CRYPTIC SPECIES AMONG SOUND-PRODUCING ENSIFERAN ORTHOPTERA (GRYLLIDAE AND TETTIGONIIDAE)

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ABSTRACT

Studies of calling songs and seasonal life histories of crickets and long-horned grass-hoppers have revealed many species that were unrecognized on the basis of morphological studies. Once recognized, such cryptic species usually prove to have identifying morphological characters. Nearly one-fourth of the ensiferan species of eastern United States are cryptic, and high proportions of cryptic species have been found in other groups that have conspicuous, non-morphological, species recognition signals or that have been intensively studied. Similarly high proportions of cryptic species must exist in many groups which have not been intensively studied and in which cryptic species are difficult to detect. The existence of cryptic species demonstrates the lack of correlation between reproductive isolation and degree of morphological differentiation. Therefore the taxonomic treatment of morphologically similar, allopatric or allochronic populations must remain subjective and arbitrary until we have reliable criteria for predicting the evolutionary consequences of such populations becoming sympatric and synchronic.

INTRODUCTION

BIOLOGISTS generally agree that species in sexually reproducing animals are best defined in terms of reproductive isolation; however, most species are still recognized and described on a purely morphological basis. For many taxonomic groups, especially among insects, such practice can be defended as all that time and manpower now allow. Furthermore, most taxonomists maintain that the species they distinguish on morphological bases usually correspond with those that would be recognized if reproductive isolation was the criterion used.

The thesis of this paper is that cryptic species are probably much more common than is supposed and that failure to recognize their occurrence may be a major source of taxonomic error. This thesis is well illustrated by studies of the Gryllidae (crickets) and Tettigoniidae (long-horned grasshoppers or katydids), the sound-producing families of the orthopteran suborder Ensifera.

Cryptic species are biological species which are difficult to recognize as distinct on the basis of generally used morphological criteria. The term *sibling species* is frequently used for the same phenomenon, but *sibling* connotes a more recent common ancestry than is the case of species that are not *"sibling."* Since morphological indistinctness and recentness of common ancestry are not perfectly correlated, *cryptic* is more descriptive than *sibling* for the phenomenon discussed in this paper.

Taxonomists relying upon morphological features of preserved specimens have studied the gryllids and tettigoniids of the eastern United States more intensively than most insect groups of comparable size and commonness. By 1931, the number of eastern species in these two families had become stable, and new species (except very localized ones) were no longer expected. However, studies of singing behavior and life histories, first made by B. B. Fulton, H. A. Allard, E. S. Thomas, and others, and later by R. D. Alexander, R. S. Bigelow, and myself, revealed that many of the morphologically defined species are actually complexes of cryptic

species and that approximately one-fourth of the species of gryllids and tettigoniids of the eastern United States had never been recognized or had been wrongly synonymized. Unless speciation in the eastern gryllids and tettigoniids has been of an unusual sort, the occurrence of similar proportions of cryptic species in other groups is likely. I believe that the unusual aspect of cryptic species in these two families is ease of detection rather than high frequency.

DETECTION OF CRYPTIC SPECIES

Calling Songs

The calling songs of the males of the Gryllidae and Tettigoniidae are the most persistently produced, loudest sounds made by these insects. Sexually responsive females respond to the calling song by approaching the stridulating male (in all gryllids and in most tettigoniids) or by producing an answering sound which directs the male in approaching the female (in phaneropterine katydids). The calling song of each species differs from the calling songs of other species stridulating in the same place at the same time. A female normally responds only to the calling song of her own species, so differences in calling songs are the principal effective isolating mechanisms. Since the calling song allows conspecific individuals of gryllids and tettigoniids to recognize one another, it is not surprising that differences in calling songs have led to the initial detection of most of the cryptic species in these groups.

The detection of species on the basis of calling songs is usually easy and reliable; however, several important qualifications must be made. First, ensiferan tympanal organs respond to sounds differently than human ears. (For recent reviews of insect hearing see Haskell, 1961, and Dethier, 1963). Two calling songs which sound alike to a human listener may be quite distinct to an ensiferan because of the ensiferan's greater sensitivity to intensity changes. Differences in pulse rates (normally corresponding to wing-stroke rate) that are scarcely detectable to a human listener are the basis of initial species discrimination by the females of some species (e.g. Walker, 1957). Analysis of calling songs by electronic means is sometimes required to detect behaviorally (and taxonomically) significant differences.

On the other hand, two calling songs which are strikingly different to a human listener may be indistinguishable to an ensiferan. The ensiferan's inability to analyze frequency and our own keen sensitivity to frequency ("pitch") are responsible for this situation. As would be expected from the characteristics of ensiferan hearing organs, intraspecific variation in tonal quality is often considerable, while intraspecific variation in pulse rate (or other behaviorally significant temporal characteristic) is slight (e.g. Walker, 1962b, 1963).

A second hazard in distinguishing species on the basis of calling songs is that some species have *two* characteristic calling songs. So far, all such species known are phaneropterine katydids. In these species, one of the calling songs of the male causes the approach of the female, and the other causes the female to produce an answering sound (Spooner, 1964a, b).

A final limitation in the use of calling songs in detecting cryptic species is that only species which stridulate at the same time and in the same place can be separated reliably on this basis. Two species that do not overlap geographically may have calling songs which cannot be separated (Alexander, 1962b), and a single species may exhibit geographical variation in calling song (Walker, 1962a, 1963). Furthermore, two species that do overlap geographically may have calling songs which are indistinguishable provided that stridulation is at different times (Alexander and Bigelow, 1960).

Life Histories

Most species of gryllids and tettigoniids in the eastern United States apparently have a single generation each year, although a few species have two or perhaps even more. Since calling songs are produced only by adults, and since these are reproductively active for only a month or so, the seasonal life history of a species is often easily inferred from records of the times when the characteristic calling song can be heard. If more than one singing period occurs each year, a study of the development of the immature stages is needed to decide whether successive generations or seasonally isolated populations are involved. Seasonally isolated populations are likely to be distinct species because

selection operates differently on the two populations in many respects.

Annual isolation occurs when populations have life cycles of more than one year and a reproductive period of less than one year. To be effective in speciation the multiannual life cycle would have to be a rigid one, with all individuals in each annually isolated population reproducing in the same year. Such is probably seldom the case. Furthermore, natural selection is closely similar in annually isolated populations (in contrast to the situation in seasonally isolated populations), so that genetic divergence between such populations is less likely. Annual isolation is common in many insect groups but probably not in ensiferan Orthoptera. Gabbutt (1959) reports an obligatory two-year life cycle for *Nemobius sylvestris* in Devon, England, but suggests that individuals of the species in France and Germany complete development sometimes in one year, sometimes in two. Hancock (1916) had eggs of *Amblycorypha oblongifolia* hatch after two and three winters under outdoor conditions, but not after a single winter. Since there is no other information on the time required for tettigoniid eggs to hatch, it is possible that many species have eggs that require more than one year to hatch and that in these species the adults of one summer are never the descendents of those of the previous summer.

Nevertheless, no species of gryllid or tettigoniid is now known to have a constant multiannual life cycle, nor can even one example be cited from any taxonomic group where such a situation has led to the detection of cryptic species. Three pairs of cryptic species among periodic cicadas were detected on the basis of life cycles lasting 13 and 17 years, but these species do not have the same, constant multiannual life cycle. In fact, any two broods of any pair of these cryptic species reproduce in perfect synchrony every 221 years. Effective annual isolation occurs among the broods of each species, but no speciation has been detected among these broods (Alexander and Moore, 1962).

Laboratory Crossing Experiments

Crossing experiments are practical in many species of ground-dwelling crickets because they can be maintained in laboratory colonies. Such experiments have shown that some species which exist in intimate association in the field without detectable hybridization do hybridize readily under laboratory conditions (e.g. Fulton, 1933; Bigelow, 1960). Therefore, production of fertile hybrids in the laboratory does not preclude that the populations involved are distinct species. On the other hand, if interpopulation crosses do *not* produce fertile offspring, whereas the control crosses do, species status for each of the populations is indicated (in the cases of sympatric populations and allopatric populations without intervening populations) or is suggested (in the case of allopatric populations with gene flow possible by way of geographically intermediate populations). Crossing experiments have proved useful in detecting cryptic species in *Acheta* (Ghouri and McFarlane, 1957; Ghouri, 1961), *Gryllus* (Alexander and Bigelow, 1960), and *Teleogryllus* (Bigelow and Cochaux, 1962).

Discussion

Each of the three methods that have proved useful in detecting cryptic species among sound-producing ensiferans involves a characteristic that is directly related to reproductive isolation. Since reproductive isolation is the definitive aspect of a species population, such characteristics are superior to all others, including most of the traditionally used characteristics (e.g., most morphological characters) and most of the newer ones (e.g., protein structure as revealed by chromatography of peptides or amino acids), in separating species.

Other characters which may be of prime value in recognition of species because of a direct relationship with reproductive isolation are color and color patterns that function in courtship, chromosome number and structure, and host organism where mating occurs only on the host.

MORPHOLOGICAL DIFFERENCES AND CRYPTIC SPECIES

By definition, cryptic species are morphologically so similar that their status as distinct species is uncertain unless confirmed by other evidence. Nevertheless, once cryptic species are recognized, non-overlapping morphological dif-

ferences are sometimes easily found. This is because it is much easier to find distinctive morphological differences between two groups of specimens known to represent distinct species than it is to decide what morphological variations (if any) are indicative of distinct species within a mixture of similar specimens.

Non-overlapping morphological differences have been detected for most of the cryptic species recognized among gryllids and tettigoniids. Differences that will separate a portion of one species from a portion of the other have been found in most of the remaining cases, and further study will undoubtedy reveal additional useful characters. Nevertheless, it is important to note that some cryptic species cannot now be identified from preserved material, and some species may never be.

Cryptic species among gryllids and tettigoniids often differ in their calling songs, so the structure of the stridulatory apparatus might be expected to provide a means of identifying preserved males. Unfortunately, differences in songs can be produced by different rates and patterns of movement of a stridulatory apparatus as well as by differences in the apparatus. Studies of the stridulatory apparatuses of cryptic species of tettigoniids have revealed few useful characters (e.g. *Amblycorypha*, Alexander, 1960; *Neocenocephalus*, Walker, unpublished; *Orchelimum*, Thomas and Alexander, 1962). On the other hand, useful characters have often been found in studies of the stridulatory apparatuses of cryptic species of gryllids (e.g. Fulton, 1931; Thomas and Alexander, 1957). Whenever closely related crickets differ significantly in the *pulse rate* of the calling song, they also differ in the length of the stridulatory file and in the number of teeth (Walker, 1963, p. 788).

A final facet of morphological distinctness between cryptic species is that geographical variation within each of two species may make it easier to identify specimens from some areas of sympatry than from others (e.g. *Gryllus veletis* and *G. pennsylvanicus*, Alexander and Bigelow, 1960; *Oecanthus fultoni* and *O. rileyi*, Walker, 1962a; *Oecanthus celerinictus* and *O. nigricornis*, Walker, 1963).

EXAMPLES OF CRYPTIC SPECIES

In ensiferan Orthoptera cryptic species detected through field work may differ in calling songs, in seasonal life histories, or both. Furthermore, once cryptic species have been detected, morphological distinctions may or may not be found. In the following paragraphs, I will give examples of cryptic species to illustrate all possible combinations of these differences and will summarize the published work.

Both seasonal life histories and songs distinctive

Studies of singing behavior and life histories of the field crickets (*Gryllus*) of the eastern United States have revealed six native species in place of the one that was recognized on the basis of careful morphological studies (Fulton, 1952; Alexander, 1957; Alexander and Bigelow, 1960). *Gryllus rubens* differs from the other five species in producing a trilling rather than a chirping calling song, that is, pulses in long sequences rather than in short groups (Figs. 1, 2, 3). It is the only species with two generations each year, all others having only a single generation. Once *G. rubens* had been separated from the other species by song and life history, morphological differences were detected (Alexander, 1957; Rakshpal, 1960; Alexander and Walker, 1962).

In the southeastern United States the cone-headed grasshoppers (Copiphorinae, Tettigoniidae), now called *Neoconocephalus triops*, belong to two species populations (A and B) which differ in both seasonal life history and in calling song. Each species has a single generation each year, but species A overwinters in the adult stage and sings and mates in early spring, whereas species B overwinters in the egg stage and sings and mates in mid-summer. The most reliable means of distinguishing the songs of the two species is by pulse rate (Fig. 11). In addition, the song of species A begins as an intermittent buzz and usually becomes continuous, whereas the song of species B nearly always remains intermittent (Figs. 4, 5). Although species A and B are distinct in their seasonal life histories and calling songs, I have found no character that will reliably separate preserved specimens (other than date of collection).

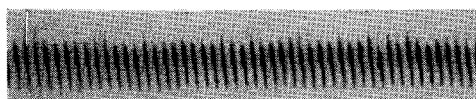An additional example of cryptic species distinguished by both song and seasonal life history
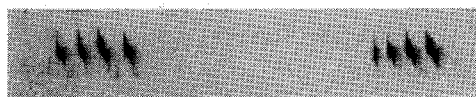
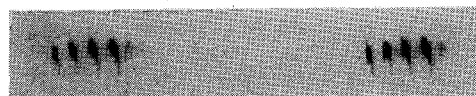Fig. 1. Gryllus rubens 25°C

Fig. 2. Gryllus pennsylvanicus 25°C

Fig. 3. Gryllus veletis 25°C

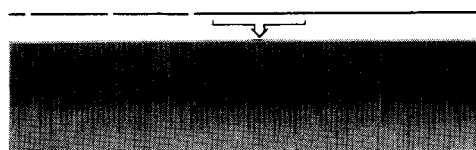Fig. 4. Neoconocephalus "triops," A 28°C
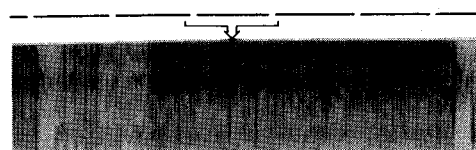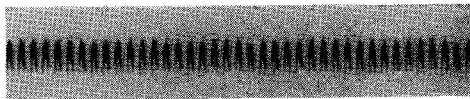
Fig. 5. Neoconocephalus "triops," B 28°C

Fig. 6. Anaxipha "exigua," triller 24°C
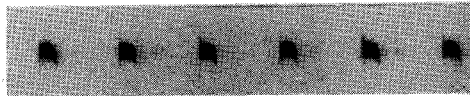
Fig. 7. Anaxipha "exigua," fast tinkler 25°C

Fig. 8. Anaxipha "exigua," slow tinkler 25°C

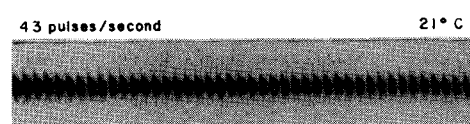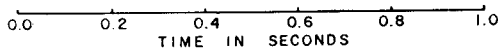53 pulses/second 21°C

Fig. 9. Oecanthus "nigricornis," fast trilling

43 pulses/second 21°C

Fig. 10. Oecanthus "nigricornis," slow trilling

0.0 0.2 0.4 0.6 0.8 1.0
TIME IN SECONDS

FIGS. 1–10. AUDIOSPECTROGRAMS OF CALLING SONGS OF CRYPTIC SPECIES

In Figs. 4 and 5, five seconds of the song is diagrammed above the one-second audiospectrogram. Frequency scales are omitted because frequency is not diagnostic within any of these four groups of cryptic species.

is *Oecanthus argentinus* as compared with fast-trilling *O. nigricornis* and, in the area of geographical overlap, with *O. quadripunctatus* (Walker, 1963).

Songs, but not seasonal life histories, distinctive

Working in North Carolina, B. B. Fulton (1951, 1956) discovered that the sword-tailed crickets known as *Anaxipha exigua* produce three different calling songs of strikingly different pulse rates (Figs. 6, 7, 8) and that any single individual produces only one of the three types of song. Fulton found no morphological differences among the three forms. Two of the

forms seemed identical in habitat distribution, and all three had the same seasonal life history. Although Fulton did not conclude that the three song forms are three species, the evidence he accumulated suggests that they are. More recent data confirm their species status. Their geographical distributions are different, the fast tinkler extending farther south and the triller extending father west and north than the others. The males are easily separated on the basis of characteristics of the stridulatory file (Table 1).

A similar example, but one in which non-overlapping morphological differences have not been found, involves two species of weed-
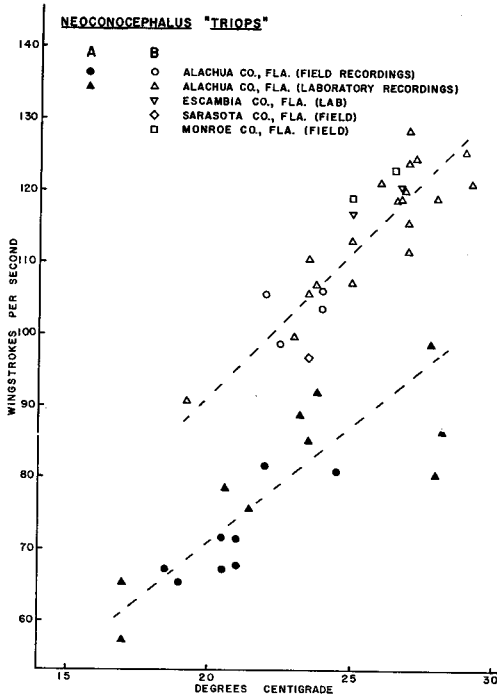
FIG. 11. RELATION BETWEEN TEMPERATURE AND
WINGSTROKE RATE IN TWO CRYPTIC SPECIES OF
CONEHEADED GRASSHOPPERS

In both species the pulses of sound are conspicu-
ously paired at low temperatures, so it is assumed
that a single cycle of wing movement ("wingstroke")
produces two pulses—one for each direction of
movement. The wingstroke rates plotted above are
those which are sustained throughout most of a
song phrase. The initial 4 to 10 wingstrokes in a
phrase are produced at a rate approximately one
fourth slower.

inhabiting tree crickets (Oecanthinae) at present
called fast-trilling and slow-trilling *Oecanthus
nigricornis* (Walker, 1963). The two species oc-
cur in the same habitats in central Ohio, have
the same seasonal life histories, and can be
recognized reliably only by the calling song.
Furthermore, the calling songs differ signifi-
cantly only in pulse rate, and the pulse rates are
so similar that electronic analysis is required
for positive identification (Fig. 9, 10). The
stridulatory files differ only on an average basis
and so are not a reliable means of identifying
individuals (Table 1).

Most examples of cryptic species among
ensiferans are like the two cases described above,
in that they involve differences in calling song
but not in seasonal life histories. Additional
published examples concern *Gryllus* (Alexander,
1957); the *Nemobius fasciatus* group (Alexander
and Thomas, 1959); *Nemobius melodius* and *N.
carolinus* (Thomas and Alexander, 1957);
Oecanthus rileyi and *O. fultoni* (Walker,
1962a); the *Oecanthus nigricornis* group
(Walker, 1963); the *Orchelimum concinnum*
group (Thomas and Alexander, 1962); and the
Amblycorypha rotundifolia group (Alexander,
1960). In all except the last of these examples,
identifying morphological characters have been
found.

Seasonal life histories, but not songs, distinctive

The most abundant field crickets of the
northeastern United States were long believed
to belong to a single species, but Alexander and
Bigelow (1960) have demonstrated that actually

TABLE 1

Characteristics of the stridulatory file of two groups of cryptic species

SPECIES	N	NO. TEETH $\bar{x} \pm$ S. D.	LENGTH (mm) $\bar{x} \pm$ S. D.	$\dfrac{\text{TEETH}}{\text{mm}}$ $\bar{x} \pm$ S. D.
Anaxipha "exigua"				
Triller	15	121 ± 8	1.00 ± .04	122 ± 6
Fast Tinkler	10	193 ± 16	1.30 ± .10	148 ± 7
Slow Tinkler	5	278 ± 14	1.56 ± .04	179 ± 6
Oecanthus "nigricornis"				
Fast-Trilling	23	38.6 ± 2.4	1.16 ± .07	33.2 ± 1.5
Slow-Trilling	20	45.8 ± 3.7	1.28 ± .09	35.9 ± 2.2

Data for *Oecanthus nigricornis* from Walker, 1963.

two species, *Gryllus veletis* and *G. pennsylvanicus,* are represented. The calling songs of these two species are not distinguishable (Figs. 2, 3), nor are there any nonoverlapping morphological differences. The seasonal life histories, however, are distinctive. *G. veletis* overwinters as a late-instar nymph, and the adults occur in spring and early summer. *G. pennsylvanicus* overwinters in the egg stage, and the adults occur during late summer and fall. The adult populations overlap slightly in midsummer, but evidently no gene exchange takes place. In laboratory crossing experiments, hybrid offspring have never been produced even though interspecific mating does occur (Alexander and Bigelow, 1960).

Other examples of cryptic species in which seasonal life histories but not calling songs are distinctive are fast-trilling *Oecanthus nigricornis* and *O. celerinictus* (Walker, 1963), slow-trilling *Oecanthus nigricornis* and *O. argentinus* (Walker, 1963), and probably *Teleogryllus* "commodus" (Bigelow and Cochaux, 1962) and *Scapsipedus* "aspersus" (Masaki, 1961).

DISCUSSION

Evolution

The most important point to make concerning the evolution of cryptic species is that there is no reason to believe that their evolution differs in any significant way from the evolution of non-cryptic species. It is true that cryptic species are likely to be of relatively recent origin, but there is certainly no exact relation between morphological indistinctiveness and recentness of common ancestry. The only peculiar aspect of cryptic species is the crypsis, which, of course, is a highly subjective phenomenon.

The initiating event of speciation (cryptic or otherwise) is some form of extrinsic isolation of conspecific populations. Once populations are extrinsically isolated, mutation, selection, and drift in the populations can result in intrinsic (genetic) differences. If these intrinsic differences make gene exchange between the originally conspecific populations severely detrimental or impossible, speciation has occurred. Cryptic species are those in which intrinsically determined reproductive isolation has developed

without conspicuous morphological differentiation. Species with conspicuous morphological differences have evolved either from cryptic species or from conspecific populations that had previously developed morphological differences.

Fig. 12 is a graphic presentation of the patterns of speciation described above. It also illustrates the idea that intrinsically determined reproductive isolation may operate prior to mating (*premating isolating mechanisms,* e.g., differences in calling songs) or after mating (*postmating isolating mechanisms,* e.g., hybrid sterility). So long as the newly evolved species remain extrinsically isolated, the type of intrinsic isolating mechanism is irrelevant, but if the extrinsic isolation breaks down, the type of intrinsic mechanism becomes important to subsequent evolution. If premating mechanisms are the only ones which have evolved while the populations are extrinsically isolated, establishment of postmating mechanisms when contact between the populations is restored should be coincidental to other changes. On the other hand, if only postmating isolating mechanisms have evolved while the populations are extrinsically isolated, gametes will be wasted when the populations resume contact, and premating isolating mechanisms should be rapidly established through selection (Fig. 12). These conjectures are supported by studies in which extrinsically isolated species seem to lack any effective premating isolating mechanism (e.g. Alexander and Bigelow, 1960, *Gryllus veletis* and *G. pennsylvanicus*), by studies in which species with overlapping distributions are shown to have greater differences in their calling songs in the area of overlap than in areas where they do not overlap (e.g. Walker, 1962a, *Oecanthus fultoni* and *O. rileyi;* Walker, 1963, *Oecanthus argentinus* and *O. quadripunctatus*), and by studies in which biologically distinct, sympatric, synchronic species seem to lack any effective postmating isolating mechanisms (e.g., Fulton, 1933, *Nemobius allardi* and *N. tinnulus;* Perdeck, 1958, *Chorthippus brunneus* and *C. biguttulus*).

These last examples make plain the prospect of two extrinsically isolated populations coming to differ *only* in calling song and remaining distinct when contact is restored. Such speciation is possible, but is probably infrequent. Calling song, like other characteristics directly
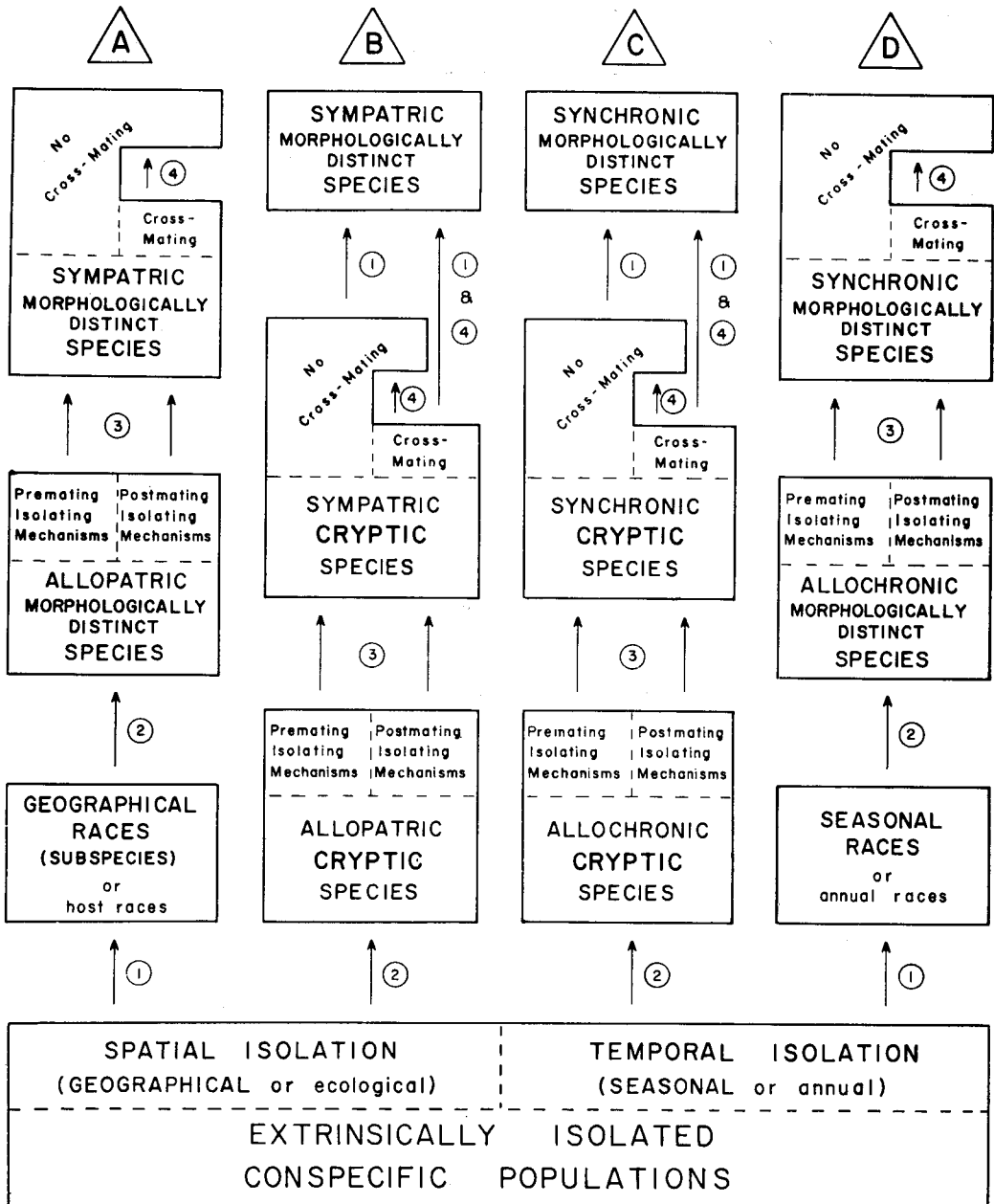
FIG. 12. MODEL FOR SPECIATION

KEY TO EVENTS

(1) Conspicuous morphological differences between populations develop

(2) Intrinsic (incorporated in the gene pool) isolation between populations develops

(3) Contact between populations restored

(4) Selection establishes premating isolating mechanisms

See text for further explanation.

KEY TO PATHWAYS

/A\ Traditional path of speciation

/B\ Usual origin of cryptic species

/C\ Occasional origin of cryptic species

/D\ Occasional path of speciation

concerned with reproductive success, should be especially resistant to nonadaptive ("random") change. However, if the two extrinsically isolated populations have different acoustical interference (e.g., the calling songs of other species), their calling songs may diverge as a result of changes which are adaptive in their respective environments. The influence of the acoustical background on the nature of the calling song is illustrated above by examples of greater differences in calling songs occurring where related species overlap. A second factor which makes less likely speciation through mere divergence in calling song is that in many species of sound-producing ensiferans response to a calling song is not a necessary prelude to mating, and population density and individual behavior may be such that the sexes meet frequently by chance. This reservation does not apply to species with sparse populations and intense calling songs (e.g. some *Neoconocephalus*).

In Fig. 12 it is further postulated that the initial extrinsic isolation leading to speciation may be temporal as well as spatial. Such *allochronic* speciation has been reviewed and discussed by Alexander and Bigelow (1960), Ross (1962), Mayr (1963a), Alexander (1963), and Mayr (1963b). In organisms with long life cycles and brief, seasonally restricted breeding periods, such speciation is an important possibility. For *Gryllus veletis* and *G. pennsylvanicus* speciation as a result of seasonally isolated populations is a simpler explanation of the present situation than is allopatric speciation (see above references).

Annually isolated populations evidently are less likely to become distinct species than are seasonally isolated populations, because annual variations in selective forces are slight and inconsistent as compared with seasonal variations. I can cite no example of speciation in which the simplest explanation is an initial annual isolation. Among insects the most striking examples of annual isolation are the various broods of each of the six species of periodic cicada (*Magicicada*). Three of these species have 13-year life cycles and three have 17-year life cycles. The major broods within a species are effectively isolated from one another, but no speciation has been detected among the broods of a single species, and the origin of the six

species is most easily explained by allopatric speciation (Alexander and Moore, 1962).

Status of allopatric and allochronic populations

A significant aspect of cryptic species is the demonstration of the lack of correlation between morphological distinctness and reproductive isolation. Sexually reproducing populations that look alike may be distinct species (cryptic species), while populations that look different may not represent distinct species. They may be polymorphs, or seasonal forms in species with successive generations during a year, or subspecies. So long as the populations in question live together, careful study should reveal their relationships and the biological species definition can be applied. For populations that are isolated in time (seasonal, annual, or geological) or in space, the species status or lack of it can only be inferred from studies of populations living together. Such inference is risky indeed, since we know of no sure correlation between reproductive isolation and any characters that can be observed in extrinsically isolated populations. Biologists must recognize that many allopatric and allochronic populations which are currently classified as conspecific are in actuality reproductively incompatible, that is, they are distinct species. This generalization includes not only populations which are partially differentiated morphologically (e.g. subspecies) but also those that are not. (The contrary error — populations mistakenly considered to be specifically distinct — is also prevalent *and for the same reason*).

The status of extrinsically isolated populations will remain a dilemma until we know what genetic divergences are irreversible and how we can detect them. Such a dilemma is preferable, however, to the dilemmas which would replace it if a phenotypic rather than a biological definition of species were to be accepted. (For the opposite view, see Ehrlich, 1961).

Prevalence of cryptic species

The commonness of cryptic species is difficult to estimate because the majority of them are undoubtedly undetected. Furthermore, the

taxonomic treatment of allopatric and allochronic populations remains at present controversial.

An important aspect of cryptic species is that they occur in all major groups of sexually reproducing animals. Mayr (1963a, pp. 37–58) discusses the presence of cryptic species among both vertebrates and invertebrates. Blair (1962) has reviewed examples of cryptic species among North American frogs, and Brown (1959) summarized what is known of cryptic species among insects.

A second important feature of the occurrence of cryptic species is that in some groups such species constitute a substantial proportion of the total number of species. For instance, among sound-producing ensiferans of the eastern United States approximately 40 of 167 species (24 per cent) were unrecognized or of doubtful status until calling songs and life histories were studied (these figures include unpublished data of Alexander and Walker). In fireflies of the genus *Photuris* a single northeastern species was recognized prior to the studies of Barber (1951), who detected 14 species, principally by their flashing behavior. High proportions of cryptic species are not restricted to groups that have conspicuous, long-range species recognition signals, although they are easier to detect in such groups. In other groups that have been intensively studied similar proportions of cryptic species have been discovered. For example, *Drosophila* have no long-range species recognition signals but a substantial proportion of the species are cryptic (Patterson

and Stone, 1952). Most of these cryptic species would still be undetected except for the fact that *Drosophila* has been more intensively studied than nearly any other group of animals. *Anopheles* and *Culex* mosquitoes are other examples of groups in which numerous cryptic species have been detected but only through unusually intensive study (Bates, 1949, pp. 244–250).

There is thus reason to believe that intensive study will reveal numerous cryptic species in most groups of sexually reproducing animals. The principal exception to this should be groups which have species recognition signals that remain conspicuous (to human beings) in the preserved specimen. Butterflies, dragonflies, and birds are examples of such groups, but within each of these groups there are species in which no conspicuous species recognition signals are preserved with the specimens. For example, Stein (1963) has described two biologically distinct species from among the birds previously known as the alder flycatcher (*Empidonax trailli*). So long as sympatric, synchronic cryptic species are still being detected among common North American song birds, no taxonomist should be complacent about the status of species classification in the groups he studies.

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