A NEW SPECIES OF *CEPHALONOMIA* EXHIBITING AN UNUSUALLY COMPLEX POLYMORPHISM (HYMENOPTERA, BETHYLIDAE)¹

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Polymorphism is well known in *Cephalonomia* and certain other genera of Bethylidae. Kearns (1934) has studied the phenomenon in *C. gallicola* (Ashmead), a species in which the females are always apterous, the males either apterous or macropterous. A different type of polymorphism occurs in *C. formiciformis* Westwood (Richards, 1939); in this species the females are either macropterous or brachypterous, the males always macropterous. In the related genus *Scleroderma*, most species appear to be dimorphic in both sexes, either fully winged or completely apterous (e.g., Bridwell, 1920). As compared to fully winged forms, brachypterous and apterous forms tend to exhibit reduction in eye size, ocelli, width of the head, and some of the sutures of the pterothorax. Thus apterous individuals may look very different from macropterous ones of the same species.

A few years ago Hugh B. Leech, of the California Academy of Sciences, sent me a series of a minute, polymorphic Cephalonomia which he reared from ciid-infested fungi collected in Baja California. More recently John F. Lawrence, of the University of California at Berkeley, has sent me examples of this same *Cephalonomia* from ciidinfested fungi collected in numerous localities in Oregon, California, Arizona, Baja California, and Navarit. This wasp is quite distinct from any other North American Cephalonomia, its closest relative apparently being the Palaearctic formiciformis, which also attacks ciid beetle larvae in fungi. This new species, described below as perpusilla, differs from formiciformis in its smaller size and also in minor details of color and structure. It also differs from formiciformis and from all other bethylids, so far as I know, in that no less than six well-differentiated types of individuals can be discerned, each type differing in certain aspects of wing development, size of the eyes and ocelli, head shape, or other details. In brief, the males are either alate (i.e., macropterous) and broad-headed or apterous and narrow-headed, the females macropterous, micropterous (in either case narrow-headed, about like the apterous males), subapterous, or apterous (in these two

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Cephalonomia perpusilla: numbers of each form arranged by locality								
Zon	e Locality	Alate	Apter- ous	Alate	Microp- terous	Subap- terous	Apter- ous	Total
		88	88	Q Q	Q Q	Q Q	Q Q	
D	CALIFORNIA							
	Plumas Co., Twain	1	2	6	0	0	0	9
	Plumas Co., Canyon							
	Dam	2	7	15	0	0	30	54
	Eldorado Co.	0	0	1	0	0	1	2
В	OREGON							
	Douglas Co.	0	0	1	0	2	0	3
	CALIFORNIA							
	Mendocino Co.	0	0	0	0	1	0	1
	Marin Co.	0	0	2	0	5	0	7
	Contra Costa Co.	0	0	1	0	1	0	2
	Fresno Co.	0	0	0	0	1	0	1
A	CALIFORNIA							
	Alameda Co.	0	0	0	5	0	0	5
	Santa Clara Co.	0	0	0	1	0	0	1
~	Santa Cruz Co.	0	0	0	2	0	0	2
С	ARIZONA							
	Rustler Park	0	1	1	0	3	1	6
	Portal & vicinity	3	1	8	0	4	6	22
-	Douglas	0	1	0	0	2	0	3
D^1	BAJA CALIFORNIA							
	San Jose Island	4	14	3	0	0	4	25
	Cerralvo Island	0	0	1	0	0	13	14
	El Triunfo	1	30	0	0	0	37	68
	NAYARIT	_			-	0	0	
	San Blas	7	6	3	0	0	8	24
	TOTALS	18	62	42	8	19	100	249

TABLE ONE

cases extremely narrow-headed). However, samples from any one locality do not in any case contain all six forms. Males appear dimorphic throughout the range, but the females appear to show geographic variation in morphism (Table I). This unusual situation is discussed further following the description of the six forms.

Cephalonomia perpusilla new species

Holotype. — & (macropterous), Twain, Plumas Co., Calif., 6. Nov. 1960 (J. F. Lawrence, no. 720, ex Polyporus versicolor on Acer sp.).

Paratypes with the following data (see Table I for numbers of each sex and form from each locality). - OREGON: 10 mi. SW Camas Valley, Douglas Co., 24 Oct. 1962 (JFL, no. 1126, ex Polyporus adustus). CALIFORNIA: Mendocino Co., 2 mi. N Piercy, 26 Oct. 1962 (JFL, no. 1131, ex Polyporus versicolor); Plumas Co., Twain, 6 Nov. 1960 (JFL, no. 120, ex Polyporus versicolor); Plumas Co., Canyon Dam, 6 Sept. 1960 (JFL, no. 713, ex Fomes pinicola);

Eldorado Co., 2 mi. N Placerville, 18 May 1961 (JFL, no 823, ex Polyporus versicolor; coll. P. Wygodzinsky); Marin Co., San Geronimo, 16 April 1961 (JFL, no. 791, ex Polyporus versicolor); Marin Co., Alpine Lake, 8 July 1961 (JFL, no. 846, ex Lenzites betulina); Contra Costa Co., 1.5 mi. W Danville, 12 Aug. 1961 (JFL, no. 938, ex Polyporus adustus); Contra Costa Co., 14 mi. S Clayton, 18 June 1961 (JFL, no. 835, ex Lenzites betulina); Alameda Co., Oakland, 26 Dec. 1959 (JFL, ex Polyporus versicolor); Santa Clara Co., 16 mi SE Sveadal, 19 June 1960 (JFL, no. 605, ex Polyporus adustus); Santa Cruz Co., Ben Lomond, 25 Feb. 1962 (JFL, no. 994, ex Fomes pinicola); Fresno Co., Huntington Lake, 31 Aug. 1960 (JFL, no. 675, ex Fomes annosus). ARIZONA: Cochise Co., Rustler Park, 8 mi. W Portal, 8 Aug. 1961 (JFL, no. 924, ex Fomes sp.); Cochise Co., 5 mi. SSW Portal, 4 Aug. 1961 (JFL, no. 899); Cochise Co., 2 mi. SW Portal, 9 Aug. 1961 (JFL, no. 928, ex Trametes hispida); Southwestern Res. Sta., 5 mi. SW Portal, 5 Aug. 1961 (JFL, no. 902, ex Ganoderma lucidum); same locality, 7 Aug. 1961 (JFL, no. 916, ex Trametes hispida); Cochise Co., 15 mi. E Douglas, 5 Aug. 1961 (JFL, no. 906, ex Trametes hispida). BAJA CALIFORNIA: San José Island, 11 April 1962 (R. Moran, no. 9415, ex Ganoderma sp.); Cerralvo Island, 16 April 1962 (R. C. Banks, ex Ganoderma on Ficus); 0.7 mi. NW El Triunfo, 9 January 1959 (H. B. Leech, ex ciid in fungus). NAYARIT: San Blas, 28 December 1960 (JFL, no. 746; coll. P. DeBenedictis, ex Ganoderma sp.).

Holotype and paratypes to be deposited in the California Academy of Sciences; paratypes at the California Insect Survey, U. S. National Museum, Museum of Comparative Zoology, and collection of J. F. Lawrence.

Description of alate male. — Total length about 0.7 mm. to 1.1 mm. Head length .253-.336 mm.; head width .80-.88 × head length (mean .84). Wings long, extending beyond apex of abdomen; ocelli strongly developed. Body dark brownish-fuscous; antennae dark brown; legs dark brown except tarsi straw-colored to light brown, tibiae often with a faint pale annulation at base; wings hyaline. Mandibles with a strong apical tooth and three small additional teeth; clypeus truncate apically, its median area roundly elevated. Antennae inserted well below level of bottoms of eyes; first four segments in a ratio of about 7:3:2:2 or 7:3:1:1, apical segment large, 2.3-2.8 × as long as wide. Eyes prominent, weakly hairy, removed from base of mandibles by about .3 × their own height, removed from vertex crest by .7-1.0 × their own height. Minimum width of front

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 $.65 \times$ width of head, 1.3-1.45 \times eye height. Head, and also thoracic dorsum, polished, weakly alutaceous, obscurely punctate. Scutellum with a straight transverse groove at base. Propodeum without a median carina or a transverse carina margining the disc behind; surface somewhat alutaceous, especially on the posterior slope and sidepieces. Fore wing with subcosta, prostigma, and stigma distinct, median and anal veins indicated by very faint, hyaline streaks. Abdomen relatively broad and short.

Alate males are remarkably similar from throughout the range. However, California and Arizona males average larger than those from Mexico, and there is relatively little overlap in size. In the three California specimens head length is .293-.320 mm. (mean .302). In the three Arizona specimens head length is .308-.336 mm. (mean .320). In the twelve Mexican specimens head length is .253-.294 (mean .281).

Description of apterous male. — Total length about 0.7 mm. to 1.0 mm. Head length .233-.320 mm.; head width .68-.77 \times head length (mean .72). Tegulae normally developed, but wings completely absent; ocelli always present, although tending to be slightly smaller than in the alate males. Color as in alate males, except basal segments of antennae light brown in some specimens. Features of head as in alate males, except the head more parallel-sided, the eyes smaller and less protruding; minimum width of front .63-.68 \times width of head, 1.50-1.65 \times eye height; distance from tops of eyes to vertex crest always greater than height of eye. Transverse groove at base of scutel-lum weak, sometimes barely apparent.

One of apterous males from Plumas Co., California is unusually large (head length .32 mm., as compared to .296 for the next largest specimen, from Arizona). The smallest male is also from Plumas Co., California (head length .233 mm.), and in fact the mean head length is nearly the same for U.S. and Mexican males.

Description of alate female. — Total length about 0.9 to 1.3 mm. Head length .288-.370 mm.; head width .68-.76 \times head length (mean .72). Wings long, extending well beyond apex of abdomen; ocelli well developed. Coloration as in male, except antennal segment two and sometimes adjacent segments tending to be lighter brown than remainder of antennae. Mandibles and clypeus as in alate males. Antennae inserted well below bottom of eyes, distinctly shorter than in male; first four segments in a ratio of about 15:5:2:2, segments three through eleven wider than long, apical segment about 1.6-2.0 \times as long as wide. Eyes weakly convex, protruding slightly from sides of head, covered with short hairs; eyes removed from base of mandibles by about .3 their own height, removed from vertex crest $1.1-1.2 \times$ their own height. Minimum width of front about .65 \times width of head, $1.35-1.40 \times$ eye height. Head and thoracic dorsum polished, obscurely alutaceous, barely punctate. Transverse groove at base of scutellum present but rather weak. Propodeum and wings as in alate male. Abdomen depressed, the sting visible in most specimens.

As in the males, alate Arizona females tend to be largest (mean head length .337), California females next (mean head length .330), Mexican females the smallest (mean head length .314). These differences are very slight, and there is a broad overlap in size in specimens from all these areas. It should also be noted that the three alate females from zones A and B in California (Table I) have a mean head length of .350, while those from zone D in California average smaller (mean head length .327), approaching the mean for the Mexican specimens.

Description of micropterous female. — Total length about 0.9-1.3 mm. Head length .336-.364 mm.; head width .71-.78 \times head length (mean .75). Wings, .09-.11 mm. long, about twice the length of the tegulae, extending slightly beyond anterior margin of propodeum; ocelli distinct, fully as strong as in alate female. Dark brownishfuscous; antennae brown, basal flagellar segments somewhat paler than the others; legs as described for alate males. Head differing from that of alate female only in having the eyes slightly smaller, removed from base of mandibles by about half their own height, minimum width of front about 1.6 \times eye height. Scutellum separated from mesoscutum by a thin line, also with a weak transverse basal groove. Other features as in alate female.

It will be noted that the micropterous females, all of which are from the San Francisco Bay region (Zone A in Table I), are considerably larger than the average for the fully alate females. The mean head length is .346 mm., considerably more than even that of the Arizona alate females. Also, the mean of the head width/length ratio is .75, considerably above the .72 mean ratio for the fully alate females. This ratio is not plotted on Figure 2, since the number of specimens is so small that one cannot be certain that there is any real difference in this regard from the alate females.

Description of subapterous female. — Total length about 0.8-1.2 mm. Head length .267-.363 mm.; head width .61-.71 \times head length (mean .655). Wings about .05-.07 mm. long, barely if at all longer than tegulae, usually reaching but scarcely exceeding anterior margin

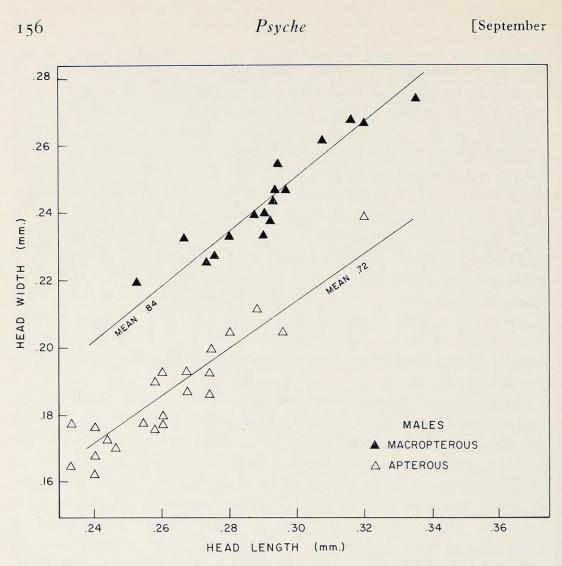


Fig. 1. Head width plotted against head length in the two forms of Cephalonomia perpusilla males.

of propodeum; ocelli present but small and weakly convex. Coloration as in micropterous female, head and thoracic dorsum polished and only very obscurely alutaceous. Sides of head subparallel except weakly converging anteriorly and posteriorly, eyes rather flat, not notably protruding from surface of head; eyes very small, weakly hairy, removed from base of mandible by $.7 \times$ their own height, removed from vertex crest by nearly twice their own height; minimum width of front 1.7 \times eye height. Scutellum weakly separated from mesoscutum, with a very thin basal transverse groove.

Subapterous females occur only in Zones B and C (Table I). The one unusually large specimen (Fig. 2) is from Marin Co., Calif., but other relatively small specimens occur in this same sample. The smallest specimen is from Rustler Park, Ariz. The two females from Douglas Co., Oregon, are exceptional in having the head width/ length ratio .68 and .71, higher than in any other specimens, and in having the wings very slightly longer than usual. These are the only two of the 27 short-winged females which are somewhat intermediate between micropterous and subapterous, though in wing length they can be regarded as subapterous. The mean head width/length ratio is not plotted on Figure 2, as it is only slightly different from that for the apterous females.

Description of apterous female. — Total length 0.7-1.0 mm. Headlength .253-.333 mm.; head width .61-.68 × head length (mean .64). Wings absent, but tegulae of nearly normal size; ocelli barely discernible, apparently absent in some specimens. Coloration and sculpturing as in subapterous female, head shape as in that form, the eyes even smaller; eyes removed from base of mandibles by .7-.9 × their own height, removed from vertex crest by 2.0-2.5 × their own height; minimum width of front 1.8-2.0 × eye height. Scutellum weakly separated from mesoscutum, with a barely perceptible basal groove.

As may be seen from Table I, apterous females occur in zones C (Arizona), D (Sierras of California), and D¹ (Mexico). Specimens from all three of these zones are exceedingly similar. Following the same trend as in the alate males and females, Arizona specimens average the largest, followed by California and Mexican specimens. The figures for head length are as follows: Arizona (zone C) .274-.333 (mean .297); California (zone D) .263-.304 (mean .290); Mexico (zone D¹) .253-.320 (mean .284).

Summary of sexual and morphic differences. — The males are readily separated from the females by the longer antennae, particularly the apical segment, which is more than twice as long as wide in the male, less than twice as long as wide in the female. In addition, the ocelli are well developed in both alate and apterous males, whereas subapterous and apterous females have the ocelli absent or barely discernible. Of course, in most females the sting is visible, and in many males the apices of the parameres can be seen.

Apterous males differ from alate males not only with respect to the wings, but also in having a decidedly more narrow head, smaller eyes, and slightly reduced ocelli. The difference in head shape of the two forms is particularly striking when the width is plotted against the length, as in Figure 1. It is interesting that the mean head width/ length ratio for the apterous males is the same as that for the alate females (.72); that is, the lower line in Figure 1 is the same as the upper line in Figure 2.

As compared to the alate females, the micropterous females have



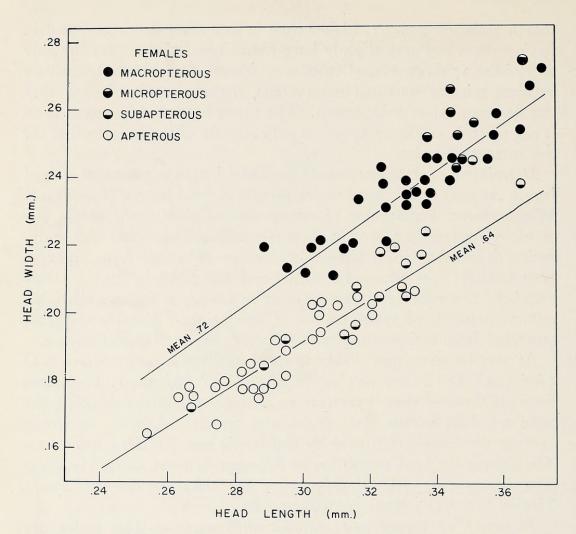


Fig. 2. Head width plotted against head length in the four forms of *Cephalonomia perpusilla* females.

the eyes very slightly smaller but the ocelli not noticeably reduced. The few available specimens (all from zone A, Table I) have the head, on the average, slightly wider than in the alate females, which is the opposite of what one would expect. As pointed out above, the mean head width/length ratio for the eight micropterous females is .75 (not plotted on Figure 1) while that for the many alate females is .72. It is probable that a larger sample would reveal no difference in this respect.

The subapterous females have the wings only slightly smaller than the micropterous females (about half to two thirds as long), a difference barely noticeable in these minute insects. Yet the head shape is different and the eyes and ocelli generally smaller in the subapterous females. Whereas the mean head width/length ratio is .75 in the micropterous females, it is only .655 in the subapterous females. There is, however, much variation in both these forms, so that in one subapterous female (from Douglas Co., Ore.) this ratio is the same (.71) as in one of the micropterous females (Santa Cruz Co., Calif.). However, there is considerable difference in wing length between these two specimens.

As compared to the subapterous females, the apterous females have a slightly smaller mean size, a mean head width/length ratio of .64, the eyes smaller and the ocelli so small they cannot be clearly discerned in many specimens. The wings are, of course, completely absent, although the tegulae are of nearly normal size. The line separating the mesoscutum and scutellum is very weak, the continuation of a trend begun in the subapterous females.

It may have been noted that there are, for most forms, fewer specimens indicated in Figures 1 and 2 than are listed in Table 1. This is a result of the fact that while wing length could be determined for all specimens, some specimens had the head missing or distorted to such an extent that accurate measurements could not be made. Also, not all specimens were measured in samples of one form from one locality of more than twenty.

Discussion. — That polymorphism for wing length occurs in both sexes of *Cephalonomia perpusilla* is not in itself surprising, for several different patterns of polymorphism are known to occur in this section of the family Bethylidae. That modifications in head shape and in size of the eyes and ocelli accompany modifications in wing length is also not surprising, since this has been reported for several polymorphic bethylids, and most aculeate Hymenoptera which are wingless also exhibit reduction in eye size and loss of the ocelli (e.g., female Mutillidae). It should be pointed out that the changes in head shape are not *merely* the result of decreased area and convexity of the eyes. In alate forms the whole side of the head is more bulging, presumably reflecting the much larger size of the optic areas of the brain, as compared to wingless and short-winged individuals. The apterous and short-winged forms of *Cephalonomia perpusilla* show only very slight reduction in thoracic structure, in contrast to other polymorphic species such as Cephalonomia gallicola and Scleroderma immigrans, in which the apterous individuals have the mesoscutum and scutellum completely fused and the tegulae absent.

What is unusual in *Cephalonomia perpusilla* is the presence of four distinct types of females. Although the two types with small wings differ only slightly in wing length, they nevertheless differ distinctly in head characters. The micropterous females are basically "alate" with

respect to the head, although their wings are only about .1 mm. long, about half as long as the hind tibiae (in fully winged individuals the wings measure .8-1.0 mm.). In the subapterous females the wings are further reduced only slightly, being .05-.07 mm. long, roughly one third the length of the hind tibiae. Yet this slight reduction seems to influence head structure profoundly, as though wing reduction had crossed a narrow threshold below which reduction in the organs of vision was essential.

What is still more surprising is that the four types of females apparently never occur together (Table I). Although macropterous females occur throughout the range (except, so far as known, in zone A), micropterous females are known only from zone A, subapterous females only from zones B and C, apterous females only from zones C, D, and D¹. These zones are arranged somewhat concentrically, zone A being more or less in the center of the range, closed in by an elongate zone B, which is followed by zone D, comprising the more mountainous parts of the northern half of eastern California. Zone C (Arizona) is interposed between B and D¹ toward the south and is the only zone in which three types of females are known to occur; in the North, zones B and D are contiguous. Zone D¹ (Baja California and Navarit) contains, like D, no short-winged females; nearly all females from this zone are apterous (7 alate females are known as compared to 62 apterous females). It looks very much as though the center of the range was the area of "greatest wingedness", and as one passes to the periphery in any direction the incidence of wing reduction increases.

It is tempting to erect hypotheses in an effort to explain this interesting situation. As I have noted, the closest relative of *perpusilla* appears to be the Palaearctic *formiciformis*, a species in which the males are always macropterous, the females macropterous or brachypterous in roughly a 1:1 ratio. Actually these short-winged females are more properly called micropterous, since the wings are scale-like and reach only to the anterior end of the propodeum; they are also like the micropterous females of *perpusilla* in lacking any substantial reduction in head width, eyes, and ocelli. Presumably the ancestor of *perpusilla* entered North America via the Bering land bridge and spread down the west coast, where selection favored smaller size and greater winglessness. The San Francisco Bay area may have served as a refugium and point of radiation for the species. As populations spread out from the center, selection favored still further reduction in the wings. Through changes in the genetics of wing inheritance, the males came to be winged or wingless in about a 1:3 ratio, the females winged or with wings reduced or absent in about a 1:3 ratio; furthermore the females came to show a distinct zonation with respect to wing-length types, the short-winged forms being entirely replaced by apterous forms at the periphery of the range. The actual figures are shown in Table I, where one notes with regret the absence of any records of males from zones A and B as well as far too few females to be sure of the present situation in the center of the range.

These 1:3 ratios suggest simple Mendelian inheritance, winglessness being dominant. I doubt very much if the situation is that simple. One notes, for example, that in the 69 available Mexican females, the winged : wingless ratio is 1:9. In the absence of careful sampling techniques and reared series, one simply cannot be sure what is happening. The genetics of *perpusilla* may not be radically different from that of *gallicola* as described by Kearns (1934), although clearly it is not quite the same for the characters of the female, since this sex is always apterous in *gallicola*.

One wonders if there is some particular selective advantage in wing dimorphism in these very small wasps. I have no new data bearing on this subject, but I suggest that this phenomenon may be related to the unusual mating behavior of these insects. Several persons have reported that in *Cephalonomia* and other gregarious Bethylidae the males emerge first and chew their way into the cocoons of the females (often their own sisters), fertilizing them before they emerge. This would result in much inbreeding unless males also flew about and mated with females elsewhere (since the females do mate again after emerging). The presence of two type of males, one fully winged and the other completely wingless, might be a mechanism for insuring that both inbreeding and outbreeding would occur. The same result would, of course, be achieved by alate males alone if they first mated with their sisters and then flew about and mated with other females, but there may be behavioral or ecological reasons why this is ineffective. It should be born in mind that these minute insects do not "fly" in the usual sense of the word. Their wings are slender and fringed with long setulae, and the venation reduced to a single short vein at the base of the fore wing. It seems quite certain that such insects are incapable of much sustained, directed flight, but after becoming airborne are merely wafted about by air currents. Since these wasps are restricted to fungi infested with ciid beetles, their available habitat is broken up into widely separated, strongly localized sites. The chances of a winged male alighting on (1) a fungus of suitable type, (2) in-

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fested with ciid beetles, (3) parasitized by this species of *Cephalono-mia*, and (4) containing females ready for mating must be fairly small. Thus the presence of wingless males may assure that most females will be mated and capable of producing female offspring, while the winged males may represent a mechanism for providing for enough outbreeding to offset the serious effects of continued inbreeding.

These remarks will apply equally well to the females if one substitutes "finding the host" for "mating." That is, the presence of winged females throughout the range may be a mechanism for spread of the species into new areas containing the ciid hosts, although many winged females are doubtless wafted into unsuitable locations. Wingless females presumably attack ciids occurring in the same or neighboring fungi, and such females might eventually exhaust the available hosts; at the very least, a given growth of fungus will die out after a period of time. Thus the occasional fertilized, winged females which locate a new supply of ciid beetles may play an important role in the survival of the species, while the wingless females are responsible for localized build-ups in the population.

Having said all this, I must state that I consider it possible that genetics is not directly involved in the polymorphism of Cephalonomia perpusilla. Salt (1952) studied the ichneumonid wasp Gelis corruptor, in which the females are always apterous, the males either macropterous or micropterous, and found that on a large host the males develop into fully winged individuals but on a small host, providing meagre nourishment, the males develop into micropterous individuals. In an earlier paper, Salt (1937) showed that Trichogramma semblidis produced apterous males when reared on one host, alate males when reared on certain other hosts of equal size (or actually smaller); in this case it is the quality of food rather than its quantity which effects morphogenesis. The polymorphic forms of the chalcidoid wasp Melittobia chalybii have also been shown to be conditioned by trophic factors: the larvae produced from the first few eggs laid on the host feed on the blood, and develop into a short-lived form with much reduced wings; larvae produced from eggs laid after the first few days feed on other tissues and develop into "typical" adults (Schmieder, 1933). In this instance the short-winged forms develop much more rapidly and permit a rapid population build-up within the large host.

Clearly such mechanisms as these may have strong selective value even if their basis is not "genetic" in the usual sense. These morphs are comparable to the castes of social insects rather than to genetically determined morphs; they are, however, "fortuitous castes", depending upon the nature of the host rather than upon food provided by adults of the same species. Perhaps the term polyphasy is more applicable to such cases, and the term "phase" better than "morph".

In the case of *Cephalonomia perpusilla*, there is no way of knowing at the present time whether the various forms are determined genetically or as the result of the influence of hosts of different sizes and species. John F. Lawrence writes that most of the fungus samples from which these bethylids were reared contained several species of ciids (up to six). However, the samples from Mexico, all of which were from *Ganoderma* rather than the more usual *Polyporus* and *Fomes*, contained only one or two species of ciids, and these ciids were only I mm. long or less. Thus the smaller size and greater degree of winglessness of the Mexican material might reflect these smaller hosts. The rearing of this species in series from specific hosts would be difficult but not impossible, and it is the only way in which these questions can be answered.

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