UNIPARENTAL, SIBLING AND SEMI-SPECIES IN RELATION TO

TAXONOMY AND BIOLOGICAL CONTROL

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ABSTRACT

Uniparental, sibling, and semi-species are defined and the taxonomic problems associated with them discussed, with special reference to parasitic Hymenoptera. It is emphasized that such species frequently are overlooked or ignored and considered to be so-called races or strains. Criteria are outlined concerning the recognition and naming of uniparental species of parasitic Hymenoptera. Such species are indicated to be much more common than realized and of considerable significance to biological control research. Likewise, sibling species of parasitic Hymenoptera are'rather common and support is developed for their recognition and formal naming whenever possible. The importance of semi-species to biological control research and application is emphasized. Examples are presented relating to each of the taxonomic categories considered.

This paper was prompted by nomenclatorial problems encountered during biosystematic studies of the genus <u>Aphytis.</u> These taxonomic studies were correlative to research on the use of <u>Aphytis</u> species in biological control of diaspine scale insects.

Taxonomists and biological control investigators share a major common interest. The identification and classification of organisms is crucial to both and both have contributed significantly to the other's field. (see: Sabrosky, 1955; Schlinger and Doutt, 1964). However, viewpoints and objectives differ somewhat. The end point for the taxonomist, briefly and broadly speaking, lies in classification and the determination of phylogenetic relationships. For the biological control worker the beginning and necessary basis for his research start with an accurate knowledge of the precise taxonomic identity of the orga- nisms involved. The taxonomist's interests tend to begin with and to range up-

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wards from the species level to supraspecific categories; the biological control researcher's interests and needs stress the species level but tend to range from this more toward sub-specific categories.

From the standpoint of practical biological control, we are vitally interested in whether natural enemies differ from one another, regardless of our ability to tell them apart morphologically. All grades of specific or subspecific gentically-based difference may be important. Obviously, different species which may be taxonomically indistinguishable can be quite distinct biologically. The importance of such sibling species to biological control has been discussed by DeBach (1960) and Schlinger and Doutt (1964). Many taxonomists tend to avoid, ignore or overlook sibling species because little can be done if only preserved specimens are available. Likewise, uniparental (or thelytokous) species are of real importance to biological control because they represent biological entities which are reproductively isolated. To taxonomists, they present thorny problems as far as the species concept is concerned; so frequently they are designated as so-called strains or races and not described or even considered to be species.

Sub-specific categories are not commonly dealt with by taxonomists, except in very thoroughly studied groups of fair-sized insects. Here, subspecies may be formally described. The term, semi-species, although not a taxonomic category, may be more useful in biological control research because it connotes partial reproductive isolation (Mayr, 1963; Rao and DeBach, 1969) which the terms race, strain or sub-species do not necessarily imply.

The following discussion regarding the aforementioned problem categories is primarily slanted towards the biological control workers' need to know whether populations of organisms are the same, or are significantly different genetically, regardless of how similar they are morphologically. In other words, the degree of reproductive isolation (with the concurrent implication of biological and/or ecological differences) is of most importance in biological control. I think most modern systematists have this opinion with respect to reproductive isolation and the usual biological species definition.

Before proceeding with the discussion it may be well to clarify briefly the concepts of species as we are considering them in this paper as shown in the following tabulation:

Biological species		Ethological (=uniparental, =ecological) species	
Main characteristics: Biparental reproduction; reproductive isolation from other species; free interbreeding within the species population.		Main characteristics: Uniparental reproduction; reproductive isolation from other species; significant differences in ethology or ecology from other species (see p.).	
Morphological species	Sibling species	Morphological species	Sibling species
Discernable morphological differences with other species.	No significant morphological differences.	Discernable morphological differences with other species.	No significant morphological differences.

From the preceding table it is clear that there are two types of biological species (morphological and sibling) and two types of ethological or uniparental species (morphological and sibling). Although the philosophical concepts concerning sibling and uniparental species are formidable, perhaps the practical procedure of applying taxonomic names is even greater in many cases. There are few practical problems when species exhibit significant morphological differences, whether they be either biological or uniparental species. However, with sibling species difficulties arise. When biological sibling species are involved, these difficulties can be solved by crossing tests where possible. In biological control research such is often the case. When uniparental sibling species are involved, more serious practical taxonomic problems arise, since reproductive isolation occurs among all individuals. The problem is compounded when there are two or more uniparental sibling species, each as alike as identical twins. A solution to this is suggested on p. 19 . Uniparental species will be discussed in the next section, keeping in mind that even though they can be either morphological or sibling species, the latter category will be emphasized in the subsequent section dealing with siblings. Here again, even though the discussion emphasizes sibling species, it should be noted that these can be either biological species or uniparental species, but not, of course, morphological species.

UNIPARENTAL SPECIES

Such species are doubtless much more common among parasitic Hymenoptera than is readily evident. Clausen (1962) states that some 30 genera of the parasitic Hymenoptera contain one or more species that reproduce uniparentally. From our own studies with the genus Aphytis and with species of the Signiphoridae it has been found, both from large series collected in the field and from live cultures maintained in the laboratory, that a surprisingly high proportion of species in these groups are uniparental. Table 1 shows

that of the 53 species of Aphytis whose sexuality is known, 16 (30 per cent) are uniparental. Other information supports this. Of the current Aphytis species cultures on hand at Riverside, which we have acquired from abroad at random with respect to sexuality, 8 out of 23 are uniparental, or about 35 per cent. An intensive one-year study of the Aphytis species present in southern Greece and Crete disclosed 9 uniparental species and 4 biparental species, or about 70 per cent uniparental (DeBach, 1964b). The study of 4 imported cultures of the Aphytis maculicornis·species complex by Hafez and Doutt (1954) indicated that at least 3 sibling species were involved, of which 2 were uniparental. Uniparentalism also is common in the Signiphoridae. From live culture studies, as well as from specimens in our collection and literature records, sufficient data are available on the sexuality of 41 species of Thysanus or Signiphora. Sixteen of these are uniparental, or about 40 per cent.

Table 1. - Sexuality and sibling status of species of Aphytis[a]

Group	No. of Species				Siblings
	Total	Sexuality status			
		Unknown	Biparental	Uniparental	
Vittatus	21	12	8	1	0
Proclia	15	2	7	6	6
Lingnanensis	21	4	15	2	8
Mytilaspidis	19	5	7	7	4
T o t a l s.	76	23	37	16	18

[a] Based upon an ongoing revision by the author and Dr. David Rosen, hence figures are not final. About 24 of the 76 species have not yet been formally named.

Even if the preceding data were not indicative of the incidence of uniparentalism in other groups of parasitic Hymenoptera, it is obviously a much more. general and important phenomenon in many respects than has been realized.

Uniparental species exhibit thelytokous parthenogenesis; females producing female progeny without fertilization by males. Occasionally males are produced by uniparental Aphytis and Signiphora, but thus far we have not found that they perform any required reproductive function. Rather, they appear to be genetic mistakes. Most current evidence indicates this to be the general rule. According to White (1964), "In this genetic system (thelytoky) fertilization is entirely suppressed. Males are absent from the population or

are only produced as occasional, non-functional anomalies, frequently inter-
sexual." I know of no hard data to dispute this statement. It has been shown
that the proportion of occasional males produced by uniparental species can
vary considerably with the season and that male production in some species
can be considerably increased - even made entirely male in a given genera-
tion - by subjection of young adult females, unemerged females, or perhaps
even female pupae, to high temperatures (Wilson and Woodcock, 1960;
McCoy, 1967). The evident explanation of this phenomenon is that abnormal
temperatures interfere with either the automictic or apomictic mechanisms of
thelytoky. Flanders (1945) has suggested that male production in uniparental
species is correlated with nutrition through the influence of environmental
factors on the primordial germ cells of the immature female. This hypothe-
sis needs collaborative proof.

Under either natural conditions or normal insectary temperatures
the proportion of males produced by uniparental species is low. Wilson and
Woodcock (1960) record the production of 126 males and 6 gynandromorphs to
14,996 females in a normal insectary culture of Ooencyrtus submetallicus
(Howard), or less than 1 per cent. In our uniparental culture of Signiphora
"borinquensis" my colleague, Dr. José R. Quezada, observed only an occasional
rare male, estimated at less than 1 per cent. A random check of 3,000 spe-
cimens from this laboratory culture yielded no males. All of the uniparental
species of Aphytis we have examined in any detail produce occasional males.
Comparative figures have not been kept, but from observation I would estimate
male production to range from about 1% to 5%. In Aphytis, any substantial
field sample consisting of less than 10% males (or perhaps even 20% males
depending on the season and temperature) could be considered to represent a
uniparental species. This is substantiated by the fact that in the many bi-
parental species of Aphytis studied, the average proportion of males is about
40 to 50 per cent.

In the parasitic Hymenoptera, I know of no valid records of cyclical
parthenogenesis (hetergony) such as occurs in the cynipids or certain aphids.
According to Flanders (1945), "The chalcid Ditropinotus aureoviridis exhibits
a unisexual overwintering generation and a bisexual summer generation.
(Phillips and Poos, 1921)" but all that Phillips and Poos (1921) actually state
regarding this is, "No males (of D. aureoviridis) normally occur in the first
generation of this species, and the females seem greatly to outnumber the
males in succeeding generations." Rather than indicating cyclical partheno-
genesis, their statement suggests thelytoky with high summer temperature-
induced production of some unessential males.

Also, there have been statements or suggestions in the literature
of reversal of uniparental parasite species to biparental reproduction or vice
versa, but there does not appear to be any rigorous experimental verification

of this. For example, Schlinger and Doutt (1964, p. 258) cite unpublished data by Schlinger and Hall to the effect that uniparental female Aphelinus, when cultured at 85°F (instead of the normal lower temperature), gave rise to 90% males "and thus a biparental stock was obtained". However, this statement does not mean what it seems. The authors have recently clarified this in conversation. Male Aphelinus were produced only when females were cultured at 85°F. These males were not known to be functional, but as long as the culture was maintained at 85°F a substantial proportion of males would be produced and it would appear to be a biparental culture. When the temperature was reduced to normal, only females were produced. Thus the stock actually never became biparental, it merely produced a high proportion of males at 85°F, presumably, as previously discussed (see Wilson and Woodcock, 1960; McCoy, 1967), due to interference of the high temperature with the automictic or apomictic mechanisms which otherwise result in thelytokous female production.

The occasional appearance of uniparental females in biparental cultures has been recorded by several authors (see Flanders, 1945). The possibility of accidentally mixed cultures in the laboratory or sympatric colonies (one being an "invader") in the field leading to competitive displacement of one or the other also is a likely explanation of a uniparental species "turning into" a biparental one or vice versa. In our experience it has occasionally happened in the insectary that one biparental species of Aphytis rapidly has "turned into" another morphologically distinct biparental species - due of course to accidental contamination and subsequent competitive displacement. Thus, it would appear to be safe to consider most, if not all, uniparental species of parasitic Hymenoptera to be essentially permanent entities in the sense that any species is permanent.

If a biological control specialist discovers a uniparental species, all is well from the immediate practical viewpoint. He can go ahead and treat it as a distinct species whether it is formally described or not. This was done with the mytilaspidis species complex in Greece (DeBach, 1964b, p. 13) wherein it was pointed out that apparently 4 sibling species occurred, all of which would run to A. mytilaspidis in the most authoritative key. Biological and experimental evidence indicated the 4 to be distinct species. One is biparental and the other 3 are uniparental. However, if a taxonomist acquires a large series from a field population which are all females, hence evidently uniparental, he may assign these to an already described biparental species, perhaps designating the uniparental population as a form or strain or even ignoring completely the fact that it is distinct biologically. It may thus remain buried for possible use in biological control for an indefinite time.

The major difficulty for the taxonomist is that uniparental species do not fully meet the most commonly accepted definition for biological species. The qualification of reproductive isolation obviously is completely met because

presumably no crossing whatsoever occurs. The qualification of free inter-
breeding among individuals of the species population is not met, obviously by
the same token, because each individual reproduces itself without crossing with
another. Thus, the dilemma arises that each individual meets a major quali-
fication of the species definition, that of complete reproductive isolation.

What should be done about this from the standpoint of practicing
taxonomy and biology? Some of the world's outstanding systematists consider
that uniparental species should be recognized and described as good species,
even though they admit difficult problems are involved. Ernst Mayr (1963)
makes the following comments: "To draw conclusions from the degree of mor-
phological difference on the probable degree of reproductive isolation is a
method of inference that has long been applied successfully to isolated popula-
tions in sexual organisms. There is no reason not to extend its application to
asexual types. It results in the combining in a single species of those asexual
individuals that display no greater morphological difference from each other
than do conspecific individuals or populations in related sexual species. "(p. 28).
"Another species class is represented by the 'parthenogenetic species' that
occur in many insects and lower invertebrates. Among the sibling species of
chrysomelid beetles described by Brown..., many are known only in the fe-
male sex and apparently reproduce strictly parthenogenetically. The same is
true of the so-called species of white-fringed weevils:..., of psychid moths of
the genus Solenobia..., and of isopods of the genus Trichoniscus... Some of
the 'biological races' of Trichogramma minutum also seem to be, at least in
part, parthenogenetic and reproductively isolated from each other.... Whether
or not to list such clones as sibling species depends on the criteria adopted
for 'species' in asexual organisms" (Chapter 15. p. 56). "Complete partheno-
genesis poses a taxonomic problem. The orthodox species criterion of inter-
breeding cannot be applied, because each clone is reproductively isolated not
only from the parental species but also from every sister clone. How to treat
clones and parthenogenetic species taxonomically must be decided for each
case. Where no essential morphological or biological differences exist, such
clones should be combined into collective species. Where a parthenogenetic line
has originated from a bisexual species by an irreversible chromosomal event
(for instance, polyploidy), it is usually advisable to consider it a separate
(sibling) species, even though the morphological difference is slight. " (p. 411).

Schlinger and Doutt (1964) discuss the 3 indistinguishable forms of
Prospaltella perniciosi in North America (1 biparental and 2 uniparental) which
are distinct biologically and which were referred to as geographical species by
Flanders (1950). They consider that these are sibling species, inferring that
they should be described. Flanders (1953) advocates the use of biological
characters in taxonomy to distinguish between "behavioral" species, and he
gives examples of the use of behavioral characters in a key to 10 species of
Coccophagus. But curiously, he does not use uniparentalism to separate species,

rather apparently considering it representative of a non-specific character, as indicated by his statement "bisexuality and unisexuality may be purely pheno-typic responses and of no value in taxonomy. " Thus for the 45 species he lists as having been studied, no information on sexuality status is given.

The consideration by taxonomists of uniparental forms as species is common in diverse groups. All of the bdelloid Rotifera, for example, are uniparental species. Many unicellular organisms lack apparent sexuality but have been described as good species. Certain higher plants which reproduce either only vegetatively or parthenogenetically likewise have been described as species.

Again to take an example from Aphytis, the uniparental species we have collected and studied seem to form just as discrete, uniform and identi-fiable populations as do the biparental species. There are hundreds of speci-mens of uniparental Aphytis chilensis (Howard) and A. chrysomphali (Mercet) in our collection from various parts of the world, yet the uniformity is remarkable. One might expect that with uniparental species rapid subspecific evolution would be going on in diverse habitats to produce a host of variants. Such does not seem to be the case. Mayr (1963, p. 27) puts it another way: "If mutation and survival were random among the descendents of an asexual individual, one would expect a complete morphological (and genetic) continuum. Yet discontin-uities have been found in most carefully studied groups of asexual organisms and this has made taxonomic subdivision possible. For this phenomenon I have advanced the explanation that the existing types are the survivors among a great number of produced forms, that the surviving types are clustered around a limited number of adaptive peaks, and that ecological factors have given the former continuum a taxonomic structure. Each adaptive peak is occupied by a different 'kind' of organism and if each 'kind' is sufficiently different from other kinds it will be legitimate to call such a cluster of genotypes a species. "

In view of the aforementioned data and discussion, it would appear particularly desirable and apropos that uniparental forms of parasitic Hymeno-ptera be formally described as new species, even in those cases where bi-parental forms exist which have identical appearing females, i. e. , where the uniparental species is also a sibling species. The latter is the most difficult case to handle from a practical taxonomic viewpoint. I propose an "ethological species concept" to cover all cases of uniparental species whether morphological or sibling species. In effect, this is already practiced in some cases. The old morphological species concept relying chiefly on morphological differences, as discussed by Mayr (1963), essentially rules out the recognition of sibling species; the biological species concept, involving interspecific reproductive isolation but intraspecific crossing, makes it difficult to include uniparental species, whereas the following ethological species concept should permit rational inclusion of such species.

The ethological species is based on ethological and biological charac-
teristics whose sum total is equivalent to those similar characteristics found
in recognized biological or morphological species. Briefly, any group of re-
productively isolated organisms that behaves like a biological species (that is,
plays a significantly different ethological or ecological role in the habitat)
should be considered to be a valid species.

The following biological tests can be applied to help distinguish such
species. Of course, if a uniparental population shows definite morphological
differences from the related biparental and/or uniparental species, the case is
even stronger and much more simple taxonomically.

Taxonomic Tests for Ethological Species

By comparison with the most closely related good morphological bi-
parental species in the same genus (if there are any - if not, compare with
other related groups), answer the following questions:

(1)   Does the uniparental population show little or no greater amount of mor-
      phological variation between individuals?

(2)   Are individuals within the uniparental population relatively uniform in
      their biology, ethology and ecology?

(3)   Does the uniparental population differ significantly in

      (a)   host (or food) specificity (including, for example, host stages or
            host organs attacked) or

      (b)   habitat specificity (including either preferences between habitats or
            within a habitat)?

(4)   Does the uniparental population show significant average differences in
      development, voltinism, diapause, fecundity, temperature tolerance, etc. ?

If the answer is yes to all or most of these questions, especially 1, 2 and 3,
it should be considered to be a valid species.

SIBLING SPECIES

This type of species has been defined as "morphologically similar
or identical natural populations that are reproductively isolated". (Mayr 1963).
It is generally accepted that the primary criterion of species rank of a natural
population is reproductive isolation. Thus sibling species are good species but
only can be recognized by biological differences, the best test of which is
complete reproductive isolation. However, other biological difference such as
host specificity, habitat specificity, fecundity, voltinism, diapause, longevity,

and temperature tolerance may be highly significant. Museum taxonomists thus rarely distinguish sibling species, whereas field biologists or ecologists are more likely to. It will be recalled that sibling species can be either biparental or uniparental.

The importance and significance of sibling species to biological control research has been emphasized before (Hafez and Doutt, 1954; DeBach, 1959, 1960; Schlinger and Doutt, 1964) and is well illustrated by the studies with Aphytis species. Suffice it to say that we now know that sibling species are common in Aphytis (about 25 per cent are siblings) and that any two such species can be importantly different biologically (see table 1). The adults of biparental Aphytis melinus DeBach and A. fisheri DeBach are indistinguishable. The former was imported from India-Pakistan, the latter from Burma, and both were colonized at the same time and in similar numbers against the California red scale in California. A. melinus has become an important part of the complex attacking the red scale, but A. fisheri did not persist.

It has been concluded on the basis of biological differences by Hafez and Doutt (1954) that there are at least 3 sibling species included under the name Aphytis maculicornis. These were imported into California and colonized against the olive scale but only one, the Persian-Indian form, became established and instrumental in successful biological control of the olive scale. These forms are currently undergoing taxonomic study but neither Dr. David Rosen nor I have yet found any morphological differences among them. One of them may be the true A. maculicornis, the others remain unnamed.

Somewhat the opposite happened with species of the aphid parasites, Trioxys. According to Hall, Schlinger and van den Bosch (1962), Dr. M. Mackauer in a 1959 revision of the European species of the genus Trioxys, placed most of them in species groups. To the pallidus group he assigned T. pallidus (Haliday), T. utilis Muesebeck, T. betulae Marshall, and T. pulcher Gautier and Bonnamour. On the basis of the morphological characters used to delimit the members of the pallidus group, Mackauer was unable to separate these four adequately. He later placed them all in synonymy with pallidus but suggested that biological studies might be essential to the proper identification of the individual species. Hall, Schlinger and van de Bosch conducted such studies on T. pallidus and utilis and found them to be distinct sibling species on the basis of reproductive isolation as well as on differences in host specificity, host habitat and slight cryptic morphological differences. Inasmuch as each attacks different economically significant aphid species, the great importance of recognizing and describing such species is evident.

There should be no reluctance on the part of a taxonomist to describe a sibling species as new. The term is really quite relative, anyhow.

Many of today's morphologically distinguishable species were once included with other species under one name. They could have been called sibling species then, had the fact of reproductive isolation been known. Once a sibling species has been recognized as being distinct, it is likely to receive further study which may well reveal morphological differences not perceived by earlier workers.

A good case in point involves some current studies nearing completion at Riverside on species of the Muscidifurax raptor complex which were imported into California from various parts of the world by Dr. Fred Legner. Studies of certain of these by McCoy (1967) and Legner (1969) indicated, on the basis of reproductive isolation and size variation, that several sibling species were involved but no reliable distinguishing morphological characters were confirmed. Drs. Marcos Kogan and Fred Legner are just completing an intensive study of these forms, utilizing both the phase microscope and the scanning electron microscope and can now separate them morphologically. Four new species will be described, all of which formerly were considered to be M. raptor (Kogan and Legner, 1969).

Biological control workers should never consider, a priori, that two similarly appearing populations in different geographical areas represent the same species, or at the very least they should maintain a reasonable doubt. It is better to err on the safe side, than it is to fail to import a natural enemy because it is considered to be already present. It was such lack of knowledge - understandable for the time - that precluded the importation of the most important parasites of the red scale into California for many years.

According to Compere (1961), during his trip to the Orient in 1932 an attempt was made to introduce into California all the parasites and predators found on California red scale with the exception of Aphytis species. This was because all the yellow species of Aphytis seen were thought to be A. chrysomphali, which already occurred in California. No attempt was made to introduce any of the Aphytis observed. It is now known that the species seen in India and elsewhere did not include chrysomphali. While returning with live material from India, by ship, Compere discovered in Hong Kong that a species of Aphytis was accidentally "contaminating" one of his scale cultures. It was believed to be A. chrysomphali and was destroyed. In the light of present knowledge, this species was doubtless either A. melinus DeBach or A. lingnanensis Compere, which are the two major species in biological control of red scale in California today and have virtually caused the extinction of chrysomphali there. This failure to recognize sibling species retarded the importation of A. lingnanensis into California by 16 years and of A. melinus by 25 years. A somewhat similar story involves the failure to recognize A. holoxanthus De-Bach as distinct from A. lingnanensis for some 12 years (DeBach, 1960). Otherwise it would have been obviously available for importation into Israel against the Florida red scale much earlier than was ultimately done.

Sibling species of parasites or predators which are unsuccessful in biological control in one country should not be ignored as possibilities elsewhere. For example, A. fisheri should not be precluded from trials in Israel or other countries merely because it was unsuccessful in California. It is well established that in cases involving ecological homologs, such as A. melinus and A. fisheri, one species may win over the other in one habitat, whereas the reverse may occur in a different habitat (DeBach, 1966). This is illustrated in California today by the interactions between A. melinus and A. lingnanensis Compere, which also are ecological homologs. A. melinus displaced, and now excludes, A. lingnanensis from interior climatic areas where the latter once was dominant; whereas in coastal areas lingnanensis remains dominant and virtually excludes melinus.

It is important to recognize that in all probability most of the so-called races, strains, stocks or forms of many authors actually are either uniparental species or sibling species or both. However, Flanders (1945) considered uniparentalism as a racial character of some biparental species of Hymenoptera; again (1950), he wrote of races of apomictic (i. e., uniparental) parasites. Hafez and Doutt (1954) demonstrated and stated that they were dealing with 3 sibling species under the name Aphytis maculicornis, yet they referred to them as strains throughout the paper. Perhaps this was a semantic problem, deriving from the fact that they did not formally name the species.

Another case where sibling species were demonstrated and recognized, but not described, and still mentioned as strains in the paper, involved a biparental and a uniparental population of oleander scale, both known as Aspidiotus hederae (Vallot) (DeBach and Fisher, 1956).

It seems apropos to conclude this section with the following quotes: "There are many more references to sibling species in the literature but those cited show some types of physiological, ecological, and ethological differences that might be expected and looked for by future systematists working with 'similar' species which are often called races, strains or forms. That the discovery of sibling species in biological control work should be carefully investigated and terminated with a full, formal description of the species seems both practical and desirable to the authors." (Schlinger and Doutt, 1964, p. 259).

"Those who adhere to a purely morphological species concept usually refer to sibling species as 'biological races.' By far the majority of the so-called biological races of the literature are now acknowledged to be sibling species. In Thorpe's words, they are forms 'which on every biological ground should be classified as distinct species.' ......there is no longer any reason why such cryptic species should be designated 'races'." (Mayr, 1963, pp. 56-57).

SEMI-SPECIES

This term has evolved to apply to conspecific populations which are partially reproductively isolated; perhaps to the extent of being thought of as incipient species (Mayr, 1963, p. 455). Obviously, such a term is not precise, hence it covers a broad range of reproductive isolation and genetic difference because the degree of isolation may range from very little to nearly complete. In biological control research, recognition and importation of a semi-species which is nearly completely isolated reproductively from the parental species, but has the same host preferences, may be essentially the equivalent to importation of a distinct species from a practical viewpoint. Sexual isolation might proceed rapidly to completion after the semi-species is colonized and one form would probably displace the other because they probably would be ecological homologs. According to competitive displacement theory, the winner should be more effective in population regulation (DeBach, 1966).

Another important possibility is illustrated by the two so-called strains or races of Comperiella bifasciata Howard, now established in California, which are morphologically indistinguishable. One, from China, develops in both the California red and yellow scales; the other, from Japan, does not develop on the red scale. These forms hybridize readily in the laboratory, so they must be considered as conspecific, but gene flow restriction is indicated in the field, hence they may be considered semi-species. Our field surveys and laboratory tests indicate that they apparently maintain their integrity as discrete "strains" in the field, even where sympatric. Parasites obtained from the yellow scale in the field are of the pure yellow scale strain; they do not develop on the red scale. We do not as yet understand how this may happen, especially since biological tests indicate that the red scale strain should be superior on both host scales, hence should displace the Japanese Comperiella. These results are still tentative but the possibility that semi-species can occur sympatrically, yet maintain their host-preference distinctness and genetic integrity in spite of some hybridization, is of considerable interest to biological control. It may also be illustrative of the possibility of sympatric speciation which Mayr (1963) argues against.

Semi-species can only be distinguished and evaluated by crossing tests between different population cultures. Our studies (Rao and DeBach, 1969) with the Lingnanensis group of Aphytis revealed a complex relationship between various species and semi-species obtained from different sources, which is of considerable significance both to taxonomy and to biological control. The results are depicted in Fig. 1.
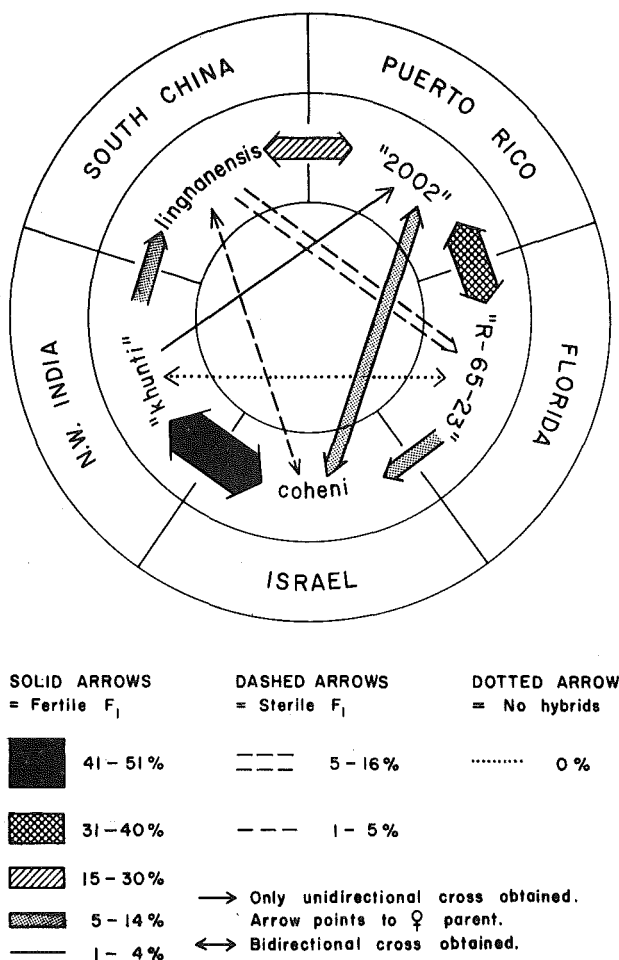
SOLID ARROWS = Fertile F_1 | DASHED ARROWS = Sterile F_1 | DOTTED ARROW = No hybrids

	41 - 51%		5 - 16%		0%
	31 - 40%		1 - 5%		
	15 - 30%				
	5 - 14%				
	1 - 4%				

→ Only unidirectional cross obtained.
Arrow points to ♀ parent.
←→ Bidirectional cross obtained.

Fig. 1 - Crossing relations within the Lingnanensis group of <u>Aphytis</u>, showing per cent of F_1 progeny which are female and the nature of the F_1 hybrids. Normal intra-species F_1 progeny production consists of 60 - 75% females. (From Rao and DeBach, 1969).

All Lingnanensis group species studied are siblings, virtually indistinguishable from one another. <u>A. coheni</u> (from Israel ex <u>Aonidiella aurantii</u> (Mask.)) and <u>A.</u> "khunti" (from N.W. India ex <u>Aonidiella orientalis</u> Newst.) hybridize readily in the laboratory, yielding fertile hybrids. However, the hybrid sex-ratio and progeny production is somewhat lower than normal, and the two show different crossing relations with <u>A.</u> "2002" (from Puerto Rico ex <u>Aspidiotus destructor</u> Sign.), <u>A. lingnanensis</u> (from S. China ex <u>A. aurantii</u>)

and A. "R-65-23" (from Florida ex Unaspis citri (Comstock)), indicating that they are genetically rather distinct and should be considered as weak semi-species with respect to each other.

Lingnanensis and "2002" hybridize fairly readily (although considerably less so than coheni and "khunti"), but show great differences in their crossability with coheni and "R-65-23". They are considered to be semi-species.

The fact that lingnanensis produces only a few sterile hybrids with coheni confirms the genetical incompatibility between the two, and confirms their distinct species status.

When crossed with "khunti", lingnanensis produces very few hybrids, but they are fertile. However, the two show great differences in their crossability with coheni, "2002" and "R-65-23." Hence, "khunti" and lingnanensis are considered species with respect to each other.

Although "2002" produces fertile hybrids with coheni and "khunti," it does so rarely and only with laboratory manipulation. Therefore "2002" is considered a good species with respect to coheni and "khunti".

On the basis of limited information, "R-65-23" is considered a semi-species with resepct to "2002," with which it hybridizes rather readily. It produces sterile hybrids with lingnanensis and does not hybridize with "khunti" so is considered a distinct species with respect to these two. "R-65-23" and coheni appear to exchange genes to such a very limited extent that hybridization in nature is highly questionable, so they also are considered good species with respect to each other.

The simplest generalizations that can be drawn from this complex situation are that the five sibling forms represent three biological species, A. coheni (with "khunti" as a semi-species), A. lingnanensis (with "2002" as a semi-species) and "R-65-23" (with "2002" as a semi-species). Thus, although A. lingnanensis and "R-65-23" are considered to be distinct biological species, they are linked through the mutual semi-species, "2002".

Aside from the fact that well developed semi-species may have significant biological differences important in biological control, the advantage in detecting and recognizing semi-species lies in the possibilities for genetic enrichment and manipulation of the species being used in biological control programs. The importance of genetics and of so-called races and strains (which may well be semi-species) in biological control research has been emphasized by several authors (Clausen, 1936; Smith, 1941; Flanders, 1950; DeBach, 1958; DeBach, 1964, pp. 449-52; Simmonds, 1963;and Force, 1967). The potential for exploratory research in genetic manipulation and in biological control importation appears great.

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