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OBSERVATIONS ON SEXUAL SELECTION

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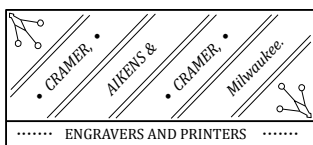
SPIDERS OF THE FAMILY ATTIDAE.

BY

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OBSERVATIONS ON SEXUAL SELECTION IN SPIDERS OF THE FAMILY ATTIDAE.

GEORGE W. AND ELIZABETH G. PECKHAM.

Introduction.

Mr. Wallace, in his well known essay on *Colours of Animals*,¹ remarks that color *per se* may be considered normal and needs no special accounting for; that amid the constant variations of animals and plants color is ever tending to vary and to appear where it is absent; and that natural selection is constantly eliminating such tints as are injurious to the species while it preserves and intensifies such as are useful; and in opposition to Darwin he has argued that the sexual diversity of color, common in many animals, has its primary cause in the special need of protection for the female, which represses in her the bright colors that are normally produced in both sexes by general laws. Or, to put it in another way, he starts with the fact of the variability of color in animals of both sexes and says that in the female, where greater protection is needed, the color is toned down or eliminated, while in the male, the need for protection being less, the color may be preserved and intensified. Mr. Wallace has supplemented this theory by another factor; he now holds that the frequent superiority, to use his own words, of the male bird or insect in brightness or intensity of color, even where the general coloration is the same in both sexes, is primarily "due to the greater vigor and activity and the higher vitality of the male. * * * This intensity of coloration becomes most developed in the male during the breeding season when the vitality is at a maximum. * * * The greater intensity of colors in the male, which may be termed normal sexual difference, would be further developed by the combats of the males for the possession of the

¹ *The colours of animals and sexual selection*, Chapter V, pp. 158—220, in *Tropical Nature, and Other Essays*, by Alfred R. Wallace, London, Macmillan and Co., 1878.

females. The most vigorous and energetic usually being able to rear most offspring, intensity of color, if dependent on or correlated with vigor, would tend to increase. But as differences of color depend upon minute chemical or structural differences in the organism, increasing vigor acting unequally on different portions of the integument, and often producing at the same time abnormal developments of hair, horns, scales, feathers, etc., would almost necessarily lead also to variable distribution of color and thus to the production of new tints and markings. These acquired colors would * * * be transmitted to both sexes, or to one only, according as they first appeared at an early age, or in adults of one sex; * * * but in all cases where an increasing development of color became disadvantageous to the female, it would be checked by natural selection; and thus produce the numerous instances of protective coloring in the female only, which occur in these two groups, birds and butterflies."¹

We have here two theories offered to explain sexual differences in color: the first is, that natural selection modifies color in the female for purposes of protection; and the second, that color may be produced or intensified where there is a surplus of vital energy, as in male animals generally, and sometimes in the females, and more especially at the breeding season. We will here consider the second theory, since Mr Wallace regards this as the more important in making intelligible cases of more brilliant coloring in the male as compared with the female.

What is meant by an excess of vital energy is not quite clear. Does this term imply that the colored modifications of the integument represent the excess of nutriment over expenditure? This seems scarcely probable, and yet what other interpretation is to be put upon such a statement? Supposing this interpretation to be correct, if the color or development of plumage represents the surplus over ordinary expenditure, should not the least active animals, rather than the most vigor-

¹ *Tropical Nature*, pp. 187 and 193-196.

ous, have the greater surplus and consequently the richer ornamentation?

Grant Allen, in his *Colour Sense*, remarks, concerning the ornamental appendages of animals: "Whatever we may think of their functions, we must agree that they are, on the whole, products of a high vitality. They represent part of the excess of nutriment over expenditure. But these dermal adjuncts do not probably take away anything from the effective energies of the organism."¹ He evidently understands Mr. Wallace to mean that these color adjuncts are by-products, or waste, from the other tissues. In this connection he quotes from Mr. Lowne to the effect that "the dermal appendages of reptiles and the feathers of birds, rich in pigment and nitrogen, are probably entirely excrementitious to the other tissues, and, without doubt, depend in great part for their origin on the solid nature of the excretion of the kidneys. Birds especially, leading a very active life, excrete material rich in nitrogen; and the feathers, which are shed periodically, enable them to throw off that element without overtaxing their renal organs."²

"Hence" says Mr. Allen, "we can understand why the more active and energetic sex should possess a greater number of highly developed dermal adjuncts, and should often display much brighter colors than the females." This, however interesting it may be as a speculation, has, so far as we are aware, no direct evidence to support it; and knowing so little as we do at present of the functions of the kidneys in birds, and of

¹ P. 188.

² The fact that closely related species annually undergo a double moult and others only a single one, and that even in the same species the sexes sometimes differ in their moulting habits, renders this proposition improbable. The habits being usually identical, why should one species depend upon moulting for the disposal of its surplus nitrogen, while in another the burden is borne by the excretory organs alone? Is there a single anatomical fact to countenance such a supposition? Darwin says that there is reason to believe that with certain bustards and rail-like birds, which properly undergo a single moult, some of the older males retain their nuptial plumage throughout the year. In the birds of paradise some have a single moult, some a double, and others, after the moult of the first year, do not cast their feathers again. For other facts bearing on this habit, see *Descent of Man*, Am. Ed., pp. 391—394.

the nature of the pigment in their feathers, it would be premature to discuss it in this connection.

Let us see how far the hypothesis that brilliant coloring is correlated with high vitality is supported by facts. Wallace makes the activity and pugnacity of an animal the criterion of its vitality; and where the male bird takes charge of the eggs and incubates them, he considers this change of habit, along with the pugnacity of the female, a proof that in such cases she possesses the higher vital energy, pugnacity being the important factor. "Of the mode of action of the *general principles of color-development in animals*,"¹ he says, "we have an excellent example in humming-birds. * * * The more vivid colors, and more developed plumage of the males, I am now inclined to think may be wholly due to their greater vital energy, and to those general laws which lead to such superior developments even in domestic breeds; but in some cases the need of protection by the female while incubating, to which I formerly imputed the whole phenomenon, may have suppressed a portion of the ornament which she would otherwise have attained." In view of the importance of this point the following evidence, offered in its support, seems rather meagre. "The extreme pugnacity of humming-birds has been noticed by all observers, and it seems to be to some extent proportioned to the degree of colour and ornamentation in the species. Thus Mr. Salvin observes of *Eugenes fulgens*, that it is 'a most pugnacious bird,' and that 'hardly any species shows itself more brilliantly on the wing.' Again, of *Campylopterus hemileucurus*,—'the pugnacity of this species is remarkable. It is very seldom that two males meet without an aerial battle,'—and 'the large and showy tail of this humming-bird makes it one of the most conspicuous on the wing.' Again, the elegant frill-necked *Lophornis ornatus* 'is very pugnacious, erecting its crest, throwing out its whiskers and attacking every humming-bird that may pass within its range of vision;' and of another species *L. magnificus*, it is said that 'it is so bold that the sight of man

¹The italics are ours.

creates no alarm.' The beautifully coloured *Thaumastura Cora* 'rarely permits any other humming-bird to remain in its neighborhood, but wages a continual and terrible war upon them.' The magnificent bartail, *Cometes sparganurus*, one of the most imposing of all the humming-birds, is extremely fierce and pugnacious, 'the males chasing each other through the air with surprising perseverance and acrimony.' These are all the species I find noticed as being especially pugnacious, and every one of them is exceptionally colored or ornamented; while not one of the small, plain, and less ornamental species are so described, although many of them are common and well observed species."¹

Here we have *six species* of humming-birds, given as all that are noticed as especially pugnacious, to establish the wide generalization that there is a causal relation between the high vital activity, as shown by fierceness and pugnacity, and brilliancy of coloring, in the family *Trochilidae*, containing 118 genera and 390 species, of which 340 are brightly colored.²

The large family of pigeons gives evidence that makes strongly against the theory. Many of them are conspicuously colored—indeed Mr. Wallace remarks, "in the Malay Archipelago and Pacific islands, they occur in such profusion and present such singular forms and brilliant colors that they are sure to attract attention. Here we find the extensive group of fruit-pigeons, which, in their general green colors, adorned with patches and bands of purple, white, blue, or orange, almost rival the parrot tribe; while the golden-green Nicobar pigeon, the great crowned pigeons of New Guinea as large as turkeys, and the golden-yellow fruit-dove of the Fijis, can hardly be surpassed for beauty."³ If the high vitality of the humming-birds will

¹ *Tropical Nature*, pp. 213, 214.

² Baird, Brewer and Ridgway, *N. A. Birds*, say that about fifty species are plainly colored.

³ *Loc. cit.* p. 103. All the pigeons build open nests and the males take part in incubation. In the case of the humming-birds, which also build open nests, Wallace has abandoned, in part, the factor of protection to the female during incubation, since, in a number of the most beautiful species, the sexes are alike, and, as Darwin says, "In the majority the females, though less brilliant than the males, are brightly

explain the unusual development of color in both sexes, and will sometimes override the action of natural selection in keeping down the brightness of the female, this is evidently not the case where the pigeons are concerned, since they are not remarkable for activity nor pugnacity, and are notoriously liable to destruction by many enemies. The further fact that the male is more highly ornamented than the female, and yet assists in incubation, is still more out of harmony with the hypothesis. That the presence of ornaments or gaudy tints is not necessarily correlated with high vitality in birds is shown by the Barbets, which are "rather clumsy, fruit-eating birds," and are clothed in green, diversified by the most vivid patches of yellows, reds and blues.¹

Again, in the birds of paradise there seems to be no relation between pugnacity and color. Mr. Wallace, in speaking of the splendid Great Bird of Paradise, which he studied in the Aru Islands, says that they congregate at "*sácaleli* or dancing parties," held in certain trees in the forest. "On one of these trees a dozen or twenty full-plumaged male birds assemble together, raise up their wings, stretch out their necks, and elevate their exquisite plumes, keeping them in a continual vibration. Between whiles they fly across from branch to branch in great excitement, so that the whole tree is filled with waving plumes in every variety of attitude and motion." Although these birds were carefully observed not a word is said of their fighting nor of any display of pugnacity. In regard to the Red Bird of Paradise, he mentions having kept a number of the magnificent male birds in the same cage; this he could not have done had they quarreled to any extent.³ He also mentions "the large cage" of two specimens of the Les-

colored." Does not the same reasoning hold good with the pigeons and a host of other birds where the nest is open and the female conspicuous? A fair consideration of the facts seems to us to confirm Darwin's supposition that the habit, common with bright colored birds, of using covered nests was acquired after, rather than before the development of the color.

¹ *Tropical Nature*, p. 105.

² *Malay Archipelago*, p. 446.

³ *Loc. cit.* p. 536.

ser Bird of Paradise, which he took with him to England, as though he kept them together.¹ If the trait of pugnacity is so closely related to brilliant ornamentation in the humming-birds, why should it not **not** be so in the birds of paradise? And why do we find brilliant color in many birds that have no more—indeed rather less—vigor than the soberly dressed birds of prey? Since, of all living naturalists, Mr. Wallace is undoubtedly the most competent to discuss this theory of the correlation of great vitality and bright color, it is surprising that he can find so little evidence in its favor.

Perhaps the most difficult fact to reconcile with the theory is the absence of ornamentation and bright color in the bats. They have wide expanse of integument, and great activity, the conditions specified by Mr. Wallace for the development of gaudy pigment, and nothing, apparently, in their habits to keep it down; but, except in the frugivorous bats, we find little difference between the sexes, nor is there any appreciable approach to bright colors. As Darwin remarks, it deserves attention as bearing on the question whether bright colors are serviceable to male animals from being ornamental, that only in frugivorous bats is the sense of sight well developed, and it is only in this group that we find any color.²

In the Araneides the great number of species and the wide differences between the several groups in habits and in amount of ornamentation, offer unusual facilities for testing Wallace's two theories of sexual color.

There is a common impression that among spiders there is little development of ornamentation, and that they are, as a rule, inconspicuous and dull. This is far from being true. Wallace, in his *Tropical Nature*, says: "The small jumping spiders are also noticeable from their immense numbers, variety and beauty. They frequent foliage and flowers, running about actively in pursuit of small insects; and many of them are so exquisitely colored as to resemble jewels

¹ *Loc. cit.* p. 557.

² *Descent of Man*, p. 534.

rather than spiders.¹ In the Malay Archipelago, also, he was struck by the "abundance and variety of the little jumping spiders, which abound on flowers and foliage, and are often perfect gems of beauty."² Bates, too, in *The Naturalist on the River Amazons*, says that "the number of spiders ornamented with showy colors was somewhat remarkable."³ A large collection of spiders from the tropics is sure to contain as great a proportion of beautifully colored specimens as would be found among an equal number of birds from the same region. Let us, then, endeavor to apply to them the hypothesis, that the brighter color of the male is due to his greater activity and vital force.

Beginning with the most brilliant family, the *Attidae*, we find that the females are, with few exceptions, larger, stronger and much more pugnacious than the males. Some four years ago we placed two females of *Phidippus morsitans* together in a glass jar. No sooner did they observe each other than both prepared for battle. Eyeing each other with a firm glance they slowly approached, and in a moment were locked in deadly combat. Within a few seconds the cephalothorax of one was pierced by the fang of the other, and with a convulsive tremor it relaxed its hold and fell dead. We placed together, in all, four females, and in each instance the fight was short but even to the death. Subsequently, we put in a well-developed male, which, though smaller, was compactly built and apparently strong enough to bring the virago⁴ to terms; but, to our surprise, he seemed alarmed and retreated, trying to avoid her; she, however, followed him up, and finally killed him. We have observed the same habits in *Phidippus rufus*. In *Dendryphantes elegans* the female is nearly a third larger than the male. During the past summer we kept a number of this species, males and females, together in a large mating-box, and were much struck by the greater quarrelsomeness of the females; they would frequently go out of their way to chase each other, and they were much more circumspect in approach-

¹ P. 97.

² Malay Archipelago, p. 437.

³ P. 54.

⁴ A *virago* is a strong, brave, or war-like woman.

ing each other than were the males. In *Icius mitratus*, neither sex was especially pugnacious, but the male was as little so as the female. In *Synageles picata* the females never came near each other without some display of hostility, though they did not actually fight.

In several species of *Xysticus*—as *ferox* and *gulosus*—the females are savage and ready to attack anything that comes in their way, while the males are smaller and more peaceable. De Geer tells of a male spider that "in the midst of his preparatory caresses was seized by the object of his attentions, enveloped by her in a web, and then devoured, a sight which, as he adds, filled him with horror and indignation."¹ The Rev. O. P. Cambridge holds that the greater ferocity on the part of the female in the genus *Nephila* has led, through the actions of natural selection, to the extreme reduction in the size of the males.² In each of two species of *Lycosa*, whose mating habits we were endeavoring to discover, two males were destroyed by a single female.

Not all female spiders are savage and quarrelsome. In some genera, as *Linyphia*, the two sexes live happily together in the same web; but Hentz, after twenty years' study of North American spiders, says that "there is less ferocity in the spiders of this division than in any other of the family. It is the only sub-genus in which the male and female may be seen harmoniously dwelling together."³ Although subsequent investigation has made it necessary to qualify this statement, the

¹ Kirby and Spence, *Entomology*, Vol. I. p. 280. 1818.

² *Proc. Zool. Soc.* 1871, p. 621. Simon has the following interesting remarks on sexual differences in size in Epeiridae: "Dans les genres où l'inégalité est faible, le nombre des mâles paraît égal à celui des femelles, car à l'époque de l'amour ces *Epeiridae* se rencontrent régulièrement par paires; mais, dans les genres où il y a grande disproportion, le nombre des mâles est beaucoup plus considérable, car il n'est pas rare de voir quatre ou cinq individus de ce sexe courtiser une seule femelle. Ces petits mâles sont adultes les premiers, mais la durée de leur vie paraît très-courte, car après l'époque de la reproduction ils disparaissent complètement; ils ne construisent point de toile propre; mais ils se tiennent à proximité des endroits habités par la femelle, attendant le moment propice pour l'accouplement, qui a lieu au milieu de la toile de celle-ci est qui est toujours précédé de longues hésitations. *Les Arachnides de France*, I, p. 20.

English translation: For genera where there is little difference in size, there appear to be equal numbers of males and females, since these *Epeiridae* are usually found in pairs during the mating season. In genera where there is a great difference in size, there are considerably more males, and it is not unusual to see four or five males courting a single female. These small males become adults first, but their life-span appears to be very short, as they disappear completely after the mating season; they do not build webs, but remain near the female site, waiting for the proper moment to mate, and then they venture onto the web only after long hesitation.

³ *Spiders of the United States*, p. 132.

broad fact remains that, as a rule, the females are more powerful and more pugnacious than the males. Walckenaer, Menge, Hentz and others give numerous instances where the male meets his death through the fierceness of his mate; in fact the danger is so imminent that after mating it is the habit in several genera (*Epeira* and *Tegenaria* are mentioned by Walckenaer) for the male to retire with precipitation² from the web of the female, as a reasonable precaution. The relations between the sexes have been admirably characterized by Romanes in *Animal Intelligence*, where he says: "In many species the male spider in conducting his courtship has to incur an amount of personal danger at the hands (and jaws) of his terrific spouse which might well daunt the courage of a Leander. Ridiculously small and weak in build, the males of these species can only conduct the rites of marriage with their enormous and voracious brides by a process of active manoeuvring, which, if unsuccessful, is certain to cost them their lives. * * * There is no other case in the animal kingdom where courtship is attended with any approach to the gravity of danger that is here observable."¹

It might be supposed that in spiders the usual conditions are reversed and that, as in some birds, the females are more beautifully colored as well as more pugnacious than the males. This, however, is not the case. Even where the coloration of the two sexes is similar the tints of the male are usually brighter; and in many cases, especially among the *Attidae*, the female is dull-colored, while the weak and unaggressive male is extremely brilliant.

There is a family of spiders, the *Gasteracanthidae*, comprising a number of genera and several hundred species, widely distributed and very rich in individuals. In the whole order of spiders there is no group where the females are so universally remarkable for inactivity and sluggishness of movement. After the web is made she remains, nearly all the time, standing motionless in the center. The males, so far as they are

¹ P. 204.

² Here *precipitation* refers to an abrupt or hasty movement by the male spider.

known, are smaller and much more active in their habits. Contrary to what we should expect on the theory, however, the males are, as compared with the females, inconspicuous and plainly colored; the females being almost always strikingly and often very brilliantly adorned with black, yellow, red, blue and white. If it be objected that the *Gasteracanthidae* do not entirely meet the point in question, since their colors have been developed as a warning of their inedibility, there are scores of edible species among the web-building spiders which are brilliantly colored and, at the same time, are very inactive; as in the genera *Epeira*, *Meta*, *Tetragnatha*, *Theridium*, *Linyphia* and others.

Turning to the family *Lycosidae*, with its numerous species, just the reverse appears, since it is among these vagabond or wolf-spiders that we find the most vigorous species, ever running about and full of restless activity. We know a good deal of their habits and of the courage of the females in defending their young; but, contrary to what we should expect, this family presents very little color development, dull grays, browns and blacks prevailing. The *Agelenidae* are very active in their movements, throwing themselves upon their prey with great vigor, and depending upon their strength, and not upon web-lines, to hold it, even when it is large and powerful. These spiders are also dull colored.

The spiders, then, seem well adapted to disprove the proposition that there is a causal relation between vital activity and color development, since in the sedentary groups, while many of the species are plainly colored, there are nearly as many that present the most beautiful tints; and, on the other hand, some of the wandering and very active groups are, for the most part, clothed in sombre hues.

Turning to the other question, how far have the females had their color toned down, as compared with the males, for purposes of protection during the nesting period? If we examine the *Attidae*, where there are marked differences in the coloration of the sexes, we find that all the females remain under

a thick, web-like covering, with their cocoons, until the eggs are hatched—that is to say, all the species of this family have covered nests. Many of these covered nests are occupied by dull-colored females, the males of the same species being showily attired. The same is true, to a great extent, among the *Thomisidae*, where the females, often protectively colored, remain near the eggs in a covered nest. The protectively colored *Lycosidae*, it is true, have practically open nests, as they carry the eggs about with them. In other families the habits vary, some leaving the eggs to their fate as soon as the cocoon is formed. while others give it much or little attention, as the case may be. A general survey of the facts shows no relation between color development in the females and their nidifying¹ habits, and it is highly probable that in spiders, as in birds, the color was developed prior to the formation of these habits.

We must then, seek further for an explanation of sexual coloring in spiders, since here we have present to account for it neither special vitality on the part of the male, nor need of protective coloring, while nidifying,¹ in the female.

MOULTING HABITS.

There is no group of facts that brings out the remarkable similarity between birds and spiders in color development more prominently than that which is gained from a study of the moulting habits of the two classes. In spiders, as in birds, the young very often differ from the adults, and in many species where the sexes differ when adult, the male being the brighter, they are alike until they reach maturity, when the male, along with his sexual development, acquires his brilliant color. Cuvier formulated, under several rules, the various changes that the plumage of birds undergoes from the nestling to the adult. These rules were extended by Blyth; and Darwin, in *The Descent of Man*, not only amplified and added to them, but also submitted them to a thorough analysis and discussion in order to discover the causes of the phenomena. In

¹ *Nidifying* refers to *nesting*, or the *making of a nest*.

looking over systematic works we unfortunately obtain little or no information about the moulting habits of spiders. Most of the species have been described by workers living in the large cities of Europe, from collections coming to them from distant parts of the world, so that an observation of habits was impossible. Then, too, such collections contain only adult or nearly adult forms, since both systematists and collectors have thus far given their attention only to these. There are, therefore, accessible on this subject, little more than the impressions of several high authorities in arachnology as published by Darwin. For some years past we have been accumulating data as to the differences in form and color between the young and the adults, and also between the two sexes in the adult stage in the same species.

Before giving the facts that we have thus far obtained it may be well to remind our readers that spiders, shortly after hatching, cast the skin, and that this moulting of the integument, including the outer coat of the eyes, is repeated, the number of times varying in the different species and possibly in the two sexes. It is probable that the *Attidae* moult from seven to eleven times before reaching maturity. In *Dendryphantes capitatus* we have counted ten moults and the spider was still immature. If one examines any of our spiders soon after they are hatched he will verify Dr. McCook's generalization that "the color of young spiders is almost without exception bright yellow or green, whitish or livid."¹ Soon after this stage, probably at the third or fourth moult, colors appear, distributed in patterns characteristic of the species, and as the spiders continue to advance in age and make their successive moults, still other and more marked changes may be noted.

Let us now pass to the consideration of the classes of cases under which the differences and resemblances, in color and form, between the young spiders and the adults of one or both sexes may be arranged. It is true among spiders as among birds, that the several classes pass into each other; and that

¹ Proc. Acad. of Nat. Sci. of Phila., 1888, p. 172.

when the young resemble their parents, the resemblance, although very strong, is not so complete as to render them exactly alike.

CLASSES OF CASES.

I. When the adult male is more conspicuous than the adult female the young of both sexes in color and form closely resemble the adult female.

II. When the adult female is more conspicuous than the adult male the young of both sexes, in color and form, more closely resemble the adult male than they do the adult female, especially in the earlier moults.

III. When the adult male resembles the adult female the young of both sexes resemble the adults.¹

In Darwin's discussion of the subject of sexual selection, he considered in great detail how far the moulting habits of birds tended to support his theory that the differences between the two sexes are attributable to female selection, rather than to natural selection acting upon the greater need for protection on the part of the female. In his profound discussion of the laws of heredity he formulates two general propositions. *First*: That variations appearing early in the life of an organism would tend to be transmitted to the offspring of both sexes. *Second*: That variations appearing late in life would be limited to the sex in which they first appeared, and would tend to appear at a corresponding age; the exception being that they might appear at an earlier age in the offspring than they did in the first instance. When the great complexity of the subject is considered, and the way in which natural selection must have sometimes modified sexual selection is taken into account, it is remarkable how fully the moulting habits of birds confirm his generalizations; and it is of the highest interest to inquire how far the moulting habits of spiders are also consistent with them.

Class I includes the cases where the adult male spider is

¹These classes are slightly modified from Darwin, *Descent of Man*, p. 466.

These rules appeared on p. 466 of a single volume Second Edition of *The Descent of Man and Selection in Relation to Sex*, published between 1875 and 1889 by D. Appleton and Co., New York. Darwin's rules (I—VI) were in fact *significantly* (not *slightly*) modified by the Peckhams. Darwin always included many more qualifications in his statements.

more conspicuous than the adult female, the young of both sexes resembling the adult female, both in color and form—or, at least, resembling her much more than they do the adult male. A good example of this class is *Phidippus johnsonii*, where the female has the abdomen red and black, with a white base and some white dots, while that of the male is bright vermillion red with sometimes a white band at the base (Plate II). The young of both sexes resemble the mother until the last moult, when the males assume their bright livery. *Philaeus militaris*, a very common *Attus*, is another illustration; in the male the cephalothorax and abdomen are bright bronze brown, the former with a wide, pure white band on each upper side and a white spot on the center of the head, the latter with a wide, white band around the base and sides; the female has a brown body covered over with white and gray hairs, which form a more or less distinct pattern of lines and spots. To give a better idea of this difference, let us suppose a male bird with the body, neck and head bright bronze brown, and the wings and a patch on the head pure white, with a female having mottled white and brown plumage.

Hentz described the female of his *Plexippus puerperus* as a different species under the specific name *sylvanus*, so little do the sexes resemble each other. *Dendryphantes capitatus* is another species in which there are great sexual differences. As in the last instance, the male and female were described by Hentz as different species. We may suppose that the sexual peculiarities of the male have been only recently acquired in *capitatus*, since he sometimes retains the markings and color of the female, these being proper to him in the immature stage. In *Icius palmarum* the sexes are very different. We shall, later on, describe the differences in the face and falcis, so that here it is enough to say, that in the male the whole body is bronze brown, covered with short, golden down, while in the female the color is rufus, with black and white markings.

For *Habrocestum splendens* the colored figures of the moults and the adult forms (Plate I) bring out the fact that while the

young are not exactly like the adult female they resemble her much more closely than they do the adult male. This is one of our most beautiful males. The highly iridescent scales, which cover the entire body, make it impossible to give, in a painting, a correct idea of its brilliancy, since the color changes in every light. The male only gets this gorgeous livery at the last moult, just as he becomes mature, though in some species the nuptial robe is acquired one moult before maturity.

The family *Attidae*, from which these illustrations have been taken, is by common consent, placed at the head of the order;⁴ and contains among its 1,500 species the greatest amount of sexual difference and the highest development of ornamentation; indeed, as we have seen, Wallace speaks of them as resembling jewels rather than spiders, and Walckenaer says that their species are well marked by the rich diversity of their colors and the variety of the designs which ornament their abdomens.¹

In the seventy-eight species described in our work on the *Attidae* of North America we have both male and female in only forty; or, to be more accurate, we have felt warranted in placing males and females together in only forty instances. Doubtless in many cases we have separated the two sexes, making two species out of one, but the difference in color is so great that, without knowledge of their habits, no other course was possible.² Of the forty species, we know the moults of thirty two, and of these, nineteen species form a group characterized by marked sexual differences, the males being very generally conspicuously colored as compared with the females, while in others only the falcis are different. Since the nineteen species represent twelve important genera³ it would seem that so far as the North American *Attidae* are concerned, the generalization is

¹ *Hist. Nat. des Insectes Aptères*, I, p. 481.

² We have, in the genus *Phidippus*, sixteen species, four pairs, four single males and eight single females. *P. cardinalis*, male, is of a splendid, uniform, cardinal red (Plate II); to which of the eight plainly attired females he belongs we do not know; and we have the same difficulty in other cases.

³ *Phidippus*, *Philaeus*, *Plexippus*, *Dendryphantas*, *Icius*, *Habrocestum*, *Astia*, *Zygoballus*, *Synageles*, *Menemerus*, *Lyssomanes*, and *Epiblemum*.

⁴ Although there is no scientific basis for this view, more than 100 years later popular authors still refer to the Salticidae (*Attidae* of the Peckhams) as the *most advanced* spiders. In the late 1800's, however, even naturalists as rigorous as Charles Darwin frequently made a distinction between *higher* and *lower* animals.

well established. If we may add to these a large number of bright-colored, undescribed species from our own Guatemala collection, in which the young closely resemble the female, the generalization is materially strengthened.

In order to estimate to what extent the sexes differ in the *Attidae*, we tabulated the species, in a number of works, giving the number of species in which both sexes, and also the number in which one only **are** described. If it may be assumed that a collector ordinarily takes as many of one sex as of the other—and our numerous collections from different parts of the world confirm this supposition¹—if the sexes were fairly alike they would be identified as one species and placed together; if, on the contrary, the sexual differences were great (the habits being unknown) many species would be founded on a single sex.

TABLE OF SPECIES DESCRIBED BY DIFFERENT AUTHORS, ACCORDING TO SEX. TOTAL 930. ² (<i>ATTIDAE</i>)				
AUTHOR.	LOCALITY.	♂ & ♀	♂	♀
Koch and Keyserling	Australia	48	47	57
Taczanowski	South America	60	27	26
C. Koch	World, except N. Am. and Europe	3	49	46
Cambridge	Various	16	27	16
Lucas	Algiers	8	13	36
Thorell	Burmah and Indian Archipelago	17	62	42
Simon	Various places, not France	8	47	22
Walckenaer	World, except N. Am. and Europe	3	11	17
Peckham	North America	40	17	21
Simon	France	94	28	11
Vinson	Madagascar, Mauritius, etc.	0	0	8
TOTAL		297	328	306

The table shows that in a total of 930² species from all parts of the world the single males just about balance the single

¹ That this is not always true in other families is shown by Stoliczka, who says: "In collecting *Epeiridae* I was particularly struck with the very great scarcity of male specimens; for, among about 200 specimens belonging to about thirty species, there were not more than five or six males." *Indian Arachnida*, Proc. Asiat. Soc., Vol. XXXVIII, p. 234. This was probably due to his having collected either before or after the mating season, when the males are always more rare.

² The numbers presented here add up to 931, not 930.

females, and that the same is true, with a few exceptions, in the individual collections. Excepting when the spiders are well-known, as in the case of Simon's *Attidae of France*, a comparison of the description of the two sexes, when they have been put together, would only serve to show a similarity between the males and females, since it would be only in the species where there was little or no sexual difference that they could be placed together. Where they are well-known, as in the *Attidae of France*, we find by such a comparison that in thirty-nine species the male is plainly unlike the female, being in twenty-six instances much more conspicuous, while in fifty-five the sexes are similar, or, if they differ, the male is no more conspicuous than the female. These facts are given to make it clear that the sexes very commonly differ, the male being brighter than the female. It is probably not too much to say, that in the *Attidae*, at least two-fifths of all the species have the male more conspicuous than the female.

Menge¹, in referring to the greater brilliancy of the male of *Micromata ornata*, says that it only assumes its bright color as a "bridal adornment," and in this connection makes the statement that in the families *Thomisidae* and *Salticidae* the males are generally more beautifully colored than the females. We have, in North America, several *Thomisidae* that are like Menge's species in the difference in color between the sexes, and also in that the young males are like the female, and only assume their bright color at the last moult. Darwin² remarks on the fact that "the female of *Sparassus smaragdulus* is dullish green, whilst³ the adult male has the abdomen of a fine yellow, with three longitudinal stripes of rich red;" while young this male resembles the female."⁴ The obvious conclusion from these facts is that it is the male that has varied, and this, too, late in life, so that his peculiarities, having been limited to one sex, do not appear in the young. We are not embarrassed in this group by any need on the part of the female for plain colors to protect her during incubation, since, without exception, the cocoon

¹ *Preussische Spinnen*, II, p. 396.

² This quote appeared in *The Descent of Man, and Selection in Relation to Sex* (Appleton and Company, New York, 1871, Chapter IX, p. 327). This statement also appeared on p. 272 of a popular American version of the Second Edition of this work (Appleton and Company, New York, 1875—1889), which appears to have been the edition (if not the version) used by the Peckhams (however, see note 4, below).

³ Spelled *while* in Darwin's original (first edition) account published by Appleton and Company, and changed to *whilst* in the Second Edition.

⁴ The last part of this sentence, *while young this male resembles the female*, was a direct quotation from Darwin's first edition of *The Descent of Man*, and did not appear in his Second Edition.

is so placed as to be concealed, or, as in the *Attidae*, is covered with a thick layer of web, under which the mother spider remains until the young appear, seldom leaving the nest to obtain food. On the whole, the explanation of sexual differences of color in spiders which is most conformable with facts, is that the males have departed from the usual colors of the genus,¹ and that most probably this departure has been brought about by sexual or female selection.

Thus in the *Habrocestum* group the general coloring of the genus is represented by the females of *cristatum* and *auratum*, which are gray, with oblique whitish bands; in *viridipes* there is a tendency to greater concentration of color, and consequently to stronger contrast, the color being blackish with yellowish white bands. In *peregrinum* and *auratum* we find that the males have gone still further in the same direction, the ground color being deep black and the bands pure white. (Plate 1.) In *splendens* the male has made a still greater departure from the typical coloring of the genus, while the female, also departing therefrom, though not in so great a degree, shows the strongly contrasting black and white that is found on the males of *peregrinum* and *auratum*.

Class II. When the adult female is more conspicuous than the adult male, the young of both sexes, both in color and form, more closely resemble the male than they do the female, especially in the earlier moults.

This class, while it is found both in spiders and birds, differs widely in the two groups, both in the number of instances and in the causes that have produced them. While in birds the number of cases in which the females are brighter is

¹This is the opinion of Blackwall and of Canestrini. Thorell, in speaking of the genus *Erigone* (of the family *Therididae*), a genus that contains an immense number of species, says: "The study of the spiders belonging to this interesting genus has hitherto been comparatively neglected, and this neglect is no doubt to be attributed partly to their diminutive size, and partly to the great similarity prevailing among the females of the different species. * * * Many a female is sometimes mated with one, and sometimes with another male; * * * the following lists of synonyms must, unless the contrary be directly stated, be considered as applying only to the *males*, which are comparatively easily distinguishable." *Remarks on Synonyms of Europ. Spiders*, p. 97.

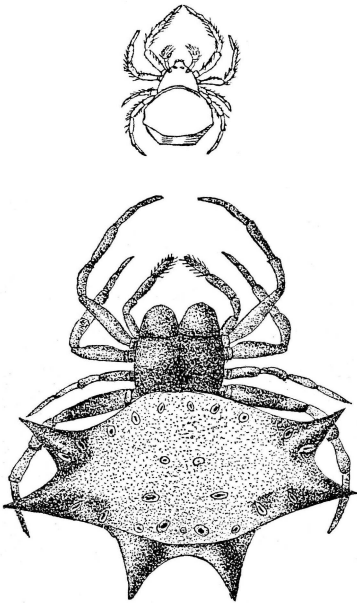


Fig. 1.—*Gasteracantha rufospinosa*. Upper figure, male enlarged seven times; lower **figurer** female, enlarged four times (from Marx.).

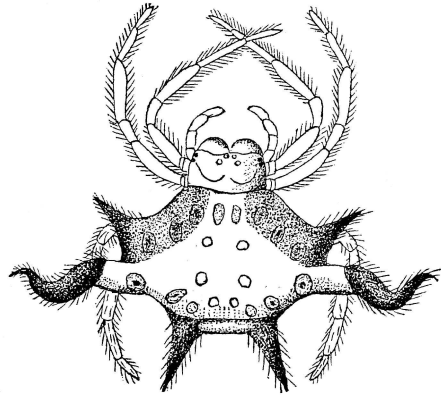


Fig. 2.—*Gasteracantha crepidophora*, female (from Cambridge).

inconsiderable, and while even in these cases the female is but little more conspicuous than the male, in spiders there are numerous species in which the female is decked in the most gaudy hues, her body being at the same time protected by strong, sharp spines, while the smaller male is unarmed and comparatively inconspicuous.¹ (Figs. 1 and 2)² The spiders to which we refer belong to the genera *Gasteracantha*, *Acrosoma*, *Phoronocidia* and others, including possibly 250 species distributed over all parts of the world. The differences between the males and females are shown in Plate III.² Only a few males are described in this group, but they all agree in the peculiarities mentioned.

The perplexing fact in this connection is that while the females at first resemble the males, it is only while they are quite young, since when they are from a quarter to a third grown they begin to assume the adult form and color, and it seems as though characteristics developing so early should have been transmitted to

¹ A seeming exception to this rule is *G. Cowani*, ♂, described in *Proc. Zool. Soc.*, 1882, p. 766. As this case was sufficient to invalidate our generalization we wrote to Mr. Butler, asking him to re-examine the spider in question to make sure that it

² Both of these figures, as well as Plate III, were also shown in, or referenced by, the subsequent paper in this volume (Protective resemblances in spiders, *Occasional Papers of the Natural History Society of Wisconsin* Volume 1, Number 2, 1889) by E. Peckham. The *shared* Plate III is also included in this edition, for reference.

both sexes. After a good deal of consideration we are inclined to believe that in the early history of the group the male and female both possessed some such form and color as is now seen in the adult male, and in the first few moults of the female; and that afterwards the adult female, probably on account of some change in habits, varied toward her present size, form and color under the action of natural selection. "As variations occurring late in life," says Darwin, "and transmitted to one sex alone, have incessantly been taken advantage of and accumulated through sexual selection in relation to the reproduction of the species; therefore it appears, at first sight, an unaccountable fact that similar variations have not frequently been accumulated through natural selection, in relation to the ordinary habits of life. If this had occurred the two sexes would often have been differently modified, for the sake, for instance, of capturing prey or of escaping from danger. Differences of this kind between the two sexes do occasionally occur, especially in the lower classes. But this implies that the two sexes follow different habits in their struggles for existence, which is a rare circumstance with the higher animals."¹

The other supposition open to us, namely, that the variation from the male form began in young females and *were* sexually limited from the first, is improbable, in view of the mass of evidence that variations before maturity are inherited by both sexes equally. The habits of the female, standing nearly all the time exposed in the web, give the clue to the occasion of her modification. The habits of the male being different, he is left unmodified; he is usually found in less exposed posi-

was a male and not a female. Mr. Pocock, who is now in charge of the *Arachnida* in the British Museum, responded as follows:

BRITISH MUSEUM (Natural History), LONDON, March 28, 1889.

* * * * * * *

You are quite right in supposing that Mr. Butler fell into error in describing his specimens of this species as being males. They are in reality females. The distal segments, however, of the palpi are considerably wider than the preceding, and no doubt the mistake arose from a superficial examination of this appendage.

¹ *Descent of Man*, p. 241.

This quotation appeared on p. 241 of the expanded Second Edition of Darwin's *The Descent of Man, and Selection in Relation to Sex* (Appleton and Company, New York, 1875—1889).

tions, and only for a few days, at the mating time, is to be seen in the web.

Class III. When the adult male resembles the adult female the young of both sexes resemble the adults.

The greater number of species in this class have dull colors, which seem to be protective, as in the *Lycosidae*, many of the *Drassidae*, *Epeiridae*, *Thomisidae* and others. The same problems are presented here that are so ably discussed by Darwin in the case of birds belonging to this class. It seems likely that in the orb-weavers a large part of the courtship is conducted by vibrating the web lines, and that the males depend upon their skill in this direction, and not upon color alone, in attracting the female. The modifications of the first pair of legs, so common in the male spiders of the group, might be explained as useful in producing variations in these vibrations. We have some little evidence on this point, but defer consideration of it until treating of mating habits. In the *Attidae*, when the male is not strikingly colored, it is more than probable that the choice of the female is determined by his antics and grace of movement. *Saitis pulex* is a good example. While in the greater number of instances in this class the colors are dull, we have many species which are brilliant. Thus, in the genus *Homalattus*, many of the species have metallic greens or lovely iridescent blues or violets, while others are soft brown, mottled with white. We have not enough data to throw any light on the very intricate problems here presented, and can only refer the reader to Darwin's work,¹ where the whole subject is admirably discussed. If, therein, he will substitute *spider* for *bird*, whenever the latter word appears, he will see how full of difficulty is the whole subject.

We have other cases that come under several classes but as the instances are few, we will simply describe them individually. In *Hasarius hoyi* the adult male is more conspicuous than the adult female, which, indeed, was first described as a separate species under the name *pinus*. The young, very early,

¹ *Loc. cit.*, p. 481.

differ from each other according to sex, the young males resembling the adult males, and the young females the adult females. In this case the law of inheritance at corresponding ages must be supposed to have failed, the young males inheriting their differential peculiarities at an earlier age than that at which the variation first appeared in their male ancestors.

Phidippus rufus, when mature, is a brick-red spider, the male being considerably brighter than his consort. When about one-seventh grown, and after the third or fourth moult, the young are very dark brown, with light yellow legs. Some moults later, they are reddish, with narrow, oblique whitish bars on the sides of the abdomen, and two dark bands on the dorsum, on each of which is a row of white dots. The appearance of the spider changes but little during the next four moults, but after the last—the tenth—both male and female become mature and acquire the adult color. The meaning of the fifth moult—that with the uniform brown body and yellow legs—we are unable to explain. The appearance of the female after the fifth moult is similar to that of many other females in the genus, and her final change is probably due to a transference to her of the male color, which, judging from the moults, must have appeared late in life.

All the cases under the first and third classes are intelligible if we suppose that the females have selected the more conspicuous males and that when variations occurred late in life they were limited to the sex in which they first appeared. There are, however, many cases in which it is probable that the color variation of the male has modified the female in a greater or less degree, and this accounts for the instances in which the female, as well as the male, is showily colored, especially since the showy color in these females usually tends to approach the coloring of the males, and to depart, in the same proportion, from the normal coloring of the genus. The second class, in which the females are more brilliant than the males, is the only one in which the moulting habits of spiders are not strikingly similar to those of birds; and it seems in the highest

degree probable that where there is so close a resemblance between two such complex sets of phenomena, in widely separate classes, they can only have been brought about by a common cause.

SECONDARY SEXUAL CHARACTERS.

It is a noticeable feature in the secondary sexual peculiarities of spiders, beside those of color, which have already been sufficiently dwelt upon, that they are very commonly found in the falces, clypeus, palpi and first pair of legs—that is to say, in those parts of the animal that are plainly in view when the male is paying court to the female; and it is a fact of great significance that even in the species where sexual differences are reduced to a minimum we usually find a modification of one or more of those parts which serve to render the male somewhat more conspicuous or showier than the female. *Synageles picata* is a case in point, the sexes being nearly alike, but the male having the first legs flattened and brilliantly iridescent. In

several species of the genus *Lyssomanes* the sexes only differ in the length of the falces and that of the first pair of legs or palpi.¹

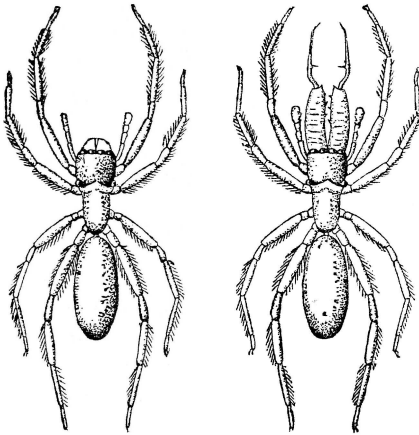


Fig. 3.—*Salticus formicarius* (from C. Koch.). Right-hand figure, male; left-hand figure, female.

The ant-like spiders are notable for differences in the falces of the two sexes. *Salticus formicarius*, (Fig. 3), a common European species, is a good illustration, the female having short, vertical, reddish black falces, while those of the male are horizontal, much enlarged, and copper green in color. In an ant-like spider from Australia, *Synemosyna lupata*, (Fig. 4, see p. 27), Dr.

Koch describes a very curious development in the falces of the male; their great length, their teeth, and their branching

¹*Lyssomanes viridis, jemieus and amazonicus.*

fangs, reminding one of the great mandibles in certain male *Lucanidae*. The female is undescribed, but we know, in this genus and in others closely related, so many males that have enlarged falces while those of the females are short, that this, too, is doubtless a sexual characteristic.¹

Cambridge has described two spiders from Ceylon² which are remarkable for the great elongation of the male falces, these being in both species longer than the cephalothorax, while the fangs are toothed and equal in length to the falx. In both species, too, the falces seem to be attractively colored, as in one they are "dark black-brown and shining," and in the other "very slightly and transversely rugose, and shining in some lights with an opaline hue." It is true in many males that the falces are not only greatly enlarged but are also brilliantly colored; and in this connection it is of high importance to note that the brightly colored hairs or metallic scales, as well as the protuberances, are either on the anterior surface, or in some way so placed as to be plainly in view from in front.

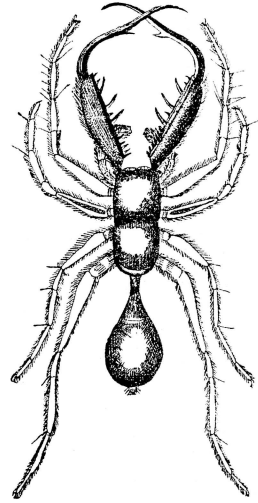


Fig. 4.—*Synemosyna lupata*.
Male (from L. Koch).

In a common spider of the Southern and Eastern United States *Icius palmarum* Hentz we have a good illustration. In the male the falces are compressed and horizontal and are three times as long as the face, the fang equaling the falx in length. The front surface of the falces is dark bronzy rufus and on each outer edge is a wide band of snowy white hairs. In

¹ We have examined 49 species of ant-like spiders, but in no instance have we found a female with long falces, while we know of 19 males in which they are much lengthened. One might have expected to find that an occasional female had inherited the modification from the male, but it seems to be, in this group, strictly limited to one sex.

² *Ann. and Mag. of Nat. Hist.*, 1869, pp. 68—70.

the female the falces are vertical and only as long as the face, the fang being equally reduced, and the white hairs are absent. The male is rendered still more striking by the long, snowy white hairs which cover his clypeus, while the forehead and a space just below the first row of eyes is covered with bright red hairs. All this ornamentation is lacking in the female, and the contrast between the showy male and his modestly attired mate is very striking. In the little cosmopolitan zebra spider, *Epiblemum scenicum* we find the same difference in the size of the falces of the two sexes, the male having them four times as long as the face, while in the female they are only one-and-a-half times as long. Dr. Koch, in his magnificent work *Arachniden Australiens*, figures and describes an *Attus Opisthonus abnormis* (Fig. 5), with curiously formed falces. Their general color is

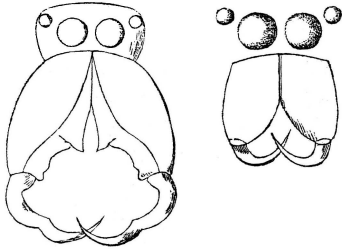


Fig. 5.—*Opisthonus abnormis* (from L. Koch.). Upper (left) figure, face and falces of male; lower figure (right), face and falces of female.

yellowish brown, but the front surface is coppery red, and toward the inner edges they are of a pretty, iridescent, bronzy green; but nature, less generous to the female, has given her only some white hairs over her small and unmodified yellowish brown falces. For purposes of offense or defense, however, the female fang is the more effective of the two, and our fine fellow doubtless hopes more from his beauty than his strength.²

In the sub-family *Tetragnathinae*, the falces are long in both sexes, but longer and much more ornamented with various processes and bunches of hair in the male than in the female.¹ (Figs. 6 and 7, see p. 29. The two figures fairly represent this greater development in the one sex than in the other.

Canestrini remarks on the sexual differences of the falces, saying: "Sometimes they are long and strong, with fine teeth,

¹ This point has also been noted by J. H. Emerton, *New England Epeirida*, p. 298. He says of the *Tetragnathinae*: "The mandibles, especially in the males, are very long, and toothed on the inner edge."

² This idiomatic expression most likely means that *the male is more 'concerned with' its appearance than with its strength (with respect to its large falces or chelicerae).*

in the male, while in the female they are short, weak and without teeth."¹ He also speaks of the entirely different colors of the male and female falces of the same species.² Not infrequently there are two forms among the males of a species, one with long and modified falces, and another having them short, and more like those of the female. In *Pensacola signata*, an Attus from Guatemala, we have two such forms. To quote a former paper of our own: "In the first, which is a little the larger, the falces are more than twice as long as the face, slightly retreating, narrow at the base and extremity, but dilated in the middle when looked at from in front. Near the anterior inner edge, in the middle, is a strong apophysis or spine in each falx which reaches nearly to the end of the fang; fang long and slightly bent. In the second form the falces are relatively shorter, and are but very little dilated in the middle so that the curve on the inner edge is not marked, and the spine is less than half as long as in the first form. We find others intermediate between these two extremes."³ Canestrini also refers to the existence of two male forms, and explains them by the supposition that we here see these secondary sexual characteristics, as it were, in process of development.⁴

Another curious modification is found in *Icius cornutus*,

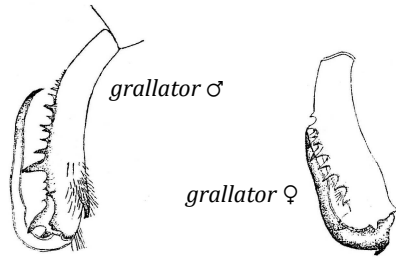


Fig. 6.—*Tetragnatha grallator* (from Emerton). Left-hand figure, falx of male; right-hand figure, falx of female.

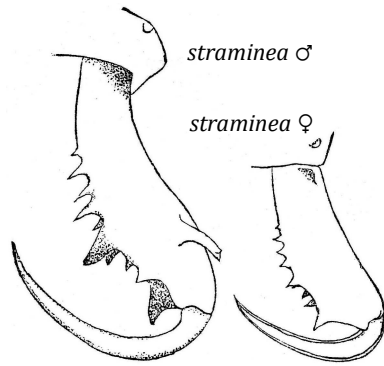


Fig. 7.—*Tetragnatha straminea* (from Emerton). Left-hand figure, falx of male; right-hand figure, falx of female.

¹ *Caratteri sessuali secondarii degli Arachnidi*, Atti della Soc. Vento—Trentina di Sc. Nat. Padova, 1, Fasc. 3, 1873.

² *Loc. cit.* This footnote was omitted in the text, and its placement above is just a guess.

³ *On Some New Genera and Species of Attidae*, G. W. and E. G. Peckham, Proc. Nat. Hist. Soc. of Wisconsin, 1887, p. 84.

⁴ The occurs in *Philaeus militaris*, *Icius palmarum*, and *Zygoballus bettini*. Canestrini mentions the genera *Linyphia*, *Theridium* and *Dysdera*.

from Madagascar, where there is long projection from the anterior face of each falx, the two processes extending forward and looking a little like a pair of horns; they are more than half as long as the cephalothorax.¹

The height of the clypeus² was formerly used in the classification of *Attidae*, but it has more recently been found to be so entirely a sexual peculiarity, as to be of little or no taxonomic value. It is frequently

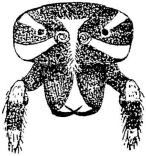


Fig. 8.—*Dendryphantes capitatus*. Male, face, falces and palpi (from nature).

adorned by colored hairs, which fall over the falces, or is diversified by curious patterns formed by bars and patches of down. The very striking appearance that a spider presents with this feature well developed is shown in *Titanattus saevus*, a male from Guatemala. In a common North American spider, *Dendryphantes capitatus*, (Fig. 8), the clypeus of the male is conspicuously marked by several white bands; one passes up between the anterior middle eyes from the

base of the falces; and two on each side pass back over the cephalothorax. The contrast between these snowy white bands and the dark color of the rest of the face is exceedingly striking. The female has the whole clypeus whitish and is not at all conspicuous. In two species of *Habrocestum*, *coronatum* and *caecatum*, the clypeus is covered with bright red hairs. In describing *H. coronatum*, Hentz says that "the bright scarlet spot on its front gives to this spider a whimsical air of fierceness, which is heightened by its attitudes and singular motions."³ In *Thorellia ensifer*, the male has two bunches of stout dark hairs projecting forward from just above the insertion of the falces, which are not present in the female.⁴ *Hyllus pterygodes*⁵ has the clypeus, or rather what might be called the cheeks, drawn

¹ *On Some New Genera and Species of Attidae from Madagascar*, G. W. and E. G. Peckham, Proc. Nat. Hist. Soc. of Wisconsin, p. 31.

² The *clypeus* is all of the face above the insertion of the falces and below the first row of eyes.

³ *North American Spiders*, p. 65.

⁴ Koch and Keyserling, *Arachniden Australiens*, p. 1353.

⁵ *Id ibid.*, p. 1339.

out and gradually coming to a point on each side, so that the face looks, from in front, very much swollen and enlarged. This surface, in both sexes, is covered with bright scales which are somewhat rosy in tint, and the points at the sides are furnished with some stout dark hairs.

In examining the upper part of the face, just above or below the first row of eyes, a number of interesting features may be observed. In one section of the subfamily *Lyssomanae* most of the species have, for the general color of the body, a tender grass green. In this group the clypeus and the region around the first row of eyes is nearly always adorned with a covering of red hairs, which are sometimes dull, sometimes very bright; this ornamentation is not usually confined to one sex, but in *L. amazonicus* the red is perceptibly brighter in the male, while though in *Asamonea puella* the eye-region of the female shows no red hairs, the male has the forehead covered in the middle by thick, silvery white, and old the sides by reddish hairs, his clypeus, also being unusually high.

The other section of this sub-family often presents dark colors, and here the clypeus and eye-region are more frequently marked with white pubescence or metallic scales than with red hairs; thus in *A. tenuipes* the dark clypeus of the male is covered with highly iridescent scales, and that of the female is light yellow, covered with thick, snowy white hairs.

The bright markings in some of these species have evidently been transmitted to the females through the males. Looking at the group as a whole, it is important to note how frequently the adornment is so placed upon the body as to be brought into view when the spiders face each other.

In *Amycus micans*, (Fig. 9), of which only male is known, the face is very high, and all its parts are covered with glittering violet, green and golden scales; above the first row of eyes is a transverse band of scale-like hairs, some few longer hairs growing out between; this band is shining, colored

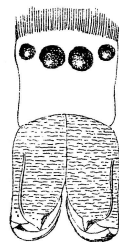


Fig. 9.—*Amycus micans*.
Male, face and palces
(from L. Koch).

like the rest of the face.¹ *Amycus tristriatus* has a high face, the hairs around the eyes being white in the lower half and yellowish red above.²

In the nine species of the genus *Amycus* described by the two Kochs, we have only males; in the South American spiders of this genus described by Simon anti Taczanowski,³ we have both sexes in four

species, and in three of these the clypeus of the female is low; in the fourth it is said to be "rather high." The great height of the clypeus in *Amycus* is, in fact a sexual peculiarity although in some instances it may have been transmitted to the female.

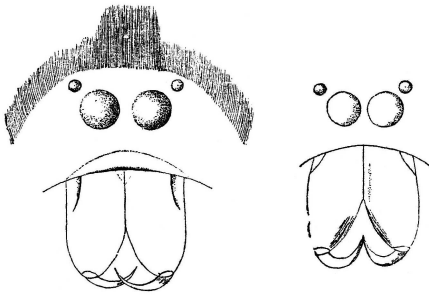


Fig. 10.—*Mopsus mormon* (from L. Koch). Upper (left) figure falces of male, showing ridge of hairs; lower (right) figure, face and falces of female.

By far the most remarkable instance of facial adornment is to be found in *Mopsus mormon*⁴ (Fig. 10.). The face of the male is dark brown,

covered with steel-blue scales; around the eyes are both brown and yellowish red hairs; the front of the long falces is also dark brown, covered with bright metallic scales; and to add to his beauty there is a high vertical ridge of variously tinted hairs extending over his forehead. The part above the middle eyes is brown, but on either side it changes to pure white, gradually becoming yellowish as it passes back on to the sides. In the female, while the general coloration is the same, the most striking ornament—the band of hairs—is entirely absent. In this species we are reminded of the wonderful crests found in humming-birds and fruit pigeons. In *Dendryphantes elegans* the male alone has two oblique converging ridges of short hairs extending from the eyes of the second row to the anterior middle eyes; and in

¹ Koch and Keyserling, *loc. cit.*, p. 1173.

² *Id ibid.*, p. 1181.

³ *A. rufifrons*, Simon: *A. fusco manus*, *A. mystacalus*, *A. scops*, Taczanowski.

⁴ *Arachnidens Australiens*, p. 1319, described as *Ascyllus penicillatus*.

the black male form of *Astia vittata* there are three long tufts of black hairs on the eye-region, which are absent not only in the female but also in the other male form (Plate II).

Leaving the *Attidae*, there are several genera described by Menge, Cambridge, Simon, Thorell, Emerton and others that illustrate curious sexual modifications of the upper part of the face. For example, in the genus *Argyrodes*, (Fig. 11), of Simon, while the head of the female is often high and somewhat notched in front, in that of the male each of these divisions of the front part of the head gives rise to a horn, covered at the extremities with hairs. The drawing shows the parts in the two sexes. Emerton in *New England Therididae*, when speaking of the genus *Ceratinella* says: "The heads of the males are usually higher than those of the females, and in some species are very large and raised into humps;" and of the genus *Cornicularia* he says that "the males have a hump or horn on the front of the head between the eyes, usually ornamented by flat, stiff hairs. In several species there are two horns, the lower one being small and partly concealed by the upper." There are many other genera in this family, with large numbers of species distributed over different parts of the world. Most of these species are small, but close inspection shows a great deal of sexual difference in the head parts and often also in the falces.

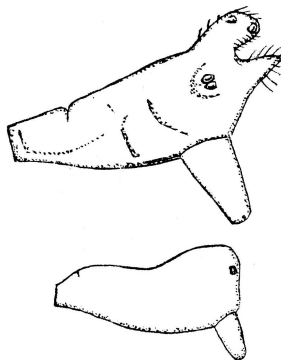


Fig. 11.—*Argyrodes argyrodes* (from Simon). Upper figure, cephalothorax of male; lower figure, cephalothorax of female.

In male spiders the palpi are modified and serve as organs for the conveyance of the sperm cells to the epigynum of the female. Beside this direct use in the reproductive act they often play an important part as ornamental appendages. The female palpi, are, speaking generally, cylindrical, five-jointed outgrowths of the maxillae, covered with hairs and varying somewhat in length and color; but throughout the order there

is but little difference among the various species. Passing over the many and great differences of structure in the last or tarsal joint of the male palpus, which are primary sexual characters, we find, in this organ, many curious modifications of form and of ornamentation the only use of which is to please the female.¹

In some species they are greatly elongated (*Lagnus longimanus*); in others there are curious enlargements and apophyses on one or more of the joints (*Plexippus puerperus*); but the most frequent and by far the most striking form of decoration is a covering of long white or yellowish hairs which gives them a plume-like appearance (*Pensacola signata*).

In many spiders the sexes differ not only in the beautiful plumose palpi of the male, but also in the locomotive organs. The legs of the first pair are lengthened, in many males, and the several joints are enlarged and brilliantly colored, or furnished with long hairs or iridescent scale-like setae. In no family of spiders does sexual selection seem to have been more effective than in the *Attidae*. Many of the species, as we have seen, are furnished with remarkable falces, elaborate head ornaments and plume-like palpi, and we have now to give an account of a further modification which has apparently been gained for the sake of ornament, or possibly through the sham battles between the males.

In an ant-like species, *Synageles picata*, the female has legs of the ordinary forms but in the male the tibia of the first leg is enlarged and flattened, and the anterior face of the enlargement is of a brilliant, steel-blue metallic color, as glossy as the breast of certain pigeons. In *Philaeus metallescens*, from Australia, the legs of the first pair in the male are 11 mm. long, while those of the female are only 9 mm.; those of the male are of a very brilliant steel-blue color, and are ornamented with rings, spots and fringes of short, scale-like hairs, and of

¹ Koch and Keyserling in *Arachniden Australiens* describe in the family *Attidae* thirty-four males having well developed fringes or tufts of hair on the palpi, while there are only five females so ornamented, and several of these to only a moderate extent.

long, white hairs; those of the female are but slightly iridescent, and lack all further ornament. In *Dendryphantes elegans* the first leg in the male has on the lower half of the tibia a wide fringe of hair, which is very conspicuous as he waves his legs while courting; while the legs of the female are plain. These leg modifications have been frequently transmitted to the female, so that not uncommonly we find both sexes presenting striking forms, which are, however, proportionately less remarkable in the females than in the males. For example, in *Diolenius phrynoides*, where the first legs are wonderfully lengthened and modified, those of the female measure $12\frac{1}{4}$ mm., and those of the male $20\frac{1}{2}$ mm., being nearly twice as long. The curious change in the legs of this species so impressed Walckenaer as to make him suggest that the spider must walk on the water, since in no other way could such legs be useful. As it is a land species his explanation must be abandoned, and we are constrained to look upon these legs as secondary sexual organs, useless for locomotion, but of high importance while mating. To gain a clearer idea of this lengthening of the first legs one has only to imagine that in some group of human beings the arms of the men were doubled in length, while in the women they remained as before. There are numerous species in this genus, all characterized by their long legs (Fig. 12.). It is not unusual for female as well as male beetles to possess well developed horns and knobs, so that there is nothing anomalous in the elongated legs of both sexes of the *Diolenii*. In *Chirothecia*, a South American genus of *Attidae*, we meet with other instances of modified legs, but here there is a marked

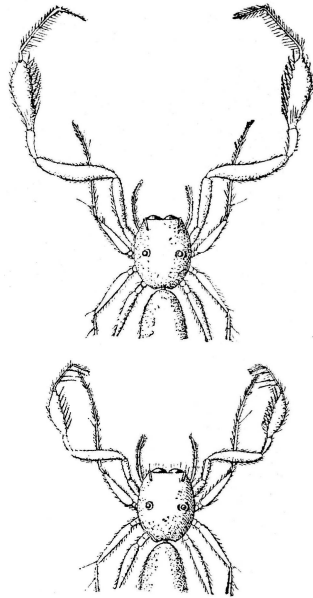


Fig. 12.—*Diolenius venustus* (from nature). Upper figure, male; lower figure, female.

difference between the sexes, the males having the legs longer, more robust, and more ornamented than the females. This is also true in the North American species *Icius palmarum*. *Saitis barbipes* has the third leg of the male fringed with hairs on either side which gives it quite a plume-like appearance, while that of the female is entirely plain. In an undescribed species of *Habrocestum* from Arizona the first leg of the female is plain, while that of the male has on the tibia a fringe of long, silky, yellow hairs, mingled with which are other hairs, which are enlarged and flattened at the end. These spatulate hairs also appear on the first legs of *Habrocestum hirsutum*; in this species we have only the male.

Walckenaer remarks that his earlier division of *Attidae* into *Sauteuses*, or short-legged, and *Voltigeuses*, or long-legged, is vicious,² since in many species of *Sauteuses* the males have very long legs, and are, therefore, if we have not seen the female, placed in the *Voltigeuses*, while the females must be put into the *Sauteuses*.¹ We may go further than this, and say that all these modifications of the legs are sexual and of little or no importance in taxonomy.

The instances which we have given of secondary sexual differences might have been indefinitely multiplied, but we have only thought it necessary to give examples of each kind or class of modification; these will serve, we trust, to establish the fact that these differences are not less numerous among spiders than among birds and insects.

MATING HABITS.

For a number of years prior to 1888, we had been much impressed by the many important differences between the sexes of our jumping-spiders, and since we thought it most probable that they had come about through sexual selection, we had often tried to watch them during their courtship, but up to that time with very little success. We had occasional glimpses of their habits, but they were so incomplete as to con-

¹ *Loc. cit.*, p. 482.

² Here *vicious* probably means *unacceptable*.

tribute but little to a thorough knowledge of the subject. Last year, we determined that, if possible, we would work out this subject so far as concerned the species in our locality. For this purpose we had made a number of mating-boxes. The larger ones were 15 inches long by $11\frac{1}{2}$ wide and 3 deep; the smaller, $7\frac{1}{4}$ long by $5\frac{3}{4}$ wide and $2\frac{1}{2}$ deep. The sides of each box were marked off into inches so that the distance of the spiders from each other could be easily noted. The floor was made of coarse cotton cloth, for the purpose of ventilation, while the top was of glass, so that the inmates of the cage could be kept fully in view at all times; this top could be opened and closed. As a usual thing we move into the country toward the last of June but this year we went out on the 22d of May, in order to be in time for those species that mature early.

The courtship of spiders is a very tedious affair, going on hour after hour. We shall condense our descriptions as much as possible, but it must be noted that we often worked four or five hours a day for a week in getting a fair idea of the habits of a single species.

SAITIS PULEX.

On reaching the country we found that the males of *Saitis pulex* were mature and were waiting for the females, as is the way with both spiders and insects. In this species there is but little difference between the sexes. On May 24th we found a mature female and placed her in one of the larger boxes, and the next day we put a male in with her. He saw her as she stood perfectly still, twelve inches away; the glance seemed to excite him and he at once moved toward her; when some four inches from her he stood still and then began the most remarkable performances that an **armorous** male could offer to an admiring female. She eyed him eagerly, changing her position from time to time so that he might be always in view. He, raising his whole body on one side by straightening out the legs, and lowering it on the other by folding the first two pairs of legs up and under, leaned so far over as to be in danger of losing his balance, which he only maintained by sidling

rapidly toward the lowered side. The palpus, too, on this side was turned back to correspond to the direction of the legs nearest it. (Fig. 13.) He moved in a semi-circle for about two inches and then instantly reversed the position of the legs and circled in the opposite direction, gradually approaching nearer and nearer to the female. Now she dashes toward him, while he, raising his first pair of legs, extends them upward and forward as if to hold her off, but withal

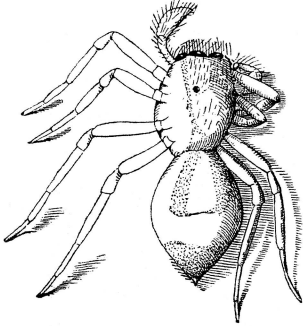


Fig. 13.—*Saitis pulex*. Male dancing before female (from nature, by Mr. Ludwig Kumlien).

slowly retreats. Again and again he circles from side to side, she gazing toward him in a softer mood, evidently admiring the grace of his antics. This is repeated until we have counted 111 circles made by the ardent little male. Now he approaches nearer and nearer and when almost within reach whirls madly around and around her, she joining and whirling with him in a giddy maze. Again he falls back and resumes his semi-circular motions, with his body tilted over; she, all excitement, lowers her head and raises her body so that it is almost vertical;

both draw nearer; she moves slowly under him, he crawling over her head, and the mating is accomplished.

After they have paired once, the preliminary courtship is not so long. When this same pair mated a second time, there were no whirling movements, nor did the female lift her body, as at first. We watched this species a great deal during the three weeks that the mating lasted. Once we saw a female approach a very glum-looking male, waving her palpi and making herself agreeable, but in vain. He was pushed a little from without, so as to make him look toward her, when she turned about, holding her abdomen high and her head low. Finally he grew excited enough to dance a little, and then they whirled round and round together in the usual manner; but she appeared the more eager of the two. This was true, however,

of only this one female. All the others were more retiring, and were never more than half willing to be wooed.

The males, while very excitable in the presence of the female, do not seem to be especially quarrelsome. When excited, they pursue and leap upon each other, but do not exactly fight. During the display of the male before the female, she is no inattentive observer, but watches him intently, turning frequently to keep him in view as he dances from side to side, and, finally, if she approves of him, yields to his desires. Often, however, the male fails to make an impression upon her, even after dancing before her for a long time, since upon his too near approach, she runs away.

EPIBLEMUM SCENICUM.

On the afternoon of the 10th of June we found two males of this species fighting on a brick wall. They held up the first pair of legs and moved rapidly in front of each other, now advancing and now retreating, in a half circle, distant from each other about four and a half inches. There was little real earnestness in the affair, and it reminded one of the bluster of two boys, each threatening the other and daring the other to strike, but neither willing to be the aggressor. In a few minutes they both wandered away. During the next two days we found eighteen males and four females on this wall, which was about 20x12 feet in size. The performances of the male are not so complicated and interesting in this as in the preceding species, nor do the males seem to be so persistent.

We placed twelve spiders, of both sexes, in one of the boxes. Soon they were all moving about, the males making advances to the females, who seemed to endeavor to escape. After about two hours we found that three pairs had come to an agreement and mated, the male, in each case, getting his female into a corner of the box and spinning a cover over and around her. Sometimes, while the male was working, the female would wander off several inches, but when the house was nearly completed, he would follow her, and half lead and half drive her home, when he would get her into the nest first,

and then follow himself. Here the mating would be accomplished, after some slight preliminaries. The females seemed to have some difficulty in choosing from among the males, but, after a decision had been reached and a male accepted, there appeared to be complete agreement, and the male, thereafter, commenced to build his house. On the next morning we found all the pairs together in different tents.

The male, when prancing before the female, stood quite high on the three posterior pairs of legs; the first pair, the palpi, and the long falces, were stretched out stiffly in an oblique direction, the spider moving rapidly from side to side.

ICIUS SP.

This species, still undescribed, we discovered last summer, in large numbers, on rail fences at the edge of woods. We had worked over the place time and again, for many years past, but had overlooked them, not only on account of their admirable protective coloring, but from the fact that they only congregate, in this way, until they have mated, and afterward wander back into the woods and are then rarely met with. This is a habit with several *Attidae*¹ and reminds one of the "*sácaleli*" or dancing-parties of certain birds, or of our own partridge dances. We were fortunate in discovering them just at the mating season. A dozen or more males and about half as many females were assembled together within the length of one of the rails. The males were rushing hither and thither, dancing opposite now one female and now another; often two males met each other, when a short passage of arms followed. They waved their first legs, sidled back and forth, and then rushed together and clinched, but quickly separated, neither being hurt, only to run off in search of other and fairer foes. We watched them for hours, and then, our patience being exhausted, filled all our bottles and carried them home. We placed them in the smaller boxes, since we have learned that propinquity² is quite as effective in hastening the courtship of

¹ In the Genus *Dendryphantes*, *capitatus* and *elegans* are examples. Going to their favorite bushes we have caught 40—50 males in a few hours' sweeping, but after the season the same locality would not yield more than 2—3.

² *Proximity or nearness, based on Latin propinquitas.*

these little creatures as it is said to be among the higher races. For several days, in visiting this fence, we found goodly numbers on each rail, but after a little they grew scarcer and scarcer and at last we were unable to find one where a short time before they had been so common.

It was much more comfortable to study them after they had been put into the mating boxes and within the next few days we had seen many of them pair. The males were very quarrelsome and had frequent fights, but we never found that they were injured. Indeed, after having watched hundreds of seemingly terrible battles between the males of this and other species, the conclusion has been forced upon us that they are all sham affairs¹ gotten up for the purpose of displaying before the females, who commonly stand by, interested spectators. This is entirely contrary to what we had expected, and early in the season we, on several occasions, forcibly parted the combatants, fearing that they would kill each other. The falces in many of the males are, it is true, much lengthened, but as weapons of offense the shorter fangs of the female are much more deadly. In twelve species, in which we witnessed numberless fights, we could never discover that one of the valiant males was wounded in the slightest degree.

In this new species the position of the female while watching the male is unlike that of any of the others. She lies close to the ground with her first legs directed upward and forward, while her second legs are held on the ground and stretched forward in front of her face (Fig. 14). The male,

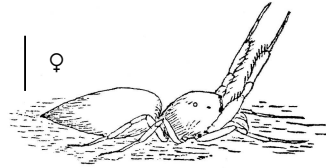


Fig. 14.—Undescribed species. Position of female when **approched** by male (from nature by L. K.).

when approaching her, does not throw his legs high over his head, as he does before another male, but raises his body on his six hind legs;

¹ Cuvier remarks that "the males sometimes engage in contests in which their manoeuvres are very singular; but which do not terminate fatally." *Animal Kingdom*, trans. by Carpenter and Westwood, London, 1863. p. 464.

Hentz (*N. A. Spiders*, p. 133) saw two males of *Linyphia communis* fighting an

the first legs are held down toward the ground, diverging slightly near the head, and are bent inward at the middle so that the tips turn toward each other and meet. (Fig. 15.) At times he turns the apex of his abdomen down; at other times he keeps it straight, as he moves from side to side; the palpi are folded under. He sometimes varies his attitude by lying flat on his venter, keeping the tips of the legs touching as before.

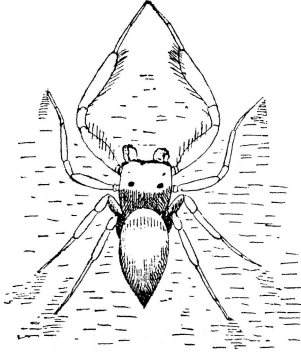


Fig. 15.—Undescribed species. Position of male approaching female (from nature by L. K.).

HASARIUS HOYI.

The sexes are very different, so much so that we at first described them as two species, the male being the more conspicuous of the two. The males are ready in the early days of June, and the females a little later. In his dance the male has several movements; most commonly he goes rapidly from side to side with his first legs obliquely up; (Fig. 16); at other times he twists the abdomen to one side and bending low on the other, something as *pulex* did, goes first in one direction for about two inches, and then, reversing, circles to the opposite point. The females are very savage, especially with each other; and even the members of the sterner sex are not always free from danger when paying their preparatory addresses. Once we saw a female eagerly watching a

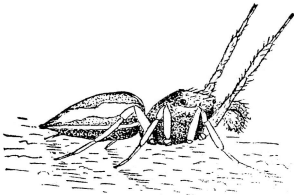


Fig. 16.—*Hasarius hoyi*. Position of male approaching female (from nature by L. K.).

prancing male and as he slowly approached her she raised her legs as if to strike him, but he, nothing daunted by her unkindly

obstinate battle; he did not watch it to the close, but believes that it was "without bloodshed."

Vinson, on the contrary, mentions a fatal combat between two males of *Epeira niger* that he had shut up in a bottle with a female. *Araneides de La Reunion, Maurices et Madagascar*, p. 190. We have a cousin of this species, *Argiope cophinaria*, and though we have seen the two or three little males that were courting a female manoeuvre together the results were never serious.

reception of his attentions, advanced even nearer, when she seized him and seemed to hold him by the head for a minute—he struggling. At last he freed himself and ran away. This same male, after a time courted her successfully.

SYNAGELES PICATA.

These are small ant-like spiders. The most important sexual difference, is the greater thickness of the first legs of the male. These are flattened on the anterior surface and are of a brightly iridescent steel-blue color. Unlike most of the *Attid* males this species keeps all his feet on the ground during his courtship: raising himself on the tips of the posterior six he slightly inclines his head downward by bending his front legs, their convex surface being always turned forward. His abdomen is lifted vertically so that it is at a right angle to the plane of the cephalothorax. In this position he sways from side to side. After a moment he drops the abdomen, runs a few steps nearer the female, and then tips his body and begins to sway again. Now he runs in one direction, now in another, pausing every few moments to rock from side to side and to bend his brilliant legs so that she may look full at them. We were much impressed by the fact that the attitudes taken by the males served perfectly to show off their fine points to the female. We had never known the male of this species until the day that we caught this one and put him into the mating-box, and it was while studying his courtship that we noticed how he differed from the female in his iridescent first legs. He could not have chosen a better position than the one he took to make a display. We had six females in the box, and saw him mate with all of them; and each, after a time, made a cocoon containing three large eggs.

MARPTUSA FAMILIARIS.

This is a rather plainly marked *Attus*, well protected by its coloring of gray and black, on the bark of trees and on fences, where it is most frequently found. There is little difference between the sexes. We placed the two together. She saw him

as he entered at the opposite side of the box, some thirteen inches away. Eyeing him attentively, she slowly changed her position to keep him in sight, and kept her palpi moving rapidly, a characteristic action with the species. As he neared her, he stretched the first and second pairs of legs sideways, but, after a moment, backed away. (Fig. 17.) These manoeuvres were repeated many times. Occasionally he would bend the tip of the abdomen down, lifting the

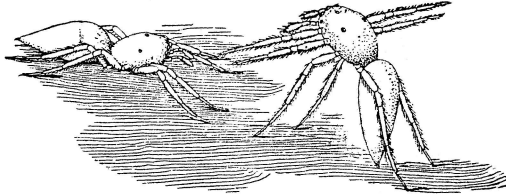


Fig. 17.—*Marptusa familiaris*. Positions in courtship: left-hand figure female, right-hand figure male (from nature by L. K.).

body up on the last joints of the two hindermost legs. The female always paid the greatest attention to his movements, lying on the ground, with all the legs flattened out and the palpi slightly raised, the only movement

visible being the vibration of the palpi. There is a certain slowness and dignity about the wooing of this species that is almost ludicrous.

PHIDIPPUS RUFUS.

The sexes are alike in general coloring, but the male has much the brighter tint. In the early days of July we found them mature and brought them together. The female standing still, the male, while some five inches away, stood high on the six back legs, turned the first pair forward and upward and crossed them at the tips; the palpi were held widely apart, parallel with the second legs. The effect of this position was to bring directly before her, as she stood watching him, the beautiful white hairs on the lower part of the palpi.¹ At the same time the abdomen dropped so that it touched the ground. In this way he advanced, with a swaying motion. The female ran away, but after a time he renewed his attentions. The

¹ These white hairs, in contrast with the bright iridescent green falces, are very striking; the female, although her falces are green, is without the white hairs.

female *rufus* is a ferocious creature, having a great advantage in size, and so it happened that our assiduous male, in an unguarded moment, was pounced upon and eaten up.

PHIDIPPUS MORSITANS.

On this species we leave but few notes. The single female that we caught during the summer was a savage monster. The two males that we provided for her had offered her only the merest civilities, when she leaped upon them and killed them. The sexes are quite alike in color and marking, but while the female has the fourth leg longest, the male has the first pair not only much the longer, but thickly adorned with white hairs, some of which are long and others short and scale-like. It was while one of the males was waving these handsome legs over his head that he was seized by his mate and devoured. The tibia of the palpus is also covered with white hairs, which make a strong contrast with the general black color, and this is held out in such a way as to make a display as he approaches the female.

DENDRYPHANTES CAPITATUS.

The sexes are entirely different. In the male the bronze brown face is made very conspicuous by some snowy white bands, as is shown in the drawing (Figs. 8, 19).¹ These are wanting in the female, her face being rufus with some few scattering white hairs. The males of *capitatus* are very quarrelsome, sparring whenever they meet, chasing each other about, and sometimes clinching. It is a very abundant spider with us, so that we often put eight or ten males into a box to see them fight. It seemed cruel sport at first, but it was soon apparent that they were very prudent little fellows, and were fully conscious that "he who fights and runs away will live to fight another day." In fact, after two weeks of hard fighting we were unable to discover one wounded warrior. When the males are approaching each other, they hold the first legs up in a vertical direction. Sometimes they drop the body on to one side as they jump about each other. These movements are very quick, and they

¹The same drawing was presented in both of these figures.

are always ready for a passage at arms. When courting the females they have another movement. They approach her rapidly until within two to five inches, when they stop and extend the first legs



Fig. 18.—*Dendryphantes capitatus*. Position of male approaching female (from nature, by L. K.).

directly forward, close to the ground, the legs being slightly curved with the tips turned up. (Fig. 18.) Whether it be intentional or not, this position serves admirably to expose the whole of the bronze and white face to the attentive female, who watches him

closely from a little distance. (Fig. 19.) The males also give their palpi a circular movement, much as a person does when washing his hands. As he grows more excited, he lies down on one side with this legs still extended. These antics are repeated for a very long time, often for hours, when at last the female, either won by his beauty or worn out by his persistence, accepts his addresses.

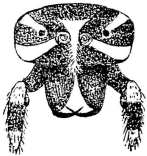


Fig. 19.—*Dendryphantes capitatus*. Face and palpi of male (from nature, by L. K.).

DENDRYPHANTES ELEGANS.

The male of the species, like many other animals, has received a number of names. Hentz called the female *elegans* and the male *superciliosus*. C. Koch called him *cristata*, and we ourselves, *tibialis*, on account of the fringe of hairs on the tibia of his first leg. Both sexes are beautiful. The male is covered with iridescent scales, his general color being green; in the female the coloring is dark but iridescent, and in certain lights has lovely rosy tints. In the sunlight both shine with the metallic splendor of humming-birds. The male alone has a superciliary fringe of hairs on either side of the head, his first legs being also longer and more adorned than those of his mate. The female is much larger, and her loveliness is accompanied by an extreme irritability of temper which the male seems to regard as a constant menace to his safety, but his eagerness being great, and his manners devoted and tender,

he gradually overcomes her opposition. Her change of mood is only brought about after much patient courting on his part. While from three to five inches distant from her he begins to wave his plummy first legs in a way that reminds one of a wind-mill. She eyes him fiercely and he keeps at a proper distance for a long time. If he comes close she dashes at him and he quickly retreats. Sometimes he becomes bolder and when within an inch, pauses, with the first legs outstretched before him, not raised as is common in other species; the palpi also are held stiffly out in front with the points together. Again she drives him off, and so the play continues. Now the male grows excited as he approaches her, and while still several inches away whirls completely around and around; pausing, he runs closer and begins to make his abdomen quiver as he stands on tip-toe in front of her. Prancing from side to side, he grows bolder and bolder, while she seems less fierce, and yielding to the excitement lifts up her magnificently iridescent abdomen, holding it at one time vertically and at another sideways to him. She no longer rushes at him, but retreats a little as he approaches. At last he comes close to her, lying flat, with his first legs stretched out and quivering. With the tips of his front legs he gently pats her; this seems to arouse the old demon of resistance, and she drives him back. Again and again he pats her with a caressing movement, gradually creeping nearer and nearer, which she now permits without resistance until he crawls over her head to her abdomen, far enough to reach the epigynum with his palpus.

ZYGOBALLUS BETTINI.

The sexual differences in this species are well marked. The male has much more silvery white on the face; the first

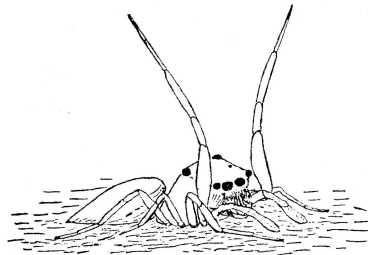


Fig. 20.—*Zygoballus bettini*. Position of male approaching female (from nature, by L. K.).

legs and falces are much longer, and on the side of the abdomen the general color is darker and the lateral bars of a much more glistening

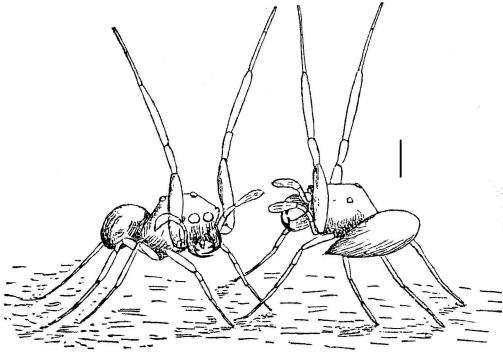


Fig. 21.—*Zygoballus bettini*. Position of males when fighting (from nature, by L. K.).

white. All the colors are far more brilliant in the male than in the female. (Plate II.) In courting the male lies flat near the female, wriggling his abdomen and frequently turning from side to side. His first legs are held up over his head, slightly diverging, and are often twisted and turned about. (Fig. 20, see p. 47.)

Two males that were displaying before one female, rushed savagely upon each other and fought for twenty-two minutes, during one round remaining clinched for six minutes. When fighting, the abdomen is held nearly at a right angle with the cephalothorax (Fig. 21.) The combatants appeared tired at the close of the battle, but after a short rest were perfectly well and fought a number of times subsequently. There are two forms of male in this species, one being twice as large as the other.

HABROCESTUM SPLENDENS.

The colored plate (Plate I) gives a good idea of the sexual difference in this species. The male, a magnificent fellow, when we first caught him, displayed for a long time before the female. He began by advancing a few inches toward her and then backing off again, this being repeated many times. After a while he settled down under a little web in the corner. The female, troubled by this indifferent treatment, advanced toward him; he came out and she fell back. This play was kept up for some time, but at length the male began his courting in earn-

est. When within a few inches of her he began a rapid dance from side to side, raising the whole body high on the tips of the legs, the first pair being directed forward and the palpi clasped together, with the abdomen turned to one side and lifted up. After a short dance he stood motionless, striking an attitude, as shown in the figure, remaining quiet for half a minute. (Fig. 22.)

Then he turned his back on her, moving irregularly about with his legs forward and his palpi vibrating. Again he dances sideways before her, strutting and

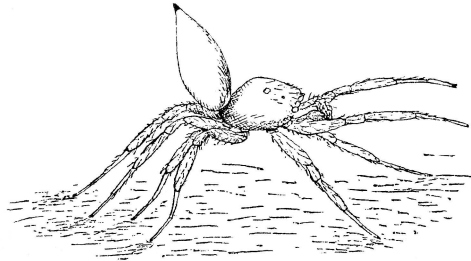


Fig. 22.—*Habrocestum splendens*. Position of male approaching female (from nature, by L. K.).

showing off like a peacock, or whirling around and around. When he turned his back we often thought that the female seemed disappointed, since she would then commonly move nearer to him and appear much excited herself. We at first supposed that this turning around was accidental, but it happened so regularly at a certain stage of the courtship that we concluded it was an important part of his display, serving to better show off his brilliant abdomen. Our artist, Mr. Kumlien, while watching the antics in order to draw the spider, called our attention to this habit, not knowing that we had observed it. The fact that among spiders the males take such attitudes as display their best points recalls this passage in one of Darwin's letters: "I am very glad to hear of your cases of the two sets of *Hesperidae*, which display their wings differently, according to which surface is colored. I cannot believe that such display is accidental or purposeless."

ICIUS MITRATUS.

The male is quite different from the female, especially in his slender, tapering body and in his long first legs. While in *splendens* the female was remarkable for the attention that she

gave the male, seeming at times to coquet with him, in this species she was remarkable for her indifference. She takes less interest in the display of the male than any spider that has come under our observation. Another peculiarity of *mitratus* is the large amount of time and strength given up by the males to fighting. They do not seem so fierce as other species, but they cannot endure each other's proximity. A male will leave a female in the midst of his caresses to

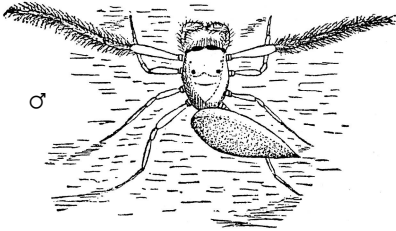


Fig. 23.—*Icius mitratus*. Male dancing before female (from nature, by L. K.).

drive off another male that comes too near. We once saw a male jump on to the back of another that was pairing with a female. The latter turned on the intruder and drove him to a distance of five or six inches, and then returned and renewed his addresses. In courting and in fighting the position of the male is the same. The body is

somewhat raised; the first legs are held at a right angle to the cephalothorax, and the abdomen is twisted to one side, and, as he dances before the female, is changed now to the right, now to the left. (Fig. 23.) In mating, the male does not usually crawl over her, but jumps upon her from a distance of one or two inches, in this respect agreeing with the following species, *militaris*. Whether or not this habit in the two species is due to the savageness of the female—the females of both species sometimes attack the males—we are unable to say.

PHILAEUS MILITARIS.

This is the only species in which we saw males take possession of young females and keep guard over them until they became mature. There is a good deal of difference in the size of the males, some being larger and some smaller than the females. We commenced our experiments by putting half a dozen mature males into a box. They at once began to chase each other about and to threaten each other with upraised legs.

The addition to the company of a number of nearly mature females considerably increased this tendency to quarrelsomeness, the males thereafter spending all the time that they spared from courtship in fighting. In approaching the female they seemed very eager, and fairly quivered with excitement. The first two legs were raised over the head and curved toward each other, so that the tips nearly met and the palpi were moved up and down. (Fig. 24.) One of them was much larger than any of the others, and from the first showed plainly that he had a strong sense of his own superiority. He drove all the others about at his pleasure, constantly interrupting their attempts at courtship. This big fellow seemed to be especially attractive to the females, of which there were always two or three standing in an admiring circle around him. When he approached them, however, they slipped away. After a time, he singled out the largest of the females, half coaxed and half drove her into a corner, and there kept her secluded, chasing away every spider that approached, irrespective of sex. He once interrupted a courtship which was going on six inches away, driving the male to a distance and then pursuing the female for a long time. This seclusion of the female was kept up until evening of the next day—a period of twenty-four hours—but on the following morning the pair had separated and he was hidden among some leaves. None of the females were yet mature. We now put into the box another male, which was nearly as large as the first. This second one adopted the same bullying manner to the smaller members of his sex that the first had done. After driving them about for a time, he secured a gnat, and was peacefully devouring it, when number one emerged from the leaves, caught sight of the new-comer, and at once approached, bristling with pride and ire, his first legs raised high, as if to strike, his palpi vibrating with excitement, and

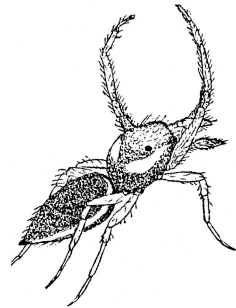


Fig. 24.—*Philaeus militaris*.
Position of male approaching
female (from nature, by L. K.).

his abdomen dragging first on one side and then on the other. Number two was evidently of good courage, for he held his ground, and, not relinquishing the gnat, raised his legs and clinched with his antagonist. The battle raged for five minutes; finally number one pulled the gnat from the other, and then chased him away.

For several days following, life in the mating box was robbed of its monotony by perpetual battles among the males. The females, in eluding them, jumped and hung from a thread. At one time a small one guarded a female for some hours in a corner; she once slipped away and ran a few inches, but when another male began to pay court to her she ran back and crept under the body of her protector. After two or three days each of the two large males took possession of a female, spun a web over her, and spinning a second sheet above as a cover for himself, remained quiet in the little nest thus formed for a week. During this time every spider that approached was driven away. They went out occasionally for food, but were not seen to carry any to their mates.

At the end of a week number one was observed to be pairing with his female, which had moulted and was now mature. The two were separated, when the male went hunting about and finally sprang upon an unmated female, three inches away from the other nest, whereupon number two ran out, attacked him violently, drove him away, and then returned to his nest. Number one, while wandering about, caught sight of his own mate and sprung upon her without any of the preliminary attention before noticed. From this time forward, the big, wandering male, his occupation gone, became a very thorn in the flesh to the other, whose female had not yet matured. Not only did he continually approach the nest, thus arousing a jealous fury in its owner, which was not called out by any of the other spiders, but whenever the rightful owner was away from home, chasing intruders or procuring food, this disturber of domestic peace made his way into the nest. The first time this happened, the owner, returning, ejected him

without ceremony; the second time they had a prolonged struggle, clinching, and falling, thus locked together, a distance of about twelve inches—the height of the box (Fig. 25); the third time number one was not discovered until he had cut the still immature female out of the web which enclosed her. She ran away, and after that the two males wandered about, fighting whenever they met. The defrauded male, as well as the other one, now courted every female in the box, although so long as they had their own mates they had paid no attention to other females, except to drive them away.

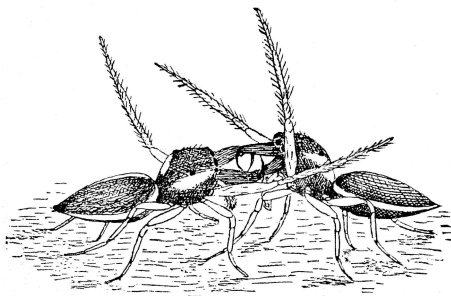


Fig. 25.—*Philaeus militaris*. Position of males when fighting (from nature, by L. K.).

The following extract from our notes shows that the guarding of young females is a habit of males in this species, and was not the result of artificial conditions:

"Aug. 17. Found a mature male *militaris* standing guard, in a tent, over an immature female (one moult from maturity). They seemed very friendly when taken out and put into a bottle. The webs and positions were as we had seen them in our mating-boxes."

ASTIA VITTATA.

There is a good deal of interest connected with the study of this species, for the reason that there are two well marked male forms; moreover their love antics are unusually curious. A description of the two males is unnecessary, since they are well represented on Plate II. The two forms grade into each other, excepting that the three hair tufts are only found in the fully developed *niger* form. The *vittata* form, which is quite like the female, when he approaches her, raises his first legs either so that they point forward or upward, keeping his palpi stiffly outstretched, while the tip of his abdomen is bent to the

ground. This position he commonly takes when three or four inches away. While he retains this attitude he keeps curving and waving his legs in a very curious manner. Frequently he raises only one of the legs of the first pair, running all the time from side to side. As he draws nearer to the female he lowers his body to the ground, and, dropping his legs also, places the two anterior pairs so that the tips

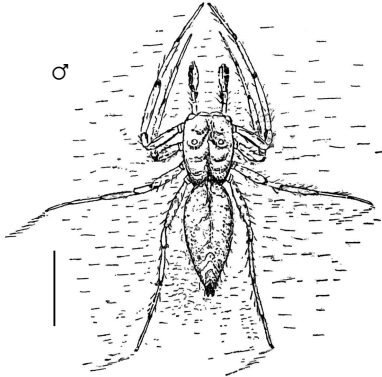


Fig. 26.—*Astia vittata*. Position of male approaching female (from nature, by L. K.).

touch in front, the proximal joints being turned almost at a right angle to the body. (Fig. 26.) Now he glides in a semi-circle before the female, sometimes advancing, sometimes receding, until at last she accepts his addresses. The *niger* form, evidently a later development, is much the more lively of the two, and whenever the two varieties were seen to compete for a female, the black one was successful. He is bolder in his manners, and we have never seen him assume the prone

position, as the red form did, when close to the female. He always held one or both of the first legs high in the air, waving them wildly to and fro, or, when the female became excited, he stood perfectly motionless before her, sometimes for a whole minute, seeming to fascinate her by the power of his glance. (Fig. 27, see p. 55.) A female that was full of eggs was looked at critically from a distance of four or five inches by several ardent males, but received no further attention. Although the males were continually waving their first legs at each other, their quarrels were harmless. It was quite otherwise with the females, since they not only kept the other sex in awe of them, but not infrequently, in their battles, killed each other. We thought it rather remarkable that the *niger* variety should not have the same antics as the *vittata*; but since closely related species often differ greatly in color, form

and habits, we should not be surprised at finding like differences between distinct varieties.

The very meager knowledge that we have of the mating habits of the *Epeiridae* has been gained at the expense of numerous hours of watching. The courtship of *Attidae* is often very tedious, but it does not compare in this respect with that of the *Epeiridae*, perhaps because the members of the former family are constantly in motion and thus hold out a hope to the observer that he is going to see something worth seeing, while the orb-weavers make nothing of remaining motionless for six or eight hours at a stretch; the observer, in the meantime, being afraid to let his attention flag for a moment lest he lose some small but significant movement on their part. We have watched the males and females of several species, but our only notes pertain to two species of *Argiope*, *cophinaria* and *fasciata*, in which the males are much smaller than the females. In the mating season each female has three or four of these little males hanging about the outskirts of her web.

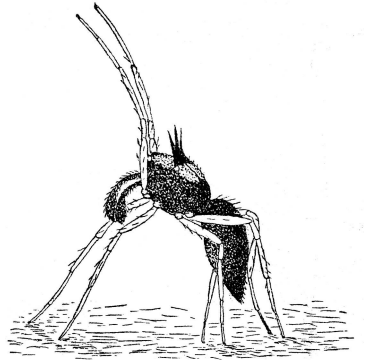


Fig. 27.—*Astia vittata*, var. *niger*. Position of male approaching female (from nature, by L. K.).

In *cophinaria*, when two of these males meet, they throw up their first legs and back away from each other, without striking or clinching as in the *Attidae*, and then one of them drops at the end of a line. When advancing toward the female, the male seems to pause and pull at the strands of web, as though to notify her of his approach. When he comes toward her from in front she imparts a slight motion to the web with her legs, which seems to serve as a warning, as he either moves away or drops out of the web. When he comes from behind she pays no attention to him until he begins to creep on to her body, when she slowly raises one of her long legs and unceremoniously brushes him off.

We passed one afternoon in watching a female of *fasciata* in her web, around the edge of which were perched four little males. The proceedings were briefly as follows:

One of the males ran lightly over the web toward the female, approaching her from behind. Before he reached her she, seemingly conscious of his approach, gave the web a violent shake, whereupon he retreated. He made three or four trials of this kind and then seemed to give up hope. His place was taken by one of the other males, which acted in exactly the same way, with no greater success, and then gave place to a third. The female was always approached from above and behind, she hanging head downward, and she usually gave her warning shake before the male came very near, although once or twice he came close enough to touch her. The males showed no ill feeling toward each other. The most interesting part of it was that she seemed to recognize from the character of the vibration that a male was approaching, not taking the motion of the web to signify that an insect was entangled in it, as in this case she would at once have turned to secure her prey.

From these slight observations we were inclined to believe that the courtship in the *Epeiridae* was carried on, to some extent at least, by a vibration of web lines. Dr. McCook subsequently confirmed that opinion, and we quote from his work on *American Spiders and their Spinning Industry*¹ the following extract, which bears directly on the subject:

"The first stages of courtship have already been indicated. Having found the snare of his partner, the male **Orbweaver** stations himself upon the outer border and awaits results. It is not difficult for him to communicate his presence. Indeed, he must take his place deftly and keep it very quietly upon the snare, or he will quickly bring down upon him the voracious lady of the house. A touch of his claw upon a radius would telegraph to the female the fact of his presence; and I believe, from what I have seen of the operations of the male in this preliminary stage of courtship, as well as from the recorded observations of others,

¹ This quote appeared in Volume II, pp. 20—22, of *American Spiders and their Spinningwork. A Natural History of the Orbweaving Spiders of the United States, with Special Regard to their Industry and Habits*, published by the author (H. C. McCook) and the Academy of Natural Sciences of Philadelphia in 1890. The Peckhams must have had access to an advance copy of this text. Missing parts of the original text have been inserted in red here.

that he does thus intimate his presence, and that the first stages of the engagement are consummated by these telegraphic communications back and forth between male and female over the delicate filaments of the silken snare.

"If matters be favorable, the male draws nearer, usually by short approaches, renewing the signals at the halting places. Sometimes this preliminary stay is very brief; sometimes it is greatly prolonged. I have observed it to be continued during several days, in which the male would patiently wait,—sometimes, but not always, changing his position—until his advances were favorably received, or were so decidedly repulsed that he was compelled to retire. With Labyrinth spiders I have generally seen the male stationed upon the maze, or that part of the snare which consists of crossed lines. Here he would make for himself, as he hung back downward, a little dome of spinning work,² which spread above him like a miniature umbrella. The male of *Argiope cophinaria* feels the web with his feet for some time before the final approach. The male of *Linyphia marginata*, as he cautiously approaches, pulls upon the threads connecting his own with his lady's bower. . . . [different context, p. 22:] The period of approach or courtship is generally terminated by a sudden rush which brings the partners into union."

The same idea was advocated many years ago by Termeyer, as follows:¹

"The *diadema* spider was that which I examined. * * * He never appears in the center of the beautiful webs, and even when I saw him he was, as to abdomen and palpi, so different from the female, which in other respects he resembled, that I should not have supposed him of the same species. He never spins webs except in the time of his amours. * * * He approaches little by little, with much caution, doubtful of the reception with which he is to meet in the web of the female, who occupies the center, intent only on her prey. He commences

¹ Researches and Experiments upon the Silk from Spiders and upon their Reproduction. Raymond Maria de Termeyer. Revised by Burt G. Wilder, M. D. Proceedings of Essex Institute, Vol. V, pp. 71—73.

²This was spelled *spinningwork*, not *spinning work*, by McCook.

by touching with one leg a thread of her web; the female approaches him; he flies, allowing himself to hang. Then he rises, winding up the thread, when he is assured, by I know not what movement, that he will not be ill-received; then he approaches her and with one of the palpi touches her stomach quickly many times. Then he returns, repeats the same act and departs, if he succeeds in leaving. I say if he succeeds, because I wish to relate what came under my observation in 1798. * * * I put a male and female of the *diadema* spider together in a box like a drum, closed with a veil at both ends. The male began by making various movements, as if to draw the attention of the female, who pretended not to perceive him, but only from time to time touched some thread of the web. He boldly approached, directing one of his palpi to her abdomen, and she extending this toward the palp. * * * But I saw also with surprise and indignation that, the work hardly finished, the male not being able to fly on account of the confinement, the female enveloped him in her thread, and having thus deprived him of every means of defense, devoured him. Perhaps overpowering hunger compelled her to it, but the act was very ferocious."

SUMMARY AND CONCLUSION.

In this paper we have considered the two theories by which Mr. Wallace explains sexual color differences in animals—primarily the greater vitality of the males, especially during the breeding season, and secondarily the greater need of protective coloring on the part of the females; and we have found that however satisfactory they may be where birds and butterflies are concerned, they fail in each important particular when applied to spiders.

In our study of moulting habits we have seen that among the *Attidae*, where the sexual differences are strongest, males are commonly more brilliant than the females; that the young males nearly always resemble the adult females; that the males, when they diner from the females, depart from the general coloring of the group; and that when the females depart from the coloring of the group they approach, in the same degree,

the coloring of the males. Mr. Wallace's theory would only partially explain these facts since although the increased vitality at the breeding season might produce variations which would tend to be inherited at that age, the assumption with which he starts out—that the male animal is constitutionally more active than the female—is not true in regard to spiders.

While studying the secondary sexual characteristics of spiders we came upon several large groups of facts which seem entirely inconsistent with Mr. Wallace's view. First, we found no evidence that the male spiders possess greater vital activity; on the contrary, it is the female that is the more active and pugnacious of the two. Second, we found no relation, in either sex, between development of color and activity; the *Lycosidae*, which are among the most active of all spiders, having the least color development, while the sedentary orb-weavers show the most brilliant hues. Third, we found that in the numerous cases where the male differed from the female by brighter colors and ornamental appendages, these adornments were not only so placed as to be in full view of the female during courtship, but that the attitudes and antics of the male spider at that time were actually such as to display them to the fullest extent possible. Moreover, we noticed that the males were much more quarrelsome in the presence of the females, and that they, to a great extent, lost their tendency to fight when the mating season was over.

With these facts in mind let us examine Mr. Wallace's two strongest objections to the theory of sexual selection.

First: "There is a total absence of any evidence that the females admire or even notice the display of the males. Among butterflies there is literally not one particle of evidence that the female is influenced by color or even that she has any power of choice, while there is much direct evidence to the contrary."¹ In butterflies and in birds, with their rapid flight, it is difficult to determine how much one sex is watched by the other; but in the *Attidae* we have conclusive evidence that the

¹ *Tropical Nature*, pp. 199-200.

females pay close attention to the love dances of the males, and also that they have not only the power, but the will, to exercise a choice among the suitors for their favor.

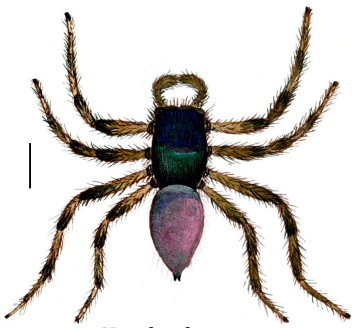
Second: The fact that every male bird finds a mate "would almost or quite neutralize any effect of sexual selection of color or ornament; since the less highly colored birds would be at no disadvantage as regards leaving healthy offspring." In spiders, as the females gradually become adult, they have a choice from among a number of males, as these mature several days earlier. The males will pair as often as they have the opportunity and as the mating season lasts for two or three weeks the more brilliant males may easily be selected again and again.

The fact that in the *Attidae* the males vie with each other in making an elaborate display, not only of their grace and agility but also of their beauty, before the females, and that the females, after attentively watching the dances and tournaments which have been executed for their gratification, select for their mates the males that they find most pleasing, points strongly to the conclusion that the great differences in color and in ornament between the males and females of these spiders are the result of sexual selection.

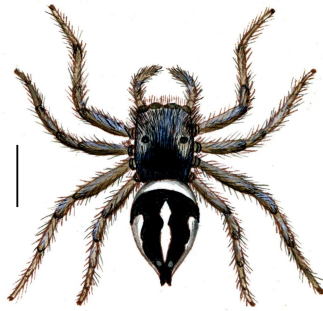
NOTE.—Since finishing the above we have seen, in the February number of the Popular Science Monthly, T. H. Morgan's article on *The Dance of the Lady Crab*. The observation therein noted is full of interest, showing, as it does, that sexual display in the invertebrates is not confined to spiders.

The three plates (I—III) referenced in this document were attached to a subsequent number (Volume 1, Number 3) of the Occasional Papers of the Wisconsin Natural History Society, issued in 1890. Here captions that originally appeared on a separate sheet have been added directly to the respective plate, to facilitate their use. Plates I and II were only associated with this document (Number 1), but Plate III, dealing with orb weavers (included in the *Epeiridae* by the Peckhams) was also referenced by a second paper in this volume (Number 2) by E. Peckham.

Plate I.



H. splendens. ♂.



H. splendens. ♀.



H. splendens.
var. ♀.



H. splendens. 1st moult.

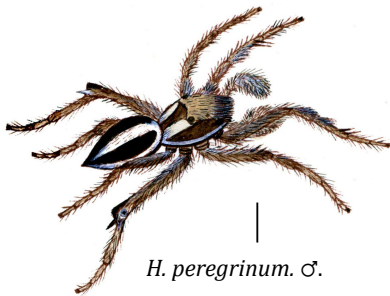


H. splendens. 2nd moult.

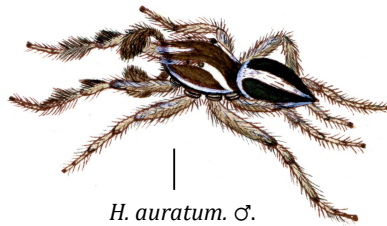


H. splendens. 3rd moult.

Habrocestum splendens: Male and female, to show the difference between the sexes; first three moults, to show the greater resemblance of the young to the female; variety of the female.



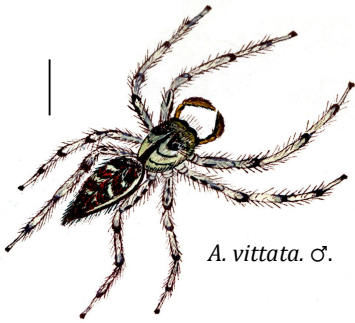
H. peregrinum. ♂.



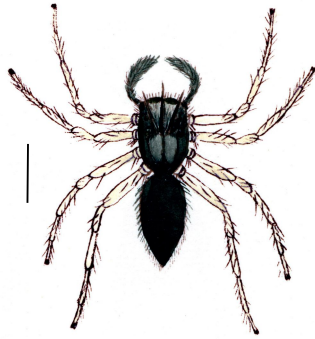
H. auratum. ♂.

Habrocestum peregrinum and *Habrocestum auratum* males, to show the departure in that sex from the general coloring of the genus; note that the female of *splendens* resembles these males more than she does the male of her own species.

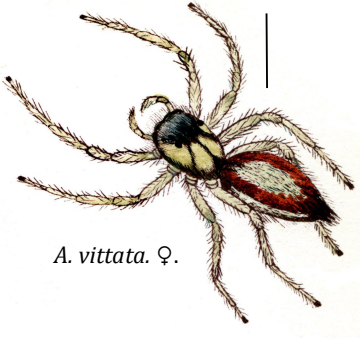
Plate II.



A. vittata. ♂.



A. vittata. var. *niger*. ♂.



A. vittata. ♀.

Astia vittata: Female and two male forms, to show the two varieties and the sexual differences.

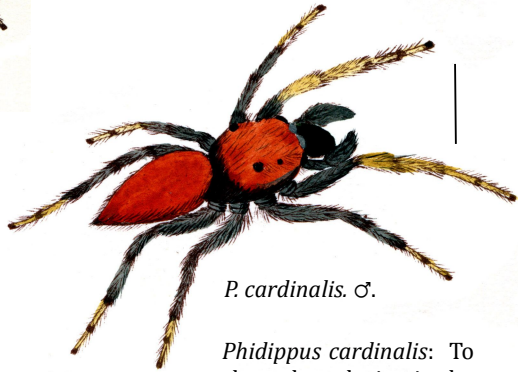


P. harfordii. ♂.



P. harfordii. ♀.

Pseudicius harfordii: Male and female, to show the sexual differences.



P. cardinalis. ♂.

Phidippus cardinalis: To show the coloring in the male.



P. johnsoni. ♂.

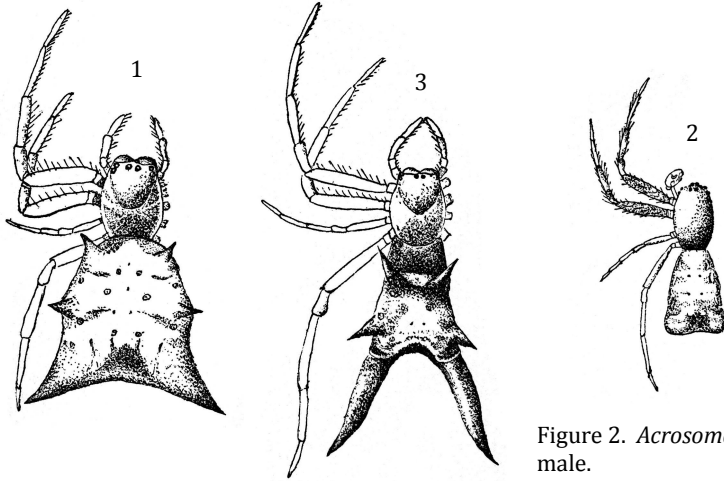
Phidippus johnsonii: To show the coloring in the male.



Z. bettini. ♀.

Zygoballus bettini: To show the coloring in the female, the male being still more brilliant.

Plate III.



Figures 1 and 3. *Acrosoma spinea*, two forms of female.

Figure 2. *Acrosoma spinea*, male.

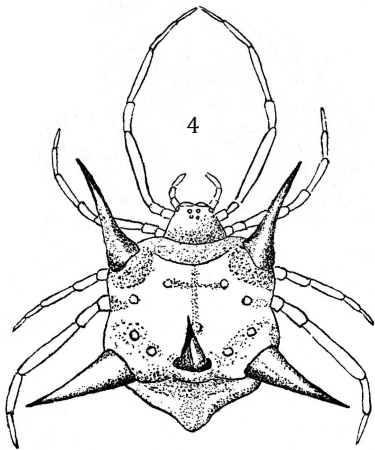


Figure 4. *Phoroncidia aurata*, female.

Note: By mistake, figures 5 and 6 were included as being drawn from nature by Mr. Kumlien.

They were, in reality, copied from Dr. Taczanowski's work, *Araneides de la Guyane Française*.

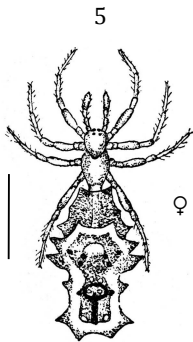


Figure 5. *Acrosoma horrida*, female (from Taczanowski).

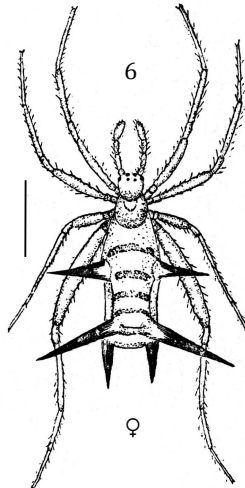


Figure 6. *Acrosoma oblonga*, m female (from Taczanowski).