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Systematic and Evolutionary Implications of Parthenogenesis in the Hymenoptera

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SYNOPSIS. Two types of parthenogenesis, arrhenotoky and thelytoky, exist in the Hymenoptera. Arrhenotoky, the development of males from unfertilized eggs, is present in all wasps and bees. Thelytoky, the development of diploid females from unfertilized eggs, is present in a few species. Two types of thelytoky, apomixis and automixis, are known. Most thelytokous Hymenoptera are automictic. No meiosis, only mitosis, occurs in apomixis. Meiosis does occur in automixis, allowing crossing-over and segregation of genes. Advantages of thelytoky are that heterotic combinations become fixed, gene loss is reduced, and reproduction requires only a single individual. One advantage of arrhenotoky is that genetic load in males is eliminated. Both environmental and genetic factors contribute to sex-determination in the haplodiploid system of Hymenoptera. Haplodiploidy can facilitate the evolution of social behavior. Parthenogenesis creates some taxonomic problems since thelytokous clones do not fit the generally accepted biological species concept. Some members of bisexual populations probably acquire thelytoky, forming their own clones, races, or species.

All Hymenoptera thus far reported are parthenogenetic. Male Hymenoptera develop by arrhenotoky from unfertilized eggs (Whiting, 1945) and are genetically haploid. In some species males are entirely absent and females develop by thelytokous parthenogenesis from other females (Whiting, 1945).

CYTOLOGICAL MECHANISM OF ARRHENOTOKY

The cytological mechanism of arrhenotoky has been intensively studied in the parasitic braconid *Bracon hebetor* by Speicher (1936). Oogenesis proceeds normally in the female, producing an egg with a haploid set of chromosomes. The inner nucleus forms the definitive egg nucleus and the middle two polar nuclei fuse with the outer nucleus and degenerate. Unfertilized egg nuclei apparently develop similarly to those of fertilized eggs prior to the first cleavage division. Cleavage is approximately synchronous until the eleventh division and there is no doubling of chromo-

some number in fertilized or unfertilized eggs.

Somatic polyploidy in males is common and in ants it may reach octoploidy. In ants autodiploidization takes place early in development, producing tissue that is somatically diploid, but genetically haploid (Whelden and Haskins, 1953). However, some tissues remain haploid. Nerve cells of *Telenomus* males have ten chromosomes while those of females have twenty (Dreyfus and Breuer, 1944, cited in da Cunha and Kerr, 1957) and brain ganglia cells of *Melipona* males have nine chromosomes while the ganglia cells of *Melipona* females have eighteen (Kerr, 1948, cited in da Cunha and Kerr, 1957).

Spermatogenesis is different in the Hymenoptera compared to that of most insects. Early workers reported that meiosis consists of two divisions, an abortive first division in which the nucleus does not divide and a second division that is equal. In some species enucleate "cytoplasmic buds" are described during meiosis (Torvik-Greb, 1935; Peacock and Gresson, 1931). These cytoplasmic buds are inter-

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preted as remnants of the abortive first division. Walker (1949), however, found that in the sawfly *Pteronidea ribesii*, cytoplasmic buds are products of mechanical interference during cell division. Whiting (1947) reports that in four species of sphecid wasps there is only a single mitotic division that produces two functional sperm. White (1954) concludes that there is a single mitotic division between the last gonial division and sperm formation in all Hymenoptera. In the bees the division is cytoplasmically unequal, so that only one functional sperm is produced (Whiting, 1947).

Diploid males occasionally arise in some species (Speicher and Speicher, 1940). Such males in *Bracon hebetor* show inherited characters from both parents, and are produced by inbreeding in the laboratory (Whiting and Whiting, 1925; Whiting, 1927). Spermatogenesis of diploid males of *Bracon* follows the same course as in haploid males, except that there are 20 chromosomes instead of 10. There is a single mitotic division, and no synapsis takes place. Two diploid sperm are produced (Torvik-Greb, 1935). Such males are not completely sterile, and when mated with diploid females give rise to triploid daughters (Bostian, 1936).

On a theoretical basis, arrhenotokous males should be four times as variable as their sisters, if no dominance or epistasis is present (Eickwort, 1969). Very little biometrical work has been done to substantiate this prediction. Eickwort (1969) studied biometrically the variance of males (haploid) and queens (diploid) of the social wasp *Polistes exclamans*. This species has only one founding queen per nest and a low frequency of transfer of adults between nests. On the basis of ten characters, males were more variable than the queens, consistent with the theoretical prediction. However, Daly (1971) compares wing lengths between sexes of the bee *Ceratina acantha* and his data are inconsistent with Eickwort's results. Daly's investigations involve nine localities in the western United States and his measurements are

transformed to natural logs (Lewontin, 1966) before variance ratios are computed. In each case the male variances ranked less than those of females. At four localities the differences were significant at the five percent or less level.

EVOLUTIONARY ADVANTAGES OF ARRHENOTOKY

Arrhenotoky and the haplodiploid system confer a considerable advantage to the Hymenoptera. Some advantages of diploidy are protection against the effects of somatic mutations, heterozygosity, and recombination, if the average fitness of the diploid population is greater than that of a haploid one (Crow and Kimura, 1965). One disadvantage of diploidy is the genetic load. Since Hymenoptera males are genetically haploid, recessive lethal mutations do not accumulate in populations. The genetic load in males is reduced to a very low level. Females in the Hymenoptera possess advantages of diploidy, while males obviate the disadvantageous aspects.

Details of the origin of arrhenotoky are not known. Whiting (1945) postulates that arrhenotoky arose in an ancestral hymenopteran species by crossbreeding between a bisexual population and a thelytokous offshoot of that population. The viable fertile types of such crosses should be, according to Whiting, the following: (1) both sexes bisexual; (2) thelytokous females; and (3) bisexual females and arrhenotokous males. Alternatively, arrhenotoky may have originated by the accumulation of recessive mutant genes for parthenogenesis, which would gain expression in an egg laid but not fertilized, and be favorably selected because of reduction in the genetic load.

CYTOLOGICAL MECHANISMS OF THELYTOKY

Thelytoky does not seem to be a common form of reproduction. Table 1 shows families and species of Hymenoptera in which thelytoky is known to occur. However, if more data on reproduction were available, thelytoky might prove to be

TABLE 1. *Hymenopteran species known to reproduce entirely or in part by thelytoky*

Tenthredinoidea
Diprionidae
<i>Diprion polytomum</i> (Smith, 1941)
Tenthredinidae
<i>Strongylogaster macula</i> (Peacock and Sanderson, 1939)
<i>Pristiphora rufipes</i> (= <i>P. pallipes</i>) (Comrie, 1938).
Ichneumonoidea
Ichneumonidae
<i>Venturia canescens</i> (= <i>Nemeritis canescens</i>) (Speicher, 1937)
Braconidae
<i>Perilitus coccinellae</i> (Balduf, 1926)
<i>Bracon hebetor</i> (= <i>Habrobracon juglandis</i>) (Speicher, 1934)
Chalcidoidea
Trichogrammatidae
<i>Trichogramma semifumatum</i> (Bowen and Stern, 1966)
Signiphoridae
<i>Thysanus</i> spp., <i>Signiphora</i> spp. (DeBach, 1969)
Eulophidae
<i>Aphytis</i> spp. (DeBach, 1969)
<i>Prospaltella perniciosi</i> (Flanders, 1953)
Encyrtidae
<i>Ooencyrtus submetallicum</i> (Wilson and Woolcock, 1960)
<i>Tropidophryne melvillei</i> (Doutt and Smith, 1950)
<i>Pauridia peregrina</i> (Flanders, 1965)
<i>Habrolepis rouxi</i> (Flanders, 1946)
<i>Encyrtus fuliginosus</i> (Flanders, 1943)
<i>Trechnites psyllae</i> (Hagen, 1970, personal communication)
Cynipoidea
Cynipidae
many cynipid spp.
Bethyloidea
Bethyilidae
<i>Scleroderma immigrans</i> (Keeler, 1929a,b)
Formicoidea
Formicidae
<i>Lasius niger</i> (Bier, 1952)
<i>Atta cephalotes</i> (Tanner, 1892)
<i>Aphenogaster rudis</i> (Haskins and Enzmann, 1945)
<i>Oecophylla longinoda</i> (Ledoux, 1949a)
<i>Formica polyctena</i> (Otto, 1960)
<i>Crematogaster</i> spp. (Soulié, 1960)
Apoidea
Apidae
<i>Ceratina acantha</i> (Daly, 1971)
<i>Ceratina dallatorreana</i> (Daly, 1966)
<i>Apis mellifera</i> (Mackensen, 1943; Tucker, 1958)
<i>Apis mellifera capensis</i> (Anderson, 1963)

more prevalent, *e.g.*, thelytoky is common in the eulophid genus *Aphytis* and in the Signiphoridae (DeBach, 1969). Of the 53 species of *Aphytis* whose method of reproduction is known, 16 (30 percent) are thelytokous; 16 (40 percent) of the 41 species of *Thysanus* or *Signiphora* are thelytokous. According to DeBach (1969), even when a high proportion of males is experimentally produced in a laboratory culture of thelytokous *Aphytis*, the population remains reproductively thelytokous.

Usually one, sometimes two, mitotic divisions occur in apomictic thelytoky.

Meiosis does not occur, thus chiasmata are not formed and the diploid number remains unchanged (White, 1954). This type of mechanism appears to be fairly common in the parthenogenetic Diptera and Coleoptera (Suomalainen, 1962), particularly in weevils (Suomalainen, 1940, 1962). Apomictic thelytoky occurs in the sawfly *Strongylogaster macula* (Peacock and Sanderson, 1939).

Meiosis does occur in automictic thelytoky. The chromosomes pair at zygonema, chiasmata are formed, and crossing over and reduction occur. The diploid

state is restored by fusion of two of the resulting four nuclei, or by fusion of two cleavage nuclei (Suomalainen, 1962). This type of mechanism has been reported in the sawflies *Diprion polytomum* (Smith, 1941) and *Pristiphora rufipes* (Comrie, 1938), in the ichneumonid *Venturia canescens* (Speicher, 1937), and in individuals of several races of the honey bee, *Apis mellifera* (Tucker, 1958).

EVOLUTIONARY ADVANTAGES OF THELYTOKY

Heterozygosity is retained in apomixis. Since there is no pairing and segregation of chromosomes, mutations can accumulate. Only mutations that are dominant lethals will be immediately eliminated. Apomixis theoretically can lead to the eventual formation of two sets of chromosomes that are quite unlike each other. Also, there is no mechanical barrier to the establishment of polyploidy (White, 1954). In the parthenogenetic weevils apomixis was followed by polyploidy (Suomalainen, 1958), and the same has apparently happened in the psychid moth *Solenobia* (Seiler, 1946, cited by Suomalainen, 1958).

In automixis, homozygosity will be produced only if cleavage nuclei fuse in pairs. Such fusion is comparatively rare, with most examples being in the whiteflies and the scale insects (White, 1970). Once homozygosity is reached, heterozygosity can arise only by mutation. In one generation homozygosity will be restored (Suomalainen, 1962). However, a mutant gene has a probability of 0.5 of being passed from mother to daughter, so that individuals in a population, although homozygous, could have different genotypes.

Heterozygosity, on the other hand, will be produced if the meiotic nuclei fuse and restore the diploid condition. A diploid organism has two homologous sets of chromosomes, x and y . During meiosis four nuclei are produced. A pair of nuclei are derived from chromosome set x , and a pair from set y . Two nuclei from set x , or two nuclei from set y , are sister nuclei, while a

nucleus from set x and one from set y are non-sister nuclei. White (1970) points out that two types of fusion are possible. In the first type, a pair of sister nuclei fuse. In the second type, a pair of non-sister nuclei fuse. If each chromosome arm forms a single chiasma, fusion of sister nuclei will maintain heterozygosity for loci distal to the chiasma. Similarly, with a single chiasma per chromosome arm, fusion of non-sister nuclei will maintain heterozygosity between the centromere and most proximal location at which chiasma-formation, or crossing-over, occurs.

Speicher, Speicher, and Roberts (1965) studied segregation of a recessive lethal mutant gene in X-irradiated wild-type females of the thelytokous ichneumonid *Venturia canescens*. The lethal gene behaves as a point mutation and produces 12.77 percent homozygous recessive eggs. Homozygous normal females also occur in about the same proportion. On the basis of these results, Speicher *et al.* (1965) conclude that, except for recessive genes that are located close to the centromere, selection against recessive lethals in *Venturia* must be slower than in arrhenotokous species, but faster than in panmictic populations of bisexual diploid species.

Thelytoky offers certain evolutionary advantages. Heterotic combinations may become fixed. Beneficial mutations are passed from individuals to their progeny. Genetic recombination and segregation can occur in automixis. Gene loss is reduced to a minimum. Except in the case of close linkage, thelytokous hymenopterans are in a better position than bisexual ones to build up coadapted complexes (Crow and Kimura, 1965). Also, since mating is not necessary, no time is lost in searching for suitable mates; a single female can disperse to a new location and reproduction can begin immediately after the maturation of the oocytes.

Since thelytoky does not require more than one animal to produce offspring, species with thelytoky have an advantage over bisexual species when population numbers are low. Tomlinson (1966) calculated

that according to the probabilities of the Poisson distribution, the advantage of parthenogenesis is very high when the probability of contact between more than one individual of the same species is low, but drops to low values when a given individual can encounter seven or more conspecific individuals of either sex. Tomlinson believes that parthenogenesis is advantageous to animals with low vagility, and to animals that are at the periphery of a species distribution. White (1964) postulates that thelytoky gives bisexual species with ordinarily poor vagility a chance to escape local climatic changes by extending their range. White further states that thelytokous species are incapable of colonizing new environments, which strong-flying bisexual species often must be able to do, and that thelytoky consequently is unlikely to arise in a species with high vagility.

In the weevil genus *Otiorrhynchus*, the parthenogenetic species that occur in northern Europe are found mostly in the regions covered by the Würm Ice Age, while related bisexual species are found mostly in areas that have remained outside the glaciation (Suomalainen, 1962). While it may be argued that weevils have comparatively low vagility and are not colonizing rapidly, the studies of Daly (1966, 1971) indicate no clear relation between vagility and thelytoky in bees of the genus *Ceratina*. *C. dallatorreana* was accidentally introduced in the Sacramento Valley of California at least as early as 1949. Subsequent collection records trace a rapid spread southward, covering 170 miles in nine years. The species now occupies most of the Sacramento Valley and portions of lower San Joaquin and Santa Clara Valleys. In the Mediterranean region, *C. dallatorreana* is bisexual, but males are extremely rare in California and thelytoky is present. On the other hand, *C. acantha* is a bisexual species widespread in California and the Pacific Northwest. In Los Angeles County, thelytokous populations have been found in three separate areas. Judging by the absence of males in earlier collections, at least two of the areas

have been occupied exclusively by thelytokous colonies for at least 50 years. During this time bisexual populations have also been in existence in nearby ranges of hills and mountains. Nothing is known of the dispersal behavior of bees in this genus, but their use of weedy plants requires active flight for food and nesting substrate. The thelytokous *C. dallatorreana* evidently rapidly colonized a new and unexploited environment while the thelytokous populations of *C. acantha* have apparently remained static. In these cases, the presence or absence of competing populations seems more important to the spread of the thelytokous form than its relative vagility.

Although the advantages of thelytoky in species with low vagility are apparent, it does not follow that species with high vagility should be unable to utilize the same advantages. Even though the genotype of a thelytokous species is fixed when thelytoky arises, there is enough mutation and, in automixis, segregation to give rise to different gene combinations. Certain of these combinations may be adapted for colonizing new, unexploited environments. In a new and possibly harsh environment bisexual species would have to establish themselves in sufficient numbers so that mates could be found. Thelytokous species would not be faced with that problem.

CYCLICAL PARTHENOGENESIS

A number of species of one group of Hymenoptera, the cynipids, utilize the benefits of both arrhenotoky and thelytoky in an alternation of generations (cyclical parthenogenesis or heterogony). Typically, there are two generations per year, a bisexual and a thelytokous one. For example, in some species of *Cynips*, the bisexual males and females emerge from oak galls in the spring, mate, and lay eggs. The eggs develop in galls during the summer, and give rise to females, which emerge in winter. These females parthenogenetically produce the males and females of the next bisexual generation, and the cycle begins again (White, 1954). In *Neuroterus* (Don-

caster, 1910, 1911, 1916), each female gives rise parthenogenetically to either males or females, but not both. These males and females form the next bisexual generation, and the cycle begins again. In some species, such as *Andricus operator*, the same parthenogenetic female produces both males and females, while in others a given parthenogenetic female produces progeny that is mostly, but not entirely, of one sex (White, 1954). Recessive mutations are removed during the sexual phase, when climatic conditions are favorable for searching out mates. The necessity of mating is removed during the parthenogenetic phase, when climatic conditions are harsher. Some cynipids have lost the sexual generation entirely.

Another form of alternation of generations may occur in ants. The life cycle of the African weaver ant, *Oecophylla longinoda*, appears to consist of an alternation between bisexual queens and apomictic workers. The cycle, described by Ledoux (1949a; 1949b) and summarized by Wilson (1970) is as follows. After mating, queens attempt to start colonies, but most of these attempts are unsuccessful. New colonies are started by groups of workers, who leave a colony to construct new nests. Most worker eggs develop into other workers, but some develop into queens. Winged queens sometimes accompany the workers that start new colonies. These queens give rise to workers if fertilized and to males if unfertilized. Thus, the queens produce workers and males, and the workers produce other workers and queens. However, these details are subject to some question (See Wilson, 1970).

According to Anderson (1963), thelytokous workers are also known in the Cape honeybee, *Apis mellifera capensis*. Workers present in normal colonies rapidly increase in number when the queen is removed. The colony may be sustained for as long as four months without a queen or drones. New queens can be reared from the eggs laid by the workers. Once established, the queens produce drones and workers in the normal manner.

ENVIRONMENTAL AND GENETIC DETERMINATION OF SEX

In most bisexual Hymenoptera, the question of whether a given egg will develop into a male or a female depends on a combination of environmental and genetic factors. A female can apparently decide from environmental stimuli whether or not to fertilize an egg. Queen honeybees will lay unfertilized eggs in the larger drone cells and fertilized eggs in the smaller worker cells (Flanders, 1946). Females of the alfalfa leaf-cutter bee, *Megachile rotunda*, lay female eggs in the deeper inner tunnels of the nest and male eggs in the shallower outer tunnels. During oviposition of the female eggs the female ceases contracting the abdomen when two-thirds of the egg is pumped out. A pause lasting about one-fifth of the total oviposition time ensues, following which the egg is laid. No such pause occurs in the laying of male eggs (Gerber and Klostermeyer, 1970). Another bee, *Agapostemon nasutus*, lays an unfertilized egg between every two fertilized ones in the cells of its nest (Roberts, 1969). Similarly, *Dahlbominus fuscipennis*, a species parasitic on the spruce sawfly normally lays fertilized eggs on large hosts and unfertilized eggs on small ones (Ullyett, 1936). Other examples are discussed by Flanders (1946, 1965).

However, in at least one known case the female has no behavioral control over fertilization. Wilkes (1964) found that the normal sex ratio of 92 percent females in the parasitic eulophid *Dahlbominus fuscipennis* can be dropped to five percent by selectively breeding for a sex-limited gene that is transmitted by females to their progeny. The low sex-ratio can be maintained over a number of generations, and is not influenced by the environment or the host.

Two major hypotheses have been proposed to explain the genetic basis of sex-determination in the Hymenoptera. One, developed by Whiting (1940, 1943) and usually called the multiple allele hypothesis, postulates the existence of a series of alleles that function in sex-determination.

If these alleles are designated as x_1, \dots, x_n , then any diploid heterozygote ($x_1/x_2, x_2/x_n$, etc.) is a female, while any haploid hemizygote (x_1, x_2, x_n) or any diploid homozygote ($x_1/x_1, x_2/x_2, x_n/x_n$) is a male. This hypothesis is consistent with the situation in *Bracon hebetor*, in which Whiting found nine sex-determining alleles. Seven to 12 alleles have been found in the honeybee, *Apis mellifera* (Mackensen, 1951; Laidlaw, Gomes, and Kerr, 1956), and are estimated by Kerr (1967) to occur in equal frequencies. Kerr and Nielsen (1967) found that inbred honeybee diploids, homozygous for x alleles, are males that possess some female-like characters.

The multiple allele hypothesis cannot explain sex-determination in species of meliponids, in which diploid homozygosity for sex alleles produces normal females in some species and sterile females in others (Kerr and Nielsen, 1967). Da Cunha and Kerr (1957) have proposed a general hypothesis that would explain sex-determination in both the meliponids and the species with multiple allele systems. According to this hypothesis, there is a series of male-tendency genes m with non-additive effects and a series of female-tendency genes f with additive effects. The male-tendency genes will produce the same effects in the hemizygote m and the homozygote mm . The effects of the m genes in either case can be represented by the constant M . The effects of the f genes, being additive, would then be F in the hemizygote and $2F$ in the diploid homozygote. Sex is determined by the relationship $2F > M > F$, in which $2F > M$ produces females and $M > F$ produces males. The multiple allele effects observed in *Bracon* and *Apis mellifera* are explained as being due to f genes that have lost their additive effects in the homozygous state but still retain it in the heterozygous one.

Although the multiple allele system is not found in the meliponids and other related apids such as *Bombus* (Kerr, 1967), a multiple allele system is involved in caste determination of *Melipona* (Kerr and Nielsen, 1966). Only a double

heterozygote for two genes, $x_1^a x_2^a, x_1^b x_2^b$, can become a queen if enough food is provided during the larval stage. Homozygotes for the two genes become workers.

EVOLUTION OF SOCIAL BEHAVIOR

The haplo-diploid system and male arrhenotoky provide a unique opportunity for the development of social behavior. Consider the number of genes which related individuals have in common. Mothers and their daughters will have one-half of their genes in common, but sisters in the haplo-diploid system will have three-fourths of their genes in common. The greatest degree of relationship will accordingly be between sisters (Crozier, 1970). According to Hamilton (1964b), it is to the advantage of the female offspring of a given mother in an aggregation or semisocial group to help their mother provision new cells and help produce more sisters, since this would lead to more of the offsprings' genes being present in the population. However, in the social Hymenoptera, the genes of the sister workers are not directly incorporated into the population, since only the queens lay eggs. Hamilton (1964a, 1964b) points out that although a gene may increase the fitness of its bearer above the average, selection will not be positive if such increase is at the expense of related individuals, since relatives carry replicas of the same gene through common ancestry. On the other hand a gene may receive positive selection even if it is disadvantageous to its bearer, provided it confers a sufficiently large advantage to the relatives of the bearer.

Censuses of adult and immature stages of several species of social Hymenoptera seem to substantiate the above hypothesis. Michener (1964) counted the number of immature individuals and females in colonies of the halictine bees *Pseudagapostemon*, a subsocial bee, *Augochloropsis*, a semisocial bee, and *Lasioglossum*, a social bee. He also considered published accounts of censuses of polybiine wasps and of

ants. By dividing the number of immatures by the number of females in a given colony, an index of the ability of the female to rear young could be obtained. It was found that the smaller the colony, the more progeny there are per female, and that isolated females living alone produce the most progeny per female. The social insects have fewer progeny per total females in a colony, but have the most progeny per reproductive female. This, together with protection of reproductives and colony homeostasis, confers a great evolutionary advantage to the social Hymenoptera.

SYSTEMATIC IMPLICATIONS OF PARTHENOGENESIS

The significance of parthenogenesis in evolutionary biology has been overshadowed by the emphasis on vertebrates. Numerically speaking, 50,000 species of vertebrates exist compared to 100,000 species of Hymenoptera (Storer and Usinger, 1957; Borror and DeLong, 1964). An appreciable fraction of living creatures do not evolve as biparental organisms with both sexes diploid, yet these creatures are considered as equivalent to biological species. Taxa in which thelytoky alternates with bisexual reproduction are also treated as equivalent to biological species, but in fact they may possess peculiar attributes. Kinsey (1936) proposed a most unconventional explanation for the evolution of species of *Cynips* which bears reinvestigation with modern techniques.

When reproduction is entirely thelytokous, the biological species concept is no longer applicable, because each individual and its descendents are genetically isolated from all other individuals. The question to be asked is whether thelytokous clones or groups of clones should receive formal taxonomic names. In practical terms, names are needed for groups in which morphological differences can be observed. Thelytokous entities can only be named on the basis of phenetic resemblance, since no gene flow at the population level is involved. Phenetic analysis by numerical

taxonomy would seem to be the method of choice for establishing species, but once the species are delimited either a phenetic or a cladistic approach could be used for the higher classification.

The most difficult decisions involve thelytokous clones which are morphologically similar to biparental populations. The taxonomist accustomed to biparental species usually refers informally to such clones as races or strains. His rationale is a practical one. The clones may be virtually indistinguishable from the biparentals in collections and, if differences do exist, the number of different clones is potentially large. It is also possible that such clones are short-lived and of little phylogenetic consequence.

DeBach (1969), however, has argued persuasively that thelytokous clones are of ecological importance, especially in biological control, and require names for the purpose of information retrieval. By proposing an "ethological" species concept and a series of taxonomic tests, DeBach has attempted to facilitate the recognition of thelytokous species. The task is also made easier by the interesting properties of such populations. They are surprisingly uniform in morphology, and are often allopatric with respect to related species. The latter attribute is further evidence of their ecological significance, because it may be explained in terms of competitive exclusion. We are unaware of cases where thelytokous females are facultative and reproduce normally when inseminated. Thelytoky is probably a uni-directional irreversible process, that is, occasional normal females of a biparental species become thelytokous and, *ipso facto*, members of the related thelytokous species. This kind of "speciation" seems absurd in the context of current thought, but it only reflects the limited view of evolutionary biology which has resulted from intensive study of the vertebrates.

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