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AND A SUMMARY OF CYTOLOGIC ORIGINS
OF SUCH MOSAIC HYMENOPTERA. BIOL-
OGY OF EUMENINE WASPS, VI.**

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A BILATERALLY GYNANDROMORPHIC *HYPODYNERUS*, AND
A SUMMARY OF CYTOLOGIC ORIGINS OF SUCH MOSAIC
HYMENOPTERA. BIOLOGY OF EUMENINE WASPS, VI.

KENNETH W. COOPER¹

SYNOPSIS: A nearly perfectly divided, left (♂)-right (♀) gynandromorph of the Chilean eumenid wasp *Hypodynerus tuberculiventris* (Spin.) and a dissection of its terminal retracted abdominal segments and genitalia are described and illustrated. A table summarizes the morphology of the seven or eight other sexual mosaics recorded in the Eumeninae (Vespidae). Although female *Hypodynerus* average considerably larger than males, the approach to dimensional symmetry of the male and female halves probably reflects nearly equal growth per food unit (at not-extreme ranges of provisioning) of male and female wasps, and not a dominant influence of the female half. Indeed, as is usual for such mosaics although not invariably so, the male and female tissues of this wasp appear to have differentiated autonomously. The rarity of collection of such mosaics (frequency < 0.01%) grossly underestimates the frequency of the cytologic mishaps giving rise to them. The known errors of oocytic meiosis, of suppression of nuclear activity, and of fertilization leading to gynandromorphy are discussed; in aggregate their raw frequencies for Hymenoptera probably lie between 0.1% and 1.0% of all eggs.

Although frequent and even mass occurrences of gynandromorphs and minor sexual mosaics are known in certain exceptional strains of honeybees (e.g., von Siebold 1864; Rothenbuhler 1958) and colonies of ants (e.g., Wheeler 1937; Donisthorpe 1946), gynandromorphic Hymenoptera are nevertheless extremely rarely encountered by collectors. Thus, to judge from the compilations and observations by Dalla Torre and Friese (1899), Wheeler (1903), Enderlein (1913), Mitchell (1929), Krombein (1949), and others, as well as from citations in Zoological Record, gynandromorphs have been described in fewer than 200 species of Hymenoptera. If some 280,000 Hymenoptera have now been described as Bernard (1951) estimates, then less than a tenth of a percent have gynandromorphic representation, and a rough estimate of the overall frequency of occurrence of gynandromorphs in collections would perhaps be an order of magnitude less than this, or roughly one-hundredth of a percent. As will be brought out in the discussion, which reviews what is now known of the origins of hymenopterous gynandromorphs, the raw frequencies of the events leading to gynandromorphy (and other mosaicism) are probably con-

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siderably higher than would be judged from the experience of collectors.

The gynandromorphic Hymenoptera now known are more or less randomly scattered among sawflies, parasitic Hymenoptera (terebibrants), ants, wasps and bees, and they probably occur in most species of Hymenoptera, if not in all. They are conveniently classified to the four main types recognized by Dalla Torre and Friese (1899): *lateral*, the two sides of the insect being of different sex; *frontal*, having a fore-aft division of the sexes; *transverse*, being dorso-ventrally divided; and *mixed*, or combinations of varying complexity of the first three types. Members of the four classes are not equally frequent, but form a series: lateral > mixed, mixed \approx frontal, and mixed or frontal > transverse. The male or female parts of gynandromorphs seem to show no tendency to be predominantly left, anterior, or dorsal. As might be expected, most gynandromorphs are only partially so, for they do not have the body equally divided into male and female sectors. Rather only a portion of the insect (*e.g.*, the head, the thorax, the head and thorax, etc.) is gynandromorphic in most cases, and total involvement of the body occurs in less than 10% to 15% of all. The small number of previously known eumenid gynandromorphs (summarized in table 1) conform with these generalizations, and the very remarkable new example now to be described is the second known instance of a total, lateral, gynandromorphic eumenid wasp (figs. 1, 2). Of special interest is the dissection of the terminal abdominal segments of this gynandromorph (fig. 2), for the only other eumenid gynandromorph having divided terminalia was not dissected (see *Hoplopus reniformis* (Gmel.) in table 1, and Leiningger 1926).

Hypodynerus tuberculiventris (Spinola)

(Figures 1, 2)

Eumenes tuberculiventris Spinola, 1851, in: Gay, Historia Fis. Pol. Chile, Zool., VI, p. 267.

Odynerus (Leionotus) tuberculiventris de Saussure, 1853, Ét. Fam. Vesp., I, p. 162

Odynerus (Hypodynerus) tuberculiventris de Saussure, 1855, Ét. Fam. Vesp., III, p. 227

Nortonia tuberculiventris Zavatteri, 1912, Arch. f. Naturgesch., LXXVIII, Abt. A, Heft 4, s. 169, Pl. II, fig. 49

Hypodynerus tuberculiventris Bequaert and Ruiz, 1943, Rev. Chilena Hist. Nat., 54, pp. 30-32, (1941).

LABEL DATA: El Canelo, Prov. Santiago, XI-XII, 1952, Chile. Collected by Louis Peña (together with some 220 other normal individuals of this species, of which no more than 5% were males).

HABITUS (fig. 1): The left side is entirely of male structure and coloration, whereas the right side is conversely entirely female. For the most part the wasp is well proportioned and nearly symmetrical in overall appearance, measuring *ca.* 2.5 mm in head width (between the outer margins of the compound eyes) and *ca.* 7.7 mm from frons to the apex of abdominal tergite-2 (foreshortened in fig. 1). The body size is accordingly that of an average female, being considerably larger than an average male. The asymmetry therefore reflects not the normal sexual dimorphism for body size, but rather the proportional differences between male and female structural parts (*e.g.*, the compound eyes, mandibles, etc.; see figure 1) normal to wasps of opposite sex but of corresponding body sizes.

The overall effect of the color pattern, like that of the morphology, is one of general symmetry. The body of the wasp is predominantly shining black with bright yellow maculations. Except as noted below, the antennae and legs (from just before the apex of the femur to the infuscated last tarsal joint) are light reddish brown or rusty. Without magnification the color pattern is disrupted by only two marked asymmetries, namely the striking bipartite black and yellow pattern of the clypeus and the unique yellow spot on the left mesocoxa (fig. 1). Despite the overall appearance of symmetry, the color pattern of the left side follows faithfully that of the average male and when magnified it markedly contrasts with that of the female right side wherever male and female patterns of normal wasps differ.

HEAD (fig. 1): Overall asymmetry slight; nevertheless when studied in face view or from below (fig. 1), or from above, individual structures of the left side—being of typical male morphology and color pattern—present striking contrasts to their counterparts in the right half which are of normal female constitution and proportions. For example, on the left side: the ocellar triangle is skewed; the compound eye is notably larger than that on the right, and of different shape; the antenna is longer than that on the right, its joints are of different proportions, and it has 13 segments (12 in ♀), the terminal one being typically hooked as in all males; the frontal carina is more narrowly separated from the antennal socket; the clypeus is less wide but proportionately longer; the gena and mandible are markedly smaller; and so on.

TABLE 1

SUMMARY TABLE OF DESCRIBED GYNANDROMORPHIC EUMENID WASPS. TYPE F, FRONTAL GYNANDROMORPHS; TYPE L, LATERAL GYNANDROMORPHS; TYPE M, MIXED GYNANDROMORPHS; NO TRANSVERSE GYNANDROMORPH HAS SO FAR BEEN REPORTED IN THE EUMENINAE,—SEE TEXT FOR DESCRIPTION OF GYNANDROMORPHIC TYPES.

Species	Type	Head	Thorax	Abdomen	Reference
<i>Eumenes flavicornis</i> Sauss.	?F	both antennae ♂; all else ♀	♂	♂	de Saussure 1856
<i>Odynerus acoelogaster</i> Perk. ¹	M	left side ♂, right ♀	left ♂; right ♀ except for mid and hind legs (♂-like)	♀ except for an incom- plete 7th dorsal segment on right (♂-like); genita- lia ♀	Perkins 1901, 1922
<i>Ancistrocerus callosus</i> (Thoms.) ²	M	left side ♂, right ♀	left ♀, except foreleg and sternum (♂); right side ♂, except legs which are ♀	outwardly purely ♀; gen- italia not examined	Rengel 1917
<i>Ancistrocerus callosus</i> (Thoms.) ²	?F	left antenna ♀ in structure except for presence of a 13th, terminal, hook-like segment (♂); right antenna broken; head otherwise ♀	♀	♀	Rengel 1917

<i>Parancistrocerus pedestris</i> (Sauss.) ²	M	head an irregular mosaic of ♂ and ♀ characters	left legs and wings ♀, right ♂	entirely ♀, including genitalia	Malloch 1924
<i>Hoplopus reniformis</i> (Gmel.) ⁴	L	left side ♀, right ♂	left side ♀; right ♂	left side ♀, right ♂; genitalia similarly divided, but may not be 50-50 for phallus of abnormal shape	Leininger 1926
<i>Pterocheilus phalerata</i> var. <i>chevieriana</i> Sauss. ⁵	L	left side ♂, right ♀	♀	♀, but apparent sternites-II, -III, -IV and -V are ♂ on the left side, ♀ on the right; sting projecting, so genitalia probably ♀	Benoist and Berland 1935
<i>Ancistrocerus parietum</i> (L.)	M	left side ♀, right ♂	left half of scutellum ♀, right half ♂; all legs ♀; upper right thorax ♂-like.	externally ♀	Kontkanen 1935

¹ J. F. Perkins of the British Museum of Natural History kindly informed me that this specimen is in the museum's collection and is to be referred to *Odynerus acoelogaster* R. C. L. Perkins. (synonyms: *O. relictus* R. C. L. Perkins and *O. lithophilus* R. C. L. Perkins).

² Recorded as *Odynerus callosus* Thoms.

³ Recorded as *Odynerus (Stenodynerus) conformis* Sauss.

⁴ Recorded as *Odynerus reniformis* Gmel.

⁵ Recorded as *Pterochilus chevierianus* Sauss.

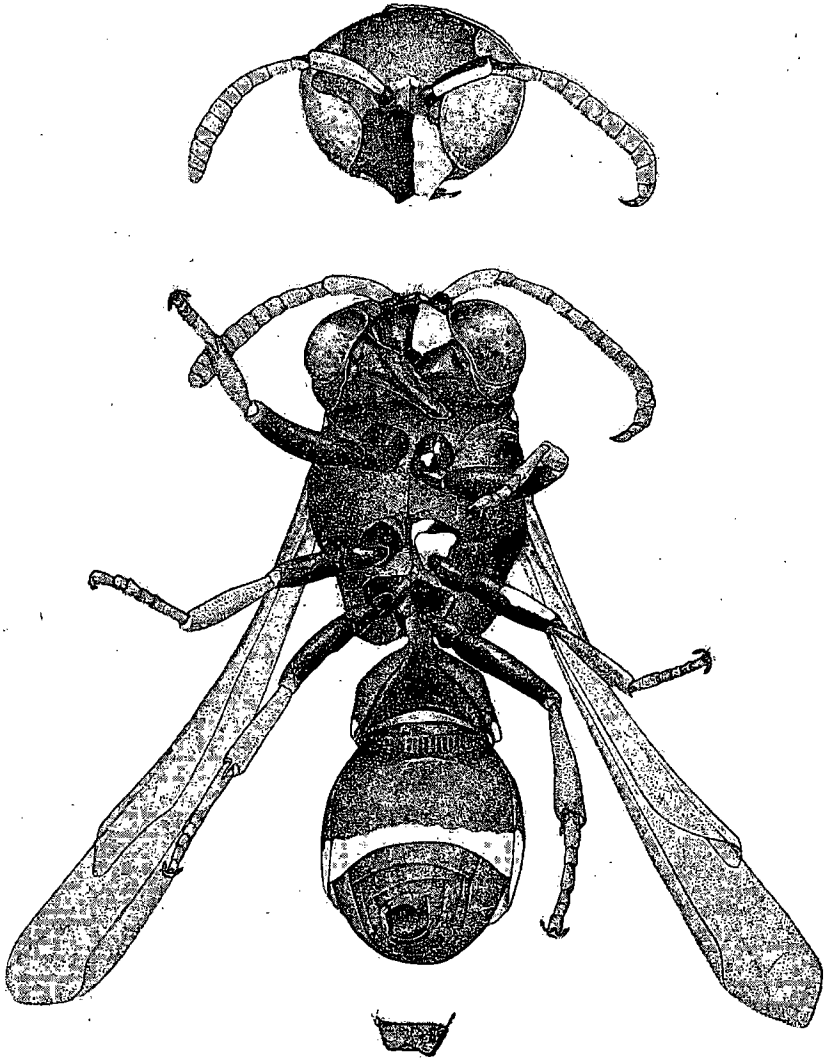


Fig. 1. Bilateral gynandromorph of *Hypodynerus tuberculiventris* (Spin.); left side of wasp male, right side female.

The body of the gynandromorph is shown in ventral view. The normally retracted abdominal segments, the genitalia, and the male tergite-VIII and sternite-IX have been dissected from it (see fig. 2 of the dissection). Above, head in full face view, maximum width *ca.* 2.5 mm.; below, sternite-VII in ventral aspect. See text for full description.

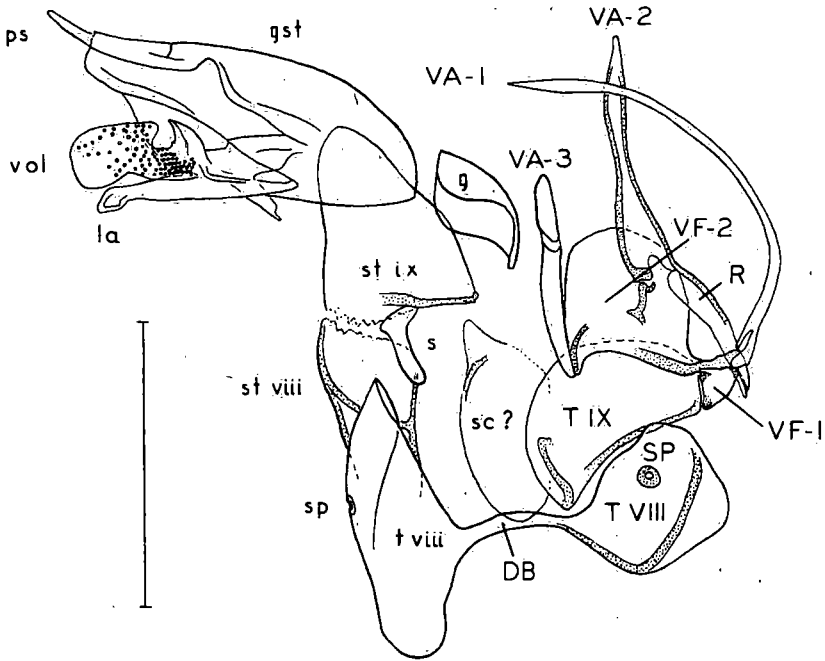


Fig. 2. Cleared dissection of terminal, retracted abdominal segments and genitalia of the bilateral gynandromorphic *Hypodynerus tuberculiventris* (Spin.). Male parts to left, their labelling in lower case; female parts to right, labelling in capitals.

The dissection is in dorsal aspect, and the female parts are displayed in their normal relations and in dorso-lateral aspect. Male sternites-VIII and -IX have broken apart, the spiculum is detached, and these elements are viewed from their internal surfaces. Phallus and gonobase have rotated 180° and are viewed from their ventral surfaces. The sclerotized apodemes of st-viii, sc ?, T-VIII, T-IX, VF-1, VF-2 are stippled. Vertical scale to left equals one millimeter.

g, gonobase or basal ring of phallus; gst, gonostipes or basiparamere; la, lamina aedeagalis, "lateral rod", or "penis valve" of aedeagus; ps, parameral spine; s, spiculum or median apodeme of sternite-IX (detached); sc ?, scalar remnant of tergite-IX ?; sp, spiracle of tergite-VIII; st-viii, sternite-VIII broken from ankylosis with sternite-IX; st-ix, sternite-IX; t-viii, tergite-VIII; vol, volsella.

DB, dorsal bridge of hemitergite-VIII; R, ramus of second valvula; SP, spiracle of hemitergite-VIII; T-VIII, hemitergite-VIII; T-IX, hemitergite-IX; VA-1, -2, -3, valvulae-1, -2, and -3 respectively; VF-1, -2, valvifers-1 and -2.

The typical and hence contrasting male morphology of the left side of the head is in turn accentuated by the color pattern differences between the sexes. Thus, on the left side: the yellow frontal spot is smaller; the scape and pedicel of the antenna are black above, light reddish brown behind, and yellow in front and below as in a typical male (on the right, as normal for the female, the scape is entirely light reddish brown, and the pedicel is black above and light reddish brown elsewhere); the clypeus is yellow, contrasting sharply with the shining black of the right or female side.

THORAX AND APPENDAGES (fig. 1): The left pronotum from above is very slightly shorter at its outer apical angle, and the left mesothorax and left propodeum are slightly less rounded and robust than on the right (female) side. The wings on the left are slightly shorter than on the right (foreshortened and not evident in fig. 1). The legs of the left side are very slightly more slender than on the right, and the left middle femur is slightly sinuate below.

The yellow ornaments on the two sides of the thorax show few differences, except that the tegulum on the left is marked basally with black overlying the rufous medial field and only the posterior tip is yellow, whereas the posterior third of the tegulum on the right is yellow and has only a suggestion of black basally. The divided yellow dot on the left anterior distal half of the left mid femur, the yellow splash on the outer distal face of the left anterior tibia and on the anterior distal half of the left mid tibia, and the small yellow spot on the outer mid sector of the left hind tibia are all male characteristics, and have no counterparts on the right (or female) side. The orange coloration of the costal field of the right forewing is somewhat brighter than that of the shorter, left (male) wing.

ABDOMEN (segments II-VII; fig. 1)²: As in the cases of the thorax and propodeum, the left side of the abdomen is slightly less robust than the right, but this is not obvious without close study. Likewise the yellow color pattern shows no certain difference on the two sides; such slight asymmetries as exist are paralleled in normal individuals of either sex. However, the left side of the undissected specimen had seven segments as in a normal male, whereas but six occurred

² The propodeum, or true first abdominal segment, has been dealt with in the discussion of the thorax; the apparent first abdominal segment, bearing the petiole, is in fact the second abdominal segment, and the numbering employed here accordingly counts the propodeum as abdominal tergite-1.

on the right side as is typical of most female aculeates. Although tergite-VII on the whole appears symmetrical, it has a small notch apically, slightly left of center at the margin of juncture of male and female sides. To the right of center, the female tergital half extends slightly more distally than does that of the male. Sternite-VII, on the other hand, is very asymmetrical (fig. 1, below), being unequally scalloped medially and somewhat prolonged on the left (or male) side. Sternite-IX (apparent seventh male sternite) projected somewhat to the right beyond the right apex of the emargination in the undissected specimen, and was overlain by what in effect is a male *hemitergite*-VIII (fig. 2, t VIII). Aside from the anomalous occurrence of an extra abdominal segment on the left side, before dissection the apex of the abdomen possessed a deceptively regular contour.³

ABDOMEN (segments VIII-IX and genitalia; fig. 2): Only in the head of this wasp is the sexual dimorphism and clearly bilateral division into a left male half and right female half as strikingly and diagrammatically displayed as in these terminalia. The left eighth tergite of the male half (t viii) is sclerotized and pigmented over its exposed apical two-thirds. Proximally, as in a normal male, this tergite is neither pigmented nor strongly sclerotized. But unlike that of the normal male it is no more than a hemitergite, and it is joined across the midline by a dorsal bridge (DB), just as a left hemitergite of a normal female would be, with the wholly retracted, structurally normal, female hemitergite of the right side (T VIII). Aside from the dorsal bridge and integumentary membranes connecting the main exoskeletal plates, there are no other unions between the left (male) and right (female) halves.

A partially successful attempt was made to keep all the exoskeletal parts in their normal array and relations during dissection and permanent mountings, yet regrettably the left (male) sternite-VIII (st viii), which is normally ankylosed to sternite-IX, and the spiculum (s) were broken from their unions. Nevertheless the arrangement and structures of sternites-VIII and -IX are clear enough and, except

³ Surely, in the field, this wasp would have appeared to most collectors quite normal and a female, just as it did to Peña. Yet there may be some sufficiently alert, discerning, and nimble to be certain death to such a diminutive freak. Consider Morice's (1901) comment, when writing of an equally cryptic gynandromorphic bee, *Podalirius retusus* (L.): "Its curious particolored face caught my eye; otherwise I should have let it pass as a female, for the other characters were too inconspicuous to attract attention as it flew past me." (1)

along their medial edges, of normal morphology. The spiculum, on the other hand, is unduly short and disproportionately broad. It is not certain whether this is an artifact resulting from damage in dissection, or whether the spiculum was in fact so modified in the gynandromorph. It may well be modified for not only is it a ventral midline structure, but to a noticeable degree the phallus is also ill-shaped (as are also the first and second valvulae on the female side), for it is both broader and somewhat shorter than normal, and has a shortened, less needle-like, parameral spine (ps). Nevertheless exactly half—the left half—of a phallus is present, containing each of the lateral components of the normal eumenid phallus (see figure 2). A flap of integument (sc P), the left half of which is elliptically curved as ordinarily is the case for eumenine scalar remnants of tergite-IX, and bears a weak apodeme along its left apical margin, completes the retracted abdominal and genital complements of a normal male.

The female morphology of the right side (fig. 2) is normal insofar as hemitergites-VIII and -IX, valvifers-1 and -2, and valvula-3 are concerned. Valvula-1, however, is shorter and somewhat more robust than usual, and valvula-2 is much shortened and deformed beyond its basal third. Nevertheless the female genitalia and retracted abdominal segments show no suggestion of "masculinization", and in every aspect the right side is completely that of a female.

COMMENT: This specimen, then, is a notably clean-cut bilateral gynandromorph, with the only obvious disturbance of symmetry being the invasion of the dorsal bridge of right hemitergite-VIII across the midline onto the male side. The minor proportional defects in the phallus, perhaps in the spiculum, and in valvulae-1 and -2, cannot be taken as evidence of "feminization" or "masculinization", and perhaps best can be understood as reflecting restraints on the symmetrical growth of these very diverse parts brought about by their apposition in the developing pupa. There is no suggestion that diffusible elements derived from one sex have notably biased the development of the other. Rather, as in the case of other gynandromorphs (but not all, see Leclercq 1953) the evidence indicates that the tissues of each sex seem largely self-determining. Nor is the general symmetry and correspondence of gross body size of the male and female halves with that of an average female suggestive of a dominant effect of the female half on the male half, even though the average female *Hypodynerus tuberculiventris* (Spin.) is considerably larger than the average male. Body size in eumenid wasps is, within limits, a function of food consumed, and the largest males in a population

are larger than the smallest females. This wasp, as a larva, very probably developed in a female cell with a provender of caterpillar prey of the bulk normally provided an average zygote (or fertilized egg, which, in Hymenoptera, ordinarily develops as a female) in contrast to that stored for an azygote (or unfertilized egg developing as a male). What is of interest, and which this wasp shows unequivocally, is that male and female eumenid larvae that have consumed an equal bulk of food (which is neither excessively large nor unusually scant) will develop to wasps of equal size, or virtually so.

THE ORIGINS OF HYMENOPTEROUS GYNANDROMORPHS

The low frequency with which hymenopterous gynandromorphs occur in the experience of collectors ($< 0.01\%$) would, were Boveri's (1888, 1915) hypothesis of their formation valid, permit a rough estimate of the lowest rate at which delayed sperm extraordinarily fertilize one nuclear product of the first cleavage division of haploid eggs. The result of such an abnormal sequence would be the entrance to second cleavage of one diploid, or $2N$, syngamic nucleus (ordinarily giving female tissues) and one haploid, or N , matroclinous nucleus (giving male tissues), the adult product thereby being a sexual mosaic. The particular pattern of sex mosaicism, and the ultimate percentage of the individual made up of male rather than female tissues, would be principally determined by the partition of the diploid and haploid nuclei of the embryo among the imaginal discs as in any case initially involving two or more classes of nuclei. Under Boveri's hypothesis each gynandromorph commences life as an inseminated egg, and this much is assuredly true for most gynandromorphs of *Habrobracon* and *Apis* where detailed genetic analysis has been possible. However it is now very clear, especially from Whiting's research on *Habrobracon* as well as from Rothenbuhler's and others' on the honeybee, that the sequence of events following fertilization that Boveri postulated occur extremely rarely, if at all, and that gynandromorphs may arise in a number of different ways.

The commonest modes of origin of gynandromorphs in *Habrobracon* and *Apis* involve events prior to cleavage in the egg. Thus the commoner origin of gynandromorphs in *Apis* (but a much rarer one in *Habrobracon*) is brought about by effective dispermy; one sperm fertilizes the haploid egg nucleus, the other sperm, instead of remaining arrested or degenerating, directly enters cleavage to give a clone of haploid nuclei (Rothenbuhler, Gowen and Park 1952; Rothenbuhler 1958; Whiting 1928, 1931, 1943). In these cases the events are just

as postulated by Morgan (1905) and, contrary to Boveri's view, the male tissues are of patroclinous or androgenetic origin. A simple but uncommon variant is known in the honeybee in which haploid nuclei derived from *two* sperm, in addition to the syngamic diploid nucleus, undergo cleavage without fusion. The resulting gynandromorph is then in addition a mosaic of two genetically different, androgenetic male tissues (Rothenbuhler 1957, 1958). Turn about, in *Habrobracon* the frequent mode of origin of gynandromorphs follows the normal fertilization of an egg (providing a 2N nucleus ordinarily developing to female tissues), but thereafter this zygotic nucleus and one remaining nuclear product of oocytic meiosis (hence N, developing male tissues) enter cleavage (Whiting 1935, 1943; Whiting and Wenstrup 1932; Whiting and Whiting 1927). The prime cytologic abnormality in this case is the production of a binucleate egg, and it can be shown that the two egg nuclei may be genetically different and hence cannot, in such a case, be identical products of a first cleavage division as Boveri postulated (Whiting 1932; Whiting and Stancati 1931). Gynandromorphs arising in this way have matroclinous or gynogenetic male parts. Though the commonest type in *Habrobracon*, gynandromorphs of such an origin are found only infrequently in honeybees (Mackenson 1951; Rothenbuhler 1958).

It might be expected that very rarely a binucleate egg would be effectively dispermic, with one sperm fertilizing one egg nucleus and both the other egg nucleus and the other sperm nucleus entering cleavage independently to give two genetically different clones of haploid nuclei. The haploid male portions of gynandromorphs arising in this way would be in part of androgenetic (paternal) origin, in part of gynogenetic (maternal) origin. Such has in fact been found in *Habrobracon* (Whiting 1943). Finally, impaternate gynandromorphs arising from wholly unfertilized eggs have been proven to occur rarely in *Apis* (Tucker 1958), and evidently are known also in *Habrobracon* (see von Borstel 1957). In these cases either the second meiotic division products of one of the two second meiotic spindles fail to be segregated, or two of the four nuclear products of meiosis fuse to form a diploid nucleus heterozygous for the sex alleles. In Tucker's (1958) opinion, the haploid products of oocytic meiosis may in certain cases undergo one cleavage division before fusing to give diploid nuclei. In any case a diploid nucleus results, and this nucleus and one of the two haploid meiotic products enter cleavage to give a wholly gynogenetic embryo that is a mosaic for female-determined (2N) and male-determined (N) nuclei. Thus hymenopterous gynandro-

morphs may arise in a number of different ways, all of which involve either oogenetic meiotic mishaps, failures to suppress the activity of all but one product of these meioses, or failures to arrest the activity of sperm not participating in syngamy, or combinations of these events.

There are, of course, still other conceivable patterns or combinations, involving no more than these meiotic and physiologic failures, by which gynandromorphs might arise. What is more, the occurrence of biparental or other diploid males (and of diploid male tissues in mosaics), and the fact that haploid-diploid sex determination may not depend upon simple heterozygosity for sex alleles in all Hymenoptera (e.g., in forms with very close inbreeding; see Whiting 1947, 1958), further complicate any basis for estimation of the average frequency of the raw events underlying gynandromorph production. Certainly, however, they are far more frequent than the gynandromorphs themselves (perhaps occurring in 0.1% to 1.0% of all eggs). On the other hand the very high rates for some special strains within species, such as Rothenbuhler's (1958) honeybee stocks which may produce up to 40% gynandromorphs, do not reflect chance breakdowns in oogenetic meiosis or in mechanisms of physiologic restraint. They have been proven to be genetically determined oocytic or gametic dysfunctions. Brief but interesting discussions of the possible nature of certain of these dysfunctions have been given by von Borstel (1957) and Tucker (1958).

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