, and another, *E. elongatus*, has been found attached to the bony gill rakers of the spoon-bill cat, *Polyodon spathula*. At the present time they have been found to infest all of the major groups of fresh-water fishes and it is likely that no species of fresh-water fish is entirely free from the possibility of becoming a host. As far as is known, fishes are the only hosts on which this genus has ever been found. (See Mueller, 1936; Tidd & Bangham, 1945; Wilson, 1911, 1916, 1925, 1932; Wright, 1844.)

The males of *Ergasilus* are free-swimming

throughout their lives. They are small and easily overlooked in plankton samples and consequently few of them have ever been described. The chief distinguishing characteristics in the males are the powerful maxillipeds, which are lacking in the females, and the small, weak second antennae.

The females are free-swimming during their early developmental stages and only attach themselves after mating. It is generally concluded (Wilson, 1911) that mating takes place only once while the female is still free-swimming. The sperms are stored in the semen receptacle and fertilize the eggs as they pass out into the ovi-sacs.

The breeding season apparently extends throughout the summer months. The length will vary from season to season, or from one region to another, depending on favorable water temperatures. In this area females were observed with fully extended egg strings on March 31. In the laboratory the incubation period was found to be around eight weeks, which is about the period of time observed by Wilson ("eight to nine weeks"). Henderson (1926) in her paper on *E. lucionercarium* from Canada, stated that it is likely that the females carry their egg strings throughout the winter. This is not the case in Westons Mills Reservoir, but it may be that in Canada, where the summer season is considerably shorter, the last batch of eggs does not get the chance to develop before cold water temperatures come and consequently must be carried over until the warmer temperatures of spring. In New Brunswick the breeding season is over by the middle of November.

OBSERVATION ON EPIDEMIC OF *Ergasilus* ON FISHES IN THE WESTONS MILLS RESERVOIR, NEW BRUNSWICK, N. J.

During the latter part of November, 1947, fishermen began to notice large numbers of fish dying in Westons Mills, a reservoir from which New Brunswick obtains its water supply. Local residents estimated that the fish were dying by the "thousands," and indeed the number of dying fish was so great

<sup>1</sup> The author wishes to express his appreciation to Mr. Herbert Groat, who first called attention to the epidemic; Dr. R. F. Nicrelli for assistance in making this paper ready for publication; and to Herbert Treuting and others who gave assistance when it was needed.

as to attract large flocks of sea gulls from the nearby Raritan River. The fish affected were apparently only two species, calico bass, *Pomoxis sparoides*, and bluegill, *Lepomis macrochirus*.

Some of these fish were brought to the Rutgers University Zoological Laboratory where they were examined for possible parasitic infestations. No intestinal parasites were found in excessive numbers nor did there appear to be any injury of body tissues, either external or internal. The gills appeared to be covered with an unusually heavy coating of mucus and microscopic examination revealed great numbers of copepod parasites of the genus *Ergasilus*. The blue color of these organisms, the three knobs on the inner edge of the second antennae towards the distal end, and the fact that they were all found in between the gill filaments seemed to indicate conclusively that these were of the species *caeruleus*. The hairs and spines on the appendages, along with other general morphological characteristics, were not quite in accord with Wilson's *caeruleus*, but there seemed to be a considerable amount of variation in this genus, depending on geographic location (Mueller, 1936). Wilson (1911) considers *caeruleus* a parasite of the vegetative Centrarchidae, and gives the explanation that the copepods on these fishes must locate themselves between the gill filaments to escape the discomfort and irritation to their gills from bits of vegetation.

A number of trips were made to the reservoir to collect fish during this period. Oxygen determinations were made at all depths and at no time was the O<sub>2</sub> concentration less than 10 ppm. Most of the fish were alive when captured. They could easily be spotted as they swam feebly on their sides on the surface of the pond. It was possible to come up alongside these fish in a boat and pick them up by hand. Occasionally a fish would sound on approach, but only to rise slowly to the surface after a short interval. On the first of such trips about a dozen fish were collected and taken back to the laboratory. These were placed in a well-aerated aquarium. At first they seemed almost dead—all lying motionless on their sides, with only an occasional movement of a fin. The next day, however, they seemed fully recovered and all were swimming about apparently quite normal. A few of these examined at this time were found to have a very heavy infestation.

In brief, the meager facts obtained on the epidemic from Nov. 27 to Dec. 10, 1947, can be summarized as follows:

1. Many calico bass and bluegills died during this period. No official estimates could be obtained, but laymen who observed the phenomenon estimated the deaths to be in the thousands.
2. One calico bass died for every ten bluegills. These were apparently the only fish affected.
3. All fish that were infested by these parasites appeared to have a heavy coating of mucus over the gills.

4. Estimated number of parasites on each fish was 250-300.
5. Age group (as determined by scale readings) was 1-2 years.

During the late fall of 1948 these observations were continued. A large fish trap was constructed and set in deep water as soon as ice covered the reservoir. All of the species of the Centrarchidae as well as one yellow perch were examined. Later in the year the fish were obtained by seining and from fishermen.

In this survey the large-mouth bass, *Micropterus dolomieu*, was found to be parasitized by a second species, *E. centrarchidarum*. This species is generally larger, broader, and found on the outside of the gill filaments, in contrast to *caeruleus* which is found between the gill filaments. In addition, there are no knobs on the inside surface of the distal end of the second pair of antennae.

Again there were morphological differences from Wilson's description of *centrarchidarum* and this phase of the work will be discussed in a later paper. Both species had the blue pigment but *centrarchidarum* was never as deeply pigmented as *caeruleus*. Strangely enough, both species had the same hair and spine formula on their appendages. This is: 1st exopod, I-0; 0-1; II-5, endopod 0-0; 0-1; II-3; 2nd exopod, 0-0; 0-1; 0-6, endopod, 0-1; 0-2; I-4; 3rd exopod, 0-0; 0-1; 0-6, endopod, 0-1; 0-2; I-4; 4th exopod, 0-0; 0-5, endopod, 0-1; 0-2; I-3.

In addition to the sampling of fish from Westons Mills, two other bodies of water in the New Brunswick area were sampled. These included the lower section of the Delaware-Raritan Canal and the small pond in Johnson's Park. The bluegills and calico bass in Johnson's Park were found to be free of ergasilids but the canal proved as fruitful as the reservoir. A summary of the fish examined is given in Table I.

Some interesting facts are foreshadowed in Table I. Although the amount of sampling from both bodies of water was not extensive enough to reveal fully the actual condition, nevertheless the methods by which these fish were obtained and the period of time over which the sampling was made certainly indicate the trend that one might expect to find if a more extensive sampling were to be taken.

For example, only five large-mouth bass were obtained—but under totally different conditions and at various times. The fact that all five had infestations does not indicate that all the bass are parasitized, yet one would expect to find a high percentage of the bass serving as hosts to these parasites. On the other hand, not once during this entire period of research has there ever been found a pumpkinseed infested with these copepods. Certainly one can say that for this species the incidence of parasitism is very low.

Again, viewing the information in the same light, one should expect the bluegills to be parasitized about 50% of the time in

TABLE I.

Result of the Samplings from Westons Mills and Delaware-Raritan Canal from Nov. 30, 1948-July 30, 1949.

Name	Total No. Caught	Percent of parasitism	Average Length	Length <sup>h</sup> . Range
Calico bass*	5	100%	5.79"	4"-7"
Bluegills	15	60%	5"	2"-7 3/4"
Pumpkinseed	6	0%	4"	3"-5"
Large-mouth bass	5	100%	6.4"	2 1/2"-12"
Yellow perch	1	0%	7"	7"

\* The highest infestation noted was on one calico bass 5 3/4" in length; 259 caeruleus were counted on this fish.

Westons Mills and the Canal. No data on calico bass could be obtained from the Canal but from the available information it would seem that these fish have become the most heavily infested in Westons Mills, not only in number of individuals but in number of parasites per fish. This is significant, for although the calico bass was found to be the most heavily infested as well as the most commonly parasitized fish, the epidemic of 1947 killed only one calico bass to ten bluegills. Unfortunately, here also, too little information is at hand. On the basis of the present data, however, there seems to be two logical explanations for this:

1. The calico bass are more resistant to the infestation of these gill parasites than are the bluegills and have been able to build up a resistance.
2. All the bluegills left are those that have built up a resistance to these parasites, or those that were only slightly parasitized.

Both fish are to be found in the same general type of environment and both have similar food habits, so apparently these two factors may be discounted.

#### PATHOGENESIS.

There has been a great deal of controversy over the extent of damage done by the ergasilids, as well as exactly what kind is done. Wilson (1911) states that "Living as they do upon the fish's gills, there can be but little doubt that they feed upon blood." Halisch (1939) in his observations on *E. sieboldi* and *E. minor* on the gills of tench states that extra-intestinal digestion is important and that much more tissue is destroyed than is ingested by the parasitic copepod. Blood may be taken in. Fungi may grow in the lesions.

In contrast to these two observations, Henderson (1926), in her work on *E. luciopercarium*, observed that "The gills may be heavily attacked without affecting the health of the fish. It is a harmless parasite, which, while it only benefits the unbidden guests, causes no lesions and consequently does no injury to the host." (If this is the case it should not even be called a parasite, but a commensal). She goes on to explain how, in her opinion, it is impossible for the parasites to injure the gill tissue, since the mouth parts of these organisms are too weak to pierce the gill tissue.

One might suspect that the claw-like, prehensile, second pair of antennae of the parasite is capable of at least some damage to the gill lamellae, although the mouth parts may be too small to cause any injury. However, the observations in the present studies showed no evidence of mechanical injury; neither was there any evidence of digested gill tissue or blood in the intestine of the numerous copepods examined, even in females with ovaries full of developing eggs.

We agree with Henderson (1926) that these parasites in all probability feed on the excessive mucus produced under the condition of the parasitism, or the many minute mucus or bits of organic debris and bacteria in this viscid material. However, it is altogether possible that the parasites may feed on sera, straining out the corpuscles.

A close examination of the mouth parts of these ergasilids will reveal the mandibles and second maxillae heavily fringed with setae. These would seem ideal for feeding on mucus or bits of organic debris and bacteria but hardly suitable for feeding on blood. Any pathological conditions of the gills may cause the mucus glands to secrete an excessive amount of mucus (Nigrelli, 1949). This has been especially apparent during infestations of trematode gill parasites. This condition has also been observed on many of the fish that were infested with these copepods<sup>2</sup>. It may be that an excess mucus secretion over the surface of the gills may lower the efficiency of the gills to absorb the dissolved oxygen in the water. Under normal water conditions when there is sufficient oxygen and all the chemical and physiological factors are in proper balance, this may not have any deleterious effects. However, if, for example, a factor such as the CO<sub>2</sub> concentration in the water should be increased, it might be sufficient to reduce the efficiency of the gills in absorbing the dissolved oxygen and so cause the fish to die of suffocation.

The highest death rate has been found among the younger fishes and it is the

<sup>2</sup> It must be kept in mind that the heavy coating of mucus which seems to accompany fish that are heavily infested with this parasite does not mean too much in itself. Fish that have been placed in preservative or that have died from other causes may show the same condition. Moreover, some fish that were heavily infested did not have an excess of mucus covering the gills. In such cases these fish exhibited no symptoms whatsoever and appeared perfectly normal. Apparently, there is a physiological balance here that is very delicately adjusted and which can be thrown out of balance only under certain specific conditions.

TABLE II.

Check List of the *Ergasilus* Found East of the Mississippi River.

Names and Synonyms	Hosts	Localities Studied	Remarks
<i>E. caeruleus</i> Wilson	Yellow perch Trout perch Wall-eyed pike	Lake Mendota Trout Lake region Lakes Erie & Michigan	
Synonyms:	Gray pike, Blue pike Rock bass, Calico bass	Oneida Lake Mississippi River, Iowa	
<i>E. confuscus</i> Bere	White bass Warmouth bass		
<i>E. skryabini</i> Mueller	Crappie Green sunfish Blue-spotted sunfish Pumpkinseed Bluegill Lake trout Cisco, White fish Sucker, Long-nosed gar		
<i>E. centrarchidarum</i> Wright	Rock bass, Calico bass, Large-mouth bass, Small-mouth bass, White bass, Warmouth bass, Green sunfish, Bluegill, Crappie, Pumpkinseed, Sunfish (?) Wall-eyed pike, Gray pike, Sauger, Silversides, Smelt, <i>Microgadus tomcod</i>	Lake Erie Lake Michigan St. Lawrence River Watershed Lake Champlain Black Lake, N. Y. Lakes St. John & Chibogamo, Quebec St. Andrew's Bay, N. B. Lake Maxinkuckee, Ind. Mississippi River, Iowa Clewiston, Fla. Woods Hole	
<i>E. chautauquaënsis</i> Fellows		Lake Champlain Lake Mendota Fairport, Iowa	Has never been found as a parasite, but may be like <i>elegans</i>
<i>E. cotti</i> Kellicot	Rainbow darter Sculpin— <i>Cottus bairdii</i>	Lake Erie Westerville, Ohio	
<i>E. elegans</i> Wilson	<i>Ameiurus</i> sp. Northern black bullhead Channel catfish Short-nosed gar Long-nosed gar	Lake Okeechobee Myakka River & Canals Peace River, Fla. Mississippi River, Ia.,	Parasitic only after eggs begin developing
<i>E. elongatus</i> Wilson	Spoonbill cat	Mississippi River, Iowa and Illinois	
<i>E. funduli</i> Krøyer	<i>Fundulus ocellaris</i>	New Orleans	Salt and brackish water
<i>E. labracis</i> Krøyer	Striped bass	Woods Hole Baltimore	Marine
<i>E. lanceolatus</i> Wilson	Gizzard shad	Cumberland River, Ky.	
<i>E. lizae</i> Krøyer	Common killifish Gulf killifish Broad killifish Striped mullet White mullet	Englewood, Fla. New Orleans	Salt and brackish waters
<i>E. luciopercarum</i> Henderson	Pike perches	Lake St. John Lake Chibogamo, Que.	
<i>E. manicatus</i> Wilson	Silversides Smelt Two-spined stickleback Top minnow ( <i>Gambusia holbrooki</i> ) <i>Jordanella floridae</i>	Englewood St. Andrew's Bay, N. B. Woods Hole Along Atlantic Coast	Marine

Names and Synonyms	Hosts	Localities Studied	Remarks
<i>E. megaceros</i> Wilson	Fulton cat Fall fish	Oneida Lake, N. Y. Mississippi River, Iowa	Found in the nasal fossae and spiracles
Synonym:			
<i>E. fragilis</i> Mueller			
<i>E. mugilis</i> Vogt	Striped mullet	Beaufort, N. C.	Marine
<i>E. nigratus</i> Wilson	Large-mouth bass	Mississippi River, Iowa	
<i>E. osburni</i> Tidd & Bangham	Burbot	North Central States	
<i>E. versicolor</i> Wilson	Fulton cat Red-mouthed buffalo fish Channel cat	Mississippi River, Iowa Florida Lake Erie	
Synonym:			
<i>E. celestis</i> Mueller	Common brown bullhead Mudcat Skip jack Yellow cat Eel cat	Lake Maxinkuckee	

younger fishes that would require the greatest amount of oxygen (in proportion to the gill area), due to their greater metabolic activity. At the same time it is the younger fishes that are more susceptible to attacks from disease and parasites since they are using all their available energy toward growth. Wilson states that it is the young fish that are most heavily parasitized and this is probably true—especially during an epidemic. However, larger fish may also be quite heavily parasitized. (See Table 1).

The ergasilids on the large-mouth bass were never very abundant—never more than thirty on any individual. Although Wilson (1916) mentions fish fatalities from the ergasilids he does not mention which species or copepod causes death, nor which species of fish are killed. In checking all the literature on *centrarchidarum*, never were their numbers found to be as great as for *caeruleus*. Therefore, one wonders if *caeruleus* is not the only one that may appear in such numbers as to bring about the death of a fish.

This leads us to speculate on how many ergasilids must be present on a fish to cause death. It would seem that numbers that lead to the death of a fish at one time, appear to have no effect at another. However, during the epidemic of 1947 none of the dead fish had less than an estimated 250 copepods. Whether fewer parasites can bring about the death of a fish remains to be determined by further study.

It is apparent from the literature that *E. centrarchidarum* is the most widespread parasite and probably the best known. It has been found in all the main regions studied, including the marine habitat, but it has not been found on as many hosts (16) as has *caeruleus* (19), nor on as great a variety.

*Caeruleus* has not been found in all the

areas that have been studied and so far has proved to be an exclusively fresh-water parasite. Additional research may also reveal that *caeruleus* is more widespread than *centrarchidarum*. It is unfortunate that most of the workers in this field have failed to make clear whether *caeruleus* has always been found between the gill filaments of its host. If it is found between the gill filaments of such clear-water fishes as the lake trout, cisco and white fish, certainly Wilson's explanation for their being found between the gill filaments is not substantiated.

*E. versicolor* is apparently third in abundance and seems to be more specific in its parasitism.

Many of the *Ergasilus* have only been found on one or a few hosts, but it is still too early to state definitely that they are specific for only those hosts.

#### CONCLUSIONS.

1. It seems quite likely that *Ergasilus* may indirectly cause death to fish, although it probably seldom causes extensive damage to any given fish population.
2. Young fish (1-2 years) are apparently the only ones on which these parasites may prove fatal. Although infestations have been found to be equally high on all age groups, more young fish appear to be heavily infested than older ones.
3. Ponds where the fish are overcrowded or that are small in area seem to be the only places where infestations become high enough to cause death.
4. Ergasilids do not feed on blood, but probably on mucus or bits of organic matter found in the viscid material.
5. Death of fish is probably due to a delicate physiological imbalance affecting the diffusion of oxygen through the gill tissues.

6. *E. caeruleus* can always be distinguished from *E. centrarchidarum* by the three knobs on the second pair of antennae, and by the fact that it is always found in between the gill filaments. Variations among these copepods are exceedingly great.
7. Although Wilson considers *E. caeruleus* a parasite of the plant-eating Centrarchidae, it is also found on species that are quite carnivorous and not generally found among aquatic vegetation. It undoubtedly is found most commonly on fishes that typically inhabit an environment of aquatic vegetation, such as the bluegill and calico bass.
8. Though *centrarchidarum* and *caeruleus* have often been found on the same fish (Wilson, 1911, 16), they were never observed together in the New Brunswick area nor was *centrarchidarum* ever observed on either bluegills or calico bass in this area. Neither was observed on any but the above species of fish.
9. It may be that certain factors, chemical, physical, physiological and environmental, or a combination of these, determine which hosts may be parasitized.
10. No reason could be found to explain why the pumpkinseed, *Lepomis gibbosus*, is free from these copepod parasites in this region.

#### SUMMARY.

An epizootic in Westons Mills Reservoir which caused the death of many bluegills and calico bass was investigated.

A copepod parasite, *Ergasilus caeruleus*, was believed to be the indirect cause of the death of these fish. Apparently, metabolic wastes from the copepod or irritation to the gill tissues causes an excessive secretion of mucus. This mucus may lower the efficiency of the gills, so that when certain other factors are not in proper balance the fish will suffocate.

Large-mouth bass were found to be infested with another species *E. centrarchidarum*.

A brief survey of two other bodies of water in the New Brunswick area revealed that the incidence of parasitism from these ergasilids is quite high for bluegills, calico

bass and large-mouth bass, but does not seem to be present on the pumpkinseed.

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## 16.

An Analysis of Reproductive Behavior in the Mouthbreeding Cichlid Fish, *Tilapia macrocephala* (Bleeker).<sup>1,2</sup>

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(Plates I-III; Text-figures 1-10).

## INTRODUCTION.

Teleosts of the family Cichlidae are noted for their elaborate patterns of courtship, mating and parental care, and for the readiness with which they breed in the restricted confines of the small aquarium. It is largely because of these attributes that cichlids have become the subjects of several extensive investigations of fish behavior. Outstanding among these studies are those of Breder (1934) on the blue acara, *Aequidens latifrons*; Noble and Curtis (1939), Peters (1941) and Seitz (1942) on the jewel fish, *Hemichromis bimaculatus*; Peters (1937) on the small Egyptian mouthbreeder, *Haplochromis multicolor*; and Seitz (1940) on a closely related mouthbreeder, *Astatotilapia strigigena*.

These students have investigated topics such as schooling, sex recognition, courtship, territory, social dominance, spawning, parental care, the stimuli causing the release of various innate responses and many other related items of behavior. In these studies, mating behavior has been described qualitatively and in varying degrees of detail. Although the reports in most cases have been based on a number of observed spawnings, the results are given in a generalized or "averaged" form and the only suggestion of variability in behavior is found in such broad phrases as "this usually happens," or "the typical mode of behavior is." Moreover, the "averaging" is often achieved by means of subjective impressions rather than in terms of a calibrated or objectively weighted evaluation of behavioral characteristics.

Variability is a fundamental characteristic of biological phenomena, a characteristic

which always merits careful consideration in studies of animal behavior. It is the writer's belief that the study of teleost behavior cannot extend very far beyond the present descriptive stages unless and until methods of a more quantitative nature are employed. Students of mammalian psychology, and particularly of rodent behavior, have made excellent progress by utilizing quantitative procedures. The present study afforded an opportunity for testing the applicability of comparable techniques in the study of the reproductive behavior of fish.

The present report is concerned with the average behavior and the range of variability under constant aquarium conditions of a type which can be readily duplicated. In other investigations now in progress, the mating activities of brain-operated and hormone-treated animals will be compared to the norms obtained in the present report.

Nothing appears to be known concerning the mating behavior of *Tilapia macrocephala* in the wild state, and the present report is hardly intended as a substitute for such an investigation. Nevertheless, wherever the behavior of fishes has been studied both under field conditions and in captivity, agreement has been fairly good, as for example in the Centrarchidae. It is anticipated that the over-all picture obtained in this study should prove to be essentially similar to conditions prevailing in the natural state, and that differences if any would be expected only in some of the lesser details.

## LITERATURE.

Information concerning the breeding habits of *Tilapia macrocephala* and of related species belonging to the same genus has been furnished for the most part by aquarium hobbyists and through cursory observations by field naturalists. It is realized that because aquarists' reports often fall below generally recognized standards of scientific accuracy, as might be expected considerable confusion exists in the literature concerning certain aspects of the breeding patterns of *Tilapia*. Some of these difficulties may no doubt be attributed to an improper identification of

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<sup>2</sup>Mrs. Magda Schonwetter assisted in many of the observations. Drs. Frank A. Beach and Charles M. Breder made numerous helpful suggestions on the conduct of the observations and experiments. Dr. Myron Gordon helped solve the feeding problem. Dr. T. C. Schneirla, Mr. James W. Atz, Mrs. Marie Holz-Tucker and Mr. Christopher W. Coates read the manuscript and made innumerable constructive criticisms. The author gratefully acknowledges his indebtedness to these people and those past and present associates of the Department of Animal Behavior who in ways too numerous to mention made possible the completion of this study.

the species in question, since aquarists sometimes trust the knowledge and dependability of fish dealers for the identity of their subjects. Nevertheless it is possible to obtain from this literature a rough picture of the reproductive habits of the genus *Tilapia*. For these reasons the inclusion of numerous aquarists' accounts is considered expedient. What may be offered herein is by no means intended to be a comprehensive review of the extensive popular literature.

Brief descriptions of the breeding habits of *Tilapia macrocephala* can be found in the aquarium texts of Stoye (1935), Arnold and Ahl (1936) and Innes (1944). In addition, reports on the spawning of *Tilapia heudeloti* (which according to Boulenger (1915) may be a variety of *Tilapia macrocephala*) have been presented by Breder (1934) and Schoenfeld (1934). These accounts tell us briefly that (1) a nest is built by the mating pair; (2) the female deposits the eggs in the nest; (3) the male fertilizes the eggs as soon as they are deposited; (4) shortly thereafter the male takes the eggs into his mouth; and (5) the eggs hatch and develop in the mouth of the male. How long the eggs are retained in the male's buccal pouch is not indicated, but Stoye (1935) reports two cases where eggs were carried 24 to 25 days respectively. Stoye considers these periods abnormally long as a result of excessive disturbances.

With four probable exceptions, all the species of *Tilapia* whose spawning habits have been reported are mouthbreeders. The four exceptional species remove their larvae to sand pits in typical cichlid fashion. These non-mouthbreeding species are (1) *Tilapia guinasana* (Rolloff, 1938, 1939), (2) *Tilapia spaarmanii* (Hey, 1945, 1947; Anon., 1948)<sup>3</sup>, (3) *Tilapia melanopleura* (Svensson, 1933; Bertram, Borley and Trewavas, 1942) and (4) *Tilapia zillii* (Bade, 1923; Stoye, 1935; Arnold and Ahl, 1936; Bertram, Borley and Trewavas, 1942). However, Liebman (1933) describes *Tilapia zillii* as a mouthbreeder. Incubation of the eggs is accomplished by the females of *Tilapia flavomarginata* (Pellegrin, 1906)<sup>4</sup>, *Tilapia galilaea* (Pellegrin, 1903, 1905), *Tilapia martini* (Boulenger, 1906), *Tilapia microcephala*<sup>5</sup> (Jungmans, 1918) and *Tilapia mossambica*<sup>6</sup> (Bade, 1923; Dietz, 1926; Rolloff, 1937; Peters, 1937a, 1939; Seleuthner, 1941; Hey, 1947). The same appears to be true for *Tilapia squamipinnis*, *Tilapia lidole*, and *Tilapia shirana* (Bertram, Borley and Trewavas, 1942).

The male is credited with the care of the eggs in *Tilapia dolloi* (Asch, 1939), *Tilapia heudeloti* (Breder, 1934; Schoenfeld, 1934),

*Tilapia macrocephala* (Stoye, 1935; Innes 1944), *Tilapia microcephala* (Schreitmüller, 1920) and *Tilapia simonis*<sup>7</sup> (Lortet, 1875; 1883). However, there is some disagreement on this point since both the male and female are believed to incubate the eggs in *Tilapia simonis* (Pellegrin, 1903; Liebman, 1933), *Tilapia galilaea* (Liebman, 1933), *Tilapia microcephala* (Locke, 1932), *Tilapia nilotica* (Boulenger, 1901) and *Tilapia zillii* (Liebman, 1933). Bodenheimer (1927) claims that females alone incubate the eggs of *Tilapia simonis*, and Arnold and Ahl (1936) claim the same for *Tilapia dolloi*.

Irvine (1947) states that the male or possibly both sexes of *Tilapia discolor* and *Tilapia heudeloti* incubate the eggs, but contrary to the findings of Boulenger, Irvine relegates this function to the female in *Tilapia nilotica*. Liebman (1933) believes that it is quite general in Palestine cichlids for both parents to incubate the eggs, but the number of females performing this function is higher than the number of males so doing.

The length of the incubatory period has been reported for only a few species. Arnold and Ahl (1936) say about 14 days for *Tilapia dolloi*; Schreitmüller (1920) gives 4 to 6 days for *Tilapia microcephala*; Rolloff (1937) reports 21 days for *Tilapia mossambica*; Bade (1923) offers a value of 15 days while Dietz (1926) and Seleuthner (1941) both give 13 days as the incubatory period of this species.

The retrieving into the female's mouth of newly released young has been reported for *Tilapia dolloi* (Arnold and Ahl, 1936), *Tilapia macrocephala* (Stoye, 1935), and *Tilapia mossambica* (Rolloff, 1937; Seleuthner, 1941) while in *Tilapia microcephala* the male is credited with that activity (Schreitmüller, 1920).

Nest making by these mouthbreeders has received some general attention. On a number of occasions, Lortet (1883) witnessed the female *Tilapia simonis* lay approximately 200 eggs in a small excavation which she had hollowed out and cleaned in the silt among the reeds. Nest building by both the male and the female *Tilapia nilotica* was observed in the field by C. L. Boulenger (1908). Rolloff (1937) describes the nest of *Tilapia mossambica* as being 20 cm. in diameter. Seleuthner (1941) reports a nest for this species which was 25 cm. in diameter and reached a depth of 4 cm. in the middle, while Hey (1947) pictures it as a "small saucer-shaped depression." Bertram, Borley and Trewavas (1942) describe the nest of *Tilapia squamipinnis* as a circular depression.

Other mouthbreeding cichlids are listed by Peters (1937) as belonging to the genera *Astatotilapia*, *Ectodus*, *Geophagus*, *Hap-*

<sup>3</sup> Also recorded in "Report No. 1 (1944) Inland Fisheries Dept., Union of South Africa"—1945.

<sup>4</sup> Designated by Boulenger (1911) as *Tilapia andersonii*.

<sup>5</sup> *Tilapia microcephala* = *Tilapia heudeloti*. According to Boulenger (1915, p. 178) *Tilapia macrocephala*, and *Tilapia multifasciata* "may ultimately have to be regarded as varieties of *T. heudeloti*. I am unable to find characters by which to separate them sharply."

<sup>6</sup> *Tilapia mossambica* = *Tilapia natalensis*.

<sup>7</sup> Placed in the genus *Tilapia* by Boulenger (1899) but now referred to a new genus *Tristramella* by Trewavas (1942). Lortet (1875) called this fish *Chromis paterfamilias*.

*lochromis*, *Pelmatochromis* and *Tropheus*.<sup>8</sup> It is to be noted that at least some of these genera also contain non-mouthbreeding species, suggesting a multiple origin of this habit even within the cichlid family. This problem has been considered in some detail by Breder (1933) and Myers (1939).

The small Egyptian mouthbreeding cichlid, *Haplochromis multicolor*, and a closely related form, *Astatotilapia strigigena*, have been the most popular and intensively studied of all the mouthbreeding fish. In addition to the scientific investigations previously mentioned, more than 30 accounts of the spawnings of these two fish have appeared in the last three decades, the majority of them in the *Wochenschrift für Aquarien- und Terrarienkunde*. These accounts, which are relatively consistent in their general implications, demonstrate that the spawning behavior of these species differs considerably from that of the various species of *Tilapia* described above. For this reason what is known about the *Haplochromis* and *Astatotilapia* mating patterns is summarized briefly for the purposes of comparison.

In these species the male does practically all of the nest building. Upon the completion of the nest, the female starts the oviposition by depositing between four and ten eggs in the nest. The male immediately fertilizes the eggs after which they are picked up by the female. This cycle is then repeated as the female lays a second batch of eggs. Between five and ten such cycles have been reported by various authors as comprising a spawning. The eggs are carried for 9 to 20 days, after which the young are released. However, the young are taken back into the female's mouth at night and at other times when disturbed. Such a retrieving of the young has been the subject of a special investigation by Peters (1937).

#### MATERIAL AND METHODS.

*Tilapia macrocephala* (Bleeker) is native to West Africa, particularly in the region of the Gold Coast. Boulenger (1915) describes the species as coming from the Gold Coast, Ashantee and Lagos. Many of his specimens were taken from the Ancobra river and Seconda lagoon in the Gold Coast, and from the Lagos lagoon. According to Arnold and Ahl (1936) the fish is found in the brackish lagoons of the coast and the swampy deltas of rivers.

The individuals utilized in this study were selected from a laboratory-bred stock which had been maintained for a number of years prior to the start of the present research.<sup>9</sup> Males were chosen for the brightness of their yellow operculum which is a secondary sex

character (Pl. I, Fig. 1). The females (Pl. I, Fig. 2) were selected on the basis of the complementary sex character, namely a deep red spot in the center of the gill cover.<sup>10</sup> These dimorphic color patterns appear at sexual maturity and disappear after castration (Aronson, in manuscript).

Pairs were established by random selection and were placed in 54-liter aquaria, 60 cm. × 30 cm. × 30 cm. each containing roughly 36 liters of water. The side and rear walls of these tanks were painted pale blue to minimize any possible disturbing influences from neighboring tanks, and also to facilitate the ability of the investigator to follow the activities of the fish. The tanks were located in a greenhouse the temperature of which was maintained throughout the year at 26° C. with a positive and negative variation of approximately 3° C. To furnish hide-outs for the fish which at the same time would not obstruct the observer's view, a mat of floating plants was placed in every tank. *Cabomba* was extensively used for this purpose, but *Sagittaria subulata* was found to be somewhat more suitable and was used whenever available.<sup>11</sup> The fish were fed mostly a dehydrated preparation consisting of dried shrimp, oatmeal, beef liver, lettuce and spinach. At times this was supplemented by live tubifex worms. Occasionally the fish nibbled at the stonewort *Nitella*, and this was paced in the tanks when available. The tanks were aerated continuously, and the water was changed whenever it became excessively murky. This was approximately once a month. Tap water brought to the proper temperature was used in washing the tanks and for replacement.

In order to avoid injury to the fish due to excessive nipping which often occurred after spawning, a transparent glass partition was placed in the aquarium, separating the male from the female as soon as observations of oviposition were completed. As the individual carrying the eggs (generally the male) eats little or nothing during the incubatory period, brooding fish were not fed during this interval. By the time that the young were released from the male's mouth, the females often were prepared to spawn again. However preliminary observations indicated that when such spawnings occurred males sometimes behaved abnormally, due apparently to the protracted period of inanition. To avoid this difficulty an arbitrary rule was established to the effect that males were separated by a transparent glass partition from females for one week after they had released their young or had swallowed their eggs. This interval allowed the males to feed and regain their strength. While thus iso-

<sup>8</sup> An older listing of mouthbreeding cichlids given by Pellegrin (1903) includes the genera *Geophagus*, *Acara*, *Chaetobranchius*, *Tilapia*, *Paratilapia*, *Pelmatochromis*, *Ectodus* and *Tropheus*.

<sup>9</sup> I am greatly indebted to Miss Ethelwyn Trewavas of the British Museum for kindly checking and verifying the taxonomic identity of the fish as *Tilapia macrocephala*.

<sup>10</sup> Examination of this spot by Aronson and Holz-Tucker (in manuscript) has revealed that it is in actuality a semi-transparent window through which the underlying red gill can be seen.

<sup>11</sup> The author wishes to express his appreciation to Dr. Myron Gordon of the New York Zoological Society for furnishing all of the sagittaria used.

lated, females often spawned alone but observations showed that a considerable amount of courtship took place through the glass partition.

To prevent the parents from eating their young after they were released, large masses of the stonewort *Nitella* were placed in all tanks where young were being incubated. The stonewort was distributed equally on both sides of the partition since the newly released fry could easily swim through the cracks at the intersection of the partition and the glass walls of the tank. Disturbances caused the young to swim into the fine interstices of the *Nitella* where they would not be followed by their cannibalistic parents.<sup>12</sup>

The criteria employed to indicate the approach of oviposition were (1) persistent nest building, mostly by the female, (2) heightened courtship activity, and (3) protruding genital tubes. When these signs were observed, continuous records were taken of the courtship and mating activities of the pair up to the time of spawning and for one-half hour thereafter. Attempts were made to secure continuous pre-spawning records for three hours. However, this goal was attained in only a small number of cases with the result that the records vary from just a few minutes before spawning up to the full three-hour span. A serious difficulty was encountered here in that the activities of many promising pairs were observed continuously for many hours up to a whole day without the fish ever ovipositing.

After the present experiment had been terminated, behavior during the interspawning interval was studied, using different pairs of *Tilapia*. The experimental conditions were the same as before with the following minor exceptions: (1) no plants were used but instead inside aquarium filters served as hide-outs; (2) the water in the tanks was never changed; (3) the males

were never separated from the females. The actual spawnings of these pairs were not witnessed, all ovipositions being recorded as having occurred at the time the eggs were discovered in the male's mouth. All pairs were checked twice daily for eggs. A 15-minute record of the behavior of a given pair was taken 5 or 6 days after the spawning and again on the 15th or 16th day. The interval between successive spawnings varies from 8 days up to almost a year with a mode of 15 days (Aronson, 1945). Approximately two-thirds of the intervals are less than 29 days. Thus the 5- or 6-day score serves as an intermediate record for the shorter interspawning intervals, while the 15- or 16-day score serves in the same capacity for the longer intervals. Obviously some of the 15-day records could not be taken because of intervening ovipositions. Many of these observations served, moreover, as behavior records for varying days before spawning.

#### QUALITATIVE DESCRIPTION OF REPRODUCTIVE BEHAVIOR.

In order to furnish the reader with the proper background for the quantitative investigation, it is appropriate to present first a general description of mating activities. This account does not take into consideration the question of the range of variability and any exceptional items of behavior. Details concerning many of the generalizations made here will be considered in the next section.

Certain of the behavioral patterns which increase in their frequency of occurrence prior to spawning and which lead up to the acts of oviposition and fertilization generally are classified as courtship activity. Such behavior appears to express the level of sexual excitability of the given individual. In accordance with the views of Huxley (1914, 1938), Howard (1929) and Marshall (1936), it is assumed that courtship tends to hold the pair together, and through mutual stimulation may lead to a well synchronized spawning. In the terms of Schneirla's (1946) discussion, such relationship may be thought of as involving trophalactic processes, and the temporal aspects of these interactivities are of significance from the standpoint of adaptive function. *Tilapia* eggs (Pl. I, Fig. 2; Pl. II, Figs. 3, 4), as well as those of other oviparous teleosts, are shed in a flaccid state, but rapidly become hard and turgid upon entering the water. That is, they "water harden" (Breder, 1943). Hence, to insure fertilization the male must deposit his sperm over the eggs within a very short time after they are laid. An adequate synchronization of the pair's reproductive processes thus appears to be critically important for effective species survival.

There follows a description of the early courtship behavior of *Tilapia macrocephala*: (1) The male and female approach each other and suddenly dip their heads; or one member of the pair lowers its head. This

<sup>12</sup> This was the author's first experience with the maintenance of tropical fish. Since then, several innovations have been developed. Inside aquarium charcoal filters are now placed in every tank. These keep the water clean and eliminate the need for changing it. Plants are not used since they grow poorly in *Tilapia* aquaria. The food formulae have been modified as follows: (1) *Wet mash*: 2½ lbs. liver; ½ lb. chopped lettuce and spinach; ½ lb. dried ground shrimp (mostly shell); ½ lb. dried and ground refined shrimp (mostly muscle); Pabulum (or other precooked infant cereal)—enough to make thick paste (approximately 3½ lbs.); 1 pinch salt. The liver is chopped, about 1 cup of water added, and the mixture is then liquefied in a blending machine. All ingredients are mixed together with sufficient Pabulum to make a paste. The food is further solidified and preserved by packing into jars and immersing them in boiling water for about 10 minutes. (2) *Dry food*: 12 lbs. dried shrimp (mostly shell); 12 lbs. dried refined shrimp (mostly muscle); 10 lbs. liver; 6 lbs. chopped lettuce; 6 lbs. chopped spinach; 28 lbs. Pabulum; 2 level teaspoons salt. The ground spinach and lettuce are mixed with the Pabulum and cooked for 15 minutes. The liver is cut into slices and boiled for 15 minutes in a minimum amount of water and then chopped. All ingredients are mixed together and the resulting paste spread about ½ inch thick on trays. When almost completely dry, the food mixture is ground and sifted through screens of several coarsenesses.

The sexes are no longer separated after the spawning. If the fry are to be saved they are forcibly removed from the parents' mouths on the tenth day post-oviposition, and are placed in small aquaria. At this age the young do very well without further parental care, and thus, losses through cannibalism are easily avoided.

behavior has been termed "head-nodding." (2) When one member of the pair approaches the other, spreads its opercula and expands its buccal pouch, we have called this act a "throat-puff." (3) The male or female ceases swimming movements and the trunk musculature appears to quiver for a fraction of a second. We have named this a "body-quiver." (4) When one member of the pair slaps the other with its tail, this has been called a "tail-slap." Included in this category were the frequent cases where tail-slapping motions were quite distinct, but where actual contact with the partner was not made.

Closely associated with the courtship acts, but displayed as well in many pairs throughout the interspawning interval, is a mode of behavior which we have termed "nipping." This occurs when a fish swims after its partner, and then with a sudden dart nips or bites the body of its mate. Nipping also occurred at times without a previous chase. Sometimes the male and female may nip each other simultaneously and occasionally they may even lock jaws. Frequently observed cases in which the pursuing fish darts ahead but misses the fleeing opponent also have been included under the general heading of nipping.

In addition to its association with courtship and spawning, nipping behavior appears to be related to the establishment of social hierarchies and the formation of territories. These further relations of nipping have not as yet been investigated.

The above-mentioned patterns of behavior usually appear as quite distinct, but occasionally they tend to merge into one another, so that discretion on the part of the observer is often called for in assigning a particular courtship act to its proper category. Oftentimes two or more courtship acts may be displayed in rapid succession, a frequent combination being a head-nod, throat-puff and body-quiver. Another commonly occurring combination is the throat-puff and tail-slap.

Readers acquainted with the courtship behavior of other cichlid fishes will readily recognize the resemblance of the *Tilapia* pattern with those of other cichlids. Reactions such as the body-quiver, the throat-puff and the tail-slap in some form seem to be prevalent throughout the family.

Nest-building is first observed after intensive courtship has been in progress for several hours or days. Most of this activity is conducted by the female who begins scooping up mouthfuls of gravel from scattered locations in the bottom of the tank. Soon the excavating is confined to one location, and the construction of a nest begins. Often two or more nests are constructed prior to the spawning, and sometimes nests are built and then destroyed during the construction of an adjoining nest. The nests are most often round or slightly oval. If the gravel substratum of the aquarium is not too thick, the fish dig down to the slate bottom of the

tank. If, however, the depth of the gravel is more than 2 or 3 cm., the nests do not reach the slate.

In our study the length of time taken to complete a nest varied considerably from as little as one-half hour up to what appeared to be several days. In the latter case, the nest-building activity occurred in spurts, followed by periods of quiescence. The rapid builders generally worked continuously until the nest was completed. A small amount of nest-building was accomplished by sweeping movements of the tail and pectoral fins. However, this has been interpreted as incidental to swimming and balancing movements and not directly related to nest building.

After the nest is more or less completed, nest-building decreases considerably and is supplanted to some extent by nest-cleaning (Pl. I, Fig. 1) in which the female, and occasionally the male, pick continuously at the bottom of the nest. Nest-building and nest-cleaning are always interspersed among various phases of courtship responses.

As the nest takes form, the genital tubes of the male and female become more prominent. At this time, the male begins to swim slowly over the nest, rubbing his genital tube over the bottom. We have called this "passing-nest." Later when the female completes the nest, she likewise "passes-nest." Thus the pair circle around and around, rubbing their genital tubes over the nest. This behavior is often interrupted by periods of courtship, nest-building and nest-cleaning activity. As soon as a fish starts passing-nest, the genital tubes become fully erected, but if this activity ceases for a time, the tubes generally recede somewhat. This suggests that mechanical stimulation is one factor causing the erection of the genital tube. Since fish not on the verge of spawning are sometimes seen with partially extended genital tubes, other stimuli seem to be involved in the partial erection of the genital tubes. Courtship activity and hormones are suggested as possible factors.

After the passing-nest behavior of the male and female has been in progress for some time, the female stops in the nest during a "pass-nest," and her body musculature quivers for a second or two. This has been called a "spawning-quiver." Males also exhibit spawning-quivers, but in the male these responses generally are less distinct and are seen less frequently.

Spawning-quivers were the final pre-spawning acts and indicated the imminence of the oviposition. During one of these quivers a batch of approximately 10 to 20 eggs is extruded by the female in what we have termed an "oviposition movement" (Pl. I, Fig. 2). The female then swims just past the nest. She is followed by the male who passes-nest, usually rubbing his genital tube over the newly laid eggs and sometimes exhibiting a spawning-quiver. This complementary act has been termed a "fertilization movement" (Pl. II, Fig. 3). Sperm

apparently are emitted at this time, although no male products were apparent in our observations. The female then repeats her oviposition movement which is followed closely by a second fertilization movement of the male. After two to four such egg-laying cycles, the female swims rapidly from the nest for a distance of 15 to 30 cm., then faces the nest. Meanwhile the male swims in the vicinity of the nest for a minute or so, then rapidly picks up the eggs with his mouth (Pl. II, Fig. 4; Pl. III, Fig. 5).

In our investigations there were a few exceptional cases where the male did not pick up the eggs. Then the female nipped and tail-slapped the male violently, exhibited some courtship behavior, and finally after 10 to 20 minutes of this activity she picked up the eggs and carried them in her mouth (Pl. III, Fig. 6). We found that at times, because of the unequal sizes of the male and female, all the eggs could not fit into the male's mouth, the female would pick up the remaining eggs, but not until 10 to 20 minutes had elapsed.

Post-spawning activity consists for the most part in poking around the nest, first by the male, and later by the female as well. If any of the eggs are missed when the original spawn was picked up, they are almost always recovered during this poking activity.

After several minutes, this poking behavior sometimes gives way to extensive nipping and mouthing in which one member of the pair, generally the female, soon dominates and the other retreats into hiding.

The eggs hatch in 5 days and are carried from 2 to 15 days further, during which time the embryos continue to develop. The young are released abruptly and most of them are sufficiently developed at this time to suggest that further parental care would not be advantageous to them. Parental care appears to end suddenly with the release of the young. In fact, parents sometimes eat their newly liberated offspring. Never did we see the young swim back into the parental mouth as has been described by some authors for this and other *Tilapia* species, and which is such a striking characteristic of the small Egyptian mouthbreeders, *Haplochromis multicolor* (Peters, 1937).

With this brief description of the mating pattern we turn now to an analysis of the actual counts made of the frequency of occurrence in relation to the time of spawning of many of the behavioral acts described above.

#### ANALYSIS OF THE MATING PATTERN.

For the purpose of analyzing the data, records were organized in the following manner. For each observed spawning, the time of appearance of the first batch of eggs was designated as the zero minute. The 15-minute period just prior to the zero minute was called the first pre-spawning interval. The period 15 minutes to 30 minutes prior to the zero minute was named the second pre-spawning interval. Twelve pre-spawning

intervals were similarly measured. Again starting from the zero minute, the 15-minute interval which followed was called the first post-spawning interval, and a second post-spawning interval was likewise measured. The number of times that the various courtship and mating activities (tail-slaps, passing-nest, etc.) were recorded during each 15-minute pre- and post-spawning interval was determined for both the males and the females for all observed spawnings. With data assembled in this manner, a series of distributions was obtained (one of each behavior pattern of both the male and female for each interval). Almost all of these were strongly skewed to the right. The arithmetical mean obviously is a poor representation of the central tendency of a markedly skewed distribution. Medians are generally more suitable, but a better method of treating such data is to employ a transformation. In many cases by use of the transformation  $X = \sqrt{x}$ , binomial distributions were obtained which could be treated as normal curves.<sup>13</sup> These were checked by plotting cumulative distributions on arithmetic probability paper. However some of the distributions were not normalized following the above transformation, but approximated closely the Poisson series. This was particularly true with infrequently occurring items, where the highest frequency was zero and where the mean was considerably smaller than one. Theoretical Poisson distributions were calculated from Pearson's (1914) tables and the goodness of fit of the actual distributions was tested by the chi-square method.

Still other distributions did not approximate either the normal or Poisson series. As will be noted later, these were not subjected to further statistical analysis.

For the normal distributions, the means, range, theoretical range ( $M \pm 3\sigma$ ), standard deviation and standard error of the mean were calculated. These were plotted graphically in a time sequence, using the method of comparing ranges and means developed by Dice and Leraas (1936) as modified by Simpson and Roe (1939). Since the length of the pre- and post-spawning records varied inadvertently for each spawning, the calculated means for each interval are based upon a varying number of spawnings. Simpson and Roe (1939) point out that the method of Dice and Leraas is less reliable when the frequencies and standard errors of the mean vary greatly. Therefore, in critical cases where the graphic method was suspected of being inaccurate, P values were calculated. The solid lines in Text-figs. 1-6, 8 and 9, indicate females; the broken lines males. The heavy vertical lines designate actual ranges of the distributions. The adjacent light vertical lines indicate theoretical ranges ( $M \pm 3\sigma$ ). The large dots represent the means, while the short horizontal lines above and

<sup>13</sup> The writer wishes to acknowledge the aid given by Dr. Charles P. Winsor in suggesting the use of this transformation.

below the means indicate the range of  $M \pm 2\sigma_M$ . When these ranges overlap, it may generally be assumed that the differences between the means are not significant. Conversely, if  $M \pm 2\sigma_M$  do not overlap, the differences between the means are significant. The limitation of this method has already been noted.

For the Poisson series, the theoretical ranges were considered to run from zero to that value of the variate having a relative frequency of .003 or less. Means were compared by the method described by Snedecor (1946). Because of the asymmetrical nature of the Poisson distribution the graphical method of comparing means described above cannot be used. Hence, in the following graphs, the range of  $M \pm 2\sigma_M$  are not indicated for the Poisson distributions.

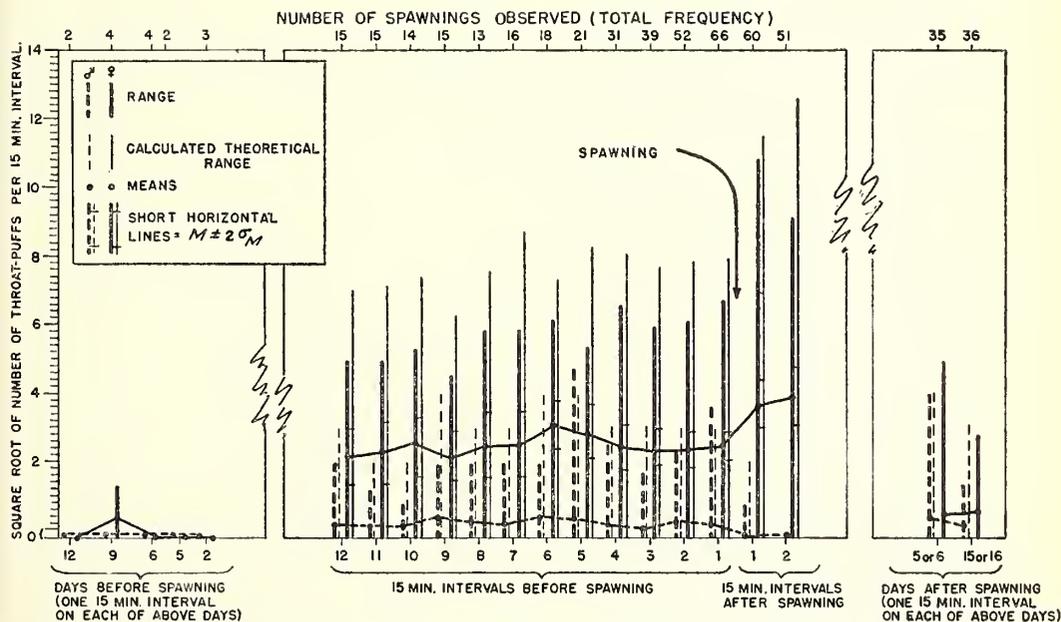
Where the distributions did not conform reasonably well to either a normal or Poisson series, only the means and actual ranges are presented on the graphs.

The 15-minute records on the 5th or 6th post-spawning day and on the 15th or 16th day were treated in a similar manner. Since a number of pairs spawned again within two weeks after these observations were made, it was possible to use some of these data as records of behavior on the 2nd, 5th, 6th, 9th and 12th pre-spawning days. Because of the small number of cases, only means and ranges are indicated graphically.

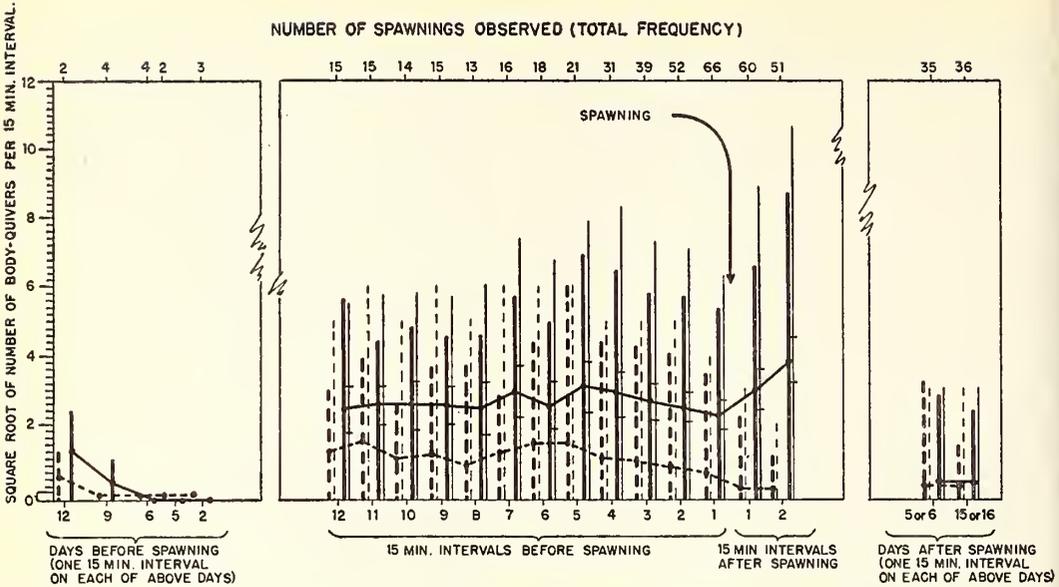
**THROAT-PUFFS.** As seen from the graph in Text-fig. 1, the females (solid lines) exhibited this behavior very rarely on the several days they were observed before the spawning. One female throat-puffed just once on the 9th pre-spawning day. However, by

three hours before spawning, the throat-puffing frequency had reached a rather high level, which was maintained with little fluctuation right up to the spawning. Immediately after the egg laying, throat-puffing activity increased sharply. To be sure that this rise was not due to chance fluctuation, the means of the first pre- and post-spawning intervals were compared and were found to differ significantly ( $P < .01$ ).

The males showed the throat-puffing behavior much less frequently than the females (Text-fig. 1, broken lines). On the several days the pairs were observed prior to the spawning, no throat-puffing by the males was seen. At three hours before the egg laying, a low frequency of throat-puffing was recorded, and this level was maintained up to the spawning. When these data were treated by utilizing the transformation  $X = \sqrt{x}$  as already described, the frequencies of male throat-puffs were found to be distributed in a Poisson fashion with zero the highest frequency, an indication that the mean frequencies were less than one. This raised the question whether the males of just a few pairs were responsible for the bulk of the throat-puffing activity. A partial answer to this question was obtained by selecting the 25 spawnings in which continuous records for the first hour before spawning were available. It was found that during this hour, 64.0% of the males exhibited no throat-puffing at all. This contrasts with the figure of only 4.0% for the female. Similarly, in the seven pairs where continuous records for the first two pre-spawning hours were available, 57.1% of the males did not throat-puff. From this we may conclude that a consider-



TEXT-FIG. 1. Fluctuation in male and female throat-puffing behavior before and after spawning.



TEXT-FIG. 2. Fluctuation in male and female body-quivering behavior before and after spawning.

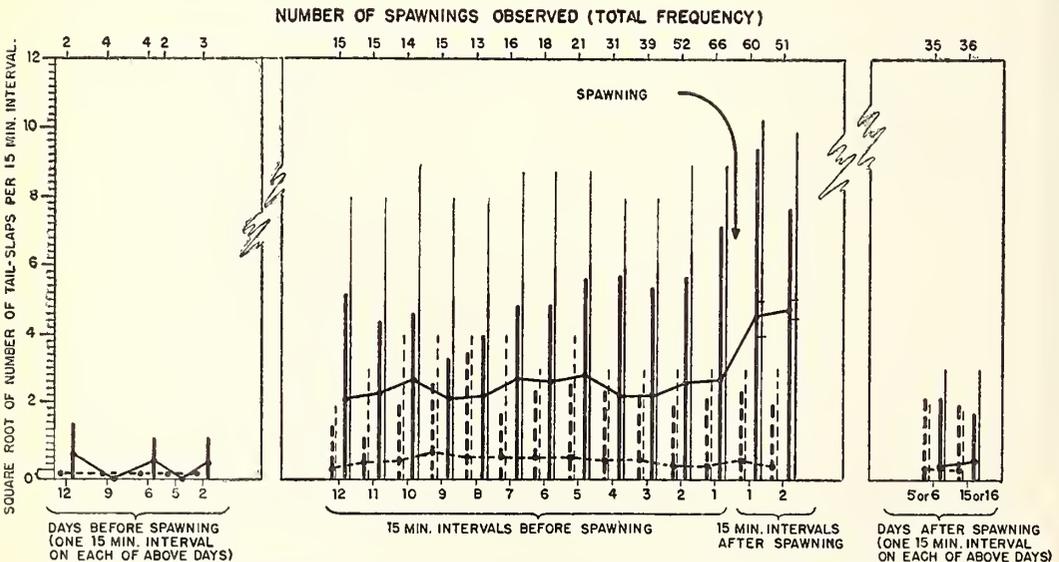
able number of males exhibited little or no throat-puffing behavior prior to the spawning.

Immediately after the egg laying, throat-puffing by the male was no longer observed. Since the mouths of the males were now filled to capacity with eggs, it seems better to say that after the spawning throat-puffing could not readily be identified. By the 5th or 6th post-spawning day, many of the males were no longer carrying eggs, and now the throat-puffing behavior had reached the pre-spawning level.

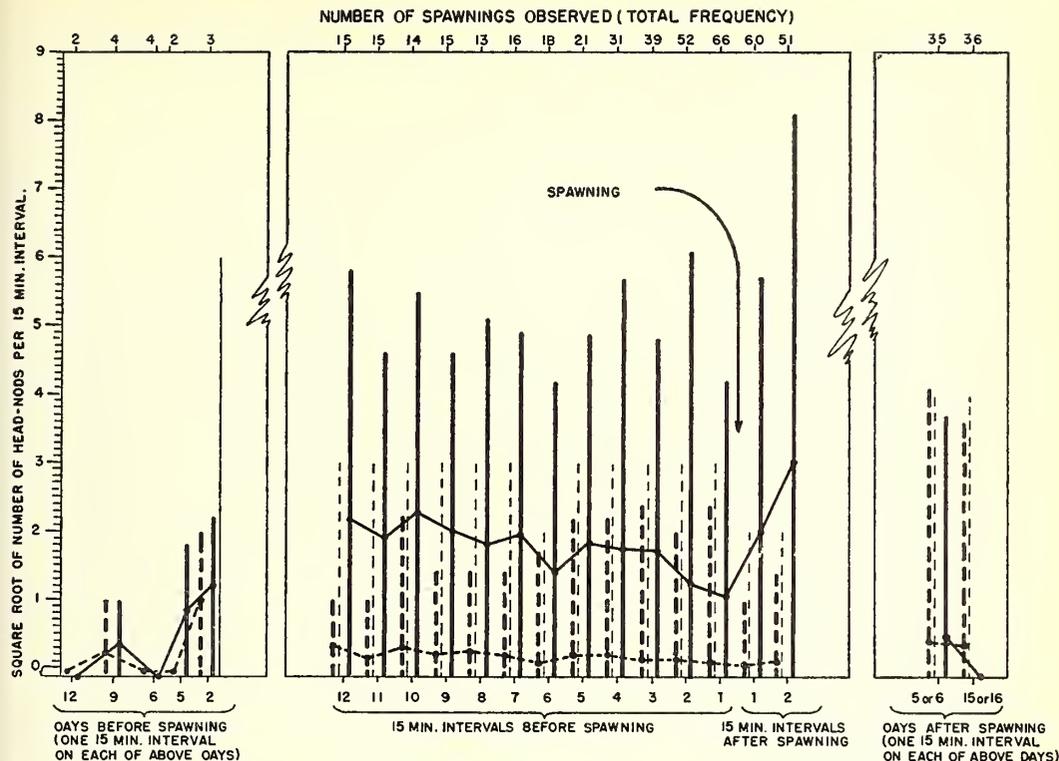
**BODY-QUIVERS.** Only an occasional body-quiver was exhibited by the males and females on the several days they were observed

prior to the spawning (Text-fig. 2), but by three hours before oviposition the body-quivers (solid lines) were very frequent occurrences in the female. They remained at this relatively constant level until the spawning, after which there was an abrupt rise. The means of female body-quivers for the first pre- and post-spawning intervals were compared, and the latter were found to be significantly higher ( $P = .021$ ). At five days after spawning the females' body-quivering had dropped far below the immediate pre-spawning level, and remained the same during the observation period on the 15th or 16th day.

The body-quiver frequency of the males at



TEXT-FIG. 3. Fluctuation in male and female tail-slapping behavior before and after spawning.



TEXT-FIG. 4. Fluctuation in male and female head-nodding behavior before and after spawning.

three hours before spawning was considerably less than the females' and again these data were best treated as Poisson distributions. The behavior remained at this level until the fifth pre-spawning interval when it started to slope off, reaching a minimum at the first pre-spawning interval. However, when the male body-quivers of the fifth and first pre-spawning intervals were compared, this slope appears not to be significant ( $P > .10$ ). On the 5th or 6th post-spawning day, and on the 15th or 16th post-spawning day, the body-quiver frequency of the males was very close to that of the females.

Of the 25 spawnings in which continuous records were available for one hour before the spawning, 100% of the females and 80.0% of the males exhibited body-quivering at least once. In the seven ovipositions in which continuous two-hour pre-spawning records were taken, 100% of the males gave body-quivers at least once. Thus while this courtship pattern is exhibited more frequently by the females, practically all males show some body-quivering activity prior to the egg laying.

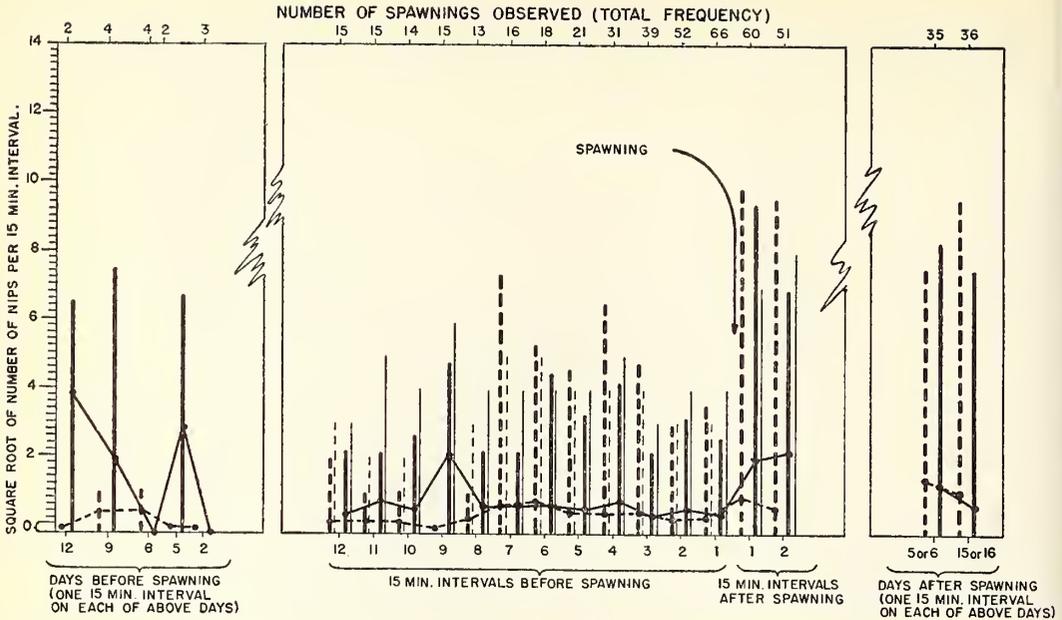
**TAIL-SLAPS.** With the transformation previously described, the data of both the male and female were found to be distributed in a Poisson fashion, excepting the first two post-spawning intervals of the female which were normally distributed (Text-fig. 3). On the several days prior to the spawning occa-

sional tail-slapping by the female was observed, but at three hours before the egg laying, the occurrence of this behavior had increased considerably. This level was maintained until the spawning, when there was another significant rise ( $P < .01$ ) during the first post-spawning period.

No tail-slapping by the male was observed on the several days prior to the spawning, and during the three-hour pre-spawning interval, the frequency of tail-slaps remained low with relatively little fluctuation. Approximately this same frequency was observed during all the post-spawning observation periods.

Of the 25 pairs for which continuous records for the first hour were obtained, 100% of the females were recorded as tail-slapping at least once, but only 48% of the males. In the seven spawnings with two-hour continuous pre-spawning records, 71.4% of the males tail-slapped at least once.

**HEAD-NODS.** Following the transformation, head-nodding data for the female was characterized by a large number of zero frequencies and a small number of rather high frequencies. These did not fit Poisson distributions. At times, head-nodding was not clear cut and easy to recognize, and it is possible that a considerable amount of head-nodding passed unrecognized. Before the spawning, head-nodding activity was quite high (Text-fig. 4), at least for some of the



TEXT-FIG. 5. Fluctuation in male and female nipping behavior before and after spawning.

females, and there was a still further rise after the egg laying.

The data for male behavior fit Poisson distributions quite closely. The low mean values indicate that this behavior occurred rather infrequently, and little fluctuation was noticeable before or after the spawning.

Of the 25 ovipositions from which continuous records were taken for the first pre-spawning hour, 84.0% of the females and only 20.0% of the males exhibited head-nodding at least once. Similarly, of the seven pairs where two-hour records were available, 100% of the females and 28.6% of the males head-nodded at least once. We may conclude that head-nodding is a typical female activity and that a small fraction of the males head-nod occasionally.

**NIPS.** Nipping data of both the male and female were treated as Poisson distributions. Both sexes displayed some nipping behavior on the several days they were observed before the spawning (Text-fig. 5). During the three-hour pre-spawning observation period, approximately the same amount of nipping was shown by both the males and females. After the egg laying there was a significant rise ( $P < .01$ ) in the nipping frequency of the females. The rise in female nipping during the ninth pre-spawning interval may be significant ( $P = .05$ ), but it was mostly due to a marked spurt of activity of a single female.

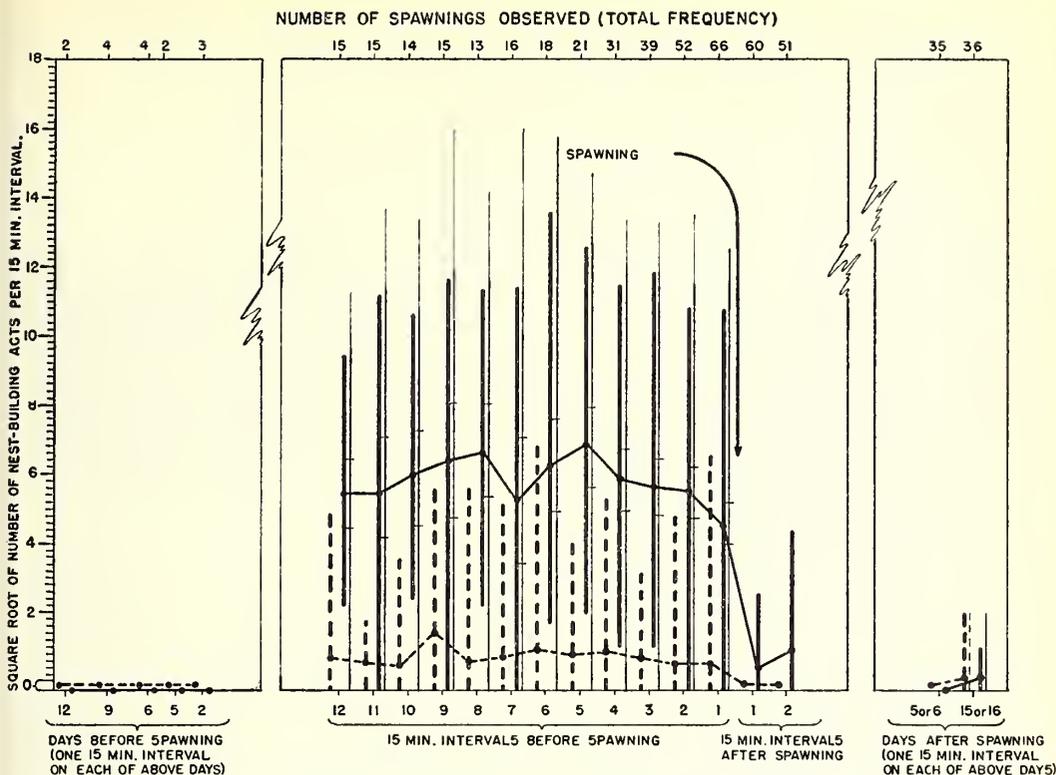
Analysis of the 25 spawnings where complete records for the first hour before spawning were taken showed that 68.0% of the females and only 28.0% of the males exhibited nipping behavior at least once. Where two-hour continuous records were available, 100% of the females, and 57.1% of the males

engaged in some nipping activity. This suggests that practically all of the females and at least half of the males do some nipping before spawning.

**NEST-BUILDING ACTS.** On the several days before spawning, nest-building by either the male or female was not observed (Text-fig. 6), but by the third hour before oviposition, female nest-building activity had reached a rather high frequency. Since the presence of a nest and the occurrence of nest-building behavior was one of the more important criteria used to determine the imminence of spawning, and hence to ascertain the appropriateness of starting the observation, these data are likely to be somewhat biased in favor of early nest-builders. Actually at three hours before spawning, the average nest-building activity of the female may not be as high as that indicated by the data.

The drop indicated in the seventh pre-spawning interval appears not to be significant if the nest-building values of the fifth and seventh intervals are compared ( $P = .13$ ). On the other hand, there is a noticeable downward slope between the fifth and first pre-spawning intervals, and when these two intervals are compared, the difference was found to be highly significant ( $P < .01$ ). It is clear that female nest-building behavior drops off as the time for the laying of the eggs approaches, and it is gradually superseded first by nest-cleaning behavior (which is clearly distinguishable from nest-building), and secondly by nest-passing activity, which, as we shall see in the next section, is increasing as the nest-building frequency is declining.

Following the oviposition episode, nest-building activity dropped to a very low fig-



TEXT-FIG. 6. Fluctuation in male and female nest-building behavior before and after spawning.

ure. On the 5th or 6th day nest-building by females was not observed, and on the 15th or 16th day only one nest-building act was observed during the 15-minute observation interval by one female out of thirty-six.

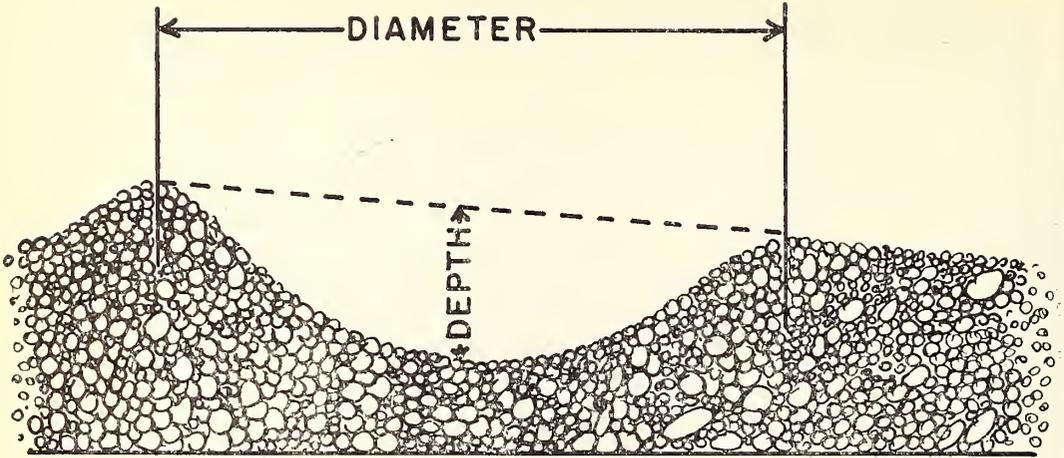
The data for the male was characterized by high frequencies of zero values and low frequencies of high values which nevertheless did not fit Poisson curves even after the aforementioned transformation. In contrast to the extensive nest-building activity of the female, that of the male was quite limited. Similar to the female, there is a downward slope in activity between the fourth and first pre-spawning intervals. However, the decline is not very pronounced and its statistical validity could not be readily ascertained. After the spawning the males no longer engaged in nest-building except for a single male which on the 15th post-spawning day nest-built four times during the observation interval. This male was paired with the one female, which was also observed to build a nest during the 15-day post-spawning interval. Two nests were present in the tank and it is apparent that this pair was approaching another spawning cycle.

Turning again to the 25 spawnings with continuous records for the first pre-spawning hour, it was found that 100% of the females and 72% of the males engaged in nest-building at least once. Of the seven pairs with continuous two-hour pre-spawning records, 71.4% of the males did some nest-building.

It is probable that only a small percentage of males do not engage in any nest-building prior to the spawning.

Fifteen nests built by ten pairs were measured shortly after the spawnings. In each case the fish were first carefully removed without damaging the nests. Since in many cases the nests were oval, two diameters were taken, namely the short diameter, and at right angles to this the long diameter. The points used in these measurements are indicated in Text-fig. 7. The average short diameter was 11.8 cm., the average long diameter 13.2 cm., and the average depth 2.6 cm. The female fish (which as shown above are primarily responsible for the construction of the nests) varied from 10.7 gr. to 19.2 gr. with an average of 15.1 gr. The males were slightly heavier, weighing on the average 18.0 gr. There was no indication from these limited data of a correlation between size of fish and size of nest.

PASSING-NEST. The earliest nest-passing by the female was recorded for the eleventh pre-spawning interval, two and one-half hours before the egg laying (Text-fig. 8). Following the previously mentioned transformation, the data for this interval fit a Poisson distribution. The same is true for the records of the 6th, 8th, 9th and 10th intervals. The data for the 2nd to 5th and the 7th intervals consisted of a series of zero or very low frequencies and a smaller group of relatively high values, vaguely suggesting



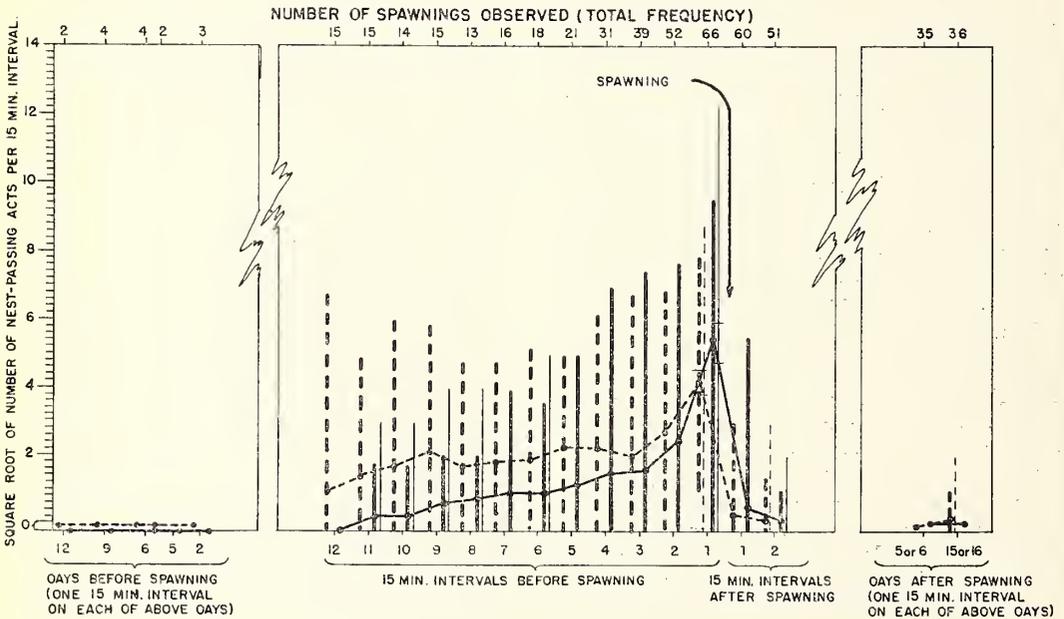
TEXT-FIG. 7. Diagrammatic section through typical *Tilapia* nest showing points used for nest measurements.

bimodal curves. The data for nest-passing for the first interval were normally distributed. These data indicate a gradually rising frequency of nest-passing as the spawning approached, with a sudden spurt of activity during the second and first intervals. After the egg laying, nest-passing activity of the female dropped to almost zero and none was recorded on the 5th or 6th and 15th or 16th days.

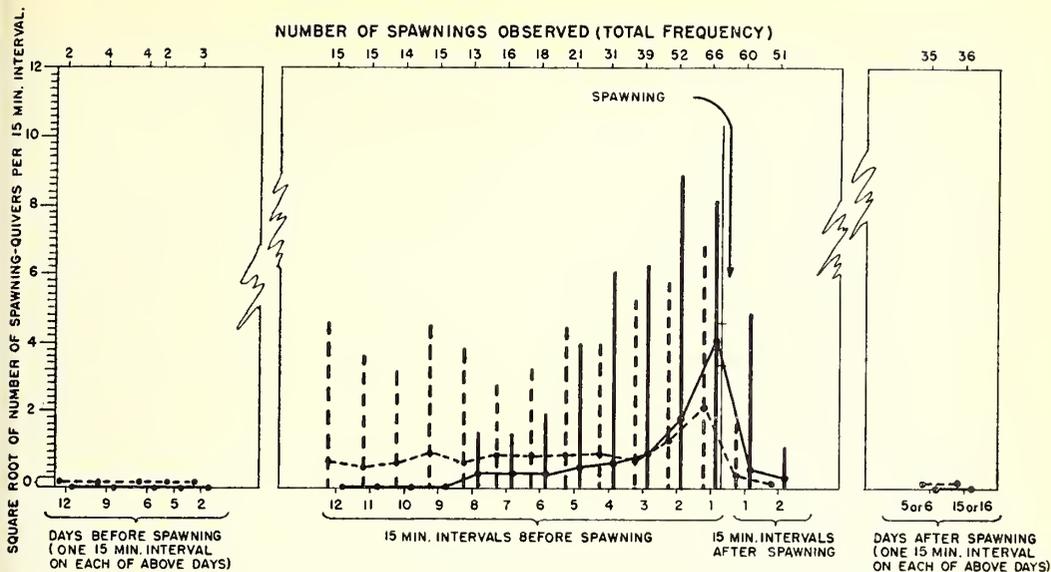
The nest-passing data of the male were normally distributed for the first interval. The records for the remaining pre-spawning intervals were highly skewed to the right with highest frequencies zero, which, however, did not fit Poisson series. While no

nest-passing was recorded for the males on the several days prior to the spawning, a substantial amount of nest-passing was observed by three hours before the egg laying. This level of activity remained fairly constant until the second interval when it started to rise precipitously. However, during the first pre-spawning interval, the nest-passing activity of the female surpassed that of the male for the first time ( $P < .01$ ). After the spawning, the frequency dropped to almost zero and nest-passing was not observed on the two post-spawning observation days.

Observations indicated that male and female nest-passing were not entirely independent of each other, and calculation of the



TEXT-FIG. 8. Fluctuation in male and female nest-passing behavior before and after spawning.



TEXT-FIG. 9. Fluctuation in male and female spawning-quiver behavior before and after spawning.

coefficient of correlation for the first pre-spawning interval yielded an  $r$  of  $+ .63$ . This was transformed to  $Z = + .74$  which is a highly significant correlation ( $P < .01$ ). The nest-passing data for the remaining pre-spawning intervals appear to be comparably correlated, but the data do not readily lend themselves to this type of statistical treatment. Prior to the spawning, all of the males and females exhibited some nest-passing activity.

**SPAWNING-QUIVERS.** This behavior was not observed during the observation periods on the several days before the spawning (Text-fig. 9). Female spawning-quivers were first seen during the 8th pre-spawning interval,  $1\frac{3}{4}$  to 2 hours before the egg laying. Their frequency gradually increased and reached a peak during the first pre-spawning interval. There was a marked drop to almost zero after the egg laying, and on the 5th or 6th days and 15th or 16th days none were seen.

A few male spawning-quivers were in evidence during the 12th pre-spawning interval, and a low level of this behavior was maintained until the second interval, 20 to 15 minutes before the egg laying, when there occurred an abrupt rise in frequency which terminated during the first interval. During the first post-spawning interval, a very few spawning-quivers were recorded, and none were seen thereafter. While a few of the males exhibited spawning-quivers long before the females, the peak of spawning-quiver activity of the females during the first pre-spawning interval was considerably higher than that of the males. However, the data did not permit further statistical analysis.

Selecting the 25 spawnings for which continuous records for the first hour before oviposition were available, it was observed

that 96.0% of the females and 72.0% of the males showed at least one spawning-quiver during this hour. Similarly, in the seven spawnings for which two-hour continuous records were available, 100% of the females and 71.4% of the males were recorded as performing at least one spawning-quiver during these two hours. It thus appears that while all the females showed this behavior, in about a fourth of the males spawning-quivers could not readily be distinguished from nest-passing behavior. Since all of the females exhibited spawning-quivers and because of the sharp peak in the frequency of occurrence of this activity just before the spawning, this behavior can also be employed as an indicator of the approaching oviposition.

**OVIPOSITION AND FERTILIZATION.** The behavioral patterns considered thus far were recorded in terms of the number of times that the acts occurred during a short interval of time (i.e., 15 minutes), and the relative infrequency of some of this behavior accounts in part for the marked skewness of the distribution curves. On the other hand, the oviposition data which follow, and the data concerning the reactions of the male and female to the eggs and young, are based upon the total frequency of the behavior during a given spawning, and as might be anticipated, these data approximated more closely binomial distributions which could be treated as normal curves.

A nest-passing act by the female during which eggs were oviposited was counted as a single oviposition movement. A nest-passing act by the male when eggs were present in the nest was recorded as a fertilization movement. Actual contact with the eggs was not considered essential as a criterion for a fertilization movement, although in most

instances the male rubbed his genital tube over some of the freshly laid eggs.

In 76 observed spawnings, the mean number of oviposition movements by the female was  $3.41 \pm .13$  with a standard deviation of 1.1 movements. The mean number of male fertilization movements was  $3.46 \pm .15$  with a standard deviation of 1.3. The difference between the means is  $.05 \pm .2$  which indicates clearly that the number of oviposition movements of the female does not differ significantly from the number of fertilization movements of the male. Finally, there is a significant positive correlation ( $r = +.48$ ,

$z = +.52$ , P calculated from  $\frac{z}{\sigma z} < .01$ ) between these two activities, indicating that the number of times the males fertilize the eggs is partly related to, and probably dependent upon the number of oviposition acts of the female.

**PARENTAL BEHAVIOR.** In a total of 76 observed spawnings, the male alone picked up the eggs in 62 cases (81.8%), the female picked up the eggs in 6 cases (7.9%) while both male and female participated in this activity in 8 cases (10.5%).

The time after the beginning of oviposition for the male to start picking up eggs varied from 20" to 2'10" with a mean of 1'3"  $\pm$  3" and a standard deviation of 23". For the female this interval varied from 3'18" to 11'14" with a mean of 7'59"  $\pm$  1'22" and a standard deviation of 3'17". The difference between the means of these two distributions is obviously significant, and from these data we may conclude that the male starts to pick up the eggs as soon as the oviposition has terminated, while the female allows several minutes to elapse before she will collect any of the eggs still available. Here then is an apportioning mechanism which results in the observed fact that the male usually incubates the eggs, and the female does so on infrequent occasions.

Eggs remain in the nest available to the female under two circumstances. First, if the male's mouth is of insufficient size to contain all of the eggs, a few may be left over in the nest. This was the situation in case 1 (Table I) where a small male was paired with a large female. It was quite clear to the observer that in this instance not all of the eggs could fit into the male's mouth. Secondly, eggs would be available to the female when the male behaved atypically and did not touch the eggs. In three of these cases males had released broods seven to twelve days previous to the spawnings, and this may be a contributing factor causing the lack of response of the males to the eggs.<sup>14</sup> In most instances where the eggs remained in the nest for any length of time, the females would chase, nip and court the males. In a few cases, the latter retaliated and violent

TABLE I.

Time from the Beginning of Oviposition for Eggs to Be Picked Up. Eight Cases Where Both Male and Female Engaged in This Activity.

Case No.	Male		Female	
	Start	Finish	Start	Finish
1	25"	50"	7'15"	—
2	11'00"	11'30"	6'50"	10'10"
3	3'00"	4'00"	2'30"	4'00"
4	4'05"	4'30"	4'15"	4'30"
5	2'05"	5'00"	4'30"	5'00"
6	4'10"	5'10"	4'10"	4'55"
7	6'24"	10'30"	5'50"	6'36"
8	3'50"	4'00"	1'25"	3'30"

fighting ensued; as a result the nests were destroyed and the eggs scattered. In cases 3, 6, and 7 (Table I), as soon as the female began to pick up the eggs, the males followed suit and both gathered up the eggs simultaneously. The typical pattern when eggs are left in the nest may be summarized as follows:

- (1) Immediately after the eggs are oviposited and inseminated, there is often a period of extreme quiescence lasting a minute or two.
- (2) This is followed by a period in which the female appears to be inhibited from approaching or touching the eggs, but at the same time she seems to be excited by the eggs, resulting in active nipping, chasing and courting of the male who sometimes responds similarly.
- (3) After several minutes the inhibitory action of the eggs begins to diminish; the female now approaches the nest, pokes around the eggs, and eventually picks them up. It was at this time that several of the recalcitrant males listed in Table I also approached the nest and in a few cases started to pick up eggs ahead of the female.

It is suggested that in cases 2 to 8 (Table I), chasing, nipping and courting by the female, and also her poking around the nest, sufficiently stimulated the male to pick up the eggs, thereby completing the pattern.

Once started, the length of time it took for males to gather up the spawn varied from 2" to 1'45" with a mean of 13"  $\pm$  2" and a standard deviation of 16". The high variability noted here is a result of two exceptional cases, one where the male took 1'7" and in the other 1'45". In the remaining 60 spawnings, the time was less than 46". On the other hand, six females took from 35" to 3' with a mean of 2'6"  $\pm$  22" and a standard deviation of 51.7". Thus we see that not only does the female wait longer before starting to pick up the eggs, but once started she performs this task at a significantly

<sup>14</sup> On the other hand, recent observations by Aronson and Holz-Tueker (unpublished) reveal that males in the process of incubating young may on occasion fertilize and pick up a new batch of eggs.

slower rate. In most cases, the males gathered up the eggs rapidly and then kept poking around the nest for some time. Thus any scattered eggs were quickly recovered. Some of the females, on the other hand, would pick up part of the eggs, swim away from the nest, return and pick up more eggs, swim away again, and so forth.

The egg-gathering records for the female were necessarily limited by the behavior of the males as noted above. It was therefore considered appropriate to use for comparison data from other experiments. Aronson and Holz-Tucker (unpublished data) observed the spawning of an isolated female that could see another female in an adjacent tank. The ovipositing female took 24' to start gathering up the eggs and the process itself took 1'25" to complete. Similarly, we observed the spawning of a completely isolated female. This female did not start to pick up the eggs for 13'5". She took 1'15" to gather up most of the spawn, but left six eggs which she did not pick up for another eight minutes. A large number of normal females were paired with males suffering various types of brain lesions (Aronson, in manuscript). In 27 spawnings, these females took on the average 12'2" to start picking up eggs and an average of 1'15" to complete the job. Hence these data support our original conclusions. However, it is likely that in our first observations, the mean time for the six females to start picking up the eggs is somewhat low, while the time it took to complete the process may be a little too high. It is of interest to note that in a few spawnings the females seemed unable to carry all of the eggs that they themselves had laid.

Both the male and female are capable of successfully incubating the eggs. The percentage of spawnings in which young were recovered at the termination of the incubatory period is shown in Table II. Where the spawnings were not witnessed, the slightly higher score made by the males may be accounted for by a possible failure to record

a few cases where the spawn was swallowed immediately after the oviposition, and before it was observed. The data for the third set of observations are taken from a second experiment, (Aronson, 1945). These spawnings were also not witnessed. In this experiment, aquarium conditions were considerably improved by the use of aquarium filters, thus avoiding any changes of water. The young were forcibly ejected from the parental mouth on or about the tenth day after spawning and were counted immediately, thus largely eliminating the possibility of losses through cannibalism.

Even with these improved techniques, only 40% of the males released viable fry. Two factors account for this low yield of young by the males. First is the failure of the eggs to be properly fertilized, or death of the embryos, with subsequent disintegration of the eggs. A second factor is swallowing the spawn. The relative importance of these two factors will now be considered.

If freshly laid unfertilized eggs are placed in a jar of *Tilapia*-conditioned water which is kept at approximately 26° C., very few of the eggs will show any gross signs of degeneration before 24 hours. Starting with the second day, however, some of the eggs will have decomposed, and in all cases few if any intact eggs remain after the tenth day. As to the variation in the length of the incubation period, it will be seen in columns 6 and 7 of Table III that females may carry unfertilized eggs for as long as ten days, after which time it may be assumed that all have decomposed. Note particularly that in almost 80%<sup>15</sup> of these cases, the dead eggs were retained longer than one day, and it is highly probable that in many of these cases the eggs were carried until they were quite degenerate. It was not unusual to examine the contents of a male's or female's mouth and

<sup>15</sup> Since the presence of incubating eggs was checked only twice daily, spawn swallowed shortly after oviposition might have been overlooked. Hence this figure may be a little too high.

TABLE II.  
Per Cent. of Spawnings in which Young Were Recovered.

	No. of spawnings in which males incubated eggs.	No. of males releasing young.	% of males releasing young.	No. of spawnings in which female incubated eggs.	No. of females releasing young.	% of females releasing young.
Spawnings witnessed.	68	22	32.4	14	3	21.4
Spawnings not witnessed.	85	33	38.8	2	0	0.0
Spawnings not witnessed, 2nd experiment.	70	28	40.0	4	4	100.0

TABLE III.  
Variation in Length of Incubatory Period.

Length of incubation.	NO YOUNG RECOVERED						YOUNG RECOVERED			
	Incubated by males <sup>1</sup> .		Incubated by females <sup>1</sup> .		Incubated by females <sup>2</sup> (unfertilized eggs).		Incubated by males <sup>3</sup> .		Incubated by females <sup>1,4</sup> .	
	No. of males.	Per cent. of males.	No. of females.	Per cent. of females.	No. of females.	Per cent. of females.	No. of males.	Per cent. of males.	No. of females.	Per cent. of females.
0-1 hr.	1	2.2	5	45.5						
1-8 hr.	1	2.2	1	9.1	54	20.1				
8-24 hr.	6	13.3	0	0.0						
2 days.	7	15.6	1	9.1	54	20.1				
3 "	13	28.9	1	9.1	34	12.7				
4 "	10	22.2	2	18.2	44	16.4				
5 "	1	2.2	0	0.0	31	11.6				
6 "	2	4.4	1	9.1	19	7.1				
7 "	1	2.2			19	7.1	1	1.2		
8 "	0	0.0			6	2.2	1	1.2		
9 "	0	0.0			5	1.9	1	1.2		
10 "	2	4.4			2	.7	2	2.5		
11 "	1	2.2					12	14.1		
12 "							8	9.4		
13 "							18	21.2		
14 "							12	14.1		
15 "							9	10.6		
16 "							4	4.7	1	33.3
17 "							11	12.9	1	33.3
18 "							2	2.5		
19 "							1	1.2	1	33.3
20 "							3	3.5		

<sup>1</sup> All spawnings witnessed.

<sup>2</sup> Females isolated from males. Spawnings not witnessed. Incubation intervals less than 1 day were recorded as one day, but some short intervals might have been missed. Data from Aronson (1945).

<sup>3</sup> Some spawnings not witnessed. Includes data from Aronson (1945).

<sup>4</sup> The young from the four females of the 2nd experiment indicated in Table II were forcibly removed from the parents' mouths on the 12th day. Hence these cases could not be included in this table.

find that the fish had been carrying a mass of badly decomposed eggs, or a mixture of decaying eggs and viable embryos. From the appearance of the eggs it was frequently apparent that the fish had been carrying the dead eggs for many days. In columns 2 and 3 are listed the durations of the incubatory intervals for males carrying fertilized eggs. It will be noted that in 17.7% of the cases, the spawn was swallowed within 24 hours. The indirect evidence cited above leads to the conclusion that these eggs were swallowed because of some failure of the male's incubatory mechanism, whereby the male failed to discriminate between eggs and food. On the other hand, those egg masses which were retained in the mouth for a number of days were only swallowed when they had become extensively decomposed. It should be noted in passing that decomposed eggs are never found in the tanks, and it is assumed that they are swallowed rather than spat out. The stomach contents of several males were examined shortly after the egg layings, while the males were carrying eggs. In two of these cases a few eggs were also found in the stomachs.

Columns 4 and 5 show that in 54.6% of the spawnings in which eggs are picked up by the females, they were swallowed within 24 hours and in most cases within the first hour after spawning. Although these data are limited, they indicate that the female's incubatory mechanism is not as dependable as the male's, and that the female fails to distinguish eggs from food much more frequently than does the male.

The length of incubation by the male in cases where young are recovered is shown in columns 8 and 9 of Table III. These data fit closely a normal curve, and from them we have determined a mean incubatory time of  $13.8 \pm .27$  days with a standard deviation of  $\pm 2.6$  days. This would give us a theoretical range of 6 days to 22 days. The few cases in which the female successfully reared young fall well within this range.

Thus far, only the presence or absence of eggs and developing embryos have been considered. Now, the relative sizes of the spawn and brood will be examined. A new group of pairs was established, and on the day of or day after oviposition, the spawn was ejected from the male's mouth and was counted. This count may be taken to represent fairly accurately the number of eggs laid by the female, since, in most instances, all of the eggs are picked up and few if any are swallowed. Eighty females whose mean weight was  $7.15 \pm .33$  gr. deposited an average of  $49.7 \pm 1.96$  eggs.

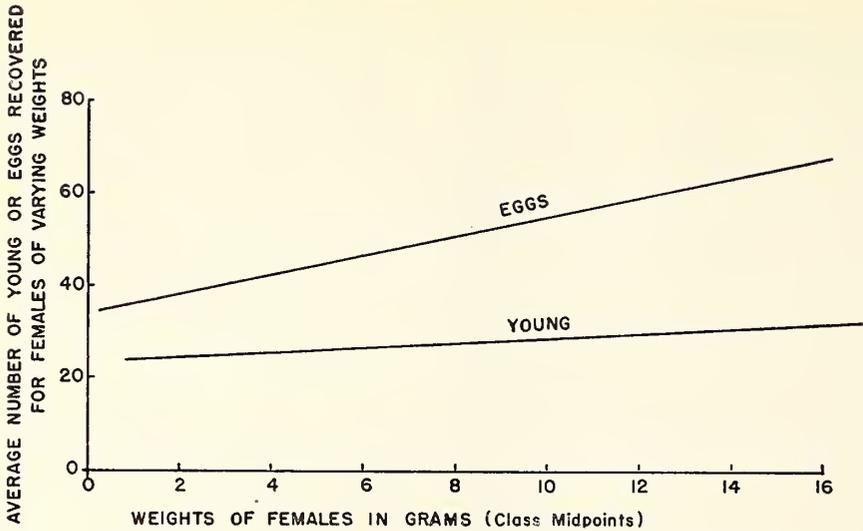
In a second group of 31 pairs in which the average weight of the females was only slightly less ( $5.6 \pm .38$  gr.), the males were allowed to incubate the eggs and the fry were counted soon after their release. Here it was found that the average brood size was only  $23.9 \pm 2.9$  young. It was thought at first that this smaller brood size might be attributed

to the lesser weights of our second group. To examine this hypothesis the body weights of the females that had just oviposited were compared with number of eggs in the spawn. A low order positive correlation was found, which was probably significant ( $r = +.23$  or  $z = +.236$ ;  $P$  calculated from  $\frac{z}{\sigma_z} = .05$ ). A similar comparison of the weights of females (determined immediately after oviposition) with the size of the brood that was eventually recovered after being incubated by the male partner did not yield a significant correlation ( $r = +.10$  or  $Z = +.10$ ;  $P$  calculated from  $\frac{z}{\sigma_z} = .6$ ). When two regression

lines are plotted (calculated by the method of least squares), one for the rise in number of eggs oviposited as body weight increases, and a second for the change in number of young recovered as body weight increases (Text-fig. 10), the relationship involved becomes clearer. From these regression lines in Text-fig. 10, it can readily be seen that for females of the same body weight, the number of young successfully incubated is considerably smaller than the number of eggs laid. This loss can best be accounted for by the failure of some of the eggs to be fertilized and by the death of some of the embryos. Since brooding fish have never been observed to spit out decomposed eggs or embryos, and since such material has rarely been observed on the gravel substrata of the aquaria, it is assumed that the incubating fish somehow manages to sort out and swallow this dead matter.

These data also indicate that while larger females tend to lay a greater quantity of eggs than smaller females, the number of fry successfully brooded by the males remains constant regardless of the weights of the females and hence of the magnitude of the spawn. Therefore the mortality of eggs and embryos must be directly proportional to the size of the female and hence to the number of eggs laid. Since the larger females were in most cases older, this difference might be based upon an aging factor. It is also conceivable that such increased mortality was due to overcrowding in the male's mouth during incubation.

It is an interesting fact that incubating *Tilapia* generally carry some gravel intermingled with eggs. Of 63 fish examined on the day or day after the egg laying, 95.2% were carrying one or more pieces of gravel. Generally between 25 and 50 pieces (commercial grade No. 2) were found along with the eggs, and occasionally the count went well over 100. The possible significance of this fact is not known at present. It is not clear whether or not the gravel is picked up accidentally along with the eggs, and whether this behavior bears some relation to the survival of the embryos. For example, it is possible that since the eggs and gravel are continuously churned around in the mouth, the



TEXT-FIG. 10 Regression lines showing relation of body weights of females to number of eggs laid during each spawning and relation of body weights of females that spawned, to number of young recovered immediately after their release by the incubating males.

latter might serve to rub off fungi or ectoparasites from the developing fish.

It is important to note that there is considerable variability in the number of days that given parents may incubate their young. It is therefore to be expected that at the time of release, the broods carried longest will be the ones furthest advanced in development. This, generally speaking, is found to be true. Thus, fry released in less than ten days still have a large yolk sac and their swimming activity is sporadic, whereas young incubated for longer intervals show little or no trace of the yolk sac, also their swimming ability is developed to the stage where they are well able to elude their enemies if reasonable shelter is provided. A complicating factor is that, as can be seen from the few samples in Table IV, there is a considerable difference in the rate at which the fry grow within the parental mouths. Thus the average size of a given brood incubated for 22 days was barely larger than another one incubated only 15 days. Similarly, a given brood retained in the mouth for only 11 days reached the same average size as another brood incubated for 16 days. It is possible the number of young in the brood may somehow be related to growth rate; however, our limited data on this point in Table IV do not suggest such a relationship. It is also of interest to note that the variation within the brood was quite low, the average coefficient of variation ( $V$ ) for nine broods being 3.7. This state of affairs is in striking contrast to the great variability ( $V = 15 \pm 1.60$ ) which resulted when a brood was kept together in a stock tank from the time of release to maturity (Aronson and Holz-Tucker, in manuscript).

#### DISCUSSION.

In most vertebrates the characteristic mating behavior patterns of the two sexes are distinctly different. Thus in the rat, the reproductive habits of which have been analyzed most intensively, the typical pattern of the estrous female, lordosis, is only occasionally exhibited by the male (Beach, 1938, 1945). Similarly, the typical male pattern of ear-wriggling, mounting and pelvic thrusts is seldom seen in the female (Long and Evans, 1922; Hemmingsen, 1933; Beach, 1938).

The sex difference in behavior generally is very clear although relative rather than absolute. Under special conditions males may be induced to exhibit female-like behavior, and the reverse can also be accomplished (Beach, 1941). The conditions producing such results often are very special in nature. Thus for example, the well known fact that estrous cows frequently exhibit male-like mounting behavior may very well result from the almost universal custom of segregating the cows from the bulls. Similarly Beach and Rasquin (1942) explain in part the high incidence of masculine behavior in their female rats as the result of repeatedly testing two females together. These authors are also aware of the possibility that the females of their particular colony may have been more active in a masculine direction than are females from most other stocks. However, we are concerned with the fact that disparity of behavior between sexes is general among the vertebrates.

A survey of the literature indicates that in reptiles a behavioral dichotomy of the sexes appears to be the rule, and the writer's extensive investigations of the sexual be-

TABLE IV.

Relation Between Average Size<sup>1</sup> of Young in Brood and the Number of Days the Brood Was Incubated.

No. of days young were carried.	No. of fry in brood.	Average length of fry <sup>1</sup> (mm.).	Coefficient of variation.
10	13	9.2 ± .08	2.9 ± .57 <sup>2</sup>
11	19	10.6 ± .10	4.0 ± .65
11	3	10.4	.....
11	8	9.8 ± .09	2.8 ± .70
12	44	10.8 ± .06	3.9 ± .41
14	18	9.4 ± .11	5.1 ± .85
15	82	11.2 ± .04	3.3 ± .26
16	58	10.6 ± .06	4.4 ± .40
16	38	10.6 ± .06	3.7 ± .43
22	58	11.5 ± .05	3.4 ± .31

<sup>1</sup> Length from tip of mouth to end of tail fin.

<sup>2</sup> Standard error of the coefficient of variation.

havior of the tailless amphibia have shown that in the Anura, male and female sexual behavior are quite specific with only occasional evidence of bisexual behavior (Noble and Aronson, 1942; Aronson, 1943, 1943a, 1944).

In many birds these distinctions are less clear. Thus in the pigeon, billing and bowing are common to both sexes (Whitman, 1919), and while it is usual for the female to squat and for the male to mount, copulation not infrequently occurs with the positions reversed (Carpenter, 1933).

While all vertebrates appear to possess the neuromuscular and hormonal mechanisms capable of eliciting most elements of the mating pattern of the opposite sex (Beach, 1942, 1944), morphological differences, particularly in the genitalia, hormones and other genetic factors, greatly limit the incidence, completeness and effectiveness of such behavior. Thus in the majority of vertebrates, behavior patterns characteristic of the male or female are readily distinguished.

In contrast to this typical vertebrate condition, *Tilapia* appears to represent an extreme condition. None of the patterns of reproductive behavior investigated are entirely characteristic of either sex. Qualitatively, male and female courtship and spawning behavior are exactly alike. Even in the acts of oviposition and fertilization, the overt motor patterns are the same in both sexes. Both fish swim slowly over the nest and rub their genital tubes on the substratum. The one observable difference occurs when eggs extrude through the genital aperture of the female, while the male's genital tube releases sperm, which, however, are invisible to the naked eye. It is only when the frequencies of the various reproductive acts are considered that behavioral differences between the sexes become apparent. It is true even so that in *Tilapia* sex differences in behavior depend in some cases on the time interval before the spawning. Thus, as we have found, the females exhibit much more court-

ship and do most of the nest-building. Males do more nest-passing than the females at one to two hours before the spawning, but at 15 minutes prior to oviposition we find this relationship clearly reversed. After the spawning, both qualitative similarity and quantitative dichotomy are still in evidence. Thus males wait on the average only 1.3' before they start to pick up eggs; whereas females require on an average 7'59". Also, males pick up the eggs much faster than the females, and are less prone to swallow their eggs.

In some of the patterns, as for example head-nodding, the quantitative difference between male and female frequency of the act is sufficiently large that such behavior could possibly be called a female pattern. However, our data have shown that in 25 pairs where continuous records for the first hour were available, almost one-third of the males exhibited some head-nodding. It is highly probable that if the entire span of the pre-spawning sex behavior could be observed, an even greater percentage of the males would be found to perform a minimal amount of this behavior. Bisexual or homosexual activity has generally been thought of as a recognizable intrusion of the characteristics of behavior in one sex to a greater or lesser extent into the behavior patterns characteristic of the opposite sex. Such partial observations of sex dichotomy are known to occur in a limited portion of the population or under special circumstances such as segregation. Thus we are justified in considering bisexual or homosexual behavior a rather restricted phenomenon in most vertebrates. It follows that in the case of *Tilapia* none of the patterns should be relegated to one particular sex as is generally done in the higher vertebrates.

One might hypothesize that this situation in *Tilapia* represents a primitive condition in the evolution of reproductive behavior patterns. This, however, is doubtful since cichlids are a highly specialized family of

teleosts, and on the other hand clearly recognizable, sexually divergent mating patterns are in evidence in some of the anatomically more primitive fishes. While our study of the described condition concerns *Tilapia*, it is apparent from the literature that qualitative similarities and quantitative differences such as we find between male and female sexual behavior in this species will be found to a greater or lesser extent in all cichlid fishes, and may well be true of several other families of fish.

Rather than being a primitive condition, we might view these behavior patterns of *Tilapia* as adjustments (in an evolutionary sense) to a specialized mode of reproduction in which the similarity of the sex behavior patterns has a considerable adaptive value. For the post-spawning parental behavior this point is fairly evident. If both sexes are capable of rearing the young, there is less likelihood of lost or wasted spawn. If we look upon the action of courtship as a mutually stimulating and a synchronizing mechanism as well as one which keeps the pair together, one might expect the sexes to develop comparable mechanisms to accomplish the same outcome when not limited by morphological dissimilarities.

Not all behavioral disparities between the sexes in *Tilapia* are readily understandable. On several occasions, males exhibited considerably more courtship activity than the females of given pairs. In no case did such excess lead to a spawning. One observation showed a male in a stock tank courting at a very high frequency as he swam around the enclosure. In the same aquarium a female was engaged in building a nest. Actually she did not court in relation to this sexually active male, but rather her activities had to do with two other males in the territory. The significance of excessive courtship by males is not clear. It is possible that it represents the equivalent of bisexual behavior, that is, of males behaving like females.

In this study we have found it convenient to group certain activities such as the throat-puff, body-quiver, tail-slap and head-nod under the category of courtship, as distinct from subsequent items of the reproductive series, namely nest-building, nest-passing, spawning-quivers, oviposition and fertilization. However, no sharp line of demarcation is implied between these. If we follow the functional definition of courtship as previously stated (page 136), one cannot altogether exclude the latter group of patterns from the courtship category. However, a separation on the basis of functional or adaptive significance seems to be in order. Thus courtship behavior is mainly concerned with the formation and maintenance of the pairs while the latter activities have most to do with the immediate preparation for spawning, as for example the building of the nest and the physiological preparation for oviposition and fertilization. Also there are indications of an organic separation. It is of

interest to note in this connection that in our observations on the several days before spawning, most of what we are terming courtship activities were seen at one time or another, but the acts of nest-building, passing-nest and spawning-quivers were never recorded. Thus in general reproductive behavior tends to arise and function in group fashion.

The quantitative records show that all of the courtship responses of the female increased in frequency directly after spawning. The same was true for nipping. Two factors appear to be responsible for this increased activity. The first is a physiological change consequent to oviposition, and the second is the presence of eggs. While we have not attempted to analyze the relative influence of these two factors, several observations are of interest here. First, the observed heightened courtship activity generally lasts several hours and subsides gradually. Secondly, the activity continues long after the eggs have been removed to the male's mouth. The freshly laid eggs might possibly release some type of chemical stimulus, but the evidence for this is not forthcoming. Moreover, if newly oviposited eggs are presented to males and females that have not spawned recently, such eggs are generally eaten within a short time, and they do not stimulate either courtship or nipping. The effect of this heightened activity is not apparent in most of the spawnings, but in the few cases where the males are slow in picking up the eggs, the courting seems to attract the male to the nest and stimulates him to gather up the spawn.

It has long been recognized that certain external morphological characteristics of an animal, together with specific modes of behavior, may act as exciting stimuli to other members of the species (and sometimes to members of another species) for the mediation of specific behavioral responses. Lorenz (1935, 1937) has developed this concept as a cornerstone of his theory of instinctive behavior. The stimulus or group of related stimuli bringing forth a reaction are called "releasers," the responding individual is designated as the "companion." Mutual instinctive responses of companions are sharply separated from learning processes although some modifications of the former are recognized. Furthermore, according to this view the release of every unconditioned reaction is considered to be dependent on a special central nervous mechanism which is called the "innate releasing schema" (Lorenz, 1935) or "innate releasing mechanism" (Tinbergen, 1939, 1948).

These hypotheses have become quite popular on the Continent. In this country they have received some consideration by students of bird behavior, but they are largely out of tune with the findings and interpretations of a large segment of the American experimental psychologists (Lashley, 1938) who in general have paid little attention to the

Lorenz movement. To say that a special "innate releasing mechanism" exists for every unconditioned reaction implies an extreme localization of function within the brain, a claim that is without special support in this country. Here the more popular view is that most responses are capable of being elicited by a broad array of well separated stimuli (Beach, 1942, 1947) and are not exclusively dependent upon any single stimulus or group of stimuli. Moreover, there is here a growing tendency to think of innate and learned factors as closely interlocked in their influence on behavior (Schneirla, 1941, 1946) with the view that in the higher vertebrates at least, purely innate behavior patterns as entities may be simply matters of a convenient terminology doubtfully related to reality. Lack (1940) has criticized Lorenz's view as being too simple. He points out that in many cases the designated releasers may not be the sole characters that bring forth the response. Rand (1941) has been to date Lorenz's severest critic. According to Rand, the releasing characters are by far too limited, and the releasers and responses are mostly unidentified. The reality of releasers has accordingly not been demonstrated but remains presumptive. Actually the experimental analytical approach to behavior is not only untried by Lorenz, but its validity is denied. Finally, according to Rand, there is in Lorenz's treatment a negativistic approach which denies the possibility of ever being able to elucidate the fundamentals of behavior.

Tinbergen (1939) has modified Lorenz's hypotheses in several respects. First, releasers are called "signals" or later "sign stimuli" and are subdivided into releasing stimuli and directing stimuli. More important, Tinbergen recognizes a closer relation than does Lorenz between innate responses released and modifiable factors such as learning, endocrine reactions and neural processes (summation, conditioning and "higher mental processes"). Most important is Tinbergen's recognition of the validity of the experimental approach, and his attempts, mostly by means of artifacts and models, to demonstrate releasers in this manner. Even so, it must be emphasized that Tinbergen sees releasers as very specific and limited morphological and behavioral characters which during the unfolding of a complex pattern of response will hold to a relatively rigid sequence.

Seitz, a follower of Lorenz and Tinbergen, has analyzed the behavior of two related cichlid fishes, namely a small Egyptian mouthbreeder, *Astatotilapia strigigena* (1940) and the jewel fish, *Hemichromis bimaculatus* (1942) in terms of the releaser concept. Seitz recognizes whole series of very specific releasers which call forth specific responses and which lead in an orderly manner to the spawning. These he has summarized in schematic form (1940, p. 82; 1942, p. 100). Thus, in *Astatotilapia*, the presence of a female releases a change to mating color-

ation in the male, and this change in its turn releases a slight but not significant color change in the female. The presence of the female also releases a mode of behavior called by Seitz an introductory presentation which in turn brings forth a passive response in the female. This in turn releases a complex of movement and color change called by Seitz a "Fegebalz" (lit., sweeping courtship dance). This Fegebalz of the male releases a following reaction on the part of the female, which in its turn releases circular swimming in the male around the spawning site. The circular swimming then releases a strong following reaction of the female to the spawning site which in turn brings forth a response whereby the male slips under the female. This releases circling movements in the female which in turn release the same movements in the male. The circling movements of the male call forth additional circling movements by the female. These release the oviposition movements and the latter release the fertilization movements of the male.

Our experiments were not designed to test the releaser concept and this discussion is not intended as a critique thereof. However, we were interested in learning to what extent our data would or would not support the releaser hypothesis or fit into that pattern of thought.

The significant correlation between male and female nest-passing behavior appeared most likely to fit in with this concept if we were to assume that nest-passing of male and female released a like behavior in the opposite sex. However, we had on record any number of cases where the females were very quiescent, exhibiting little or no courtship or pre-spawning behavior of any kind, and yet the males nest-passed consistently. Of course, the nest itself might be a releaser of nest-passing, but this would contradict a large portion of our data where nest-building by the female and the presence of a well-formed nest was not followed by nest-passing on the part of the male. Similarly in the spawning of the completely isolated female previously referred to, the order of magnitude of nest-passing behavior was well within the range of variability of our control pairs. Yet there was nothing in that situation which could be considered a releaser. In an attempt to follow the lead of Seitz, we could possibly view the various courtship patterns previously described as releasers. For example, the approach-throat-puff of the female might be construed as a releaser of similar behavior by the male which in turn might be thought of as releasing female nest-building behavior. This may be especially so since an approach-throat-puff by a female was often followed by a similar pattern in the male, and soon thereafter the female turned to the construction of the nest. However, no consistent pattern of this type was in evidence. Female throat-puffs were also followed by almost any of the other courtship patterns or by no particular re-

sponses of the male. Again, female nest-building was sometimes preceded by the throat-puffs but often by head-nods, tail-slaps or body-quivers. It is recognized that in general observation, that is in "just watching" these fish, one could easily gain the impression that certain acts are in effect releasers, and others a response to these releasers. However, when observational technique involves an orderly and complete quantification of response according to condition of occurrence, the data do not support such an interpretation.

We are inclined to view the courtship and pre-spawning items of behavior together with the territory and nest as having a general stimulatory effect upon the other member of the pair which would tend to raise the level of sexual excitability in the latter. Or, to put the matter in another way, the given conditions may serve to lower the threshold for the elicitation of various courtship and pre-spawning patterns. Here the particular response obtained would depend upon a whole complex of factors including the neural threshold, the immediate topographic relation to the partner, the territory, the nest and other environmental conditions, as well as the internal physiological balance of the individual at the moment. In this sort of system, no specific releasing stimuli may be properly postulated. For example, a series of weak or only partially effective tail-slaps by the female might bring forth a response in the male similar to one very effective approach-throat-puff. Moreover, as the general level of excitability of both members of the pair increased, there would be a gradual shift in the statistical probability of the elicitation of a given type of response. In other words, throat-puffing during the early stages of the pre-spawning history of a pair might bring forth additional throat-puffing or other phases of the courtship, while later, such behavior might elicit return to the nest or nest-passing. As spawning approached, nest-passing behavior of one member of the pair was often followed by like behavior of the other member of the pair, but this was often interrupted by some of the early phases of courtship such as head-nodding and tail-slapping. In many of the records, interruptions of the smooth flow of passing-nest and spawning-quivers were noted within minutes of the actual oviposition. While these data do not altogether contradict the releaser concept, it is believed that these findings can be more satisfactorily understood by adhering to a considerably more generalized interpretation of the complexity and effectiveness of the stimuli than the "releaser concept" implies.

Seitz (1940) and Tinbergen (1948) in their discussion of releasers refer to the "rule of heterogeneous summation" which states that the release of a given behavior pattern may result from the summation of several different stimuli. Tinbergen also

emphasizes that "high internal motivation may cause the reactor to respond to all objects offering the minimum adequate external stimulation." Finally, Tinbergen observes that some releasers have a general excitatory influence, rather than to direct the reactor's response. If these three principles noted here are sufficiently expanded, some of the major objections to the releaser concept are thus overcome, and except for the sharp lines drawn between instinct and learning processes, we begin to arrive at a common ground for the understanding of the nature of sexual behavior.

#### SUMMARY AND CONCLUSION.

Qualitative descriptions and quantitative measurements of the patterns of reproductive behavior of the African mouthbreeding cichlid fish, *Tilapia macrocephala* (Bleeker), have been presented. These patterns have been grouped into three categories. The first, namely courtship, includes head-nods, approach-throat-puffs, body-quivers and tail-slaps. Most of the females exhibited these courtship items during the observation periods, and at a relatively high frequency. The males performed these courtship acts at a considerably lower frequency. A high percentage of males showed some tail-slaps and body-quivers, and it is believed that if the entire spans of the pre-spawning activity of the pairs could have been observed, all of the males would have performed these courtship patterns. On the other hand, it appears that a measurable portion of males do not head-nod or approach-throat-puff prior to the spawning.

It is hypothesized that courtship behavior is an expression of the level of excitability of the individual. It may be thought of as a trophallactic process which through mutual stimulation serves to regulate the behavioral activities and physiological processes of the male and female so that well synchronized spawnings result.

Nipping, which is closely related to courtship and which also appears to be mutually stimulating, was performed equally by the male and female before the spawning, but nipping on the part of the female rises sharply directly after oviposition. Similar post-spawning increases on the part of the female were noted for all of the courtship patterns. It is suggested that the physiological changes following oviposition plus the presence of eggs are the factors responsible for this heightened activity. During the inter-spawning interval, a low level of courtship is in evidence, especially on the part of the females.

The second group of reproductive patterns includes those acts which are concerned with the immediate preparation for spawning. Included here are nest-building, nest-passing, spawning-quivers, oviposition movements and the act of fertilization. Considerably more nest-building is exhibited by the

female than by the male, but it is likely that all males do some nest-building before every spawning. With passing-nest and spawning-quivers the frequency is somewhat higher for the males an hour or so before spawning, but at 15 minutes before spawning this relationship is clearly reversed, with the females at the height of their nest-passing and spawning-quivers. A significant correlation between male and female nest-passing during the first pre-spawning interval suggests that this behavior is mutually stimulating. The mean number of oviposition movements of the female did not differ significantly from the mean number of fertilization acts of the male. Moreover these behavior patterns are highly correlated, suggesting that the number of times the male fertilizes the eggs is partly related to and probably dependent upon the number of oviposition movements of the female. In contrast with the courtship patterns, behavioral items in the present category were not observed during the inter-spawning interval.

The third category of reproductive acts are those associated with the care of eggs and young. Males start picking up eggs on an average of 1'3" from the beginning of oviposition. Females, if given the opportunity, took on the average 7'59". This is the apporportioning mechanism whereby males usually incubate the eggs, and females do so only on infrequent or special occasions. Similar quantitative differences were found in other phases of the parental pattern. Thus females gather up the spawn more slowly and are more prone to swallow the eggs.

A low order positive correlation was found between the size of the female and the number of eggs laid during a given spawning. Since brood size shows no correlation with the size of the female, it is concluded that a greater mortality occurs in the larger broods. Incubating fish generally carry some gravel intermingled with the spawn, but it was not clear whether this bore any relation to the survival of the embryos.

In the majority of vertebrates there are distinct qualitative differences between the patterns of reproductive behavior of the male and female. While both sexes have the neuromuscular mechanism capable of eliciting both the male and female patterns, bisexual or homosexual behavior is limited and generally appears under special conditions. *Tilapia* are exceptional in this respect insofar as there are no distinct qualitative differences between male and female in their sexual activities. However, there are marked quantitative differences in all of the patterns.

Several previous investigators have analyzed cichlid mating behavior in terms of Lorenz's releaser concept. It is felt that even in the expanded and modified form presented by Tinbergen, this concept is still too restricted to form an adequate basis for the analysis of *Tilapia* reproductive behavior.

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## EXPLANATION OF THE PLATES.

## PLATE I.

- Fig. 1. Male cleaning nest.  $\times .5$   
 Fig. 2. Oviposition. The male is behind the female, waiting for her to move along so that he can pass over and fertilize the eggs.  $\times .5$

## PLATE II.

- Fig. 3. The male is fertilizing the eggs while the female is circling the nest. By the time fertilization was completed the female was directly behind the male, ready to lay a second round of eggs.  $\times .5$   
 Fig. 4. Male picking up the eggs. All of the eggs were gathered up in less than one minute.  $\times .5$

## PLATE III.

- Fig. 5. Male carrying eggs.  $\times .7$   
 (Photo. by S. C. Dunton, N. Y. Zool. Soc.).  
 Fig. 6. In special circumstances the female may carry the spawn. An egg can be seen at the tip of the open mouth of the female.  $\times .5$

## ADDENDUM.

When this report was in page proof an article by Alfred Seitz (1948)—Vergleichende Verhaltensstudien an Buntbarschen (Cichlidae).—Zeitschrift für Tierpsychologie, 6 (22): 202-235, was received from Germany. Here Seitz analyzes fighting and courtship behavior in two cichlid species, *Tilapia heudeloti* and *Tilapia natalensis*, in accordance with the theory of instinctive movements of Konrad Lorenz. On page 134 of the present paper we have noted the very close similarities of *T. heudeloti* and *T. macrocephala*; they may in fact be varieties or subspecies. However, the pictures of *T. heudeloti* presented by Seitz, the descriptions of the external morphology, particularly coloration, as well as the descriptions of courtship and fighting behavior, all suggest that he was dealing with a very different fish. It is not possible at this time to comment further on Seitz's paper, nor do we wish to venture any opinions concerning the complex problems of cichlid taxonomy, except to suggest to the reader who may wish to compare Seitz's paper with the present report that the *T. heudeloti* of Seitz and our *T. macrocephala* are perhaps very different species. —L.R.A.

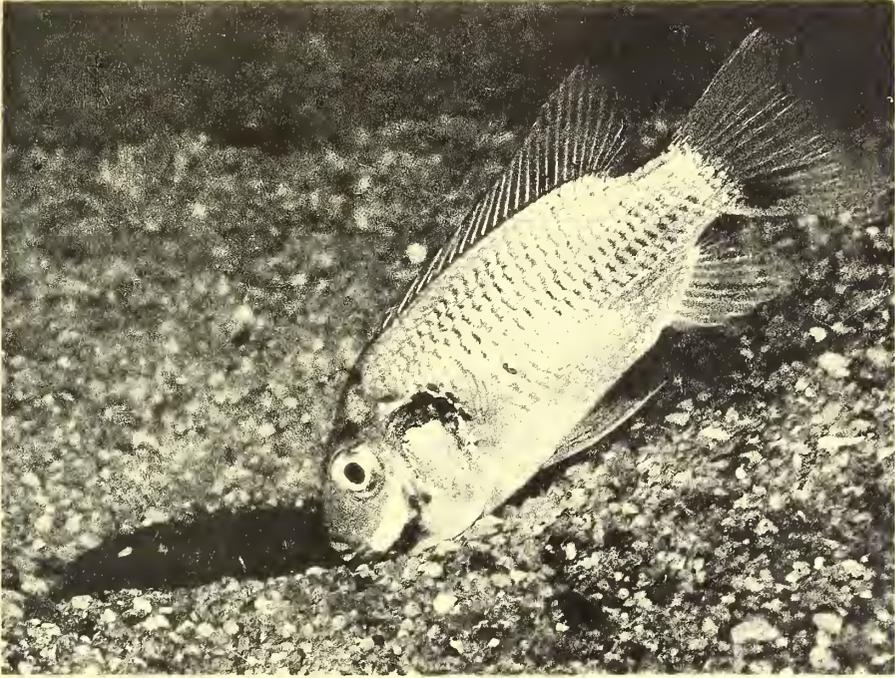


FIG. 1.



FIG. 2.

AN ANALYSIS OF THE REPRODUCTIVE BEHAVIOR OF THE  
MOUTHBREEDING CICHLID FISH, *TILAPIA MACROCEPHALA* (BLEEKER).



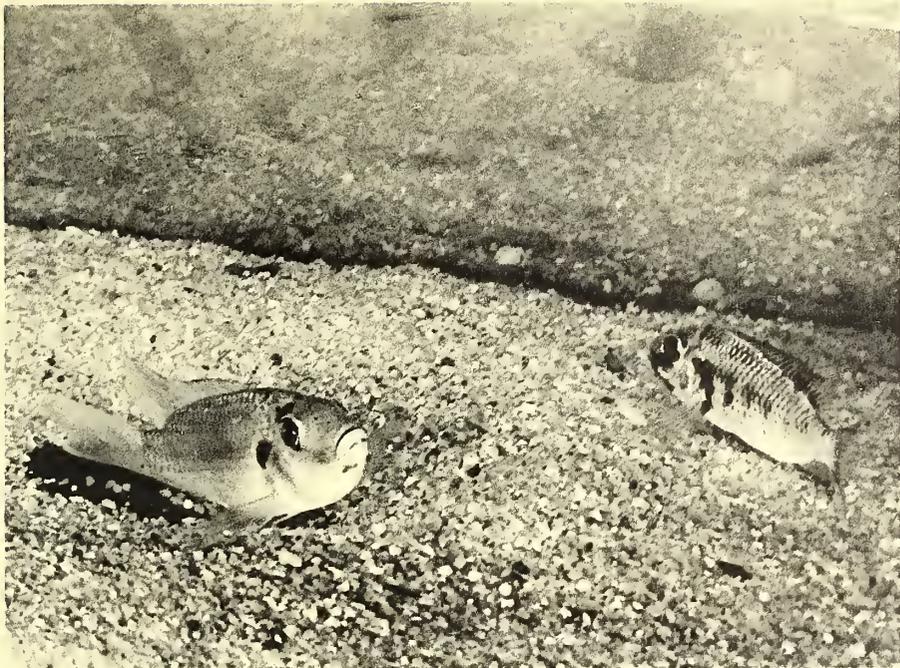


FIG. 3.

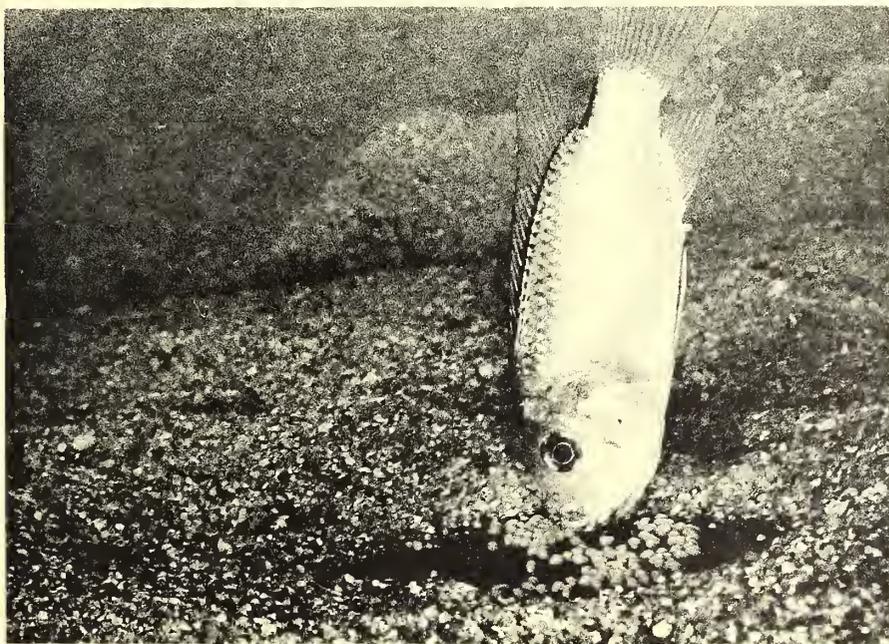


FIG. 4.

AN ANALYSIS OF THE REPRODUCTIVE BEHAVIOR OF THE  
MOUTHBREEDING CICHLID FISH, *TILAPIA MACROCEPHALA* (BLEEKER).



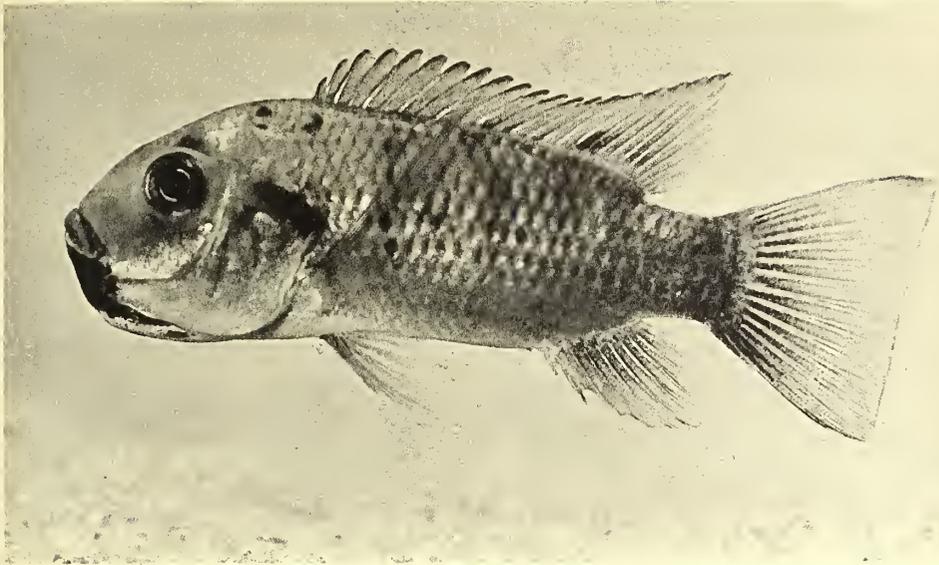


FIG. 5.

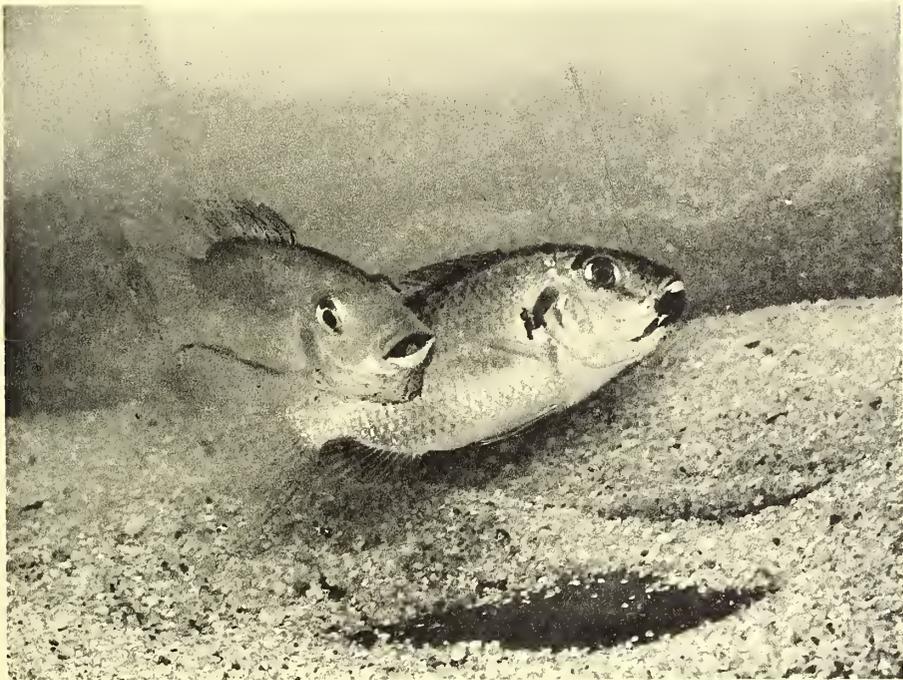


FIG. 6.

AN ANALYSIS OF THE REPRODUCTIVE BEHAVIOR OF THE MOUTHBREEDING CICHLID FISH, *TILAPIA MACROCEPHALA* (BLEEKER).



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## 17.

# Comparative Biology of Salticid Spiders at Rancho Grande, Venezuela.

## Part IV. An Analysis of Display.<sup>1</sup>

JOCELYN CRANE.

Research Zoologist, Department of Tropical Research,  
New York Zoological Society.

(Plate I; Text-figures 1-9).

[This is one of a series of papers resulting from the 45th, 46th and 47th Expeditions of the Department of Tropical Research of the New York Zoological Society, made during 1945, 1946 and 1948 under the direction of Dr. William Beebe, with headquarters at Rancho Grande in the National Park of Aragua, Venezuela. The expeditions were made possible through the generous cooperation of the National Government of Venezuela and of the Creole Petroleum Corporation.

[The characteristics of the research area are in brief as follows: Rancho Grande is located in north-central Venezuela (10° 21' N. Lat., 67° 41' W. Long.), 80 kilometers west of Caracas, at an elevation of 1,100 meters in the undisturbed montane rain forest which covers this part of the Caribbean range of the Andes. Adjacent ecological zones include seasonal forest, savanna, thorn woodland, cactus scrub, the fresh-water lake of Valencia and various marine littoral zones. The Rancho Grande area is generally subtropical, being uniformly cool and damp throughout the year because of the prevalence of the mountain cloud cap. The dry season extends from January into April. The average humidity during the expeditions, including parts of both dry and wet seasons, was 92.4%; the average temperature during the same period was 18° C.; the average annual rainfall over a five-year period was 174 cm. The flora is marked by an abundance of mosses, ferns and epiphytes of many kinds, as well as a few gigantic trees. For further details, see Beebe and Crane, *Zoologica*, Vol. 32, No. 5, 1947. Unless otherwise stated, the specimens discussed in the present paper were taken in the montane cloud forest zone, within a radius of one kilometer of Rancho Grande.]

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### I. INTRODUCTION.

This is the fourth of a series of papers dealing with the salticid spiders of Rancho Grande, Venezuela. Part I (Crane, 1948.1) discussed the taxonomy and life histories of three species of *Corythalia*, Part II (1948.2) described methods of study and Part III (1949) dealt with systematics and behavior in eight new species of various groups of genera, as a basis for this and subsequent sections. The present paper on display, while an independent unit, will be followed by sections on comparative post-embryological development and on evolutionary trends, which must, to some extent, be anticipated in the present paper.

My deep appreciation goes to Dr. William Beebe for his continued advice, encouragement and patience during the progress of this study. Special thanks are due Miss

<sup>1</sup> Contribution No. 858, Department of Tropical Research, New York Zoological Society.

This paper was awarded Honorable Mention in the A. Cressy Morrison Prize Competition of the New York Academy of Sciences for 1949.

Louise A. Moore and Mr. Douglas G. Boyden for their work on the drawings and diagrams, respectively.

## II. PURPOSE.

The purpose of this paper is two-fold: first, to analyze the innate releasing mechanism of display behavior in salticids; second, through a comparison of display and related behavior in widely scattered genera, to shed light on evolutionary trends within the family.

## III. MATERIAL AND METHODS.

The observational and experimental material in this paper has been drawn primarily from about fifteen species of salticid spiders which are common around Rancho Grande, Venezuela. They were carefully selected from among some thirty-five species in the same locality, in which display behavior was to some degree observed, on the following bases:

1. They represent a wide divergence of salticid forms, belonging to seven relatively well-defined groups of genera. These groups, although they have so far defied satisfactory divisions in keys to include all their borderline genera, are still rather generally recognized as composed of naturally related forms. For convenience, Petrunkevitch's (1928, 1939) practice of terming the groups "subfamilies" is followed, although their unequal values and the usual difficulties of salticid systematics are fully recognized. Since the tracing of a pattern of relationships is one of the purposes of this paper, groupings must be attempted. The genera chosen are relatively non-controversial, as are, in their broad outlines, the subfamilies to which they are referred; borderline cases have purposely been omitted. The selected forms are fairly typical members of the following subfamilies designated by Petrunkevitch: Marpissinae, Synagelinae, Dendryphantinae, Magoninae, Hyllinae and Plexippinae. The *Lyssomanes* group, however, in spite of its aberrant characters will be given only subfamilial status. These terms will be used throughout, in order to simplify correlation by future workers, in spite of questionable validity or priority in any of the old, type genera. Each subfamily corresponds to a group in Chickering's 1946 arrangement, based on Panamanian genera, except that in the present paper the plexippinids and hyllinids will be kept separate, largely in deference to basic behavior differences. From these limitations, it will be seen that the study cannot be expected to help in practical fashion in the determination of fine points of relationship among puzzling genera; rather, it is hoped only to clarify some of the broad outlines of the family's organization.

2. The second criterion of selection has been that each subfamily have a northern as well as neotropical distribution. This has

a double advantage, since some comparable display behavior has in each case been already recorded and future comparisons will be facilitated.

3. In three genera, *Sassacus*, *Phiale* and *Corythalia*, intrageneric behavior patterns could be compared.

The thirteen species listed in Table I form the paper's foundation, in the sense that most of the observations and experiments were performed on them. Ten of them were described as new in Parts I and III of this study (1948.1, 1949); the remaining three are well known in the tropics. For further comparison, a few casual references will be made to the following Rancho Grande species which are systematically undetermined: Magoninae: *Hypaeus* sp., Dep't. of Tropical Research Cat. No. 45138; Hyllinae: *Phiale* sp., Cat. No. 481408; Plexippinae: *Eustromastix* sp., Cat. No. 45110; Plexippinae: a genus, probably new, near *Capidava*, Cat. No. 4586.

In Table II an effort has been made to correlate the relevant observations made upon northern species of the same subfamilies by previous investigators. Complete spider display references to 1939 are given in Bonnet's bibliography (1945, p. 718). Kaston (1936) and Bristowe (1941) give excellent selected references on the subject.

The general methods of observation and experiment at Rancho Grande have already been recorded (Part II, 1948.2). Special information regarding particular experiments will be presented in the body of this paper. See also Pl. I, Fig. 2.

It remains to remark on the usage of several terms. The phrase "epigamic display" has been advocated by a number of behaviorists to replace "courtship," a word which has an undesirable historical burden of anthropomorphism. In the study of salticids, the choice is complicated by the wide range of distinctness of male-female, female-male and inter-male display; a general term seems necessary to cover the entire field. Again, "aposematic display" has been proposed to designate inter-male encounters; in the literature, however, this term is used so widely to cover displays against potential predators—a type of display which is not known to occur in salticids—that a more restricted name appears desirable. Therefore, for present purposes, the following terminology has been adopted: *Epigamic display* refers to special behavior of either sex which is normally used in any sexual situation, including encounters between males. *Courtship* applies to those forms of epigamic display which normally precede copulation. *Threat display* is used for all inter-male display, whether or not it is visually distinct from courtship, and whether or not occasional contact fighting occurs.

"Ornamentation" is used as a convenient term to cover special colors, patterns, tufts, brushes, etc., which, conspicuous to human eyes, are specializations possibly connected

TABLE I.

Subfamily acc. to Petrunkevitch (1939)	Group acc. to Chickering (1946)	Name
Lyssomaninae	Lyssomaninae	<i>Lyssomanes bradyspilus</i> Crane, 1949
Marpissinae	<i>Marpissa</i> Group	<i>Menemerus bivittatus</i> (Dufour, 1831)
Synagelinae	<i>Zuniga</i> Group	<i>Semorina brachychelyne</i> Crane, 1949
Dendryphantinae	<i>Metaphidippus</i> Group	<i>Ashtabula furcillata</i> Crane, 1949
Dendryphantinae	<i>Metaphidippus</i> Group	<i>Sassacus flavicinctus</i> Crane, 1949
Dendryphantinae	<i>Metaphidippus</i> Group	<i>Sassacus ocellatus</i> Crane, 1949
Magoninae	<i>Amycus</i> Group	<i>Mago denticheles</i> Crane, 1949
Hyllinae	<i>Phiale</i> Group	<i>Phiale dybowskii</i> (Taczanowski, 1871)
Hyllinae	<i>Phiale</i> Group	<i>Phiale flammea</i> Crane, 1949
Plexippinae	<i>Phiale</i> Group	<i>Plexippus paykullii</i> (Audouin, 1827)
Plexippinae	<i>Phiale</i> Group	<i>Corythalia chalcea</i> Crane, 1948.1
Plexippinae	<i>Phiale</i> Group	<i>Corythalia fulgipedia</i> Crane, 1948.1
Plexippinae	<i>Phiale</i> Group	<i>Corythalia xanthopa</i> Crane, 1948.1

with epigamic displays. It and similar words are put in quotation marks when it seems wise to emphasize their non-anthropomorphic use. The quotations will simultaneously act as reminders, as advocated by Korzybski (1948), of the every-day, inexact connotations of the terms; another of his safety devices, the frequent use of *etc.*, is employed, not to disguise ignorance, but to emphasize the incomplete state of our knowledge.

The terms *sign stimulus*, *releaser*, *director*, *innate releasing mechanism*, *stimulus configuration* and *heterogeneous summation* are used with the meanings attached to them in Tinbergen's general discussion, in English, of social releasers (1948).

Throughout the present paper, the terms *reaction* and *response* are used interchangeably to indicate overt display behavior discernible to the human observer.

Kaston's (1948) nomenclature is followed in all references to species of salticids occurring in the United States.

#### IV. SURVEY OF SALTICID DISPLAY.

##### A. FORM AND VARIETY.

The general habits and life histories of all salticids are similar and typical of many hunting spiders; they spin no snares, but stalk and leap upon their prey, which they eat promptly; the male copulates in the dorsal position; the female guards the egg cocoon until the emergence of the spiderlings. In the development of their eyes, however, salticids are unique even among long-sighted hunting spiders. In company with the latter, notably the lycosids, and correlated with the acute vision, the salticids have evolved a courtship display which is primarily visual. This is in contrast to the behavior of short-sighted forms, such as the web-spinning epeirids, in which courtship depends on senses other than vision.

As in all groups, there is considerable intra-family variation in details of behavior, particularly in the form and care of the cocoons, in jumping methods, in preferred ecological niches and in physiological tolerances of various kinds. A most

important series of differences is based upon an apparently unreported correlation between visual acuity and chemical dependence on the one hand, and method of locomotion on the other. Because of its basic connection with display behavior, this subject will be considered in detail further on (p. 173).

The outstanding directions of development within the family are shown in the very remarkable variety of epigamic display patterns and in the apparently correlated ornamentation of the spiders. All salticids, before inserting the sperm-charged palps into the epigynum of the female, perform some sort of preliminary motions, the form of which, under natural conditions, is a fixed part of the behavior pattern for the species. These movements range from brief and simple elevations of the first legs to complicated and prolonged sequences involving most of the other appendages.

In some salticids there are clear visual distinctions between courtship and intermale threat display, which often employ not only distinctive motions but also different appendages. In each kind of epigamic display, when complete, there are always distinguishable two major stages. Specific display differences, as well as distinctions between courtship and threat, always lie principally in Stage I. Stage II, which immediately precedes either copulation or true fighting as the case may be, is very similar throughout the family; it consists in extending the first legs forward, parallel to each other and slightly elevated. (Pl. I, Fig. 1).

Although salticid display is dominantly visual, the role of other senses is proving of considerable secondary importance. Unfortunately, because of the limitations of human sense organs and the lack of appropriate instruments, specific display descriptions must still be largely confined to the reporting of gross visual components. For instance, possible changes in chemical stimuli, which may be emitted in sequence during display, are still necessarily overlooked.

Table II presents correlated data on the displays recorded within the subfamilies

TABLE II.  
Comparative Display Data in Seven Subfamilies of Salticid Spiders.

Name	Display References	Courtship Posture (Stage I)
MARFISSINAE		
<i>Marpissa undata</i> (De Geer)	Peckham, '89, p. 43; fig. ("Marptusa familiaris") (U.S.A.)	Carapace high. 1st & 2nd legs raised slightly, stretched laterally. Abdomen pendent.
<i>Marpissa rumpfi</i> Scop.	Bristowe, '29, p. 330-352. Bristowe, '41, p. 480; fig. (England)	Carapace high. 1st legs raised vertically, parallel. Abdomen raised.
<i>Menemerus bivittatus</i> (Dufour)	Crane (Unpublished observations) (Venezuela)	Carapace low. 1st legs raised slightly, stretched antero-laterally; 2nd legs ex- tended forward. Abdomen level.
<i>Hytia nivoyi</i> Luc.	Berland, '27, p. 15; fig. Bristowe, '29, p. 329; fig. Bristowe, '41, p. 484; fig. (Europe)	1st legs stretched forward @ $\angle$ of 45°; raised & lowered. Abdomen often bent sideways. (cf. Dendryphantinae).
<i>Hytia pikei</i> Peckham	Kaston, '48, p. 455; fig. (U.S.A.)	Carapace low. 1st legs raised vertically @ $\angle$ of 45°. 2nd legs extended forward. Abdomen raised.
<i>Salticus cingulatus</i> Panz.	Bristowe, '29, p. 332. (England)	Similar to <i>S. scenicus</i> .
<i>Salticus scenicus</i> (Linn.)	Peckham, '89, p. 39. ("Epiblemum scenicum") Gerhardt, '21, p. 131. ("Epiblemum scenicum") Monterosso, '24, p. 1. Bristowe, '29, p. 332. Bristowe, '41, p. 480, 499; fig. (Europe & U.S.A.)	1st legs slightly raised, stretched laterally. Chelicerae opened. Palps stretched laterally.
SYNAGELINAE		
<i>Synageles venator</i> Luc.	Bristowe, '41, p. 485. (England)	1st legs stretched forward, parallel. Abdomen wriggled or waved from side to side, sometimes raised a little.
<i>Semorina brachychelyne</i> Crane	Crane, '49, p. 37. (Venezuela)	1st legs stretched forward, @ 90° $\angle$ , slightly raised. Abdomen raised; tends to remain high with increasing excitement.
<i>Gertschia noxiosa</i> (Hentz)	Kaston, '48, p. 451; fig. (U.S.A.)	1st legs braced laterally. Abdomen raised vertically & swung from side to side.
<i>Peckhamia picata</i> (Hentz)	Peckham, '89, p. 43. Peckham, '90, p. 121; fig. (U.S.A.)	Carapace high. 1st legs on ground, bent, convex sur- face forward. Abdomen raised vertically. Spider sways from side to side.

TABLE II (cont.)

Comparative Display Data in Seven Subfamilies of Salticid Spiders.

Threat Posture & Fighting	Principal Apparent Morphological Adaptations to Display	Locomotion & Remarks
	MARPISSINAE (cont.)	
	Slight enlargement basal half of 1st & 2nd legs.	♀ vibrates palps.
Jaws opened; pressed against those of opponent.	1st legs elongated, enlarged, darkened.	
Usually ♂♂ pay no attention to each other; no distinctive motions; rarely courtship to mirror image in closed vial.	1st legs elongated, enlarged, darkened.	Runs; jumps only on prey or to cross gaps. 1st legs little used in walking. ♀ vibrates pale palps.
	1st legs elongated, enlarged, darkened.	
	1st legs elongated, enlarged, darkened. Abdomen boldly striped.	1st legs not used in walking, extended forward & raised to clear ground.
	Chelicerae elongated, enlarged, darkened. 1st legs slightly elongated.	
Like courtship, but jaws opened wider and palps not stretched to sides. (No mirror display. Crane obs. U.S.A.)	Chelicerae elongated, enlarged, darkened. 1st legs slightly elongated.	Jerky walk; hops when pursued. (Crane obs. U.S.A.).
	SYNAGELINAE (cont.)	
	1st legs enlarged.	
Apparently no inter-male display. No mirror display.	1st legs elongated, enlarged, darkened. Abdomen dark with 2 dorsal white spots.	Runs; jumps only on prey or to cross gaps. 1st legs stretched to front, parallel; do not touch ground. ♀ vibrates palps.
	1st legs elongated, enlarged, darkened. Abdomen dark with dorsal white bands.	Runs slowly, irregularly, like ant. (Emerton, 1909).
	1st legs elongated, enlarged, darkened. Abdomen dark with dorsal white bands.	



TABLE II.

Comparative Display Data in Seven Subfamilies of Salticid Spiders.

Name	Display References	Courtship Posture (Stage I)
MARPISSINAE		
<i>Marpissa undata</i> (De Geer)	Peckham, '89, p. 43; fig. ("Marpissa familiaris") (U.S.A.)	Carapace high. 1st & 2nd legs raised stretched laterally. Abdomen pendent.
<i>Marpissa rumpfi</i> Scop.	Bristowe, '29, p. 330-352. Bristowe, '41, p. 480; fig. (England)	Carapace high. 1st legs raised vertically, parallel. Abdomen raised.
<i>Menemerus bivittatus</i> (Dufour)	Crane (Unpublished observations) (Venezuela)	Carapace low. 1st legs raised slightly, stretched antero-laterally; 2nd legs extended forward. Abdomen level.
<i>Hycitia nivoyi</i> Luc.	Berland, '27, p. 15; fig. Bristowe, '29, p. 329; fig. Bristowe, '41, p. 484; fig. (Europe)	1st legs stretched forward @ $\angle$ of 45°; raised & lowered. Abdomen often bent sideways. (cf. Dendryphantinae).
<i>Hycitia pikei</i> Peckham	Kaston, '48, p. 455; fig. (U.S.A.)	Carapace low. 1st legs raised vertically @ $\angle$ of 45°. 2nd legs extended forward. Abdomen raised.
<i>Salticus cingulatus</i> Panz.	Bristowe, '29, p. 332. (England)	Similar to <i>S. scenicus</i> .
<i>Salticus scenicus</i> (Linn.)	Peckham, '89, p. 39. ("Epiblemum scenicum") Gerhardt, '21, p. 131. ("Epiblemum scenicum") Monterosso, '24, p. 1. Bristowe, '29, p. 332. Bristowe, '41, p. 480, 499; fig. (Europe & U.S.A.)	1st legs slightly raised, stretched laterally. Chelicerae opened. Palps stretched laterally.
SYNAGELINAE		
<i>Synageles venator</i> Luc.	Bristowe, '41, p. 485. (England)	1st legs stretched forward, parallel. Abdomen wriggled or waved from side to side, sometimes raised a little.
<i>Semorina brachychelyme</i> Crane	Crane, '49, p. 37. (Venezuela)	1st legs stretched forward, @ 90° $\angle$ , slightly raised. Abdomen raised; tends to remain high with increasing excitement.
<i>Gertschia noziosa</i> (Hentz)	Kaston, '48, p. 451; fig. (U.S.A.)	1st legs braced laterally. Abdomen raised vertically & swung from side to side.
<i>Peckhamia picata</i> (Hentz)	Peckham, '89, p. 43. Peckham, '90, p. 121; fig. (U.S.A.)	Carapace high. 1st legs on ground, bent, convex surface forward. Abdomen raised vertically. Spider sways from side to side.

TABLE II (cont.)

Comparative Display Data in Seven Subfamilies of Salticid Spiders.

Threat Posture & Fighting	Principal Apparent Morphological Adaptations to Display	Locomotion & Remarks
MARPISSINAE (cont.)		
	Slight enlargement basal half of 1st & 2nd legs.	♀ vibrates palps.
Jaws opened; pressed against those of opponent.	1st legs elongated, enlarged, darkened.	
Usually ♂♂ pay no attention to each other; no distinctive motions; rarely courtship to mirror image in closed vial.	1st legs elongated, enlarged, darkened.	Runs; jumps only on prey or to cross gaps. 1st legs little used in walking. ♀ vibrates pale palps.
	1st legs elongated, enlarged, darkened.	
	1st legs elongated, enlarged, darkened. Abdomen boldly striped.	1st legs not used in walking, extended forward & raised to clear ground.
	Chelicerae elongated, enlarged, darkened. 1st legs slightly elongated.	
Like courtship, but jaws opened wider and palps not stretched to sides. (No mirror display. Crane obs. U.S.A.)	Chelicerae elongated, enlarged, darkened. 1st legs slightly elongated.	Jerky walk; hops when pursued. (Crane obs. U.S.A.).
SYNAGELINAE (cont.)		
	1st legs enlarged.	
Apparently no inter-male display. No mirror display.	1st legs elongated, enlarged, darkened. Abdomen dark with 2 dorsal white spots.	Runs; jumps only on prey or to cross gaps. 1st legs stretched to front, parallel; do not touch ground. ♀ vibrates palps.
	1st legs elongated, enlarged, darkened. Abdomen dark with dorsal white bands.	Runs slowly, irregularly, like ant. (Emerton, 1909).
	1st legs elongated, enlarged, darkened. Abdomen dark with dorsal white bands.	

TABLE II. (cont.)  
Comparative Display Data in Seven Subfamilies of Salticid Spiders.

Name	Display References	Courtship Posture (Stage I)
LYSSOMANINAE		
<i>Lyssomanes bradypilus</i> Crane	Crane, '49, p. 34; see also Text-fig. 8, this paper. (Venezuela)	Carapace high, occasionally bobbed No legs raised; 1st 3 prs. brace forward. Palps sometimes tap ground. Abdomen pendent, twitched. Prolonged posing in this position as— Rate of retinal motions within AMI are accelerated.
DENDRYPHANTINAE		
<i>Ashtabula furcillata</i> Crane	Crane, '49, p. 41; fig. (Venezuela)	Carapace high. 1st legs stretched laterally, wave up & down. Palps jerk; later are quiet. Abdomen turned to side.
<i>Hentzia mitrata</i> (Hentz)	Peckham, '89, p. 49; fig. ("Icius mitratus") (U.S.A.)	Carapace high. 1st legs stretched laterally, held a right $\sphericalangle$ to body. Abdomen twisted to side.
<i>Icius elegans</i> (Hentz)	Peckham, '89, p. 46. ("Dendryphantes elegans") (U.S.A.)	1st legs waved "in way that remind one of a wind-mill". Later, re volves on tip-toe.
<i>Sassacus ocellatus</i> Crane	Crane, '49, p. 45. (Venezuela)	Carapace scarcely elevated. 1st legs stretched up & out at right $\sphericalangle$ to each other. Chelicerae closed. Palps vibrated occasionally. Abdomen sometimes twisted slightl to side, held motionless.
<i>Sassacus flavicinctus</i> Crane	Crane, '49, p. 41. (Venezuela)	Carapace moderately high. 1st legs stretched up at wide $\sphericalangle$ t each other. Chelicerae stretched sideways, bu closed. Palps stretched sideways. Abdomen trailed inconspicuousl from side to side. Later: Carapace & abdomen slowl rocked from side to side.
<i>Metaphidippus protervus</i> (Walck.) and/or <i>M. galathea</i> (Walck.)	Peckham, '89, p. 45; fig. ("Dendryphantes capitatus") (U.S.A.)	Carapace low. 1st legs stretched forward, close t ground, slightly curved with tip turned up. Palps given circular movement. Later, lies on side, legs still extend ed.
<i>Paraphidippus marginatus</i> (Walck.)	Peckham, '89, p. 50; fig. ("Philaeus militaris") (U.S.A.)	1st legs raised, curved toward each other, tips nearly meeting. Palps moved up and down.

TABLE II (cont.)  
Comparative Display Data in Seven Subfamilies of Salticid Spiders.

Threat Posture & Fighting	Principal Apparent Morphological Adaptations to Display	Locomotion & Remarks
LYSSOMANINAE (cont.)		
Threat display rarely induced; posture as in courtship, but no bobbing, no abdominal twitching, no acceleration of retinal motions. Fighting & mirror display absent.	Distal portion of black retina contrasts with green surroundings. Chelicerae elongated but not specially displayed.	Runs in short spurts. Jumps only in final pounce on prey. Palps pendent, pat ground during pauses. 1st legs take part in locomotion. ♀ sags to side when watching display; muscular activity in eyes increase as in ♂.
DENDRYPHANTINAE (cont.)		
Apparently no inter-male display. No mirror display.	1st legs elongated, enlarged, darkened, fringed. Abdomen with lateral white stripe bounded by iridescence.	Runs; jumps only on prey or to cross gaps. 1st legs unused in progress, held forward, they & palps tap ground; waved in air in pauses. ♀ vibrates palps.
Same as courtship. Chases rivals away.	1st legs elongated, fringed. Abdomen with lateral white stripe bounded by darker.	♀ "indifferent"; sometimes attacks ♂.
Stage I: Similar to courtship, except chelicerae partly unsheathed, & no distinct abdominal twisting. Stage II: Actual fighting, 1st legs raised vertically; chelicerae wide open; palps extended laterally. Clinching frequent, with occasional injury; no deaths seen.	Carapace with frontal tufts. 1st legs elongated; tibia fringed, black-spotted. Both sexes covered with iridescent scales.	♀ irritable, prone to attack; later raises abdomen or turns it sideways.
Stage I: Like courtship except no rocking. Stage II: (Rare). Chelicerae unsheathed, extended forward; 1st legs raised vertically; clinching; no injuries seen. Occasional mirror display.	1st legs elongated, enlarged, darkened, with white scales. Chelicerae elongate, enlarged darkened. Clypeus with white band. Abdomen with large, sub-distal, white-barred black spots.	Runs; jumps only to catch prey & cross gaps. 1st legs held forward, scarcely touch ground; these & palps wave in air & tap ground, during pauses. ♀ once did weak mutual display.
Distinct from courtship. 1st legs raised. Sparring, chasing & clinching without injury.	1st legs elongated, enlarged, darkened. Chelicerae elongate, enlarged, darkened. Clypeus with yellow band.	Runs; jumps occasionally when pursued, as well as to catch prey & cross gaps. Palpates ground & waves 1st legs less than <i>S. ocellatus</i> .
Distinct from courtship. 1st legs raised. Palps vibrated. Abdomen dragged to either side. Chasing and clinching without injury.	1st legs elongated, enlarged. White markings on dark palps & clypeus.	Runs, but hops freely when pursued, as well as to catch prey to cross gaps. Palps often jerk. 1st legs not waved. Take some part in walking. (Crane obs. U.S.A.)
Distinct from courtship. 1st legs raised. Palps vibrated. Abdomen dragged to either side. Chasing and clinching without injury.	1st legs elongated, enlarged. Chelicerae elongated.	♂♂ guard immature ♀♀ until molt.



TABLE II. (cont.)

Comparative Display Data in Seven Subfamilies of Salticid Spiders.

Name	Display References	Courtship Posture (Stage I)
LYSSOMANINAE		
<i>Lyssomanes bradyaspilus</i> Crane	Crane, '49, p. 34; see also Text-fig. 8, this paper. (Venezuela)	Carapace high, occasionally bobbed. No legs raised; 1st 3 prs. braced forward. Palps sometimes tap ground. Abdomen pendent, twitched. Prolonged posing in this position, as— Rate of retinal motions within AME are accelerated.
DENDRYPHANTINAE		
<i>Ashtabula furcillata</i> Crane	Crane, '49, p. 41; fig. (Venezuela)	Carapace high. 1st legs stretched laterally, waved up & down. Palps jerk; later are quiet. Abdomen turned to side.
<i>Hentzia mitrata</i> (Hentz)	Peckham, '89, p. 49; fig. ("Icius mitratus") (U.S.A.)	Carapace high. 1st legs stretched laterally, held at right $\Delta$ to body. Abdomen twisted to side.
<i>Icius elegans</i> (Hentz)	Peckham, 89, p. 46. ("Dendryphantans elegans") (U.S.A.)	1st legs waved "in way that reminds one of a wind-mill". Later, re- volves on tip-toe.
<i>Sassacus ocellatus</i> Crane	Crane, '49, p. 45. (Venezuela)	Carapace scarcely elevated. 1st legs stretched up & out at right $\Delta$ to each other. Chelicerae closed. Palps vibrated occasionally. Abdomen sometimes twisted slightly to side, held motionless.
<i>Sassacus flavicinctus</i> Crane	Crane, '49, p. 41. (Venezuela)	Carapace moderately high. 1st legs stretched up at wide $\Delta$ to each other. Chelicerae stretched sideways, but closed. Palps stretched sideways. Abdomen trailed inconspicuously from side to side. Later: Carapace & abdomen slowly rocked from side to side.
<i>Metaphidippus protervus</i> (Walck.) and/or <i>M. galathea</i> (Walck.)	Peckham, '89, p. 45; fig. ("Dendryphantans capitatus") (U.S.A.)	Carapace low. 1st legs stretched forward, close to ground, slightly curved with tips turned up. Palps given circular movement. Later, lies on side, legs still extend- ed.
<i>Paraphidippus marginatus</i> (Walck.)	Peckham, '89, p. 50; fig. ("Philaenus militaris") (U.S.A.)	1st legs raised, curved toward each other, tips nearly meeting. Palps moved up and down.

TABLE II (cont.)

Comparative Display Data in Seven Subfamilies of Salticid Spiders.

Threat Posture & Fighting	Principal Apparent Morphological Adaptations to Display	Locomotion & Remarks
LYSSOMANINAE (cont.)		
Threat display rarely induced; posture as in courtship, but no bobbing, no abdominal twitch- ing, no acceleration of retinal motions. Fighting & mirror display ab- sent.	Distal portion of black retina contrasts with green sur- roundings. Chelicerae elongated but not specially displayed.	Runs in short spurts. Jumps only in final pounce on prey. Palps pendent, pat ground during pauses. 1st legs take part in locomo- tion. $\varphi$ sags to side when watching display; muscular activity in eyes increase as in $\delta$ .
DENDRYPHANTINAE (cont.)		
Apparently no inter-male dis- play. No mirror display.	1st legs elongated, enlarged, darkened, fringed. Abdomen with lateral white stripe bounded by irides- cence.	Runs; jumps only on prey or to cross gaps. 1st legs unused in progress, held forward, they & palps tap ground; waved in air in pauses. $\varphi$ vibrates palps.
Same as courtship. Chases rivals away.	1st legs elongated, fringed. Abdomen with lateral white stripe bounded by darker.	"indifferent"; sometimes at- tacks $\delta$ .
Stage I: Similar to courtship, except chelicerae partly un- sheathed, & no distinct ab- dominal twisting. Stage II: Actual fighting, 1st legs raised vertically; chel- icerae wide open; palps ex- tended laterally. Clinching frequent, with occasional in- jury; no deaths seen.	Carapace with frontal tufts. 1st legs elongated; tibia fringed, black-spotted. Both sexes covered with iri- descent scales.	$\varphi$ irritable, prone to attack; later raises abdomen or turns it sideways.
Stage I: Like courtship except no rocking. Stage II: (Rare). Chelicerae un- sheathed, extended forward; 1st legs raised vertically; clinching; no injuries seen. Occasional mirror display.	1st legs elongated, enlarged, darkened, with white scales. Chelicerae elongate, enlarged darkened. Clypeus with white band. Abdomen with large, sub- distal, white-barred black spots.	Runs; jumps only to catch prey & cross gaps. 1st legs held forward, scarce- ly touch ground; these & palps wave in air & tap ground, during pauses. $\varphi$ once did weak mutual dis- play.
Distinct from courtship. 1st legs raised. Sparring, chasing & clinching without injury.	1st legs elongated, enlarged. White markings on dark palps & clypeus.	Runs; jumps occasionally when pursued, as well as to catch prey & cross gaps. Palpates ground & waves 1st legs less than <i>S. ocellatus</i> .
Distinct from courtship. 1st legs raised. Palps vibrated. Abdomen dragged to either side. Chasing and clinching without injury.	1st legs elongated, enlarged. Chelicerae elongated.	$\delta$ guard immature $\varphi$ until molt.

TABLE II. (cont.)  
Comparative Display Data in Seven Subfamilies of Salticid Spiders.

Name	Display References	Courtship Posture (Stage I)
DENDRYPHANTINAE (cont.)		
<i>Phidippus audax</i> (Hentz)	Peckham, '89, p. 45. ("Phidippus morsitans") Kaston, '36, p. 120; fig. (U.S.A.)	Carapace moderately high. 1st legs raised in 2 jerks, stretched obliquely out at $\angle$ of 45° to ground; later waved alternately Palps raised and lowered rapidly when close to ♀.
<i>Phidippus clarus</i> Keyserling	Kaston, '36, p. 118; fig. (U.S.A.)	Carapace moderately high. 1st legs stretched out, the femur obliquely up, other segments paralleling ground. Palps sometimes widely spread. Abdomen now & then moved from side to side.
<i>Phidippus purpuratus</i> Keyserling	Kaston, '36, p. 121; fig. (U.S.A.)	Carapace high. 1st legs stretched out, held higher than in <i>clarus</i> & <i>audax</i> ; waved. Palps held wide apart, parallel with each other, occasionally drummed on ground. Abdomen dropped.
<i>Phidippus whitmanii</i> Peckham	Peckham, '89, p. 44. ("Phidippus rufus") (U.S.A.)	Carapace high. 1st legs stretched forward & up, crossed at tips. Palps held wide apart, parallel with 2nd legs. Abdomen dropped. Sways during advance.
HYLLINAE		
<i>Evarcha falcata</i> Bl.	Bristowe, '29, p. 333. Bristowe, '41, p. 480. (England) Homann, '28, p. 249; fig. ("E. blanchardi") (Germany)	Some waving of 1st legs & twitching of abdomen, but tends to leap on ♀ with almost no display.
<i>Philaeus chrysops</i> Poda	Berland, '14, p. 116. Thomas, '29, p. 267. Bonnet, '33, p. 139; fig. (France)	Carapace high. 1st legs raised & waved up & down. Palps vibrated. Abdomen slightly elevated. Courtship sometimes almost absent. Leaps on ♀ suddenly.
<i>Phiale flammea</i> Crane	Crane, '49, p. 48. (Venezuela)	Carapace high. 1st legs raised at 45° $\angle$ to each other & ground. Palps vibrated irregularly. Abdomen lowered. Carapace rocked from side to side. Later, sinks low, 1st legs stretched to front.

TABLE II (cont.)  
Comparative Display Data in Seven Subfamilies of Salticid Spiders.

Threat Posture & Fighting	Principal Apparent Morphological Adaptations to Display	Locomotion & Remarks
	DENDRYPHANTINAE (cont.)	
like courtship, until opponents close; then chelicerae & fangs opened wide; some ♀ fighting.	1st legs elongated, enlarged, with white fringes and scales. Palps with white scales.	Both sexes savage, prone to eat mate.
as in <i>P. audax</i> .	1st legs elongated, enlarged, lightly fringed. Palps with white band.	
	1st legs elongated, enlarged, heavily fringed. Clypeus with white fringe.	
	1st legs elongated, enlarged, heavily fringed.	Hopping well developed.
	HYLLINAE (cont.)	
	1st legs elongated, enlarged, darkened; palps pale, white-haired.	
	1st legs elongated, darkened with light tufts & scales.	Excellent visual acuity; hops skilfully when pursued. Berland & Thomas saw frequent leg-waving when spiders were alone in field and in clean boxes; Bonnet saw waving only before ♀♀.
differs from courtship in quiet palps & absence of low stage. At close quarters, chelicerae open, 1st legs spread widely, often touch opponent's; no injuries. displays freely to mirror.	1st legs elongated, darkened. Clypeus & palps with buffy yellow bands against black.	Basically a runner although jumps readily over gaps; 1st legs little used in walking, habitually waved during pauses; true also of ♀♀ & young. ♀ raises 1st legs & vibrates palps during display.



TABLE II. (cont.)  
Comparative Display Data in Seven Subfamilies of Salticid Spiders.

Name	Display References	Courtship Posture (Stage I)
DENDRYPHANTINAE (cont.)		
<i>Phidippus audax</i> (Hentz)	Peckham, '89, p. 45. ("Phidippus morstians") Kaston, '36, p. 120; fig. (U.S.A.)	Carapace moderately high. 1st legs raised in 2 jerks, stretched obliquely out at $\angle$ of 45° to ground; later waved alternately. Palps raised and lowered rapidly when close to ♀.
<i>Phidippus clarus</i> Keyserling	Kaston, '36, p. 118; fig. (U.S.A.)	Carapace moderately high. 1st legs stretched out, the femur obliquely up, other segments paralleling ground. Palps sometimes widely spread. Abdomen now & then moved from side to side.
<i>Phidippus purpuratus</i> Keyserling	Kaston, '36, p. 121; fig. (U.S.A.)	Carapace high. 1st legs stretched out, held higher than in <i>clarus</i> & <i>audax</i> ; waved. Palps held wide apart, parallel with each other, occasionally drummed on ground. Abdomen dropped.
<i>Phidippus whitmanii</i> Peckham	Peckham, '89, p. 44. ("Phidippus rufus") (U.S.A.)	Carapace high. 1st legs stretched forward & up, crossed at tips. Palps held wide apart, parallel with 2nd legs. Abdomen dropped. Sways during advance.
HYLLINAE		
<i>Evarcha falcata</i> Bl.	Bristowe, '29, p. 333. Bristowe, '41, p. 480. (England) Homann, '28, p. 249; fig. ("E. blanchardi") (Germany)	Some waving of 1st legs & twitching of abdomen, but tends to leap on ♀ with almost no display.
<i>Philaeus chrysoptus</i> Poda	Berland, '14, p. 116. Thomas, '29, p. 267. Bonnet, '33, p. 139; fig. (France)	Carapace high. 1st legs raised & waved up & down. Palps vibrated. Abdomen slightly elevated. Courtship sometimes almost absent. Leaps on ♀ suddenly.
<i>Phiale flammea</i> Crane	Crane, '49, p. 48. (Venezuela)	Carapace high. 1st legs raised at 45° $\angle$ to each other & ground. Palps vibrated irregularly. Abdomen lowered. Carapace rocked from side to side. Later, sinks low, 1st legs stretched to front.

TABLE II (cont.)  
Comparative Display Data in Seven Subfamilies of Salticid Spiders.

Threat Posture & Fighting	Principal Apparent Morphological Adaptations to Display	Locomotion & Remarks
DENDRYPHANTINAE (cont.)		
Like courtship, until opponents close; then chelicerae & fangs opened wide; some ♀ fighting.	DENDRYPHANTINAE (cont.) 1st legs elongated, enlarged, with white fringes and scales. Palps with white scales.	Both sexes savage, prone to eat mate.
As in <i>P. audax</i> .	1st legs elongated, enlarged, lightly fringed. Palps with white band.	
	1st legs elongated, enlarged, heavily fringed. Clypeus with white fringe.	
	1st legs elongated, enlarged, heavily fringed.	Hopping well developed.
HYLLINAE (cont.)		
	1st legs elongated, enlarged, darkened; palps pale, white- haired.	
	1st legs elongated, darkened with light tufts & scales.	Excellent visual acuity; hops skillfully when pursued. Berland & Thomas saw fre- quent leg-waving when spiders were alone in field and in clean boxes; Bonnet saw waving only before ♀♀.
Differs from courtship in quiet palps & absence of low stage. At close quarters, chelicerae open, 1st legs spread widely, often touch opponent's; no in- juries. Displays freely to mirror.	1st legs elongated, darkened. Clypeus & palps with buffy yellow bands against black.	Basically a runner although jumps readily over gaps; 1st legs little used in walk- ing, habitually waved dur- ing pauses; true also of ♀♀ & young. ♀ raises 1st legs & vibrates palps during display.

TABLE II. (cont.)  
Comparative Display Data in Seven Subfamilies of Salticid Spiders.

Name	Display References	Courtship Posture (Stage I)
PLEXIPPINAE		
<i>Plexippus paykullii</i> Aud.	Crane (unpublished obs.); Pl. I, fig. 1, this paper. (Venezuela)	Carapace very high. 1st legs stretched forward, up & out at varying wide $\angle$ , higher with excitement; no waving. Palps quiet. Abdomen pendent. Prolonged posing in display posi- tion.
<i>Eustiromastix</i> sp.	Crane (unpublished obs.). (Venezuela)	Carapace high. 1st legs raised antero-laterally @ $\angle$ of $45^\circ$ to ground; sometimes jerked, & raised higher. Palps vibrate. Abdomen horizontal. Some posing in display position.
<i>Saitis barbipes</i> Sim.	Berland, '23, p. 206. Berland, '27, p. 15; fig. (France)	3rd legs wave.
<i>Corythalia xanthopa</i> Crane	Crane, '48.1, p. 35; figs. (also, see footnote, this paper, p. 183). (Venezuela)	Carapace moderately high. Palps hanging, motionless. Abdomen slightly below horizontal Stage Ia: Side-to-side rocking, all feet on ground. Stage Ib: 1st legs stretched for- ward, straight, parallel @ $\angle$ of $45^\circ$ to ground. No posing in display position.
<i>Corythalia chalcea</i> Crane	Crane, '48.1, p. 21; figs. (Venezuela)	Carapace moderately high. Palps hanging, motionless. Abdomen about horizontal. 3rd legs stretched out, waved up & down in unison above the hori- zontal. No posing in display position.
<i>Corythalia fulgipedia</i> Crane	Crane, '48.1, p. 28; figs. (Venezuela)	Carapace progressively lowered. Palps jerked in unison. Abdomen about horizontal. 1st, 2nd, & 3rd legs stretched far out to sides, the 3rd legs being slight- ly intermittently raised & vi- brated up & down in unison with body. No posing in display position.

TABLE II (cont.)

## Comparative Display Data in Seven Subfamilies of Salticid Spiders.

Threat Posture & Fighting	Principal Apparent Morphological Adaptations to Display	Locomotion & Remarks
PLEXIPPINAE (cont.)		
No inter-male displays seen. Mirror response not tested.	1st legs elongated, enlarged, darkened. White clypeus band against black.	Hops often even during ordinary progress. ♀ completely passive.
Scarcely developed; rarely, brief threat similar to early courtship but abdomen lowered & palps quiet. Occasional brief mirror display, sometimes ending in attack.	1st legs slightly longer, thicker, blacker than others.	Hops often even during ordinary progress. 1st legs take active part in walking. Palps quiet. ♀ extremely savage both before & after mating; often kills ♂.
Same as courtship.	3rd legs elongated, compressed, fringed.	Performs display motions even when alone in clean boxes.
Completely distinct from courtship. Carapace very high. Palps motionless, flexed, their yellow scales continuing band of clypeus. Abdomen pendent. 2nd, 3rd & 4th legs off ground, raised successively higher. Prolonged posing. No fighting. Displays freely to mirror.	Palps & clypeus with yellow bands. 2nd, 3rd & 4th legs fringed, compressed, with iridescent patches; 3rd & 4th legs elongated.	Ordinary progress consists largely of hopping. 1st legs take active part in walking. Palps quiet. ♀ not aggressive; when watching display, sits high with braced legs until receptive, then crouches.
Distinct from courtship, although same legs used. Differs in waving 3rd legs below horizontal, often in an arch; prolonged posing. Palps flexed & stiff. No fighting. Displays freely to mirror.	1st, 2nd & 3rd legs fringed, compressed, with iridescent patches; 3rd legs elongated.	Locomotion as in <i>xanthopa</i> . ♀ sometimes aggressive, may do some form of reciprocal display.
Distinct from courtship, although similar in very first phase, & same legs used throughout. Whereas in courtship carapace sinks lower, in threat it rises higher. At peak, all legs are drawn close in & stretch up, 2nd tarsi leave ground & 3rd legs are raised slightly; body rocks from side to side; posing with 3rd legs arched frequent. Palps jerked at beginning, later flexed & stiff. No fighting. Displays freely to mirror.	1st, 2nd & 3rd legs fringed, compressed, with iridescent patches strongly developed; 3rd legs elongated. Palps with white patches.	Locomotion as in <i>xanthopa</i> . ♀ more aggressive than most salticids, although not seen to injure ♂; when stimulated performs rough, reciprocal display.



TABLE II. (cont.)

## Comparative Display Data in Seven Subfamilies of Salticid Spiders.

Name	Display References	Courtship Posture (Stage 1)
PLEXIPPINAE		
<i>Plexippus paykullii</i> Aud.	Crane (unpublished obs.); Pl. I, fig. 1, this paper. (Venezuela)	Carapace very high. 1st legs stretched forward, up & out at varying wide $\angle$ , higher with excitement; no waving. Palps quiet. Abdomen pendent. Prolonged posing in display position.
<i>Eustiromastix</i> sp.	Crane (unpublished obs.). (Venezuela)	Carapace high. 1st legs raised antero-laterally @ $\angle$ of 45° to ground; sometimes jerked, & raised higher. Palps vibrate. Abdomen horizontal. Some posing in display position.
<i>Saitis barbipes</i> Sim.	Berland, '23, p. 206. Berland, '27, p. 15; fig. (France)	3rd legs wave.
<i>Corythalia xanthopa</i> Crane	Crane, '48.1, p. 35; figs. (also, see footnote, this paper, p. 183). (Venezuela)	Carapace moderately high. Palps hanging, motionless. Abdomen slightly below horizontal. Stage Ia: Side-to-side rocking, all feet on ground. Stage Ib: 1st legs stretched forward, straight, parallel @ $\angle$ of 45° to ground. No posing in display position.
<i>Corythalia chalcea</i> Crane	Crane, '48.1, p. 21; figs. (Venezuela)	Carapace moderately high. Palps hanging, motionless. Abdomen about horizontal. 3rd legs stretched out, waved up & down in unison above the horizontal. No posing in display position.
<i>Corythalia fulgipedia</i> Crane	Crane, '48.1, p. 28; figs. (Venezuela)	Carapace progressively lowered. Palps jerked in unison. Abdomen about horizontal. 1st, 2nd, & 3rd legs stretched far out to sides, the 3rd legs being slightly intermittently raised & vibrated up & down in unison with body. No posing in display position.

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TABLE II. (cont.)

Comparative Display Data in Seven Subfamilies of Salticid Spiders.

Name	Display References	Courtship Posture (Stage I)
<b>MAGONINAE</b>		
<i>Maevia vittata</i> (Hentz)	Peckham, '89, p. 54; fig. ("Astia vittata") (Wisconsin, U.S.A.) Painter, '13, p. 625. (Connecticut, U.S.A.)	Displays of the 2 forms differ. <i>Gray form</i> : Carapace high; 1st leg raised, waved, palps stretched sideways; abdomen down; later whole body low, 1st & 2nd leg forward, tips touching; palp forward. (Peckham, Wisc.). Low stage precedes high stage (Painter, Conn.). <i>Black, tufted form</i> : Carapace very high; 1st legs raised & waved, held high in pose. (Peckham & Painter).
<i>Mago denticelis</i> Crane	Crane, '49, p. 48; fig. (Venezuela)	Carapace slightly raised. 1st legs stretched sideways & slightly forward; waved alternately up and down or held in pose. 2nd tarsi touch ground, far out & slightly forward. Abdomen sometimes vibrated.
<i>Ballus depressus</i> Walk.	Bristowe, '31, p. 1409; fig. Bristowe, '41, p. 484; fig. (England)	All legs on ground, drawn in, sway; body from side to side.

under consideration in this paper. Text-fig. 1 and Table III will give some idea of the variety of display motions throughout the family. All displays unite at least several of the listed movements, and many involve all of the major headings except that of retinal motion, which so far appears to operate as part of the signal mechanism only in *Lyssomanes*.

No less varied are the forms of "ornamentation" in the family; these occur too often on displayed appendages to be explained only by chance mutations, metabolic processes, other behavior patterns, etc. They include many specializations of size, shape, hair concentration, scalation and pigmentation, several forms usually occurring in a single spider. For example, the first legs, which always enter at least into Stage II courtships, are often elongated, thickened and much darker than the others; in addition, the palps, which frequently vibrate during display, in many species show patches of shiny white scales. Again, in *Corythalia xanthopa*, the fourth legs, elevated only in threat display, are prominently fringed; in the related *C. chalcea*, in which they never leave the ground, fringes are absent. Many other examples occur in the literature, of which the Peckham's original series are among the best (1889, 1890). The striking

point is that any appendage specially exhibited in epigamic display usually shows some differentiation which is to human eyes conspicuous.

However, two other obvious points must be kept in mind. First, not all parts active in display are so ornamented; an example is the brown abdomen of *Semorina*, relieved only with small, pale inconstant spots. Second, not all parts conspicuously ornamented (again, to human eyes) play any demonstrable part whatsoever in display. Examples are the bright scarlet abdomen of *Phiale flammea* and the striking carapace bands of various *Phiale* and *Corythalia*.

#### B. HISTORICAL REVIEW.

The history of the study of salticid display reflects the changing ideas of evolutionists. The Peckhams pioneered both in the recording and explanation of epigamic display and of the apparently correlated ornamentation (1889, 1890). According to them, the phenomena were due to direct Darwinian sexual selection; the females, consciously or unconsciously, were affected by the performances, colors and beauty of the males, selecting the most handsome or at least the most striking. Male battles were initiated both for simple possession of a mate and as sham contests for the females' edification. The Peck-

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Comparative Display Data in Seven Subfamilies of Salticid Spiders.

Threat Posture & Fighting	Principal Apparent Morphological Adaptations to Display	Locomotion & Remarks
MAGONINAE (cont.)		
Wave 1st legs at each other but "quarrels . . . harmless" (Peckham). Displays to mirror.	Tufted form is black anteriorly, has cephalic tufts.	Peckham & Painter disagree on selection value of dimorphism. ♀♀ irritable; fight each other.
Stage I: Similar to courtship. Stage II: 1st legs waved higher, almost meet overhead; when lowered, 1st & 2nd tarsi rub together. Rarely, chelicerae opened and knocked repeatedly against opponent's; no injuries. Displays to mirror.	1st & 2nd legs enlarged, blackened.	5 other Venezuelan magoninids use all legs actively in walking, hop freely during ordinary locomotion. All include rubbing of 1st & 2nd tarsi in display. ♀ usually extends 1st legs during courtship.
	1st legs enlarged, partly blackened.	♀ vibrates light palps.

hams disagreed strongly with Wallace (1878, 1889), who attributed both performance and ornamentation to the greater vigor of the male, especially during the breeding season. Montgomery (1910) in general held Wallace's views; furthermore, he thought the displays originated in self-defense movements, which were combined with external evidence of physiological excitement. Berland (1923, 1927) attributed the behavior altogether to the exceptional physiological activity of the breeding season and its correlated excitement.

Bristowe (1941 *et ante*) has held the view that courtship in spiders in general has two fairly distinct functions, namely recognition and stimulation. Recognition he holds to be particularly important, since in spiders the female is not only carnivorous but often much larger than the male. Inter-male display and fighting he attributes essentially to mistaken identity: "It, would appear from what has been said above that the battles, which are preceded by normal courtship reactions, are the outcome of frustrated instinct, and are modifications of courting procedure brought about as a result of the different reception experienced at the hands of another male to that of a female." (1929, p. 352). He believes that display arose from the groping and chemotaxing motions of primitive spiders,

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Savory agrees with Bristowe, except that he considers the division between "recognition"—for which he prefers the term "realization"—and stimulation invalid. He gives the following summary of his views on spider courtship: "If we may venture to summarize in a few words the results of so complex an activity as courtship, we may say that courtship is a chain of related instinctive actions, in which the reproductive urge suppresses the normal habits of self-protection and self-nourishment, and is accompanied internally by the physiological changes necessary to make the subsequent union possible." (1928, p. 221).

Gerhardt, who has recorded numerous spider pairings, has been most interested in copulation methods, showing that the various positions assumed by the male shed light on phylogeny. In salticids the copulation position is invariably dorsal and similar throughout the family. He has made few observations on the courtship phases of reproduction.

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There has been as great discrepancy in

views regarding the senses involved in salticid display, as in those concerning its origin and functions. The Peckhams (1894) concluded that sight was essential, both for recognition and as stimulus for display; Petrunkevitch (1910) agreed. Montgomery (1910) apparently saw a salticid court after merely touching a female. Berland (1914, 1923, 1927) thought smell must be involved in locating the female though sight was needed to stimulate courtship. Bristowe and Locket (1926) and Bristowe (1929, 1941) thought that both sight and chemotaxis (referred to as "smell" in the earlier papers) were involved. Savory (1928, p. 215), after speaking of inter-male courtships, of the courting of immature individuals and those of other species, sometimes through glass, says in regard to spider courtship in general: "It is clear, therefore, that the stimulus which initiates the male's performance is vague, rather than definite and specific. It may act upon the sense of sight, of smell, or of touch, but the appearance or the scent of the female does not seem to be readily distinguishable from that of the male."

The most recent group of observers have concluded, along with the Peckhams and Petrunkevitch, that sight alone among salticids is the only adequate and necessary stimulus for salticid display; these workers include Homann (1928), Bonnet (1933), Heil (1936) and Kaston (1936). The latter gives a detailed review of previous work, followed by a report and discussion of observations and experiments of his own; these were conducted on thomisids, pisaurids, lycosids and salticids. His salticid examples are distributed among four Connecticut species of the genus *Phidippus* (Dendryphantinæ). His conclusions, which include his results with that genus, are as follows (p. 152): "On the basis of a large number of observations and experiments with the males of 19 species from 4 families of vagabond spiders, it is pointed out that the senses involved in courtship may vary with the species. There is no evidence that a sense of smell is used in sex recognition by any spiders. At least this sense plays no part in initiating courtship activity in the male. There is no evidence that Attid males can 'recognize' the females by any sense other than sight. At any rate, it appears that the visual stimulus is the only one that suffices to incite courship in this family."

### C. BASES FOR DISAGREEMENTS.

The disagreements and uncertainties among previous investigators appear to have been due principally to the following causes:

1. Although all observers have realized that display stimuli among the various families differed, and were roughly dependent on the development of vision, yet it does not seem to have been clear that there are large differences within the family, at least in salticids, in the relative importance of the

senses. On these sensory differences depend many differences in behavior.

2. Systematic attention does not seem to have been paid to the fluctuating physiological states of individual spiders.

3. The early experiments, as usual throughout the history of biological science, were not properly organized to ensure the testing of only one stimulus or characteristic at a time.

4. In later work, the compound natures of such concepts as "visual stimuli" do not seem to have been taken fully into account.

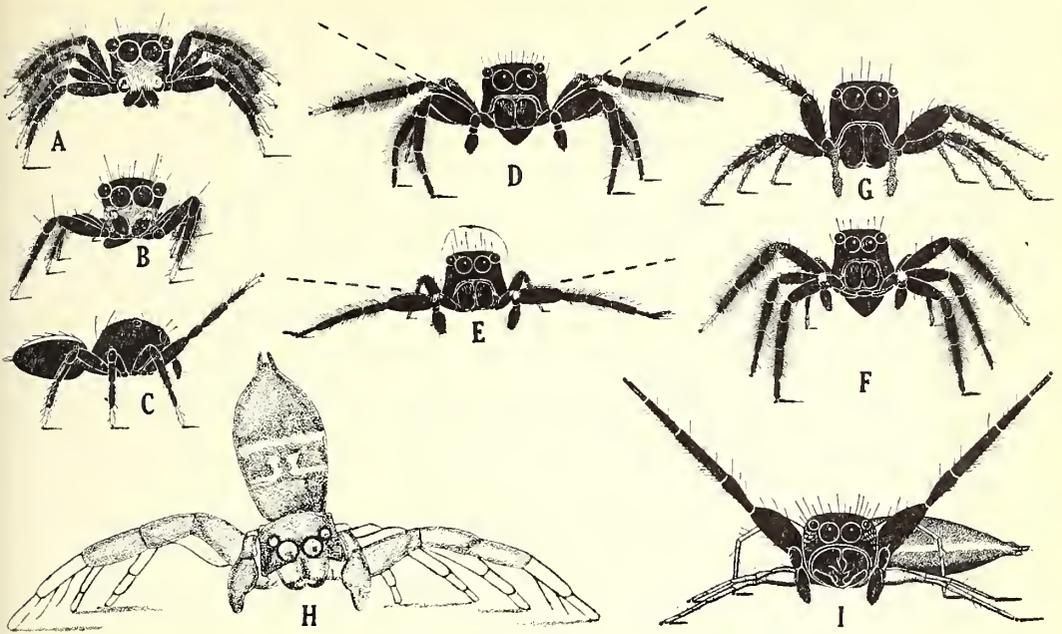
5. The recent concepts of innate releasing and directive mechanisms, as developed by Lorenz, Tinbergen, and their co-workers, do not appear to have been applied to spiders.

6. Certain motions involving sensory perception, such as waving of the first legs, have perhaps occasionally been mistaken for epigamic display.

### TABLE III.

#### Principal Motions Reported in Salticid Display Literature.

1. General manoeuvres, involving spider as a whole.
  - a. Tacking.
  - b. Direct approach.
  - c. Leaping.
  - d. Sidling.
  - e. Semi-circling and circling.
  - f. Posing.
  - g. Crawling.
  - h. Elevation of carapace.
  - i. Rocking motions.
  - j. Bouncing motions.
2. Retinal motions within antero-median eyes.
3. Palp motions.
  - a. Vibrations, jerks, rotations; synchronized or alternate.
  - b. Flexion or extension in special attitudes.
  - c. Palpation of female or opponent.
4. Chelicerae motions.
  - a. Lateral extension of basal segment.
  - b. Extension of distal segment.
  - c. Clinching.
  - d. Biting.
5. First leg motions.
  - a. Elevation and extension forward, up or out, and to any intermediate degree.
  - b. Vibrations, waves, jerks, rotations; synchronized or alternate.
6. Second leg motions.
  - a. Extension forward, to rub second tarsus against first.
  - b. Elevation to form portion of fan-type display.
7. Third and fourth leg motions: Elevation and extension to various degrees, sometimes forming part of fan-type display involving all legs.
8. Abdominal motions.
  - a. Depression, when carapace is raised.
  - b. Twitching or vibration; vertical or horizontal.
  - c. Twisting or bending to side.
  - d. Elevation.



TEXT-FIG. 1. Examples of display motions in salticid spiders. A-F, Subfamily Plexippinae; G, Magoninae; H, Synagelinae; I, Dendryphantinae. A, *Corythalia xanthopa*, threat; B, C, same, courtship; D, *C. chalcea*, threat (dotted lines indicate peak position of legs during courtship); E, *C. fulgipedia*, threat; F, same, courtship; G, *Mago dentichelis*, courtship; H, *Gertschia noxiosa*, courtship (from Connecticut, U. S. A.; similar to that of the Venezuelan genus *Semorina*); I, *Ashtabula furcillata*, courtship. H, after Kaston, 1948; others reprinted from Parts I and III.

7. The great range of development of threat display within this single family does not appear to have been recognized, since the days of the Peckhams' scattered remarks on the subject.

#### D. PROGNOSIS OF EVOLUTIONARY PATTERN.

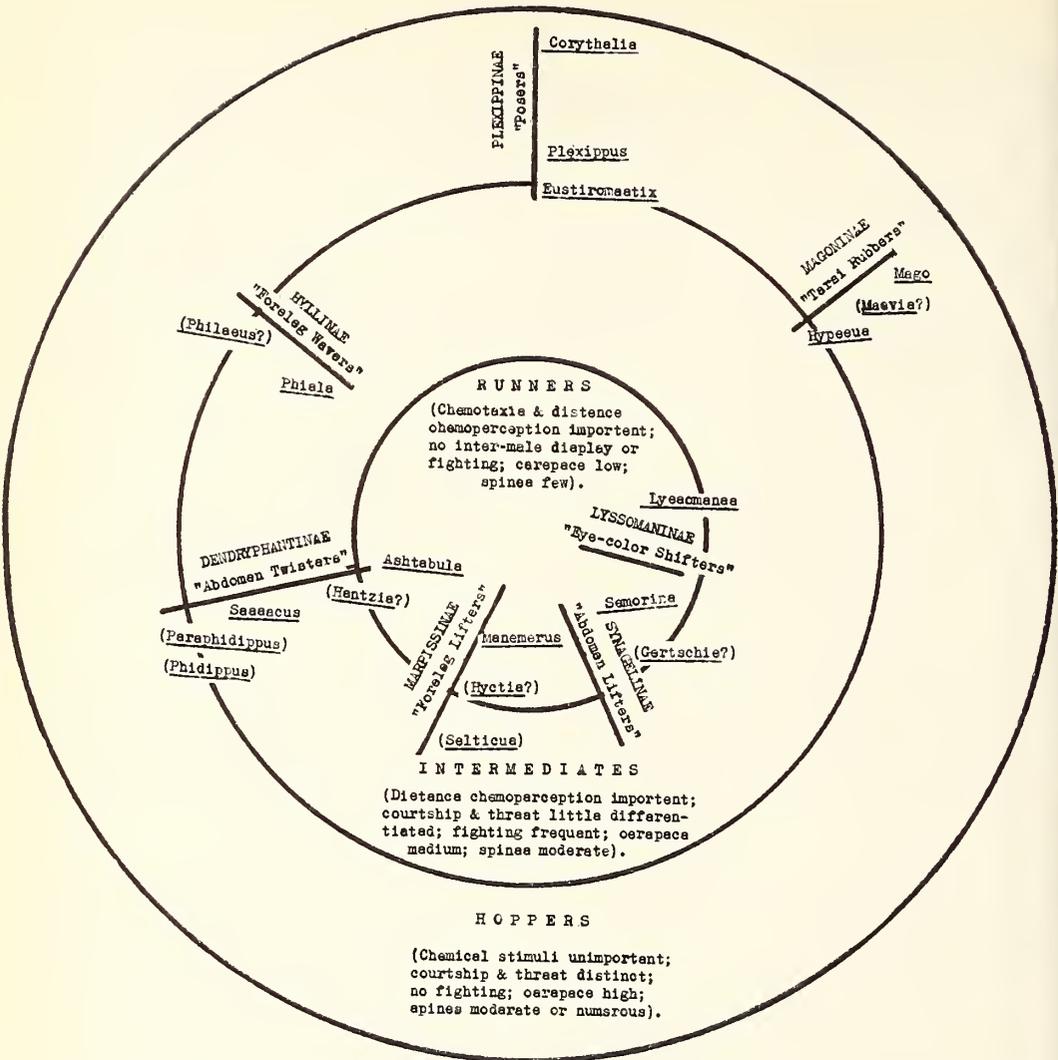
In order to bring into perspective the material in the following pages, it is necessary to anticipate some of the conclusions reached not only in this paper but in future sections of the series on post-embryology and general evolutionary trends.

1. *Correlation of Jumping with Sensory Development.* The genera studied at Rancho Grande showed great variety in the frequency of jumping in the course of normal, unexcited progress. Taking into consideration their behavior in other fields, notably display, it seems certain that this variety is based on differences in the dependence on various senses. In some forms more dependence is placed on chemical senses and less on vision. Evidence is presented later showing that these chemical senses include both chemotaxis and a distance chemoperception appearing very similar in its operation to the vertebrate sense of smell. In other forms, vision seems both more acute and more farsighted, while the chemical senses are relegated to relative unimportance. Experiments have not yet been performed at Rancho Grande on variations in visual acuity, al-

though several experimenters, notably Homann (1928) and Heil (1936), present modern data on visual perceptions in species of the subfamilies Marpissinae and Hyllinae.

A few minutes' observation of unconfined salticids of selected genera will, I think, give convincing empiric support of the hypothesis. For example, in *Ashtabula* the progress is "a scurrying run, the first legs held flat and low, straight in front of the body; both they and the palps palpate the surface almost constantly during progress. During pauses the first legs are usually elevated, and they and the palps jerked rapidly up and down." (Part III, 1949, p. 41). These "runners," as salticids of similar habits will be called, never resort to hopping or jumping except in crossing gaps in the surface and in the final stages of prey capture. In contrast to other kinds, they are more easily observed in glass-covered dishes than when permitted to run freely on a table (cf. Part II, p. 143). Their comparatively poor vision and their dependence on chemotaxis, or near-chemotaxis, make their exploration of a new environment a highly "restless" and "nervous"-appearing proceeding, as they race to and fro.

In strong contrast is the behavior of an almost completely vision-dependent salticid, such as a *Corythalia*. When allowed to drop on an unfamiliar surface, he tends to pivot almost where he is placed while he looks all around; finally he moves off, without haste or



TEXT-FIG. 2. Tentative basis for a hypothetical phylogeny in salticids. See text (pp. 205 and 175) for explanation; cf. Table II. Non-Venezuelan genera are enclosed in parentheses; those not observed alive by the author are followed by a question mark. The characteristics ("foreleg lifters" etc.) under each subfamily indicate the most generally present display distinction; it usually is not found in every genus, and occurs sporadically in other subfamilies as well; cf. Lorenz (1941) on the phylogeny of display in ducks.

visible agitation, in a series of short runs and hops, interspersed with pauses for further observation. His palps, usually motionless, are held quite clear of the ground; his first legs are used as much in walking as all the others. To the human observer, in an anthropomorphic moment, the contrast in "poise" between a chemotaxis-dependent and a strongly vision-dependent salticid is ludicrous. When startled or pursued he hops almost altogether. In the future, salticids progressing in the *Corythalia* fashion will be called "hoppers."

*Phiale* is a good example of an intermediate stage, in which hopping is moderate and eyesight obviously keen. Considerable dependence appears to be placed on distance

chemoperception, however, although not on chemotaxis. The specially sensitive first legs and palps are often carried up, in normal progress, and during the pauses they are waved up and down, without touching the ground; it seems certain that they are receiving sense impressions which, by definition, are not chemotactic.

Characteristics of locomotion, where known, are included in Table II.

2. *Preliminary View of Evolutionary Pattern.* It is generally agreed that the salticids are more specialized than the lycosids, particularly in regard to the development of vision. In this characteristic, indeed, they lead all other families. It seems likely, therefore, that the salticids in which vision is

best developed are those farthest from the primitive stock. This hypothesis is supported by evidence from a number of other fields, although the pattern of specialization, as shown even in these few present-day genera, is far from a simple "family tree." As in all other groups, salticids having many primitive characteristics may be extremely specialized in a few directions.

Briefly summarized, the hypothetical pattern may be stated as follows:

The evidence in regard to salticid evolution—based on post-embryology, external morphology, ornamentation, locomotion, general habits and epigamic display—all points to a radiative type of development. Many forms with primitive characteristics still survive. Each subfamily so far studied in any detail includes genera ranging through at least two stages (Text-fig. 2).

The first, most primitive stage includes species with low carapaces (Text-fig. 3), low visual acuity, high dependence on chemotactic stimuli, locomotion of the running type, courtship simple and threat display absent.

The second stage is characterized by intermediate carapaces, visual acuity, hopping proficiency and courtship development; by depending on distance chemoperception rather than on chemotaxis; and, especially, by the presence of threat display which is based on the mistaking of males for females, and is undifferentiated from courtship except that it often ends in true fighting.

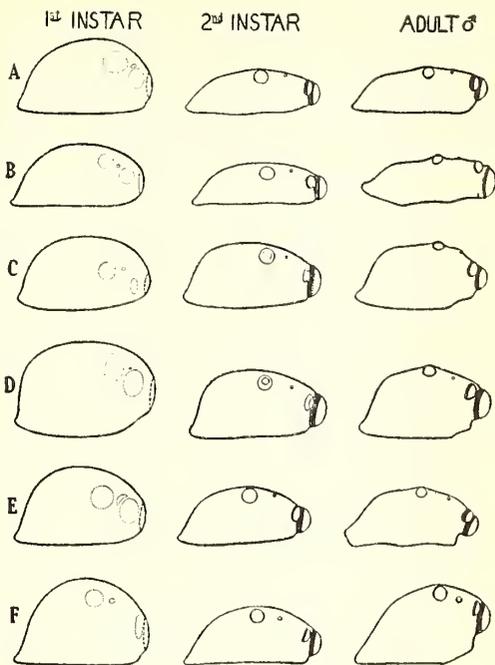
The third and most specialized stage is represented by species with high carapaces, extreme visual acuity, chemical perceptions of minimized importance, locomotion consisting principally of hops, courtship often complex but sometimes secondarily simplified, and threat display separate from courtship and altogether ritualistic.

I realize keenly the extremely small number of forms investigated at Rancho Grande in relation to the large size of the family. However, published records, in so far as they can be analyzed from modern points-of-view, and my own sporadic observations in other localities, appear to lend support to the hypothesis. It seems that the basic framework will prove to have validity.

## V. FACTORS IN DISPLAY.

The releasing and directive mechanisms of salticid display have proved much more varied and their interrelationships more complex than was expected. Although all epigamic display is fundamentally visual in this family, chemoperception is important in certain phases; simple adulthood is not the only physiological essential for performing or responding to display; vision itself must be divided into perceptions of motion, distance, size, form, intensity, pattern and color for an approach to understanding display stimuli.

In the following pages an attempt is made to isolate and evaluate these factors, giving



TEXT-FIG. 3. Change of carapace proportions with growth in representative genera of salticids. Left column, 1st instar; center column, 2nd instar; right column, adult male. **A**, *Menemerus bivittatus*; **B**, *Semorina megachelyne*; **C**, *Sassacus flavicinctus*; **D**, *Mago denticheles*; **E**, *Phiale flammea*; **F**, *Corythalia chalcona*.

in each case a summary of the observations and experimental results upon which the conclusions are based. Because of space limitations, it is impossible to publish full details of field and laboratory data; however, descriptions of especially illustrative observations and experiments are quoted now and then directly from the original notes. Laboratory procedures have already been described (Part II, 1948.2). Reference to Text-fig. 6 will help clarify the relationships of display elements during the course of this analysis; in the subsequent section on innate releasing mechanisms, beginning on p. 199, these factors are viewed as closely integrated, mutually dependent series of stimuli activating, controlling and directing both courtship and threat.

### A. FACTORS OF THE INTERNAL RELEASING MECHANISM.

1. *Age*. In general, no sexual interest appears between the sexes until both are adult. Exceptions occur when a mature male in a particularly responsive state briefly courts a pre-adult female of similar appearance to the adult; such displays never pass beyond Stage I. A number of workers have reported behavior of this kind and I have seen it in various genera, always of the hopper type, especially in *Corythalia*. Very rarely juvenile individuals perform abortive displays; examples will be given below.

The Peckhams (1889, p. 50) recorded the interesting case of *Philaeus militaris* (= *Paraphidippus marginatus*) in which the adult males actually kept guard over individual preadult females until they molted. The nearest approach to this seen at Rancho Grande was the behavior of a single male *C. fulgipedia*. He was captured clinging to the outside of a cocoon, within which a female was molting to the adult instar. He did not even wait for her to dry and harden, but raced through the briefest display as she emerged, and mated. She was still soft and weak, and gave no resistance or apparent response at all. The eggs appeared on schedule, some two months later, and were fertile. This was an exception to the general behavior pattern of the genus.

Similarly, mature males rarely display to juvenile males except in reinforced experimental situations.

During experiments on display sign stimuli with *C. xanthopa* and *C. chalcea*, several cases of display behavior were noted in immature individuals of both sexes. They were exceptions, however, to the rule. Once a preadult (6th instar) male *chalcea* leapt repeatedly on a dead, mounted adult male, when the latter was appropriately moved. He then gave a medium complete threat display, through the fan stage with stiffened palps, following this with a Stage I courtship, and ending with a clumsy attempt to mate, approaching atypically from the rear. When a normal adult male was presented to him, without a rest period, the young one at once gave a complete threat display; when the adult responded in kind, the other retreated. When a preadult female was presented to the young one, she attacked him, whereupon he retreated, turned and courted briefly, Stage I. This sequence with the female happened four times, she charging him each time.

A single case of display in a 5th (pre-preadult) instar *chalcea* was recorded. This individual did a moderately complete threat display (through the arch phase) to two different adult males, punctuating them with retreats. One of the adults responded with threat. There was no courting or other reaction to females.

Preadult females of both *xanthopa* and *chalcea* gave incipient threat displays on a number of occasions, to adult displaying males, alternating the rudimentary fan-pose with the usual abortive attacks and retreats. In each case, it was clearly rudimentary threat, not courtship. These motions were never made in the presence of potential prey or predators, even of similar size.

Display is usually delayed, however, even after the final molt has taken place. *Corythalia* males normally do not display to each other or to a female until at least two days thereafter. One exceptional *xanthopa* did his first threat displays on the third and sixth days, but did not court at all until the seventh and then only a rudimentary Stage I; full threat and courtship were not attained until

the tenth day. Although freshly molted females are both attractive and receptive, they normally do not emerge from their cocoons for two or three days. Judging by the responses of males, female *xanthopa* do not attain their maximum attractiveness until about the fifth day.

The age at which males and females lose interest in display varies with the species. After two months in the adult stage, unmated *C. fulgipedia* males usually cease to initiate display in threat or courtship, and do not respond to threats of other males. However, one example, reared from the egg, three months after the final molt briefly courted an aged female who had completed molting more than six months before. Unmated males of *C. xanthopa* are in their adult prime less than a month; for several weeks thereafter they may respond to stimulus situations which are both complete and reinforced, but never to the extent of carrying a courtship beyond Stage I. An exception was a 32-day-adult male which mated with a 33-day-adult female, after a courtship of 13 minutes; the usual courting period for the species is three to five minutes. Their healthy brood was reared through several instars.

Unmated females of *fulgipedia* remain attractive to males and will accept them at least four months after the final molt, even though they have, at the usual time (about two months after molting), started laying the customary successive clutches of eggs. Females of *xanthopa* start losing both their responsiveness to display and their attractiveness after about three weeks, although the eggs in this species are not laid until about the fortieth day after molting.

No Rancho Grande female, in spite of repeated attempts on a number of well-distributed genera, was ever found to mate more than once, when more than a few hours had intervened; usually, also, she lost most of her attractiveness. However, there are a number of recorded northern observations of repeated salticid matings by both males and females (e.g., Peckham, 1889, p. 38). Rancho Grande males, as in the north, copulated readily at least several times in *Corythalia*, *Phiale* and *Menemerus*; other genera were not investigated, nor were such aspects as the duration of fertility and the effect of copulation on subsequent display initiation and duration.

*2. Fluctuating Epigamic Rhythm.* Not only is the period of display and acceptance at Rancho Grande limited to moderately young adults of both sexes and to unmated females, but there is also a definite fluctuation in both sexes from day to day in sexual aggressiveness and receptivity. Such fluctuations are of course well known, and are in fact the rule in higher vertebrates. Hints of it have also been detected in fiddler crabs (Crane, 1941, p. 153 ff.), but it does not seem to have been much investigated in invertebrates.

In all salticids under special observation at Rancho Grande, it was noted repeatedly that young, vigorous adults of either sex varied daily in behavior. Those which were particularly lively in display or responsiveness on one day might, on the next, be altogether unresponsive to sexual situations, although their general health and activity seemed unimpaired. These individuals had not been allowed to mate on the preceding day, nor had there been a break in the feeding routine, or noticeable changes in other conditions such as moisture or general weather. A day or more later, they might recover all their previous epigamic energy.

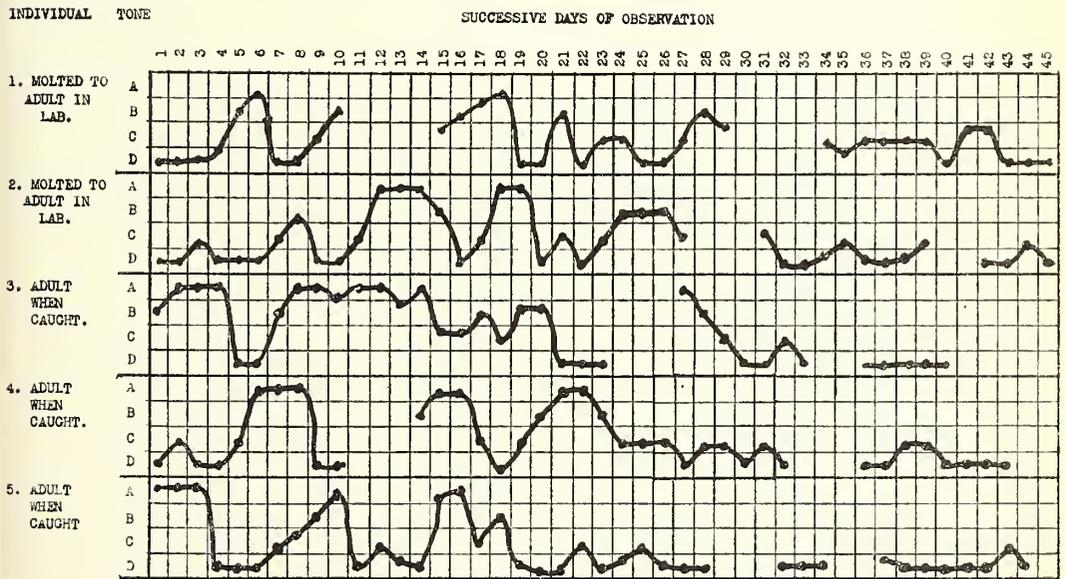
This phenomenon was specially investigated in more than twenty adult *Corythalia xanthopa* males of varying ages. About half of them passed the final molt in the laboratory, so that their exact length of adulthood was known. None of this group was allowed to mate. All were kept under conditions as similar as possible, although all twenty were not observed simultaneously, but in small, overlapping groups. All were tested for various periods up to 43 days with stimuli of such proven efficacy that they came to be termed "standard stimuli" for the species. They consisted of a particular, normal male, dried and mounted in semi-threat stance (see p. 169), a mirror image, young and older adult females, and live normal males.

In the case of low-threshold males, various unnatural or incomplete stimuli were also presented. The mounted specimens and mirror were each presented in a series of up to a dozen successive jerking approaches to the tested male, after his attention had been

caught by the stimulus. The quickness of response (if any) was taken into account when determining his sexual tone, because, obviously, a stimulus which drew a response only on repetition was reinforced by summation. Again, the "startle" element of repeated presentations of the same stimulus in quick succession, rather than continuously, was important in drawing responses from low-tone individuals; hence all hand-controlled stimuli, for the sake of uniformity, were presented in this fashion: the mount or mirror was lifted high in the air for an instant after each approach to the spider. The working of the law of heterogeneous summation (Tinbergen, 1948, p. 35) was minimized by always working with a group in every test period; each individual could thus be tested with one stimulus followed by a rest, yet with a minimum wastage of experimental time. The same general rules were followed in all salticid testing (see also, Part II, p. 143).

In the course of the work, the fluctuating internal drive appeared divisible into four major degrees of sexual tone, with the following characteristics:

A-Tone. Internal drive strong, that is, male with low epigamic threshold. Only minimal stimulus needed for maximal response, which follows promptly and appropriately to all normal stimuli and to many deficient stimulus situations as well. Display follows through swiftly into Stage II in courting receptive young females; old females courted with considerable persistence. Responses continued during a prolonged test-period. No "vacuum responses," however, have ever



TEXT-FIG. 4. Daily fluctuation of epigamic threshold in five male *Corythalia xanthopa*. Spiders of A tone are most responsive to epigamic stimuli, those of D tone unresponsive. The tone was determined by the individual's response to three standard stimuli: his own mirror image, a particular dead male mounted in a semi-threat position, and a young, living female. See p. 177. Blanks in the graphs indicate days when observations were not made.

been observed, in this or any other salticid; that is, no display is performed without some external stimulation.

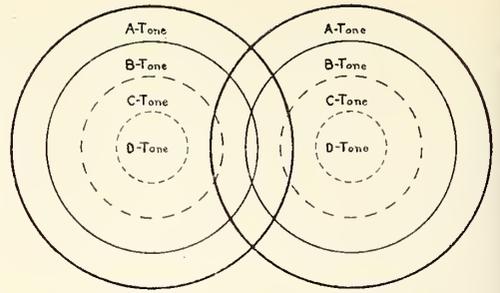
**B-Tone.** Internal drive moderate, the epigamic threshold being moderately low. Maximal stimulus needed for normal response; either threat or courtship or both may be elicited, but only through summation, though display is eventually complete. Courtship of a young female may be energetically performed throughout its entire course, but older females attract little or no attention. All courtships are likely to die out in the middle, when the male, instead of following up the female during her normal, periodic retreats, simply circles around her previous resting place, palpating the ground in the manner of less specialized, runner-type salticids. Again, the male sometimes gives atypical responses, leaping briefly at the threat stimulus before performing threat display, or even courting it; equally briefly and rarely, he may threaten a female. He may or may not respond to one or two slightly incomplete stimulus situations. Invariably ceases to respond in a test period after relatively few stimuli have been presented.

**C-Tone.** Internal drive weak, the epigamic threshold being moderately high. Maximal stimulus needed for minimal response. Male responds either to normal threat or normal courtship stimuli, but not both; summative threat stimuli more often draw a response even than young females. No courtship is ever followed through to completion, and the palpating of the female's resting place is pronounced, the male spending much of his attention on one of her former positions, even though she is at the moment sitting in full view, and facing him, only an inch away. Leaping at threat stimuli is frequent and, unlike the case in B-tone spiders, is rarely followed by the normal response. Incomplete stimulus situations attract no attention, except, sometimes, brief notice followed by escape behavior. The attention of C-tone spiders is difficult to attract and hold, they often move about in "restless" fashion, and always stop responding quickly, often after only one or two stimuli have been presented.

**D-Tone.** Internal drive imperceptible, the epigamic threshold being very high. Male does not respond with display to stimuli of any kind, although other daily activities, such as feeding and moving about, are unimpaired.

The above four states naturally merge into one another, and in recording the daily changes of tone, it was found convenient to recognize plus and minus degrees. For example, a spider which did not display, but nevertheless showed enough interest to follow a jerked mount or a young female with with his eyes (through the twisting of his carapace), was counted D-plus.

Typical examples of daily fluctuations are shown in Text-fig. 4. Text-fig. 5 diagrams the degree of influence on each other of spiders of various tones.



**TEXT-FIG. 5.** Diagram showing mutual influence of salticids of various epigamic tones. For example, even an A-tone spider never draws a display response from one of D tone, although he himself displays readily toward individuals of any tone and either sex; B- or C-tone spiders may respond to the displays of an individual of higher tone, but rarely initiate it themselves. The boundaries between tones should not be regarded as hard and fast lines. See pp. 176-179. In salticids, courtships are rarely completed in the field, or threat displays energetically prosecuted, except by spiders of A tone, that is, of the lowest epigamic threshold. This is in contrast to the condition in some vertebrates, where the behavior of a correspondingly low-threshold individual is not regarded as typical (cf. Part II, 1948.2, p. 143, and Tinbergen, 1948, p. 39).

The one result that emerged clearly from the records was the complete lack of a definite rhythm in *xanthopa*. In general, however, individuals in their prime remained from one to four days in A-tone, then dropped within 24 hours to C or D; they remained at these high-threshold levels from one to three days, and then climbed back to B-plus or A in about 48 hours. Some spiders attained A-tone only once in the course of their four weeks of prime, the rest of their top display levels being B's, with prolonged C and D stretches between. A rarely active male, caught adult, had three A-periods of three, four and one day each, during a period of two weeks, with only one day of D intervening; the subsequent portion of his active display prime tapered off in irregularly alternating B's and C's of one to three days each.

Just-molted males start at D, paying no attention whatever to epigamic stimuli during at least the first two days; they then climb, gradually or abruptly, to their first B or A period, which may come at any time from the third day to the tenth. After about the 28th day, display responses taper off, fluctuating gently between C's and D's. Often they flow along for four or five days on about a C-minus level, responding, for example, one day to a single, summative threat stimulus situation, and the next with a series of leaps only to the same stimulus, but with the addition of a few abortive rocks to a young female.

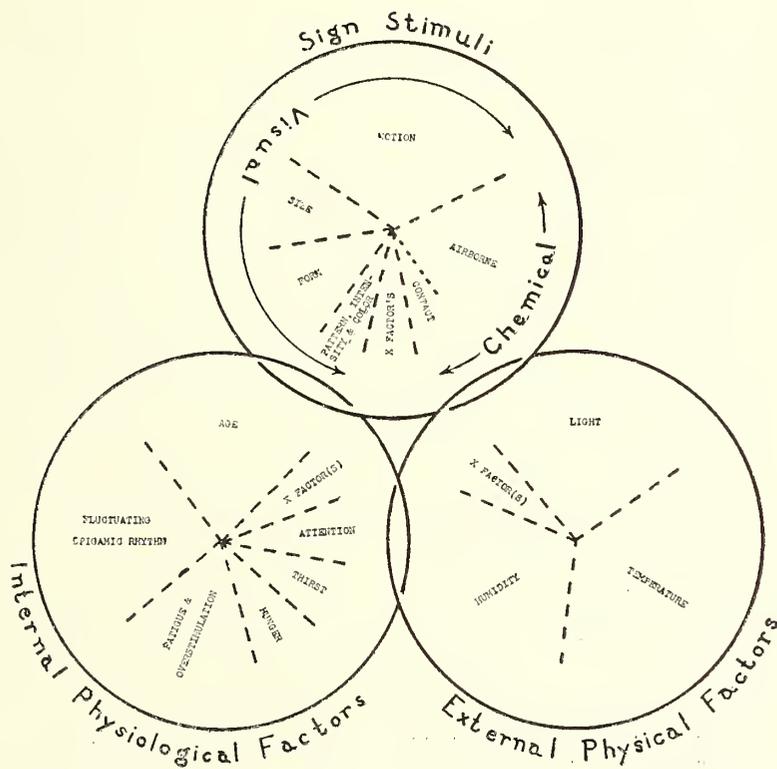
That the above phenomena are not the results of laboratory conditions is proved by the fact that a number of males were tested

in the field, before capture, and their behavior was found to correspond to that immediately afterwards in the laboratory; also, these and other males were taken, as adults, in all four phases, some young, judging by their future plotted curves, some old. Their behavior curves differed in no wise from those of males reared through at least one molt in the laboratory, except that in general the wild-caught adults tended to hit and hold A-tone oftener and longer.

Although males of other genera and species were not tested systematically, there is no doubt but that they do have periods similar to those of *xanthopa*. Females, too, show noticeable behavior fluctuations, both in general aggressiveness and in reciprocal display, although their periods were not studied. One *C. chalcea*, for example, was especially

prone during several days to do a particular type of jiggling in mutual display; I never saw it in another of her species, and it soon dropped from her usual behavior, reappearing only sporadically. Although she was exposed to the display of a number of males during and after this time, she was not allowed to mate for another two weeks, when the process went off perfectly normally.

3. *Hunger and Thirst.* Hunger, as might be expected, was an important factor in the behavior of females, since a hungry female was usually far more aggressive and needed far longer courting than one which was well-fed. However, in no genus except *Eustiromastix* have I ever seen a female try seriously to kill a male, although occasionally she will leap at him. Moderate hunger in males lowers their epigamic tone only



TEXT-FIG. 6. Factors of the innate releasing mechanism in salticid display. The circles are represented as loosely interlocking to indicate the interdependence of the three groups of factors. Similarly, the spokes are not continued to the circumference in order to show the mutual influence of the sections. Finally, the spokes are represented as broken lines, to emphasize the variability and instability of their relative importance; this varies not only throughout the family, but even in the same spider under different conditions. For example, among the Synagelinae, the chemical factors are more important than among the Plexippinae, while the same sections are of still different relative value in the end-forms of the Dendryphantinae. The sizes of the sections, therefore, are merely a guide to their average apparent importance. The term "X-factor(s)" is included in each circle to emphasize the incomplete state of our knowledge. "Distance" is omitted from among the sign stimuli since it seems to be more of a compound factor in display than do the others, based largely on apparent size, on chemical stimuli or their absence, and on physiological conditions; perception of distance and depth does exist however (see Homann, 1928; Heil, 1936). Tactile factors are omitted since they do not release display in salticids, although they are important in the final display stages. The sign stimuli circle applies to courtship; for threat display, the chemical factors should be eliminated.

slightly—from B-minus to C-plus, for example. In all the experimental work, no spiders were tested without having been fed at most 48 hours previously.

Thirst cannot of course properly be separated from the external factor of humidity, although spiders do drink water as needed. Salticids that for some days had been kept without special moisture in the laboratory went into silk shelters, if they did not die first, became semi-torpid and did not react to display stimuli; this behavior is doubtless equivalent to aestivation in the field.

4. *Fatigue and Overstimulation.* These two factors have not been properly distinguished. Actual physical fatigue, however, sometimes appeared clearly involved during experiments. Often initially restless individuals, even of hopper-type genera, were tested which raced about the table before settling down to attending to stimuli; they often had even to be pursued to the floor; afterwards, even when otherwise of A- or B-tone, they always reacted to stimuli for a shorter length of time than those which responded without preliminary activity. On the other hand, overstimulation appears to be a better term for the cessation of reaction that takes place in spiders at the peak of their internal drive, when they have had practically no exercise but have been presented with a succession of stimuli. In every individual the moment is reached, as in other animals, when no further response is drawn, no matter what the stimulus. The length of reaction time is highly variable; *C. xanthopa* is, however, as typical as any: A-tone males may be tested for around half an hour with only minimum pauses between stimuli (about three minutes). When a large group is used (the customary experimental procedure) responses may spread over three or four hours, the long rotation period allowing individual rests of 10 to 30 minutes between stimuli presentations. An individual which is tested in the morning to the point of complete non-response is usually again responsive by mid-afternoon; full recovery (regardless, that is, of internal drive changes) is the rule by the next day. Spiders with low internal drive, e.g., of C-tone, have extremely short response periods, usually totaling only five or ten minutes; often there is only a single response, regardless of length of rest between stimuli.

5. *Attention.* This factor is quite distinct from the others, and a *sine quo non* of display. Although spiders with strong drive undeniably are more easy to stimulate with display situations than weak-drive individuals, all vary irrespective of sexual tone in the amount of time needed to attract their attention to a stimulus. Sometimes they are so restless when first put on the table that their only motive appears to be to get somewhere else; some minutes pass before they seem suddenly to "wake up" with an almost literal jerk and "notice" the stimulus, which may have been equally close in front of them

many times before. This applies to both threat and courtship stimuli. The same is true of a spider engaged with one display stimulus, or with food, when another and, at the moment stronger, situation is presented.

## B. FACTORS OF THE EXTERNAL RELEASING AND DIRECTIVE MECHANISM.

1. *Physical Environment.* The effect of the physical environment has not been precisely analyzed in regard to exact tolerances and requirements of temperature, humidity, light and altitude. However, the following facts have been determined:

*Corythalia xanthopa* in the Rancho Grande laboratory displayed readily at temperatures between 65° and 80° Fahr., the extremes tested. As has been noted by others, responses were somewhat accelerated at the higher temperatures. The humidity varied from 50 to 95 per cent. The same species displayed at Weston photometer readings as low as 0.8 foot candles; below that there was no response. During regular experimental sessions, reflected daylight from the laboratory table ranged from about 25 to 75 foot candles, Weston; these readings were comparable to those obtained in *xanthopa's* natural habitat during periods of high activity. *Menemerus*, with apparently poorer vision, seemed to need considerably more light, but no accurate measurements were taken.

*Corythalia fulgipedia*, *C. chalcea*, *Eustromastix* and *Phiale flammea*, although captured at 3,500 feet, all displayed at sea level in New York, having been brought there alive in the early instars. They displayed upon reaching maturity regardless of the month, of the highly variable and unnatural extremes of temperature and humidity in which they had been reared, and of the lower altitude.

Displaying individuals of most species could be found at Rancho Grande from February to September, the period of our residences, which includes most of the dry season and half of the wet. However, as in other groups, most species had a clear peak of breeding adults in May, June and July, the early part of the rainy season.

Both in Venezuela and in New York, spiders displayed under extremely unnatural conditions, with no time whatever needed for adjustment, short of their being literally frozen, deeply chloroformed, dried out or far overheated. That is, if the spider were not injured physically beyond recovery, if he remained capable of primary activities—moving freely, catching prey and spinning a shelter—he could and did display when in a period of moderate or strong drive and when properly stimulated. All salticids observed displayed as readily in a glass container or on a table top as in their own forest environment, and in every case the pattern of display behavior in captivity was identical with that recorded in the field. The only exception was that, rarely, captive

*Corythalia* males, in close quarters under hot lights, occasionally injured each other in actual fights; ordinarily, aggressive behavior was confined to highly ritualized threat display.

In the field, salticids invariably disappeared under leaves and therefore presumably did not display, both during every shower beyond a drizzle and during all hours of intense heat, drought or baking sunlight. Display during the night in the laboratory was successfully stimulated in A- or B-tone *Corythalia* and *Phiale* which were forced out of their shelters and provided with adequate light. Hence an innate diurnal rhythm does not appear to exist in these forms.

In brief, the only external physical requirements for display appear to be tolerable conditions of temperature and humidity, along with adequate light (sun, photoflood or mazda). In *Corythalia* at least, this illumination is less than that sufficient for comfortable reading by a human being.

2. *Sensory Elements and Sign Stimuli.* The sign stimuli (or perceptual signs) considered here are those external signals which are involved in releasing or directing epigamic display in salticids. They are unexpectedly complex, especially in courtship, in which they customarily involve compound tactile, chemoperceptual and visual stimuli. Of them all, only two or three combinations of a few visual stimulus-elements can be termed primary releasers, since no salticid displayed at Rancho Grande unless the antero-medial eyes were photopically stimulated.

Reference to Table II and Text-fig. 2 will be helpful in maintaining orientation in regard to the various displays and the presumed degree of specialization of species discussed.

a. *Tactile Perceptions.* Although in many web-spinning spiders tactile perceptions are of great importance in courtship, in salticids their role is confined to advanced Stage II, where the stimuli are probably mingled with chemotactic stimuli. They will be discussed together on p. 182.

b. *Chemoperception.* For many years a possible "sense of smell," as earlier observers called it, in spiders has been the subject of extended experiment and considerable controversy. In their studies of courtship in various spiders, modern workers, particularly Kaston (1936) and Bristowe (1941), have drawn necessary and precise distinctions between contact chemoperception and distance chemoperception.

In contact chemoperception, conveniently called chemotaxis, the spider must actually touch the female herself, her silk or exuviae, or at least her trail, in order to receive a sensory chemical impression. This sense, both authors agree, often enters into spider courtship, although it is not always essential for the stimulation of display, and, in their experiments, was not necessary in salticids.

The Rancho Grande results were in agreement with these conclusions.

On the other hand, in courtship stimuli involving distance chemoperception, a spider would have to react to volatile, airborne particles given off by a female, her silk or exuviae, or her trail. Such stimuli have not been found by these authors to take any part in stimulating courtship display in any spiders which they have studied, nor do they consider that evidence has yet been brought forward which necessitates the operation of such a sense in spider courtship. Here the Rancho Grande results differ; it seems necessary to postulate the use as a secondary sign stimulus in courtship of a sense analogous to smell.

The two aspects of chemoperception—contact and distance—will now be considered in reference to the Rancho Grande salticids.

i. *Chemotaxis.* In some other groups of spiders, all with vision less well developed than in salticids, chemotaxis is a primary releaser of courtship, with or without sight of the female. In salticids this is certainly not the case. Kaston, reexamining the situation in 1936 (pp. 129-130), concluded that it was not essential in two species of *Phidippus*, and Bristowe (1941 *et ante*) agreed. Similarly, at Rancho Grande, when chemotaxis was positively eliminated from the stimulus situation, in every genus tested A-tone males displayed without chemotaxis. Contrariwise, no individual ever displayed on the stimulus of chemotaxis alone, although excitement over chemotactic stimuli was often shown. The tested forms were the following: *Menemerus*, *Semorina brachychelyne*, *Ashtabula*, *Sassacus* (2 spp.), *Phiale* (2 spp.), *Plexippus* and *Corythalia* (3 spp.).

However, in all of the numerous observations and experiments, variations were very obvious in the minor exercise of chemotaxis. These were present on all levels—generic, specific and individual. When chemotaxis was allowed, the initiation of display in all the runner genera (*Menemerus*, *Semorina*, *Ashtabula*) was definitely expedited, although that of the hopper and intermediate forms (e. g., *Corythalia*, *Phiale*) was apparently not affected in the case of A-tone spiders. However, many individuals in all genera, when of B-tone, initiated display only when chemotaxis was included in the stimulus situation.

Salticids of all conditions, except those of D-tone, and in all genera, but particularly among the runners, often paid great attention to the recent resting places of females, tapping them with palps and forelegs and revolving round and round the area. All B-tone or tiring spiders tended to break off display and palpate at length her just-vacated resting spot even as the aroused female sat and watched only an inch or two away; sometimes, absorbed in these palpations, a male allowed a prospective mate to wander completely out of sight; this reaction was noted

most frequently in the hopper genus *Corythalia*.

In the runners there was more of a tendency to follow a trail, by intermittent palpation of the ground, over which the female had passed. In *Sassacus ocellatus*, *Phiale* and *Corythalia*, there were no tendencies to trail-following chemotaxis at all; once a female had attracted his attention, a male often followed her zigzag or curving retreat by taking the most efficient short-cuts, whether or not display had been initiated.

The latter half of Stage II is so similar and well known throughout the family that it will not be specially treated here. It begins with the male climbing over the female, patting her carapace with palps and first legs, and follows through to the twisting of the abdomen and successive insertion of the palps into the epigynum, usually after some palpation of its surface. Here it will only be pointed out that chemotactic as well as purely tactile perceptions are probably involved.

Chemotactic perceptions are also not necessarily eliminated from the stimuli which continue to lower the female's threshold during the same period. Her final resistance is probably broken down by the stimulating action of the patting motions; however, since her chemotactic receptors appear to be scattered over her entire body, as well as concentrated on the appendages (Kaston, 1936 & ref.), they very likely are stimulated at this time.

Except in the advanced stage noted above, chemotaxis certainly plays no important part in the acceptance of a male by a female. Since she usually retreats a number of times during normal courtship, she infrequently crosses a male's trail during display in the field. It is true that some individual males have a tendency to circle the female completely during display. Also, females of *Phiale* and *Menemerus* have often been seen to palpate a male's recent resting place, while he is still displaying. Nevertheless, on open table tops in more than 20 experimental situations and in uncounted casual observations, involving all the experimental genera, males were accepted without the females once crossing their trail.

I can find no evidence whatever that chemotaxis plays any part in inter-male display; I have never seen a male palpate the surface or show apparent excitement of any kind when placed on the spot recently vacated by another male, even when both have been or are displaying to each other. However, a male *Menemerus*, a typical runner, could be induced to display to his mirror image only by corking him in a clean glass vial and holding the mirror against the glass end. After a few minutes, display sometimes took place in A-tone individuals, each presumably activated by his own strongly reinforced chemical stimuli. This experiment was performed on six different males; the display was indistinguishable from Stage I of

courtship and was always of very brief duration.

The occasional males in various genera that enter upon Stage II of threat, when the first legs of each opponent touch, practically always finish the encounter at this point with no damage done to either. The fangs are very rarely unsheathed during these moments. Chemotaxis, or, rather, the absence of the female chemotactic stimulus, may be involved here.

ii. *Distance Chemoperception.* The apparent part played in display by a sense analogous to olfaction will now be discussed. The majority of previous experiments concerned with it have dealt with the reactions of spiders to essential oils, chiefly of an apparently irritating nature. It has been pointed out several times (e.g., Kaston, 1936, p. 146) that sensitivity to these stimuli does not necessarily indicate possession of a true olfactory sense. Such a sense has, however, been proved to occur in a number of terrestrial invertebrates, including moths, beetles and bees. The only aspect directly concerned in the present display study is the part, if any, taken by a sense analogous to odor perception.

If such a sense exists, the necessary affectors do not, of course, necessarily consist of volatile particles; they need only be airborne and, presumably, invisible to human eyes. It is regrettable but natural that we human beings, as visually dominated organisms, should tend to be impressed with and to study chiefly visually or at least aurally dominated displays in animals. Moths and other nocturnal creatures, both vertebrate and invertebrate, may, for all we know, give off in epigamic display regular symphonies of smells in a rhythmic succession. More difficult to imagine, but perhaps easier to check, is the following possibility: Females of certain animals, at the peak of physiological readiness, may actually radiate certain wavelengths invisible to us. These may be either infrared or ultraviolet, using those terms in their broadest sense. An alternative possibility is that these frequencies may be reflected rather than radiated. The emission, of whichever type, would doubtless be under hormonal control, and would have some signal values for males. It would not necessarily of course be perceived visually. In that connection may be mentioned the old, recurrent speculations on possible wave-perceptive functions of insect antennae. The claims of some investigators that blind-folded human beings respond muscularly to red light is another related topic (See Birren, 1938, ref.).

Toward the proof or disproof of the possibility of such emissions, not one jot of experimental proof is offered here. The subject is mentioned only because of its potential connection with salticid display, and in the hope of stimulating investigation. If found valid, it would explain one or more aspects of

animal display which at present are inexplicable. The proving of the perception of special frequencies would solve puzzles in certain fiddler crabs and birds, for example. In each of these cases, males appear instantly to distinguish receptive females of their own kind from non-receptive ones in some fashion which does not appear to depend either on her behavior or on her emission of any recognized sensory signal (see Beebe, 1928, p. 64; Crane, 1941, p. 157; and Armstrong, 1947, p. 340 & ref.).

It is true that the operation of scent has not yet been eliminated under experimental conditions in the above instances. Since the published work on crabs, however, many field examples have been seen where the particularly stimulating female crab was several yards to leeward in a stiff wind; the poor olfactory development in birds is well known. According to Kettlewell (1946), however, moths have not yet been proved ever to approach females with the wind, the contrary evidence of earlier experiments having been due to incomplete observations.

In view of its highly controversial aspect, therefore, this present speculation may be on the order of postulating improbable sunken continents in order to explain an inconvenient distribution of fauna, flora or culture. Nevertheless, it is set down in the hope that adequate instruments will soon be developed capable of testing the possibility. Proofs of the use of supersonic signals by bats (Hartridge, 1945) and the perception of polarization of light by bees (von Frisch, 1949; Thorpe, 1949) are suggestive recent results of research in unusual directions. In our own future researches and experiments we certainly intend to take such possibilities into account.

In regard to salticid spiders, however, it seems that the phenomena described below can be most simply and adequately explained by postulating the action of typical, airborne, volatile, chemical particles acting upon appropriate receptors. They will be so considered in this paper.

The work at Rancho Grande seems to point conclusively to the existence of such a chemical sense. It appears likely that it is merely a further development of chemotaxis, in that the affectors, and perhaps the receptors, are basically similar or identical. This sense plays an important secondary role in courtship.

The evidence for this conclusion is based chiefly on the following observation: Young, living, unmated, adult females at Rancho Grande were in general markedly more successful in drawing courtship display from males than were females in other categories.

Their superior attraction was noted in more than 25 species, in fact, in all material plentiful enough to yield comparative observations; these included all the Rancho Grande forms discussed in this paper. The Peckhams (1894, p. 251) attributed a similar observa-

tion to the fact that females about to lay eggs were so heavy that they tended to move about less, and that it was the lack of movement which made them relatively unattractive. In the basic experiments at Rancho Grande, this factor was eliminated by chloroforming the subjects. They were then presented alternately as motionless, or uniformly moving stimuli on L-mounts. Chemotaxis was ruled out as previously described (Part II, pp. 143 and 144). The males were allowed only front views on a plane surface, to avoid the visual variables of large vs. small abdomens, or fresh vs. rubbed patterns. The effects of summation were guarded against, as usual. For experimental purposes, a female was counted as "young" when she had been adult for less than two weeks, "old" when more than four.

The general results, in this and other genera, were as follows: A-tone males, when given a choice, almost always devoted their attention to a young female, although an old or mated individual was usually courted energetically if no other was available. B-tone and C-tone males, as well as all near-senile males, showed no courtship display response at all to any but young females. A-tone males often courted a young female which was chloroformed, placed on a mount and held motionless; males of the same tone rarely took any notice of an old or mated individual similarly presented. Dead, thoroughly dried females of all ages either drew no reaction when motionless, or, when appropriately moved, occasionally drew confused threat display. Finally, although certain paper models of *C. xanthopa* males successfully drew threat display, models of females were never successful.

Special test situations, involving *C. xanthopa*<sup>2</sup> and *Phiale*, gave the following results which are pertinent:

The abdomen of a young adult female *xanthopa* had been painted black for another experiment on the tenth day after her molt. After repeated intermittent chloroforming, she died about five o'clock one afternoon. At that time, when crumpled, motionless and of atypical coloring, she readily drew display from several males. Chemotaxis had, as usual, been eliminated from the test situation. By seven o'clock the next morning, although she was not yet stiff, she had lost attraction for three A-tone males to the extent that, although some attention was paid her when she was jerkily moved, no display whatever was drawn. The normally colored abdomen of a chloroformed female, adult for fourteen days, was then cut off from the cephalothorax

<sup>2</sup> The published description of *C. xanthopa* display (Part I, p. 36) erroneously states that rocking precedes threat as well as courtship; further observation showed that this occurred only in small, closed dishes involving strong reinforcement of chemical stimuli. Normally, rocking does not occur in threat display. See Table II, this paper, for synopsis of threat and courtship distinctions. Also, the threat display figured (i.e., Text-fig. 14 C) represents a moderate phase; in the extreme form the 4th legs are held even higher, well above the carapace, and the second tarsi leave the ground.

and placed on the mount 10 mm. from the dead female. Two males now displayed promptly to the black corpse, following through to attempted mating with it, disregarding completely the normally colored, detached abdomen.

The detached abdomen was then rubbed over a dried, mounted male, which had heretofore always drawn prompt threat display. It drew brief, confused display, with both threat and courting elements, from a male which had threatened it a few moments before, and threatened standard stimuli immediately after (without a rest period). During the test, however, he followed the confused display with a leap at the mount and finished with an abortive attempt to mate.

On another occasion, a male *xanthopa* was threatening a dried male mount. Another freshly detached abdomen of a young female was hidden under a tiny paper tent, 5 mm. to the left of the displaying male which in turn was 50 mm. from the mount. The male stopped threat display, went into a courtship stance and rocked. When the mount was removed, there was no further reaction.

A *xanthopa* male paid no attention to a scrap of black cloth alone on a mount, or to the same cloth with a young female underneath it, with or without motion of the mount. Then a large, dried *Eustiromastix* male was given a yellow clypeal band similar to that of *xanthopa*, and placed on another mount. This stimulus drew prompt threat display when the mount was moved. The piece of cloth was then placed in a heap under the *Eustiromastix*. Threat again followed. However, when the chloroformed female was once more hidden beneath the cloth and the whole placed under the *Eustiromastix*, the test male paid swift attention without display, then vibrated the palps, took a courtship stance, and, finally, after one or two rocks, leapt on top of the *Eustiromastix* and tried to mate with it. This involved such a violent attempt to twist the stiff abdomen that the whole structure toppled over. With a changed sequence of stimuli, the same series was presented to two other males, with similar results, except that the courtship response died out before mating attempts.

Young females of both *Corythalia* and *Phiale*, when painted to resemble males, drew unmixed courtship, not threat, although old painted females drew mixed display (p. 194).

When female epigyna of *Menemerus*, *Phiale* and *Corythalia*, in a total of six individuals, were sealed with paraffin, no diminution in attraction was noted; the attractive substances are probably secreted rather generally by body and appendages; the experiments of Kaston (1936) and others on non-salticids support this idea.

It should be mentioned incidentally that young adult females have a stronger odor to human noses than either males or older females, at least in *Menemerus* and all three species of *Corythalia*. In a series of tests on *Corythalia*, the odor of

young females was the only one perceptible to two of five observers; the other three people in every case considered the young female's odor strongest, but indistinguishable in quality from that of males or other females. The latter seemed stronger than the males'. No generic or specific differences were detected, during casual tests with various genera. The terms used in attempts to describe the salticid odors included "spicy," "pungent," and "faintly antiseptic."

Further incidental data, by no means to be regarded as actual evidence for distance chemoperception, include the different methods of using palps and first legs in the various genera (Table II). This seems to be in accord with the various degrees of reliance on contact and distance chemoperception.

The chemoreceptors (including those of chemotaxis and the distance chemoreceptors, whether or not they are distinct), have been shown to be generally distributed on the spider, but concentrated near the tips of the palpi and first legs (Kaston, 1936 and ref.). With this view the Rancho Grande experiments agree. Females without palps or without first legs readily accepted males in *Menemerus* and *Corythalia*. When both palps and first legs were removed, reaction time was slowed in *Menemerus* but not in *Corythalia*. Males similarly handicapped displayed right through to mating attempts. When use of the first legs was the essential part of display, spiders without them would suddenly leap at the female after a prolonged period of attention. This response was specially noted in *Menemerus*. Reaction time was decidedly slowed in handicapped males in initiating courtship, but not in responding to any of the threat stimuli, including the mirror and painted mounts. It was much slower in mutilated runners of the genus *Menemerus* than in the hopper genus *Corythalia*.

In summary, the following conclusions appear valid. At Rancho Grande, distance (airborne) chemoperception is a positive factor in courtship, but not in threat display. A strong, invisible stimulus is given off by young females, serves as a secondary sign stimulus for releasing courtship and is surpassed in importance only by the male's ability to use his antero-median eyes. It appears to have little directive value. When courtship and threat are distinct, the addition of airborne chemical stimuli from a young female to a stimulus configuration tends to change threat to courtship.

#### b. Vision.

i. *Vision as a primary stimulus to display.* Use of the AME (antero-median eyes) by the male is the only single, *sine qua non* of display. The investigators who have experimented with the reactions of blinded male salticids agree that they will not display when the eyes are completely covered, no matter what other stimuli (e.g., contact and airborne chemical stimuli) are present. Apparent excitement caused by other stimuli

has sometimes, however, been observed. The species previously tested are well distributed among a number of subfamilies: *Dendryphantas elegans*, *Saitis pulex*, *Phidippus rufus* and *Astia vittata* (Peckham, 1894, p. 248); *Evarcha blancardi* (Homann, 1928, p. 254); *Aelurillus v-insignatus* (Bristowe, 1929, p. 343); *Phidippus clarus*, *P. audax* (Kaston, 1936, p. 131). Homann confined some of his blinding experiments to the AME, finding that display failed to occur as completely as when spiders were totally blinded.

The present experiments support and extend these previous conclusions. Two males each of *Corythalia xanthopa*, *C. chaleea* and *Menemerus bivattatus*, all of A-tone, were used. In one of each pair all eyes except the AME were painted, as described in Part II (1948.2, p. 144); in the other, only the AME were covered. After the spiders had apparently recovered from the chloroform (the minimum time allowance was one hour), standard test stimuli (p. 177) were presented on three successive days, unless a positive response was obtained earlier. Regardless of all-negative responses, the paint was then removed and, in tests counted as successful, positive responses obtained to at least one of the standard stimuli within one hour.

In each species, the males with the AME uncovered performed complete display (both threat and courtship, in the case of *Corythalia*) within the allotted period, although their reaction time in general appeared a little slowed. In contrast, those with the AME painted never displayed at all. The latter did, however, show some awareness of moving objects, including females, by shifts in position and slight "following" with the eyes at distances of half an inch or less. This note is typical: "X64 male sat quiet, although he ran and jumped when prodded. Took no notice of X34 female, as she watched him only one-half inch away; although she actually brushed against him several times, even his palps hung quiet. Later he moved off, crossing her trail and very recent resting place without pausing. Finally, when she jumped past him, he did turn toward her; the stimulus, however, could have been a vibration of her jump, rather than either a chemical or visual stimulus. Even in the same vial with her, with all her chemical stimuli reinforced, there was no reaction."

The most interesting result, from the viewpoint of phylogeny, was that *Menemerus*, which appears to depend more on chemotaxis and distance chemoperception and less on vision than *Corythalia*, was decidedly less handicapped by the loss of the AME. He moved around much more actively, and palpated the females' resting places in apparent excitement. No attempt was made by either genus to pursue prey without the use of the AME.

The AME of a single young female *C. xanthopa* were covered. Just before the operation she had allowed a male to reach an

advanced Stage II, when the pair was purposely separated. After painting, she refused him and four other actively displaying males which subsequently displayed to her, two or three in succession, on four successive days. One male, on the third day, reached Stage II repeatedly, ". . . but at the least touch, or before, she moved off. Male was very persistent. She did not turn to keep him in view; her palps hung motionless. Since he circled her time after time in displaying, as usual, she crossed his trail frequently during her retreats. She never once assumed the raised-carapace stance so many *xanthopa* females temporarily adopt when attention is gained. He persisted for twenty minutes, then gave up. I cleaned her eyes, introduced the same male within half an hour, and they were mating five minutes later." (Field lab. note.)

No other female blinding experiments were completed through the final stage of obtaining positive mating responses after the AME were uncovered. However, all the indirect evidence—in the observations of others and in my own—points to the usual necessity for the female to see the male before allowing mating to take place.

In summary, use of the AME, and of the AME only, is a prime requisite in salticid courtship.

ii. *Motion*. It seems well established that at least some salticids will not only leap on motionless prey, but will display to a motionless female (e.g., Peckham, 1894, pp. 243-248; Heil, 1936, p. 10). Nevertheless, the present study showed that movement is the most important single element in the visual sign stimulus pattern, in both courtship and threat display, in all the salticids tested. Although display was occasionally obtained by a motionless spider, the courtship response always occurred under the following conditions: first, the stimulus was a female; second, the displaying male was of A-tone with exceptionally low threshold; third, the motionlessness of the stimulus was the only unusual factor in the situation. On other experimental occasions in which the above conditions were fulfilled, however, only negative responses were drawn. Table IV gives test data and results of pertinent experiments.

In many (certainly more than twenty) unrecorded, casual observations, a normal spider, which was sitting quietly when the male to be tested was introduced, would not draw a display until it moved, even though the two spiders were close together and the test male, judging by his actions—his turning, or moving toward the stimulus—had certainly become aware of the stimulus.

In more than 300 tests on 10 species, in which the stimulus was in some way unnatural, no positive response was ever obtained until the stimulus was moved. Many times the slightest, brief, manual twitching of the cardboard mount was enough of an

TABLE IV.

## Responses of Males to Motionless Females.

*Series A. Conditions.* Male of A-tone; normal female chloroformed, placed on cardboard mount in approximately natural position; chemotaxis, but not distance chemoperception, eliminated (i.e., fresh sheet of paper on open table used for each test); same female in experimental session drew display from same male both before test (followed by rest) and immediately after. Exposure of each male to stimulus consisted in allowing him to drop near, or run toward, female, chivvying him gently with brush if necessary, to ensure her being in his direct line of vision. Even in negative responses, attention was often gained, even extending to feeling of the female with palps and legs, although display was not released.

Species.	No. of Individuals.	No. of Tests.	Negative Responses.	Positive Responses.
<i>Menemerus bivittatus</i>	5	7	6	1
<i>Semorina brachychelync</i>	1	2	2	0
<i>Sassacus flavicinctus</i>	2	2	2	0
<i>Phiale dybowskii</i>	1	5	0	5
<i>Phiale flammea</i>	2	3	0	3
<i>Corythalia chalcea</i>	1	1	0	1
<i>Corythalia xanthopa</i>	4	12	11	1 (delayed)
Total	16	32	21	11

*Series B. Chemotaxis permitted.* Conditions as in A, but males permitted to cross repeatedly trails of the now motionless females.

Species.	No. of Individuals.	No. of Tests.	Negative Responses.	Positive Responses.
<i>Menemerus bivittatus</i>	4	9	8	1
<i>Sassacus flavicinctus</i>	2	2	2	0
<i>Corythalia xanthopa</i>	4	8	8	0

*Series C. Elimination of Distance Chemoperception and Motion.* Conditions as in A, but female isolated in glass vial. No tests completed, since males did not display even when the stimulus female regained consciousness and moved naturally. However, in spite of the imperfect conclusions, it is worth recording that not one positive response was drawn in a total of more than 20 tests involving the same species listed in Series A. The enclosing of tested males, rather than stimulus females, would not have given significant results, since the effect of possible self-stimulation through crossing of their own tracks or responding to their own distance chemical stimuli, would not be eliminated. Similarly, mirror responses automatically involved sight of the males' own motions (however slight).

*Series D. Alteration of Female Appearance.* Conditions as in A, but female painted or upside-down. More than 25 tests, using stimuli which gave positive responses when moved, were all negative when motionless. See pp. 191 and 193 for tested species; all were given motion response tests in the same session. No stimulus which was unsuccessful when moved drew display when motionless.

*Series E. Use of Models.* No motionless model, even when successful in motion, drew a positive response. See p. 190. Test individuals were given motion-response tests in the same session.

addition to the stimulus situation to draw a prompt display.

This manual jerking of the mount of a chloroformed or fresh dead female was as effective as the female's own motions in drawing display. Her further motion was not essential, once the male had initiated display; it is, however, customary in normal courtship for even A-tone females to turn and twist and, especially, to retreat a few inches at least once or twice during courtship.

Also, the finer motions of females during male display almost certainly have value. In various species—in *C. xanthopa*, for example—females early in courtship brace themselves high in a position similar to a pre-threat stance in males. Just before or after the beginning of the male's Stage II, they crouch low. Again, in very many species, the females vibrate the palps rapidly during the early stages of courtship. Finally, in a few species, notably *C. fulgipedia* and *Sassacus ocellatus* among Rancho Grande examples, excited females often make weak copies of the males' motions, with occasional individual quirks of their own. None of these female motions ever proved to be in the least necessary either to release or to direct male display. There seems no question, however, but that they have minor directive value, and the female's eventual, crouching quiescence, as in other animal groups, certainly acts as a positive factor in permitting the continuation of Stage II. Also, it is this crucial point which in intermediate genera largely determines the continuation of display as Stage II courtship or as contact threat or actual fighting. In final summary, however, the function of female posture and motion changes is minor: in no genus which I have observed closely does the release of Stage II depend, in lock-and-key fashion, on any motion, or cessation of motion, in the female.

From the female's viewpoint, the sight of a male making appropriate courting motions is essential for acceptance. Exactly what constitutes, for each species "appropriate motion" is, however a completely unsolved question of obvious evolutionary interest. Since no method has yet been devised of testing this aspect, only the following general remarks may be made.

Little or no notice is taken of motionless males, although occasionally an A-tone female will approach or even touch one, without any attempt to injure or eat him (cf. behavior toward a partly blinded male, p. 185). No male was ever allowed to mate without complete courtship for the species, although sometimes the whole display was raced through in less than a minute, with no repetitions of stages, where both individuals were of high tone. In the occasional instances where males, because of low tone or a confusing experimental factor, omitted display and leapt directly on the female, she invariably drove him off or escaped.

Many males of high tone court females of similar-appearing or closely related species.

These females are often attentive for long periods and make no effort to attack or retreat. It is usually the female that withdraws, often before Stage II is reached. It has yet to be determined how much her withdrawal depends on the, for her, "incorrect" pattern of male motion, and how much on the unsatisfactory character of other elements in the stimulus configuration.

In the release of inter-male threat display, motion is usually essential. Once a *C. xanthopa*, of especially high A-tone, did perform threat to a chloroformed male; this, however, was the only exception in more than 25 trials on different species. Those males which react to their mirror images will very rarely display unless the mirror is moved jerkily forward.

One more point should be emphasized in regard to motion in general. The positive responses to motionless stimuli, of whatever nature, usually occur when the test spider is dropped suddenly near the stimulus. It seems likely that the visual effect to the spider may be similar to that obtained when the stimulus is moving—roughly analogous to a human passenger's confusion when one of two parallel trains starts to move.

To sum up: Male display is sometimes released in the presence of motionless females. In these cases, however, the males are of extremely high epigamic tone (A-plus), the females of unaltered appearance, and the general external conditions propitious. Therefore, although movement of the stimulus is not a primary releaser for courtship, it is an important secondary releaser, and, doubtless, a director as well. Appropriate motion of the male is essential for acceptance by females. The response to motion does not appear to vary with the degree of specialization within the family.

iii. *Distance.* The distance at which salticids perceive their prey and mates, and at which they start display, has been measured for a variety of species (e.g. Peckham, 1894, p. 242; Homann, 1928, p. 247 ff.). In this study it is pertinent to add the following remarks and conclusions.

*Corythalia xanthopa*, which averages around 4.3 mm. in length, is typical of moderately small species at an advanced stage of visual evolution. Males will come to a state of attention and approach a female on the same level, from a maximum distance of ten inches, but the usual limit of attention (as distinct from display) is not more than six inches for courtship, much less for threat. Neither courtship nor threat usually takes place at more than three inches, and usually at 1.5 to two inches. At the resumption of an interrupted series, however, it may start at 3.5 to four inches. Stage II, in courtship or threat, starts at less than one inch, usually at about half an inch. *C. chalcea* and *fulgipedia*, which have apparently equal visual dependence with *xanthopa*, are both somewhat larger than the latter; in correlation



TABLE VI.

## Spectral Reflectance of Paints Used in Salticid Experiments.

Conditions: Ultraviolet (UV) reflectance judged optically from comparative inspection of negative images of paint samples; lens, Leitz 50 mm. Summar; film, Eastman Super XX; filter, Wratten No. 18A; exposure, 1 sec. @ F 3.5; illumination, light from north sky, partly cloudy, noon, June, latitude 10° 21' north. Spectral reflectance readings from curves furnished by Electrical Testing Laboratories, N. Y., made from same samples on Hardy spectrophotometer; reflectance factor in terms of magnesium oxide.

Wave-length (m $\mu$ )	Reflectance Factor										
	White (Devoe)	Blue (Devoe)	Green (Devoe)	Yellow-green (Devoe)	Yellow (Devoe)	Yellow (Flo- quil)	Orange (Devoe)	Red (Devoe)	Red (Flo- quil)	Red-&- white (Devoe) (Pink)	Black (Devoe)
UV	very strong	strong	weak	very weak	very weak	very weak	very weak	weak	very weak	strong	very weak
400	.715	.432	.080	.067	.115	.067	.050	.080	.030	.450	.025
410	.725	.450	.082	.070	.120	.067	.055	.087	.032	.462	.032
420	.735	.480	.090	.075	.130	.067	.057	.092	.033	.477	.035
430	.750	.515	.095	.082	.145	.067	.058	.095	.035	.492	.035
440	.755	.535	.110	.090	.165	.068	.060	.098	.035	.512	.035
450	.765	.550	.135	.107	.197	.070	.063	.103	.035	.522	.035
460	.770	.545	.180	.145	.250	.070	.065	.102	.037	.520	.035
470	.775	.505	.255	.215	.330	.075	.067	.095	.038	.518	.035
480	.780	.440	.365	.345	.425	.078	.068	.087	.040	.513	.035
490	.782	.365	.475	.475	.520	.087	.072	.085	.043	.507	.036
500	.785	.280	.545	.565	.597	.105	.075	.077	.045	.498	.037
510	.785	.215	.552	.617	.640	.157	.077	.072	.052	.492	.037
520	.787	.160	.520	.637	.667	.265	.080	.068	.057	.488	.037
530	.787	.125	.470	.637	.680	.402	.083	.070	.060	.493	.037
540	.790	.097	.405	.620	.685	.515	.105	.070	.062	.502	.037
550	.790	.080	.335	.592	.692	.575	.160	.067	.067	.507	.038
560	.792	.067	.275	.560	.697	.615	.270	.068	.075	.510	.038
570	.795	.060	.220	.535	.700	.640	.420	.075	.080	.530	.038
580	.800	.057	.185	.525	.705	.657	.550	.100	.085	.580	.039
590	.805	.055	.167	.523	.713	.670	.625	.180	.115	.650	.040
600	.810	.057	.155	.525	.715	.677	.665	.335	.195	.715	.040
610	.812	.060	.147	.532	.725	.678	.688	.550	.310	.747	.040
620	.817	.062	.137	.550	.737	.678	.705	.575	.395	.755	.040
630	.820	.067	.132	.577	.747	.678	.718	.625	.450	.777	.040
640	.825	.080	.135	.615	.752	.677	.735	.657	.478	.787	.040
650	.830	.092	.145	.640	.763	.677	.750	.680	.493	.798	.040
660	.835	.115	.167	.657	.777	.678	.765	.700	.502	.807	.041
670	.845	.145	.195	.665	.790	.680	.780	.722	.510	.818	.041
680	.850	.190	.225	.657	.795	.683	.792	.740	.513	.827	.042
690	.855	.242	.280	.653	.805	.685	.802	.755	.522	.838	.042
700	.860	.315	.342	.663	.815	.688	.813	.767	.527	.843	.043
710	.863	.392	.407	.692	.820	.690	.820	.773	.532	.850	.043
720	.865	.465	.463	.720	.823	.693	.827	.787	.535	.853	.042
730	.867	.530	.515	.745	.827	.697	.832	.795	.538	.858	.042
740	.870	.577	.558	.770	.830	.698	.835	.780	.540	.860	.042
750	.872	.610	.595	.790	.834	.702	.840	.887	.542	.862	.042

they have slightly greater attention and display limits, thus illustrating a general principle of the spatial limits of salticid responses.

In comparison with *Corythalia*, species which still place a relatively high dependence on chemotaxis and/or distance chemoperception, appear relatively short-sighted. Thus, *Ashtabula* and *Semorina*, although similar in length to *C. xanthopa*, rarely give evidence of first attention at more than four inches, and usually much less. Display begins even closer, and, as always, Stage II starts closer than Stage I.

It must be kept in mind that two spiders are seldom in the same plane in the field; therefore, one customarily enjoys the advantage of an obliquely downward view on the expansive dorsal surface of the other.

Once more the importance of the physiological state should be emphasized: A-tone males tend to start attention and display responses at greater distances than others.

iv. *Size*. The display responses of salticid males to stimuli of unusually large and small size do not appear to have been previously investigated. In this study *C. xanthopa* was subjected to a series of experiments, the

distinctness of its threat and courtship responses making it an especially interesting species. Because of the importance of distance chemoperception in its courtship releasing mechanism, males rather than females were usually selected as stimuli. The results of the tests appear in Table V. In casual observations on other species, primarily concerned with inter-specific display, it was always true that where two species had display relations, there was never much discrepancy in size.

Conclusions: First, Appropriate size is an important secondary sign stimulus to display. No male *xanthopa* will give any kind of a positive display reaction to a spider with a frontal area of more than five times, or less than one-third, of his own. In other words, in linear measurements, positive responses may be given to stimuli measuring up to about twice natural size and down to about one-half.

Second. The responses within this range are highly variable and signs of confusion are frequent. The courtship response is often given in these unusual size ranges to stimuli to which a threat response would seem more appropriate.

Third. Addition of a clypeal band of yellow paint to an otherwise black frontal view, sometimes changed negative to positive responses. This yellow resembled, to human vision, that of *xanthopa* males. Both brands used had slight reflectance below about  $520 \mu$  (Table VI).

Fourth. As usual with unnatural stimuli, responses were usually obtained only by deliberately reinforcing the stimuli. This was accomplished by repeated presentations in quick succession, and constant chivvying to keep them moving in the direct front visual field of the spider. Spiders below A-tone gave consistently negative results.

Fifth. There was a tendency to respond to large stimuli at longer range than the normal.

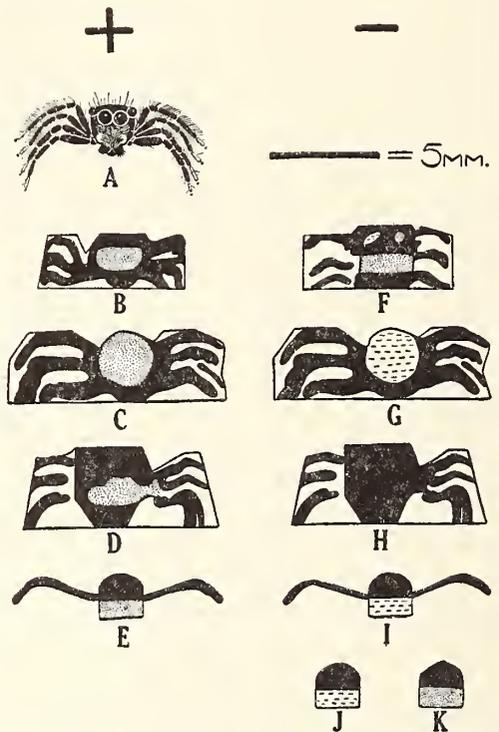
v. *Form*. The general shape of the spider is another secondary sign stimulus for releasing display. Heil (1936), working with life-size pictures of *Evarcha*, performed some experiments on this subject. He found that the number of positive display responses decreased rapidly with the simplification of the drawing, particularly in the reduction of lines representing the legs. The following results, which support and extend those of Heil, were obtained at Rancho Grande.

As in other factors, the importance of form varies inversely with the normality of the test situation, and with the drive of the individual; an A-tone *C. xanthopa* of especially strong drive will respond (with threat) to a jerked, life-size paper model of great simplicity, to the jerked carapace of a dried male, or to a jerked or naturally moving normal male with a high black paper "hat." None of these extremes is successful under other conditions, or in combination with one an-

other. For example, none of them draws display from a male of mediocre drive, while a legless paper model or a motionless carapace is unsuccessful even with males of the highest tone.

Because of the variety of contributing factors, a tabular representation of the experiments in this series would not give as true a synopsis of the results as the following running account with selected and annotated field notes. All of the experiments were performed under the conditions described under Table VI. In this series the tested species were *Corythalia xanthopa*, *C. chalcea* and *Phiale flammea*, all visually advanced species in which chemotaxis and distance chemoperception are of reduced importance.

*Models*. Cardboard models were tested on male *C. xanthopa*. Drawings of successful and unsuccessful models, made through a binocular microscope, are shown in Text-fig. 7. "A" represents a careful drawing of a male in threat position, for comparison, and was not used as a model; such detail, of course, have been impossible to include on a



TEXT-FIG. 7. Examples of models used in experiments on form-pattern-color perception in *Corythalia xanthopa*. The stippled areas were painted yellow, the dashed areas white, the backgrounds light green; spectrophotometric data in Table VI. A, detailed drawing of *C. xanthopa* in threat position; B-E, drawings of pasteboard models which drew threat responses, in order of their success, from the most (B) to the least (E); F-J, unsuccessful models. Note that the only difference between successful and unsuccessful in some cases was the presence or absence of a yellow median area. See text.

surface 5 mm. across. Similar models, but relatively larger or smaller than those shown were never successful. Even the unsuccessful models (right column) drew some attention from A-tone males. All were drawn in Higgins India Ink on bits of pasteboard; interstices between "legs" were painted pale green (see wave length analysis, p. 189 for this and other colors mentioned hereafter), from the same jar as the mounts and similar in reflectance curve to the paper substratum. This tint, used frequently as background in series of experiments involving living stimuli, appeared, from the tested spiders' behavior, to provide for them excellent contrast.

The most successful model was B, the least successful in the positive series, E. The best of them, however, drew only delayed display. It will be noted that all successful models had the following characteristics: a roughly squared or rounded central portion, painted matte black and yellow, with a greater or lesser series of lateral extensions. The "eyed" model (F) was never successful, nor were models similar to or identical with the successful one except for black or white in place of yellow in the central region. Plain black quadrilaterals—i.e., without "legs," but covering the same area as B and D—were always unsuccessful, even when furnished with a median yellow spot or bar. Also unsuccessful were all more extreme models, including equilateral and isosceles triangles; the latter were tried both vertically and horizontally, and all were furnished with a median yellow area. Finally, no small, median portion, representing the carapace only, ever drew a response.

#### *Form Experiments with Specimens.*

*General Shape.* The following experiments also show the necessity for a general shape approaching the normal. A young adult female *C. chalcea* was lightly chloroformed, placed on an L-mount and covered with a bit of flimsy black silk (chiffon), which scarcely enlarged her, but effectively concealed her shape. When she was jerked before a high tone male, no display was drawn. However, when the whole was surmounted by a large, dried *Eustiromastix* sp. (a male, plain dark brown with a painted yellow clypeus), the *chalcea* promptly courted, following through to attempted mating—not with the hidden *chalcea*, but with the *Eustiromastix*. Single, fresh abdomens, of both males and young females, were presented to males of *xanthopa*, *chalcea* and *P. flammea*; none ever drew display, or even attention, from a total of about 25 tests. Detached fresh legs, singly or in groups, were equally ineffective.

*Importance of Legs.* A legless, dried male *xanthopa* cephalothorax was very rarely successful in drawing threat display. Similarly, a legless and palpless young female *chalcea* (but with abdomen intact) drew delayed display in only three of nine tested males. However, none of these positive responses was complete: one male broke off display and

jumped, several times in succession, at the female; another, after a delayed Stage I, merely climbed onto the cardboard mount beside her, palpating its surface; a third reached Stage II, but did not follow through to twisting the abdomen, his display dying out in palpation of her body and the surrounding mount.

A single real leg was then laid flat at each side of the female, without drawing a response; but when two pairs were used, delayed but complete courtship followed.

When a sling of stiff black cotton, shaped like a broad, inverted W, was substituted for real legs, brief and abortive display followed. When a second sling was added, so that the front view showed lateral stripes of alternating light and dark, prompt, complete courtship ensued. When the second sling was removed, there was once more no response, which however followed promptly upon the second sling's replacement.

Throughout all the experiments with *xanthopa*, it proved axiomatic that mounted dried or chloroformed males with the legs stretched out at the sides drew threat display from males of mediocre drive faster than those in a huddled position.

Upsidedown females of *xanthopa*, *chalcea* and *P. flammea* were tested. These almost never drew display, the rare exceptions being from males of the very highest tone. The display never started until abnormally close to the stimulus and Stage I was exceptionally brief; occasionally a male would approach a female without display, palpating her for a time before wandering off. No actual mating attempts, which were always preceded by some display, were ever successful, the males groping about in evident confusion. Upsidedown males, on the other hand, never drew threat display or, in fact, more than passing attention.

*Importance of Carapace Height.* Compared with the legs, the height of the carapace is of very minor importance. Its elevation off the ground has no perceptible significance, judging from the prompt response of male *xanthopa* to the various mounts and of other forms, including *Menemerus*, *Sassacus*, *C. chalcea* and *Phiale*, to various dried or chloroformed mounted examples of their own species, none of which was ever presented balanced in life-like fashion on the legs. It must be remembered, however, that in normal display one of the most usual factors is the elevation of the carapace high on the legs.

Black and white paper "hats" of various sizes and shapes were fastened above the eyes to males and females of *C. chalcea* and *P. flammea* with rubber cement. So long as other conditions approached the normal, appropriate display was delayed little or not at all, and a female *chalcea* readily accepted a black-hatted male. However, in the case of hatted females, the males did not carry display through to actual mating attempts, in

this small set of "hat" tests which totalled about a dozen. The highest addition tried measured twice the height of the clypeus-plus-AME-diameter.

*Conclusions.* First, shape is of secondary significance in the release and direction of display.

Second, deviations in shape which do not hinder display release nevertheless often prevent mating.

Third, the primary shape requisite for releasing and directing either courtship or threat in *Corythalia* and *Phiale* are a roughly quadrilateral figure, broader than high, the lateral portions of which show some suggestion of dark and light horizontal stripes.

Fourth, the vertical dimension is less important than the horizontal as a factor in display.

Fifth, when the shape of a stimulus deviates from the normal range of variation, the tested spider must be of high tone and the other factors in the display situation must in general be normal, in order to draw a display response.

vi. *Pattern, Intensity and Color.* The parts played by pattern, intensity and color in courtship and threat displays are, as in other groups, exceedingly difficult to determine and to distinguish; in the present study only the surface of the question has been scratched. It should be pointed out that the distinction made here between "shape" and "pattern" is obviously artificial, although, in the preceding section on shape the emphasis was on the general form of the figure, rather than on the details; however, the stimulus value of the legs certainly belongs as much under "pattern" as under "shape."

The Peckhams (1887, p. 403) were the pioneers, as usual, in investigating color perception in spiders. Working altogether with lycosids, they approached the problem through a choice method, the lid of the cage being covered with glass squares differing in color. Since neither intensity nor wavelength was controlled, their results can have no final significance for modern workers. Nevertheless, it is very suggestive that the vast majority of *Lycosa* chose "red," since these spiders are largely negatively phototropic; very likely the hunting spiders in general, like the majority of insects, will prove to be relatively insensitive to the red end of the spectrum.

The Peckhams performed another series of experiments, painting female salticids partially or completely "blue." Following painting, the previously displaying males paid them much less attention, either not displaying or delaying the response, although it was resumed promptly when normal females were introduced. A number of uncontrolled factors were of course involved in this series (1894, p. 249).

Kaestner (1949) has just published a preliminary report indicating that color percep-

tion does occur in the European genus *Evarcha*.

Apart from the question of actual color perception in salticids, the minor role played by color, or at least by lightness and darkness, in courtship is shown by *Maevia vittata*, the North American salticid with dimorphic males. Painter (1913) seems to have been the most recent worker on the subject. The dimorphism is controlled by the presence or absence of a small sex chromosome, and in the population studied the two forms were about equally abundant. The principal distinctions consist of general color—black in one, gray with orange palps in the other—and the presence of a pair of tufts on the carapace in one, absent in the other. In spite of considerable individual variation, the two forms are quite distinct visually; in addition, the display patterns show differences. Nevertheless, both were readily accepted by females, as were dark males with their tufts missing. According to the Peckhams (1889, p. 54), who worked in a different part of the United States, the darker, tufted form was more aggressive, and was preferred by the females; also, differences in display of the gray form from that described by the Peckhams were reported by Painter. In spite of the fact that in neither study were controlled experiments performed, which guarded against summation, etc., it still seems likely that a most interesting series of behavior differences has evolved in this widespread species. Here is certainly splendid material for worthwhile work.

The disagreements between the Peckhams and Painter do not affect the conclusion that degree of lightness or darkness in males is not, in that species, of primary importance in gaining acceptance by the female.

In the present experiments, two groups of colors were used, the Floquil "Flo-paque" series and Devoe opaque water colors. Since spectrographic analysis could not be conducted in the field, library cards were painted with each hue and combination used; later these were analysed spectrophotometrically (Table VI), along with fresh samples from new jars. The latter check was employed to determine the degree of changes in the samples since their field use; these differences proved insignificant. Although the paints are far from a theoretical monochromatism, most of the hues do show steeply ascending curves near the regions of highest reflectance.

During the field experiments, the paints and the yellow of *C. xanthopa* (cut in two, without exposure to chemicals, just before the photograph was made) were photographed through Wratten Filter No. 18A, which screens out virtually all light except the ultraviolet; the spider's yellow areas did not perceptibly affect the negative according to observations through a binocular microscope. (Spider photographic data: lens, Leitz 90 mm. Ektar; exposure, 13 sec. @ F12.7; other data as in Table VI). In view of these

negative results, it is apparent that ultraviolet is not a factor in the effect of *xanthopa* yellow as a sign stimulus; they do not of course, preclude the possibility of the spider's visual sensitivity to ultraviolet wave-lengths. So far the yellow of the spiders has not been further analyzed: dried specimens appear to be too changed to give trustworthy results.

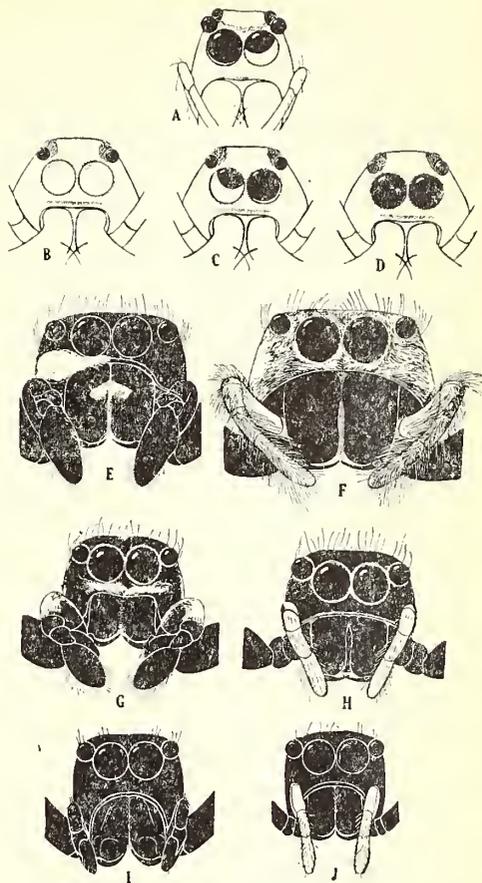
It will now be shown that the various characteristic "display ornaments" are in themselves of minor importance in the samples studied as display sign stimuli, except in certain inter-male relationships. *C. xanthopa* was the subject of most of the experiments; *C. chalcea*, *C. fulgipedia*, *Menemerus bivittatus*, *Phiale flammea* and *P. dybowskii* were used to a lesser extent; a few illustrations were taken from *Semorina*, *Ashtabula* and *Sassacus*.

*The Role of Female Pattern, Intensity and Color in Stimulating Male Display.* The female's pattern and color equipment may be divided between that of the frontal and the dorsal (particularly abdominal) regions. It must be kept always in mind, however, that in practice the male's first view of the female is often obliquely downward, so that both regions are simultaneously visible. In the experiments below, the two regions were kept separate, the stimuli being presented on a plane surface in direct frontal or rear views.

*Frontal pattern.* (Text-fig. 8). In females, this may be divided functionally into two well-marked classes; first, differentiation of frontal markings, including those of clypeus and palps as a unit, and, second, distinctions concerning the palps alone. The sexual difference of frontal markings is noticeable in many salticids, but ranges through all degrees and is often absent. The following examples are from the present series: In *C. xanthopa* and *Phiale* spp., the females are black-faced while the males have strong yellow or white clypeal bands which continue, when the palps are bent, onto certain palpal segments. In contrast, in *C. chalcea*, *C. fulgipedia* and *Eustiromastix* sp., the females are frontally moderately or very hairy, chiefly gray and white, while the males are almost completely black and naked. In *Menemerus bivittatus*, both sexes have the hairs pale, but the female more so than the male, where they are confined to a white clypeal band. Finally, in *Mago acutidens*, the frontal region is black and naked in both sexes. It should be remembered that the legs, particularly the first, are often much darker in males than in females.

Experiments were made with *C. xanthopa* and *P. flammea*, both having sexual dimorphism in this respect, to determine the effect on the male of alteration of the clypeus.

When normally black-faced young female *xanthopa* were given yellow clypei and palpi, resembling those of the male, the courtship display was always drawn as promptly as ever with no hint of threat or confusion. Chemotaxis, but not motion or distance chem-



TEXT-FIG. 8. Examples of frontal sexual dimorphism and types of "ornamentation" in representative salticid genera. A, *Lyssomanes bradyspilus*, female; B, C, D, same, male, showing three positions of ocular color "change"; E, *Menemerus bivittatus*, male; F, same, female; in the male, one-half of the white clypeal band has been shaved off to show narrowness of true clypeus; G, *Phiale flammea*, male; H, same female; I, *Mago denticheles*, male; J, same, female. All figures drawn to same scale; note how in *Mago* the individual female depicted happens to be smaller than the male; this often occurs in salticids, although the carapace size of the average female in a given species is always somewhat larger than that of the average male.

The adaptive value of the "ornamentation" is by no means equal throughout the family. In *Phiale*, the clypeal band of the male is a releaser for threat display; in *Menemerus* there seems normally to be no inter-male display at all, although a similar clypeal band is well developed, nor is it of apparent importance in courtship; *Mago*, lacking all clypeal "ornamentation", but having a plain, high, black carapace and clypeus, has both courtship and threat well developed and moderately well differentiated. Note the prevalence of pale palps in the female; these are usually vibrated during display, but do not, in the several tested genera, function as either primary or secondary releasers of male courtship. Sexual dimorphism varies from negligible (e.g., *Mago*) to extreme (e.g., *Menemerus*); see also Part I, 1948.1, text-figs. 12-15 incl., for examples of the latitude of dimorphism within a single genus, *Corythalia*.

ical stimuli, was excluded. (Test-material: 2 females, 6 males, 9 tests).

Four weeks later, one of the same females, still unmated, but now more than "middle-aged" for that species, was given a new coat of paint and presented to a fresh series of males. The results were quite different: (Test-material: 1 female, 7 males, of which 6 were of A-tone and 1 of B-tone; 10 tests.) First round: 2 threat, 3 courtship, 2 undecided; second round (3 only tested): 1 threat (last time this individual was uncertain), 1 courtship (last time this individual also courted), 1 courtship (last time this individual was uncertain). Total of responses: 3 threats, 5 delayed courtships, 2 confused responses (including that given by the low-tone individual). The threat reactions were all promptly given, while courtship followed a period of uncertainty characterized by attention, "following" with the eyes, and intermittently dropping the abdomen (i.e., alternating in courting and threat position). It seems apparent, in conjunction with other experiments, that the waning airborne chemical stimuli of the female were here responsible for the inclusion of threat and uncertainty in the results.

Two male *xanthopa* were now altered; in one the yellow scale-hairs of clypeus and palps were painted black; in the other the palps were detached and the clypeal scales scraped off with a razor. The results (5 males tested, 5 tests) consisted of 2 very rudimentary brief courtships (1 single rock each), 1 abortive, brief, courtship-plus-threat and 2 responses which were negative except for brief attention. When a mirror was presented to the palpless, shaved male, as he stood on the same spot where a young female had just been sitting, he gave prompt attention, courtship stance and a few rocks, then retreated briefly, and ended by leaping at the mirror, but above the image level. The same response was repeated on fresh paper, but since no rest time was given in this instance, summation may well have been involved; unfortunately because of an accident to the shaved male, and lack of time for repetition, the testing was not resumed.

When similar experiments were conducted on *Phiale*, the results were as follows:

When a normally black-faced young *P. dybowskii* female was given white spots on the palps and, later, a white clypeal band similar to those of the males, repeated tests always drew complete courtship, not threat.

When an old *P. flammea* female was similarly treated, two males courted relatively promptly so long as she was motionless, but approached her, for mating, from the side, out of sight of the abnormal, white palps and never got properly oriented toward the abdomen.

When the female mount was moved during the presentation, the male first gave threat, changing to a prolonged, side-approach courtship only when he was unusually close to her.

When her paint was washed off, both males gave prompt, normal, complete courtships.

The entire frontal aspect of a young chloroformed *C. chalcea* female, excepting the eyes, was painted white. As she sat motionless on a mount, an A-tone male was introduced with the following results: "He soon vibrated palps in the air, making semi-circles until he came close to the mount. Then he palpated and further vibrated the palps, circling off on the surrounding paper and returning to mount time and again. However, there was no trace of display, and no attempt to mate. It was exactly like the behavior of a male introduced to the spot where a female had recently been sitting or moving about. Finally, after more than five minutes, he went away. When he was brought back, to a distance of about two inches, the female was jiggled infinitesimally. He displayed at once, with good courtship. The first mating attempts in Stage II were from her unpainted rear. Then he displayed Stage I again and approached with a typical Stage II from the front." (Field lab. note).

One typical feature of the female frontal appearance in many species is the rapid vibration of contrastingly pale palps at a certain stage of courtship; it occurs usually in the earlier phases, during her first apparent awareness of the male's Stage I. Sometimes, as in *Semorina*, *Ashtabula*, *Phiale* and *Mago*, contrast to the otherwise dark front (including or excluding legs), is attained principally through pale integument; sometimes, as in *Menemerus*, the effect is accentuated by long white fringes. In species such as *C. chalcea*, where vibration of the palps by the female is of casual and infrequent occurrence, they are not notably lightened or "ornamented." When present, the paleness and "ornamentation" usually extends to most segments, unlike special spotting with scale-hairs of certain segments which is so typical of some males, as in *C. xanthopa* and *Phiale*.

In order to determine their importance as display sign stimuli, the female's palps were removed from examples of *Menemerus* and *Phiale*. In every case the males courted the mutilated females as readily as normal forms. (*Menemerus*: 1 female, 8 males, 10 tests; *P. dybowskii*: 1 female, 1 male, 2 tests.) Palps were not removed from any of the other species, but males of all genera mentioned in the preceding paragraph always displayed as readily to a chloroformed female when her mount was slightly twitched as to a normally moving individual; the separate motion of contrasting palps is certainly not even a secondary sign stimulus.

In most females, as in males, the eyes are rimmed more or less conspicuously with reddish, yellowish or white scales. Since males display as readily to clumsily blinded females, in which all trace of the scales is covered, as to normal ones, these scales seem to have no primary or secondary display value in modern times.

*Dorsal pattern:* Dorsal carapace markings are almost always absent in the species studied, except in *C. fulgipedia* and *Phiale*, where they are highly variable and practically identical with those of the male; the white submarginal carapace bands characteristic of many species do not appear to be displayed in any of the ones I have observed and, indeed, short of a theoretical lateral display, involving flattening of the legs, it is difficult to see how they would ever be plainly visible.

The females of *C. xanthopa* have a naked black carapace, but a prominent abdominal pattern, consisting of a pair of broad, longitudinal, yellow stripes on a black ground. Males frequently display to the rear view of normal females before they have seen her dark front view at all. Blackening of the female abdomen produced no change in reaction time (1 female, 2 males, 6 tests). Then two young females were selected, of similar age and condition; the abdomen of one was blackened; they were then placed, facing away from the center, about eight inches apart on the ten-inch line of the concentric test circles (Part II, 1948.2, p. 145), this being about the limit of perception-response in this species. Six males in A-state were then placed in succession in the circle's center, facing exactly between the two females. In every case the male became first aware (as judged by his shifting position to look toward her, and the adoption of preliminary courtship stance) of the female whose mount was twitched first, no matter how slightly. His progress toward her was invariably interrupted by a movement from the other female, regardless of her color. By the time the male arrived within actual courting distance (several inches away), he would either court first one, then the other, impartially, or simply sit, restlessly, between them in apparent confusion. In all, four of the six males courted somewhat, and two sat quiet at courting distance and eventually retreated. Of the courters, two eventually stopped and ran between the females out of range, one retreated, and the fourth's test was broken up when the normal female came out of the chloroform and moved off. At that point the male made no attempt to follow, but concentrated at once on the black female nearby, now not being twitched, and followed through into advanced Stage II before they were forcibly separated. A second round of tests, using the same males, brought similar results, although a given male did not always behave in the second test as in the first. The overwhelming effect in all tests was uncertainty and conflict. The only possible difference noted in the response to the two females was a very slight tendency to notice the normal female first at the greatest distance (10 inches), when both were twitched simultaneously.

Thus, although the female's pattern certainly has no value as a releasing stimulus, it seems likely that in the long run the two

light stripes may have some slight directive value in the field. Under those natural conditions, three-dimensional vision is of course the rule. Therefore, the striking contrasts may make the attraction of the male's attention from farther than 10 inches, beyond the range of distance chemoperception, easier, among the dead leaves and shadows. To human vision, both males and females of this species are conspicuous in their normal habitat. However, I have never been able to gather the least evidence of this possible function, although it has been kept constantly in mind in field observations. In regard to *C. fulgipedia* females, which exhibit an abdominal pattern and color striking enough with their strong black and white, there are no distinctions from either immature specimens of almost equal size or from those of adult males; therefore the adaptive nature of abdominal pattern in any fashion, except that perhaps of disruptive coloration, is even more unlikely.

In female *chalcea*, any adaptation to display use is the most questionable of all; its dull bronzes, pale gold and black bandings are not only indistinguishable without a microscope from those of the preadult female, but they merge exceedingly well into dead-leaf or tree-trunk backgrounds, and when the spider moves it is even less conspicuous than an all-black form. If the color and pattern have any adaptive significance, it would appear to be as disruptive coloration of a protective nature; certainly it cannot help in attracting the attention of the male. A further point is that *chalcea* and *fulgipedia* females, although of strikingly different appearance, each draws display from males of the alternate species even when the males have only a posterior view.

When the abdomens of *xanthopa* females were painted solidly yellow to resemble those of males, there was no confusion: as when the clypeus and palps were painted, the male courted from the rear if the female was a young adult; as in the case of the altered front view, he became confused with old painted females.

In *Phiale*, the quite constant flaming rusty red of many species in the male is variable in females, ranging from almost male vividness to nearly black. The white spots and bars, though also variable, are nevertheless always present and, to human eyes, conspicuous, especially posteriorly. However, when the female abdomen was painted uniformly black in *P. flammea*, three males courted her promptly from the rear at close range. Nevertheless, in this genus pursuit is a fundamental, normal part of the courtship, and as often as not the male is displaying for a time to the female's posterior view. It seems therefore that while female white posterior markings have no releasing value, they, like the *xanthopa* stripes, are probably directive in the sense that they facilitate following.

In perhaps a majority of genera, the abdominal pattern appears completely undistinguished, except as probable examples of protective coloration. In *Sassacus ocellatus*, one of the species in which the female abdomen is both striking and closely similar to that of the male—i.e. iridescent green with posterior black-and-white spots—it is noteworthy that abortive female display was once observed (Part III, 1949, p. 46).

There is, however, one female abdominal marking which appears of importance in courtship. This is the sub-basal pale band, usually white, which is of such frequent occurrence in both sexes throughout the family. It is found even more often in females than in males. It is present in all of the adult females discussed in the present paper except *Lyssomanes*, *Semorina*, *Ashtabula* and *Corythalia xanthopa*. It always crosses the highest point of the abdomen and is preceded only by the naked black region immediately behind the pedicel.

In order to test its display value, abdomens were variously covered with white, yellow, black or red paint in females of *C. xanthopa*, *C. chalcea* and *P. flammea*. In painted *xanthopa*, in which the abdomen is normally striped, display proceeded though normal mating, as described earlier. In the other two species, which normally have sub-basal bands, the males appeared to become confused in the middle of Stage II, when the time came for twisting the abdomen. The following instance is typical: A *chalcea* female was painted completely white above, except for the thoracic slope of the carapace, which was inadvertently left black. Three males in seven tests courted normally until advanced Stage II, whereupon all of them tried to twist the carapace, not the abdomen, and made fumbling efforts to insert the palp too far forward. All of them gave up and moved off. When black paint was applied to this area also, lest the behavior difference involve negative chemical or other stimuli from paint, the same reaction followed. Finally, the base of the abdomen was blackened, the crest and all posterior to it remaining white. The two males still in display condition now promptly started mating after normal courtship, in the typical position. Cases of similar confusion occurred in *Phiale*: When the female abdomen was completely blackened, the males did not locate the epigynum; when a sub-basal white band was added in the usual position, courtship was completed without delay. (1 female; 3 males; 3 tests). The confusion following lateral approach in response to legless females has already been discussed (p. 191).

The following interim summary may now be made in regard to the role of female pattern and color in stimulating male display:

First. They are of the most minor importance, in comparison with other stimulus situation components, having no releasing functions and only rarely a directive value.

Second. Young adult females in the tested species, when painted to resemble males, or when the typical pattern is severely altered, are nevertheless courted as females, so long as the remainder of the stimulus configuration remains normal; otherwise there is no response.

Third. Old females so painted, or males painted to resemble females, draw delayed or confused responses, or, sometimes, complete threat display.

Fourth. The correlation of palp ornamentation and vibration in females, although it may well increase visibility to and/or excitement in the male, is certainly not even of secondary releasing value; males court palpless females of *Menemerus* and *Phiale*, as well as chloroformed—and hence quiet-palped—females of these and other genera, promptly and completely.

Fifth. While the white posterior markings or other patterns of some females may increase visibility to pursuing males, this is pure speculation; the markings are not necessary to release display, nor are any of the other tested female abdominal patterns.

Sixth. The white sub-basal abdominal band, which occurs so frequently in the family, proves to be a directing mechanism for copulation in *Corythalia chalcea* and *Phiale flammea*, the only two species tested. There is contributory evidence that this is also true in other species.

*The Role of Male Pattern and Color in Gaining Acceptance by the Female*: The following paragraphs summarize the experiments in this series. The difficulty in assembling data was in bringing treated males back to full A-tone display condition after the operation, and in having receptive females on hand at the right time.

*Menemerus bivittatus*. Five females all paid prompt attention to the display of two males, each with the white clypeal bands and palpal spots scraped off, showing black integument beneath. Though all the females allowed a male to reach the part of Stage II in which he was entirely out of range of her AME, on top of her, mating was not completed in any case. However, these females on the test days rejected even normal males, and two of them proved to be already fertilized.

*Phiale flammea*. Four females paid prompt attention to two displaying males, each with



TEXT-FIG. 9. Antero-dorsal view of a female abdomen (*Phiale flammea*). The pale band acts as a director for turning the abdomen in the final part of Stage II courtship display.

the white clypeal bands and palpal spots scraped off (as in *Menemerus*); in two cases the males, during prolonged (20 minute) sessions, were allowed to reach Stage II; there were no acceptances; the females appeared very sluggish, but normal, control males were not then available for determining the females' true tone.

*Corythalia chalcea*. A female accepted promptly a male painted to resemble *C. fulgipedia*, having white pigment on the femur and patella of the normally black palps. These two species display to one other freely, but never, in numerous observations, did display proceed beyond early Stage II.

*C. fulgipedia*. A female accepted promptly a male with the white-spotted palps blackened to resemble those of *C. chalcea* (see above). Another female accepted a male with the frontal aspect, including the legs, completely covered with white. It will be recalled that in *fulgipedia* the iridescence and fringes of the legs are displayed in courtship as well as in threat. Complete blackening of the legs did not affect the female's reaction in the least, nor did removal of the fringes. In three other pairs the male was variously painted with red, from a median red spot above the AME through covering of the clypeus and palps to a complete coating of the frontal aspects (excepting the eyes) including again the legs. Once more acceptance was complete in each case, and within the normal acceptance time of the species (3 to 6 minutes).

*C. xanthopa*. Two females each accepted a male with the yellow of palps and clypeus changed to white, and another in which the clypeus had been painted black and the palps removed. When the latter male reached advanced Stage II, he could not of course proceed and eventually backed off the carapace; the female, however, had showed no signs of restlessness. Another female accepted a male with the yellow areas replaced with orange.

From these examples it appears that deviations in the color and pattern of the male play a very minor part in acceptance by the female. To summarize: In three species of *Corythalia*, altered males were readily accepted by six individuals. In *Menemerus* and *Phiale*, although mating was not completed by frontally altered males, they were allowed to reach advanced Stage II; in these two genera the available females during the tests appeared to be in non-receptive condition.

*The Role of Pattern and Color in Inter-male displays*. This aspect was investigated rather fully in *C. xanthopa* and less so in *C. chalcea* and *P. flammea*. The following results were obtained:

*C. xanthopa*. Males of A-tone responded invariably with more or less prompt threat display to the following moving stimuli in which the yellow clypeal band and spotted palps appear to be involved: conscious,

chloroformed or mounted-and-dried males with yellow, orange or yellow-plus-white paint covering the front yellow areas; legs painted dark brown or black (covering iridescence); two-dimensional models of appropriate size and general shape so long as a yellow or orange bar or spot appeared across the middle; dried females painted like males; unrelated species of large size with a yellow clypeal band added; preadult male *xanthopa*, or other *Corythalia* species of similar sub-*xanthopa* size, in which males were painted like adult *xanthopa* males.

On the other hand, males responded with incomplete courtship or did not respond at all to the following stimuli: conscious, chloroformed or mounted-and-dried males with the yellow of palps, clypeus and abdomen altered to any of the following colors: red, blue, blue-plus-white, red-plus-blue; six intensities of black-plus-white which included values comparable, by Weston meter, to those of the yellow, yellow-plus-white and orange which elicit threat display; to receptive young adult females of other species of *Corythalia* painted like male *xanthopa*.

To the stimuli listed below, the reaction was variable and included incomplete courtship, threat, no reaction and a confused mixture of threat and courtship. The variability was not only between individuals, but in the same individual on different days or even at different parts of the same test period. These borderline stimuli are the following: males, or the testee's mirror image, with the yellow parts painted black as in females, white, red-plus-white or green; males with the black legs altered to white, yellow or red; females, middle-aged or old, painted to resemble males; a normal male *Phiale flammea*, characterized frontally by strong white markings on a black ground. When a male *xanthopa* face was blackened and the legs painted yellow, there was no reaction. When, as occasionally happened, a blackened, chloroformed male suddenly became conscious and threatened a normal subject, the latter either appeared startled, leaping in the air, and retreated, or, if he were courting, stopped courting and, in several instances, changed the courtship to threat display.

Male *xanthopa* in B-state responded to very few unnatural stimuli, and the few reactions which did result were so erratic and variable that no general listings would be profitable. The only invariable reaction was that orange or buff-faced males were threatened as promptly as yellow-faced examples.

The solid abdominal yellow of *xanthopa*, as seen from the rear, drew as prompt threat display as a front view; males with the abdomen striped black and yellow like females, also drew threat display. Males with the abdomens blackened, however, drew confused responses.

Unfortunately, during the inter-male series of *xanthopa* tests, which took place early in the salticid experimental period, the full

importance of the amount of mount-jerking in some species was not fully realized (*infra*). Nevertheless, in all the *xanthopa* tests, the responses did not appear in general to be dependent on the type of motion. It can be stated without reservation that the stimuli which drew the most variable, confused or inappropriate reactions (i.e., anything except threat) were almost always ineffective unless strongly reinforced by constant jerking and repeated presentations: in other words, the single twitch which in *C. chalcea* and *Phiale* sometimes made the difference between threat and courtship responses (see below) was inadequate for the less successful stimuli of the *xanthopa* series.

*C. chalcea* and *C. fulgipedia*. These two species, in one of which the palps are black and in the other spotted with white, display to each other freely, each maintaining rigidly its own threat pattern.

Under experimental conditions, the following tests were made: Two *chalcea* males each displayed promptly with threat to another male with his normally black face painted yellow (as in the smaller *xanthopa*, to which species it will not display). They also displayed to a larger male *Eustiromastix* sp., dried and mounted, his normal dark brown having a painted yellow clypeus. Again, a chloroformed, mounted male *chalcea* with the legs whitened, drew various responses from a single A-tone male; these ranged from incomplete courtship with a poorly oriented side approach, to prompt threat, depending on the motion of the mount: when the latter was not moved, attention only resulted; a single twitch was followed by courtship; continued jerking drew threat. When the same mount was presented to the same male on one of his B-tone days, the incomplete courtship responses occurred, with the previously successful single twitch, but no threat could be drawn with any type of motion. A male *chalcea*'s legs were blackened, to eliminate iridescence, and the now completely black individual mounted on a black background, and jerked slightly before an A-tone individual. Incomplete courtship was eventually drawn, with no trace of threat.

From the above it appears that at least in *chalcea*, change of the normal black color on the mid-frontal region to white or yellow does not affect threat response, while confusion may result when the legs are painted white; this complex would seem however to be more concerned with shape than with pattern and color in the sense used in this section; the importance of type of motion is once more emphasized; the response to the mount on black seems to be connected with visibility.

*Phiale flammea*. The white scales were scraped from the palps and clypeus of two males, so that they now had in frontal view the wholly black appearance of females. Neither male was chloroformed thereafter and each was of A-tone. When placed to-

gether, both gave complete threat displays starting at three inches, followed by brief sparring, in six tests on two successive days. The displays were never mixed with courtship, except that on one day the larger, less aggressive male tended to start with a generalized display (high stance, first legs high). However, when another male was chloroformed, palps and clypeus blacked and the whole mounted, the following occurred: "A normal male took no notice when the mount was not moved. When the mount was given a single twitch, the testee hesitated, adopted a high, generalized stance, then, at one inch (unusually close) he changed into a typical crawling courtship; he continued to persistent attempts to mate, even including complete twisting of the mount's abdomen." (Field lab. note). On the second round, when the mount was persistently jerked, prompt threat response was drawn; courtship resulted once more when the movement was restricted to a twitch. Here again, as in *chalcea*, the significant difference was in the amount and type of motion; and as in the yellow of *xanthopa*, the median white frontal markings were, under appropriate conditions, badges of masculinity. (cf. also p. 194 for threat display toward females with whitened palps, and the role played by distance chemoperception, p. 183).

When the first legs of a normal male were painted white, incomplete threat was drawn from three individuals.

When the flame-red abdomen of a dried male was painted completely black, including the white terminal spots, prompt threat display was drawn from three individuals; the same results followed when the white carapace stripe and submarginal band were also removed. However, when the abdomen was whitened, there was no display from any of the three in a total of ten tests; one of them stalked and leapt upon it once, apparently treating it as prey, but dropped it promptly (perhaps because it was stiff). When it was re-blackened, all three males once more threatened promptly. Intensity, rather than hue, seems to be the important factor here.

The abdominal red of *Phiale* shows no evidence of being an aposematic hue. Small frogs and lizards of several species stalked and ate *Phiale* without hesitation or apparent distaste. Furthermore, a *Phiale*, in all three tests made, showed a decided fear-flight response when dropped near a young *Anolis*; this occurred several seconds before the lizard appeared aware of the spider.

The results of inter-male display experiments may be summarized as follows:

First. The light-colored contrasting clypeal and palp markings of male *Phiale* and *C. xanthopa* have definite releasing value for threat display, subject to superior control by airborne chemical stimuli and motion. White clypeal and palp markings in the naturally black-fronted *C. chalcea* have no such value.

Second. Reflected light appearing in the (to human eyes) yellow region of the spec-

trum has threat releasing value in *xanthopa*, irrespective of intensity, when occurring in the palp-clypeal region. Other spectral regions in general release incomplete or inappropriate responses.

Third. Reflected light in the red region, added to the black frontal view, does not affect threat display in *C. chalcea*.

Fourth. When the scarlet abdomen of *Phiale* is covered with black, threat responses are not affected.

Fifth. White paint applied to legs or abdomen of male *chalcea* or *Phiale* usually draws an incomplete response, or none.

Sixth. The obliteration of iridescence in *Corythalia* legs by black or brown paint does not affect display responses.

#### *General Summary of Value of Color-Pattern-Intensity in Epigamic Display.*

First. Pattern, color and intensity are of minimum importance in the stimulus configuration of courtship, at least in *Menemerus*, *Phiale* and *Corythalia*: Male or female "ornamentation" is not a primary or secondary releaser for either female acceptance or male courtship display, respectively.

Second. It is probable, however, that in both sexes, certain spots and patterns, particularly when correlated with motion (as in spotted palps) have definite directive and/or excitatory value, or at least function as visual aids. An example of an unquestionable directive stimulus is the pale sub-basal abdominal band which, at least in *Phiale* and *Corythalia* functions during advanced Stage II as a copulation guide for twisting the abdomen.

Third. Clypeal and palp markings contrasting strongly in brightness with the black integument and present only in the male have definite releasing value in intermale display at least in two species, *Phiale flammea* and *Corythalia xanthopa*. In two other *Corythalia*, however, one with minor markings and one with none, facial ornamentation is not a threat releaser.

Fourth. There is some evidence that at least *Corythalia* and *Phiale* have poor sensitivity in the red region.

Fifth. The application of white paint to extremities in *Corythalia* and *Phiale* sometimes affects display reactions, perhaps because of apparent form alteration.

Sixth. The obliteration of leg iridescence in *Corythalia* has no perceptible affect.

The significance of deviate responses will be discussed under displacement behavior (p. 202).

## VI. INNATE RELEASING AND DIRECTIVE MECHANISMS.

From data given in the preceding sections, the innate mechanisms in courtship and threat may now be viewed as integrated patterns. In all display, adequate physical conditions, including light, humidity and tem-

perature, are prerequisites, as described earlier; they, as well as the general good health and nourishment of the spiders are essential and will not be referred to again in the following discussion. Courtship and threat displays as a whole will be taken up in turn, from the points of view of both sexes, followed by a more general discussion.

### A. COURTSHIP.

#### 1. Mechanisms of courtship display in males.

##### a. *Releasers in A-tone males of hopper groups.*

i. The stimulus must be within range of the AME.

ii. It must fulfil certain rough size-shape-distance requirements.

iii. One of the following factors must be present.

(a). Airborne chemical stimuli.

(b). Generalized motion (for Stage I); lack of motion is customary for advanced Stage II.

iv. The following often contribute to the configuration, but are not essential as releasers:

(a). Special frontal and/or abdominal patterns, often displayed with special motions, such as the vibration of pale palp.

(b). Chemotaxis.

(c). Cessation of motion, including that of palps, often accompanied by crouching; this behavior has releasing value for Stage II, although it is not essential; close proximity is of first importance, with or without crouching.

##### b. *Directors of A-tone males of hopper groups.*

Groups iii and iv above are probably partly and primarily, respectively, directive in function. A light, sub-basal abdominal band is sometimes a specific director for copulation.

##### c. *Releasers and directors of A-tone males in runner groups.*

These differ from the hopper group requirements in the greater importance of both airborne and contact chemical stimuli, as well as of proximity. The visual stimuli of i and ii remain essential, however, as releasers;

the visual stimuli of iv are probably of less importance as directors.

- d. *Releasers and directors of males of lower tones.* Stimuli from all groups, acting in conjunction when necessary. Alternatively, a few stimuli may release and direct courtship display when strongly reinforced.
2. Mechanisms for courtship response in females.
    - a. The stimulus must be within range of the AME.
    - b. It must fulfil certain motion requirements.
    - c. Airborne chemical stimuli are probably involved at close range in Stage I, at least in the runner groups.
    - d. Tactile (and probably chemotactic) stimuli are essential in Stage II.
    - e. No obvious secondary sexual character, including special structures, "decorations" and colors, is essential to successful mating in the genera studied.
  3. Course of mutual display in courtship.
 

In general, a system of progressive, mutual stimulation exists between the sexes, on the order of that demonstrated in sticklebacks (Tinbergen, 1948 *et ante*). However, in the salticids, especially in the more specialized forms, the situation is far less clear-cut. Omitting, for the sake of clarity, special exceptions and qualifications, the usual course of normal field or laboratory display in salticids is presented in Table VII.
  4. Comments on various aspects of courtship.

Stage II is never entered upon without at least a rudimentary Stage I, even when it is only a resumption of a display briefly broken by the female's temporary retreat during Stage II, or even in the middle of copulation.

The role played from the female viewpoint by the size and shape of the male, as well as by his motion-configuration, has so far unfortunately proved impossible to test. The most pertinent data bearing on this are supplied by observations on the behavior of females watching males other than those of their own species in display; in each case the size and shape were similar to those of their own males, and they always retreated before allowing Stage II to commence; this subject will be further discussed under species barriers.

The female's own occasional reciprocal display during Stage I and early Stage II is not a vital factor in self-stimulation, at least in *Phiale* and *Corythalia*, since it is not of regular occurrence; it is practically absent in *xanthopa*, and only fairly common in the other two *Corythalia* species; much of the apparent display in *Phiale* females probably should be interpreted rather as distance chemoperception ("sniffing") motions with the front legs and palps.

B. THREAT DISPLAY. The mechanism of threat display differs from that of courtship in the absence of positive releasing or directive value of any chemical stimuli and of the greater importance of special colors or "decorations." These badges combine with non-female behavior—i.e., height and width accentuation, plus increasing instead of decreasing activity—to release threat. The various signals, in order of importance, are general motion, motion configuration, a form-size element and, finally, any special male pattern-and-color badge. In nature, all normally act together as a configuration.

In runner genera, inter-male displays practically never occur; when they do, they are indistinguishable from courtship and break off before actual contact, probably because of the absence of female chemical releasers and/or directors. In intermediate genera, courtship and threat are usually identical until the spiders are practically touching. As in the runners, inter-male displays in these groups probably are the result of a male treating another male as a female. When the requisite close-range signals—visual, chemical or both—are not forthcoming, displacement behavior then occurs as special fighting or sparring. In hopper genera, cases of mistaken identity appear to occur only rarely, since threat and courtship are usually distinct throughout display.

C. COMPARISON AND COMMENT ON INNATE RELEASING MECHANISMS IN COURTSHIP AND THREAT. Before proceeding to a discussion of the functions and evolution of display, it may be helpful briefly to compare the principal aspects of the innate releasing mechanisms of display.

The perceptual sign stimuli for releasing display are overwhelmingly visual in both courtship and threat, involving motion, form and size. Neither contact nor airborne chemical stimuli alone will release display of any form in the genera studied, no matter how great the reinforcement, nor how strong the internal drive. However, both forms of chemical stimuli play an important differential role in display, their importance varying phylogenetically: in general, the presence of an airborne and/or contact chemical signal is a positive differentiator for courtship, while a pattern-and-color signal in some species plays a corresponding positive role in threat. Absence of either one usually acts as a positive signal for the alternative

type of display, other factors being equal. Airborne chemoperception takes precedence over a color-pattern badge in test situations where both are present, since males court, not threaten, young adult females painted like males. Motion-configuration also supercedes color-and-pattern, since males change courtship to threat when a previously quiescent, female-painted male starts threat display. Motion-configuration itself is a strong differentiator of the two types of display, particularly in the earliest and late stages; in the middle portions of courtship (i.e., late Stage I), the tendency of some females to reciprocal display never confuses the male.

As in other groups of animals, deficiency of one signal can often be compensated for by increase in another in the same stimulus situation. An example may be given of an unnaturally painted spider, which stimulates no response when running freely in the field. When it is chloroformed or killed, and mounted, so that it can be persistently manipulated with appropriate jerks close to the tested spider, it will frequently arouse a response through reinforcement. The same situation occurs when an old female is placed with a male in a small, closed container; with either contact or airborne chemical stimuli reinforced, the male frequently displays, although he would not be sufficiently stimulated to do so in the field.

Also as in other groups, maximal stimulus is needed to arouse minimal response in

spiders of weak internal drive, while spiders of strong internal drive give a normal response to a minimal stimulus, often responding to fraction of the usual configuration. As previously noted, summation readily occurs in this family.

Highly stimulated spiders in unnatural test situations, and spiders in states of moderate and low internal drive, frequently confuse threat and courtship reactions and behave inappropriately in other respects. These actions, which may often be classed as typical displacement behavior, give provocative clues to evolution; they will be considered later.

Wholly aside from test situations, however, the reaction of spiders in the field is to complex, closely integrated, mutually dependent configurational stimuli. Although there are no simple, lock-and-key arrangements, the more the stimulus situation departs from the normal, the less likely is it to release display.

In an over-all view, salticid display presents a complex combination of rigid and fluid aspects. It is true that display patterns are wholly fixed and instinctive. Learning plays no discernible part in this field of activity, since males reared in solitude perform either courtship or threat to perfection on their first attempt. Again, there is no evidence that imprinting ever takes place. Finally, when two males of different species display, each maintains rigidly his own dis-

TABLE VII.

## Generalized Course of Display in Salticids.

*Male.*

Becomes aware of ♀; starts display, Stage I. (*Minimal releaser*: several sight factors; airborne chemical stimuli also usually involved).

Approaches, in zigzags, or follows (if female retreats), continuing or resuming display. (*Minimal releaser and director*: above sight factors, plus type of female motion or lack of it). Special ♀ signs, such as vibrating palps and light abdominal spots probably have directive value.

Speeds up display tempo. (*Releasers and directors*: reduced motion of female, plus chemical stimuli. Self-stimulation is doubtless also a factor).

Enters Stage II.

(*Releasers*: primarily, proximity of female; also involved, usually, her lack of motion, low position, and, doubtless, reinforced chemical stimuli). Copulation follows unless female withdraws. (*Director*: sometimes a pale abdominal cross-bar).

*Female.*

Retreats, or watches ♂, usually in braced, high position, often vibrating palps. Rarely attacks. (*Minimal releaser and director*: several sight factors).

Becomes completely attentive; sometimes gives weak reciprocal display. (*Minimal releaser*: summative effect of display motions).

Ceases motion and, usually, crouches low, legs drawn in.

play pattern; no temporary modifications were ever seen to occur; by contrast, imitative behavior is frequent in vertebrates, as in the cormorants which altered their flight pattern to match that of their pelican companions (Beebe, 1938, p. 106).

Nevertheless, in working with living salticids, both their own individuality and the dynamic, unfinished, untidiness of display mechanisms are constantly apparent. A given spider's behavior is scarcely more predictable than that of a single electron. It depends, at any given instant, on great numbers of factors, external and internal, all in various stages of evolution, all related, and all themselves in a state of constant change. Wasted energy, abortive displays and lost opportunities are the rule. Altogether, the lumbering, complex, display mechanisms do not appear efficient. The most that can be said of them is that they work adequately enough, often enough, to ensure the perpetuation of the species. In the end, however, all the billions of salticids, hopping at this moment about the globe, are lively proof of their success.

#### VII. BEHAVIOR RELATED TO DISPLAY.

The basic similarity of behavior trends in all higher organisms—whether invertebrate or vertebrate—becomes increasingly clear. Not only do animals agree in the obvious, basic activities essential to all life, but they prove also to be surprisingly similar, among the end forms, in the more complex aspects of behavior. It has long been recognized that when vision becomes the dominant sense, elaborate, visually dominated courtships often evolve; the principle applies in certain cephalopods, crabs, spiders and insects as well as among fish, lizards and birds. The importance and frequent distinctness of threat display in salticids has been emphasized throughout this paper, and is in accord with results of recent behavior studies of birds and other vertebrates. Similarly, it is increasingly evident that dominance hierarchies, social and territorial behavior and displacement activities very often occur in higher invertebrates, though usually in primitive form. Although these latter aspects were studied only incidentally in the Rancho Grande salticids, the following observations appear to be worth recording.

A. DISPLACEMENT OR SUBSTITUTE BEHAVIOR. Experimental work sometimes drew inappropriate responses which correspond closely with typical displacement behavior in birds and other groups. When a stimulus configuration, while partly effective, was yet too exaggerated or incomplete to draw an appropriate display, the spider either retreated, attacked or by-passed the stimulus, exchanged threat for courtship and courtship for threat or regressed to a more primitive level of display behavior. It is interesting, however, that at no time were the substitute

activities wholly outside the sexual field. That is, never did the spider stalk an insect, pick up a discarded fly, spin a retreat, or even resort to grooming—that substitute action so common throughout much of the vertebrate world.

This restriction of displacement behavior appears to be an example of the rigidity typical of higher invertebrates. The compartments of life are kept distinct even in the midst of "mental" confusion, shock or frustration. With such restrictions, a girl would not reach for her lipstick when frightened by a bomb, nor a startled bird fidget with the makings of an off-season nest. To lapse into anthropomorphism, a salticid, when his prey escapes, never picks a fight with another male, nor does a rejected suitor gorge on extra flies.

B. DOMINANCE. In salticids, little hint has yet been found of long-term dominance relationships. Day to day variation, as shown in energetic courtship and threat or apathy and retreat, is on a rhythmic, physiological basis. It is true that some males never develop as high tone levels as others, the peaks of their rhythm curves being lower; in this sense dominance may be said to occur. I have never found, however, that rank is altered by a series of successes or failures in threat display or in actual combat. In primitive groups, where inter-male combat does not ordinarily exist, nothing approaching dominance relations was seen (apart from the usual physiological fluctuations, which determined the degree of courtship activity at a given time). In groups of young and old spiders placed together in a cage, the small ones invariably showed a healthy wariness of the large individuals; in view of the carnivorous character of the spiders, however, this behavior certainly needs no more explanation than the obvious one of self-defense. (See also p. 203).

C. SOCIALITY. *C. xanthopa* was one species in which traces of social behavior occurred. Along the leaf-strewn Water Trail, the richest habitat for this species, three to ten individuals were often found fairly close together. These groups included individuals of various ages and both sexes. They occurred in an area of about a square yard or two, divided by 10 to 20 feet from the next group. There was absolutely no discernible difference in the ecological characteristics of the populous and barren stretches, and indeed they shifted back and forth in quite irregular fashion over a period of weeks. Intra-specific relations within a group appeared purely casual. Abortive courtships and threat displays were brief and frequent. There was a high degree of mutual toleration, but, except for sexual situations, no inter-individual associations. It is noteworthy that quite small individuals, measuring less than half the size of the adults, were included in these groups, and apparently not stalked as food. Often their attention was attracted by the

displays of nearby adults, and at times they appeared to watch attentively these encounters of their elders, although they took no part whatever. The same behavior was noted in non-displaying adult males, and in fat females, obviously soon to lay eggs. On other occasions, these non-displaying members of the group simply continued their previous occupations, paying no attention to the others; they either maintained hour-long lookouts from the top of a projecting twig, stalked prey with indifferent success, hopped slowly along a meandering course, or simply moved occasionally out of the shifting sunlight.

An example of more advanced sociality was found in *Semorina megachelyne*. A large silk shelter was taken containing a group of 14 individuals of various instars, including several adult males and females. The young ranged from the first through the preadult stadia, the youngest being sheltered in a subcocoon. The morphologically primitive position of *Semorina*, compared with the advanced niche of *Corythalia*, indicates that sociality is not dependent in this group on phylogenetic specialization. Comparable dissociation of these two factors is found in other groups, including non-salticid spiders, lepidopteran caterpillars and birds.

It is probably significant that in neither of these examples of incipient sociality, *Semorina* and *Corythalia*, is inter-male fighting developed; in the one case the males follow the primitive pattern of mutual disregard; in the other, combat has been sublimated into threat. Never have I seen any signs of group formation in the more pugnacious genera.

**D. TERRITORY.** A territorial concept almost certainly exists in salticids, but work has scarcely been started on this angle. In captivity, all salticids generally returned to the same shelter, if they made one, night after night, even occupying it through several successive molts, so long as it was undisturbed. It seems probable that such a practice occurs also in the field. It is certainly a likely beginning for a concept of territory, or at least of home range. When siblings of *Phiale*, *Corythalia* and *Eustiromastix* young were reared in groups of three or four through the early molts, they not only got on peacefully at all times, but each always—on the many occasions when they were observed with this point in mind—returned to his own shelter at night and during ecdysis. One group of three *Phiale dybowskii* was reared to adulthood in this fashion. Individual variations in size and pattern made the identification of individuals easy after the second instar.

Cannibalism is exceedingly rare in this family, and when it occurs it is only under extreme provocation of hunger or gross size disparity. In the few cases where females killed the males, they were eaten only twice, both in *Eustiromastix*. After inter-male

battles, the losers were never eaten, even when they had been disabled or killed.

On the other hand, there is no evidence yet that salticids actually defend a territory, even in the case of adult males. I am quite sure that the young at least do not have one, although the concept of home range seems applicable, at least in *C. xanthopa*. This term, as defined by Burt (1943), signifies that wandering of individuals is limited, although the area is shared at least tolerantly with others of the same species.

It is notable that although in the orb-weavers the adult males wander, in *Corythalia xanthopa*—the only species where field marking has been initiated—the females did the roaming. One female, recaptured after 34 days, was taken 186 feet from her original location, while several marked males were seen repeatedly during a single month within two feet of their original positions. A similar situation exists in fiddler crabs (Crane, 1941, p. 160) and, of course in vertebrates (e.g., Evans, 1938; Lack, 1943).

When a strong adult male *xanthopa* in A-tone was dropped close to a wild male who had hitherto been undisturbed, the usual threat display took place, but I saw no sign whatever that the strange male was usually driven off by the previous "tenant," or showed much perturbation. The response was tested more than ten times. This result is in strong contrast to the behavior of an orb-weaver dropped into a strange web. The retreat of a protagonist seemed to depend only on his physiological condition, rather than on any general reduced pugnacity or sense of security when out of his own range.

The other intermediate and hopper group salticids were in general strongly individualistic; two or more adult males were rarely shaken from the same herb or bush, and it may be that in these cases definite territories are maintained and defended. On the other hand, possession or invasion of a territory is certainly not a prerequisite to display, indeed by the prompt reactions of A-tone males dropped simultaneously on a strange table-top. Altogether, development of territoriality appears to be a very primitive level.

## VIII. FUNCTIONS OF DISPLAY.

### A. COURTSHIP.

The theories concerning the functions of courtship display in spiders have already been reviewed (p. 170). The conclusions resulting from the Rancho Grande studies are as follows: First, courtship display is unquestionably a necessary preliminary to mating, and not merely an outlet of excess energy for males in breeding condition, as suggested by Wallace and Berland. Second, sexual selection in the original sense used by Darwin and the Peckhams is not operative. Third, as Savory points out, the concept of recognition as distinct from, and preceding stimulation, does not appear to be necessary.

Indeed, any concept of preliminary recognition seems to be highly questionable, even when recognition is regarded merely as a kind of realization by the female that a potential meal is not at hand. Rather, it seems probable that it is through her sexual stimulation that her feeding impulses are inhibited. In this view, the two processes are merely different results of the same psycho-physical sequence, developing simultaneously and governed by the same stimulus configuration. To distinguish between recognition and stimulation in salticids seems as difficult as to differentiate temporally between human fear and loss of appetite when a charging bull interrupts a picnic: in each case two emotions, or at least sensations, are involved, one positive, one negative, and bearing an inverse ratio to each other.

As modern observers agree (e.g., Savory, 1928), the stimulation of the female is probably physically as well as psychologically necessary, since alterations appear to be made in the epigynum itself in order to permit the insertion of the palps.

The following summary may now be given of the functions of salticid courtship, as they appear from the Rancho Grande studies. It is, in essence, a selection and elaboration of certain earlier views, especially those of Savory and Bristowe. Most of it applies to animal courtship in general. The term "courtship," as used throughout this paper, includes the responses of the female as well as those of the male, and the production as well as the reception of sign stimuli.

The primary functions of courtship in salticids, then, may be expressed as follows: Courtship serves to bring to mutual attention and proximity two individuals of the same species, opposite sex and requisite physiological condition; simultaneously it inhibits their usual predator and self-protective behavior while stimulating each sex so that copulation may take place. These are the primary functions, of obvious and immediate biological use in the life of the individual.

Secondary functions, which may be considered by-products of the above, are of importance in the life of the species. First, sexual selection operates in the sense that males of chronically mediocre drive—among which are doubtless individuals of genetic weakness—do not use sufficient energy and persistence to win acceptance by females. Second, courtship display acts as an effective isolating mechanism between similar but well-evolved species: Since crosses would, judging by analogy in other animals, often prove sterile or unfit, the progressively exclusive action of individual courtships must prevent considerable germ cell wastage. The effectiveness of display as an isolating mechanism will be discussed in the section on evolutionary aspects.

## B. THREAT.

Earlier views on the cause and function of fighting and/or threat display among salticid males were summarized on p. 170. To recapitulate briefly the two extreme hypotheses, the Peckhams accepted the unmodified Darwinian premise that inter-male fighting was brought on by rivalry; as a result, the females mated with the strongest or bravest or boldest, either through male conquest or female choice. Bristowe, on the other hand, holds that inter-male display occurs when males temporarily mistake each other for females; actual fighting sometimes results through frustration.

Neither of these views explains satisfactorily the condition in many salticids, including *Corythalia*. Against the Darwinian hypothesis stand the facts that the winner of a combat does not necessarily get the adjacent female, females certainly do not necessarily "choose" the winners, the fights are usually no more than slight psychological sparring matches, at which females may or may not be present, and the winners—that is, the more aggressive—are certainly not necessarily the largest or brightest of the males. I have seen a six or seven-legged male, of small size, prevail over larger individuals on successive days; almost certainly the epigamic physiological rhythm was involved; but some individuals appear regularly to be more dominant (in their A-tone periods) than others of the same threshold. (See also p. 202). In the species Bristowe observed in England, courtship and threat display were identical. For such as these, his hypotheses of mistaken identity is completely satisfactory. According to the hypothesis of phylogeny presented in the present paper, these represent an intermediate phase of development of dependence on sight practically superseding dependence on chemical stimuli. In genera taken to represent more primitive forms, such as *Menemerus*, *Ashtabula* and *Semorina*, all far more dependent on chemical stimuli, threat display is apparently nonexistent and mirror display never occurs (except in self-stimulation in *Menemerus*, p. 182). Finally, in the most visually dependent genera, the hopper groups, of which the best ultimate examples are in *Corythalia*, threat and courtship are completely divorced. In *C. xanthopa* such an extreme is reached that different appendages are used in the two kinds of display, and true fighting has never been known to occur except under extremes of crowded, hot laboratory conditions. It seems that here there is a sublimation of aggressive impulses, as in many birds, and that a type of mutual stimulation takes place which is useful in maintaining or increasing sexual tone.

Just as in courtship display, it must be kept always in mind that male spiders are potentially dangerous to one another, both because of their carnivorous habits and their poison glands; this is rarely the case in other

groups of animals. Where mistaken identity in salticids results in actual fighting, with consequent frequent casualties, the following conclusions concerning its functions appear to be valid. All of them are of the secondary type, of importance to the species, rather than to the individual.

1. The elimination through disability or death of weaker males, thus strengthening the strain through natural selection.

2. The prevention of weaker males mating as often as do stronger individuals.

3. The encouragement of excess males to go elsewhere in search of mateless females, and so ensuring the more even distribution of the sexes.

These three points conform to Darwin's general hypothesis, excepting only that females do not deliberately choose superior males. Although it is true, as Bristowe and others maintain, that actual fighting, to the point of inflicting injury or death, is rare among spiders, it most certainly does occur, under natural conditions at that, among some salticids at Rancho Grande. For example, an apparently new genus near *Capidava* (not yet described) time and again fought to the death in large display boxes and on open table tops; twice they were seen fighting beside trails in the forest; in one of the latter cases a male was killed; in the other both were injured.

In the majority of salticids, and especially in *Corythalia*, where threat display is highly ritualized and actual fighting occurs only rarely and atypically, the physical elimination of males does not take place. In these cases, the threat display undoubtedly represents an advance over the more wasteful practice of actual fighting.

In these ritualized displays, the additional function of maintaining emotional tension is probably of importance to the species as a whole, although it is not necessary to individuals. Perhaps males having frequent opportunity for epigamic display maintain A-tone for longer periods. Armstrong, 1947, discusses tone maintenance in birds and gives excellent examples. No experiments whatever appear to have been done on this question in spiders, but its importance is becoming increasingly recognized in other groups. Experiments at Rancho Grande proved only that threat display is not a prerequisite to successful mating, either from the male or female point of view. *Phiale* and two species of *Coruthalia* all showed conclusively that virgin males displayed promptly and completely to virgin females and were accepted by them, without any of the males ever having seen another male, much less practised or observed threat display. Each of the individuals tested was reared through at least three previous instars, and permitted to molt to the adult, in complete solitude. Precautions were taken, as in all display experiments, to eliminate the danger of chemical stimuli remaining from previous spiders.

Conversely, virgin male *Phiale*, *C. chalcea* and *C. xanthopa* performed threat display perfectly to virgin males of their own species without ever having laid eyes on or received chemical stimuli from a female or another male.

Nothing is known of territoriality in any of the species except in *xanthopa*: here it appears to exist, but in rudimentary form (p. 203). This amount, however, might account for the development and maintenance in this species of a completely separate threat display. But it seems certain, as said above, that at least equally important to the species is its function of mutual stimulus and of keeping males to some pitch of excitement, perhaps in a state of long-sustained A-tone for dealing with wandering and scattered females. There is no question but that males tend to display to each other more promptly in the presence of a female: in photographing threat displays, one female was always placed with the two male subjects, since females were repeatedly found to have this decided catalytic effect. Often the males spent more time displaying to each other than to the female.

Another function of threat display doubtless is its usefulness as a "safety valve," its displacement behavior aspect, for spiders already keyed to display pitch (p. 202).

No true group displays, comparable to those reported by the Peckhams (1889, p. 40) for several dendryphantinids, were seen at Rancho Grande. They undoubtedly should be regarded as rudimentary social affairs, again with the double function of inhibiting hunger and stimulating sex.

#### IX. EVOLUTIONARY ASPECTS OF DISPLAY.

The purpose of this section is to interpret salticid display from an evolutionary point of view. Although the dangers of top-heavy generalizations are fully realized, it seems advisable to organize the limited data available. As Menninger puts it, "Classifications must never be taken too seriously—but the fear to use them has prevented much more thinking." (1945, p. 34).

##### A. HYPOTHETICAL PHILOGENY.

While many display similarities obviously coincide with natural affinities, others reflect only an extensive parallelism among the subfamilies. The salticids show a "bush type" of evolution, with similar basic trends in each branch.

The parallelism is well shown in the locomotive, sensory and display differences that have been discussed from time to time in this and preceding papers (Parts II and III). At Rancho Grande, *Menemerus*, *Semorina* and *Ashtabula* are examples of the apparently primitive "runner" group; *Sassacus* and *Phiale* are intermediate forms; and *Corythalia* and *Mago* are advanced "hoppers." Each of these groups contains representatives of two or more subfamilies, and each

subfamily usually includes genera in two or more groups. Their various characteristics will now be assembled.

The "runners" never jump or hop during horizontal progress except to cross a gap or leap on prey. According to experiments, they depend more on chemotaxis than do the other groups, court less readily in its absence, rarely or never respond to a mirror image and are rather strongly affected by the loss of their palps and first legs. The first legs are often held in front of them, not helping in locomotion, but barely clearing the ground, while the palps may pat the ground lightly. When in a strange place, they run to and fro, palpating ceaselessly and appearing endlessly "restless" and "nervous." Although they stalk and leap on prey like the hoppers, they nevertheless tackle large prey in preference to small. *Menemerus* chooses moths and the larger Diptera instead of *Drosophila*; in captivity, when no choice is given, they miss fruit flies repeatedly and eventually become thin. Large, hopper-group *Corythalia* of similar size, in contrast, can live out their lives on a fruit fly diet, catching them with ease. Morphologically, the most obvious characteristics of the runners are low carapaces and few, weak leg spines.

The intermediate group seems to be in the middle of changing from moderate chemotactic to nearly complete visual dependence by way of distance chemoperception. They are long-sighted, hop when hard-pressed, pursue their mates via efficient short-cuts and are relatively little affected in display when deprived of palps and first legs. Yet they appear to gain chemical sense impressions from a distance largely through these members which, from the second instar, often wave in the air during normal exploration. *Phiale*, when near mates or food, before display or stalking begins, is especially prone to wave the first legs up and down. It seems probable that they are "sniffing" the air. Berland's accounts of *Philaeus chrysops* and others (1914, 1923, 1927), waving their legs when completely alone in clean boxes, sound as though these were intermediate-group spiders. *Philaeus*, incidentally, is a close relative of *Phiale*. Bonnet's (1933) *Philaeus*, studied in another part of France, never waved the legs except in true display; why these observations should differ so radically remains, for the present, a mystery. Berland's *Saitis barbipes* waved the third legs at random, as well as in display.

Among salticids generally, it may be that the female is "sniffing" the male when during display she often vibrates the palps and first legs; if so, the sense of distance chemoperception may evolve through the female. Certainly in the runners, the female's palps are usually particularly active, whether or not they quite touch the ground in true chemotaxis. It does not seem advisable to consider this activity solely as a symptom of nervous tension.

The "hoppers" are the visually dominated salticids; chemotaxis means little or nothing to them under natural conditions; distance chemoperception operates as a secondary releaser for courtship display. Their sight is magnificently developed, and their courtship sign stimuli overwhelmingly visual. These are the "poised" spiders; they sit quietly when dropped on the table, look about them, then hop away, at leisure and with frequent pauses, interspersed with a measured walk. All eight legs remain firmly on the ground except during a hop or display; there is otherwise no raising at all of the first legs, or carrying of them clear of the ground. Carapaces are high and leg spines strong and numerous.

An inspection of Table II and Text-figs. 2 and 6 will show that among runners courtship is simple and threat practically nonexistent. In intermediate groups, actual fighting is frequent, but its early stages are little or not at all differentiated from courtship. In the hoppers, true fighting is rare and special threat display the rule.

The divisions appear to be based primarily on the different degrees of visual dominance. The eyes in each successive group seem to take over more and more from the chemical senses. And it is the dependence on the latter which appears, both functionally and morphologically, the closer to the pre-salticid stock. But, as in various studies of animal and human societies, the forms in midevolution seem most subject to combativeness. They appear to be in the middle of changing from one way of life to another, mistakes are made, frustration results and combat ensues.

One vitally interesting clue to the evolution of salticid display is given in the behavior of the highly specialized hopper, *Corythalia xanthopa*. Senile, over-stimulated or low-tone spiders often use primitive chemotaxis during courtship to the frequent and inappropriate exclusion of other sign stimuli (p. 178). These and other hoppers in a similar condition tend to leap at threat stimuli rather than perform their characteristic displays. This behavior seems unquestionably atavistic, regressive in a phylogenetic sense. Similar examples among displacement behavior (p. 202) consist in the replacement of threat with physical attack in experimental situations.

## B. ORIGINS OF DISPLAY MOTIONS.

The biological principle of least effort, as presented by Zipf (1949), proves to be of considerable help in this attempt to understand the development of salticid display. The subprinciples of permutation (i.e., combination) and multiple function seem especially applicable. Armstrong in particular has implied their operation throughout his discussion of bird display (1947, e.g. p. 61).

From this point of view, display evolved through the use, with modification, of actions, senses and structures already serving

less specialized purposes in the economy of the organism. Only rarely would a display action evolve especially to fill an epigamic need.

In direct agreement with this general concept is Bristowe's view of the origin of salticid display. It appears to him that the rituals grew from the groping and fending-off motions of the primitive stock. Certainly, it seems far more likely that display grew from gestures like these, which had a different original function, than that an entire new series of motions arose for display alone.

The acceleration and exaggeration of simple motions, so typical of display, are clearly related to the excitement, to the nervous agitation, connected with breeding activity. The difference between this view and those of Wallace and Berland is that, to them, display appeared to have no function; it was simply an expression of high vitality or excitement.

The "groping" motions certainly included chemotaxic behavior, such as is used by many runners in casual exploration as well as in responding to the trails of females. The similar behavior of very young runners, just out of the cocoon, contributes largely to this conclusion. Again, high-in-air leg waving, found in numerous displays throughout the family, seems to have an undoubted origin in distance chemoperception of air-borne stimuli.

Plausible origins of a number of other common display gestures may be proposed. Thus, the vibration of palps originated in the "sniffing" motions so characteristic of chemoperception, including both contact and distance types. The vibration is perhaps also useful in dissipating nervous tension during courting excitement.

Twitching or lowering the abdomen is another frequent display gesture which may be due to permutation. Probably it was concerned originally only in attaching silk to the substratum, in the usual salticid fashion of ensuring a quick escape. An almost universal part of display is the habit of approaching a female in zigzags, which obviously gives added time for necessary stimulation. When zigzagging was first combined with lowered spinnerets, it is easy to see how a side-swinging abdomen could have developed; in the more primitive, long-abdomened Dendryphantinae, it seems a natural result analogous to that of a train rounding a bend.

The elevation of the abdomen is characteristic of all the ant-mimicking or pseudo-scorpion-like salticids in which display is known. It was also typical of normal progress in *Semorina* and related genera as early as the second instar. Its ultimate origin is not yet clear. Possibly the gesture started as the end of the dropping motion, as a spider hits the ground at the end of a silk cable. Possibly, actual scorpion or pseudo-scorpion mimicry was involved among larger for-

bears; these hypothetical spiders may well have been large enough to win a mimic's protection from frogs and lizards (cf. Part III, p. 37).

Again, it is possible that abdominal lifting, quiverings, and even the swift rockings of some displays are concerned in the emission and wafting of a chemical display signal. I have as yet no corroborative experimental data; work with sealed genital grooves and epigyna—a promising approach—has not been adequate. The possibility is mentioned here as a potential X-factor, an "etc." that may prove important.

In *Lyssomanes* the retinal motion within the light-green, antero-median eyes seems to play a definite role in courtship. The resultant color shifts increase in tempo with excitement. They seem clearly to be a ritualization of incidental effects resulting from the mechanics of vision. Although the same motions occur throughout this and other large-eyed families, they are rarely as noticeable because of the dark pigment which usually surrounds the retina. The morphological basis has been discussed by Homann (1928, p. 235).

All of the display motions mentioned up to this point can have evolved through permutation of activities normally occurring in the simplest epigamic situations as well as in other fields—dropping from overhead, fixing a silk drag-line for quick escape, groping forward, and so on. In this way these postulated display origins parallel the epigamic character of displacement reactions (p. 202). Several possible exceptions will now be discussed.

The display crawling motion may have originated from the hunting rather than the sexual field of behavior. In this phase, the male lowers the carapace and creeps directly forward. Usually it occurs during late Stage I or early Stage II of courtship. It crops up sporadically, with variations, in almost every subfamily observed. It may have grown from a displaced stalking motion, definitely outside the sexual field. It appears more probable, however, that there is a sort of innate, anticipatory imitation: the crouch is extremely similar to that usually assumed by the female during the latter stages of courtship. As in many birds, this position often acts as an important releaser for the latter part of the male's display. Its previous assumption by salticid males, in combination with a typically masculine approach and leg stretching, perhaps has value in empathically inducing the female to assume a similar position. Whatever the origin, this motion is one of the most remarkable in all salticid display.

Two widespread groups of display gestures do not seem to be based on economical permutation, on made-over motions. They are the lateral leg displays and the stretchings up to maximum height. It seems, rather, that these salticids have evolved independently the widely successful animal custom of ap-

pearing larger than life in a crisis. It is exceedingly interesting that they never use the technique in other departments of living; never do they display before prey or hungry enemies; in salticids, the "big bluff" is reserved solely for an epigamic crisis.

Posing is a frequent occurrence in displays of the size-increasing type, particularly in threat and especially among the plexippinids. The motionless state, amounting to a kind of catatonia, often persists for many seconds after the exciting object has been removed. Similar behavior occurs in many animals under various conditions; it has been discussed at length by Armstrong in connection with bird display (1947). Its origin in salticids remains obscure.

This effect of seeming larger—whether in connection with courtship or threat—is of special interest in comparing displays within the advanced genus *Corythalia*. Courtship and threat display are distinct in the three species studied. However, in *xanthopa*, courtship is simple and primitive, exhibiting only the first two legs, while the remaining pairs, all specialized, are reserved for the highly developed threat display. In *chalcea* and *fulgipedia*, on the other hand, the first legs are used only in Stage II of courtship, while more posterior legs take part in Stage I of both courtship and threat. It seems that *xanthopa* represents the more primitive form, with the size-increasing threat fan occurring first. Then, by permutation with modification, the original threat function was extended, in the other species, to form a more complicated courtship. In support of this hypothesis, *xanthopa* appears decidedly more generalized than the other two species in several structural and developmental characters; these include eye proportions, spinulation, course of color development and dentition of tarsal claws.

The displays of two advanced Dendryphantinae give similarly interesting clues to their relative evolutionary status. One species, *Sassacus ocellatus*, shows a vestige of the side-swing typical of the subfamily; in the other, *S. flavicinctus*, no swinging occurs. It is the latter form which is morphologically more advanced.

The subject of vestigial behavior characters is, of course, one of the most controversial. Which traits are to be considered vestigial and which rudimentary? One point, however, appears increasingly clear. Any successful animal species includes in its organization a hodgepodge of behavioral relics in addition to the usual morphological trash. When a dog revolves before lying down on a grassless rug, he is performing a well-worn example of a functional antique. Similarly, *Sassacus*, in a moment of face-to-face courting, swings his stubby abdomen sideways, even though it and its ocellus are well hidden behind the sturdy legs; surely this example belongs equally in a behavioristic museum.

### C. RELATION OF SECONDARY SEXUAL CHARACTERS TO DISPLAY.

The question of vestigial characters leads directly to the problems of ornamentation, where morphological and behavioral relations are even more involved. Some "ornaments," including the fringes and iridescence on the displayed legs of *Corythalia*, are probably recently evolved structures; they are highly variable in individuals; their adaptive value is so slight that it has not been proved experimentally to exist at all; they develop (as do most epigamic characters) only in the final instar; and they are confined altogether to males. Yet their place in the perceptual sign situation seems unquestionable; on a mathematical basis these recent refinements would doubtless prove to have definite adaptive value, at least to the extent of making their possessor more conspicuous during display.

Next to these come such signs as the yellow or white clypeal bands of *C. xanthopa* and *Phiale* males, which have decided, contemporary releasing value for threat display.

Finally, in a confusing mixture, comes the mass of "decorations," including vestiges, characters linked genetically to selected structures, patterns aiding in camouflage, and mere byproducts of metabolism. Only rarely can their origins be satisfactorily discovered or inferred. They include the sex-chromosome-controlled tufts of dark-phase male *Maevia vittata* (Painter, 1913), the scarlet-red of *Phiale* abdomens and the circles of colored scales around most salticid eyes. These circles occur as early as the second instar and are irrespective of sex. Possibly, among primitive salticids, they had adaptive value, making the large eyes or frontal regions more conspicuous in display; now they have no demonstrable function, and their early appearance, far back in ontogeny, indicates a vestigial, if not a purely metabolic, character.

A related instance is the occurrence of white scales on the legs of intermediate instars in *Corythalia*, followed by their obsolescence on the front of legs in adult males; they may well represent an old secondary or minor display character which has been superseded by iridescence; a similar explanation may apply to the reduction of clypeus white in adult male *chalcea* and *fulgipedia*.

The variable distal abdominal ocelli of *Sassacus ocellatus*, mentioned above, seem to belong rather definitely among the vestigial character group.

All of these relics, again in agreement with the principle of least effort, persist unless it takes less "effort" for the organisms to drop them than to carry them along.

The old question as to the significance of elongate chelicerae recurs. Bristowe has pointed out that they are only rarely used in courtship or fighting, and also are unquestionably less efficient than those of the usual size (1929, p. 339). It seems to me that

they are enlarged, not to aid fighting, but much as first legs are specialized, primarily for an increase in conspicuous area. It appears, too, that secondarily their very inefficiency may be adaptive in the way that a threat display is adaptive: the danger of mutual injury is reduced without reduction of the presumable toning value of aggressive behavior.

It is noteworthy that these enlarged chelicerae, in the genera with which I am familiar, occur in the middle groups: in the Dendryphantinae, and in *Salticus* (morphologically an advanced marpissinid), in which aggression reaching the contact stages is most developed. Elongate jaws occur also in the highly aberrant lyssomaninids, but I have never been able to induce any threat display in them whatsoever. Another point is that in some genera, for example *Sassacus* and *Ashtabula*, the length of the chelicerae is highly variable among individuals, exactly as in certain beetles (e.g., Beebe, 1947) without any reference to their general tone or health. No use as a specialized, female-holding tool, as is found in *Pachygnatha*, has ever been observed in a salticid.

In salticids, as seems increasingly clear in other groups, function appears basic, structure follows after. The male salticid raises his forelegs or middle legs, or jiggles his palps; elongation, thickening, blackening, whitening, polishing or fringing may or may not follow. A spider does not, as the older naturalists naively implied, show off his decorations; rather, his decorations evolved in a conspicuous position. Every experiment made in this study showed that motion—function—was of more importance than morphological detail. This view does not, of course, rule out the obviously great reciprocal influence of behavior and morphology during selection. Nevertheless, in any general trend, it must be the function which usually changes first, while vestigial tufts and spots, seemingly placed to accent an obsolete display, persist indefinitely.

#### D. SEXUAL DIMORPHISM AND DISPLAY.

The correspondence in forms of sexual dimorphism in both salticids and birds was discussed at length by the Peckhams (1889, 1890). Here their general points will only be summarized and remarks made concerning the relationship of dimorphism to female behavior. As in birds, dimorphism is of three principal types. First, and apparently most primitive, neither sex is strikingly marked, or greatly differentiated in secondary characteristics; display is primitive and the female remains completely passive (examples: *Semorina*, *Mago*); in the second type, sexual dimorphism is strong, the female remaining dull and adolescent in coloring and her behavior passive (examples: *Sassacus flavicinctus*, *Plexippus paykullii*, *Corythalia chalcea*); in the third, both sexes are strikingly marked and similar, with the

female often acting aggressively or, in advanced groups, tending to reciprocal display with the male (examples: *Sassacus ocellatus*, *Corythalia fulgipedia*). However, there is by no means a fixed correspondence between female aggression and striking pattern: for example, the most aggressive females found at Rancho Grande were those of *Eustiromastix* sp.; structurally, this species is strongly dimorphic with the females dull and little differentiated from the young; they always killed the males shortly after mating if kept together, and, in courting, the males had to be excessively cautious. A similar situation occurs in some dendryphantinids (cf. Peckham, 1889). As in birds, all degrees of dimorphism, both of morphology and behavior, can sometimes be found at low taxonomic levels, including the genus. It seems certain that hormones and neurohumors are as deeply concerned in these characteristics as in vertebrates.

#### E. CLIMATE AND DISPLAY.

Another interesting aspect of phylogeny refers to a possible effect of climate on the development of display. It seems likely that there are fundamental differences in behavior in the tropics and in the north, which may well be responsible for some of the differences between the Rancho Grande observations and those in the temperate zone.

The differences in breeding season length is usually considerable. At Rancho Grande it is months long, while in the north the adult males are often active only a few days or several weeks. In the short-summered north the relatively few salticids which adapted themselves to the severe winters also had to adjust in less obvious ways. Basically this meant the more perfect coordination of the breeding mechanisms of the two sexes; in a short season there would be little time for the vagaries of physiological rhythms or of regressive behavior, both of which are so evident at Rancho Grande. Also, in a climate where many individuals of few species are the rule, instead of vice versa, there would be no economy in restricting a female to the single insemination which appears typical at Rancho Grande. Again, the same northern conditions might encourage the development of the almost communal displays described by Peckham (1889, p. 40), and which I have never had the fortune to see in the tropics. It must be remarked, however, that communal displays in birds reach a high tropical development, as in birds of paradise and cocks-of-the-rock.

Finally, in the brief northern summer persistent courtships and protracted fights apparently are usual, from accounts in the literature. By contrast, in Venezuela courtship and threat displays are almost always short; either they are unsuccessful, which is usually the case, and quickly broken off, or else they are consummated in a few minutes. This difference is probably also tied up

with the leisure of physiological rhythm in the tropics, with the lack of a pressing hurry to coordinate the mechanisms.

#### F. DISPLAYS AS SPECIFIC BARRIERS.

Almost every student of salticid behavior is familiar with the frequent occurrence of display between different species, both in courtship and in threat. At Rancho Grande, it was found that in general any A-tone male would initiate appropriate display before any moving male or female that showed a few sign stimuli roughly similar to those of its own species. The females, presumably because of the chemical factors, were invariably close relatives; the males, in inter-male display, had to conform in appearance only. The heterosexual pairs of species which displayed regularly to each other, under unconfined laboratory conditions, were the following: *Corythalia chalcea* and *C. fulgipedia*; *Plexippus paykulli*, female, and *Eustiromastix* sp., male; any two species of *Phiale*.

This weak selectivity would, on first sight, seem to indicate that differences in display have little value in erecting or maintaining specific barriers. Closer study, however, results in the following observations.

First, display is only initiated; it is rarely carried on beyond early Stage I. When it is continued longer (in courtship only), by a male of exceedingly high tone, the female always breaks away well before the end of Stage II. Even in experimental situations with chloroformed females, the male himself was never, in more than a dozen trials, seen actually to copulate; it seemed that in each case a mechanical barrier was reached in the epigynum. On the other hand, fertile eggs were secured after copulation with chloroformed females in one pair of *Eustiromastix* sp. and one of *Corythalia chalcea*, showing that the drugged condition of the female was not the final deterrent.

Second, when individuals of their own species are introduced to a pair of mismatched displaying spiders, attention is quite promptly turned to the appropriate newcomer.

The above does not of course show that inter-specific crosses may not occur in nature; it only indicates that, if they do so, they are probably unusual in the area studied, even though several pairs of closely related species occur, each having similar displays and occupying overlapping ecological niches. These include *Phiale dybowskii* with *Phiale* sp.; the latter with *P. flammea*; and *Corythalia fulgipedia* with *C. chalcea*.

The particulate nature of display explains its apparent inefficiency. It does not act as a single unit, but rather as a series of strainers of progressively finer mesh. An interspecific display is interrupted when the constantly changing stimulus configuration—releasing, directive or both—becomes too weak, from the viewpoint of one partner, to draw the requisite response. This positive response

may, of course, appear active or passive, depending both on the stage of display and on the sex of the partner. The point at which the display breaks off depends largely on the physiological conditions of the two protagonists.

It was pointed out on p. 204 that display may aid in the economy of germ cells by preventing unproductive mésalliances. It seems clear, however, that as a practical barrier between established species it has relatively little importance; the primary walls are ecological and morphological. As in most other animal groups, there is usually slight overlapping of the microgeographical ranges, of the ultimate ecological niches, in closely related species; under natural conditions, interspecific display must occur but rarely. Also, even if such display runs its full course, the specific differences of palps and epigyna are probably in most cases effective final barriers.

In the formation of species, display may prove of more importance. As Mayr emphasizes (1947), the growth of geographic isolation is doubtless the essential factor in all species formation. Granting this precedence, it seems likely that cumulative slight differences in display, as in other behavior, often pave the way for final morphological breeding isolation. No one who has been struck, in other animal groups, by display distinctions within a species or subspecies in different parts of its range can doubt that functional change tends to precede structural differentiation. To give examples from my own experience, a crab and a bird may be mentioned. The waving rhythm of the fiddler, *Uca pugnax rapax* (Smith), varies from Porto Rico down through the islands to Trinidad and British Guiana, and on west through Venezuela to reach a peak of complexity in Cartagena, Colombia. Similarly, the choruses of chachalacas, *Ortalis ruficauda* (Jard.), when heard in Tobago and Caracas, sound as distinct as the calls of ducks and turkeys in a barnyard. The apparent display differences in *Maevia vittata* in Wisconsin and Connecticut (Peckham, 1889, p. 53; Painter, 1913, p. 634) hint at similar geographic distinctions, of obvious evolutionary interest, among salticid spiders.

#### X. SUMMARY.

(See also sectional summaries on pp. 184, 185, 187, 190, 192 and 196-199).

1. A study was made of the epigamic display behavior of fifteen species of salticid spiders distributed through seven subfamilies. All observations and experiments were made at Rancho Grande, Parque Nacional de Aragua, Venezuela.

2. The factors comprising the innate releasing mechanisms prove to be similar throughout the family, but their relative importance varies from genus to genus even within the same subfamily, and, in minor sign stimuli, from species to species.

3. The principal controlling factors of the internal releasing mechanism appear to be age, fluctuating epigamic rhythm, hunger, thirst, fatigue, overstimulation and attention.

4. The epigamic rhythm plays an especially important part in daily responses. Only spiders of the highest tone (i.e., lowest epigamic threshold) usually carry courtship to completion in either field or laboratory. No regular periodicity, however, was observed.

5. The controlling factors of the external releasing and directive mechanisms are divided into those of the physical environment and of the configurational stimulus situation (sign stimuli).

6. Temperature, humidity and light are recognized as the principal environmental variables. Display may be released throughout a wide range of these factors.

7. Tactile, chemical and visual stimuli are regarded as the major components of the configurational stimulus situation.

8. Display cannot be released through touch, although it plays an important role in the final stages of courtship.

9. Neither is display released through chemical stimuli alone although, in the presence of certain visual stimuli, they are important secondary releasers of courtship. They appear to stimulate two overlapping senses, contact chemoperception (chemotaxis) and distance or airborne chemoperception (apparently akin to odor). The importance of each type, both in comparison with each other and with visual stimuli, depends on the degree of visual dominance of the genus; in the more primitive genera, although they too are visually dominated, greater dependence is placed on chemical senses than in more advanced forms. Absence of chemical stimuli sometimes changes courtship to threat display or actual fighting.

10. Visual stimuli alone are sufficient to release display. The principal factors of the visual stimulus situation appear to be motion, distance, size, form, pattern, intensity and color. The relative importance as well as the characteristics of these factors varies throughout the family, and no single one ever proved to be an essential, primary releaser.

11. In general, motion, form and apparent size are the most important factors, and the sign stimuli among these categories in each genus or species may vary within fairly wide limits. Pattern, intensity (except for visibility contrast) and color, on the other hand, have little releasing value. Sometimes, however, a special contrasting or colored marking does act as a definite releaser or director for display. An example is the yellow clypeal band of *C. xanthopa*, which, in combination with an adequate supporting visual configuration, is a releaser for inter-male threat display. An undoubted director is the

white sub-basal abdominal band of many females, which acts as a copulation guide. Most clypeal and palp markings, iridescent patches, leg fringes, etc., have no high releasing value, since complete display readily takes place in their absence without strengthening of other elements in the stimulus configuration.

12. This apparent uselessness of epigamic "decorations" does not, of course, mean that they are necessarily lacking in adaptive value for display or that selection has not been acting upon them toward that end. It is merely a further instance of the unequal value of sign stimuli, and of the lack of a lock-key releasing formula: the effective configuration is made up of many small bits; together, they have cumulative releasing, directive or merely excitatory value, but a number may be missing from an individual situation without noticeable effect. To only one dynamic compound element can the term "primary releaser" be applied: this is a unit composed of any of several adequate visual stimuli; very few releasers and directors are of even secondary importance.

13. Evidence is presented that color perception occurs at least in the yellow region; the two tested genera, *Corythalia* and *Phiale*, appear to be insensitive to the red end of the spectrum.

14. All of the components—external and internal—of the innate releasing and directive mechanism form a closely woven, mutually dependent, dynamic whole. When one important part of the normal configuration is weak or absent, reinforcement of another part—including especially high tone in the receptor spider—can bring a complete response: the concept of heterogeneous summation is as important in salticids as in other animal groups.

15. Nevertheless, in the field courtships are usually incomplete when the stimulus configuration is weak in any particular.

16. Although individual spiders, particularly females, sometimes showed slight, temporary idiosyncrasies, display patterns are fixed and instinctive. No evidence at all was found of display learning, imprinting or copying of other species' patterns.

17. Displacement behavior is confined to actions which normally occur in the sexual field.

18. Little evidence has been found of dominance relationships in the vertebrate sense; temporary dominance seems to be due to fluctuating epigamic rhythms.

19. Sociality and home range concepts apply in some species on a primitive level; no defended territories were observed.

20. The functions of courtship in this family are held to be stimulatory with a simultaneous blocking of hunger drives; the concept of "recognition" does not seem to be necessary.

21. The explanations and functions of threat display depend on the phylogenetic position of the genus in reference to chemical dependence. In the apparently most primitive groups, the males take little or no notice of one another; there is neither fighting nor threat display, nor even inter-male courtship; mirror display does not normally occur. In intermediate genera, with greater visual dependence but strong reliance on airborne chemical stimuli, courtship and threat are similar, usually identical in the first stage, and appear to result from the mistaking of males for females, as suggested by Bristowe. When the mistake is "discovered," fighting often results. In the genera with the least dependence on chemical stimuli, however, courtship and threat are distinct, fighting does not occur and mirror display is readily induced. In these forms, and to some extent in the intermediate group, threat display seems clearly to have a stimulatory function which is totally apart from any direct competition for mates, and which is not concerned in territorial defense.

22. A tentative hypothetical phylogeny is presented, in which the studied genera and some northern relations are placed according to dependence on chemical stimuli, display criteria and method of locomotion. The correlation with morphological characters, to be specially treated in a subsequent paper, are indicated. The evolutionary trend within all the subfamilies appears to be similar in various major characteristics.

23. The origins of most display movements appear to be in accordance with the principle of economical permutation, since the majority probably developed from ordinary motions connected with daily activity.

24. Atavistic behavior was noted in which low-tone, overstimulated or senile individuals of advanced genera resorted to inappropriate aggression and chemotaxis; this was strikingly similar to the normal behavior of more primitive groups.

25. It is held that in salticids, the display motions probably preceded most morphological secondary sexual characteristics, and that the latter often persist vestigially after they have ceased to function as part of the display stimulus configuration.

26. In salticids, as in other groups, sexual dimorphism may occur in all degrees within a closely related group, even within the same genus, and appears to hold little phylogenetic significance. In species having both sexes strongly and similarly marked, the females are often more aggressive than usual and tend to perform definite reciprocal or mutual displays.

27. It is suggested that tropical salticids may differ in behavior from northern forms because of the prolonged breeding season, which necessitates less close correlation of breeding rhythms between the sexes.

28. Although it is agreed that geographic

isolation is the prime essential of species formation, it appears that growing display differences may be a strong secondary factor in salticid speciation. As a barrier between species already established, however, display seems to be an effective, but usually super-numerary, isolating mechanism.

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## EXPLANATION OF THE PLATE.

### PLATE I.

- FIG. 1. *Plexippus paykullii*. Courtship, Stage II. Typical of Stage II courtship in the Salticidae. In this family, specialization of display occurs principally in the earlier phases.
- FIG. 2. Observation table at Rancho Grande, showing presentation of a dried spider to a test salticid. The spider is mounted on an L-shaped strip of pasteboard. The table is covered with oilcloth ruled in concentric circles for distance observations. When chemotaxis was to be eliminated, fresh sheets of paper were used in each test.



FIG. 1.

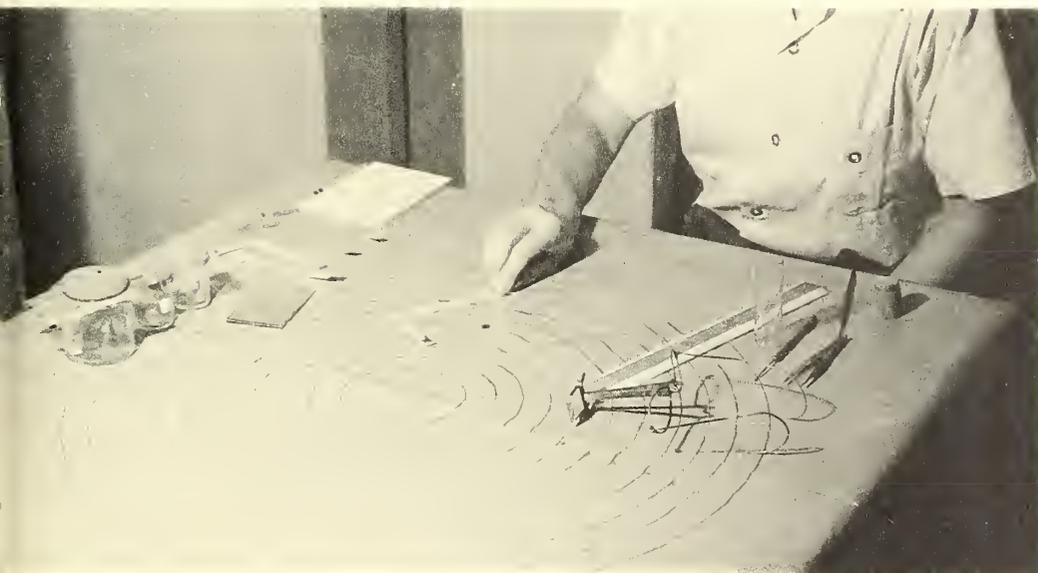


FIG. 2.

COMPARATIVE BIOLOGY OF SALTICID SPIDERS AT RANCHO GRANDE, VENEZUELA.  
PART IV. AN ANALYSIS OF DISPLAY.



## 18.

Differential Effects of Estradiol, Estradiol Benzoate and Pregneninolone on *Platypoecilus maculatus*.MARGARET CORDSEN TAVOLGA<sup>1</sup>.*New York University and The American Museum of Natural History.*

(Plates I-V; Text-figures 1-5).

Androgenic effects of estrogens have thus far been described as affecting only secondary sex organs in mammals (Allen, Hisaw and Gardner, 1939; and Witschi, 1939). In the present work, data are presented to show gonadal stimulation and androgenic effects of an estrogen in the platyfish.

The platyfish, *Platypoecilus maculatus* Günther, is a viviparous cyprinodont belonging to the family Poeciliidae. It has been used frequently for genetic studies (Bellamy, 1928 and 1933; Fraser and Gordon, 1929; Gordon, 1927, 1931, 1937a, 1947a and b), for studies of melanoma (Gordon, 1937b, 1948a; Gordon and Flathman, 1943; Levine and Gordon, 1946), and for embryological studies (Tavolga and Rugh, 1947), but until 1940 it was not used as an experimental animal for endocrinological work.

In 1941, Cohen, Gordon and Nigrelli reported on the spontaneous development of gonopodia in females of *Platypoecilus*, while in 1940 and 1942 Grobstein worked out the development of, and endocrine effects on, gonopodium differentiation. Cohen in 1942 and 1946 did the first work on the effects of sex hormones on the platyfish. At that time he found that pregneninolone has an androgenic effect upon the gonads and anal fins of the fish and that alpha estradiol benzoate has feminizing effects on the male. Pregneninolone, in mammals, has been known as a progestogen, although its effects have been discredited in recent years as ineffective and partially androgenic (Corner, 1942; Freed, 1942 and 1943). As above indicated, it has been found since that time that on lower vertebrates, such as fishes, the hormone has an entirely androgenic effect. In experiments preliminary to the present work, it was found that the effects of free estradiol did not coincide with those produced by the benzoate ester, and it was decided to continue and expand this aspect of the work as well as to determine the effects of androgens on the male and estrogens on the female. Pregneninolone was used as an androgen with which to compare the effects of alpha estradiol when

it was found that this substance did not exhibit strictly estrogenic activity.

MacBryde *et al.* (1942) found differential effects of estrogenic substances on the mammalian liver. It was decided, therefore, to investigate the effects of the treatment upon the liver of the experimental animals as a possible source of information as to the reason for the differential effects of the two estrogens. With these purposes in mind the present experiments were undertaken.

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## MATERIALS AND METHODS.

The fishes used for these experiments were platyfish, *Platypoecilus maculatus*, of the New York Zoological Society's Genetics Laboratory Culture 180 (Gordon, 1948b), their immediate offspring and those of several subsequent inbred generations. In this strain the males are the heterogametic sex (XY). The Y chromosome carries the "spotted" gene (*Sp*), regularly transmitted from father to son when a spotted male (X)<sup>+</sup>/(Y)*Sp* is mated to the recessive female (X)<sup>+</sup>/(X)<sup>+</sup>. The effect of the *Sp* gene is such that

<sup>2</sup> These animals were obtained from the Genetics Laboratory of the New York Aquarium, New York Zoological Society. The work of this laboratory is supported by a research grant from the National Cancer Institute of the National Institute of Health, U. S. Public Health Service.

<sup>1</sup> Submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy at New York University.

groups of macromelanophores are distributed over the major part of the body. The pigment cells begin to show immediately after the birth of the animals, affording a convenient method of identifying males and females within a day or two after birth. The females carry the recessive gene for macromelanophores (+ or *sp*) and appear as gray. In other strains of the platyfish which do not possess this or a similar feature, sex identification is delayed until such time as the fish mature, when the anal fin of the male is transformed into an "intromittent" organ, the gonopodium. Experiments carried out on such fish necessitate knowledge of the ratio of males to females usually derived in a brood from these fish and the use of statistical methods in determining the deviation from such a ratio when the work involves the use of hormones which produce effects on primary and secondary sex organs. This type of analysis is unnecessary with the strain used.

In seven generations only one crossover occurred, and this was in the control group. An animal in that group appeared to be a normal female 21 mm. long, but on sectioning she was found to possess normal testes for a fish of that age (66 days). Fraser and Gordon (1929) indicated that crossing over of the sex chromosomes in the platyfish is likely to occur at the rate of 1%.

The experimental individuals were kept in two-gallon tanks, approximately eight immature specimens of both sexes to a tank. Plants and gravel were removed at the beginning of each experiment in order to secure more uniform conditions. The room in which the tanks were kept was maintained constantly at a temperature of 80° F., plus or minus 3°.

The fish were fed daily on a fresh liver-Pablum mixture (Gordon, 1943) in amounts such that each tank received approximately 1.5 cc. per week. The method of introduction of hormones received a considerable amount of attention. The literature contains accounts of hormone administration both by dropping hormones into the water and by injection (Berkowitz, 1937; Eversole, 1941; Grobstein, 1942a). It was felt that the animals used in these experiments were too small to receive injections, since at the beginning of treatment they were only two to ten days old and averaged only 8 mm. in length. Therefore, dropping powdered hormone into the tanks was attempted.

It was soon noted, however, that the animals learned early to distinguish between food and hormone. At first they ingested it freely, but after a day or two they were observed to ignore it completely and the powder settled to the bottom of the tank, where it remained until removed. Thus the greater part of the hormone was not utilized. The possibility that it may have dissolved and been absorbed was not overlooked, and experiments designed to check this possibility will be discussed later. However, since the solubility of the hormones is known to be relatively small, another method of more direct

administration was attempted, and was found to give good results.

The powdered hormone was introduced into the semisolid liver-Pablum paste and thoroughly mixed. The food was given in small lumps each day and the fish were observed to pick at and ingest it freely each time it was given for the duration of the experiment. They consumed the amount given in about twenty minutes and close observation showed that they did not reject any part of the food, nor could any be seen at the bottom of the tank when later observed. Because of this it was assumed that the entire amount was ingested, and with it all the hormone which did not dissolve in the twenty-minute period which was needed for ingestion. Although no accurate measurement could be made of the amount taken in by any individual fish, it was seen that all the fish had access to the food and that there was little fighting among them for it. Each animal, therefore, received approximately the same amount of food and of the hormone. The hormone in oil preparation was mixed into the liver paste in the same manner, and though it changed the consistency of the paste to a slight degree, the preparation which was chosen contained a high concentration of hormone per cubic centimeter and little of the solution was needed to secure the necessary concentration in the food.

The hormones used were pregnenolone (Pranone, Schering), alpha estradiol (Progynon DH, Schering), and alpha estradiol benzoate (Progynon B, Schering). The first two were prepared in tablet form. The initial supply of estradiol benzoate was in powder form and the remainder in solution in sesame oil. The two forms of estradiol benzoate produced indistinguishable results and so are considered together.

The amounts of hormone used were selected in an attempt to secure doses which would be adequate to gain results and at the same time avoid much of the toxicity which was found to occur, especially from pregnenolone (see Text-fig. 1). Pregnenolone was used in doses of 5, 2.5, 1.25 and 0.625 mg. per 3 cc. of food. Estradiol and the crystalline estradiol benzoate were used in doses of 0.5, 0.25, 0.13 and 0.06 mg. per 3 cc. of food. The estradiol benzoate in oil was obtained in ampules containing 1000 rat units per cubic centimeter of solution in sesame oil, corresponding to 0.166 mg., and the doses given per 3 cc. of food measured 0.166, 0.083, 0.0415 and 0.0275 mg. These dosages were obtained by mixing 1, 1/2, 1/4, etc. cc. of the solution or the same fraction of tablets with 3 cc. of food.

Control tanks containing littermates of the experimental animals were run simultaneously with each experiment. In experiments where oil solution of estradiol benzoate was used, tanks of littermates which were fed with a mixture of food and sesame oil alone were also used.

The doses were given for various intervals,

varying from ten days to seven weeks, and at the end of each interval at least one male and one female were removed from each experimental tank and from the control tank. They were immediately fixed in Bouin's picro-formol and preserved after fixation in 70% alcohol. Each fish was then prepared for further study as follows: the anal fin or gonopodium was removed, cleared and mounted entire, and the belly of each animal was slit to facilitate infiltration of solutions. The animal was decalcified in a nitric acid-phloroglucinol mixture for a period of 24 to 48 hours, depending on the size of the fish, placed in several changes of 70% alcohol to remove the acid, and dehydrated by means of Dioxan. After infiltration in 60-62° paraffin, the animals were cut at 10  $\mu$  and the sections stained with Harris' haematoxylin and eosin, or with acid fuchsin and aniline blue (modification of Masson trichrome stain).

The sections thus obtained were examined to ascertain the condition of the ovary or testis, and the general condition of the other organs, and the anal fins were examined for signs of structural changes which might indicate a progressive shift toward maleness or femaleness. The sizes of the gonads were determined by measuring the widths of these glands. It was found that while the lengths of the gonads were roughly correlated with the standard length (length from the tip of the snout to the base of the caudal fin) of the animals, the width of the gonad was also correlated with the development and apparent activity of the gland as induced by hormone treatment.

In order to determine size differences between the eggs of the treated animals and those of the controls, one or more widely separated sections of each treated and control animal was subjected to analysis. The sections selected were as widely separated as possible in order to insure that no duplicate measurements could be made on any egg. Except for this consideration, the sections were chosen at random. In each case, 100 eggs were measured in order to obtain a good distribution and a sufficient and representative sample. The means and standard errors of the means were obtained and according to the formulas given by Simpson and Roe (1939) the significance values were calculated. These results are given in Text-fig. 4 and Table IV. In the case of the testes, the same method of analysis was applied to primary spermatocytes, secondary spermatocytes and spermatophores. In addition, an adult control male was sectioned in order to afford a comparison between the testes of the treated young animals and a normal adult testis. The testis of this animal was analyzed in the same manner.

#### RESULTS.

Two hundred forty-six animals were used experimentally. Each experimental group contained 26 to 33 animals when finally prepared and sectioned. Since with the dosages

used there was no statistical difference between those treated for different periods and with different dosages, the descriptions given will cover all periods of treatment and all dosages, except where otherwise indicated.

#### General Considerations.

As was stated above, the animals ate the hormone-impregnated food freely and there was observed to be no fighting among the members of any tank for greater amounts of food. Each pellet of food was eaten within about twenty minutes of its introduction into the tank, assuring almost complete introduction of the hormone into the animals. It was possible, however, that the hormone might be entering the animals by way of absorption taking place from the amount of hormone which dissolved into the water during the time when the food was present in the tank. In order to establish whether such dissolution took place, and whether, if it did, the dissolved hormone remained in an active state, two experiments were set up.

In the first of these, the water between two tanks was circulated through glass wool by a conventional air-lift filter in such a way that the water passed from one tank to the other without any undissolved particles passing in either direction. To the immature fishes of the same strain which were placed in the first tank was fed the same liver-Pabulum paste as was used for the main experiments. The fishes in the second tank received the same food without the hormone. The water was transferred from one tank to the other at the rate of about 240 cc. per hour, with a complete turnover at the rate of once in every 30 hours. At the end of a week, the fish in the second tank, which received no hormone in their food, had developed the same effects as those in the first tank which were fed directly, showing, first, that dissolved hormones or their metabolic products affected the animals; second, that dissolution had taken place in an amount great enough to produce an effect on the animals; and third, that the hormone was stable during the time taken for the change of water from one tank to the other.

Three weeks to a month after the termination of the main experiments, immature fish were placed in the tanks used for these experiments without changing the water or washing the tanks. The animals showed no effects of any sort and matured into normal adults, showing that after this period of time the hormone was no longer active.

During the main body of the experiments, the effect of the hormones on the experimental animals was first noticed on the males which were treated with pregnenolone. Within four to five days after treatment was begun, when the animals were six to fifteen days old, and measured 8 to 9 mm. in length, each animal's anal fin was modified into the general form of a gonopodium. A few days later, the anal fins of the females in the same

tanks had also acquired this characteristic. At about the same time (ten to twelve days), the males in the estradiol tanks developed the same type of modification, also followed in a few days by the females. Note that the estradiol, while it had superficially the same effect, was delayed in its action in comparison to the pregneninolone. Those fish in the tanks treated with estradiol benzoate, both males and females, for the duration of experimentation never developed any structures even superficially resembling a gonopodium. That the gonopodia developed by the androgen-treated animals were not typical nor perfect gonopodia with the characteristic hooks, spines, serrae, etc., of the platyfish gonopodium will be discussed later. It should be said here, however, that they were modified in the male direction sufficiently to be considered greatly affected by the hormone treatment, and that the fins of the pregneninolone- and estradiol-treated animals reacted in the same general manner.

Pregneninolone in the amounts given had a serious effect on the viability of the treated animals (see Text-fig. 1). Forty-eight percent. (32) of these animals died before the termination of the experiment and therefore were not considered in the results given. It is believed, however, that this death rate must be a significant consideration in the general effect of the hormone on the metabolism of

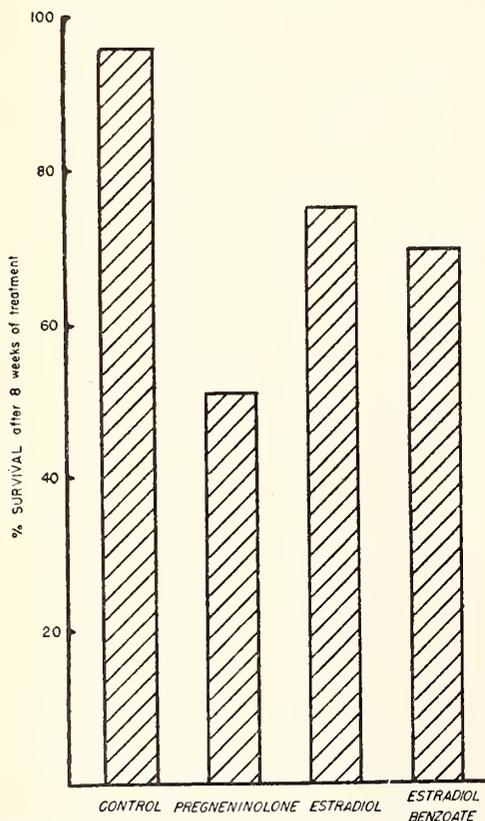
the animals, and should therefore be included in the general results. The effect of estradiol was similar, but again quantitatively less, as only 24% (17) of the animals treated in this manner succumbed. This number was significant as compared to the death rate of the control, where there was only 4% mortality, but not as compared to the estradiol benzoate-treated group, since 30% (20) of the estradiol benzoate-treated animals also died.

The locomotor activity of the treated animals was not impaired in any way. Sexual activity, normally absent at this stage of development, appeared precociously, and the tiny animals with miniature gonopodia were seen vigorously following the females, in a manner suggestive of precopulatory behavior of adults, as early as one week after the beginning of treatment, when they were but two weeks of age. This type of activity continued until the end of the experimental period. The females of the group, although they exhibited the male type of behavior, showed it to a lesser degree. Although they tended to follow each other, they did so less often and less vigorously. Females were not seen following males. In the estradiol benzoate tanks there was no evidence of male behavior during the entire course of the experiment on the part of either males or females.

#### Effect on Gonads.

##### Control Males.

All animals in the experiments were young healthy specimens, ranging in size at the end of the experimental period from 8 mm. for those treated for one week to 22 mm. for those treated for seven weeks. None of the animals at the end of the experiments were old enough to be normally sexually mature, and they would not normally have become so for about two months, as *Platypecilus maculatus* matures at the age of about four to six months under the laboratory conditions maintained here. At the ages of one to seven weeks, therefore, the testes were small compact masses, fused but showing their primary bilobed nature, their anterior ends appearing between two coils of the intestine at approximately the same cross sectional level as the caudal tip of the liver. They were attached to the dorsal peritoneum by a short mesorchium and in a few cases were seen dorsal to the intestines. See Pl. I, Fig. 1. They ranged in width from 0.08 mm. for the smallest animals (7.0 mm.) to 0.35 mm. for the larger ones (19.0-21.0 mm.). The younger gonads could be seen to contain numerous groups of cells (cysts) which could be only poorly differentiated from the main mass of tissue, except under the higher powers of magnification at which they could be seen to be spermatogonia. Between these cysts existed numerous connective tissue cells and fibers, making up the stroma of the gland. The sperm duct in these smaller animals was poorly differentiated. In the larger specimens, none of which was more than eight



TEXT-FIG. 1. Percentage survival of control and treated animals over a period of eight weeks.

weeks old, the cysts were slightly better differentiated. They could be seen to be separated from their surrounding stroma, which was less distinct, and the smaller cysts had now taken up a position relatively peripheral. At this stage these cysts measured 20 to 33  $\mu$  in width. A few larger cysts, 36 to 46  $\mu$  in width, could be seen toward the center of the gland. These, under higher magnification, could be seen to be primary spermatocytes. These cysts, when present, surrounded the now well formed duct. These descriptions confirm those of Wolf (1931) on the development of the testis in *Platypecilus maculatus* at this stage. In no case did the gonads contain any cellular formations acceptable as secondary spermatocytes, spermatids, mature sperm or spermatophores.

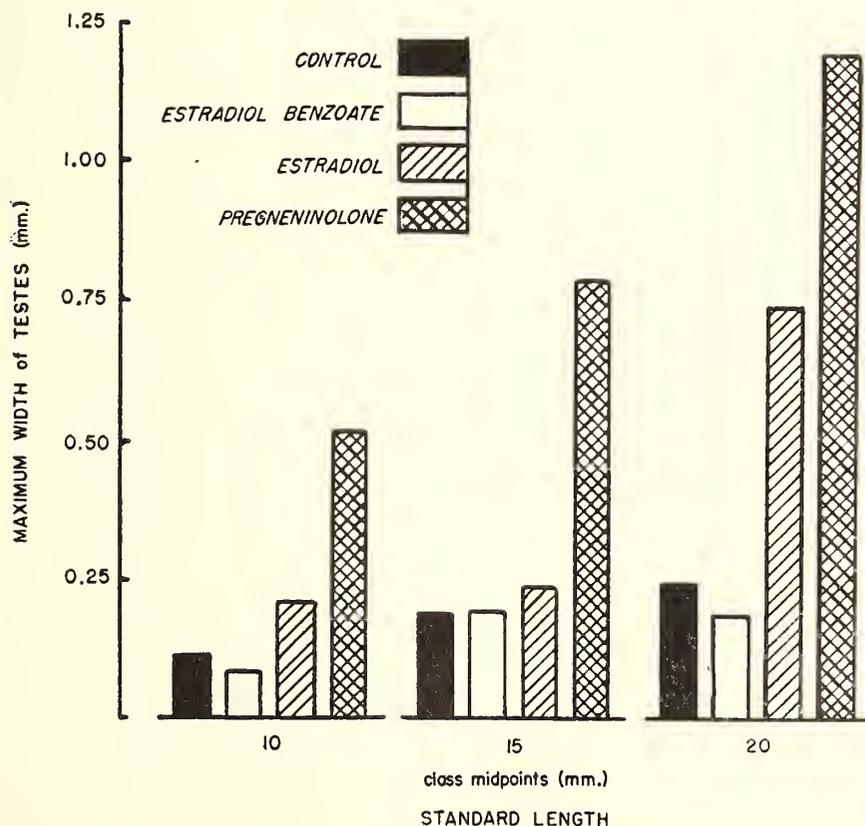
#### Males Treated with Alpha Estradiol Benzoate.

The testes of these animals showed a slightly retarded development as compared with the controls (see Pl. I, Fig. 2). Their size range was equal to that of the normals (0.10-0.34 mm.). The mean was 0.19 mm. The two testes were slightly separated, indicating an inhibition of their development toward a fused gland. The gland in general consisted of a number of peripheral cysts, surrounding stroma cells which were abun-

dant and ducts which were slightly less well formed than the normal. The cysts measured 11 to 21  $\mu$  in width, but since the testes were so small there were not enough of them to justify a statistical analysis. A few larger cysts were present, but they were less distinctly demarcated than those of the control. There were no statistically significant differences between the widths of the testes of this group and those of the controls ( $P = .05$ —see Table II).

#### Males Treated with Pregneninolone.

Pregneninolone has been shown to have androgenic activity in the guppy by Eversole (1941) and in the platyfish by Cohen (1946). It was expected, therefore, that it would have a similar effect here. That expectation was justified. The testes of even the smallest of the males thus treated showed definite stimulation effects. These testes were significantly larger than those of the control ( $P = .001$ ), measuring from 0.36 to 1.50 mm., with a mean of 0.81 mm. (see Text-fig. 2 and Table II). In each case, whether the animal was treated for a short period or a long one, the results were the same except for the general size of the gland, which had sufficient time to grow larger in the animals which were treated for a longer period. The cellular effects, in



TEXT-FIG. 2. Growth of control and hormone-treated male gonads as determined by measurements of testis widths.

TABLE I.  
Comparative Sizes of Gonads in Treated and Control Females.

Treatment	Number of animals	Mean length	Range	Mean gonad width	Extremes
Control	13	13 mm.	8-19	0.42 mm.	0.11-1.40
Estradiol benzoate	13	17 mm.	8-24	0.31 mm.	0.11-0.61
Pregneninolone	12	16 mm.	13-23	0.45 mm.	0.30-0.85
Estradiol	16	16 mm.	13-23	0.45 mm.	0.20-0.88

every case, were the same. The effect was to stimulate the testes to maturity far ahead of the time at which it would ordinarily be functional. Cysts of spermatogonia were present, measuring 30 to 51  $\mu$  in width, but in all the animals of the group the spermatogenic process had gone far beyond the stage of spermatogonia and primary spermatocytes into secondary spermatocytes, spermatids and spermatophores, the presence of which is the usual sign of a functional gland (see Pl. I, Fig. 3). The groups of cells had become differentiated into cysts of maturing primary spermatocytes measuring 93  $\mu$  plus or minus 2.1 (see Table III), secondary spermatocytes measuring 97  $\mu$  plus or minus 1.5, or later stages, each cyst containing only one stage of spermatogenesis, as is found in mature fish. Many of the cysts contained spermatids in the process of growing tails. Others contained nearly mature spermatozoa with heads embedded in Sertoli cells, beginning the formation of the typical ring of the spermatophore. Still others were found (69  $\mu$  plus or minus 1.5  $\mu$ ) which possessed the completed ring form of the spermatophore, containing mature spermatozoa, tails inward, dark heads forming a ring and massed together. In many cases the released spermatophores were found in the ducts, which is typical of the testis of the mature fish. In all the cases spermatogenesis was active in all its stages; there was an abundance of every stage from the earliest spermatogonia to spermatophores. In a general way the progress of spermatogenesis was from the outer portion of the gland inward toward the duct, and spermatogonial cysts were found mainly at the peri-

phery progressing through primary and secondary spermatocytes to spermatids and spermatophores which were located near the center of the gland and adjacent to the ducts. Since the animals were not treated for more than seven weeks, it is possible that the maximum effects were not obtained. Exhaustion effects in *Lebistes*, in which all spermatogenesis is in very late stages and no spermatogonia are present (Eversole, 1941), were not found. It is possible, therefore, that a longer treatment would have produced glands showing lack of germinal elements such as those described by him.

The position of the glands was also different in the treated fish. In the controls at this age they tended to be placed, as stated before, between the coils of the intestine, and only rarely were situated dorsal to this general position. In the pregnenolone-treated animals, however, the testes had grown so large that they pushed dorsally. They often occupied a position completely dorsal to that of the normal gonad, while in all other cases at least part of the gland projected above the coils of the intestine in cross section. Often they occupied the major part of the body cavity.

The interstitial tissue had also changed. In comparison to the size of the treated gland it was very sparse, being seen as mere threads between the cysts of maturing germ cells. However, toward the center of the gland, where it filled in spaces between the cysts and the sperm duct, slightly more abundant interstitial tissue was often seen. In the main it appeared like connective tissue, often with large oval cells. A few collecting tubules lined with cuboidal epithelium could also be seen.

TABLE II.  
Comparative Sizes of Gonads of Treated and Control Males.

Treatment	Number of animals	Mean length	Range	Mean gonad width	Mean W/SL*	t	P
Control	13	15.1 mm.	7.0-21.0	0.20	0.0122		
Estradiol benzoate	12	16.0 mm.	8.5-21.5	0.19	0.0125	.17	.05
Pregneninolone	10	16.2 mm.	8.5-21.5	0.81	0.0518	8.9	.001
Estradiol	17	15.2 mm.	8.0-22.0	0.35	0.0209	2.4	.02

\* W/SL equals the ratio of the gonad width divided by the standard length.

TABLE III.

Sizes of Spermatogenetic Cysts of Treated and Control Males.

Treatment	Structure of testis	Number of animals	Sample	Mean diam. (micra)	$\pm \sigma_M^*$	General effect
Control at experimental stage	Primary sp. cytes	14				Few—insufficient for significant count
	secondary sp. cytes	14				None present
	sp. phores	14				None present
Control mature male	primary sp. cytes	1	100	60	1.4	
	secondary sp. cytes	1	100	73	1.3	
	sp. phores	1	100	49	.9	
Estradiol benzoate	primary sp. cytes	12				Very few
	secondary sp. cytes	12				None present
	sp. phores	12				None present
Pregneninolone	primary sp. cytes	10	100	93	2.1	Enlarged over mature control
	secondary sp. cytes	10	100	97	1.5	Enlarged over mature control
	sp. phores	10	100	69	1.5	Enlarged over mature control
Estradiol	primary sp. cytes	2	100	56	1.4	Not significantly smaller than control
	secondary sp. cytes	2	100	56	1.1	Significantly smaller than control
	sp. phores	2	100	42	1.1	Significantly smaller than control

Significance Values Calculated from Means in Table III.

Significance values are calculated as the difference between two means divided by the standard error of the difference.

## Primary spermatocytes

	Estradiol	Pregneninolone
Control mature male	2.0†	13.0
Pregneninolone	14.8	

## Secondary spermatocytes

	Estradiol	Pregneninolone
Control mature male	9.9	12.1
Pregneninolone	22.2	

## Spermatophores

	Estradiol	Pregneninolone
Control mature male	5.0	11.2
Pregneninolone	14.6	

\*  $\sigma_M$  equals standard error of the mean.

† These values are not to be considered significant.

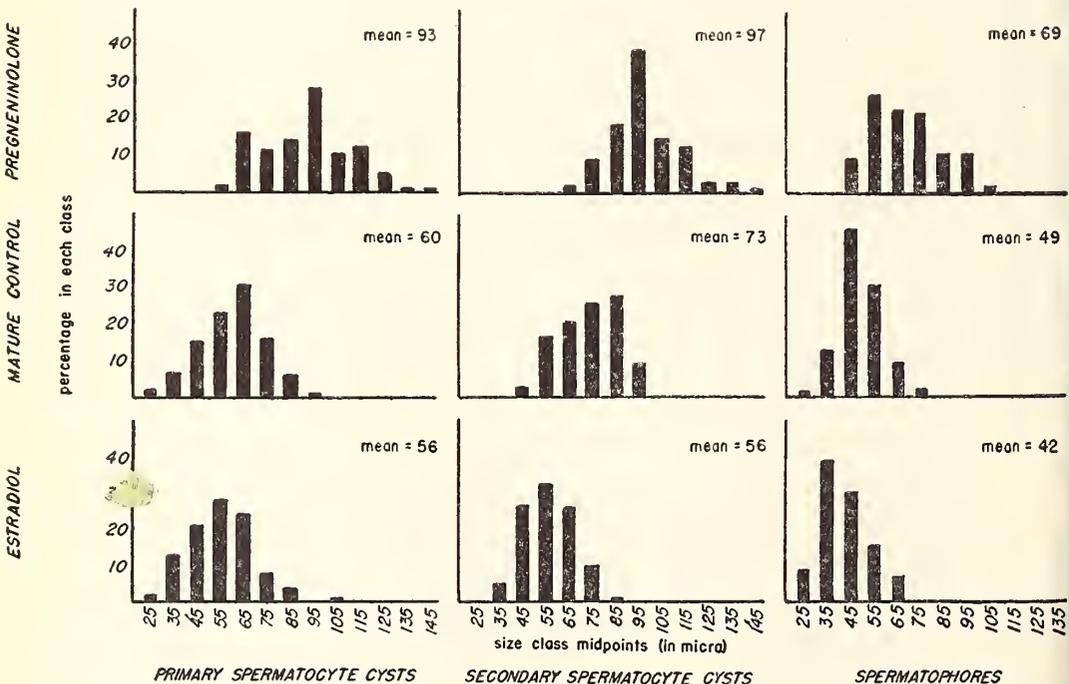
These observations corresponded very well to Wolf's (1931) description of the interstitium of a young mature male.

Males Treated with Alpha Estradiol.

In mammals it has been found that alpha estradiol is usually an estrogenic hormone (Willier, 1939; Witschi, 1939), although in some cases paradoxical effects have occurred which have affected the secondary sex organs. However, the gonads are not ordinarily changed in these cases. When the present experiments were in their earliest stages, it was found that apparently this was not true in the platyfish. Therefore further experiments were carried out in order to determine the effects of this substance. The animals in this group fell into two sets, the difference being one of size and depending not at all on dosage or length of treatment. In all animals under 18 mm. in length, the testes presented a normal control picture. The testes were small, compact, showed spermatogonia and early spermatocyte stages, compared well in size with those of the controls, except for a very small increase, and generally showed no significant effects. In all animals, however, over 19 mm. in length, the developmental picture was entirely changed. The gonads in these cases were intensely stimulated organs, showing all stages of spermatogenesis. Discrete cysts of primary and secondary spermatocytes, 56 plus or minus 1.4 μ, and 56 plus or minus 1.1 μ, respectively, spermatogonia 25 to 30 μ at the periphery, and normal spermatophores of 42 plus or minus 1.1 μ at

the center were present. Note that the sizes of these cysts were significantly smaller than those of the pregneninolone animals (see Text-fig. 3 and Table III). The ducts also were large and well formed, typical of the ducts of a mature male, and they were frequently filled with spermatophores. These spermatophores, like those of the pregneninolone-treated animals, were well formed and showed no sign of precocious extrusion from the cysts or of abnormal cells despite their comparatively small size (see Pl. I, Figs. 4 and 5). The picture approximated that of animals treated with the known androgen pregneninolone, in every detail except size. It seems, then, that estradiol, far from being an estrogen, acts much like an androgen in the stimulation of the testes in these fish. The position of the testes in the abdominal cavity of the animal and the appearance presented by the interstitial tissue corresponded in every way to the pregneninolone-treated animals.

In order to determine the size relationship of these stimulated spermatogenic cysts to those of the normal testis, an adult untreated male was sectioned and prepared in the same manner as the experimental animals. As with the experimentals, 100 cysts of each type, primary and secondary spermatocytes and spermatophores, were measured by means of the ocular micrometer and statistical analyses were made (see Table III and Text-fig. 3). In each case the cysts of the pregneninolone-treated animals were significantly larger than those of the adult control and



TEXT-FIG. 3. Comparative size ranges of primary and secondary spermatocyte cysts and spermatophore cysts of pregneninolone- and estradiol-treated animals as compared with those of a normal adult male.

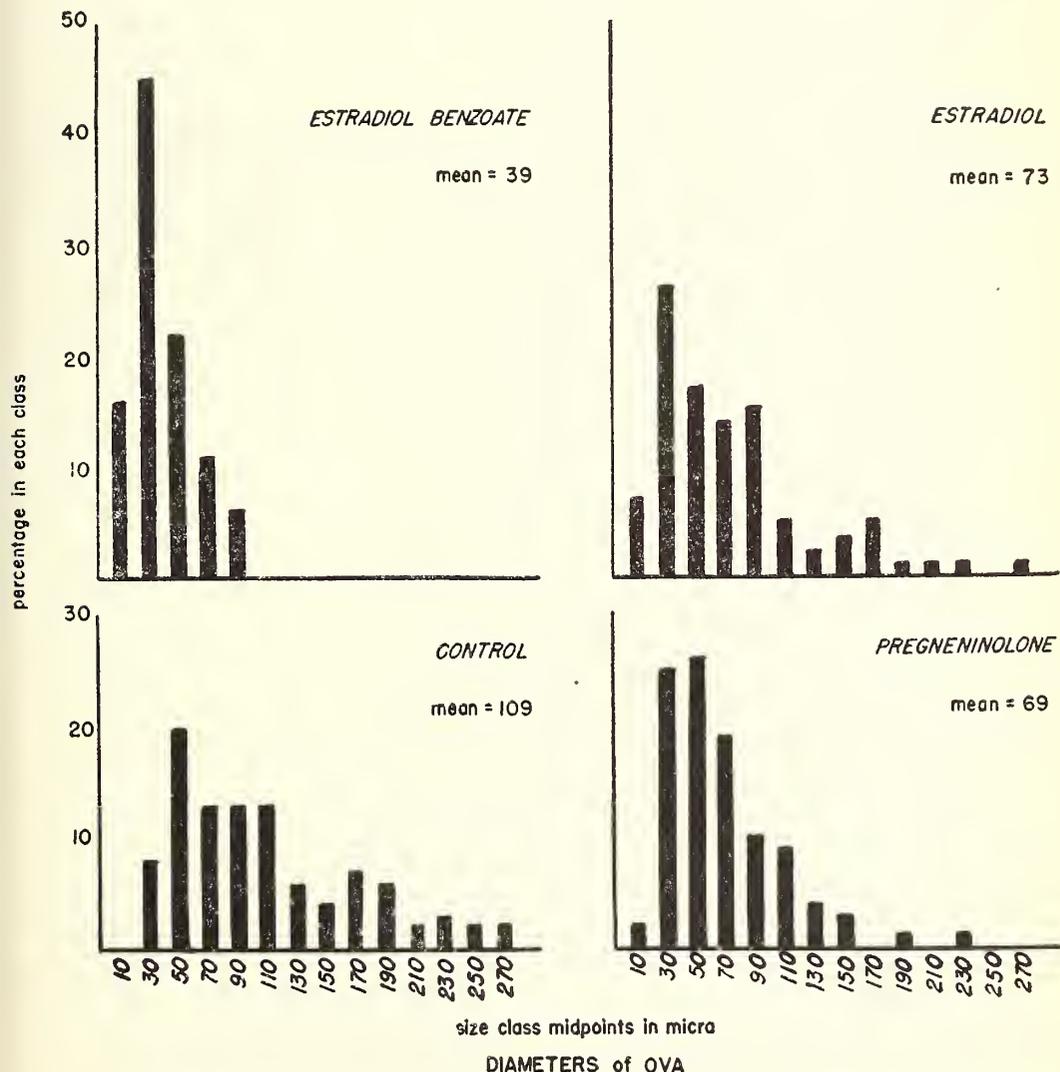
with one exception the cysts of the estradiol-treated animals were smaller. In the case of the primary spermatocytes the cysts of the estradiol-treated animals were not significantly smaller than those of the control adult.

#### Control Females.

The typical female ovary of a platyfish of two to eight weeks of age was located in serial cross sections between two coils of the intestine, suspended from and approximating the dorsal peritoneum. The ovary ranged in size from 0.11 to 1.40 mm. and the mean value was 0.42 mm. Posteriorly it lay free of contact with surrounding organs, and far posteriorly, just anterior to its posterior margin, it lay almost if not completely free in the abdominal cavity. At the young stages studied here, it consisted of a single mass composed mainly of young circular or ovoid ovocytes, before, or in the larger animals

during, the process of yolk deposition. The mean size of these ovocytes was  $109 \mu$  plus or minus  $6.5 \mu$  (see Text-fig. 4 and Table IV). The ovary as a whole was compact, little if any space being present between adjacent eggs. Any space which was present was almost filled with small amounts of stroma. Stroma also filled spaces between the outermost eggs and the peripheral flattened epithelium (see Pl. II, Fig. 6).

In the younger stages the ovocytes were yolk-free, with slightly reticular cytoplasm and a lighter-staining nucleus. Each nucleus contained one or two deeply-staining, prominent nucleoli. The nucleoplasm itself was reticular in appearance, studded with chromatin granules. These larger eggs were located mainly at the periphery of the organ and each was bounded by epithelial cells constituting the follicle. The younger cells, oogonia,  $21$  to  $45 \mu$  in diameter, were situated



TEXT-FIG. 4. Comparative size ranges and distributions of eggs of control, estradiol benzoate-, pregneninolone- and estradiol-treated females.

TABLE IV.  
 Sizes of Eggs of Treated and Control Females.

Treatment	Number of animals	Sample	Mean diam. (micra)	$\pm \sigma_M$	General effect
Control	12	100	109	6.5	Great inhibition
Estradiol benzoate	13	100	39	2.1	
Pregneninolone	12	100	69	3.9	Partial inhibition
Estradiol	16	100	73	4.8	Partial inhibition

Significance Values Calculated from Means in Table IV.

	Control	Estradiol benzoate	Estradiol
Pregneninolone	5.2	6.7	0.6*
Estradiol	4.3	6.1	
Estradiol benzoate	10.2		

\* These values are not to be considered significant.

nearer the ovarian cavity. They were sometimes imbedded in the stroma immediately surrounding it, but usually maintained contact with the epithelium of the cavity. Their cytoplasm was more deeply stained and presented a more homogeneous appearance.

In the later stage the situation was much the same except for the appearance of the larger eggs. These had now grown considerably in size, measuring 100 to 280  $\mu$ , and their cytoplasm presented a far more reticular appearance than was true of the younger eggs. Near the periphery of some of them yolk granules were discerned, but this was true only in the largest of them. In all cases intermediate stages were present between the largest and smallest eggs.

#### Females Treated with Alpha Estradiol Benzoate.

The ovaries of the animals treated with alpha estradiol benzoate were more compact and smaller than those of the controls, measuring 0.11 to 0.61 mm. and averaging 0.30 mm. in width. The eggs appeared tightly pressed together and were deformed by this pressure in some cases. The ovaries were more closely pressed between the coils of the intestine. Although the arrangement of the eggs appeared normal and a fairly well formed duct was present, the eggs themselves showed an inhibition of development (see Pl. II, Fig. 7). The larger eggs were peripheral, gradating to smaller ones in the center of the organ. In size they ranged from 11 to 96  $\mu$  (see Text-fig. 4 and Table IV), and none of them approached the size of eggs found in the control fishes of the same size. No evidence of yolk deposition was present in any of the eggs in this group. The cytoplasm of these eggs was more homogeneous than was true of the ova of the controls, and they compared in size and structure to a much younger

stage than that which would be expected from the age and size of the fish. It is evident, then, that though few acute abnormalities were present in the structure of the individual eggs, their size and appearance indicated that they were greatly inhibited by the treatment.

#### Females Treated with Pregneninolone.

The ovaries of these animals were again slightly smaller than those of the controls, measuring from 0.30 to 0.85 mm. and averaging 0.45 mm. in width. The sizes of the groups overlap a great deal (see Table I), but the largest ovaries of the pregnenolone-treated animals did not reach the size of the largest ovary of the control group. The main effects, however, were those appearing in the size and structure of the eggs. The ovaries of these animals presented an extremely abnormal appearance. The greater number of them were shrunken and small, appearing completely pressed out of shape by the surrounding coils of the intestine, as in the estradiol benzoate-treated animals (see Pl. II, Fig. 8). It is doubtful, however, whether this shrunken appearance was due to the pressure caused by the intestine, since the control ovaries were subjected to the same pressures and did not show the deformities. Also the pregnenolone ovary, like the controls, lay, at its posterior end, free in the abdominal cavity, and the deformities were equally great there. Therefore some other cause must be assigned to this phenomenon, presumably one due to the hormones involved. The ovaries contained in most cases little interstitial tissue, and while this was more deeply stained than the normal, it did not appear especially abnormal. The eggs themselves, however, showed definite effects. They were seldom as large as those of the control, having a mean size of 69  $\mu$  plus or minus

3.9  $\mu$  (see Text-fig. 4 and Table IV). In a few cases large eggs could be found and these were the most nearly normal-looking ones. Even they appeared degenerate, however, showing deeply-staining cytoplasm, slightly irregular nuclei and a partially deformed appearance. The remaining eggs were uniformly deformed in shape, the main body of them having irregular depressions in their sides and usually one concave side, so that the individual eggs took on the appearance of pushed-in balls. The nuclei were also misshapen, showing elongations and irregularities, each one staining deeply. The cytoplasm often had a mottled appearance, in contrast with the even staining of the control. This resulted, presumably, from some effect on the cytoplasm, which caused parts of it to stain deeply and others lightly, without any regularity. Another significant point was in regard to the size of the eggs. All those which were not included in the groups of larger eggs mentioned first were extremely small as compared to eggs in the same stage of a control, measuring from 11 to 60  $\mu$ . No evidence of yolk deposition could be seen in any individual eggs.

In most of these ovaries the duct was poorly formed and the edge of the epithelium was ragged and abnormal, showing cells and bits of tissue sloughing off into the duct.

Two variations of these conditions were found. In two cases the ovary was large but the eggs were scattered and large spaces were present between them (see Pl. II, Fig. 9). While the eggs in these specimens were not usually as deformed as they were in the cases described above, they were deeply stained and appeared to be in a state of degeneration. As above, few eggs could be found which were as large as those of the control of the same age and size, but several appeared which had been approaching this size and condition before treatment with hormones was begun. These eggs showed approximately the same irregularities as the large ones described above. The epithelium surrounding the gland was ragged and shredded in many places and the cells of the duct were ragged.

In two other cases a definite bi-partite ovary was found. In one of these the eggs were fairly large and normal-looking, measuring between 90 and 130  $\mu$  (see Pl. II, Fig. 10), and appeared to be comparable to the eggs of the majority of the control ovaries. In the other case, however, the eggs were small and degenerate-looking, measuring about 40 to 60  $\mu$ , and were stained deeply, showing deformities. In this ovary there appeared two definite ducts, one for each half of the gland, which showed fairly regular epithelium. The first case contained a duct which was wide and flat horizontally, apparently serving both sides of the gland. It is believed that this remaining evidence of the bi-lobed nature of the embryonic gonad may have been caused by the inhibitory effects of the androgenic hormone applied. All

variations of the ovarian conditions were used together in making the statistical analysis of the eggs in this group.

#### Females Treated with Alpha Estradiol.

In general terms, the ovaries of this group showed the effects expected of an androgen. The results were very similar to those produced by pregnenolone. The majority of the animals possessed ovaries which appeared as shrunken masses, with deformed eggs such as those described for the pregnenolone-treated animals, staining poorly and in a mottled fashion. The size also, of both the ovaries and the eggs, was comparable to the size of those of a pregnenolone-treated female, since measurements of the ovaries ranged from 0.20 to 0.88 mm. with a mean size of 0.45 mm. (see Table I). The eggs had a mean size of 73 plus or minus 4.8  $\mu$ , a size which is not significantly different from that of the pregnenolone-treated eggs.

There were several exceptions to this general picture. In two cases the ovary showed the same scattering which appeared in some of the pregnenolone-treated animals (see Pl. II, Fig. 11). The same larger degenerating eggs, and the same type of atretic appearance in the small eggs was present. In one case, there appeared a bi-lobed ovary such as that described above, which possessed one duct to serve both parts of the gland. In this specimen the eggs were small, measuring 40 to 60  $\mu$ , and while not as deformed as the typical eggs of this group, some atypical shapes were present and the eggs generally stained more deeply than the controls. In some cases there appeared a variety of degeneration not seen in the pregnenolone-treated group. In these ovaries there were a few eggs which appeared to be almost normal, both in size and general appearance. The remainder of the comparatively large gland was composed of a substance which at first appeared to be adipose material. Upon closer inspection, however, it was concluded that at the places where this material was seen, there had once been large eggs in the process of yolk deposition (see Pl. II, Fig. 12). The eggs had apparently degenerated, since the masses contained no recognizable structures, and left behind them a mass of fatty yolk-filled material. Vacuoles were present, which showed the presence of lipoids. Some yolk granules were to be seen. At certain points about the periphery of these masses there appeared epithelium of a largely degenerate nature which was broken and sloughed in parts. Since there had been several eggs of this nature, it might have been expected that there would be some type of separation between them. For the most part, however, this was not true, and the masses were indistinguishable from one another, showing no evidence of where one egg ended and another began. In some places a portion of the above-mentioned epithelium remained, to give some indication of the limits of the egg, but this was true only in a few cases. The masses

of material were of various shapes so that no indication remained of the original shape of the ovum. The remaining eggs were of the small deformed type mentioned above and were pushed to one side of the organ. The ovary, because of this peculiar content, was quite large, although the egg content was extremely small. The appearance of the organ as a whole was a degenerate one. The outline of the organ, even where the eggs were present, was ragged and appeared degenerate, as the epithelium was ragged and uneven in contrast to the smooth epithelium of the control.

#### *Effects on the Anal Fin.*

Grobstein in 1940 published a complete description of the developmental stages in the transformation of the platyfish's anal fin into the gonopodium. In 1942, however, he partially changed the terminology used in order to conform to prevailing taxonomic usage. In all the following descriptions, the terminology used in the 1942b paper will be employed.

#### Control Males.

The anal fin of the control male fish at the ages studied here was one in which no differentiation or growth had taken place in the change from the undifferentiated fin toward the typical gonopodium. The fin looked like the female fin of the same age (see Pl. III, Fig. 13). The fins were well formed, the third ray slightly thicker than the others. The fourth and fifth rays, particularly the fourth, projected slightly beyond the others. No bifurcations were present in the younger fins and the larger ones possessed only primary bifurcations. Secondary and tertiary bifurcations which, according to Grobstein, depend on age, had not yet appeared in any of the fins studied. No growth of the third ray, which indicates the beginning of differentiation into the gonopodium, had begun in any of the fins. The only difference between the male and female control fins at this age was the presence of macromelanophores in the male fin, due to the *Sp* gene. The females did not possess these macromelanophores.

#### Males Treated with Alpha Estradiol Benzoate.

Fins of the males treated with alpha estradiol benzoate presented the same picture as did the controls. In all the fins, which came from animals not more than eight weeks old, no differentiation of any sort tending in the male direction was seen. The fourth and fifth rays projected slightly beyond the others, but no more so than is normal in the female fin and certainly not enough to give the impression that they are beginning the gonopodial growth phase (see Pl. III, Fig. 14). They appeared as normal fins for this age of fish, but since no animals were carried to maturity it is not known whether the hormone would have been enough to prevent gonopodial differentiation entirely.

#### Males Treated with Pregneninolone.

The anal fins of all animals in this group were affected by the hormone treatments. In the case of the smallest animals, ten days to two weeks of age and 8 to 9 mm. in length, which had been treated for one week to ten days, the transformation had proceeded only into Phase I, and all these fins possessed third rays which were segmenting and growing, producing an elongation of the cephalad portion of the fin. All those treated for three weeks or longer, however, showed a completely modified picture. In these groups, every fish possessed an almost completely differentiated gonopodium (see Pl. III, Fig. 15). Most of these were almost perfect, although a few existed which were lacking in certain elements present in a normal fin. The usual element missing in such an incomplete fin was the spines, which in most cases, if present, were flattened and smaller than normal. Some fins were seen where no spines at all were present. Since the oldest fish in the group were not more than eight, or at most, nine weeks old, it can be assumed that this precocious development was due to the effects of the hormones administered. That the modifications of the fins correlated well with the growth and differentiation of the gonads is further evidence for this assumption.

#### Males Treated with Alpha Estradiol.

Anal fins of males treated with alpha estradiol could be placed in two groups. These corresponded directly to the division which occurred in the description given already of the gonads of this group. In those animals which were below the size of 18 mm. at the end of the experiments, the fins, like the gonads, did not show the usual effect of the androgen. Each of the anal fins observed in this group was in Phase I of growth and elongation of the third ray. The fins appeared as modifications of the female condition in which the third, fourth and fifth rays had grown long enough to project beyond the others to about one-third of their length. In the majority of the animals, the third ray was found to be segmented as in Phase I, rather than like the control, in which segmentation was far less definite.

The group comprising those animals which reached a size of 19 mm. or more contained fins which were modified far more toward the typical male condition. They were almost complete but showed more variability than did the pregnenolone-treated males. Elements which were present consistently were the subterminal segments with the terminal hook, the elongation of the fourth ray, with its cephalic ramus curved in a cephalad direction, spines and proximal serrae. Elements which were absent or incomplete in the imperfect fins were distal serrae, the spoon and spoon support, and the blade. These were absent in different combinations. Although the fins of this group were not complete, they showed a definite tendency toward the male form (see Pl. III, Fig. 16). If,

as Grobstein postulates, the gonopodium is under the control of the testis, the present evidence supports that view.

#### Control Females.

The anal fin of the female control animals, like the males at this age, showed no signs of differentiation toward the adult form. The structures possessed by these fins were those typical of the young female (see Pl. IV, Fig. 17). The fins did not differ materially from the adult female type except that, as in the male, only primary bifurcations of the fourth to ninth rays had taken place. The third, fourth and fifth rays projected slightly beyond the others, as is normal. The thickening of the third ray present in the male fin at this age was present to a lesser degree in the female. No macromelanophores were present, since the female does not carry the *Sp* gene. Except for this last distinguishing characteristic, present only in this strain, the fins were structurally similar.

#### Females Treated with Alpha Estradiol Benzoate.

In animals treated with this estrogen, the condition of the anal fin was indistinguishable from that of the control fin (see Pl. IV, Fig. 18). The third, fourth and fifth rays showed the same slight extension. The third ray was again slightly thicker than the others. Bifurcations of the rays in animals of the same age were identical.

#### Females Treated with Pregneninolone.

The fins of the animals in this group presented a varied picture. None of them possessed a complete and normal gonopodium, but neither did any possess the typical female anal fin. All animals possessed fins which had progressed far beyond the first phase of gonopodium formation and many had gone into the third phase (see Pl. IV, Fig. 19). All animals had completed the preliminary growth phase, in which the 3, 4, 5 ray complex segmented and pushed out in the cephalo-distal portion of the fin to form a promontory there. Elongation of these rays continued throughout Phase II of gonopodium formation. At the beginning of this growth new segments appeared in the third ray, and at the end of the first phase there were generally nine segments present (Grobstein, 1940). During the second phase, these segments increased in number to twenty-two when the gonopodium had completed its growth. All animals in the group possessed at least ten segments and specimens were found in which the complete number was present. At the end of Phase II differentiation of the various specialized parts of the gonopodium began. The great majority of the animals had arrived at this stage. In many, however, the differentiation was aberrant, showing certain completely differentiated parts, while other parts, which should have differentiated concurrently, were still in an undifferentiated or partially differen-

tiated state. Plate IV, Fig. 19, shows a gonopodium of this group in which the differentiation was almost complete. This fin had progressed as far as the "blade stage" (Grobstein) and shows most of the elements of a complete gonopodium in a more or less normal state. The fin possessed proximal and distal serrae, the blade, the spoon and spoon support, the terminal hook and subterminal segments and other elements. Other gonopodia were found which possessed good segmentation of the third ray and a perfect terminal hook, which should not appear until the time at which the distal serrae differentiate and after the formation of the proximal serrae, but both sets of serrae were missing. Such varied differentiations were common but the general rule in this group was partial or complete differentiation of all parts, many with slight deformations.

#### Females Treated with Alpha Estradiol.

Alpha estradiol was found to have almost the same effects as pregneninolone, although they were somewhat delayed (see Text-fig. 5). Thus the majority of the fins in this group had begun differentiation but had progressed to a lesser degree than those of the previous group. All the fins had entered the first or preliminary growth phase, since all of them showed at least the segmentation and strengthening of the third ray, and the resulting promontory forming on the cephalo-distal border. Most of them had in addition entered the second phase, in which growth had gone on to form a great elongation of the fin. About one-third of them went on into the third phase, in which they showed various stages of differentiation. In this group no complete gonopodia were found, but many fins showed the beginnings of the differentiated elements. There were present terminal hooks together with subterminal segments, proximal serrae, a few sets of distal serrae, the cephalic turning of the fifth ray, and the cephalic ramus of the fourth ray. All these, however, while they appeared together in a few animals, were usually present in less complete combinations. Alpha estradiol, while it is androgenic to a great extent, since it induces the formation of gonopodia, does not produce nearly as complete gonopodial structures as does pregneninolone (see Pl. IV, Fig. 20). The presence of an androgenic effect, however, is easily seen.

#### *Effects on the Liver.*

##### Control Animals.

The liver in the platyfish was divided into several large lobes. Lobules were not separated as in the mammal, and the entire gland appeared as a compactly arranged mass of cells. Cords of cells were present, though not as distinctly as in the livers of higher forms. The cells themselves measured about 8  $\mu$  in diameter and were weakly eosinophilic. The nuclei averaged about 2  $\mu$  in diameter. The stroma was poorly distinguished from the epithelial cells. The mass of homogeneous-

appearing cells was profusely supplied with blood vessels of all sizes. The nuclei, from 2 to 3  $\mu$  in diameter, were nearly circular and thickly granular. The cells were of three types, non-vacuolated with weakly eosinophilic cytoplasm, partially vacuolated with one or two vacuoles filling about one-third of the cytoplasm, and a third type in which larger vacuoles filled most of the cell. In all the vacuolated cells, the vacuolated ends aggregated together in a direction farthest from the blood vessels, producing pale blotches in the structure of the liver from 10 to 20  $\mu$  in diameter and very irregularly placed. The predominant type of cell was the partially vacuolated one. The second cell type in order of predominance was the one which was non-vacuolated and weakly eosinophilic. See Pl. V, Fig. 21.

Animals Treated with Alpha Estradiol Benzoate.

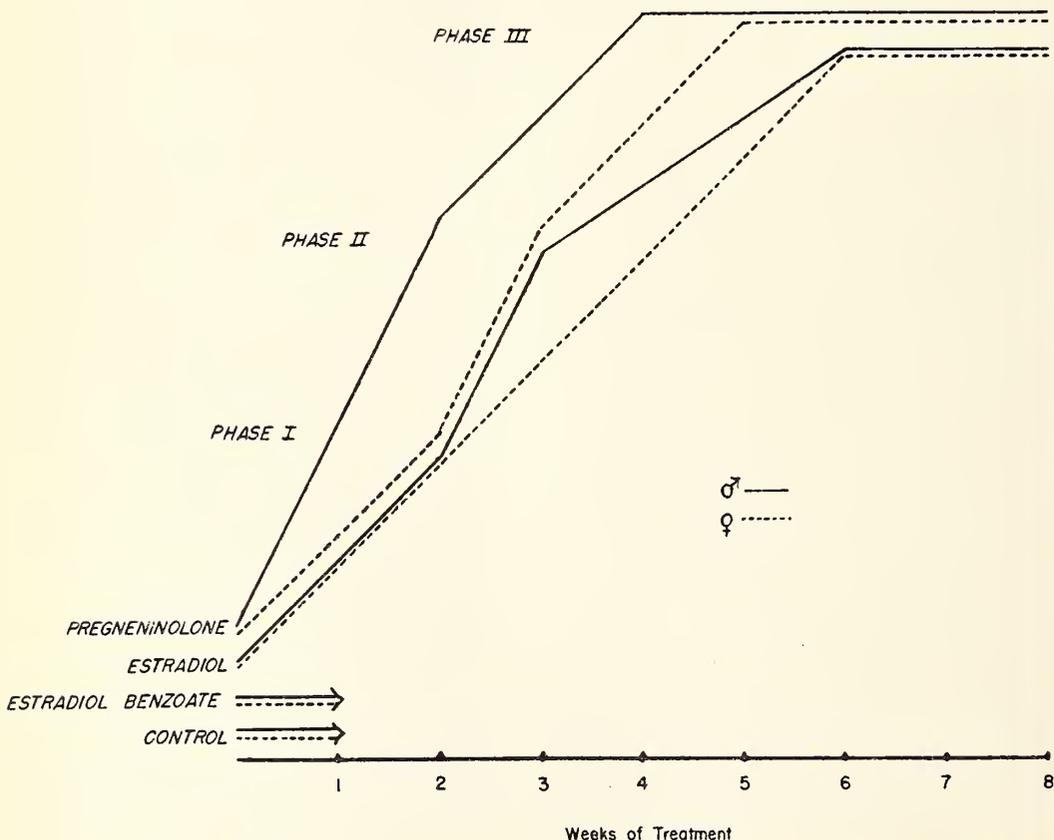
The liver cells of these animals averaged 8 to 12  $\mu$  in diameter. Three types of cells were present, one non-vacuolated and weakly eosinophilic, another containing a vacuole which filled one-third to two-thirds of the

cytoplasm, and a third which was highly vacuolated. The predominant type was that in which one-third to two-thirds of the cytoplasm was vacuolated, followed by the non-vacuolated type. The organ as a whole presented a compact appearance much like that of the control. The stroma network resembled that found in the control. No degenerative effects could be noted. See Pl. V, Fig. 22.

Animals Treated with Pregneninolone.

The cells of the livers of these animals averaged from 10 to 15  $\mu$  in diameter, being generally much larger than those of the control. The cells were all more or less vacuolated. The type of cell which predominated was one in which the cytoplasm was occupied almost completely by a large vacuole. The vacuoles occupied, on the average, about nine-tenths of the cytoplasm and as a direct result the nucleus and remaining cytoplasm were pushed to one side. The general arrangement of the cells about the capillaries was as in the control and the entire organ presented a highly vacuolated appearance (see Pl. V, Fig. 23). Vascularization appeared increased, with a capillary for every

RATE OF GROWTH & DIFFERENTIATION OF THE GONOPODIUM



TEXT-FIG. 5. Graph showing growth of gonopodium of control, estradiol benzoate, pregneninolone- and estradiol-treated animals.

seven to ten cells. The stroma network appeared more distinctly as a result of the extreme vacuolization of the parenchyma cells. The entire organ showed changes in structure, fatty in nature as demonstrated by the application of Sudan IV in frozen sections. The controls used for these reactions were normal livers of the same age, which showed comparatively few sudanophilic globules. The experimental animals, on the other hand, showed an abundance of these globules in their liver cells.

#### Animals Treated with Alpha Estradiol.

The liver cells in these animals averaged about the same size as those of the estradiol benzoate-treated animals, but the great majority of them showed vacuoles. Occasional cells showed the extreme vacuolization of the pregnenolone-treated livers, nine-tenths of the cell being occupied by a vacuole. For the most part, however, the cells contained vacuoles which occupied about one-half their volume and there appeared frequently cells with several small vacuoles instead of one large one. In general, the organ showed signs of far greater vacuolization than the control, and, therefore, partial changes similar to those shown by the livers of the pregnenolone-treated animals, but in a stage which was far less advanced. See Pl. V, Fig. 24.

#### DISCUSSION.

Regnier in 1938 made a comprehensive survey of the history of fishes as experimental animals in sex hormone studies, and in addition described her own experiments on *Xiphophorus hellerii* with anterior pituitary hormones and ovarian and testicular powders and extracts. Essenberg (1926) described sex reversal in *Xiphophorus*. Blacher in 1926 found that testicular hormones are necessary for secondary sex characteristics in *Lebistes*. Castration and implants of gonads in *Xiphophorus* was carried out by van Oordt and van der Maas (1926). Berkowitz, in a series of papers (1937, 1938, 1941a and b), described the effects of estrogens and mammalian gonadotrophins in *Lebistes*, while Eversole (1939 and 1941) worked on the effects of androgens in this animal. In two papers in 1941 (a and b), Turner tested the effects of androgens on *Gambusia*. Scott (1941 and 1944) worked on the effects of steroids on the skeleton of *Lebistes*.

Eversole (1941) mentioned that testes of *Lebistes* treated for 42 days with pregnenolone showed all stages of spermatogenesis, with later stages predominating, that the spermatids and spermatophores produced were abnormal, and that in animals treated for 50 days, later stages in spermatogenesis were present almost exclusively, spermatids and spermatophores were atypical and that the gonad was generally in a degenerate state because of a rapid maturation of the germinal elements which left few spermatogonia. He also stated that the epithelium of the ducts tended to dismember at that time and

that the stroma was hypertrophied. These observations were not seen in the present studies. Most of the animals, it is true, were not treated for more than six weeks, but some were treated for seven weeks, and even these did not show the degeneration of the gonad which was described by Eversole. Whether this difference was caused by the difference in experimental animals used, by the different method of administration of the hormone, by differences in dosages or ages, or by different conditions under which the animals were kept, is not clear. However, the gonads of the animals in the present work, while they showed great stimulation, were seen to contain germinal elements and abundant primary and secondary spermatocytes as well as spermatophores. This was true whether the animals were treated for two weeks or for seven. In the case of the animals treated for six to seven weeks, the picture of the gonad was equivalent to a normal mature testis, both in size and in quality of the elements contained. Spermatogonia were present, both primary and secondary spermatocytes were abundant, and the later stages of spermatogenesis were abundant and appeared normal. No signs of degeneration of any sort could be distinguished. As was stated in the results, it is possible that a longer period of treatment might have produced the exhaustion effects spoken of by Eversole.

Winge (1934) has shown that sex reversal may be detected by genetic means in the guppy. These reversals, however, were always from female to male. It is evident, however, that the sex determining mechanism in the guppy is less stable than that of the platyfish, since only two cases of sex reversal in *Platypoecilus* have been mentioned in the literature. Both of these were naturally-occurring phenomena (Breider, 1942; Gordon, 1947a). No sex reversal in the platyfish has ever been reported as having been induced by hormonal or any other means. Because of this relatively unstable sex mechanism in the guppy, it is easier to understand why Berkowitz (1937) was able to secure sex reversal and ovotestes in this form. No such phenomena were found in the present work. Although degeneration of the gonads was common as a result of hormone introduction, no sign of any transformation in the gonads was obtainable, either from male to female, or from female to male.

Berkowitz (1937, 1938, 1941), in work on the guppy, mentioned several hormones and combinations of these which were administered, and combined the results into a general statement. It is possible, therefore, that the divergent results of one or more of the hormones given by him went unnoticed because of this procedure. Although the results appear to be consistent, no mention is made of exactly which results were occasioned by which hormone and slight differences which might have led to a suspicion of the present findings might have been overlooked. A re-

grettable tendency evident in many papers is to administer "estrogens" without regard to which estrogen is being administered. The present work indicates that such a procedure is not safe.

Essenberg in 1923 stated that the oviduct in *Xiphophorus* was derived from a fusion of the two embryonic components of the ovary in such a way as to leave a space between them which later developed into the oviduct. Wolf (1931), on the other hand, who worked out the embryology of the gonads in the platyfish, stated that the oviduct originated by what may be considered the classical method, the degeneration of the medulla of each embryonic gonad accompanied by the development of the cortex (Willier, 1939). Goodrich *et al.* (1934) found that the oviduct of the guppy originated in the same way. Two such opposing views in two forms which are comparatively closely related seems to be unusual. Evidence for the double origin of the oviduct, in which the duct develops in two parts, one in each embryonic ovary, fusing to form one duct when the ovary itself fuses (Wolf's version), is given by the occurrence of the degenerate ovary under androgen treatment found in this work which possessed two distinct ducts. Such a condition, under the terms of Essenberg's hypothesis, would be unlikely. A further investigation into the origin of the oviduct in *Xiphophorus* would seem to be in order.

Regnier (1938), in her description of the origin of the oviduct in *Xiphophorus*, quoted Essenberg, but since this phase of her work was a review of the literature, no further evidence was to be found there. Regnier mentioned the effects of testis powder as producing bi-lobed and retarded ovaries in *Xiphophorus* when these animals were treated when very young. She also mentioned the comparatively great mortality present when this treatment was given, but said that with the addition of anterior pituitary lobe powder to the water in which treated individuals were placed, the mortality markedly decreased. After injections of testosterone for two months, her animals showed mature sperm in the testes, but no mention is made of presence or absence of spermatophores. Therefore it is not known whether the treated males in that group were fertile. She also discussed sex reversal due to hormones and the prevention of sex reversal by injections of appropriate hormones, but since it is known that the sex determining mechanisms of *Xiphophorus* are somewhat labile (Essenberg, 1926; Witschi, 1939), these results are not inconsistent. Mention was made of certain residual bodies which were derived from the degenerating follicles of the sex reversing ovaries and which traveled to nearby organs where they established themselves. Although evidence of such bodies was sought in the surrounding organs of the fish in the present work, no results were obtained.

Cohen in 1942 and 1946 treated female platyfish with pregnenolone and males with

estradiol benzoate. He found at that time that estradiol benzoate had feminizing effects on the male platyfish over a twelve-week period. The other results produced were similar to those found in the present experiments within the time limits used here, except that Cohen showed evidence that mature ova were found in normal control ovaries of fishes only eight weeks old. In the entire group of control females used in the present work, only one such ovary was found. This lack of yolk-filled eggs in the ovaries was not considered unusual, since, although growth rates vary with environment, feeding and other factors, *Platypoecilus*, even under ideal conditions, does not usually mature until the end of the fourth month after birth or later, as will be shown. Under normal conditions, no mature ova would be expected to occur until or just before that time. The effects of pregnenolone which were repeated in the present experiments were in the main more pronounced than those shown in Cohen's work, probably because of the larger amount of hormone actually introduced into the fish as a result of the different method of administration used here. It is believed that this method has been more effective, since the main portion of the hormone was introduced into the fish orally. However, the experiments run subsequently show that some of the drug was dissolved into the water, either during the time when the food lay at the bottom of the tank or after it was egested or excreted by the fish in a still potent state. That these drugs affected the fish within a short time, through whatever means they became dissolved, is also evident. The evidence brought out by the later experiment showed, however, that the hormones are not stable under aquarium conditions for more than about three weeks, since after that time immature fish introduced into the tanks with the same water showed no effects whatsoever. Whether the hormone was destroyed by the microscopic population of the tank, adsorbed to the glass, or otherwise inactivated in some way is not known, but after that time it was no longer present in a form which had any perceivable effect on the fish. Further work is being done to determine the exact time when this inactivation takes place, and also, if possible, what the cause for the inactivation may be.

As to the effects of estradiol benzoate on the male, Cohen showed no figures on the development of either the control or the treated testes for eight-week-old fish, and therefore it is difficult to compare results at that age. In the present work, however, the testes so treated were slightly retarded in differentiation though not in size because of the administration of the hormone. Whether these effects are similar to those found by Cohen for an eight-week period is difficult to judge, because his descriptions did not cover that period.

Some support for the theory that different esters of the same hormone may bring about

different effects was given by Grobstein (1942b), when he found that different esters of testosterone may show different effects on the regenerating anal fin of the platyfish. Even this paper, though, showed that all the esters used produced masculinization of the fin, as might have been expected. That a hormone and its ester should bring about diametrically opposed effects is unique. Grobstein also showed that the effects of these hormones is not to produce a normal gonopodium, but one that is imperfect. That evidence is substantiated here. In all cases there was produced a fin which was not precisely like the typical male gonopodium as it is seen in a normal adult animal. Even in those cases where the differentiated parts appeared to be almost normal, two differences in size were noted. The fin as a whole was smaller than the normal, and within this smaller fin the proportions existing between the length and width of the fin were changed. The 3, 4, 5 ray complex in each smaller fin was approximately one-third shorter than would normally have been found in a fin of the same width. The cause of this difference is apparently the result of differentiation of the fin beginning before it had time to grow to its full length, because of the relatively rapid action of the hormone. In the normal fish, the testis develops more slowly and therefore apparently controls the fin in such a way as to produce a lower amount of hormone until the fin has reached its maximum length, at which time the testis releases more hormone and differentiation takes place. This theory of hormone levels controlling the growth and differentiation patterns was postulated by Turner (1941b) and was adopted by Grobstein.

It should be established that under normal developmental conditions the young fish involved in these experiments would not have matured for about two months after the termination of the treatment, since they mature at approximately four to six months of age. Littermates of the experimental animals matured under conditions equivalent to those used in the experiments within these time limits, and averaged five months from birth to sexual maturity.

It can be assumed that a testis may be considered functional when it is producing spermatophores. Although no correlation has been found as yet to support this assumption in hormone-treated animals, it is always found that a normal functional male possesses spermatophores, while a non-functional male, otherwise normal, or an immature male, does not. Because of this evidence, it is assumed that the testes of the animals treated with pregnenolone, and the larger animals treated with estradiol were functional. Even if free sperm are produced under experimental conditions, the fish will not be sexually functional because of the necessity for transferring the sperm in a clump from the gonopodium of the male to the vent of the female. If this transfer is not carried out

by way of the spermatophore, the sperm will presumably be lost in the water and fertilization will not result. Therefore, the important feature of the pregnenolone-treated testes was the large number of spermatophores present in both the acini and the duct. Since the normal testis at this age shows none of these features, the indication is that a great stimulation had occurred. Another feature to be mentioned is the difference in reaction of fish of the same age and size to the two hormones which produced stimulation of the testes. In the case of pregnenolone, the stimulation was a steady one, producing in every fish some sign of stimulation, the amount of growth and differentiation depending on the size and age of the fish. It was, however, never completely without effect. This may be seen from the sizes of the testes shown in Text-fig. 2 and Table II. Alpha estradiol, on the other hand, produces quite a different effect. In all the small fish, those below and including 18 mm., the effect was negligible. The testes appeared like normal control testes of the same age. When, however, the fish reached the size of 19 mm., the effect was different. The testes of the fishes of this size were immediately and greatly stimulated (see Pl. I, Figs. 4 and 5), and the testes resulting appeared to be functional, considering the great number of spermatophores present in the acini and duct.

As to the difference in size of the spermatogenic cysts present in the two types of treated animals, it is possible that the sudden arrival at a threshold level of hormone in the case of estradiol was responsible for a rapid differentiation of the gland, causing the smaller size of the spermatogenic elements. The pregnenolone-treated animals, which received a longer and steadier stimulation, were capable of producing cysts which were larger than those normally seen (see Text-fig. 3).

In order to suggest an explanation for the above effects and the others found in the present work, several assumptions must be made. First, it is well known that the liver of mammals inactivates steroid hormones which pass through the portal circulation (Biskind and Mark, 1939; Burrill and Greene, 1942; Cantarow *et al.*, 1943; Heller, 1940; Israel *et al.*, 1937; Segaloff, 1943; Talbot, 1939; Teague, 1941; Westerfeld, 1940). It is assumed that the same action takes place in the liver of teleosts. Some hormones, however, are inactivated more than others. Estradiol is inactivated more than estradiol benzoate because the benzoate ester protects the molecule from destruction. According to Heller (1940), the oxidation of the estradiols takes place at carbon 3 in ring A. Since the benzoate radical is attached at this position, its presence protects the molecule from oxidation (Segaloff, 1943). Therefore it can be assumed that the effective dose of estradiol, that is, the dose which produces the effects in the animal, is less than the effective dose of

estradiol benzoate, if identical oral doses are given.

The toxicity of the hormones must also be taken into consideration. Plate V, Fig. 23, shows the appearance of the typical liver of an animal treated with pregnenolone. The cells are greatly enlarged and vacuolated and are presumably in a condition caused by the relatively great toxicity of the pregnenolone, which may be interpreted as a type of fatty change. Because of this toxicity, the liver, which at first probably rapidly inactivated the hormone, was rendered unable to do so, and the main portion of the hormone passed through the liver intact, producing a large effective dose and intense effects. The estradiol, which is partially inactivated, causes also a partial vacuolization of the liver, suggesting a cumulative effect on the liver, which results in an increase in effective dose. This eventually has an effect on the gonads.

If these hypotheses are true, they present new evidence for the action of abnormal quantities of metabolic substances on the liver, since till now the only conclusive evidence for the inhibition of inactivation by the liver has been derived from work on experimental Vitamin B deficiency (Biskind and Biskind, 1941, 1942, 1943; Biskind, 1946).

A further assumption concerns the stage of growth and differentiation in which the gonads are found during the period of the experiment. During this period the testes are, for the purposes of this explanation, in a relatively undifferentiated state and not yet under the influence of the pituitary. Gonadotrophic hormones are known to be present in fishes (Scheer, 1948). There is evidence to support the above assumptions. The testes, as shown by Text-fig. 2, grow very little during the period of the experiment. They contain essentially the same elements at the end of eight weeks as they possessed about one week after birth. The ovaries, on the other hand, grow considerably during the same period, and yolk deposition is begun and progresses considerably. The ovaries and eggs are much larger at the end of the period than they were at one week of age. The growth of the gonads is known to be under the control of the pituitary (Matthews, 1939a).

If these assumptions are admitted, at least as possibilities, a hypothesis may be advanced as to the method by which the hormones produce their results in these experiments.

In the case of the testis, the first effective doses of pregnenolone were small because the substances were largely inactivated by the liver tissue. These relatively small doses stimulated the pituitary rather than inhibited it because of the smallness of the dose. The estradiol had a delayed effect because it continued to be inactivated for a longer period of time, and therefore needed a longer period of time in which to reach an effective dose. The dose which was effective in the case

of estradiol was a cumulative one and required a longer period in which to operate and a larger animal on which to operate because of some type of threshold reaction. The estradiol benzoate went through the liver tissue undestroyed and reached the pituitary in doses large enough to cause an inhibition rather than a stimulatory effect. Thus the testis, which was not yet under pituitary control, showed little effect from the administration of this drug.

In the case of the ovaries, which were already under pituitary control, the effects were different. The smaller doses of estradiol and pregnenolone acted as partial inhibitors, shown by the partial inhibition of the eggs in these specimens, while the estradiol benzoate, again passing through the liver undestroyed, caused an almost complete inhibition of growth of the eggs.

To suggest an explanation for the action on the gonopodium is a more difficult problem. In both males and females, the effect on the gonopodium was similar. Pregnenolone stimulated at least some growth in all gonopodia, and all older animals treated for a longer period of time showed almost perfect transformation of the fin. Estradiol stimulated all gonopodia to a slight growth, and the largest ones to the same type of differentiation shown by the pregnenolone animals, though the differentiation was slightly less advanced. Estradiol benzoate had no effect on any of the animals. There are a number of hypotheses which may be advanced.

First, the gonopodium might be under purely genetic control. It is known that this is not true because the treated females showed differentiation to a gonopodium as readily as did the males.

Second, the ovarian hormone might inhibit the gonopodium. If we can assume that an inhibited ovary is producing little or no hormone, the above hypothesis cannot be true because under these conditions a greatly inhibited ovary would allow a better differentiated gonopodium than a partially inhibited one. The estradiol benzoate-treated ovary was inhibited to the greatest degree, but there was no gonopodium, while the animals which possessed partially inhibited ovaries formed well differentiated gonopodia.

Third, the reactions cannot be due to a non-specific reaction to steroids because the different substances produced different effects.

Fourth, if the reactions are due to the action of the fish testis hormone, or to an androgenic effect directly, it must be hypothesized that estradiol has a direct androgenic effect, while an effect based on dosage difference would be more plausible, since in mammals the substance has an estrogenic effect.

Fifth, control from the pituitary gland entirely could explain the effects in the males, where pregnenolone and estradiol stimulate the pituitary. In the females, however, the pituitary, according to the above assumptions, and based on its action on the gonads,

inhibits the ovaries, and presumably would not at the same time stimulate the differentiation of a gonopodium. This of course assumes that the gonadotrophins secreted by both male and female pituitaries are qualitatively identical and stimulate the gonads of the animals in which they exist. This has been shown to be true for amphibians (Rugh, 1935).

Sixth, the theory that pituitary control plus male gonads or androgenic hormone cause the effects is the most nearly complete explanation. In this case, pregnenolone and estradiol stimulate the pituitary and therefore stimulate the gonopodium through the gonad. Estradiol benzoate inhibits the pituitary. Since the testis is not as yet under pituitary control, the testis shows no effects. No androgenic hormones are produced and the lack of these produces, in turn, lack of a gonopodium. In the females, however, an androgenic effect of the substances administered is necessary to explain the results. Pregnenolone and estradiol inhibit the pituitary and through it inhibit the ovary. The pituitary inhibition plus the androgenic effects of the hormones cause the differentiation of the gonopodium. Estradiol benzoate inhibits the pituitary, but, having no androgenic effect, does not cause the formation of the gonopodium.

A detailed cellular examination of the pituitary gland in these fish may reveal significant differences between controls and experimental animals, presumably involving the cells which secrete gonadotrophic hormones. This may furnish a partial explanation for the results described above and indicate whether the action may take place through the pituitary or is a direct effect of the hormones upon the gonads, as has been shown to happen in other animals (Nelson, 1937). A careful examination of the interstitial tissue of the testes may also aid in determining the possible effects of the hormones upon this tissue.

These hypotheses were constructed in an attempt to correlate the actions of the various hormones on the gonads and on the anal fin. Perhaps the effects on the two are entirely separate, however. The effect of the pituitary may be brought in to account for the effects on the gonads, but an androgenic effect of estradiol and pregnenolone would account alone for the effects on the gonopodium. It cannot be assumed, however, in view of the evidence brought out by estradiol benzoate treatment, that the effect is the paradoxical estrogen effect mentioned above caused by high dosage with estrogens. The effective dose of estradiol benzoate is higher than that of the others because it is protected in the liver. Therefore, under these conditions, one would be led to expect that it would produce a more definite effect than either of the other hormones. Since this is not true, some other hypothesis must be advanced to explain this effect. The other possibility

which is most plausible is one in which the hormone has a directly androgenic effect.

The fact that the hormones which were used produced uniform results in spite of more than a tenfold range in dosage is an unusual finding. The toxicity which was found to be present with large dosages has also been found in mammals, but no sub-maximal results were found here.

It might have been useful also to treat the fishes with other benzoates as a control for the possible action of the benzoate ester exclusive of estradiol. The use of an inactive free compound with an active benzoate ester would be helpful in this work.

Turner (1941 a and b) brought to light various factors affecting the growth of the gonopodium. He stated that, first, the growth of the gonopodium depended on a certain low concentration of hormone and the differentiation of the fin depended on a higher concentration; second, that there existed certain dominances in the ray complexes which governed the differential growth of the various rays in such a way as to produce what we know as a complete gonopodium if the fin is left undisturbed; and third, that castration at any time during the growth of the gonopodium would stop its growth, while the administration of androgens thereafter would renew its growth. These findings on *Gambusia* have important bearings on the present studies. It was suggested above that the effect of estradiol was a cumulative one. This might account, on the basis of Turner's first statement, for the anal fin growth shown by the smaller estradiol-treated animals, where no differentiation was present. Pregnenolone caused an immediate and sustained effect on the gonopodium, suggesting that this hormone reached the threshold level almost immediately. Such a hypothesis would aid in explaining the effects on both testes and gonopodia.

As to the effect on the females, the hormones, as suggested above, may have had a direct effect on the fins.

The differential growth of the 3, 4, 5 ray complex was apparently governed by a low concentration of hormone. Dominance then shifted, according to Turner, so that the rays outside the 3, 4, 5 complex were subordinated to these three. This might explain the rapid growth of these rays in the young estradiol males and others in which a low level of hormone existed.

Castration with the effect of termination of growth of the fin, followed by androgenic restimulation, shows that the testis itself is not necessary for the growth of the fin, but that a hormone similar to that produced by the testis is required. This might aid in explaining the cases in which the females grew well-formed gonopodia.

The above hypotheses are far from clear and more work must be done in order to determine the explanation for these seemingly opposite and confusing effects. Hypophyse-

tomy, castration and a combination of the two performed on animals which were later treated with hormones would aid in determining the mechanisms which govern these effects. Preparations for such work are going on now.

More work is necessary on the general problem of the differential effects of these two estradiol compounds. The exact stage when the differential effect on the male begins should be studied in more detail. Smaller dosages should be used in an attempt to discover a dose small enough to secure a less than maximum effect, as such an effect does not appear in the present work. Finally, an investigation into the differential effects of more compounds related to these should be carried out, since the exact effect of any one of them is now doubtful, whereas heretofore they have been used interchangeably, at least on experimental animals.

#### SUMMARY.

1. The experimental animal used was a strain of the platyfish in which males could be distinguished from females at birth as a result of a Y chromosome sex linked, spotted factor, whereas usually the sexes are indistinguishable until maturity, when the anal fin of the male is transformed into an intro-mittent gonopodium.

2. The hormones used were alpha estradiol, alpha estradiol benzoate and pregnenolone, a synthetic progestogen. These were administered by mixing the powder or oil solution with the food.

3. Pregneninone exhibited a strong stimulating effect on the males, with precocious maturation of the testes and well-formed gonopodia. In females, development of the ovaries was inhibited, and gonopodia produced.

4. Estradiol benzoate was inhibitory on the testis and greatly so on the ovary. No gonopodia were produced.

5. Alpha estradiol had no effect on the testes of males under 18 mm. in standard length and produced slight growth of the anal fin. In males over 19 mm. in length, the testes were greatly stimulated and large, well-formed gonopodia were found. All females so treated showed ovarian degeneration and partial to nearly complete gonopodia.

6. Studies on the liver showed that pregnenolone and estradiol produced great vacuolization of the parenchyma cells and resulted in an organ which showed fatty changes, while the benzoate-treated livers appeared like those of the controls.

7. It is to be emphasized that although in the amniotes, estradiol and its ester are used interchangeably, in this species the two compounds produce diametrically opposed effects under the conditions of these experiments.

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## EXPLANATION OF THE PLATES.

## PLATE I.

- Fig. 1. Testis of control male eight weeks of age.  $\times 100$ .
- Fig. 2. Testis of estradiol benzoate-treated male eight weeks of age.  $\times 100$ .
- Fig. 3. Testis of pregneninolone-treated male eight weeks of age.  $\times 100$ .
- Fig. 4. Testis of estradiol-treated male eight weeks of age.  $\times 100$ . Compare with Fig. 3.
- Fig. 5. Testis of estradiol-treated male eight weeks of age.  $\times 100$ . Compare with Figs. 3 and 4.

## PLATE II.

- Fig. 6. Ovary of control female eight weeks of age.  $\times 100$ .
- Fig. 7. Ovary of estradiol benzoate-treated female eight weeks of age.  $\times 100$ .
- Fig. 8. Ovary of pregneninolone-treated female eight weeks of age.  $\times 100$ .
- Fig. 9. Ovary of pregneninolone-treated female eight weeks of age.  $\times 100$ . Note scattering.
- Fig. 10. Ovary of pregneninolone-treated female eight weeks of age.  $\times 100$ . Note bilobed appearance of organ.
- Fig. 11. Ovary of estradiol-treated female eight weeks of age.  $\times 100$ . Compare with Fig. 9.

## PLATE III.

- Fig. 12. Ovary of estradiol-treated female eight

weeks of age.  $\times 100$ . Note large degenerating eggs and small abnormal eggs.

- Fig. 13. Anal fin of control male.  $\times 34$ .
- Fig. 14. Anal fin of estradiol benzoate-treated male.  $\times 34$ . Compare with Fig. 13.
- Fig. 15. Anal fin of pregneninolone-treated male.  $\times 34$ . Note almost complete differentiation of gonopodium. Compare with Fig. 13.
- Fig. 16. Anal fin of estradiol-treated male.  $\times 34$ . Compare with Figs. 13 and 15.

## PLATE IV.

- Fig. 17. Anal fin of control female.  $\times 34$ .
- Fig. 18. Anal fin of estradiol benzoate-treated female.  $\times 34$ . Compare with Fig. 17.
- Fig. 19. Anal fin of pregneninolone-treated female.  $\times 34$ . Compare with Figs. 15 and 17.
- Fig. 20. Anal fin of estradiol-treated female.  $\times 34$ . Compare with Figs. 16, 17 and 19.

## PLATE V.

- Fig. 21. Liver of control animal.  $\times 960$ .
- Fig. 22. Liver of estradiol benzoate-treated animal.  $\times 960$ . Note similarity to Fig. 21.
- Fig. 23. Liver of pregneninolone-treated animal.  $\times 960$ . Note extensive vacuolization. Compare with Fig. 21.
- Fig. 24. Liver of estradiol-treated animal.  $\times 960$ . Note vacuolization—approaching but not equalling that of Fig. 23.





FIG. 1.



FIG. 2.

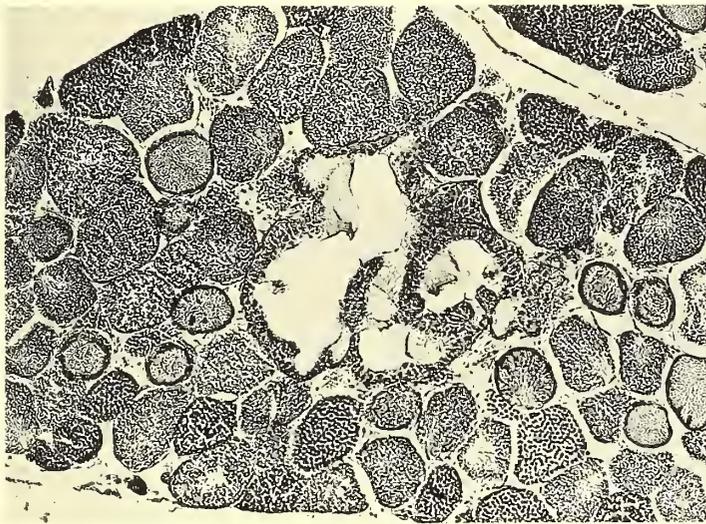


FIG. 3.

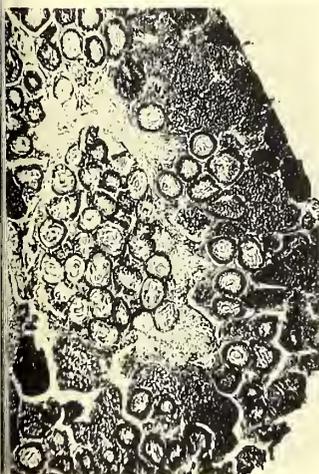


FIG. 4.

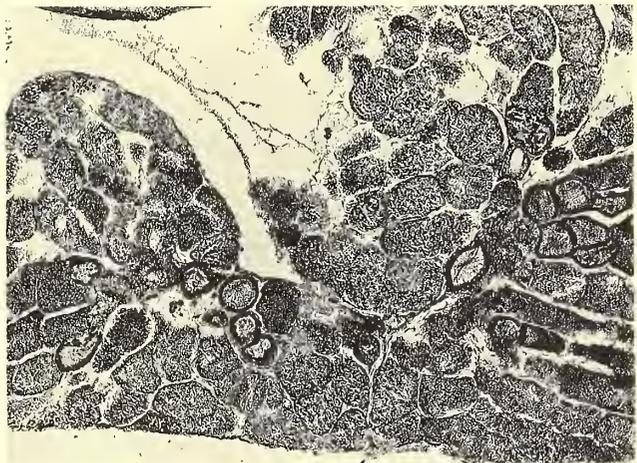


FIG. 5.

DIFFERENTIAL EFFECTS OF ESTRADIOL, ESTRADIOL BENZOATE  
AND PREGNENINOLONE ON PLATYPOECILUS MACULATUS.



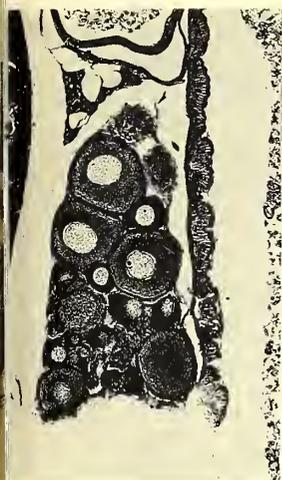


FIG. 6.

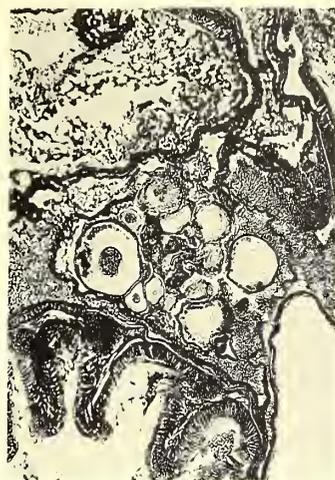


FIG. 7.



FIG. 8.

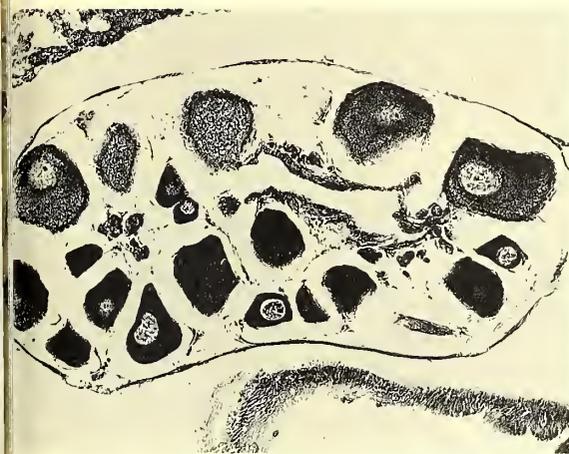


FIG. 9.



FIG. 11.

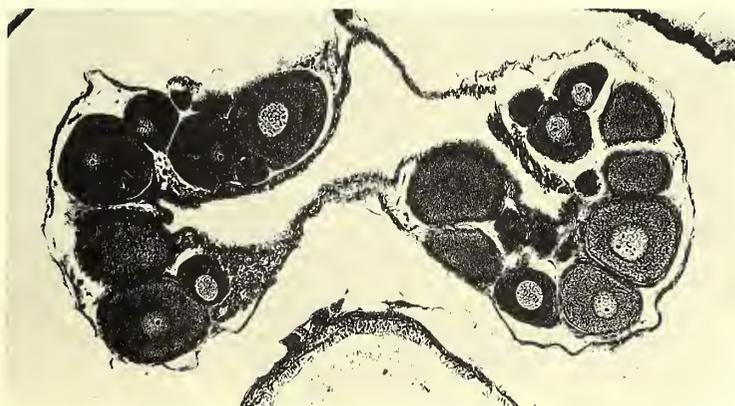


FIG. 10.

DIFFERENTIAL EFFECTS OF ESTRADIOL, ESTRADIOL BENZOATE  
AND PREGNENINOLONE ON PLATYPOECILUS MACULATUS.





FIG. 12.



FIG. 13.



FIG. 14.



FIG. 15.



FIG. 16.

DIFFERENTIAL EFFECTS OF ESTRADIOL, ESTRADIOL BENZOATE  
AND PREGNENINOLONE ON PLATYPOECILUS MACULATUS.



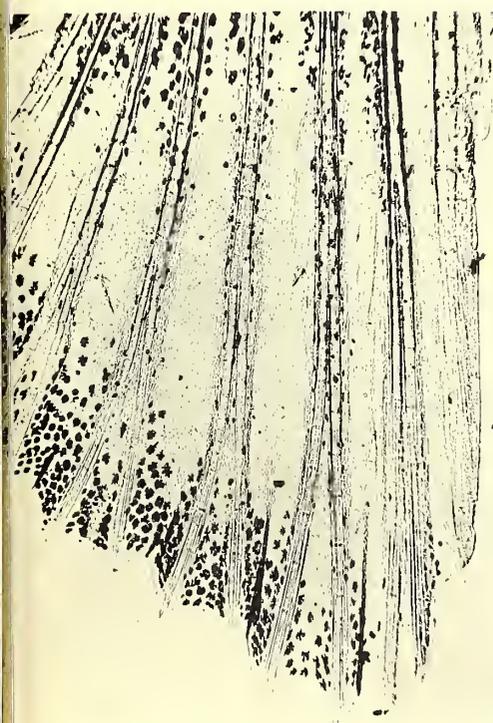


FIG. 17.



FIG. 19.



FIG. 18.



FIG. 20.

DIFFERENTIAL EFFECTS OF ESTRADIOL, ESTRADIOL BENZOATE  
AND PREGNENINOLONE ON PLATYPOECILUS MACULATUS.



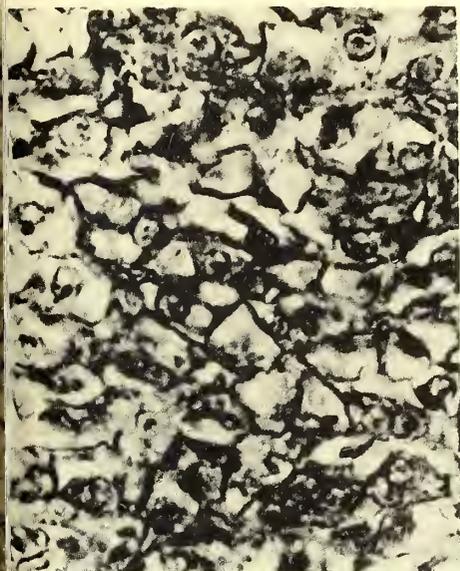


FIG. 21.



FIG. 22.



FIG. 23.



FIG. 24.

DIFFERENTIAL EFFECTS OF ESTRADIOL, ESTRADIOL BENZOATE  
AND PREGNENINOLONE ON PLATYPOECILUS MACULATUS.



## 19.

Eastern Pacific Expeditions of the New York Zoological Society. XLI.  
Mollusks from the West Coast of Mexico and Central America. Part VIII.<sup>1</sup>

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(Plate I).

[This is the forty-first of a series of papers dealing with the collections of the Eastern Pacific Expeditions of the New York Zoological Society made under the direction of William Beebe. The present paper is concerned with specimens taken on the Templeton Crocker Expedition (1936) and the Eastern Pacific Zaca Expedition (1937-1938). For data on localities, dates, dredges, etc., refer to *Zoologica*, Vol. XXII, No. 2, pp. 33-46, and Vol. XXIII, No. 14, pp. 287-298.]

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## INTRODUCTION

This is the eighth of a series of papers dealing with collections of mollusks taken on the Templeton Crocker Expedition (1936) and the Eastern Pacific Zaca Expedition (1937-1938). The general plan of presentation followed in the present con-

tribution is that mentioned in Part II of this series of papers<sup>2</sup>. Formal headings and keys are given for the species collected by the expeditions of 1936 and 1937-1938. Occasionally additional species are included in the keys for convenience but in such cases it is indicated which species do not occur in the present collection.

Acknowledgment is due Dr. G. D. Hanna, Curator, Department of Paleontology of the California Academy of Sciences, Mr. A. G. Smith, Research Associate of the same institution, and Dr. A. Myra Keen, Stanford University, California, for assistance and suggestions. The photographs used for illustrations on the plate were prepared by Mr. Frank L. Rogers.

## FAMILY SEMELIDAE.

A paper by Dall<sup>3</sup> dealing with the west American Semelidae and one by Lamy<sup>4</sup> which contains a revision of the species of this group in the Natural History Museum in Paris are useful to anyone studying the Recent west American forms of this family.

## KEY TO THE GENERA OF THE SEMELIDAE.

- A. Pallial sinus free from the pallial line  
*Semele*
- B. Pallial sinus confluent with the pallial line  
 a. Length exceeding 10 mm.; moderately thick.....*Cumingia*  
 aa. Length rarely exceeding 10 mm.; very thin; usually smooth.....*Abra*

Genus *Semele* Schumacher.KEY TO THE SPECIES OF *Semele*.

- A. Concentrically sculptured with coarsely corrugated or wrinkle-ribbed ridges  
 a. Exterior with radial striae or wrinkled and granulated sculpture  
 b. Interior white; dorsal margin purple; truncated posteriorly  
*decisa*

<sup>1</sup> Contribution No. 859, Department of Tropical Research, New York Zoological Society.

<sup>2</sup> Hertlein, L. G., and Strong, A. M. Eastern Pacific Expeditions of the New York Zoological Society. XXIII. Mollusks from the West Coast of Mexico and Central America. Part II. *Zoologica*, New York Zool. Soc., Vol. 28, Pt. 3, December 6, 1943, pp. 149-168, 1 pl. See especially pp. 149-150.

<sup>3</sup> Dall, W. H. Notes on the Semelidae of the West Coast of America, including some new species. *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 67, issued March 2, 1915, pp. 25-28.

<sup>4</sup> Lamy, E. Révision des Scrobiculariidae vivants du Muséum d'Histoire Naturelle de Paris. *Journ. de Conchyl.*, Vol. 61, No. 3, March 25, 1914, p. 243-368, pl. 8, also figs. in text.

- bb. Interior brown, orange or yellow  
 c. Interior brown; corrugated  
*tabogensis*  
 cc. Interior yellow or orange;  
 wrinkle-ribbed exteriorly  
*californica*  
 aa. Exterior without radial sculpture  
*craneana*
- B. Concentrically sculptured with raised threads, lamellae, or growth lines only  
 a. Concentric sculpture of growth lines only  
 b. Diagonal striae present  
*sparsilineata*  
 bb. Diagonal striae absent; smooth, pure white.....*laevis*  
 aa. Concentric sculpture of raised threads or lamellae  
 c. Escutcheon wide, strongly beveled .....*flavescens*  
 cc. Escutcheon very narrow or lacking  
 d. Shell without radial sculpture; white  
 e. Interspaces with fine concentric striae  
*paziana*<sup>5</sup>  
 ee. Interspaces without fine concentric striae  
*simplicissima*  
 dd. Shell with radial sculpture  
 f. Shell with incised radial grooves on part or all of valves  
 g. Incised sculpture along anterior dorsal margin only  
 h. Concentric ribs closely spaced, fine  
 i. Shell thick, fairly high; interior with a deep purple blotch *pulchra*  
 ii. Shell thinner, more elongate; less purple coloration  
*quentinensis*  
 hh. Concentric ribs more widely spaced, coarse  
*guaymasensis*  
 gg. Incised sculpture present along anterior and posterior margins  
 j. Concentric ribbing fine  
*jaramija*  
 jj. Concentric ribbing coarse;
- entire valve often reticulatedly sculptured *pacifica*  
 ff. Shell without incised radial grooves; fine radial striae present, stronger in interspaces  
 k. Shell suborbicular or roundly ovate  
 l. brownish - red with white medial streak on umbos; large  
*jovis*  
 ll. Yellowish or white  
*mediamericana*<sup>5</sup>  
 kk. Shell elongate  
 m. Concentric lamellae high; shell large; white with purple spots  
 n. Lamellae with scalloped scale-like projections  
*verrucosa*  
 nn. Lamellae without scale-like projections; more rounded ventrally  
*formosa*<sup>5</sup>  
 mm. Concentric lamellae low; shell small; umbos purplish or brownish  
 o. Thick; end of pallial sinus slightly attenuated  
*venusta*  
 oo. Thin; end of pallial sinus blunt  
*incongrua*<sup>5</sup>

***Semele corrugata californica* Reeve.**

*Amphidesma californica* Reeve, Conch. Icon., Vol. 8, *Amphidesma*, October, 1853, species 19, pl. 3, fig. 19. "Gulf of California."

<sup>5</sup> Not represented in the present collection.

*Semele californica* A. Adams, *Proc. Zool. Soc. London* for 1853 (issued July 25, 1854), p. 96. "Hab. Gulf of California. Mus. Cuming."

*Type Locality*: Gulf of California.

*Range*: Magdalena Bay, Lower California, to the Gulf of California.

*Collecting Station*: Mexico: Cape San Lucas, Lower California, beach.

*Description*: Shell ovately oblong, sub-equilateral, dirty pale brown, radiately striated; transversely sulcated, ribs elevated, subcorrugated, ornamented, interspaces closely longitudinally striated; anterior side rounded, posterior subtruncated, very flexuous; interior yellowish, margin yellow. (Free translation of Adams' original description.)

The shell of this subspecies is characterized by the concentric wrinkle-ridged ribs and the dense minute radial striae. A small lunule is present but no appreciable escutcheon. Exteriorly the shells are usually yellowish or yellowish-white in color. The umbos are often yellow and on some specimens a few faint brown transverse markings are present on the dorsal margin both anterior to and posterior to the beaks. Interiorly the shells are usually yellow, sometimes a beautiful golden or orange-yellow. The pallial sinus ascends gently and is rounded at the end which extends forward a little over one-half the length of the shell.

A left valve from Cape San Lucas, in the present collection, measures: length, 40.2 mm.; height, 36 mm.; convexity (one valve), 7.3 mm. A specimen from Magdalena Bay, Lower California, in the Henry Hemphill Collection of the California Academy of Sciences measures: length, 37.5 mm.; height, 33.6 mm.; convexity (both valves together), 15.2 mm.; pallial sinus extends anteriorly 22 mm. from the posterior margin of the shell.

This form apparently is, as stated by Dall, closely related to *Semele corrugata* Sowerby<sup>6</sup>. The specimens which we have seen from Magdalena Bay and the Gulf of California appear to be a little smaller than those of *S. corrugata* Sowerby which was described from Peru. Furthermore these do not have

<sup>6</sup> *Amphidesma corrugatum* Sowerby, *Conch. Illustr.*, Catal. issued with Pt. 19, species No. 8, issued between January 18 and March 8, 1833. [Not illustrated]. "Iquiqui. Peru. Mr. Cuming." Ref. to "Spec. Conch. f. 18." The exact dates of issue of the *Species Conchyliorum* is unknown to us. A copy of Volume 1, Part 2, in the library of the California Academy of Sciences is not dated. In Hanley's edition of Wood's *Index Testaceologicus*, 1856, p. XIX, the dates cited for Sowerby *Species Conchyliorum* are, "part 1. 1830: part II. (imperfect) not published until Nov. 1855" I. —Sowerby, *Proc. Zool. Soc. London* for 1832, issued March 13, 1833, p. 200. "Hab. in Peruvia et ad Iquiqui." "Dredged from coarse gravel in ten fathoms water."—Reeve, *Conch. Icon.*, Vol. 8, *Amphidesma*, October, 1853, species 4, pl. 1, fig. 4 (as *Amphidesma corrugata*). [Locality same as in preceding reference].

Shaw (*Proc. Malacol. Soc. London*, Vol. 8, No. 6, 1909, pp. 333-340), in a collation of the Conchological Illustrations, indicated that Parts 17, 18, 19, and the catalogue of species of *Amphidesma* issued with Part 19, appeared between January 18 and March 8, 1833. The species of *Amphidesma* named and illustrated in those parts for the first time take their date of publication from the Conchological Illustrations rather than the *Proceedings* of the Zoological Society of London where the descriptions appeared on March 13, 1833.

the purple coloration on the anterior portion of the hinge as shown on Reeve's illustration of *Semele corrugata*. That species has been recorded as occurring at Magdalena Bay and in the Gulf of California, and it is possible that the present specimen might be referable to Sowerby's species. However, for the present at least, we are inclined to regard these northern shells as belonging to a subspecies of *S. corrugata*, at least until a comparison can be made with a series of specimens from Peru, the type locality of Sowerby's species.

It appears that in some cases, *Semele corrugata californica* has been confused with *Semele flavescens* Gould, a different shell.

*Distribution*: A single valve of this subspecies was taken by the expedition on the beach at Cape San Lucas. It also occurs in the Pleistocene of Magdalena Bay, Lower California. The record "*Semele cf. pulchra* Sowerby" in the list of species cited by Jordan, 1936, as occurring in the Pleistocene of Magdalena Bay, is referable to *S. corrugata californica*. Olsson has recorded "*Semele cf. californica* Con." as occurring in the Pleistocene of Panama. Records of the occurrence of this shell in Asiatic seas are referable to some other species.

#### *Semele craneana* Hertlein & Strong, sp. nov.

Plate I, Figs. 19, 22.

Shell oval, compressed, thin, with the beaks a little nearer the posterior end, yellowish, with faint, pinkish, interrupted radial stripes; posterior dorsal margin sloping, slightly convex, forming a distinct angle with the truncated posterior end, anterior dorsal margin more direct, slightly concave, anterior dorsal margin well rounded; lunule very small, indistinct; outer surface smooth near the beaks gradually developing concentric ridges which are strongest near the margins, with deep interspaces which about equal the ridges in width; posterior end with a depression running from near the beaks to the lower end of the truncation, posterior to which the shell is flattened and somewhat flexed; radial sculpture entirely absent; interior white, somewhat iridescent, showing the concentric sculpture and pinkish rays quite distinctly; pallial sinus broad, ascending, rounded at the end and projecting about two-thirds the length of the shell; two cardinal teeth, the posterior one the larger, lateral teeth small. The type measures: length, 38 mm.; height, 29.5 mm.; convexity (one valve), 6.5 mm.; pallial sinus projects forward 24 mm. from the posterior margin of the shell.

Holotype, a left valve, (Calif. Acad. Sci. Paleo. Type Coll.), dredged in the Gulf of California. One left valve was dredged on Arena Bank, Gulf of California, Station 136-D-24, Lat. 23° 29' N., Long. 109° 23' 30" W., in 50 fathoms (91 meters), mud, *Arca* conglomerate; one young specimen and a single right valve were dredged in the same general locality, Station 136-D-26, Lat. 23° 27' N., Long.

109° 24' W., in 45 fathoms (82 meters), sand, crushed shell; a single valve was dredged 3 miles off Pyramid Rock, Clarion Island, Station 163-D-2, Lat. 114° 45' N., Long. 114° 45' W., in 55 fathoms (100 meters), rock, coral.

This shell is similar in size and shape to *Semele tabogensis* Pilsbry & Lowe. The sculpture is similar but lacks the fine radial ornamentation of that species and the posterior area is more distinct.

The shell of *Semele craneana*, although less arcuate ventrally, is similar to that of *S. martinii* Reeve<sup>7</sup> which was originally described from Brazil.

This species is named for Miss Jocelyn Crane, Technical Associate, Department of Tropical Research, New York Zoological Society, who accompanied the Templeton Crocker Expedition, 1936, during the course of which the type specimen of the present species was collected.

*Distribution*: This new species is at present known only from the southern portion of the Gulf of California and from off Clarion Island, in 45-55 fathoms.

#### *Semele decisa* Conrad.

*Amphidesma decisa* Conrad, *Jour. Acad. Nat. Sci. Philadelphia*, Vol. 7, 1837, p. 239, pl. 19, fig. 2. "Inhabits with the preceding" [which is "Inhabits deep water in the vicinity of Sta. Diego"].—Reeve, *Conch. Icon.*, Vol. 8, *Amphidesma*, 1853, species 24, pl. 4, fig. 24. San Diego, California.

*Semele decisa* Conrad, Grant & Gale, *Mem. San Diego Soc. Nat. Hist.*, Vol. 1, 1931, p. 376, pl. 14, figs. 13a, 13b. Earlier records cited. Pleistocene and Recent.

*Type Locality*: San Diego, California, in deep water.

*Range*: San Pedro, California, to Cape San Lucas, Lower California.

*Collecting Station*: Mexico: Cape San Lucas, Lower California.

*Description*: Shell rounded, thick, sub-equilateral, the anterior side the longer, the end rounded; posterior dorsal margin nearly straight, the posterior end truncated; posteriorly biangulate, the area between somewhat concave; ornamented with numerous, thick, unequal concentric rugose ribs, the entire surface covered with fine radial grooves or fine wrinkled and granulated sculpture; colored exteriorly by whitish-gray with occasional purple in the concentric grooves; cardinal teeth obsolete, laterals present; pallial sinus wide, rounded at the end, slightly ascending and extending forward about five-eighths the length of the shell which is past a line vertical with the beaks; interior white with purple around the dorsal margin.

A specimen from Cape San Lucas, Lower California, measures: length, 45 mm.; height, 42.5 mm.; convexity (both valves together), 19.8 mm.; pallial sinus extends an-

teriorly 27 mm. from the posterior margin of the shell. A large specimen of this species from Magdalena Bay, Lower California, in the Henry Hemphill collection of the California Academy of Sciences measures: length, 94 mm.; height, 86.5 mm.; convexity (both valves together), 45.5 mm.; pallial sinus extends anteriorly 59 mm. from the posterior margin of the shell.

The shell of *Semele punctata* Sowerby<sup>8</sup>, which was described from the Galápagos Islands, is more elongate in outline and less truncated posteriorly than that of *S. decisa*.

*Semele nisigotoensis* Nomura & Hatai<sup>9</sup>, described from the Miocene of Japan, was compared to *S. decisa*.

*Distribution*: A few specimens of this species were collected by the expedition at Cape San Lucas, Lower California. This is an extension south of the known range of the species. It also has been recorded as occurring in the Pleistocene of Tomales Bay in Central California, in southern California, and south to Magdalena Bay, Lower California.

#### *Semele flavescens* Gould.

*Amphidesma flavescens* Gould, *Proc. Boston Soc. Nat. Hist.*, Vol. 4, November, 1851, p. 89. "San Diego, Lieut. Green."—Gould, *Boston Jour. Nat. Hist.*, Vol. 6, 1853, p. 392. Original locality cited.

*Amphidesma proximum* C. B. Adams, *Ann. Lyceum Nat. Hist. New York*, Vol. 5, July, 1852, pp. 513, 547 (separate, pp. 289, 323). "Habitat. — Panama."—Hanley, *Cat. Rec. Bivalve Shells*, p. 341, 1856, pl. 12, fig. 5, 1843 (cited as *Amphidesma corrugatum* on expl. to plate). "Mexico."

*Amphidesma proxima* Adams, Reeve, *Conch. Icon.*, Vol. 8, *Amphidesma*, 1853, species 20, pl. 3, fig. 20. "Hab. Panama." [A reproduction of this figure given by M. Smith, *Panamic Mar. Shells (Tropical Photogr. Lab., Winter Park, Florida)*, 1944, fig. 805].

*Semele flavescens* Gould, Lamy, *Journ. de Conchyl.*, Vol. 61, No. 3, 1914, p. 358. Gulf of California; Panama.

*Semele proxima* C. B. Adams, Olsson, *Nautilus*, Vol. 37, No. 4, 1924, p. 129. Zorritos, Lobitos, Negritos, Peru.

*Type Locality*: San Diego, California.

*Range*: Catalina Island, California (Dall), to Negritos, Peru.

*Collecting Station*: Costa Rica: Golfito Bay, Gulf of Dulce.

*Description*: Shell subrotund, compressed, sculptured by concentric lamellar decussate striae, orange becoming white in later stages and covered with a periostracum which is

<sup>8</sup> *Amphidesma punctatum* Sowerby, *Conch. Illustr.*, *Amphidesma*, Catal. issued with Pt. 19, No. 18, pl. 18, fig. 7, issued between January 18 and March 8, 1833. "Galapagos Islands. Mr. Cumins."—Sowerby, *Proc. Zool. Soc. London* for 1832 (issued March 13, 1833), p. 200. "Hab ad Insulas Gallapagos."—Reeve, *Conch. Icon.*, Vol. 8, *Amphidesma*, October, 1853, species 26, pl. 4, fig. 26 (as *Amphidesma punctata*). Galápagos Islands.

<sup>9</sup> *Semele nisigotoensis* Nomura & Hatai, *Saito Ho-On Kai Mus. Res. Bull.*, No. 10, 1936, p. 131, pl. 16, figs. 8, 9. Nisigoto, Tanagura Beds, northwest Honsyu, Japan, middle Miocene.

<sup>7</sup> *Amphidesma martinii* Reeve, *Conch. Icon.*, Vol. 8, *Amphidesma*, November, 1853, species 43, pl. 6, fig. 43. "Hab. Rio." [A. Adams' description of this species did not appear until July 25, 1854].

brown shaded with gray (fusco); beaks median, acute, not at all elevated; anterior dorsal area excavated, posterior lanceolate, concave bounded by a line; interior tinted yellow, marked with shiny dots; pallial sinus spatulate, sculptured by close divergent striae; ligamental pit deep, elongate; anterior lateral teeth approximate to the beaks. Long.  $2\frac{3}{8}$ ; alt.  $2\frac{1}{8}$ ; lat.  $1\frac{1}{4}$  poll. (Translation of Gould's original description).

"Usually found about half the above size; the concentric lamellae become worn off and more irregular towards the margin. The interior is faintly tinted yellow when young, but very richly so when old. It is near *A. corrugatum*, Sowb."

The description given by Gould in 1853 is an enlargement of the original. He stated: . . . "posterior dorsal edge long lanceolate, concave, bounded by a distinct angle; surface pale orange near the beaks, becoming dingy white at the older stages, and covered by a dirty greenish epidermis; marked by concentric lamellar striae, crossed by fine radiating striae, especially across the disk."

A left valve in the present collection measures: length, 47.5 mm.; height, 43.8 mm.; convexity (one valve), 11.2 mm. A specimen from Loreto, Lower California, in the collections of the California Academy of Sciences measures: length, 58.5 mm.; height, 55.4 mm.; convexity (both valves together), 28.3 mm.; pallial sinus extends forward 36 mm. from the posterior margin. A large single left valve from Magdalena Bay, Lower California, in the collection of the same institution measures: length, 64.4 mm.; height, 63.4 mm.; convexity (one valve), 15 mm.; pallial sinus extends anteriorly 40 mm. from the posterior margin of the shell.

Gould's type specimen has never been illustrated but the foregoing description applies exactly to specimens of a species in the collection of the California Academy of Sciences which were collected from Lower California to Panama. This species is identical with the one illustrated by Reeve under the name of *Amphidesma proxima* Adams. According to Dall<sup>10</sup> Adams' species is identical with *Semele flavescens*. *Amphidesma proximum* C. B. Adams was founded upon a specimen from Panama 1.8 inches in length. It was said to be closely related to *Semele elliptica* Sowerby and *S. lenticulare* Sowerby. Carpenter<sup>11</sup> regarded *S. proxima* as identical with *S. elliptica*. Whether or not *S. proxima* is identical with *S. flavescens* may be open to doubt but certainly Reeve's figure attributed to that species is referable to *S. flavescens*.

In some cases *Semele flavescens* has been identified under the name of *Semele striosa* C. B. Adams<sup>12</sup>. That species was based upon

a single specimen from Panama .78 inch in length and it appears uncertain exactly how it differs from related forms. In the original description it is mentioned . . . "corselet and lunule not well defined." This does not agree with *S. flavescens* which has a well developed escutcheon.

*Semele mediamericana* Pilsbry & Lowe<sup>13</sup> differs from *S. flavescens* in lacking the strong escutcheon and in the sculpture in which . . . "there are narrow, thread-like concentric ridges, coarser and more raised than in *S. flavescens*, a little less than one mm. apart on the lower part of the valve, and a very minute, dense, even radial sculpture throughout, diverging at both ends, and seen under the lens to be totally unlike the radial striation of *S. flavescens*."

*Distribution*: A single left valve of *Semele flavescens* was taken by the expedition at Golfito Bay in the Gulf of Dulce. It occurs fairly commonly from Magdalena Bay to the Gulf of California and south to Panama and apparently to Peru. We have not seen specimens from north of Magdalena Bay, but the type locality is San Diego, and Dall cited it as occurring north to Catalina Island. It also occurs in the Pliocene of the Gulf of California region and in the Pleistocene of Magdalena Bay, Lower California, and it has been recorded as occurring in the Quaternary of Ecuador. Olsson, 1932, cited "*Semele* cf. *flavescens* Gould" as occurring in the Miocene of Peru.

#### *Semele guaymasensis* Pilsbry & Lowe.

*Semele guaymasensis* Pilsbry & Lowe, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 84, May 21, 1932, p. 92, pl. 12, figs. 8 and 9. "Guaymas, 20 fathoms."—E. K. Jordan, *Contrib. Dept. Geol. Stanford Univ.*, Vol. 1, No. 4, 1936, p. 145. Magdalena Bay, Lower California, Pleistocene. Also Gulf of California, Recent.

*Type Locality*: Guaymas, Sonora, Mexico, in 20 fathoms.

*Range*: Punta Penasco, Sonora, Mexico, to La Paz, Lower California.

*Collecting Station*: Mexico: Santa Inez Bay, Gulf of California (145-D-1, 3), 4-13 fathoms, sand.

*Description*: The shell is light buff, faintly mottled or obscurely rayed with dull light purple, the dorsal borders dark purple. Shape irregularly oval, nearly equilateral, strongly compressed; dorsal margin slightly convex behind, straight in front of the beaks; ends rounded; ventral margin strongly convex. Sculpture of strong, concentric ridges generally a little wider than their intervals, a little lamellar at the border of the escutcheon, and on the anterior end cut by about seven radial grooves. Escutcheon very narrow, flattened, with weak growth lines only, purple. Lunule small, sunken, the dorsal area beyond it pur-

<sup>10</sup> Dall, W. H., *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 67, 1915, p. 25.

<sup>11</sup> Carpenter, P. P., *Proc. Zool. Soc. London*, 1863, p. 367. Reprint in *Smithson. Miscell. Coll.*, No. 252, 1872, p. 203.

<sup>12</sup> *Amphidesma striosum* C. B. Adams, *Ann. Lyceum Nat. Hist. New York*, Vol. 5, July, 1852, pp. 513, 547 (separate pp. 201, 323). "Habitat.—Panama."

<sup>13</sup> *Semele mediamericana* Pilsbry & Lowe, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 84, May 21, 1932, p. 92, pl. 12, figs. 1, 1a, 2 (as *Semele mediamericum* on expl. to pl.). "Nicaragua (McNeil)."

ple and smooth except for lines of growth. The interior is stained with dull purple on a buff or white ground, with purple markings on the ventral border. The pallial sinus occupies about two-thirds of the length. Length, 16 mm.; height, 12.3 mm.; semidiam. (right valve), 2.6 mm. Length, 22 mm.; height 17 mm.; semidiam. (right valve) 4 mm. (Original description.)

This species differs from *Semele pulchra* Sowerby and *S. quentinensis* Dall in the much coarser and more widely spaced concentric sculpture.

*Semele anteriocosta* Vokes<sup>14</sup>, described from the Miocene of Trinidad, is similar to *S. guaymasensis* in its general characters but the strength of the ribbing appears to be intermediate between that of this species and *S. quentinensis*.

*Distribution*: A few specimens referable to this species were dredged by the expedition in Santa Inez Bay, in the Gulf of California, in 4-13 fathoms, on a sandy bottom.

#### *Semele jaramija* Pilsbry & Olsson.

Plate I, Fig. 12.

*Semele jaramija* Pilsbry & Olsson, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 93, September 9, 1941, p. 70, pl. 17, fig. 5. "Canoa formation, Punta Blanca." Ecuador, Pliocene.

*Type Locality*: Canoa formation, Punta Blanca, Ecuador, Pliocene.

*Range*: Santa Inez Bay, Gulf of California.

*Collecting Station*: Mexico: Santa Inez Bay, Gulf of California (145), on shore.

*Description*: Shell small, suboval in form, with the beaks placed a little in back of the middle; but little convex; the sculpture consists of strong, regular, concentric threads, well developed over the whole shell and at the anterior-upper end, these concentric threads are cut by a series of small radial grooves; at the posterior end the grooves, about 8 in number, are crossed by the concentric threads, the sculpture being beautifully cancellated. Length, 21 mm.; height, 16 mm.; semidiameter, 3.5 mm. (Original description.)

A left valve of this species in the present collection measures: length, 16 mm.; height, 12.2 mm.; convexity (one valve), 2.9 mm.; pallial sinus extends anteriorly 9.5 mm. from the posterior margin of the shell.

The present specimen agrees exactly with the illustration of *Semele jaramija* given by Pilsbry & Olsson.

As mentioned in the discussion of *Semele pacifica*, that species always has radial sculpture on both the anterior and posterior dorsal areas. The variation in *S. pacifica* Dall is so great that it appears quite possible that the form here cited as *S. jaramija* may be merely a subspecies of it.

<sup>14</sup> *Semele anteriocosta* Vokes, *Amer. Mus. Novit.*, No. 983, May 16, 1938, p. 14, fig. 5. Upper Miocene of Springvale, Trinidad, British West Indies.

*Semele guaymasensis* Pilsbry & Lowe and *S. quentinensis* Dall have radial sculpture usually only on the anterior dorsal area and when present at all posteriorly it is much less strongly developed than that on *S. jaramija*.

*Distribution*: A single left valve here referred to *Semele jaramija* was taken by the expedition on shore at Santa Inez Bay in the Gulf of California. This species has also been recorded as occurring in the Pleistocene of Panama and in the Pliocene at Punta Blanca, Ecuador.

#### *Semele jovis* Reeve.

*Amphidesma jovis* Reeve, *Conch. Icon.*, Vol. 8, *Amphidesma*, November, 1853, species 34, pl. 5, fig. 34. "Hab.—?"

*Semele jovis* A. Adams, *Proc. Zool. Soc. London* for 1853 (issued July 25, 1854), p. 94. "Hab. ? Mus. Cuming."

*Tellina barbarae* Boone, *Bull. Bingham Oceanogr. Coll.* Peabody Mus. Yale Univ., Vol. 2, Art. 5, December, 1928, p. 9, pl. 1 (upper figure). "Pearl Islands, depth 12 fathoms."

*Type Locality*: Port Parker, Costa Rica (here designated as type locality). No locality cited originally.

*Range*: Kino Bay, Sonora, Mexico, in the Gulf of California, to the Las Perlas Islands, Panama.

*Collecting Stations*: Mexico: Port Guatulco (195-D-2), 3 fathoms, sand; Nicaragua: Corinto (200-D-19), 12-13 fathoms, mangrove leaves; Costa Rica: Port Parker (203-D-1-3), 12-15 fathoms, sandy mud, crushed shell, shelly sand, algae, shelly mud.

*Description*: Shell somewhat roundly ovate, somewhat ventricose, anterior side slightly the longer; posterior side with a flexure, the end truncated; ornamented with rather thin, close-set, concentric lamellae; the interspaces with fine concentric lineation; extremely fine radial wrinkling present on fresh specimens but clearly noticeable on worn specimens; color rose-fawn, beaks red with a medial white streak; hinge with two cardinals and laterals in each valve; pallial sinus broadly elliptically rounded, projecting forward about four-sevenths the length of the shell; interior rose and white.

A right valve from Port Guatulco, Mexico, measures: length, 54.5 mm.; height, 45 mm.; convexity (one valve), 10.3 mm.; pallial sinus extends anteriorly 32.5 mm. from the posterior margin of the shell. A specimen collected by H. N. Lowe at Kino Bay, Sonora, Mexico, in the Gulf of California, measures 59 mm. in length.

*Semele rosea* Sowerby<sup>15</sup>, described from Peru, is more orbicular in outline than *S. jovis*.

<sup>15</sup> *Amphidesma roseum* Sowerby, *Conch. Illustr.*, Catal. issued with Pt. 19, species No. 5, pl. 17, fig. 1, issued between January 18 and March 8, 1833. "Tumbez, Peru. Mr. Cuming."—Sowerby, *Proc. Zool. Soc. London* for 1832 (issued March 13, 1833), p. 199. "Hab. ad littora Peruviae." "A single valve was found at Tumbez in Peru."—Reeve, *Conch. Icon.*, Vol. 8, *Amphidesma*, October, 1853, species 17, pl. 8, fig. 17 (as *Amphidesma rosea*). Tumbez, Peru.

According to Verrill the lamellae are more closely spaced and the plication of *Semele jovis* is nearer the outer edge as compared to that of *S. junonia* Verrill<sup>16</sup> which was described from La Paz, Lower California. He mentioned the presence of radiating striae in the interspaces of *S. junonia*, a feature also present and especially noticeable on somewhat worn specimens of *S. jovis*. According to Lamy<sup>17</sup> *Semele junonia* is only a variety of *S. rosea*.

**Distribution:** A few single valves of *Semele jovis* were dredged by the expedition off western Mexico, Nicaragua, and Costa Rica.

#### *Semele laevis* Sowerby.

*Amphidesma laeve* Sowerby, Conch. Illustr., Catal. issued with Pt. 19, No. 22, pl. 18, fig. 6, issued between January 18 and March 8, 1833. "Xipixapi. W. Col. Mr. Cuming."—Sowerby, *Proc. Zool. Soc. London* for 1832 (issued March 13, 1833), p. 199. "Hab. ad Xipixapi, Columbiae Occidentalis." "A single specimen of this very delicate species was dredged from a depth of ten fathoms in sandy mud."

*Amphidesma laevis* Sowerby, Reeve, Conch. Icon., Vol. 8, *Amphidesma*, November, 1853, species 50, pl. 7, fig. 50. Original locality cited.

**Type Locality:** Xipixapi [Jipijapa], Ecuador, in 10 fathoms, sandy mud.

**Range:** Champerico, Guatemala, to Jipijapa, Ecuador.

**Collecting Stations:** Guatemala: 7 miles west of Champerico (197-D-1-2), 14 fathoms, mud; El Salvador: La Libertad (198-D-1-2), 13-14 fathoms, mud; Costa Rica: Gulf of Dulce.

**Description:** Shell elongately ovate, inequilateral, the anterior side the longer, smooth, exterior and interior white; anterior dorsal margin nearly straight, sloping, anterior end tapering and rounded; ventral margin curved; posterior dorsal margin rounded and highest just back of the beaks, posterior end rounded; a broad, shallow, radial groove is present on the posterior area and where this meets the ventral margin there is sometimes a vague truncation; surface smooth except for concentric lines of growth and an occasional concentric groove and sometimes with fine submicroscopic radial striae; hinge of right valve with two small cardinals, the posterior one bifid, the anterior one thin, two laterals present, left valve with two cardinals, the anterior one bifid, the posterior one thin, also projections of the margin which fit into corresponding sockets in the right valve; pallial sinus somewhat elevated above then broadly tapering to a rounded point which projects forward about five-eighths the length of the shell.

A large right valve from off La Libertad, El Salvador, measures approximately: length, 68 mm.; height, 53 mm.; convexity (one valve), 13 mm.; pallial sinus extends anteriorly 48.4 mm. from the posterior margin of the shell.

*Semele laevis* var. *costaricensis* Olsson<sup>18</sup> has been described from the Miocene of Costa Rica and later was cited as also occurring in the Miocene of Peru.

*Semele pallida* Sowerby<sup>19</sup>, described from Ecuador, bears a resemblance, in general features, to *S. laevis* but differs in that it is less elongate anteriorly, less rounded posteriorly, the beaks are more anteriorly situated and the coloration was described as pale purple-fulvous.

**Distribution:** Specimens of this species were dredged off Guatemala and El Salvador in 13-14 fathoms and were taken on the beach of the Gulf of Dulce. These occurrences extend the known range of the species considerably to the north as heretofore it has not been reported north of Panama. This species also has been recorded as occurring in the Pleistocene of Panama and in the Pliocene at Puerto Jama, Ecuador.

#### *Semele pacifica* Dall.

Plate I, Fig. 11.

*Semele pacifica* Dall, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 61, March 2, 1915, p. 27. "Catalina Island, California, to Acapulco, Mexico, in 9 to 21 fathoms."—I. S. Oldroyd, *Stanford Univ. Publ. Univ. Ser. Geol. Sci.*, Vol. 1, 1924, p. 180, pl. 3, fig. 5. Original range cited.—J. Q. Burch, *Min. Conch. Club South. Calif.*, No. 43, January, 1945, p. 17. "Dr. A. M. Keen advises 'Type locality of *S. pacifica* is: U. S. B. F. Sta. 2022, off La Paz, in 21 fms.'"

**Type Locality:** Off La Paz, Lower California, in 21 fathoms (Keen).

**Range:** Catalina Island, California, to the Gulf of California and south to Taboga Island, Panama.

**Collecting Stations:** Mexico: Santa Inez Bay, Gulf of California (145-D-1, 3), 4-13 fathoms, sand, also on shore; Costa Rica: Port Parker (203-D-3), 12 fathoms, shelly mud; Golfo, Gulf of Dulce.

**Description:** The shell of this species is very similar to that of *Semele cancellata* Sowerby<sup>20</sup> which occurs in Atlantic waters.

<sup>18</sup> *Semele laevis* Sowerby, var. *costaricensis* Olsson, *Bull. Amer. Paleol.*, Vol. 9, Bull. 39, Pt. 2, June 21, 1922, p. 430 (258), pl. 32 (29), fig. 1. "Gatun Stage: Hill No. 3, Banana River," Costa Rica, Miocene.

<sup>19</sup> *Amphidesma pallidum* Sowerby, Conch. Illustr., Catal. issued with Pt. 19, sp. No. 3, pl. 17, fig. 3, issued between January 18 and March 8, 1833. "Salango, W. Col. Mr. Cuming."—Sowerby, *Proc. Zool. Soc. London* for 1832 (issued March 13, 1833), p. 199. "Hab. ad Salango, Columbiae Occidentalis." "Dredged in sandy mud at a depth of seven fathoms."—Reeve, Conch. Icon., Vol. 8, *Amphidesma*, 1853, species 22, pl. 4, fig. 22 (as *Amphidesma pallida*). Original locality cited.

<sup>20</sup> *Amphidesma cancellatum* Sowerby, Conch. Illustr., Catal. issued with Pt. 19, species No. 13, issued between January 18 and March 8, 1833. "Antigua and St. Vincents." Ref. to "Spec. Conch. f. 8."—Reeve, Conch. Icon., Vol. 8, *Amphidesma*, 1853, species 44, pl. 7, fig. 44 (as *Amphidesma cancellata*). "Hab.—?"

<sup>16</sup> *Semele junonia* Verrill, *Amer. Jour. Sci.*, Ser. 2, Vol. 69, No. 146, March, 1870, p. 217. "Near La Paz,—Capt. J. Pedersen."

<sup>17</sup> Lamy, E., *Journ. de Conchyl.*, Vol. 61, No. 3, 1914, p. 357.

Dall stated in the original description that it . . . "differs from that Atlantic species in its smaller lunule, shorter and weaker right lateral tooth, and sharper and more delicate concentric sculpture."

A left valve in the present collection from Golfito, Gulf of Dulce, Costa Rica, measures: length, 20 mm.; height, 16.6 mm.; convexity (one valve), 4.6 mm.

*Semele pacifica* is a very variable species. Young specimens have rather flattened shells and strong cancellate sculpture with the concentric lamellae well developed. In the adult stage the shells become thicker, more ventricose, and with the radial element in the sculpture as strong or stronger than the concentric. The radial sculpture is always present near the anterior and posterior dorsal margins and sometimes covers the whole shell.

*Semele pacifica* is one of a group of related species which vary in details of sculpture. *Semele venusta* Reeve has no radiating sculpture. *Semele guaymasensis* Pilsbry & Lowe has strong concentric sculpture but with incised radiating sculpture only on the anterior dorsal area. *Semele quentinensis* Dall has very fine concentric sculpture with radial sculpture on the anterior dorsal portion and, rarely, with a few faint striae along the posterior dorsal margin. *Semele pulchra* Sowerby has concentric and radial sculpture similar to that of *S. quentinensis* but the shell is higher in proportion to the length as compared to Dall's species. *Semele jaramija* Pilsbry & Olsson, described from the Pliocene of Ecuador, has concentric sculpture intermediate in strength between that of *S. quentinensis* and *S. guaymasensis*, but in addition to similar radial sculpture on the anterior dorsal area it also has strong, incised radial sculpture on the posterior dorsal area. *Semele pacifica* has strong well developed concentric sculpture with radials on both the anterior and posterior portions and sometimes all over the shell.

*Distribution*: A few specimens of *Semele pacifica* were dredged by the expedition in 4-13 fathoms in Santa Inez Bay, in the Gulf of California, at Port Parker, Costa Rica, in 12 fathoms, and at Golfito in the Gulf of Dulce.

### *Semele pulchra* Sowerby.

Plate I, Fig. 15.

*Amphidesma pulchrum* Sowerby, *Proc. Zool. Soc. London*, June 5, 1832, p. 57. "Hab. in Sinu Caraccensi, Americae Meridionalis."—Sowerby, *Conchyl. Illustr.*, Catal. issued with Pt. 19, species No. 2, pl. 17, fig. 2, issued between January 18 and March 8, 1833, "St. Elena W. Columbia." Var. fig. 2\*. Panama.

*Amphidesma pulchra* Sowerby, Reeve, *Conch. Icon.*, Vol. 8, *Amphidesma*, October, 1853, species 2, pl. 1, fig. 2. Original locality cited.

*Type Locality*: Bay of Caraccas, Ecuador.

*Range*: Gulf of Fonseca, Nicaragua, to Ecuador.

*Collecting Stations*: Nicaragua: Potosi and 5 miles SSW. of Monypenny Point, Gulf of Fonseca.

*Description*: Shell trigonally ovate, fairly thick, anterior side the longer, sloping and rounded at the end; posterior side with a fold, the end roundly truncated; ventral margin rounded; sculptured with fine close concentric riblets, on the anterior end these are decussated by several (10-15) incised radial lines; color pale yellowish-gray with purple blotches and ^-shaped markings; pallial sinus higher in front of the adductor impression then gently sloping to a broadly rounded end which projects forward about three-fifths the length of the shell; hinge normal; interior colored white with the umbonal half and the hinge purple or tinged with purple.

A typical specimen from Nicaragua measures: length, 31 mm.; height, 25.4 mm.; convexity (both valves together), 12.5 mm.; pallial sinus projects anteriorly 19.8 mm. from the posterior margin of the shell.

The shells here referred to *Semele pulchra* agree exactly with the figures of that species given by Sowerby and by Reeve. *Semele quentinensis* Dall, a closely related species which has usually been cited under the name of *S. pulchra*, occurs from southern California to Central America. It is more elongate in outline, the anterior dorsal margin slopes more gently from the beaks, the shell is thinner and the purple coloration is more weakly developed.

*Distribution*: Only three specimens of this species were taken by the expedition in the Gulf of Fonseca. It ranges south to Ecuador.

### *Semele quentinensis* Dall.

Plate I, Fig. 10.

*Semele quentinensis* Dall, *West Amer. Sci.*, Vol. 19, No. 3, June 15, 1921, p. 22. "Pliocene or Early Pleistocene of San Quentin."—Dall, *Proc. U. S. Nat. Mus.*, Vol. 66, No. 2554, Art. 17, 1925, p. 26, pl. 8, fig. 4. "Pliocene (?) of San Quentin Bay, Lower California."

*Type Locality*: San Quintin, Lower California, Pleistocene.

*Range*: Point Mugu, Ventura County, California, to Costa Rica.

*Collecting Stations*: Guatemala: 7 miles west of Champerico (197-D-2), 14 fathoms, mud; El Salvador: Meanguera Island, Gulf of Fonseca (199-D-1), 16 fathoms, sand, mud, crushed shell; Nicaragua: Corinto (200-D-19), 12-13 fathoms, mangrove leaves; Costa Rica: 1 mile south of Golfito.

*Description*: Shell small, inequilateral, inequivalve, rather compressed, anterior end longer, terminally rounded; posterior end obscurely subtruncate, base moderately arcuate; beaks inconspicuous; surface finely concentrically closely sculptured, with fine radial threads chiefly visible in the sulci; at the anterior end are about a dozen stronger sulci, cutting and more or less beading the concentric sculpture, but this feature is not

repeated at the posterior end; hinge normal, well developed; pallial sinus large, subovate, nearly reaching the anterior adductor scar, and entirely free from the pallial line; the left valve slightly flatter than the right valve. Length, 24; height, 19; diameter, 8 mm. (Original description).

A large specimen from the Gulf of Fonseca in the present collection measures: length, 27.3 mm.; height, 20.8 mm.; convexity (both valves together), 8.9 mm.; pallial sinus extends anteriorly 18 mm. from the posterior margin of the shell.

The shell of this species is very similar to that of *Semele pulchra* but the length is greater in proportion to the height and the anterior dorsal margin slopes more gently from the beaks. The specimens in the present collection are thinner and the purple coloration is less pronounced than that of *S. pulchra*. These shells possess fine, even, concentric sculpture which along the anterior dorsal margin is crossed by incised radial lines giving a beaded appearance to that portion of the shell. These specimens agree exactly with Dall's description and illustration of *Semele quentinensis* which was based on a fossil specimen from the Pleistocene of San Quintin, Lower California. These appear to be identical with the species occurring in southern California which generally has been cited in the literature under the name of *Semele pulchra*. The only difference seems to be in size, those from southern California seldom exceeding 20 mm. in length. A few specimens of this northern form also possess a few incised radial lines along the posterior dorsal margin but they are fewer and much weaker than those on the anterior dorsal margins and thus differ from the sculpture of *Semele jaramija* Pilsbry & Olssen which was originally described from the Pliocene of Ecuador. *Semele guaymasensis* Pilsbry & Lowe has more widely spaced and coarser concentric sculpture.

**Distribution:** Specimens of *Semele quentinensis* were dredged by the expedition in 12 to 16 fathoms from Guatemala to Costa Rica. It also is known to occur in the Pleistocene of southern California and Lower California.

#### *Semele simplicissima* Pilsbry & Lowe.

*Semele simplicissima* Pilsbry & Lowe, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 84, May 21, 1932, p. 93, pl. 12, figs. 6, 6a. "Acapulco, 20 fathoms."

**Type Locality:** Acapulco, Mexico, in 20 fathoms.

**Range:** Santa Inez Bay, Gulf of California, to Acapulco, Mexico.

**Collecting Stations:** Mexico: Arena Bank (136-D-2, 5), 33-45 fathoms, mud, *Arca conglomerates*, sand, weed; Santa Inez Bay (143-D-2, 3, 4), 25-35 fathoms, mud, crushed shell; Santa Cruz Bay (195-D-21), 18 fathoms, mud; Costa Rica: Port Parker (203-D-3), 12 fathoms, shelly mud; 14 miles S. X

E. of Judas Point (214-D-1, 4), 42-61 fathoms, mud, shell, rocks.

**Description:** Shell ovate, thin, moderately inflated at the umbos, beaks near the middle; anterior dorsal margin sloping, nearly straight, end rounded, ventral margin broadly rounded, posterior end a little higher than the anterior, convex dorsally, in large specimens decidedly truncated at the end where the fold reaches the margin; sculpture of very fine, fairly regular, low, concentric ridges which are covered by such fine, concentric lines that they disperse light into spectral colors; the interspaces are flat and without either concentric or radial striation; lunule lanceolate and rather deeply concave; pallial sinus ascending, rounded at the end and projecting a little beyond the middle of the shell; color dingy white and on the interior of fresh specimens a salmon pink or dark orange flush covers the umbonal half of the shell.

Some specimens in the present collection are much larger than the type of this species. The largest shell, a left valve, measures: length, 33 mm.; height, 24.3 mm.; convexity (one valve), 6.4 mm.; pallial sinus projects anteriorly 19 mm. from the dorsal margin of the shell. One pair of valves from Arena Bank measures, approximately: length, 29.5 mm.; height, 22.8 mm.; convexity (both valves together), 12.2 mm.; pallial sinus extends anteriorly 16.5 mm. from the posterior margin of the shell.

The present specimens have been identified after a comparison with paratypes of *Semele simplicissima* in the H. N. Lowe collection in the San Diego Society of Natural History. This species appears to be very similar to the one described as *Semele regularis* Dall<sup>21</sup> [= *Semele paziana*, new name], but differs in that the intervals between the ribs are smooth and usually not ornamented by concentric striations. However, some specimens here referred to *S. simplicissima* bear sub-microscopic striae in the interspaces.

*Semele sayi* Toulou, 1909, described from the Gatun Miocene of Panama, and especially *S. quirosana* H. K. Hodson, 1931, described from the Upper Oligocene or Miocene of Venezuela, bear a resemblance to *S. simplicissima*.

**Distribution:** Specimens of this species were dredged by the expedition from Santa Inez Bay in the Gulf of California, to off Judas Point, Costa Rica, at depths of 12 to 61 fathoms. These records of occurrence furnish new extensions both north and south of the known range of the species.

#### *Semele sparsilineata* Dall.

Plate I, Fig. 8.

*Semele sparsilineata* Dall, *Proc. Acad. Nat.*

<sup>21</sup> *Semele regularis* Dall, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 67, issued March 2, 1915, p. 27. "Gulf of California, off La Paz, in 10 to 30 fathoms."

Not *Semele regularis* E. A. Smith, *Sci. Res. Voy. Challenger*, Zool., Vol. 13, Lamell., 1885, p. 87, pl. 5, figs. 4, 4a, 4b. East of Cape York, North Australia in 155 fathoms.

A new name *Semele paziana* is here proposed for the west American species named *Semele regularis* by Dall.

*Sci. Philadelphia*, Vol. 67, issued March 2, 1915, p. 26. "Panama, 18 fathoms." Also recorded from "Chile, Hupé."

*Type Locality*: Panama, in 18 fathoms.

*Range*: Corinto, Nicaragua, to Taboga Island, Panama. To Chile (Dall).

*Collecting Station*: Panama: Gulf of Chiriqui (221-D-1, 5), 35-40 fathoms, sandy mud.

*Description*: Shell ovately oblong, the anterior portion much the longer, the end rounded, ventral margin rounded, posterior end slightly higher, slightly subtruncated, a flexure present; sculptured by fine concentric lines of growth which, sometimes anteriorly and sometimes medially, are crossed by fine oblique striations; pallial sinus ascending, broadly rounded at the end, projecting forward about three-fifths the length of the shell; color dingy white with traces of brownish-purple stains.

The larger specimen in the collection, a right valve, measures approximately: length, 25.5 mm.; height, 20.8 mm.; convexity (one valve), 4.7 mm.; pallial sinus extends anteriorly 15.8 mm. from the posterior margin of the shell.

The present specimens are somewhat worn but they show the oblique striae characteristic of this species. It was upon the basis of sparser oblique striae that Dall separated this species from the east American *Semele purpurascens* Gmelin<sup>22</sup>.

*Distribution*: Only two single valves of this species were dredged by the expedition in the Gulf of Chiriqui, Panama, in 35-40 fathoms.

#### *Semele tabogensis* Pilsbry & Lowe.

*Semele tabogensis* Pilsbry & Lowe, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 84, May 21, 1932, p. 91, pl. 12, figs. 5, 5a, 5b. "Taboga Island, among rocks near the bathing beach."

*Type Locality*: Taboga Island, Panama, among rocks.

*Range*: Tangola-Tangola Bay, Mexico, to Taboga Island, Panama.

*Collecting Station*: Mexico: Tangola-Tangola Bay (196-D-7), 6 fathoms, sand.

*Description*: The shell is thin, orange, shading through pink into light coral red near the umbones; very shortly oval, strongly compressed, slightly inequilateral. The broadly rounded anterior end is somewhat lower than the posterior end, which is noticeably truncate. Dorsal margin somewhat

concave in front of the beaks, convex behind them. In the right valve these margins are produced towards the other valve, covering the ligament. Ventral margin is strongly convex. Sculpture of regular, recurved concentric riblets, which become laminar near the dorsal margin, and are somewhat darker colored than their intervals, in which fine, weak, radial striation is seen. Beaks smooth. Lunule extremely small, confined to the right valve. The interior varies in color from carnelian red to apricot orange, smooth, with some scattered glossy dots. Teeth are lighter or whitish in large individuals. Anterior lateral short, the posterior long and thinner. The pallial sinus reaches well past the middle. Length 37.5 mm., height 30.3 mm., semidiam. (right valve) 6.5 mm. (Original description).

The present specimen, a left valve, measures approximately: length, 22.3 mm.; height, 17.3 mm.; convexity (one valve), 4.3 mm.

*Distribution*: A single left valve of this species was dredged by the expedition in Tangola-Tangola Bay, Mexico, in 6 fathoms. This is an extension north of the known range of this species.

#### *Semele venusta* Reeve.

Plate I, Fig. 13.

*Amphidesma venusta* Reeve, *Conch. Icon.*, Vol. 8, *Amphidesma*, October, 1853, species 3, pl. 1, fig. 3. "Hab. West Columbia."—A. Adams, *Proc. Zool. Soc. London* for 1853 (issued July 25, 1854), p. 96. "Hab. West Columbia. Mus. Cuming."

*Type Locality*: West Colombia.

*Range*: Acapulco, Mexico, to west Colombia.

*Collecting Stations*: Mexico: Port Guatulco (195-D-9), 7 fathoms, gr. sand, crushed shell; Santa Cruz Bay; Tangola-Tangola Bay (196-D-8), 9 fathoms, sand.

*Description*: Shell oblong, transverse, ventricose, rather shining, dull flesh-color, obscurely rayed with rose, anterior side much the longer, posterior slightly truncated, flexuous at the ventral margin; concentrically grooved; purple within, edged with white (Reeve).

A left valve in the present collection from Santa Cruz Bay, Mexico, measures: length, 21.9 mm.; height, 15 mm.; convexity (one valve), 4.2 mm.; pallial sinus extends anteriorly 14 mm. from the posterior margin of the shell.

The pallial sinus of this shell is a distinctive feature. It extends forward about two-thirds the length of the shell; it is broad and higher in front of the posterior adductor impression then tapers elliptically to a rounded point.

The ribbing of *Semele venusta* is somewhat irregular toward the anterior and posterior ends similar to that of *S. incongrua* Carpenter<sup>23</sup> although coarser ventrally. The

<sup>23</sup> *Semele incongrua* Carpenter, *Rept. Brit. Assoc. Adv. Sci. for 1863* (issued August, 1864), pp. 611, 640. "Catalina

<sup>22</sup> *Venus purpurascens* Gmelin, *Syst. Nat.*, ed. 13, Vol. 1, Pars. 6, 1791, p. 3288. Habitat unknown. Ref. to: "List. Conch. t. 303. f. 144."; "B (List. Conch. t. 304. f. 145."; "Klein. ostr. t. 11. f. 57".)

*Tellina obliqua* Wood, *Gen. Conch.*, 1815, p. 152, pl. 41, figs. 4, 5.

This is not *Amphidesma purpurascens* Sowerby (*Conch. Illustr.*, Pt. 19, species No. 19, pl. 18, fig. 5, issued between January 18 and March 8, 1833. "St. Elena. W. Col. Mr. Cuming."—Sowerby, *Proc. Zool. Soc. London* for 1832 (issued March 13, 1833), p. 199. "Hab. ad Sanctam Elenam." "A single valve of this elegant species was picked up on the sands at St. Elena."—Reeve, *Conch. Icon.*, Vol. 8, *Amphidesma*, November, 1853, species 37, pl. 6, fig. 37); which was renamed *Semele sowerbyi* by Lamy (*Bull. Mus. Nat. Hist. Nat.* (Paris), Vol. 18, No. 3, 1912, p. 165, footnote).

shell in adult forms is thicker than that of Carpenter's species. Fine radial sculpture is present in the bottoms of the interspaces.

A few small specimens in the present collection from off western Mexico are remarkably similar to *Semele incongrua*. Traces of the pallial sinus appear to be narrowly elliptical at the end similar to that of *S. venusta* rather than broadly rounded as in *S. incongrua*.

The form described as *Semele pulchra* var. *montereyi* Arnold<sup>24</sup>, based on a Pleistocene fossil from San Pedro, California, is, as mentioned by Dall, a subspecies of *S. incongrua*. The type specimen has not been illustrated but the figure given by Arnold represents a shell which appears to be a little more rounded, with sharper, more erect concentric lamellae and with stronger radial ornamentation than that of *S. incongrua*.

Verrill<sup>25</sup> considered *Semele venusta* to be but a young form of *S. formosa* Sowerby. The pallial sinus, elliptically pointed in *S. venusta*, is quite different from the broadly rounded ascending pallial sinus of *S. formosa*.

*Distribution*: A few valves of *Semele venusta* were taken by the expedition at Port Guatulco, Santa Cruz Bay, and Tangola-Tangola Bay, Mexico, in 7 to 9 fathoms.

#### *Semele verrucosa* Mörch.

Plate I, Figs. 21, 24.

*Semele* (*Amphidesma*) *verrucosa* Mörch, Malakozool. Blätter, Bd. 7, December, 1860, p. 190. "Los Bocorones ad prof. 20 org. spec. 2". Costa Rica.

*Type Locality*: Los Bocorones Islands, Costa Rica.

*Range*: Los Bocorones Islands, Costa Rica, to Hannibal Bank, Panama.

*Collecting Station*: Panama: Hannibal Bank (Sta. 224), 35-40 fathoms, rocks, coral, mud, sand, shells, algae.

*Description*: Shell elongately ovate, inequilateral, whitish blotched with purple; anterior side the longer, the end rounded, ventral margin broadly rounded, posterior end broadly rounded and with a gentle fold; sculpture consists of close concentric ribs, these especially anteriorly and posteriorly are wrinkled and give rise to scalloped scale-like projections, the whole finely radially wrinkled; hinge (right valve) with two cardinals and laterals; pallial sinus broadly rounded at the end and gently ascending to about five-eighths the length of the shell.

Is., 40-60 fm.; common." Reprint in *Smithson. Miscell. Co'l.*, No. 252, 1872, pp. 97, 126.—Carpenter, *Proc. California Acad. Nat. Sci.*, Vol. 3, February, 1865, p. 208 (as *Semele incungrua*). "Hab. Santa Barbara, 16 fm. 1 valve; Catalina Island, 40-60 fm., not uncommon; Cooper."—I. S. Oldroyd, *Stanford Univ. Publ. Univ. Ser. Geol. Sci.*, Vol. 1, 1924, p. 181, pl. 11, figs. 12, 13. "Type locality, Santa Barbara." Range, Monterey, California, to the Coronado Islands, Lower California.

<sup>24</sup> *Semele pulchra* Sowerby, var. *montereyi* Arnold, *Mem. Calif. Acad. Sci.*, Vol. 3, 1903, p. 166, pl. 15, figs. 3, 3a. Lower San Pedro series, San Pedro, California. Pleistocene. Recent in Monterey Bay.

<sup>25</sup> Verrill, A. E., *Amer. Jour. Sci.*, Ser. 2, Vol. 69, No. 146, March, 1870, p. 219.

A right valve measures approximately: length, 43 mm.; height, 32.4 mm.; convexity (one valve), 7.1 mm.; pallial sinus extends anteriorly 26.6 mm. from the posterior margin of the shell.

Mörch pointed out that the shell of *Semele verrucosa* is more elongate in outline, more subtruncate posteriorly, and that the ventral margin is more gently arcuate in outline than that of *S. formosa* Sowerby<sup>26</sup>. The present specimen possesses those characters as well as the pronounced scaly verrucose sculpture characteristic of Mörch's species.

*Distribution*: A single right valve of this species was dredged by the expedition on Hannibal Bank, Panama, in 35-40 fathoms. This is an extension south of the known range of the species.

#### Genus *Abra* Lamarck.

*Abra* Lamarck, *Hist. Nat. Anim. s. Vert.*, Vol. 5, July, 1818, p. 492. Species cited: "*Amphidesma tenuis*" in the synonymy of which was included, "*Maetra tenuis*. Maton, act. soc. linn. 8. p. 72. no. 8" and "*Abra tenuis*. Leach". "Habite les mers d'Angleterre. Communiqué par M. Leach"; "*Amphidesma prismatica*" in the synonymy of which was cited, "*Ligula prismatica*. Montagu. test. brit. suppl. 23. t. 26. f. 3. Ex D. Leach." and "*Abra prismatica*. Leach." "Habite les côtes d'Angleterre. Communiqué par M. Leach."—Gray, *Proc. Zool. Soc. London* for 1847, p. 187. Type: *Maetra tenuis*.—Dall, *Trans. Wagner Free Inst. Sci.*, Vol. 3, Pt. 5, 1900, p. 995. Type: *A tenuis* Montagu.—Woodring, *Carnegie Inst. Washington, Pub.* 366, 1925, p. 179. Type: *Maetra tenuis* Montagu.

*Type* (designated by Gray, 1847): *Maetra tenuis* [Montagu, *Test. Brit.*, Pt. 2, 1803, p. 572, Suppl., 1808, pl. 17, fig. 7. "Southampton, where it is not uncommon on the shore to the west of the town." Also from "Weymouth"—Forbes & Hanley, *Hist. Brit. Moll.*, Vol. 1, 1853 (issued 1848), p. 323, pl. 17, fig. 7. Various localities in England.] [For dates of publication of this work see Fisher and Tomlin, *Jour. Conch.*, Vol. 20, No. 5, August, 1935, pp. 150-151].

Shell small, trigonal; sculpture consisting of incrementals; ligament narrow, resilium seated on a wide, deeply inset chondrophore; hinge of right valve consisting of 2 cardinals (3a, 3b), the posterior one (3b) heavier, and slender anterior and posterior laterals; hinge of left valve consisting of 2 cardinals (2a, 2b), the posterior one (2b) very small; pallial sinus deep, very wide, confluent with pallial line (Woodring).

The genus *Abra* has been recorded as occurring from Eocene to Recent.

<sup>26</sup> *Amphidesma formosum* Sowerby, *Conch. Illustr.*, Catal. issued with Pt. 19, No. 4, pl. 19, fig. 8 [two figs.], issued between January 18 and March 8, 1833. "St. Elena. Mr. Cuming."—Sowerby, *Proc. Zool. Soc. London* for 1832 (issued March 13, 1833), p. 199. "Hab. ad Sanctam Elenam." "Only two odd valves were dredged in seven fathoms water."—Reeve, *Conch. Icon.*, Vol. 8, *Amphidesma*, 1853, species 27, pl. 4, fig. 27 (as *Amphidesma formosa*). Original locality cited.

Lamy<sup>27</sup> cited *Maetra tenuis* Montagu, the type of *Abra*, and similar species, under the genus *Syndesmya* Recluz, 1843, with the type *Maetra alba* Wood, 1801.

*Iacra* H. & A. Adams, 1856, a subgenus of *Abra*, with the type *Scrobicularia seychellarum* A. Adams, 1856, possesses divaricate radial sculpture.

*Abranda* Iredale, 1924, is based upon *Abranda rex* Iredale, an Australian species.

#### KEY TO THE SPECIES OF *Abra*.

- A. Shell elongate  
 a. Posterior end pointed ..... *pacifica*<sup>28</sup>  
 aa. Posterior end blunt ..... *tepocana*<sup>28</sup>  
 B. Shell short; high, inflated ..... *palmeri*

#### *Abra palmeri* Dall.

Plate I, Figs. 16, 18, 20, 23.

*Abra palmeri* Dall, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 67, March 2, 1915, p. 28. "Ballenas Lagoon on the west coast of Lower California; the Gulf of California (Dr. E. Palmer) and Panama Bay in 26 fathoms (U. S.N.Mus.). Type locality, Panama Bay. (U. S.N.Mus., No. 96,301.)"

*Type Locality*: Panama Bay, in 26 fathoms.

*Range*: Ballenas Lagoon on the west coast of Lower California, and the Gulf of California to Panama Bay.

*Collecting Station*: El Salvador: Meanguera Island, Gulf of Fonseca (199-D-1), 16 fathoms, sand, mud, crushed shell.

*Description*: Shell short, high, inflated, white, with a silky surface, and a very thin, polished, pale yellow periostracum; anterior end and base rounded; beaks subcentral, dorsal margins descending, posterior end attenuated and with the extremity rounded; right valve with a deeply bifid (or double) cardinal tooth, the laterals obsolete; left valve with a single cardinal and no laterals. Length 10, height 8, diameter 5.5 mm. The pallial sinus rounded, 6 mm. deep. (Original description).

This species is nearest to *A. lioica* Dall, of the Atlantic Coast of the United States (Dall).

The largest specimen in the present collection measures: length, 10.5 mm.; height, 9.2 mm.; convexity (one valve), 2.8 mm.

The short and high outline of *Abra palmeri* separates it from the two other species described from west American waters, *A. pacifica* Dall, 1915, and *A. tepocana* Dall, 1915, both of which were said to be elongate in outline.

*Distribution*: Several specimens of this species, mostly single valves, were dredged off Meanguera Island, El Salvador, in the Gulf of Fonseca, in 16 fathoms. This is the first record of the occurrence of the species since its original description.

<sup>27</sup> Lamy, E., *Journ. de Conchyl.*, Vol. 61, No. 3, 1914, pp. 268-297.

<sup>28</sup> Not represented in the present collection.

#### Genus *Cumingia* Sowerby.

#### *Cumingia lamellosa* Sowerby.

*Cumingia lamellosa* Sowerby, *Proc. Zool. Soc. London*, May 17, 1833, p. 34. "Hab. prope littora Oceani Pacifici." "Found at Payta in hard clay at low water; and at Panama in deep water."—Sowerby, *Gen. Rec. and Foss. Shells, Cumingia*, Vol. 2, No. 40, ?1833, pl. 244, fig. 3.—Sowerby, *Conch. Icon.*, Vol. 19, *Cumingia*, 1873, species 5, pl. 1, fig. 5. "Hab. Chili".—Lamy, *Journ. de Conchyl.*, Vol. 61, No. 3, 1914, p. 310. Paita, Peru.

*Cumingia coarctata* Sowerby, *Proc. Zool. Soc. London*, May 17, 1833, p. 34. "Hab. ad Sinum Caraccensem." "Dredged from a sandy muddy bottom in seven fathoms water in the Bay of Caraccas". [Ecuador].

*Cumingia trigonularis* Sowerby, *Proc. Zool. Soc. London*, May 17, 1833, p. 35. "Hab. ad Sanctam Elenam." "Found among stones in deep water."—Sowerby, *Gen. Rec. and Foss. Shells*, Vol. 2, No. 40, ?1833, *Cumingia*, pl. 244, fig. 2.—Sowerby, *Conch. Icon.*, Vol. 19, *Cumingia*, 1873, species 4, pl. 1, fig. 4. "Hab. Chili?"

*Cumingia adamsii* Carpenter, *Proc. Zool. Soc. London*, June 23, 1863, p. 367. Reprint in *Smithson. Miscell. Coll.*, No. 252, 1872, p. 203. Name proposed for *Cumingia*, sp. indet. c of C. B. Adams, *Ann. Lyceum Nat. Hist. New York*, Vol. 5, July, 1852, p. 512 (separate p. 288). "Near Panama."

*Cumingia moulinsii* De Folin, *Les Méléagrines* (Havre), 1867, p. 16, pl. 2, figs. 12, 13, 14, 15. . . . "l'Océan pacifique" . . . "pêchées aux environs des Negritos" . . . or . . . "autour des îles aux Perles, dans la baie de Panama".—De Folin & Périer, *Les Fonds de la Mer*, Vol. 1, 1867, p. 8. Bay of Panama. [For dates of publication of this work see H. A. Rehder, *Proc. Malacol. Soc. London*, Vol. 27, Pt. 2, September 5, 1946, pp. 74-75].

*Type Locality*: Paita, Peru, at low water, in hard clay (here designated as type locality). Panama, in deep water, also cited originally.

*Range*: San Martin Island, Lower California, to the Gulf of California and south to Paita, Peru.

*Collecting Stations*: Mexico: Port Guatulo (195-D-9), 7 fathoms, gr. sand, crushed shell; Nicaragua: Corinto (200-D-10, 16, 17, 19), 4-13 fathoms, mangrove leaves, sand, also on shore; Costa Rica: Port Parker.

*Description*: Shell oblong, regularly concentrically laminated, laminae narrow, standing out, distant; anterior side short, rounded; posterior side angular, acuminate, substrated; ventral margin contracted near the end; dorsal margin sloped (Sowerby, *Conch. Icon.*, Vol. 19).

Some of the larger specimens in the present collection are about 12 mm. in length. Some specimens attain a length of 20 mm. or more.

*Cumingia lamellosa* lives in sand, sponges and in fissures in rocks. Consequently it

shows great variation in the shape of the shell and in the development of the lamellae. This variation has led to the publication of a number of different names for this species by various authors.

The more northern *Cumingia californica* Conrad, has a larger and thicker shell. *Cumingia similis* A. Adams is a synonym of Conrad's species.

*Cumingia mutica* Sowerby<sup>29</sup>, which occurs in Peru and Chile, possesses a large shell for the genus. It is ornamented by finely decussated sculpture. *Cumingia clerii* A. Adams<sup>30</sup>, *C. grandis* Deshayes<sup>31</sup>, *C. striata* A. Adams<sup>32</sup> and *C. ventricosa* Sowerby<sup>33</sup> were referred to the synonymy of *C. mutica* by Dall.

*Cumingia lamellosa* Sowerby is not to be confused with *Thyella lamellosa* H. Adams, 1885, described from the island of Mauritius, later renamed *Cumingia elegans* by Sowerby, 1873.

*Cumingia tellinoides* Conrad, 1831, *C. tellinoides coarctata* Sowerby, 1833, and *C. tellinoides vanhyningi* Rehder, 1939, occur in east American waters.

*Distribution*: Specimens of *Cumingia lamellosa* were taken by the expedition off western Mexico, Nicaragua and Costa Rica. Specimens questionably identified as this species have been recorded as occurring in the Pleistocene of Magdalena Bay, Lower California.

#### FAMILY DONACIDAE.

##### KEY TO THE GENERA OF THE DONACIDAE.

- A. Inner margin crenulated.....*Donax*  
 B. Inner margin smooth.....*Iphigenia*

#### Genus *Donax* Linnaeus.

##### KEY TO THE SPECIES OF *Donax*.

- A. Shell more than twice as long as high  
 a. Anterior dorsal margin concave  
     *transversus*  
 aa. Anterior dorsal margin straight or convex  
 b. Posterior dorsal area flattened or rounded  
 c. Shell flattened; very elongate  
     *gracilis*

<sup>29</sup> *Cumingia mutica* Sowerby, *Proc. Zool. Soc. London*, May 17, 1833, p. 34. "Hab. prope littora Maris Pacifici." Obtained "at Conception in seven fathoms, sand and mud; at Iquiqui in nine fathoms, gravel and mud; at Payta in hard clay at low water; and at Muerte."—Sowerby, *Conch. Icon.*, Vol. 19, *Cumingia*, 1873, species 3, pl. 1, fig. 3. "Hab. Chili, Peru."

<sup>30</sup> *Cumingia clerii* A. Adams, *Proc. Zool. Soc. London*, November 12, 1850, p. 24, pl. 8, fig. 3. "Found at Talcahuano, Chili, by Capt. Cleri, French Marine, attached to fucl in shallow water. (Mus. Cum.)."—Sowerby, *Conch. Icon.*, Vol. 19, *Cumingia*, 1873, species 2, pl. 1, fig. 2. "Hab. Chili."

<sup>31</sup> *Cumingia grandis* Deshayes, *Journ. de Conchyl.*, Vol. 5, 1857, p. 281, pl. 8, figs. 4 and 5. "... provient des mers du Chili."—Sowerby, *Conch. Icon.*, Vol. 19, *Cumingia*, 1873, species 11, pl. 2, fig. 11. "Hab. Chili."

<sup>32</sup> *Cumingia striata* A. Adams, *Proc. Zool. Soc. London*, November 12, 1850, p. 25, pl. 8, fig. 5. "Hab. Conception; seven fathoms, sandy mud; H. C. (Mus. Cuming)."

<sup>33</sup> *Cumingia ventricosa* Sowerby, *Conch. Icon.*, Vol. 19, August, 1873, species 10, pl. 2, fig. 10. "Hab. Probably Chili."

- cc. Shell moderately inflated; higher .....*californicus*  
 bb. Posterior dorsal area concave; posterior area smoky-black; shell subrhomboidal .....*navicula*  
 B. Shell less than twice as long as high  
 a. Shell with a sharply angled umbonal carina posteriorly  
 b. Thin; anterior end acutely rounded; highly polished.....*carinatus*  
 bb. Thick; anterior end more broadly rounded .....*rostratus*<sup>34</sup>  
 aa. Shell with a rounded umbonal angulation posteriorly; strongly sculptured  
 c. Interspaces punctate (with a row of fine pits)  
 d. Shell subtriangular (typical), high; posterior margin sloping rather steeply; ventral margin sometimes slightly expanded medially  
     *punctatostratus*  
 dd. Shell elongate, lower; flatter; posterior margin sloping more gently, posterior end rostrate; base more broadly rounded  
 e. Moderately elongated  
     *contusus*<sup>34</sup>  
 ee. Extremely elongated; posterior dorsal margin somewhat rounded  
     *culter*<sup>34</sup>  
 cc. Interspaces not punctate

f. Length not exceeding 15 mm.; sculpture finely cancellate  
     *obesus*

ff. Length exceeding 15 mm.; sculpture coarsely cancellate; thick

g. Beaks subcentral; shell high, trigonal

h. Ribs on posterior area of about equal size .....*asper*

hh. Ribs on posterior area with 1-3 coarser than the others  
     *dentiferus*<sup>34</sup>

gg. Beaks decidedly posterior; shell more elongated  
     *assimilis*

#### *Donax asper* Hanley.

*Donax asper* Hanley, *Proc. Zool. Soc. London*, Pt. 13, April, 1845, p. 14. "Hab. Tumbes, Peru (Cuming)."—Reeve, *Conch. Icon.*, Vol. 8, *Donax*, September, 1854, species 12, pl. 2,

<sup>34</sup> Not represented in the present collection.

fig. 12. Original locality record cited.—Sowerby, *Thes. Conch.*, Vol. 3, 1866, p. 307, pl. 280 (*Donax*, pl. 1), fig. 24. Tumbez, Peru.

*Donax (Hecuba) asper* Hanley, Römer, *Syst. Conchyl.-Cab. Martini-Chemnitz*, Bd. 10, Abt. 3, *Donacidae*, 1869, p. 14, Tab. 3, figs. 7-10. Tumbez, Peru; Puntarenas, Costa Rica, in the Gulf of Nicoya.

*Donax aspera* Hanley, Dall, *Proc. U. S. Nat. Mus.*, Vol. 37, 1909, pp. 159, 273, pl. 28, fig. 7. Central America to Tumbez, Peru.

*Type Locality*: Tumbez, Peru.

*Range*: Tangola-Tangola Bay, Mexico, to Tumbez, Peru.

*Collecting Stations*: Mexico: Tangola-Tangola Bay; Costa Rica: Port Culebra, beach; Culebra Bay; Cedro Island, Gulf of Nicoya, beach; Gulf of Dulce, beach; Panama: Bahía Honda.

*Description*: Shell triangular, beaks subcentral, elevated, and rather gibbous; the anterior end is rather acutely rounded, the posterior end somewhat concavely truncated; ornamented by radiating riblets which are especially well developed toward the posterior end and on the posterior area where they are crenated by concentric lines; inner margin crenulated; the color is ashy-white or purple.

A large right valve in the present collection from the Gulf of Dulce measures, approximately: length, 35 mm.; height, 26 mm.; convexity (one valve), 8.5 mm.

Compared to *Donax assimilis* Hanley, the shell of *D. asper* is much higher in proportion to the length and the beaks are much more centrally located. The shell of *D. asper* differs from that of *D. dentiferus* Hanley<sup>35</sup> in that it is thicker, more acutely rounded anteriorly and lacks the raised ribs (1-3) which are coarser than the others on the posterior area of that species.

*Distribution*: This species was collected by the expedition from Mexico to Panama but nowhere in large numbers. Several single valves were taken on the beach in the Gulf of Dulce, Costa Rica, and at Tangola-Tangola Bay, Mexico.

#### *Donax assimilis* Hanley.

*Donax assimilis* Hanley, *Proc. Zool. Soc. London*, Pt. 13, April, 1845, p. 17. "Hab. Panama. Mus. Cuming, Hanley, &c."—Reeve, *Conch. Icon.*, Vol. 8, *Donax*, September, 1854, species 10, pl. 2, fig. 10. Panama.

*Donax panamensis* Philippi, *Zeit. f. Malakozool.*, Jahrg. 5, No. 10, 1848, p. 145. "Patria: Panama." [According to Römer, 1869, this species is a synonym of *D. assimilis*.]

*Donax cayennensis* Lamarck, Reeve, *Conch. Icon.*, Vol. 8, *Donax*, September, 1854, species 22, pl. 4, figs. 22a, 22b. "Hab. Panama and St. Elena, West Columbia; Cuming."

Not *Donax caianensis* Lamarck, *Anim. S. Vert.*, Vol. 5, July, 1818, p. 550. "Habite

l'Océan de la Guyane."—Delessert, *Rec. Coq. décrites par Lamarck et non encore figurées*, 1841, pl. 6, figs. 13a, 13b. See also Hanley, *Cat. Rec. Biv. Shells*, 1843, p. 82, footnote.—Lamy, *Bull. Mus. Nat. Hist. Nat.* (Paris), Vol. 20, No. 6, 1914, p. 339.

*Donax reevei* Bertin, *Nouv. Arch. Mus. Hist. Nat.* (Paris), Ser. 2, Vol. 4, 1881, p. 85. [Name based upon Reeve's pl. 2, fig. 10. Panama (Reeve).]

*Donax sowerbyi* Bertin, *Nouv. Arch. Mus. Hist. Nat.* (Paris), Ser. 2, Vol. 4, 1881, p. 85, pl. 4, figs. 2a, 2b, 2c. Based upon Sowerby's (*Thes. Conch.*, Vol. 3, 1866, p. 307), pl. 280 (*Donax*, pl. 1), fig. 21. "Panama."

*Type Locality*: Panama.

*Range*: Mazatlan, Mexico (Carpenter), to Santa Elena, Ecuador.

*Collecting Stations*: Nicaragua: Isla Encantada, Corinto; Costa Rica: Culebra Bay; Cedro Island, Gulf of Nicoya, beach; Gulf of Dulce, beach; Panama: Isla Parida, Gulf of Chiriqui.

*Description*: Shell elongately triangular, beaks posterior to the middle, anterior end the narrower, rounded, posterior end truncated; ornamented with radial riblets which are stronger toward the posterior end and on the posterior area which sometimes bears a faint subangulation; inner margin crenated; color, usually some shade or combination of gray and purple.

A large specimen in the collection of the California Academy of Sciences, collected by James Zetek at Chame Island, Panama, measures: length, 41 mm.; height, 26.8 mm.; convexity (both valves together), 17.5 mm.

Compared to *Donax asper* the shell of *D. assimilis* is much more elongate, the beaks are more posteriorly situated and the posterior area is more rounded. The more posteriorly situated beaks and more elongate shell are characters which serve to separate the present species from *D. dentiferus*.

*Distribution*: This species was taken by the expedition on the beach at a few localities from Nicaragua to Panama. It occurs commonly at Panama where it is used for food by the natives.

#### *Donax californicus* Conrad.

Plate I, Figs. 2, 5.

*D[onax]. californica* Conrad, *Jour. Acad. Nat. Sci. Philadelphia*, Vol. 7, 1837, p. 254, pl. 19, fig. 21. "Inhabits the coast of California in sand, near Sta. Barbara."

Not *Donax californica* Conrad, Reeve, *Conch. Icon.*, Vol. 8, *Donax*, September, 1854, species 40, pl. 6, fig. 40. "Hab. Gulf of California." [Carpenter, 1855, referring to some of the shells in the Gulf of California region labeled as *D. californicus*, stated, "The shells wrongly called *D. californicus* are simply the white variety of the forms *contusus* and *culter*"].

*Donax californicus* Conrad, Arnold, *Mem. Calif. Acad. Sci.*, Vol. 3, 1903, p. 170, pl. 13,

<sup>35</sup> *Donax dentifera* Hanley, *Proc. Zool. Soc. London*, Pt. 11, July, 1843, p. 6. "Hab. ?"—Reeve, *Conch. Icon.*, Vol. 8, *Donax*, September, 1854, species 2, pl. 1, figs. 2a, 2b. "Hab. Panama."

fig. 9. Lower San Pedro Series at Deadman Island, and San Pedro, California. Lower Pleistocene. Also upper Pleistocene and Recent.—Weymouth, State of Calif. Fish & Game Comm., *Fish Bull.* No. 4, 1920, p. 47, pl. 16, fig. 1. Localities cited from San Pedro to False Bay, California.

*Type Locality:* Near Santa Barbara, California, in sand.

*Range:* Santa Barbara, California, to Magdalena Bay, Lower California.

*Collecting Station:* Mexico: Cedros Island, Lower California.

*Description:* Shell elongated, somewhat pointed at both extremities; disks with very minute radiating lines; color yellowish, obscurely rayed; a brown stripe on the anterior and posterior sub-margin; within white and purplish brown; margin beautifully crenulated. (Original description.)

A specimen of this species in the collections of the California Academy of Sciences, collected by Henry Hemphill at Cape San Lazaro, Lower California, measures: length, 24.6 mm.; height, 11 mm.; convexity (both valves together), 7.4 mm.; from beaks to posterior end, 10 mm. Large specimens attain a length of about 30 mm.

*Donax californicus* can be referred to the subgenus *Serrula* Chemnitz in Mörch.

The posterior dorsal area of the shell of this species is flattened or gently rounded rather than concave as in *D. navicula*.

*Donax gracilis* Hanley is a similar southern species whose shell is more elongated and whose posterior dorsal margin slopes more gently ventrally.

*Distribution:* A few small specimens of *Donax californicus* were dredged off Cedros Island by the expedition. We have not seen specimens from south of Cape San Lazaro, Lower California<sup>36</sup>. It is also known to occur in the Pleistocene of southern California and western Lower California.

### *Donax carinatus* Hanley.

Plate I, Fig. 9.

*Donax carinata* Hanley, *Proc. Zool. Soc. London*, Pt. 11, July, 1843, p. 5. "Hab. —? Mus Stainforth, Metcalfe."—Hanley, *Cat. Rec. Bivalve Shells*, p. 84, 1843, p. 349, pl. 14, fig. 28, 1856 (as *Donax carinatus* on expl. to plate). [No locality cited.]—Reeve, *Conch. Icon.*, Vol. 8, *Donax*, September, 1854, species 11, pl. 2, fig. 11. "Hab. San Blas, California."

*Donax carinatus* Hanley, Sowerby, *Thes. Conch.*, Vol. 3, 1866, p. 305, pl. 280 (*Donax*, pl. 1), figs. 4 and 5. "California."—Römer, *Syst. Conchyl.-Cab. Martini-Chemnitz*, Bd. 10, Abt. 3, *Donacidae*, 1869, p. 10, Taf. 3, figs. 4, 5, 6. "Fundort: Der Stille Ocean bei Californien, (St. Blas, Tumaco, Mazatlan)."

*Donax culminatus* Carpenter, *Cat. Mazat-*

lan Shells, September, 1855, p. 43. "Hab. — 1 young specimen; L'pool Col."

*Type Locality:* San Blas, Mexico (here designated as type locality). No locality cited originally.

*Range:* Altata, Mexico, to Tumaco, Colombia.

*Collecting Station:* Nicaragua: Corinto (200-D-16, 19), 4-13 fathoms, mangrove leaves.

*Description:* Transversely elongated, convex, very inequilateral, purplish-brown, with more or less distinct radiating striae, (usually with obsolete darker rays and polished), ventral edge little arcuated and forming a very acute point with the nearly straight edge of the obliquely truncated and almost flattened anterior [posterior] slope, which is sharply carinated and sculptured by close decussated radiating striae: inside purple, two lateral teeth in each valve, the ventral edge crenated, anterior crenulated. 4/5 . . . 1 2/5 [inches] (Hanley, *Cat. Rec. Biv. Shells*, 1843).

The largest specimen in the present collection measures 33.2 mm. in length and 18 mm. in height. A large right valve collected by the senior author at Corinto, Nicaragua, measures approximately: length, 39.4 mm.; height, 22 mm.; convexity (one valve), 7.6 mm.

This species can be easily recognized by the comparatively thin, polished shell with a sharply angled umbonal ridge posteriorly.

The only other west American shell that might be confused with *Donax carinatus* is *Donax rostratus* C. B. Adams<sup>37</sup>. The shell of Adams' species is thicker, less sharply carinated, and is less sharply pointed where the carina joins the ventral margin, the anterior end is more broadly rounded, and the color of the exterior is lighter.

A subspecies, *Donax carinatus galvestonensis* Harris<sup>38</sup>, has been described from an artesian well in Galveston, Texas, and was considered to be of upper Miocene age. Harris did not consider Reeve's plate 2, figure 11, as representing Hanley's species.

*Distribution:* This species was dredged by the expedition off Corinto, Nicaragua, at depths of 4-13 fathoms. It also has been collected by the senior author at Corinto and at Mazatlan, Mexico. Römer cited the occurrence of the species as far south as Tumaco, Colombia.

### *Donax gracilis* Hanley.

Plate I, Figs. 4, 6.

*Donax gracilis* Hanley, *Proc. Zool. Soc. London*, Pt. 13, April, 1845, p. 15. "Hab. Bay of Guayaquil. Var. *b.* Chiriqui. Var. *c.* Bay of Caraccas (Cuming)."—Reeve, *Conch.*

<sup>37</sup> *Donax rostratus* C. B. Adams, *Ann. Lyceum Nat. Hist. New York*, Vol. 5, July, 1852, pp. 502, 545 (separate pp. 278, 321). "Panama."—Römer, *Syst. Conchyl.-Cab. Martini-Chemnitz*, Bd. 10, Abt. 3, *Donacidae*, 1869, p. 11, Taf. 3, figs. 1-3.

<sup>38</sup> *Donax carinata* var. *galvestonensis* Harris, *Bull. Amer. Paleol.*, Vol. 1, No. 3, December 2, 1895, p. 92 (10). Well at Galveston, Texas, depth, 2,552 to 2,920 feet. Upper Miocene.

<sup>36</sup> According to Miss Viola Bristol, specimens of this species from Magdalena Bay, Lower California, are in the collections of the San Diego Society of Natural History (*Min. Conch. Club South. Calif.*, No. 47, back page, April, 1945). On the same page of this paper Eyerdam is cited as having found this species at Corinto, Nicaragua.

Icon., Vol. 8, *Donax*, September, 1854, species 38, pl. 6, fig. 38. "Hab. Gulf of Guayaquil; Cuming."—Sowerby, Thes. Conch., Vol. 3, 1866, p. 314, pl. 282 (*Donax*, pl. 3), figs. 76, 77, 78, 79. Gulf of Guayaquil.—Römer, Syst. Conchyl.-Cab. Martini-Chemnitz, Bd. 10, Abt. 3, *Donacidae*, 1869, p. 80, Taf. 14, figs. 4, 5, 6. [?7, 8]. "Fundort: Der Stille Ocean bei Mittelamerika und Ecuador, (Guayaquil, Chiriqui, Panama)."

*Type Locality*: Bay of Guayaquil, Ecuador (here selected as type locality). Chiriqui [Panama] and Bay of Caraccas [Ecuador] also cited originally for varieties of this species.

*Range*: Lat. 24° 18' N., west coast of Lower California, to the Gulf of California and south to Negritos, Peru.

*Collecting Station*: Nicaragua: Corinto (200-D-10, 11, 16, 17, 19), 7-13 fathoms, sand, mangrove leaves, also in beach drift.

*Description*: Shell narrowly elongate, polished, rather compressed, beaks nearer the posterior end; anterior end acutely rounded, posterior end acutely roundedly pointed; posterior dorsal margin straight or slightly produced; inner margin finely crenulated; color of the exterior is usually brown and that of the interior brownish-purple.

A large left valve from off Potosi and Monypenny Point, Nicaragua, measures approximately: length, 22.5 mm.; height, 9.4 mm.; convexity (one valve), 3 mm.; distance from beak to posterior end, 9 mm.

The shell of *Donax gracilis* differs from that of *D. navicula* in the much more elongate outline and in that the posterior dorsal margin is straight or slightly produced rather than concave. Compared to *D. californicus* the shell of *D. gracilis* is longer in proportion to the height, more compressed, the posterior dorsal margin slopes more gently and the posterior end is more acutely pointed. It can be referred to the subgenus *Serrula*.

*Donax punaensis* Pilsbry & Olsson<sup>39</sup>, described from the Pliocene of Ecuador, is a very similar species but the beaks appear to be more centrally situated and the posterior end is more broadly rounded.

*Donax petersoni* Olsson, described from the Oligocene of Peru, is a somewhat similar species.

*Donax owenii* Gray in Hanley<sup>40</sup> of the Atlantic fauna appears to be somewhat similar to *D. gracilis* but the posterior end appears

<sup>39</sup> *Donax punaensis* Pilsbry & Olsson, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 93, September 9, 1941, p. 72, pl. 12, fig. 2. "Pliocene of the north end of Puna Island." Ecuador.

<sup>40</sup> *Donax owenii* Gray in Hanley, *Cat. Rec. Bivalve Shells*, 1843, p. 81. "Africa?"—Reeve, *Conch. Icon.*, Vol. 8, *Donax*, September, 1854, species 37, pl. 6, fig. 37. "Hab. West Coast of Africa."

Dall (*Nautilus*, Vol. 5, No. 4, August, 1891, p. 44), recorded this species from Montevideo and Maldonado. Maury (Serv. Geol. & Min. Brasil, Mon. No. 4, 1924, p. 455) also cited the species as occurring at Montevideo, Uruguay. Melvill & Standen recorded a species under the name of *Donax (Machaerodonax) owenii* Gray, from Karachi, India (*Proc. Zool. Soc. London*, November 13, 1906, p. 826). Carcelles recently cited *Donax owenii* as occurring along the coast of Argentina (*Rev. Mus. de La Plata (New Ser.)*, Sec. Zool., Vol. 3, 1944, p. 303).

to be shorter and the margin is said to be smooth not crenulated.

*Distribution*: Specimens of *Donax gracilis* were taken by the expedition in the beach drift as well as dredged in 7 to 13 fathoms at Corinto, Nicaragua.

#### *Donax navicula* Hanley.

Plate I, Fig. 1.

*Donax navicula* Hanley, *Proc. Zool. Soc. London*, Pt. 13, April, 1845, p. 15. "Hab. Gulf of Nicoya, Central America (Cuming)".—Reeve, *Conch. Icon.*, Vol. 8, *Donax*, September, 1854, species 18, pl. 4, fig. 18. Original locality cited.—Sowerby, Thes. Conch., Vol. 3, 1866, p. 314, pl. 282 (*Donax*, pl. 3), fig. 80. Original locality cited.—Römer, Syst. Conchyl.-Cab. Martini-Chemnitz, Bd. 10, Abt. 3, *Donacidae*, 1869, p. 56, Taf. 10, figs. 1-3. "Fundort: Der Stille Ocean bei Californien und Mittelamerika, (Nicoyia, Panama, Mazatlan, Reallejos)."

*Type Locality*: Gulf of Nicoya, Costa Rica.

*Range*: Gulf of California to Panama.

*Collecting Stations*: Mexico: Santa Inez Bay, Gulf of California; Cape San Lucas; Cape San Lucas Bay; Nicaragua: Potosi and Monypenny Point, Gulf of Fonseca; Corinto (200-D-10, 16), 4-7 fathoms, mangrove leaves, also in beach drift.

*Description*: Shell elongately rhomboidal, moderately inflated, fairly thick, obsolete, finely radially grooved; anterior end the longer, acutely rounded, posterior end acuminate truncated, the extremity roundly pointed; posterior area concave; ventral margin rounded and somewhat expanded just anterior to the middle, often with a compressed area between this portion of the valve and the posterior angulation; inner margin crenulated; color white or brownish with the posterior and anterior dorsal areas black or grayish-black; periostracum greenish.

One of the largest specimens, a right valve, from the beach drift at Corinto, Nicaragua, measures approximately: length, 21 mm.; height, 10 mm.; convexity (one valve), 3.9 mm.; distance from beaks to posterior end, 8.5 mm.

The shell of *Donax navicula* differs from that of *D. gracilis* in the more rounded base and rhomboidal form, more inflated valves and especially in that the posterior area is concave. It can be referred to the subgenus *Serrula*.

The concave posterior area and higher more triangular form are features which serve to separate *Donax navicula* from *D. californicus*.

*Distribution*: This species was taken abundantly by the expedition in the beach drift at Corinto, Nicaragua. A few specimens were also taken as far north as Santa Inez Bay in the Gulf of California.

#### *Donax obesus* d'Orbigny.

Plate I, Fig. 7.

*Donax obesa* d'Orbigny, Voy, Amér.

Mérid., Vol. 5, 1846, p. 541, pl. 81, figs. 28, 30. "Elle a été pêchée à Payta (Pérou) par M. Fontaine."—Reeve, Conch. Icon., Vol. 8, *Donax*, October, 1854, species 49, pl. 7, fig. 49. "Hab. Real Llejos, Central America; Cuming."

*Donax obesus* d'Orbigny, Sowerby, Thes. Conch., Vol. 3, 1866, p. 310, pl. 281 (*Donax*, pl. 2), figs. 42, 43. "Real Llejos, Central America."

*Type Locality*: Paita, Peru.

*Range*: Corinto, Nicaragua, to Paita, Peru.

*Collecting Station*: Nicaragua: Corinto (200-D-11, 19), 8-13 fathoms, mangrove leaves.

*Description*: Shell small, subtriangular, inflated; the anterior end the longer, sloping, acutely rounded at the extremity, posterior end broadly and roundly truncated; umbonal ridges rounded; ornamented with fine radial grooves which are crossed by somewhat flexuous concentric grooves forming a fine cancellated pattern of punctate appearance; inner margin finely crenulated; color white with dark purplish-brown on the posterior end and on the anterior dorsal margin.

The largest specimen in the collection, a right valve, measures: length, 13.4 mm.; height, 10.9 mm.; convexity (one valve), 4.2 mm.

The shell of *Donax obesulus* Reeve<sup>41</sup> is much more abruptly truncated than that of *D. obesus*, and the posterior umbonal ridge is decidedly angulated rather than rounded.

*Distribution*: This species was dredged by the expedition at two localities off Corinto, Nicaragua, at depths of 8-13 fathoms.

### *Donax punctato-striatus* Hanley.

Plate I, Fig. 17.

*Donax punctato-striata* Hanley, *Proc. Zool. Soc. London*, Pt. 11, July, 1843, p. 5. "Hab.—? Mus. Stainforth, Metcalfe, Hanley, &c."—Hanley, *Cat. Rec. Biv. Shells*, 1843, p. 84, pl. 14, fig. 24 (as *Donax punctato-striatus* on expl. to plate). [Not the record "China"].—Reeve, *Conch. Icon.*, Vol. 8, *Donax*, September, 1854, species 16, pl. 3, figs. 16a, 16b. "Hab. Mazatlan, Gulf of California."—Sowerby, *Thes. Conch.*, Vol. 3, *Donax*, 1866, p. 310, pl. 281 (*Donax*, pl. 2), figs. 49, 50 (as *Donax punctato-striatus*). Reeve's locality cited on expl. to pl.

*Type Locality*: Mazatlan, Mexico (here designated as type locality). No locality cited originally.

*Range*: San Ignacio Lagoon, Lower California, to the Gulf of California and south to Negritos, Peru.

*Collecting Stations*: Mexico: Santa Inez Bay, Gulf of California; Cape San Lucas; Chamela Bay; Tenacatita Bay; Sihuatanejo;

Tangola-Tangola Bay; Nicaragua: Gulf of Fonseca; Potosi and Monypenny Point; Corinto (200-D-19), 12-13 fathoms, mangrove leaves, also beach.

*Description*: Subtriangular, very convex, pale livid brown, with strong radiating punctated striae, becoming very fine and close on the anterior [posterior] slope, whose edge is rounded, posterior and anterior edges much sloping, ventral arcuated in the middle; inside stained with violet, the ventral margins dentated, the anterior [posterior] crenulated: two cardinal and lateral teeth in each valve. Long.  $4/5$ — $1-1/5$  [inches] (Hanley, *Cat. Rec. Biv. Shells*, 1843). "When full grown less inequilateral than most of this genus."

A very large specimen of this species in the Henry Hemphill collection in the California Academy of Sciences, collected at Magdalena Bay, Lower California, measures: length, 44.8 mm.; height, 30 mm.; convexity (both valves together), 17.4 mm.

The subtrigonal form and the row of fine pits, which occur in the radial grooved striae, are characteristic features of this species. It belongs to the subgenus *Chion* Scopoli.

Hanley once reported *Donax punctato-striatus* from China but it was later recognized as occurring commonly in tropical west American waters.

The variety described by Carpenter as *Donax punctato-striatus* var. *caelatus*<sup>42</sup> appears not to have been recognized since its description. It was described as possessing short impressed lines rather than pits in the interspaces.

Sowerby (1866) pointed out that there are specimens which intergrade between *Donax punctato-striatus* and *Donax conradi* Reeve<sup>43</sup>. The latter species is now known to be identical with *D. contusus* Reeve<sup>44</sup> (see our Pl. I, fig. 14), as pointed out by Tomlin<sup>45</sup>. *Donax vellicata* Reeve (fig. 66) and *D. bitincta* Reeve (fig. 68), both described without information as to the locality from which they came, are likewise identical with *D. contusus* according to Tomlin.

Typical forms of *Donax punctato-striatus* are more subtrigonal and higher than those of typical *D. contusus*, which are lower and more elongate in outline. Large specimens of *D. punctato-striatus* are sometimes slightly expanded medially along the ventral margin and the posterior dorsal margin often slopes more steeply than that on *D. contusus*, but as mentioned by Sowerby, there is intergradation between the two forms. The most elongate form of this variable group is *Donax*

<sup>42</sup> *Donax ?punctato-striatus*, var. *caelatus* Carpenter, *Cat. Mazatlan Shells*, September, 1855, p. 46. "Hab.—Mazatlan; very rare."

<sup>43</sup> *Donax conradi* Reeve, *Conch. Icon.*, Vol. 8, *Donax*, September, 1854, species 29, pl. 5, fig. 29. "Hab. Gulf of California."

<sup>44</sup> *Donax contusus* Reeve, *Conch. Icon.*, Vol. 8, *Donax*, September, 1854, species 24, pl. 4, fig. 24. "Hab. Mazatlan, Gulf of California."

<sup>45</sup> Tomlin, J. R. leB., *Nautilus*, Vol. 40, No. 2, October, 1926, p. 52.

<sup>41</sup> *Donax obesula* Reeve, *Conch. Icon.*, Vol. 8, *Donax*, September, 1854, species 30, pl. 5, fig. 30. "Hab. Peru."—Deshayes, *Proc. Zool. Soc. London*, 1854 (issued May 16, 1855), p. 352. "Hab. Central America."

*culter* Hanley<sup>46</sup>, as pointed out by Carpenter<sup>47</sup>. Very elongate forms of *D. culter* are somewhat reminiscent of *Amphichaena kindermanni* Philippi<sup>48</sup> as is *Donax petalinus* Reeve<sup>49</sup>.

*Donax aricanus* Dall<sup>50</sup>, recorded as occurring from Paita, Peru, to Arica, Chile, appears to be very similar to *D. punctatostratus* and possibly some of the records of the occurrence of the latter species in South America may be referable to Dall's species. Römer considered *D. radiatus* Valenciennes [= *aricanus*] to be only a variety of *D. punctatostratus*.

*Donax striatus* Linnaeus, which occurs in the Caribbean region, is a similar species.

**Distribution:** This species was collected by the expedition on the beach and dredged at depths of 12-13 fathoms, from Santa Inez Bay in the Gulf of California to Corinto, Nicaragua. It is a variable shell found commonly from the Gulf of California to Peru. It has been recorded as occurring in the Pleistocene of southern California, Magdalena Bay, Lower California, and at Oaxaca, Mexico.

#### *Donax transversus* Sowerby.

##### Plate I, Fig. 3.

*Donax transversa* Sowerby, Cat. Shells Tankerville, 1825, Ap., p. IV. [No locality cited].—Reeve, Conch. Icon., Vol. 8, *Donax*, September, 1854, species 36, pl. 6, fig. 36. "Hab.—?"

*Donax transversus* Sowerby, Sowerby, Thes. Conch., Vol. 3, 1866, p. 306, pl. 280 (*Donax*, pl. 1), fig. 11. "Hab.—?"—Carpenter, Cat. Mazatlan Shells, September, 1855, p. 44. Mazatlan, Mexico.

**Type Locality:** Corinto, Nicaragua (here designated as type locality). No locality cited originally.

**Range:** Mazatlan, Mexico, to San Juan del Sur, Nicaragua.

**Collecting Station:** Nicaragua: Corinto (200-D-19), 12-13 fathoms, mangrove leaves.

**Description:** "D. testâ transversim elongatâ, laevi; latere postico brevi, biangulato, carinato, obliquè truncato, longitudinally sulcato; extus albidâ; fulvo obsoletè radiatâ". (Original description).

The shell of this species is very elongated, very inequilateral, rather thin, moderately inflated, gaping at each end, polished and obsoletely radially striated; anterior dorsal margin slightly concave; anterior end elliptically rounded obliquely joining the slightly rounded ventral margin; posterior end truncated, set off by a carina, the area fairly broad, concave, with a faint rounded angulation medially, the whole area finely radially striated and at the end obliquely truncated; color yellowish-white with purple rays; ventral margin finely crenated.

Specimens of this species in the present collection are small. A large left valve collected at Corinto, Nicaragua, by the senior author measures: length, 36.4 mm.; height, 14.5 mm.; convexity (one valve), 4.5 mm.; distance from beak to posterior end, 14 mm.

This appears to be the species which authors have cited from western Mexico and Central America under the name of *Donax scalpellum* Gray. *Donax scalpellum* Gray<sup>51</sup> was originally described without information as to locality. Hanley<sup>52</sup> later cited it from "California" and Reeve<sup>53</sup> cited it from the Gulf of California. E. A. Smith<sup>54</sup> in 1891 cited it from Aden, in the Gulf of Aden, and stated: "The above named locality, given by Reeve (Conch. Icon. sp. 39), has never been confirmed, and I think there is little doubt that it is incorrect. The specimens from Aden agree in form, color, sculpture, and every other respect with that figured by Reeve." Later Melvill & Standen<sup>55</sup> cited the species as occurring at Karachi, India, in the Arabian Sea.

The concavity of the anterior dorsal margin, obliquely elliptically rounded anterior end, and much wider and radially striated posterior area are features separating *Donax transversus* from *D. scalpellum*. *Donax transversus* belongs to the subgenus *Machaeodonax* Römer, the type of which is *D. scalpellum* Gray.

**Distribution:** Three small specimens of *Donax transversus* were dredged by the expedition in 12-13 fathoms off Corinto, Nicaragua. It also has been collected by the senior author on the beach at the same locality.

<sup>46</sup> *Donax culter* Hanley, Proc. Zool. Soc. London, April, 1845, p. 14. "Hab. Var. a. Matzellan [Mazatlan] Gulf of California (Cuming). Var. b. Acapulco (Cuming)."—Reeve, Conch. Icon., Vol. 8, *Donax*, September, 1854, species 21, pl. 4, fig. 21. "Hab. Gulf of California."

<sup>47</sup> Carpenter, P. P., Cat. Mazatlan Shells, September, 1855, pp. 47-48.

<sup>48</sup> See Palmer, R. H., and Hertlein, L. G., Bull. South. Calif. Acad. Sci., Vol. 35, Pt. 2, May-August (issued September 10), 1936, p. 71, pl. 18, figs. A, B, C, pl. 19, figs. 5, 6, 7, 8, 9, 10. Mazatlan; Petatlan Bay; Tenacatita Bay, Mexico, Recent. Also Oaxaca, Mexico, Pleistocene.

<sup>49</sup> *Donax petalina* Reeve, Conch. Icon., Vol. 8, *Donax*, October, 1854, species 51, pl. 8, fig. 51. "Hab.—?"—Deshayes, Proc. Zool. Soc. London for 1854 (issued May 16, 1855), p. 350 (as *Donax petalina*). "Hab.—? Coll. Cuming."

This species was described without information as to the locality from which it came. Bertin (Nouv. Arch. Mus. Hist. Nat. (Paris), Ser. 2, Vol. 4, 1881, p. 84), stated that he found an indication in Deshayes' collection that the species came from Chile. Dall, 1909, and Gigoux, 1934, also cited it from that country. Pilsbry & Lowe, 1932, and Bales, 1938, cited it from Acapulco, Mexico.

<sup>50</sup> *Donax radiata* Valenciennes, Rec. d'Obs. Zool. Humboldt & Bonpland, Vol. 2, 1832, p. 221, pl. 1, figs. 3a, 3b, 3c, 4. "Habitat in Oceano Pacifico ad Americae calidioris litora." Not *Donax radiata* Gmelin, 1791.

*Donax aricana* Dall, Proc. U. S. Nat. Mus., Vol. 37, November 24, 1909, p. 273. New name for *Donax radiata* Valenciennes, 1832, not *D. radiata* Gmelin, 1791. Paita, Peru, to Arica, Chile.

<sup>51</sup> *Donax scalpellum* Gray, Ann. Philos., Vol. 25, February, 1823, p. 136. [No locality cited].—Wood, Index Test., Suppl., 1828, p. 4, pl. 2, *Donax*, fig. 1. [No locality cited].

<sup>52</sup> Index Test. by W. Wood, edit. by S. Hanley, 1856, p. 202, Suppl. pl. 2, *Donax* fig. 1. "California."

<sup>53</sup> Reeve, L. A., Conch. Icon., Vol. 8, *Donax*, September, 1854, species 39, pl. 6, fig. 39. "Hab. Gulf of California."

<sup>54</sup> Smith, E. A., Proc. Zool. Soc. London, 1891, p. 427.

<sup>55</sup> Melvill, J. C., and Standen, R., Proc. Zool. Soc. London, November 13, 1906, p. 826.—Melvill, Proc. Malacol. Soc. London, Vol. 18, Pt. 3, 1928, p. 115.

Genus *Iphigenia* Schumacher.

*Iphigenia* Schumacher, Essai Nouv. Syst. Test., 1817, pp. 51, 155. Sole species, *Iphigenia laevigata* (*Donax laevigata* Chemnitz.). Ref. to Chemnitz, Vol. 6, p. 253, pl. 25, fig. 249. Illustrated by Schumacher on pl. 17, figs. 4a, b.—Dall, *Trans. Wagner Free Inst. Sci.*, Vol. 3, Pt. 5, 1900, p. 962. Type: *Donax laevigata* Chemnitz.—Pilsbry & Bequaert, *Bull. Amer. Mus. Nat. Hist.*, Vol. 53, Art. 2, May 9, 1927, p. 369. *Donax laevigata* "Chemnitz" Gmelin accepted as type.

Type (by monotypy): *Donax laevigata* Chemnitz [Neues Syst. Conchyl.-Cab., Bd. 6, 1782, p. 253, Tab. 25, fig. 249. "Es wohnt diese Muschel in den ostindischen Meeren. Bey Tranqueber wird sie nur selten gefunden". Also illustrated by Schumacher, pl. 17, fig. 4a, b].

Shell large, subtriangular, subequilateral, without radial sculpture; thick, with entire ventral margins; two cardinals, the larger bifid, in each valve and two obsolete laterals in the right valve. (Dall).

The genus *Iphigenia* is known to occur in the Miocene of Venezuela and Peru. At the present time it often occurs in estuarine or brackish water conditions and is known to occur in greatest abundance from the coast and rivers of West Africa and from the tropical Atlantic and Pacific coasts of Central and South America. *Iphigenia centralis* Germain, an African species, ranges from the middle Niger river to strongly saline waters. One species occurs on the coast of Florida and one species occurs in tropical west American waters.

*Iphigenia altior* Sowerby.

*Capsa altior* Sowerby, *Proc. Zool. Soc. London*, Pt. 2, for 1832 (issued March 13, 1833,) p. 196. "Hab. in Peruvia et America Centrali." "Dredged among coarse gravel, in twelve fathoms water, in the Gulf of Nocojo. A smaller variety, which is also rather higher, was found at Tumbez, at a depth of five fathoms, in thin mud."—Hanley, *Cat. Rec. Bivalve Shells*, p. 86, 1843, pl. 14, fig. 34, 1844, p. 349, 1856. Peru and Central America.—Römer, *Syst. Conchyl.-Cab. Martini-Chemnitz*, Bd. 10, Abt. 3, *Donacidae*, 1869, p. 114, Tab. 21, figs. 1-4. Earlier records cited.

*Iphigenia ambigua* Bertin, *Nouv. Arch. Mus. Hist. Nat.* (Paris), Ser. 2, Vol. 4, 1881, p. 120, pl. 4, figs. 4a, 4b, 4c . . . "habite l'océan Pacifique, sur les côtes de l'Amérique centrale."

*Iphigenia altior* Sowerby, Dall, *Proc. U. S. Nat. Mus.*, Vol. 37, 1909, p. 159, pl. 25, fig. 8. Capon to Tumbez, Peru. Range, Gulf of California to Tumbez, Peru.

Type Locality: Gulf of Nicoya, Costa Rica, in 12 fathoms, coarse gravel. Tumbez, Peru, also cited originally for a small variety of this species.

Range: Gulf of California to Tumbez, Peru.

Collecting Stations: Mexico: Chamela Bay, beach; Nicaragua: Potosi and Moneypenny Point; Corinto, beach; Costa Rica: Port Culebra; Culebra Bay; Golfito Bay; one mile south of Golfito Bay.

Description: Shell subtriangular, the anterior side the longer, thick, moderately inflated, base rounded, anterior dorsal margin gently arcuate and sloping, rounded at the end, posterior dorsal margin more steeply sloping, more flattened and subtruncated at the end, a slight depression often present anterior to the posterior umbonal ridge; smooth except for lines of growth and submicroscopic radiating striae; two cardinal teeth in each valve, the right posterior and left anterior bifid or medially grooved; inner margin smooth; pallial sinus extends for about five-eighths the length of the shell, rounded at the end, and along the base for about a third of its length confluent with the pallial line; color yellowish or purplish-white under an olive periostracum, the umbos dark, the interior white and violet.

A very large right valve in the present collection from one mile south of Golfito Bay, Costa Rica, measures: length, 79 mm.; height, 57.3 mm.; convexity (one valve), 18 mm.; pallial sinus extends anteriorly 45 mm. from the posterior margin of the shell. A specimen in the collection of the California Academy of Sciences collected in Panama Bay by F. M. Anderson, measures: length, 68 mm.; height, 51.5 mm.; convexity (both valves together), 31 mm.; pallial sinus extends anteriorly 39 mm. from the posterior margin of the shell.

The specimen described as *Iphigenia ambigua* by Bertin may be slightly longer in proportion to the height as compared to some specimens of *I. altior*. In the absence of any other differences and in view of the variation shown in a series of shells, we have placed Bertin's species in the synonymy of *I. altior*. Carpenter<sup>56</sup> mentioned an elongate specimen from Mazatlan with a strong posterior ventral sinus which he referred to "*Iphigenia ?laevigata, ?cujus*." According to Carpenter, Gray considered the specimen to be an abnormal variety of *I. altior*. In general features *I. altior* is quite similar to *I. laevigata*, the type of the genus, from West Africa.

Compared to *Iphigenia brasiliiana* Lamarck, which occurs in the Caribbean region, the shell of *I. altior* is considerably higher proportionately from beak to base and it has a much fainter depression anterior to the posterior truncation.

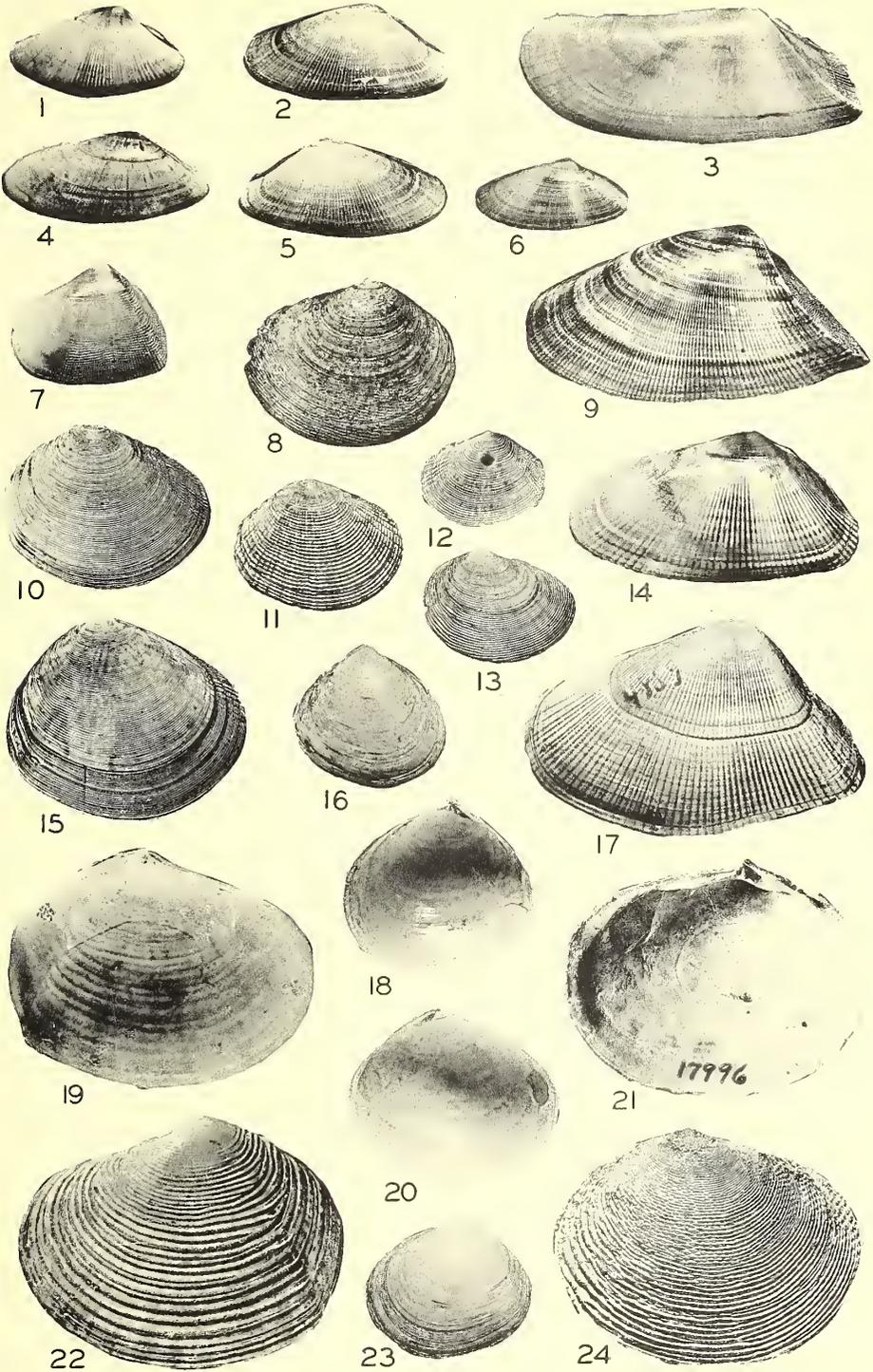
Distribution: Specimens of *Iphigenia altior* were collected by the expedition on beaches from Chamela Bay, Mexico, to Golfito Bay, Costa Rica. Dall mentioned that this species was found at a depth of 4 to 6 inches in sand, on flats and tidal lagoons of Peru.

<sup>56</sup> Carpenter, P. P., *Cat. Mazatlan Shells*, September, 1855, p. 42.

## EXPLANATION OF THE PLATE.

- Fig. 1. *Donax navicula* Hanley. Hypotype, left valve, from Corinto, Nicaragua. Length, 18.8 mm.; height, 9.2 mm. P. 254.
- Fig. 2. *Donax californicus* Conrad. Hypotype, left valve, from San Pedro Bay, California. Length, 22 mm.; height, 9.8 mm. P. 252.
- Fig. 3. *Donax transversus* Sowerby. Hypotype, left valve, from Corinto, Nicaragua. Length, 36.6 mm.; height, 14.5 mm. P. 256.
- Fig. 4. *Donax gracilis* Hanley. Hypotype, left valve, from Potosi and 5 miles west of Monypenny Point, Nicaragua. Length, 22 mm.; height, 9.7 mm. P. 253.
- Fig. 5. *Donax californicus* Conrad. View of right valve of the specimen shown in Fig. 2.
- Fig. 6. *Donax gracilis* Hanley. Hypotype, left valve, from Loc. 27588 (C.A.S.), about 13 miles southeast of Cape Tosco, Santa Margarita Island, west coast of Lower California. Collected by the Templeton Crocker Expedition, 1932. Length, 15.8 mm.; height, 7.3 mm. P. 253.
- Fig. 7. *Donax obesus* d'Orbigny. Hypotype, left valve, from Station 200-D-19, Lat. 12° 28' 03" N., Long. 87° 12' 39" W., Corinto, Nicaragua, in 12-13 fathoms (22-24 meters). Length, 11.1 mm.; height, 8.9 mm. P. 254.
- Fig. 8. *Semele sparsilineata* Dall. Hypotype, left valve, from Station 221-D-1, Lat. 7° 54' 45" N., Long. 82° 04' 32" W., Gulf of Chiriqui, Panama, in 35 fathoms (64 meters). Length, 22 mm.; height, 17.4 mm. P. 247.
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- Fig. 24. *Semele verrucosa* Mörch. View of the exterior of the specimen shown in Fig. 21.

All the specimens illustrated on this plate are in the type collection of the Department of Paleontology of the California Academy of Sciences.





## 20.

Tettigellidae and Gyponidae (Homoptera) of Kartabo,  
Bartica District, British Guiana.<sup>1</sup>

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(Text-figures 1-8).

[This contribution is a result of various expeditions of the Department of Tropical Research of the New York Zoological Society to British Guiana during the years 1917, 1919, 1920, 1921, 1922 and 1924, under the direction of Dr. William Beebe. For maps and ecological data refer to *Zoologica*, Vol. VI, 1925, pp. 1-193.]

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## INTRODUCTION.

In 1945 the writer (Metcalf, 1945b) reviewed the Fulgoroidea from Kartabo collected by Dr. William Beebe and his associates. Included with these were a small number of leafhoppers belonging to the groups Tettigellidae (formerly Cicadellinae) and Gyponidae. While the number of species in the present collection is not large, they are of sufficient interest to be worth reporting. A number apparently belong to species previ-

ously described and in these cases I have attempted to redescribe and illustrate these so as to bring them into line with modern taxonomic practices. A disproportionate number of species are apparently new. This number, however, does not seem to be out of line with the apparent number of new species from other parts of the world where, likewise, only incidental collections of these small and often inconspicuous insects have been made. No species has been described as new, nevertheless, until a thorough search has been made of the literature and careful comparisons made with the original descriptions of these species. As is well known to the students of these groups, the older descriptions are often totally inadequate. The writer is under no delusions as to his ability to place these older species accurately from the descriptions. However, since so many of these types are not readily available, the best the modern taxonomist can do is to try to correlate these older described species with the material at hand.

For the present the writer proposes to treat these two groups, Tettigellidae and Gyponidae, along with some other groups of leafhoppers, as families. Whether they are coordinate with other families of Homoptera or with families in other orders has not as yet been determined. But until the groups of the Homoptera have been studied more thoroughly, it is deemed best to treat them as distinct families of the superfamily Iasodea.

## Family TETTIGELLIDAE.

Most of the species of this family are large or medium sized leafhoppers, very few are small. The body is cylindrical or more or less fusiform. The head is usually large and in a few species is produced into a definite cephalic process. The anteclypeus is large. The lora conspicuous. The postclypeus large, sometimes inflated, definitely projected onto the crown, facial portion usually with distinct transverse ridges. The lateral postclypeal sutures usually extending to the crown. Crown large, usually distinctly triangular in outline. Cephalic process sometimes distinct, short, triangular or elongate

<sup>1</sup> Contribution No. 860, Department of Tropical Research, New York Zoological Society.

terete. Paired ocelli on the crown remote from the anterior border of crown. Pronotum usually large, flat, more or less quadrangular in outline; anterior margin usually broadly curved; posterior margin usually broadly incised; lateral margins usually distinct. Mesonotum small, triangular. Tegmina elongate, usually narrow, coriaceous; venation usually distinct, sometimes strongly reticulate apically. Radius with two distinct branches; media unbranched; cubitus 1 unbranched, joined to the claval suture (cubitus 2) by a short but usually distinct cross vein. Usually two, (sometimes three or more) radial-medial cross veins and one (sometimes two) medial-cubital cross vein. Thus there is formed usually two (sometimes three) basal cells, two or three ante-apical cells and four or five apical cells, with the ante-apical and apical cells sometimes strongly reticulate. Wings transparent with a distinct submarginal vein which is incomplete on the costal margin. Radius with two branches, the first incomplete. Media with two branches. Media 1 plus 2 with a distinct radial cross vein and media 3 plus 4 with a distinct cubital cross vein. Cubitus 1 unbranched.

#### Subfamily TETTIGELLINAE.

Head, including compound eyes, usually narrower than the pronotum. Antennal ledges indistinct, not conspicuously separated from the coronal portion of the postclypeus. Lateral margins of the pronotum divergent caudad; or rounding, not distinctly separated from posterior lateral margins. Anterior tibiae not sulcate or expanded. Tegmina broader, usually covering the lateral margins of the abdomen.

#### *Erythrogonia* Melichar, 1926a:373.

Orthotype *Erythrogonia laeta* Fabr.

The species of this genus are generally small slender tettigellids with the head including the eyes wider than the pronotum. The tegmina elongate, narrow with nearly parallel sides.

Crown shorter than the greatest width between the eyes; the ocelli usually on the posterior half; face somewhat angled to the crown, strongly impressed. Pronotum usually about as long as the crown, width usually greater than the median length. Mesonotum large. Legs slender. Tegmina elongate, rounded at the apex with three elongate ante-apical cells and three shorter apical cells.

#### *Erythrogonia bicolor* n. sp.

Text-fig. 1 A-E.

This species closely resembles *Tettigonia rutilans* Walker (*Tettigonia carminata* Signoret) in general coloration but differs as follows: the apical margin of the tegmina translucent, not blackish, and the head, more elongate. Since neither the male nor female genitalia of *rutilans* have been described and since the head characters of the present species are decidedly different, together with

the fact that *rutilans* has been recorded only from Brazil, it is believed to be better to describe this as a new species.

Crown about as long as broad, slightly impressed from the posterior lateral margins around the anterior margin, leaving the anterior margin as a broad slightly elevated border; ocelli on a line with the anterior margin of the compound eyes; face strongly produced, longer than its greatest width. Pronotum as long as crown, about one and a half times as broad as the median length; the anterior margin broadly curved; the posterior margin nearly straight; mesonotum large, nearly as long as pronotum.

Female last ventral segment four times as long as the penultimate, longer than broad, curvingly acuminate to the obtuse apex with a distinct median carina. The male genitalia with the genital plates with a broad base, slender, triangular acuminate apex about half as long as the pygofers; the pygofers when viewed ventrad, elongate, triangular, gradually acuminate from the base to the apex, not as long as the anal segment; when viewed laterad, broad with the apex broadly rounded; genital styles short, acuminate, broadly curved outward. Aedeagus shorter than pygofers with a strongly developed dorsal lobe and two elongate acuminate spines at the apex.

This is a small slender species with the head including the compound eyes, the pro- and mesonotum, and the basal angle of the tegmina blackish fuscous. Beneath, including the legs and abdomen, blackish fuscous. Tegmina bright red with the venation brown. Wings transparent with scarlet red veins. Crown black, almost as long as its width between the compound eyes.

Length to apex of tegmina: 9.75 mm.

Holotype: ♂ Kartabo, Bartica District; May 10, 1924. Allotype: ♀ Kartabo, Bartica District; July 4, 1922. Paratypes: 1 ♂ July 4, 1922; 1 ♂ May 10, 1924; 3 ♀♀ May 10, 1924.

#### *Amblyscarta* Stål, 1869a:71.

Logotype *Amblyscarta modesta* Fabr.

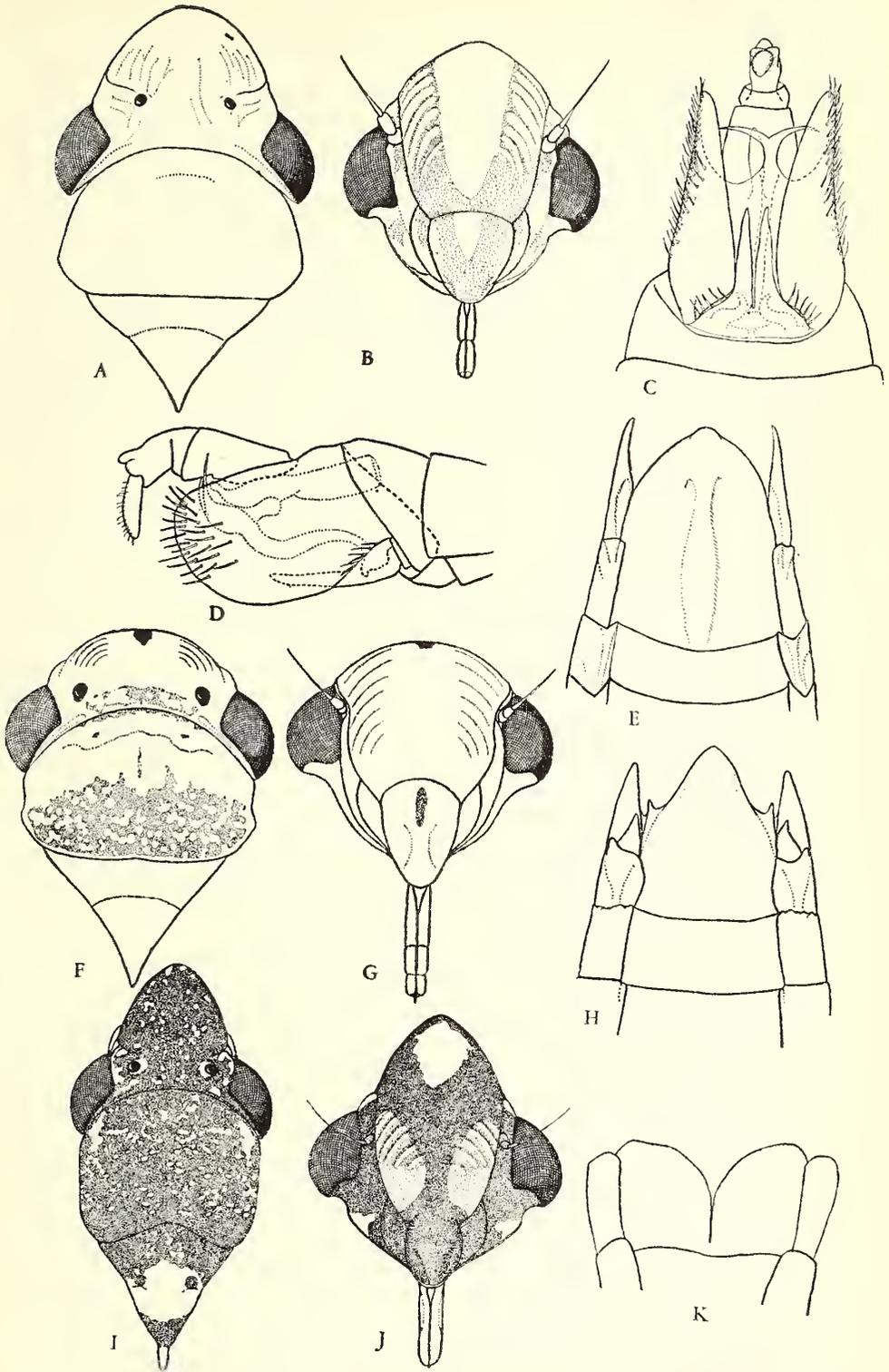
In this genus the head is broader than the pronotum. The crown is short and broad, length on the median line more than half the width between the eyes, broadly rounded to the face; face somewhat elongate. Pronotum about twice as long as the crown. Mesonotum large, almost as broad as the pronotum. Tegmina elongate, apical margin somewhat obtuse; anterior tibiae with a distinctly ciliated inner margin.

#### *Amblyscarta aurulenta* Fabr.

(*Cicadella aurulenta* Osborn, 1926b:199).

(Text-fig. 1 F-H).

This common and well-known species is apparently widely distributed in South America, having been previously recorded from British, French and Dutch Guiana, Bolivia and Matto Grosso and Rio de Janeiro, Brazil. There are numerous specimens in the



TEXT-FIG. 1. *Erythrogonia bicolor*: A, head thorax; B, face; C, male genitalia ventral; D, male genitalia lateral; E, female genitalia. *Amblyscarta aurulenta*: F, head thorax; G, face; H, female genitalia. *Orectogonia flavoscutellata*: I, head thorax; J, face; K, female genitalia.

present collection from Kartabo, Bartica District, British Guiana.

While the color is quite variable, the head, pronotum and mesonotum are chiefly ochraceous orange with the legs and venter bright yellowish, the abdomen usually carmine red. The tegmina vary considerably in color and color markings. More typical specimens in the present collection have the basal third of the tegmina velvety brown with numerous irregular light bluish spots, the apex testaceous brown, the posterior border of the crown irregularly irrorate with brownish and the posterior third of the pronotum usually marked like the tegmina with a broad brownish band more or less irregularly spotted with light bluish. The brown spot at the apex of the head usually distinctive.

Female with the last genital segment more than twice as long as the penultimate, projecting caudad in a broad triangular lobe; the lateral margins usually projecting as a pair of small lateral teeth.

Length to apex of tegmina: 9.5-11.0 mm.

**Orectogonia Melichar, 1926a:345.**

Logotype *Orectogonia sparsuta* Sign.

This is one of the genera established by Melichar in his key that has never been fully described. It may be characterized as follows: head including the compound eyes broader than the pronotum; crown elongate, conical, flat with the disc distinctly impressed with a very faint longitudinal furrow on the median line. Face somewhat inflated. Pronotum large, lateral margins parallel; anterior margin broadly curved; posterior margin triangularly incised. Mesonotum large, nearly as broad as pronotum. Caudal area distinctly produced. Tegmina translucent; venation distinct with three ante-apical and four apical cells, the fourth apical cell elongate. Legs short and slender, posterior tibiae with about six short stout spines on the outer margin; the anterior margin with numerous slender hairs, those on basal half short, those on apical half elongate, posterior margin with numerous short hairs.

**Orectogonia flavoscutellata Signoret.**

(*Tettigonia flavoscutellata* Signoret, 1855c:509).

(Text-fig. 1 I-K.)

This species is apparently very close to *Orectogonia sparsuta* Sign., but it differs decidedly in coloration and in size.

Crown longer than the width between the eyes, the median impressed line rather indistinct. Ocelli large, close to compound eyes. Face strongly inflated; anteclypeus small. Pronotum slightly wider than long. Mesonotum large, distinctly bi-impressed behind the middle. Tegmina elongate, rather narrow; venation distinct, the ante-apical cells nearly three times as long as the apical cells. Claval veins distinct. Legs short and slender.

Female genitalia with the last ventral segment elongate, deeply incised on the poste-

rior border, the incision almost reaching the anterior margin of the segment.

General color of the head, including the compound eyes and the thorax, blackish with numerous small round spots, yellowish or pale bluish-green, with a few larger irregular spots on the crown and the pronotum, and a large central area on the mesonotum, pale yellowish. Tegmina translucent, the veins blackish. Beneath general color blackish with a large median yellowish spot on the apex of the face and a pair of large yellowish spots at base of antennae, irregular yellowish spots on the sides of the thorax and the venter of the abdomen. Legs chiefly yellow with the posterior tibiae and the base of the posterior tarsi chiefly blackish.

Length to the apex of the tegmina: 11 mm.

Single female specimen from Kartabo, Bartica District, British Guiana, March 18, 1922.

Subfamily PROCONIINAE.

Head, including compound eyes, usually broader than the pronotum. Antennal ledges distinct, projecting, conspicuously separated from the coronal portion of the postclypeus. Lateral margins of the pronotum usually parallel. Anterior tibiae sulcate or expanded toward the apex. Tegmina narrow, not covering the lateral margins of the abdomen.

**Acrocampsia Stål.**

(Melichar, 1925a:337).

Haplotype *Fulgora pallipes* Fabr.

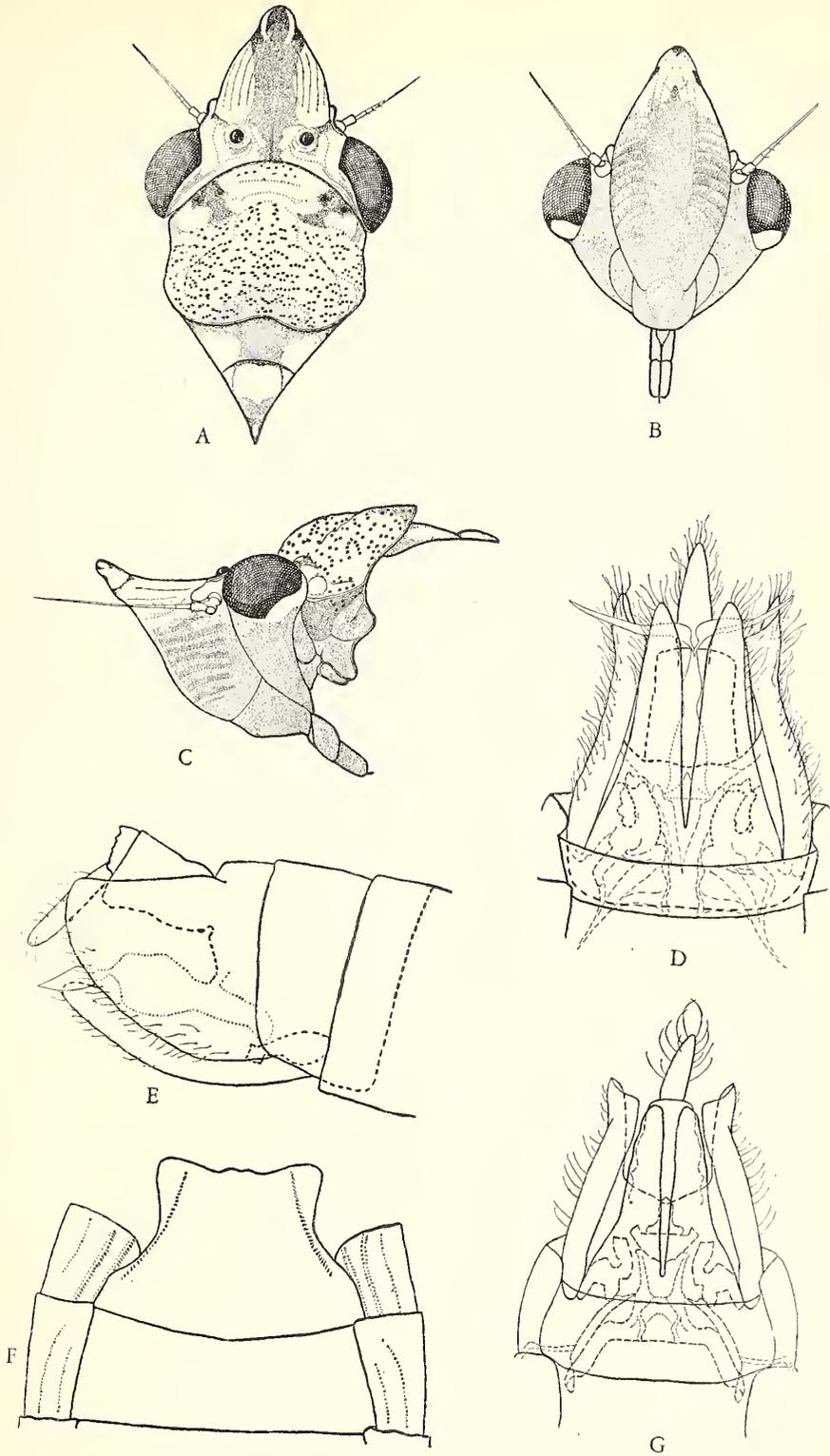
Head including the compound eyes wider than the pronotum; crown suddenly constricted in front of the compound eyes, then broadly triangularly produced to the apex which is slightly upturned. Apex with a deep longitudinal furrow both above and below. Face strongly produced; anteclypeus viewed laterad somewhat angular. Pronotum narrow with the sides parallel; anterior margin broadly curved; separated into two distinct parts—the anterior part depressed, about the same level as the crown; posterior part strongly elevated, trilobed. Mesonotum broad, not very long; apex produced into a rather slender process. Anterior tibiae broadened at the apex; posterior tibiae elongate, nearly twice as long as the femora, with a few rather stout spines on the anterior and posterior ventral margins; basitarsi not longer than the two apical segments. Tegmina rather narrow, coriaceous; venation not very distinct; the whole surface finely rugulose. Costal and commissural margins nearly parallel; apical margin obtuse.

**Acrocampsia pallipes Fabr.**

(*Fulgora pallipes* Fabricius, 1787a:261).

(Text-fig. 2 A-F).

This species may be readily distinguished from *Catorthorrhinus resinus* by the following combination of characteristics and distinctive coloration:



TEXT-FIG. 2. *Acrocampsia pallipes*: A, head thorax; B, face; C, lateral head thorax; D, male genitalia ventral; E, male genitalia lateral; F, female genitalia. *Acrocampsia rufa*: G, male genitalia ventral.

Crown somewhat longer than greatest width between the eyes, equalling the pronotum in length; cephalic process short, broadly rounded, deeply impressed, semi-erect; ocelli large, projecting; compound eyes large; face elongate, nearly twice as long as greatest width; postclypeus nearly elliptical in outline; median impression on face deep.

Female last ventral segment broad, not quite twice as broad as median length; caudal area nearly quadrangular; posterior margin shallowly incised with a median third broadly produced with a median incision at the apex. Male genitalia last ventral segment short and broad, nearly four times as broad as its median length; genital plates nearly as long as pygofer; aedeagus elongate with pair of elongate, slender, acute apical processes.

Length to apex of tegmina: 13.5 mm.

***Acrocampsia rufa* Melichar.**

(Melichar, 1925a:339).

(Text-fig. 2 G).

This species may be recognized by the following points: crown, pronotum and mesonotum chiefly yellowish, more or less clouded with light brown. Tegmina chiefly bright reddish-brown, base usually greenish-fuscous; apex transparent bordered with blackish basad. Beneath, including the legs and venter of the abdomen, chiefly pale ochraceous.

Male genitalia last ventral segment about three times as broad as its median length; genital plates slightly shorter than pygofers, obtuse; aedeagus less than half as long as genital plates.

Length to apex of tegmina: 13.5 mm.

***Dichrophleps* Stål.**

(Melichar, 1925a:327).

Haplotype *Cicada aurea* Fabr.

This genus has recently been reviewed by Melichar. He describes this genus and gives a key to the species including *aurea* Fabr. The species of this genus are quite variable in color markings and it is by no means certain that there is more than one species in Central and South America.

Head, including compound eyes, broader than pronotum; crown flat. Anterior margin acutely parabolic; face fairly flat. Pronotum rather cylindrical, lateral margins impressed; mesonotum large, triangular; tegmina transparent; venation distinct; three ante-apical and four apical cells, inner apical cell rather large. Legs rather slender, hind tibiae elongate, twice as long as the femora.

***Dichrophleps despecta* Mel.**

(Melichar, 1925a:330).

(Text-fig. 3 A-E).

I place the series of specimens in the present collection under this name because they resemble more closely the color markings described by Melichar for this species

than they do the other species from British Guiana. Melichar describes the head as shorter than the pronotum, whereas in the present series the crown is longer than the pronotum.

The genital plates of the male when viewed ventrad are short, triangular, somewhat asymmetrical at the apex; the pygofers elongate, narrow, nearly as long as the anal segment, somewhat truncate at the apex, the whole surface set with short stout spines; the aedeagus elongate, stout, somewhat membranous with a pair of ventral spines which are asymmetrical, the right spine being almost as long as the pygofer, the left spine shorter than the aedeagus; the apical area of the aedeagus is thin, irregularly broken into lobes. When viewed laterad the pygofer is about half again as long as its greatest width, thickly set with short, fairly stout spines.

Length to apex of tegmina: 16.3 mm.

Redescribed from 5 males from Kartabo, Bartica District, British Guiana. Dec. 5, 1920; April 4, 1924; April 6, 1924.

***Poeciloscarta* Stål, 1869a:73.**

(*Cardioscarta* Melichar, 1932a:285).

Logotype *Tettigoniella* (*Poeciloscarta*) *cardinalis* Fabr.

Stål established this genus as a subgenus of *Tettigonia* as indicated above, for thirteen species from South America. Melichar established the new genus *Cardioscarta* for species from America and assigned Stål's genus to species from Madagascar and Africa. On what basis this was made has never been revealed as Melichar did not finish his work on this group.

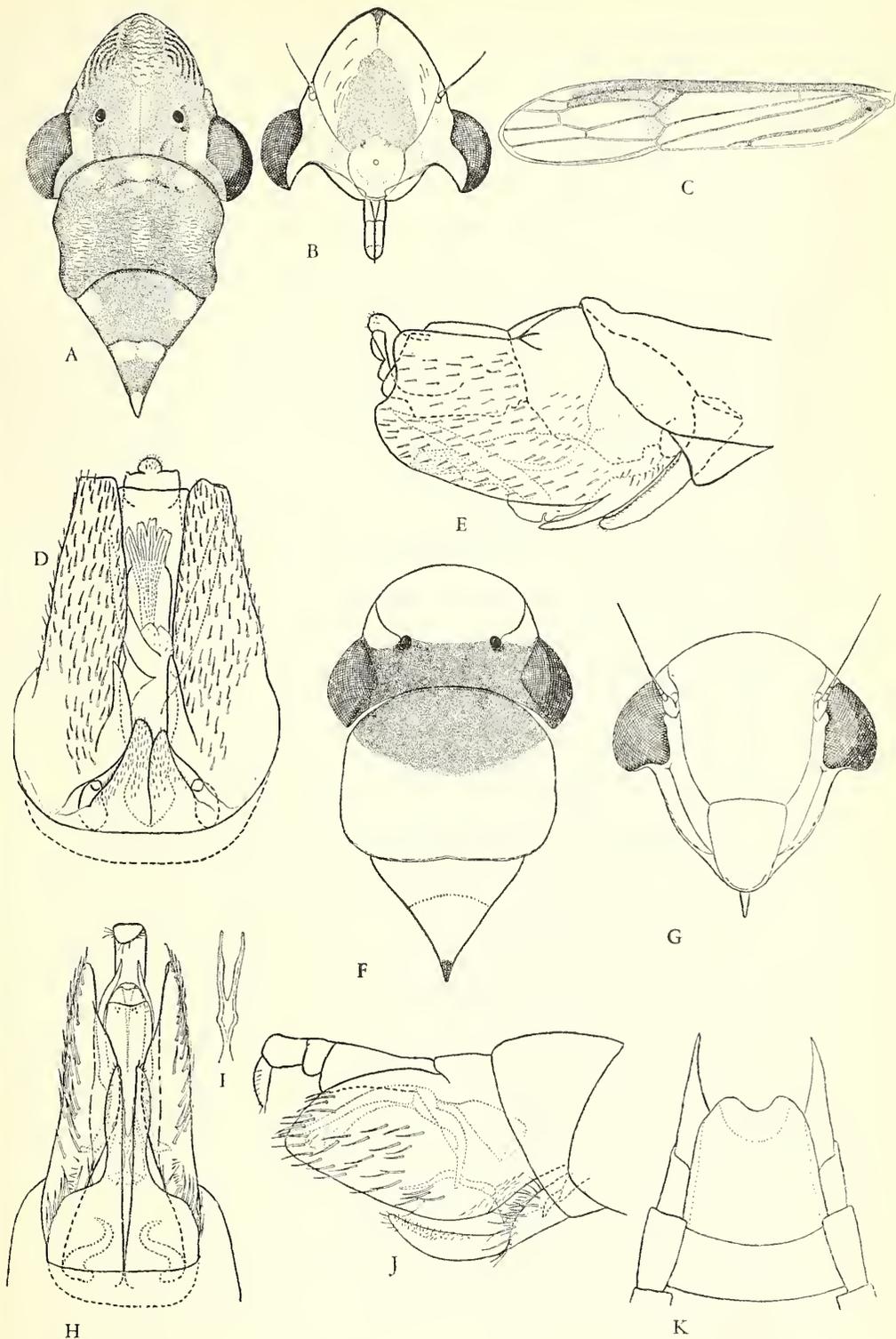
The genus may be defined briefly as follows: head including compound eyes broader than the pronotum; crown somewhat elongate, usually distinctly broader than long; anterior margin broadly parabolic; face elongate, not impressed. Pronotum broader than long, longer than the crown; anterior margin broadly curved; posterior margin nearly straight. Mesonotum large, shorter than the pronotum. Tegmina with the basal area of the corium and the clavus coriaceous with the venation indistinct; apex beyond the clavus translucent.

***Poeciloscarta quadrifasciata* Linnaeus.**

(*Cardioscarta fasciata* Melichar, 1932a:300).

(Text-fig. 3 F-K).

There has been a great deal of confusion in the nomenclature of this species. It was described originally as *Cicada quadrifasciata* Linnaeus, 1767a:706. In this he was followed by the earlier subsequent writers who merely repeated his short but distinctive description and added the reference to the original description. Goeze, 1778a:130; Fabricius, 1781a:329, 1787a:274, 1794a:51 and 1803a:72; de Tigny, 1802a:152; Donovan, 1820a: [6]; and Stoll, 1788a:82; pl. XXI, fig. 114A



TEXT-FIG. 3. *Dichrophleps despecta*: A, head thorax; B, face; C, tegmen; D, male genitalia ventral; E, male genitalia lateral. *Poeciloscarta quadrifasciata*: F, head thorax; G, face; H, male genitalia ventral; I, aedeagus ventral view; J, male genitalia lateral; K, female genitalia.

and 1792a:64; pl. XXI, fig. 114A described and illustrated this species as *fasciata* Linnaeus. In this they were followed by Blanchard, 1840a:190, and again in 1850a:190.

This species varies somewhat in color from light yellow to brilliant orange. Marked dorsad with four broad blackish fasciae, the first across the compound eyes, the posterior margin of the crown and the anterior margin of the pronotum; the second across the basal part of the tegmina beyond the sutural angle; the third across the apex of the clavus; and the fourth at the apex of the tegmina. The dark bands on the tegmina are quite variable in width and in color. The band at the apex of the tegmina is especially variable and is in some specimens reduced to a small fuscous spot with the apex of the tegmina translucent fuscous. The wings are translucent smoky with two blackish fuscous bands similar to the middle and the apical bands of the tegmina. The dorsal part of the abdomen is more or less marked with black; the venter and legs usually pale yellowish.

Crown broader than long, distinctly impressed in front of the compound eyes, broadly rounded to the face; the anterior margin parabolic; the posterior margin broadly sinuate. Pronotum quadrate; the anterior margin broadly rounded, the posterior margin nearly straight; face narrow, the anteclypeus large and protuberant.

Female genitalia with the last ventral segment elongate, nearly three times as long as the penultimate, the posterior border deeply and roundly emarginate; the male genitalia with the anal segment longer than the pygofer; the pygofer elongate, when viewed ventrad, broadened from the base to the middle and then constricted to the narrow apices; genital plates nearly as broad at the base as the last ventral segment, suddenly constricted at the middle and continued as a biramose process for half the length of the pygofer; the aedeagus elongate, stout with a biramose process, ventrally at the apex of the basal third, and a pair of elongate acute spines at the base of the apical third.

Length to apex of tegmina: 9.5 mm.

Described from numerous specimens from Kartabo, Bartica District, British Guiana.

Melichar distinguishes another species under the name of *Cardioscarta quadrifasciata* Fabr. under the assumption that *Cercopis quadrifasciata* Fabr. was a distinct species from Linnaeus's *Cicada quadrifasciata*. This cannot be true, however, as Fabricius, 1781a:329, merely copies Linnaeus's description and cites *Cicada quadrifasciata* as a synonym. Melichar distinguishes the two species in his key on the basis that *fasciata* Linnaeus (*quadrifasciata* Linnaeus) has two narrow bands on the tegmina, *quadrifasciata* Fabr. has three broad bands. This cannot be correct, however, as all of the descriptions and illustrations of the true *quadrifasciata* Linnaeus show three broad bands on the tegmina. As shown above *quadrifasciata* Fabr. is the same as *quadrifasciata*

Linnaeus and I would synonymize *quadrifasciata* Melichar with *quadrifasciata* Linnaeus but for the fact that Melichar describes the male genitalia of the latter species as having the genital plates short; whereas in *fasciata*, that is, the true *quadrifasciata* Linnaeus, the genital plates are described as long. Until we can know more about these two species, it would seem best to give a new name to Melichar's *quadrifasciata* Fabr. and I propose *Poeciloscarta nigrofasciata* nom. nov. for *Cardioscarta quadrifasciata* Melichar nec *Cercopis quadrifasciata* Fabr. This species should not be confused with *Tettigonia fabricii* which Signoret proposed for *Fulgora fasciata* Fabr. under the assumption that *fasciata* Fabr. was a secondary homonym of *Cicada fasciata* [sic] Linnaeus. But since *fasciata* Linnaeus is a typographical error for *quadrifasciata* Linnaeus and belongs to the genus *Poeciloscarta*, and *fasciata* Fabr. belongs to the genus *Raphirhinus*, the correct synonymy for Fabricius' species is as follows:

*Raphirhinus fasciatus* Fabr.

*Fulgora flammea* [nec Linnaeus] Stoll, 1781a:28; pl. VI, fig. 29.

*Fulgora fasciata* Fabricius, 1787a:261.

*Raphirhinus obliquatus* de Laporte, 1832d:415.

*Tettigonia fabricii* Signoret, 1855c:521; pl. 21, fig. 12.

*Raphirhinus* de Laporte, 1832d:413.

Orthotype *Fulgora abscondens* Fabr.

i.e., *Fulgora phosphorea* Linnaeus.

This is one of the most distinct genera of the subfamily Proconinae. It may be characterized briefly as follows:

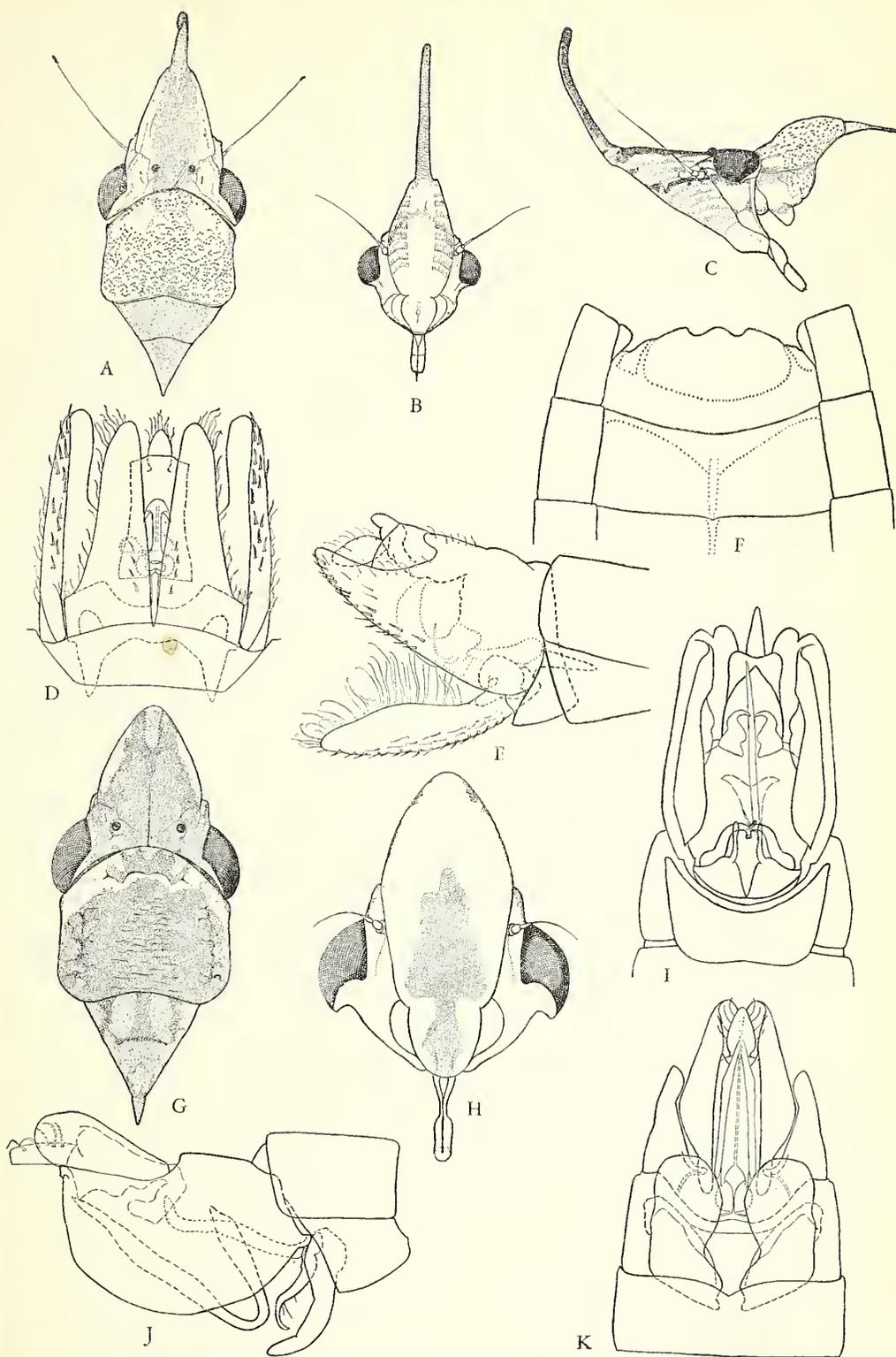
Head including compound eyes as wide as the pronotum suddenly constricted in front of compound eyes, triangularly produced to the obtuse apex which is continued into an elongate, terete, erect, somewhat recurved slender process. Pronotum usually slightly broader than long; lateral margin slightly divergent; anterior margin broadly curved, the posterior margin triangularly incised, sinuate. Mesonotum nearly as long as the pronotum, triangular. Legs slender; the anterior tibiae broadly expanded apically. Tegmina elongate, slender, coriaceous; venation fairly distinct.

*Raphirhinus phosphoreus* Linnaeus.

(Melichar, 1925a:354).

(Text-fig. 4 A-F).

This species is very variable in color. The females are chiefly ferruginous, heavily speckled with light yellow dots dorsad. Ventrals chiefly ochraceous. Males chiefly blackish fuscous, dorsad with the median area of cephalic process, lateral margins of crown, and pronotum yellowish testaceous. Beneath chiefly light testaceous yellow with postclypeus pro- and meso-plura twice banded



TEXT-FIG. 4. *Raphirhinus phosphoreus*: A, head thorax; B, face; C, lateral head thorax; D, male genitalia ventral; E, male genitalia lateral; F, female genitalia. *Capinota virescens*; G, head thorax; H, face; I, male genitalia ventral; J, male genitalia lateral; K, female genitalia.

with blackish fuscous; the fore tibiae and middle tarsi and hind tarsi apically blackish fuscous.

Female last ventral segment slightly longer than preceding segment; the apical margin on the median third shallowly bisinuate with a broad obtuse tooth. Male genitalia with pygofers, genital plates and anal segments all approximately the same length. The genital plates elongate, somewhat triangular, obtuse at the apex. The aedeagus capitate with the lateral margins strongly produced.

Length to apex of tegmina: 13.7-18.5 mm.

British Guiana, French Guiana and Surinam. Kartabo, Bartica District.

***Raphirhinus fasciatus* Fabr.**

(*Fulgora fasciatus* Fabricius, 1787a: 261).

This common and well-known species has been recorded previously from Surinam, French Guiana, Peru, Bolivia and in Brazil from Amazonas, Para and Bahia. It may be recognized by its large size and its characteristic color and markings. The dorsal surface is chiefly testaceous brown with a central vitta on the cephalic process, lateral margins of the crown, most of the pronotum, the basal area of the tegmina, a narrow fascia beyond the apex of the mesonotum, a broader fascia covering the apex of the clavus and an irregular fascia just before the apical cells, grayish or greenish-yellow. Beneath, the color is pale yellow with two narrow brownish vittae extending across the face, the lateral margins of the head, the pro- and meso-pleura to the base of the tegmina. The dorsal vitta extends just below the compound eyes and the lateral margins of the pronotum; the ventral vitta just above the clypeal suture and then curved upward to the base of the tegmina. The tips of all the tarsi and tibiae blackish fuscous.

The female last ventral segment is longer than the penultimate with the lateral margins broadly sinuate; the median area broadly and shallowly sinuate, with a broad obtuse tooth on the median line.

***Capinota* Melichar, 1926a:319.**

Orthotype *Capinota fowleri* Mel.

This genus was described originally for a single species from Mexico. The present collection contains a single species which I assigned to this genus with some hesitation, but apparently the present species should be included here.

Head including compound eyes broader than pronotum. Crown elongate, produced, suddenly but not strongly constricted in front of the compound eyes. Apex broadly upturned, impressed on the median line; lateral margins of the impression slightly carinate; a fine median carina from the base to the indented apex. Ocelli behind the anterior margin of the compound eyes. Face strongly inflated. Anteclypeus rather large, strongly inflated. Pronotum slightly broader

than long; anterior margin broadly rounded; lateral margins nearly parallel; posterior margin slightly indented. Mesonotum large, nearly as long as the pronotum. Legs slender; anterior tibiae not grooved; posterior tibiae elongate, about twice as long as the femora; basitarsus elongate, longer than the other two segments combined. Tegmina narrow; costal and commissural margins nearly parallel, coriaceous; venation regular but not very distinct; claval veins parallel.

***Capinota virescens* n. sp.**

(Text-fig. 4 G-K).

This species may be recognized by its general fuscous color above with a decided greenish cast; beneath chiefly ochraceous yellow with the tibiae of the legs chiefly ochraceous orange; ventral portion of the postclypeus clouded with blackish; anteclypeus chiefly blackish fuscous on the median line. Crown nearly one and one-half times as long as the width between the compound eyes. Ocelli nearly three times as far from each other as from the compound eyes. Pronotum slightly broader than long; sides nearly parallel; the whole surface finely but irregularly rugulose.

Male genitalia with the genital plate broadly triangular at the base, deeply incised on the median line. Inner caudal angles produced into two elongate, slender processes. Genital styles elongate, slender, curving inward, hooked at the apex. Pygofers large with a distinct ridge on the inner ventral margin. Aedeagal strut elongate, slender, acuminate and recurved at the apex. Aedeagus elongate, needle-like, sharply elbowed on basal third: basal area broadly Y-shaped when viewed ventrad. Anal segments elongate, terete, with a pair of ventral hooks at the base. Anal style elongate, slender, somewhat sagittate with a pair of distinct leaf-like processes arising at the base of the anal segment and covering most of the anal segment and anal style laterad and dorsad.

General color of the male above fuscous with a greenish cast; lateral margins of the crown, anterior border of the pronotum, and costal margin of the male greenish-yellow. Beneath ochraceous yellow except the conspicuous blackish cloud on the anteclypeus and postclypeus and the ochraceous orange tibiae and tarsi. Dorsum of the abdomen blackish fuscous; lateral margins ochraceous yellow; tips of tegmina translucent.

Length to apex of tegmina: 10.52 mm

Holotype ♂: British Guiana without definite date or locality.

Allotype ♀: Kartabo, Bartica District. British Guiana, September 20, 1922

Paratypes: 1 ♂: Kartabo, Bartica District. British Guiana, August 13, 1920; 1 ♀: British Guiana without definite date or locality.

***Rhopalogonia* Mel.**

(Melichar, 1926a:341).

Logotype *Rhopalogonia scita* Walk.

Head broad, including compound eyes

broader than pronotum; crown much broader than long, broadly rounded to face. Ocelli placed near the posterior border of the crown and near the compound eyes. Pronotum broad, nearly twice as broad as the median length. Mesonotum broad, not as long as the pronotum. Tegmina coriaceous, elongate, narrow; apical margin broadly rounded; venation indistinct, regular with four apical and three ante-apical cells, claval veins nearly parallel, complete. Legs elongate, slender; all tibiae more or less quadrangular; fore tibiae slightly longer than femora, middle tibiae more elongate and hind tibiae nearly twice as long as the femora.

*Rhopalogonia purpurata* Germ.

(*Tettigonia purpurata* Germar, 1821a:63).

(*Tettigonia purpurata* Signoret, 1853b:325, Pl. 8, Fig. 2).

(*Tetigonia purpurata* Osborn, 1926b:200).

(Text-fig. 5 A-E).

There is a small series in the present collection which I believe represents this species as described by Germar and described and illustrated by Signoret, despite the differences in coloration.

Head short and broad, crown nearly three times as broad as the median length, distinctly bi-impressed. Impressions including the large ocelli connected by a broad transverse groove; posterior border broadly carinate; anterior border broadly curved; posterior margin nearly straight. Face inflated, the postclypeus distinctly angulate near the middle. Pronotum about half again as broad as the median length, anterior margin broadly rounded, posterior margin nearly straight; mesonotum large, broader than long.

Female last ventral segment longer than broad, more than three times as long as the penultimate with a broad triangular median tooth and a pair of small lateral triangular teeth at the apex. Male genitalia with the genital plates, anal segment and pygofer all about the same length. Genital plates elongate, slender, obtuse at the apex; pygofer elongate, slender, very obtuse at the apex; aedeagus about half as long as the genital plates, broadened into two distinct lobes apically, with the outer posterior angle broadly produced; genital styles elongate, slender, curving outward; apices reflexed.

General color chestnut brown, usually distinctly lighter on the head, with a distinct round spot at the apex of the crown, blackish fuscous. Pronotum chiefly chestnut brown with a broad fascia across the middle, grayish-white. Tegmina crossed by two bluish-white fascia, one immediately posterior to the apex of mesonotum and the other near the apex of the clavus. Venter including legs chiefly chestnut brown.

Length to apex of tegmina: 11.0-11.5 mm.

Redescribed from a series of four specimens, two from Georgetown, British Guiana, and two from Bartica District, British Gui-

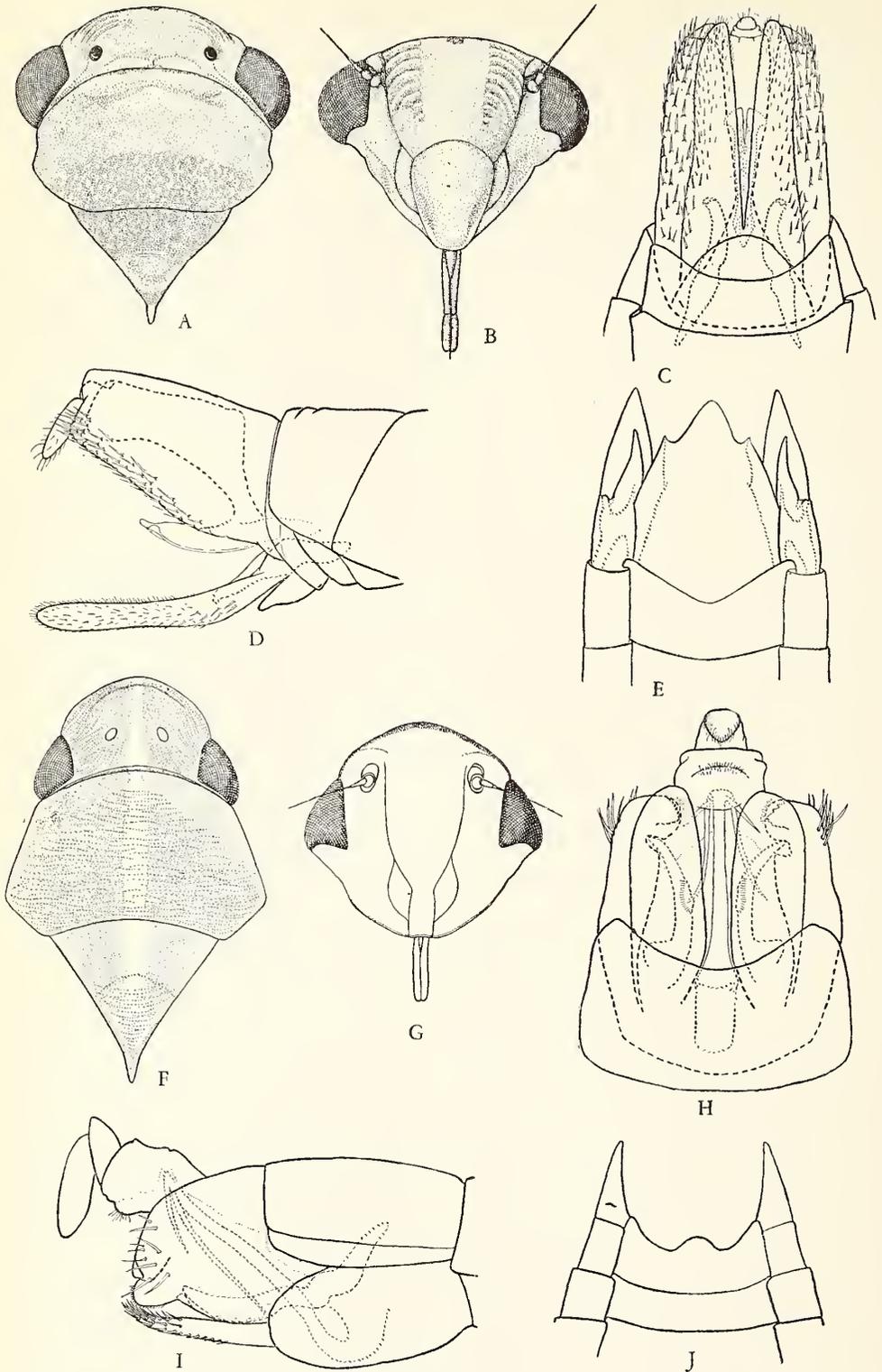
ana. This species has previously been recorded from Surinam, French Guiana, and various localities in Brazil.

Family GYPONIDAE.

In this family the body is elongate, depressed. The head is usually broad but narrower than the pronotum at the posterior lateral angles. The crown is usually longer than broad with the ocelli on the disc. The anterior margin of the crown is thin and foliaceous, or broadly thickened or rounded to the face. The face is usually broad, usually suddenly widened at the level of the antennae and forming a distinct antennal ledge. The postclypeus is narrow and elongate. The lora conspicuous. The genae broad and flat. The pronotum is large with the anterior lateral margins rounding into the anterior margin with the anterior lateral angles inconspicuous. Posterior lateral angles usually conspicuous. The posterior lateral margins distinct. The posterior margin usually broadly incised. Mesonotum large, nearly as broad as long. Anterior and intermediate femora and tibiae with distinct spines. Posterior tibiae with the internal and external dorsal margins and the external ventral margin with several fairly close set heavy spines; the internal ventral margins fringed with numerous more or less hair-like spines. Tegmina coriaceous or translucent; venation distinct, sometimes reticulate over the whole surface or the apical third only; radius 2 branched; media unbranched; cubitus 1 with two branches; cubitus 2 unbranched; first and second anal veins distinct. There are typically a single cross vein between the radial sectors; two radio-medial cross veins; and two medio-cubital cross veins thus forming three ante-apical and four apical cells.

KEY TO GENERA OF GYPONIDAE.

- A. Head with a cephalic process.  
*Ohausia* Schmidt, 1911b:299
- AA. Head without a cephalic process.
- B. Tegmina uniformly deeply pitted, body dorsoventrally wedge-shaped anteriorly, transversely wedge-shaped posteriorly, tegmina vertical, laterally compressed at apex.  
*Dragonana* Ball and Reeves, 1927a:489
- BB. Tegmina not pitted except along veins, tegmina not appressed at apex.
- C. Tegmina with numerous reticulate veins, at least on apical portion.
1. Tegmina rugose or roughened, often with white mottling, crown and pronotum usually rugose, two round black spots on pronotum.  
*Rugosana* DeLong, 1942a:64
1. Tegmina with venation often prominent but not rugose or



TEXT-FIG. 5. *Rhopalogonia purpurata*: A, head thorax; B, face; C, male genitalia ventral; D, male genitalia lateral; E, female genitalia. *Gypona thoracica*: F, head thorax; G, face; H, male genitalia ventral; I, male genitalia lateral. *Gypona bigemmis*: J, female genitalia.

- roughened, crown and pronotum never rugose.  
*Gyponana* Ball, 1920a:85
- CC. Tegmina without reticulate veins, typically with four apical and three subapical cells.
1. Face narrow, deeply excavate; pronotum and tegmina coarsely rugose.  
*Rhogosana* Osborn, 1938a:14
  1. Face not deeply excavated, flat or inflated .....2
  2. Crown acutely angled with front, margin thin, sharp, or foliaceous .....3
  2. Crown with thick margin or broadly rounding to front. 6
  3. Crown flat with longitudinal furrows, ocelli on furrow each side of median line. Tegmina usually marked with brownish dots or lines in areoles.  
*Prairiana* Ball, 1920a:90
  3. Crown without longitudinal furrows, tegmina usually without brownish markings in areoles, or if present without small brown punctate spots on vertex.....4
  4. Body usually dorsoventrally thickened, pronotum and crown depressed anteriorly, strongly sloping to anterior foliaceous margin .....5
  4. Body usually dorsoventrally flattened, pronotum and crown almost flat or gently sloping to foliaceous margin.  
*Acusana* DeLong, 1942d :57
  5. Color black, green, or orange-yellow; crown with narrow longitudinal stripes, or two round black spots on pronotum, or both.  
 Male styles short, blunt, or truncate at apex.  
*Gypona* Germar, 1821a: 73
  5. Color green or brown, without stripes on crown or round black spots on pronotum. Male styles long, slender, apex with curved, pointed tips.  
*Hamana* DeLong, 1942d:85
  6. Crown with distinct thick margin .....7
  6. Crown without definite margin, broadly and evenly rounded to front as viewed laterad .....11
  7. Face strongly inflated or bulbous .....8
  7. Face not inflated, almost straight in profile, color some shade of yellow or brown usually with distinct dark markings .....9
  8. Crown elongate, ocelli near anterior margin. Mesonotum not longer than pronotum.  
*Bulbana* DeLong, 1942d:107
  8. Crown short and broad. Ocelli about equi-distant from anterior and posterior margins. Mesonotum longer than the pronotum.  
*Scaris* LeP. and Serv.
  9. Pronotum conspicuously wider than crown, ocelli large, located almost half the length of crown from anterior border.  
*Ponana* Ball, 1920a:93
  9. Pronotum scarcely wider than crown, ocelli anterior to middle in the depression above margin .....10
  10. Anterior margin of crown quadricarinate.  
*Marganalana* Metcalf
  10. Anterior margin of crown not quadricarinate.  
*Marganana* DeLong, 1948b:101  
 [Margana DeLong, 1942d:109]
  11. Ocelli on anterior border of crown.  
*Polana* DeLong, 1942d:110
  11. Ocelli on disc.....12
  12. Head including compound eyes nearly as broad as pronotum.  
*Scaroidana* Osborn, 1938a:49
  12. Head including compound eyes decidedly narrower than pronotum .....13
  13. Crown short and broad, usually more than three times as broad as its median length .....14
  13. Crown and pronotum longer, usually not more than twice as broad as their median lengths.  
*Scarisana* Metcalf
  14. Pronotum short and broad, more than three times as broad as median length; humeri prominent; the anterior lateral and posterior lateral margins about the same length.  
*Clinonana* Osborn, 1938a:13
  14. Pronotum not more than twice as broad as long; humeri not prominent; anterior lateral margins longer than the posterior lateral margins.  
*Clinonaria* Metcalf

**Gypona** Germar, 1821a:73.

Haplotype *Cercopis glauca* Fabr.

This is a large genus of about 153 species, widely distributed from Canada, the United States, to Mexico, Central and South America as far south as Argentina and Chile. The genus formerly contained many species which are now distributed in other genera of the family Gyponidae. Many species now included in the genus *Gypona* undoubtedly belong to other genera which have been proposed recently. The correct disposition of many of the species described by Spangberg and earlier students has not been determined.

There are in the present small collection no less than 10 species of which 8 seem to be new. The genus may be described briefly as follows: body usually dorsoventrally thickened; pronotum and vertex depressed anteriorly, strongly sloping from the posterior margin of the pronotum to the anterior foliaceous margin of the crown which may be slightly upturned. Head narrower than the pronotum; crown usually elongate, sometimes almost as long as the width between the eyes. Ocelli variously placed on the crown; the anterior margin of the crown thin and foliaceous; face flat. Pronotum usually large with the anterior margin about as wide as the greatest width of the eyes; lateral margins strongly divergent, usually distinctly carinate; anterior and posterior margins strongly curved; mesonotum large; venation of the tegmina simple, the veins not punctate, with three ante-apical and four apical cells. Anterior and intermediate legs slender, short; posterior tibiae elongate with stout, close-set spines on the lateral and ventral borders. Male styles usually short and blunt at the apex. In color the species are usually decidedly variable with considerable sexual dimorphism. The females are usually light green or orange yellow, frequently unmarked, sometimes with narrow vittae on the crown or two black spots on the anterior border of the pronotum or both. Males are frequently black above, with or without pale vittae.

**Gypona fusiformis** Walker, 1858b:257.

There is a single female specimen in the present collection which agrees with Walker's short description. It may be described briefly as follows: head distinctly narrower than the pronotum; crown elongate, more than half as long as the pronotum; the anterior margins nearly parallel for a short distance in front of the compound eyes, then broadly and obtusely angulate. Ocelli behind the middle about as far from each other as from the compound eyes. Pronotum large, the lateral margins strongly divergent, anterior margin broadly rounded. Mesonotum large.

Tegmina translucent with the median apical cell clouded with blackish fuscous. Head, pronotum and mesonotum ochraceous tawny, the anterior margin of the crown

narrowly blackish, veins of the tegmina, except the concolorous subcostal vein, blackish fuscous; wings translucent, the narrow apical margin blackish fuscous; beneath, ochraceous yellow, the claws of the anterior and middle legs blackish; tips of posterior tibiae and the tarsi blackish.

Female last ventral segment slightly longer on the median line than the penultimate. Lateral posterior angles broadly rounded; the posterior margin broadly, triangularly incised for nearly half the length of the segment.

Length to apex of tegmina: 14.5 mm.

**Gypona thoracica** Fabr.

(Osborn, 1938a:21).

(Text-fig. 5 F-I).

This species was described from South America without definite locality and has been recorded from various states in Brazil. There is a good series in the present collection from Bartica District, British Guiana, collected from March through May but none later in the year.

All specimens in the present collection are males. Most of them are black in color, dorsad, with a narrow longitudinal median vitta from the apex of the crown to the apex of the mesonotum. One specimen has the posterior half of the pronotum bright orange yellow; another specimen has the entire pronotum and mesonotum bright orange yellow, with the crown with a narrow median vitta and two large pale comma-shaped marks curving between the ocelli and the compound eyes. Beneath, all the specimens are pale yellow with the posterior tibiae and tarsi and the anterior margins of the segments black.

Crown elongate, more than half as long as the pronotum, about two-thirds as long as the greatest width between the eyes. Ocelli behind the middle about as far from each other as from the compound eyes. The anterior margin of crown broadly parabolic, slightly concave. Pronotum nearly twice as broad as median length, the anterior margin broadly curved, the posterior margin broadly sinuate.

Male genitalia with the pygofer and genital plates about the same length, shorter than the anal segment. The genital plates with parallel sides, obtuse at the apex. Pygofer when viewed laterad about as long as broad with a distinct ventral apical lobe. Genital styles elongate, acuminate and diverging caudad. Aedeagus elongate, slender with two pairs of spines at the apex, the ventral pair short, strongly divergent, the apical pair elongate, slightly divergent at the apex, about half as long as the aedeagus.

Length to apex of tegmina: 13.8-14.5 mm.

**Gypona bigemmis** Spangb.

(Osborn, 1938a:25)

(Text-fig. 5 J).

This species has been reported previously

from Rio de Janeiro, Colombia and Guatemala. It may be recognized by its small size, uniform pale greenish color, and distinctive female genitalia. Head broad and short; crown broadly rounded before, slightly more than twice as broad as the median length; ocelli slightly before the middle as remote from each other as from the compound eyes. Pronotum more than twice as long as the crown, more than twice as broad as its median length. Female last ventral segment slightly longer than the penultimate, deeply excavated with a broad, round median lobe.

Length to apex of tegmina: 6.5-7.5 mm.

There is a single female in the present collection from Kartabo, Bartica District, British Guiana, March 6, 1924.

***Gypona flavolimbata* n. sp.**

(Text-fig. 6 A-E).

This is a medium large species closely resembling *Gypona glauca* Fabr. in general coloration but differing decidedly in female genitalia.

Head broad, only slightly narrower than the pronotum; crown twice as broad as its median length; ocelli just behind the middle as far from each other as from the compound eyes. Pronotum twice as broad as its median length; anterior margin broadly rounded; anterior lateral margins nearly straight, slightly divergent; posterior margin shallowly rounded almost parallel to the anterior margin. Mesonotum large.

Female with the last ventral segment only slightly longer on the median line than the penultimate; the posterior margin shallowly incised with a broad median tooth with a small triangular notch at the apex; the posterior lateral angles only slightly produced. Male genitalia when viewed ventrad with the pygofer narrow, distinctly appendiculate. Genital plates shorter than the pygofer with the apex obtuse; genital styles elongate, acute at the apex, as long as the pygofer; aedeagus as long as the pygofer, the apex with two elongate slender spines. The pygofer when viewed laterad about as broad as long with the posterior dorsal angle distinctly produced.

Length ♂: 9.75 mm.-10 mm. Length ♀: 10.75-11 mm.

Holotype ♂: British Guiana without definite date or locality.

Allotype ♀: Kartabo, Bartica District, British Guiana, March 25, 1922.

Paratypes 1 ♂: British Guiana without definite date or locality; 1 ♀: Kartabo, Bartica District, British Guiana.

***Gypona translucens* n. sp.**

(Text-fig. 7 A-C).

This species resembles *Gypona fusiformis* Walk. very closely. Head narrow, broadly triangularly produced, the crown more than half as long as the pronotum. The ocelli behind the middle, about as far from each other as from the compound eyes. Pronotum large,

the lateral margins strongly divergent, the whole surface coarsely rugulose; tegmina semitransparent.

Female last ventral segment about as long on the median line as the penultimate segment; lateral posterior angles strongly produced, the posterior margin broadly, parabolically incised with the incision slightly produced either side of the median line in short, blunt lobes.

General color tawny; the tegmina translucent; the anterior border of the crown narrowly blackish; the veins of the tegmina blackish fuscous except subcosta, which is chiefly yellowish-brown; beneath, including the legs, pale ochraceous yellow; the claws and some of the spines blackish fuscous.

Length to apex of tegmina: 17.0 mm.

Holotype ♀: Kartabo, Bartica District, British Guiana, August 18, 1920.

Paratype ♀: Kartabo, Bartica District, British Guiana, August 9, 1920.

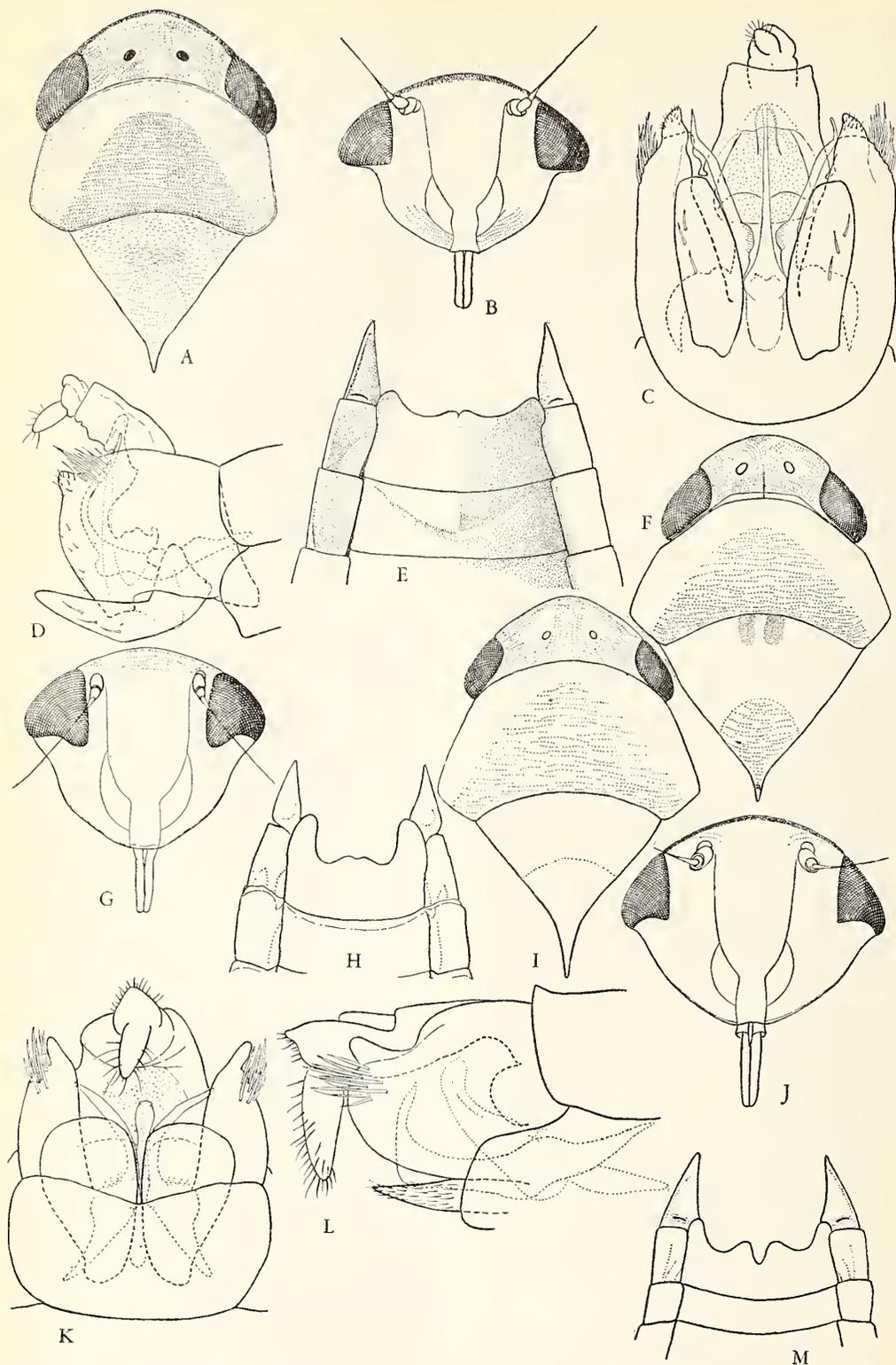
***Gypona picturata* n. sp.**

(Text-fig. 6 I-M).

This is one of the most conspicuously colored Gyponas known to me. In general structure it resembles somewhat *Gypona peruviana* Osb. but differs in essential details of the female genitalia and decidedly in coloration. Head narrow, crown short and median length about one-half as long as the greatest width between the eyes. Pronotum short and broad, about twice as long as the crown, its median length about one-half its greatest width; the anterior margin broadly curved, anterior lateral borders carinate, about twice as long as the posterior lateral margins; posterior margin nearly parallel to the anterior margin. Tegmina short and broad; venation regular.

Female last ventral segment nearly twice as long as the penultimate; the lateral posterior angle strongly produced, broadly rounded. Median area strongly produced with a deep notch on the median line. Male genitalia with genital plates short and broad, broadly rounded at apex; pygofer shorter than anal segment distinctly appendiculate; genital styles slender, elongate, strongly diverging caudad; aedeagus elongate, somewhat bulbous with a distinct process apically directed dorsad.

General color above, pale greenish-yellow with the crown with a bright red anterior border and a pair of pale reddish vittae through the ocelli; the pronotum with three pairs of reddish vittae; the tegmina chiefly translucent greenish-yellow, more or less clouded with brownish and blackish; the clavus is chiefly brownish with a broad saddle of white just before the apex; the claval border and the sutural border and the veins chiefly blackish; some of the veins on the corium are blackish or brownish and the apex is narrowly bordered with blackish fuscous with a cloud of blackish or brownish fuscous across the apical cross-veins. Be-



TEXT-FIG. 6. *Gypona flavolimbata*: A, head thorax; B, face; C, male genitalia ventral; D, male genitalia lateral; E, female genitalia. *Gypona castanea*: F, head thorax; G, face; H, female genitalia. *Gypona picturata*: I, head thorax; J, face; K, male genitalia ventral; L, male genitalia lateral; M, female genitalia.

neath, pale ochraceous yellow with all the tibiae and tarsi brownish fuscous.

Length ♀ to apex of tegmina: 13.5 mm.; ♂: 11.5 mm.

Holotype ♀: Kartabo, Bartica District, British Guiana, March 17, 1922.

Allotype ♂: Georgetown, November 15, 1933.

Paratype ♀: Kartabo, Bartica District, British Guiana, March 17, 1922.

*Gypona opaca* n. sp.

This is another large species somewhat similar in coloration to *Gypona fusiformis* Walk. and *Gypona translucens* Metc. in that the head and pronotum are generally lighter than the tegmina. It differs, however, in that the crown is very much shorter, the tegmina are opaque and variegated, and the anterior margin of the crown is without the narrow black border.

Head narrow; crown broad and short, about half as long as the short pronotum; the anterior margin broadly parabolic; the ocelli slightly behind the middle, about as far from each other as from the compound eyes; the anterior margin thin and foliaceous. Pronotum short and broad, nearly twice as broad as the median length; the lateral margins short, strongly carinate, slightly divergent; the posterior lateral margins about half as long as the anterior lateral margins; anterior margin broadly curved with posterior border nearly parallel. Tegmina opaque, somewhat rugulose. Face very flat; the dorsal margin distinctly impressed with a nearly quadrate impressed point.

Female last ventral segment somewhat longer than the penultimate on the median line. The lateral posterior angles broadly produced, somewhat obtuse. The posterior margin broadly, roundly incised either side of a strongly produced, rounded tooth.

General color of the head and thorax above, yellowish-tawny; the ocelli and compound eyes black; tegmina generally reddish-brown, variegated with pale yellowish over most of the surface; the costal margin with the reddish-brown and yellowish spots rather regularly distributed. The whole area of the tegmina somewhat rugulose but the venation regular. General color beneath, yellowish-tawny with the dorsal margin of the face infuscated; legs chiefly reddish-brown with the spines of the hind tibiae blackish fuscous.

Length to apex of tegmina: 15 mm.

Holotype ♀: Kartabo, Bartica District, British Guiana, April 4, 1922.

*Gypona castanea* n. sp.

(Text-fig. 6 F-H).

This is an almost uniformly castaneous brown species of fairly large size with the venter of the abdomen a little paler and two conspicuous black spots on the anterior border of the mesonotum.

Head narrower than the pronotum; the crown about twice as broad as its median

length; the ocelli almost equidistant from each other and the eyes, placed near the middle of crown; the anterior margin strongly curved. Pronotum twice as long as the crown, more than twice as broad as its median length; anterior margin broadly curved; anterior lateral margins nearly straight, not quite twice as long as the posterior lateral margins; posterior margin deeply incised; surface of pronotum strongly rugulose.

Last ventral segment of the female longer than the penultimate, deeply, almost quadrately incised with a broad median tooth which is notched at the apex; posterior lateral angles strongly produced, distinctly rounded at the apex.

Color almost uniformly castaneous above and beneath, except the basal segments of the abdomen which are slightly paler. Mesonotum with two conspicuous black spots on the anterior border. Tegmina with a row of inconspicuous brownish-yellow spots in the costal cell and a few irregular scattered spots on the corium and the clavus; apex of the tegmina infuscate.

Length to apex of tegmina: 11.7 mm.

Holotype ♀: British Guiana without definite date.

*Ponana* Ball.

*Gypona* (*Ponana*) Ball, 1920a:93.

Orthotype *Gypona scarlatina* Fitch.

This genus may be recognized by its narrow head, narrower than the posterior angles of the pronotum, crown short with a distinct thick margin separating it from the face. Face flat, distinctly impressed beneath the broad border. Mesonotum large. Tegmina coriaceous, venation regular. Pronotum broad; anterior margin broadly curved, almost continuous with anterior lateral margin; posterior margin nearly straight. Whole surface finely rugulose.

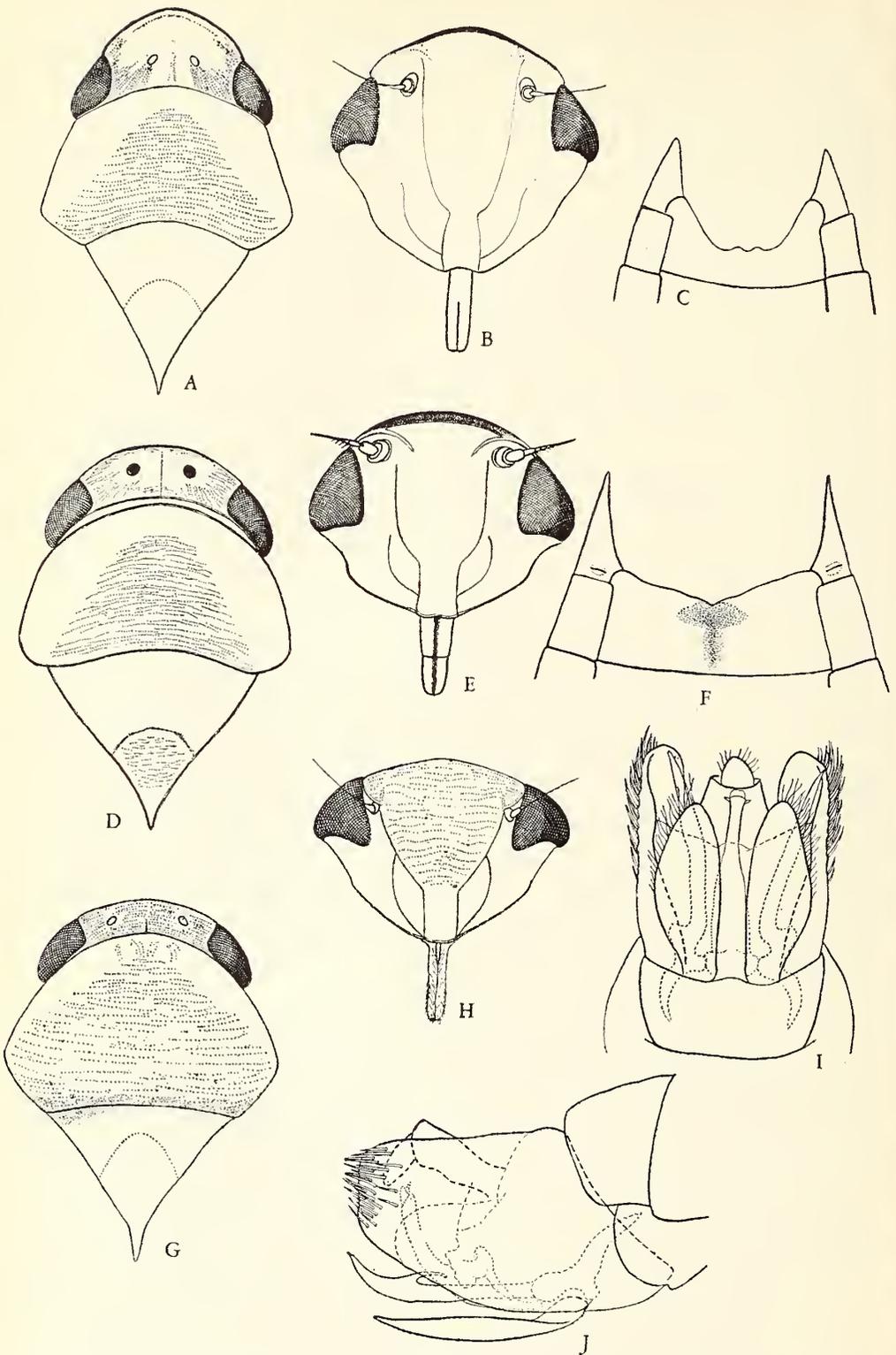
*Ponana fulva* n. sp.

(Text-fig. 7 D-F).

This is an almost uniformly tawny-colored species with the thick anterior margin brown, the ocelli and compound eyes black. Dorsal margin of abdomen chiefly bright carmine red. Crown broad and short, nearly two and a half times as broad as its median length; anterior margin broadly thickened. Ocelli about as far from base as from apex, almost equidistant from each other and the compound eyes. Face distinctly impressed beneath a broad dorsal margin. Pronotum not quite twice as broad as its median length; anterior lateral margins not distinctly separated from anterior margin; posterior lateral margins short; posterior margin broadly incised. Mesonotum nearly as broad as the head, broader than long.

Female last ventral segment about as long as penultimate; posterior margin broadly V-shaped; posterior lateral angles not produced.

Length to apex of tegmina: 9.50 mm.



TEXT-FIG. 7. *Gypona translucens*: A, head thorax; B, face; C, female genitalia. *Ponana fulva*: D, head thorax; E, face; F, female genitalia. *Clinonaria bicolor*: G, head thorax; H, face; I, male genitalia ventral; J, male genitalia lateral.

Holotype ♀: British Guiana without definite date or locality.

*Clinonaria* gen. n.

Orthotype *Clinonaria bicolor* n. sp.

This genus may be recognized by its narrow head with short broad crown. The pronotum is not especially broad and the humeri are not very prominent. When viewed laterad the pronotum is strongly declivous and the crown is broadly rounded to the face. Tegmina somewhat rugulose but the venation is distinct.

*Clinonaria bicolor* n. sp.

(Text-fig. 7 G-J).

This species resembles *Clinonana declivata* Osb. but differs in detail and decidedly in color. Head narrow; crown very short and broad with the ocelli near the anterior margin. Anterior margin broadly rounded to the face. Pronotum short, not very broad; mesonotum large.

Male genitalia with the pygofer rather broad, obtuse at the apex. Genital plates shorter than pygofer, narrow at the base, broadly curved on the lateral margins; apices obtuse; genital styles elongate, as long as the pygofer with an obtuse basal expansion; aedeagus large on the basal half, gradually narrow to the apical third with two short spines at the apex.

General color of the crown and pronotum ochraceous orange; compound eyes and ocelli black; narrow posterior border of the pronotum brown, margined anteriorly with pale green; mesonotum and tegmina auburn brown; tegmina with irregular blackish fuscous spots along the costal margin and on the basal and apical thirds; face chiefly ochraceous orange. General color beneath yellowish ochraceous with the apex of the fore, middle and hind femora with a large blackish spot near the apex; spines on the middle and hind tibiae with large black spots at their bases; apex of the hind tibiae black.

Length to apex of tegmina: ♂ 11.75 mm.; ♀ 13.0 mm.

Allotype ♀: British Guiana without definite locality or date.

Holotype ♂: Kartabo, Bartica District, British Guiana, July 20, 1922.

*Marganalana* n. gen.

Orthotype *Marganalana testacea* n. sp.

This genus is close to *Marganana* DeLong (*Margana* DeLong) but differs in several respects. Head narrower than the pronotum; crown twice as broad as long; anterior margin parabolic; ocelli nearly equidistant from the anterior and posterior margin. Anterior margin of the head conspicuously thickened, quinquecarinate, not distinctly impressed above or below. Face flat, narrow; pronotum slightly more than twice as long as the crown, not quite twice as broad as long; anterior lateral margins elongate; posterior lateral margins short; anterior margin broadly

curved in an almost continuous line from the humeri; posterior margin nearly straight. Mesonotum large. Tegmina with the venation regular. The main veins of the corium and clavus with a few indistinct punctures.

*Marganalana testacea* n. sp.

(Tex-fig. 8 A-D).

Crown distinctly broader than long; anterior margin broadly curved; median length greater than length next to compound eyes. Ocelli conspicuous, about as far from each other as from the compound eyes. Pronotum not twice as broad as long, scarcely longer than mesonotum. Female last ventral segment nearly twice as long as the penultimate with a broad V-shaped shallow notch on the posterior border; posterior lateral angles not produced.

General color above and below tawny, with anterior margin of crown, compound eyes and ocelli black. The apex of the tegmina infusate. Dorsal segments of the abdomen chiefly scarlet red.

Length to apex of tegmina: 8.5 mm.

Holotype ♀: British Guiana without definite date or locality.

*Scarisana* n. gen.

Orthotype *Scarisana variabilis* n. sp.

This genus may be recognized by the long broad head which is nearly as broad as the pronotum. Crown long and broad; anterior margin broadly parabolic; pronotum short and broad; anterior lateral and anterior borders making a continuous broad circle from the shoulders; posterior lateral borders short; posterior border straight. Mesonotum large. Face strongly inflated. Tegmina coriaceous, venation fairly regular, rather indistinct with three ante-apical and four apical cells; claval veins nearly straight and parallel. Legs rather short and stout; anterior tibiae with numerous rather long stout spines on the posterior border. Hind tibiae half again as long as the posterior femora.

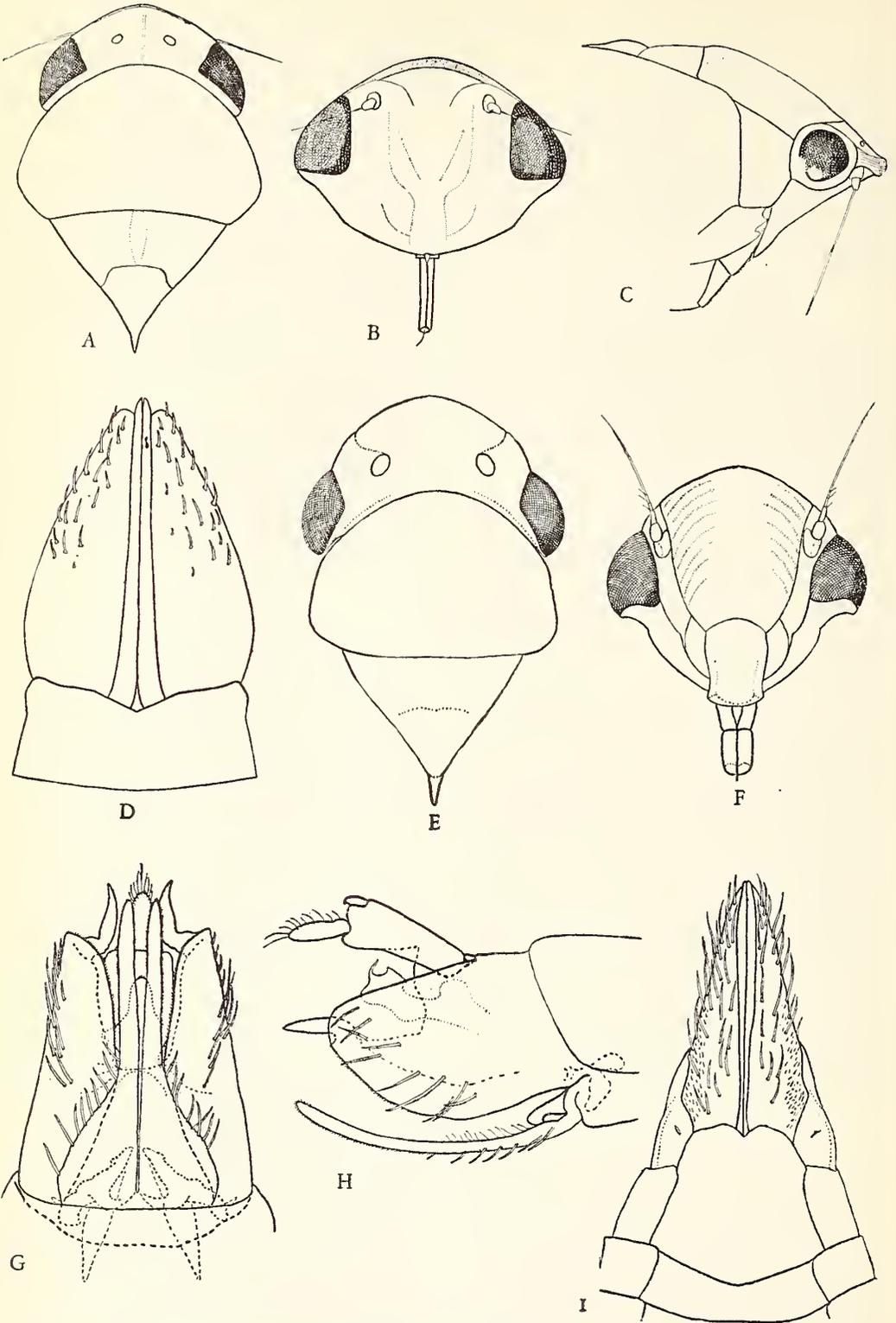
*Scarisana variabilis* n. sp.

(Text-fig. 8 E-I).

This is a variable species as far as color is concerned. Some specimens are light ochraceous buff, others are deep tawny.

Crown rather long and broad, nearly twice as wide as the median length; anterior margin broadly parabolic. Ocelli behind the middle farther from each other than from the compound eyes. Pronotum about one and one-half times as broad as its median length; anterior lateral and anterior borders broadly curved; posterior border nearly straight. Mesonotum large, broader than long. Apex produced into a distinct spine-like process.

Female last ventral segment about four times as long as the penultimate with a distinct V-shaped notch on the posterior border. Male genitalia with genital plates broad at the base, gradually restricted to near the



TEXT-FIG. 8. *Marganalana testacea*: A, head thorax; B, face; C, head thorax lateral; D, female genitalia. *Scarisana variabilis*: E, head thorax; F, face; G, male genitalia ventral; H, male genitalia lateral; I, female genitalia.

middle then nearly parallel to the apex. Pygofers with a distinct apical process.

Length to apex of tegmina: 11.25 mm.

Holotype ♂: British Guiana.

Allotype ♀: Kartabo, Bartica District, British Guiana.

Paratypes 3 ♂♂, Kartabo, Bartica District, British Guiana, various dates. 4 ♀♀ Kartabo, Bartica District, British Guiana, various dates.

**Scaris** Le Peletier and Serville, 1825a:609.

Haplotype *Iassus ferrugineus* Fabr.

This genus is unknown to me. I repeat below the more essential portions of the original description, as there is no modern description. Germar, 1833a:179, separated it from his new genus *Gypona* as having the ocelli remote from each other, whereas in *Gypona* the ocelli are approximate. Subsequent authors added but little. Evans, 1947a:215; fig. 30 G, has an excellent illustration of the head and thorax of the species *Scaris ferruginea* Fabr.

Body somewhat triangular. Crown short, transverse, much narrower than the pronotum but of the same width as the anterior margin of the pronotum, with anterior border of the head thick, rounded. Ocelli remote from each other. Pronotum not dilated laterad, transverse, rather long, narrowed anteriorly and also a little posteriorly, truncate on posterior margin. Mesonotum triangular, prolonged caudad into an elongate sharp process.

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