DISTRIBUTION PATTERNS AMONG ARTHROPODS OF THE NORTH TEMPERATE DECIDUOUS FOREST BIOTA[1]

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ABSTRACT

The distribution patterns of seven different arthropod taxa representing eleven individual monophyletic lineages with representatives in eastern North America, Europe, and northeastern Asia were analyzed. Taxon cladograms representing relationships among taxa were converted to area cladograms representing relationships among areas. Nine of the area cladograms were found to represent one congruent repetitive distribution pattern. The two remaining cladograms represented two additional independent distribution patterns. The distribution patterns were correlated with geological events that have alternately divided and reunited the principal land areas during the past 180 million years.

The largest and most diverse segments of the biota of the North Temperate Deciduous Forest presently occur in three disjunct areas: (1) eastern North America, (2) Europe, and (3) northeastern Asia. This has been known for almost one hundred and forty years. What is not known is the definitive relationships of these three related biotas to one another or the relationships of these biotas to other, perhaps more distantly related biotas. To establish definitive relationships among biotas one must practice a science of comparative systematic biology and employ an objective methodology.

The objective of this paper is two-fold. First, an objective comparative methodology will briefly be outlined whereby biotas may be analyzed and definitive relationships established. Second, a number of monophyletic, arthropod taxa occurring in North America (NA), Europe (EU), and northeastern Asia (AS) will be analyzed to determine the cladistic and biogeographic patterns of these taxa.

AN OBJECTIVE METHODOLOGY FOR COMPARATIVE SYSTEMATIC STUDIES

Let us consider how we might compare the biotas of the three areas under consideration. We might begin by making lists of the similar endemic taxa common to two or more areas. A number of such lists have been made. Asa Gray (1846) made such a list and recorded a number of plant species and higher taxa that were endemic to eastern North America and Japan. Some one hundred years later Li (1952) reanalyzed the floristic similarities between eastern North America and northeastern Asia in the light of modern systematic botanical data. These new data, presented by Li, showed that the species Gray had thought to be the same in the two areas were, in fact, different species. Li did, however, record 52 genera that were endemic to eastern North America and northeastern Asia. A number of additional papers (Graham, 1972) since the work of Li have further documented the similarities of the floras in these two areas.

Similar studies comparing the biotas of Eastern North America and Europe have also been published. Lindroth (1957) presented a comprehensive list comparing the faunas of the arctic, boreal, and temperate regions of North America with comparable areas in Europe. The symposium papers contained in Löve and Löve (1963) also document the similarities of the biotas of the North American and European continents. Numerous additional papers, particularly those of a taxonomic nature treating taxa common to North America and Europe, give examples of taxa with disjunct distributions on the two continents.

Studies comparing the biotas of Europe and northern Asia or comparing the biotas of Europe, northern Asia, and North America are limited. The work of Hara (1952, 1956) does compare the plants of the three areas. But the majority of the published literature compares only two of the

areas and we may be able to form only two sets of comparative statements: (1) the biota of NA(e) (North America, east) is related to the biota of AS (Asia) (Fig. 1) and (2) the biota of NA(e) is related to the biota of EU (Europe) (Fig. 2). These statements may be considered two-entity comparisons and as such have "low" informational content (Platnick & Nelson, 1978).

Since two-entity statements are prevalent throughout systematic biological literature it is important to clarify the statement just made, i.e., that two-entity statements have "low" informational content. In systematic biology two-entity statements may be of two types: (1) two-taxon statements—species A is related to species B; (2) two-area statements—the biota of area *a* is related to the biota of area *b* (Fig. 3). If one accepts the idea that extant taxa come from preexisting taxa through a series of interconnected, related ancient ancestors, i.e., evolution, then all taxa and biotas are related to one another at some level. The question, then, is at what level the two taxa or biotas are related. To answer this question, a third entity must be considered so that a comparative statement may be formed.

Consider the proposition that A and B are more closely related to one another than either is related to C (Fig. 4). This is a three-entity comparative statement with a higher informational content than the two-entity statement. In an evolutionary context we may see that A and B shared a more recent common ancestor, hypothetical ancestor 2, than either did with C, and C's hypothetical ancestor 1 (Fig. 4). We may also deduce that A and B share one or more attributes in common that are not shared with C.

If the discussion just given seems too simple for the advanced student or practitioner of systematic biology, consider the published literature. This body of information is replete with example after example of two-entity statements. If we are to move toward an objective, analytical format in systematic biology as suggested by Ian Ball (1975), we must begin constructing comparative statements composed of a minimum of three entities.

The construction of a comparative three-entity statement in systematic biology begins with a cladistic analysis of three or more taxa believed to have a monophyletic relationship. The methods and procedures for executing a cladistic analysis have been discussed at length by a number of authors including Hennig (1966), Ross (1974), Crisci and Stuessey (1980), and Wiley (1982).
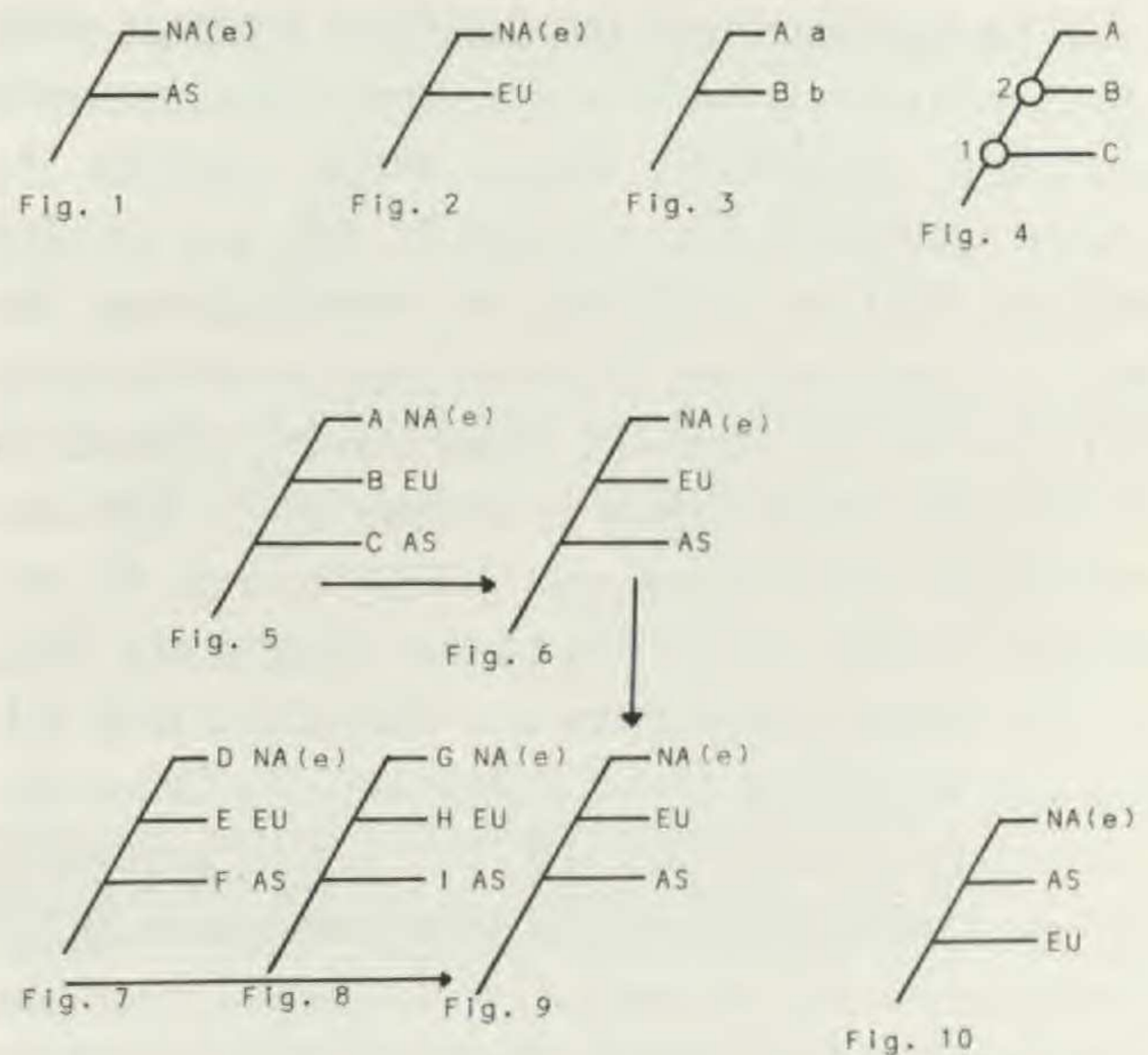
FIGURES 1–10. 1–2. Two area statements illustrating the relationships between North America east (NA(e)), Asia (AS), and Europe (EU).—3. A two taxon statement illustrating the relationships between hypothetical species A, and B occurring in *a* and *b*.—4. A three taxon statement illustrating the relationships between hypothetical species A, B, and C.—5. A cladogram of relationships existing among hypothetical species A, B, and C occurring in eastern North America, NA(e), Europe, EU, and Asia, AS.—6. An area cladogram derived from Figure 5 illustrating the relationships among three disjunct geographical areas.—7–8. Taxon/area cladograms of two hypothetical monophyletic lineages.—9. An area cladogram depicting the congruent distributional patterns illustrated in Figures 6, 7, and 8.—10. An area cladogram illustrating a second type of distributional pattern that might exist between eastern North America, NA(e), Asia, AS, and Europe, EU.

Here we need only note that there are four basic tenets necessary for a cladistic analysis of any taxon: (1) an analysis and comparison of characters and character states in the taxon being studied and in suspected related taxa; (2) the postulation of apomorphic (derived) and plesiomorphic (ancestral) states for as many characters as possible from the analysis and comparison of character states in the study group and related groups; (3) the establishment of relationships (monophyletic lineages) based on the possession of shared apomorphic characters and the graphic illustration of these relationships in the form of a taxon cladogram; (4) an analysis of the biogeographic relationships of the taxa and the areas in which they occur by converting the taxon cladograms to area cladograms. Let us consider a hypothetical example in which we cladistically and biogeographically analyze a monophyletic taxon with representatives in three disjunct areas.

Let us suppose that we discover a genus with representatives in each of the three disjunct north temperate deciduous forest areas: species A, NA(e); species B, EU; species C, AS. Let us also suppose that by applying the methodology for determining cladistic relationships we determine that species A and B are more closely related to one another than either is to species C. This information concerning relationships may be expressed in the form of a taxon cladogram (Fig. 5). This taxon cladogram is a statement that fulfills the following three requirements for a scientific hypothesis (Ball, 1975): (1) the cladogram fits the known data about relationships; (2) the cladogram may be tested by a reanalysis of the known data and/or the discovery of new character state data; (3) the cladogram predicts that the relative relationships of the three known taxa will remain the same no matter how many additional species may be discovered, i.e., species A and B will always share a more recent common ancestor with one another than either will ever share with species C.

Once the cladistic relationships of a monophyletic lineage have been established, other types of data, for example distributional data, may be plotted against the cladogram. Rosen (1975, 1978) and Nelson and Platnick (1981) have discussed the methodology as well as the scientific basis for converting taxon cladograms into area cladograms by plotting distributional data on the taxon cladogram. When this distributional data is plotted on the cladogram (Figs. 5, 6), we may see that we have a hypothesis relevant to the relationships of the three disjunct areas in which species A, B, and C occur: eastern North America [NA(e), species A] and Europe [EU, species B] have shared a more recent common biota with one another than either area has shared with northern Asia [AS, species C] (Fig. 6). Using this methodology, it is necessary for a worker to make only two assumptions: (1) that extant organisms have evolved from preexisting organisms and (2) that extant species have evolved due to an allopatric speciation model.[4] Note that the hypothesis does not involve nor suggest mandatory, long-distance dispersal.

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[4] I fully realize that perhaps one-third of the plant species (as well as some animal taxa) have originated due to processes other than allopatric speciation. Nevertheless allopatric speciation does appear to be a viable process that plays an important role in the origin of many animal species including the taxa discussed in this paper.

The hypothesis about the relationships of biotas in NA(e), EU, and AS may be tested in at least two ways. It has already been suggested that the taxon cladogram may be tested by the further study of the characters on which the cladogram is based and the study of additional characters not previously used. In addition to this test on character states, a search may be made for additional monophyletic taxa with a distribution range similar to the first taxon. If such taxa are discovered, taxon cladograms may be deduced (Figs. 7, 8) and these taxon cladograms may be converted into area cladograms (Fig. 9). If the area relationships of the new, additional taxa are the same as the first taxa, the hypothesis is corroborated and may suggest a generalized distribution pattern (Fig. 9). If the new, additional taxa suggest a different set of area relationships (Fig. 10), then the original hypothesis may be incorrect or a second distribution pattern may exist. In either case, corroboration of the first hypothesis may be objectively pursued.

Once corroborated and generalized distribution patterns emerge, we may consider the phenomena that have contributed to the evolution of these patterns. We might ask, "Are the patterns due to the dispersal of organisms across pre-existing barriers and to the subsequent isolation and evolution of the organisms?" or "Are the patterns due to historical factors that divided ancient cosmopolitan populations and set the stage for allopatric speciation to occur?" Before attempting to answer these questions, let us consider the literature that is available and search for taxa that are informative about biotic relationships between NA, EU, and AS, and describe how we can fit the available information into the objective methodology that has been outlined.

USING PUBLISHED DATA IN A CLADISTIC-BIOGEOGRAPHIC ANALYSIS

To objectively analyze distribution patterns, two prerequisites are necessary: (1) a monophyletic taxon with distinct taxa, endemic to three or more areas and (2) a taxon cladogram or data from which a taxon cladogram may be postulated. These two prerequisites may be satisfied through original research or, in some instances, by utilizing previously published information. The analysis of north temperate distribution patterns presented in this paper relies heavily upon the work of other authors. These previously published data are not always in a form that can be directly used in a cladistic biogeographic analysis

and some rearrangement of the data is necessary. The following is a brief statement of how previously published data used in this paper are adapted in order to perform a cladistic-biogeographic analysis. Three subject areas need to be considered: (1) the conversion of phylogenetic diagrams to cladograms; (2) the conversion of taxon cladograms to area cladograms; and (3) the accuracy of distribution records.

Diagrams representing the relationships of taxa to one another have been a part of systematic literature since the time of Haeckel (1866). These diagrams have been referred to by a variety of names, but the most common name appears to be "phylogenetic tree." More recently (1960s to the present), the diagrams have been referred to as cladograms.

It has only been within the past thirty years that definitive and objective methods have been proposed for the construction of cladograms. Central to this methodology is the establishment of relationships based on the possession of shared apomorphic (derived) characters. The validity of previously published phylogenies or cladograms stands or falls on whether or not the author postulated relationships based on shared apomorphic characters. In those instances where the method of determining relationships is clear, one may proceed with the use of the cladistic and distributional information. Frequently it is difficult to determine what method an author used to determine relationships. In those instances where the method of determining relationships is unclear or where relationships are based on some factor other than the possession of shared apomorphic characters, the published data is better left to rest in peace.

Relationship diagrams have also been published in a variety of formats. In this paper all of these formats have been changed to a single type of branching diagram. The use of a single format is extremely helpful in searching for and detecting redundant distribution patterns. In no case have the original data been changed, i.e., the relative relationships of all taxa (those taxa at the ends of the diagram branches) have not been changed. For example, in a diagram representing the relationship of four taxa A, B, C, and D (Fig. 11) where A and B are more closely related to one another than either is to C or D, and where A, B, and C are more closely related to one another than they are to D, the positions of the taxa have been scrupulously maintained. However, in some instances the location of taxa at terminal nodes, in this case A and B, have
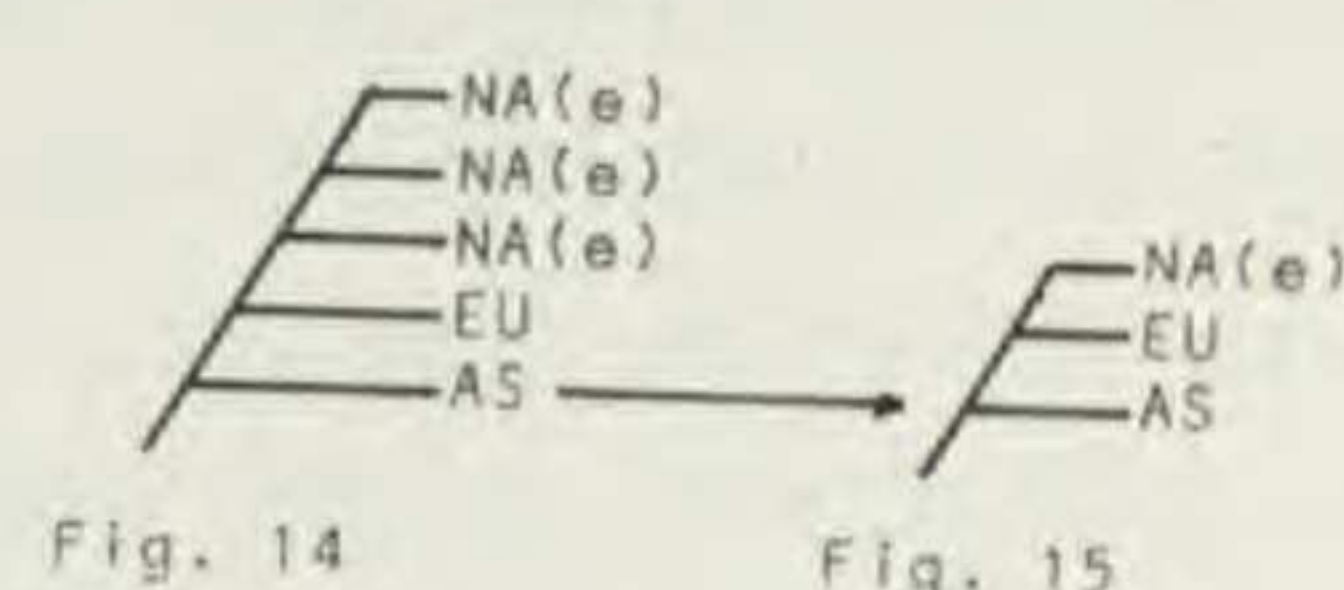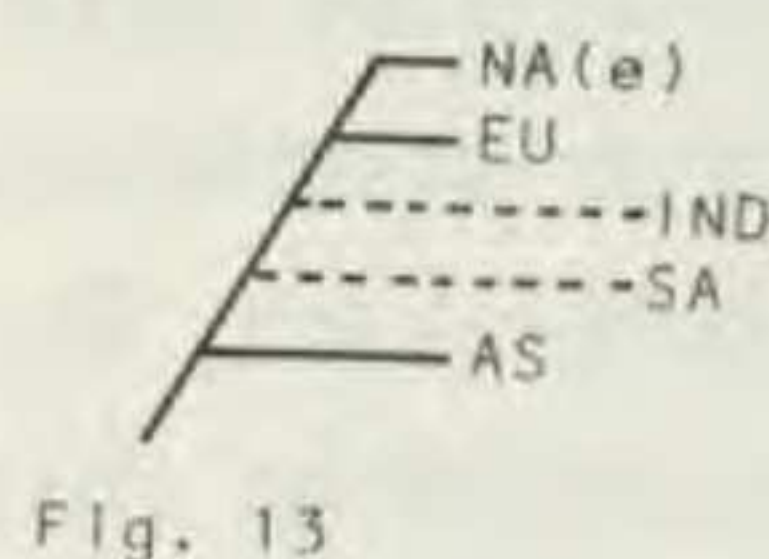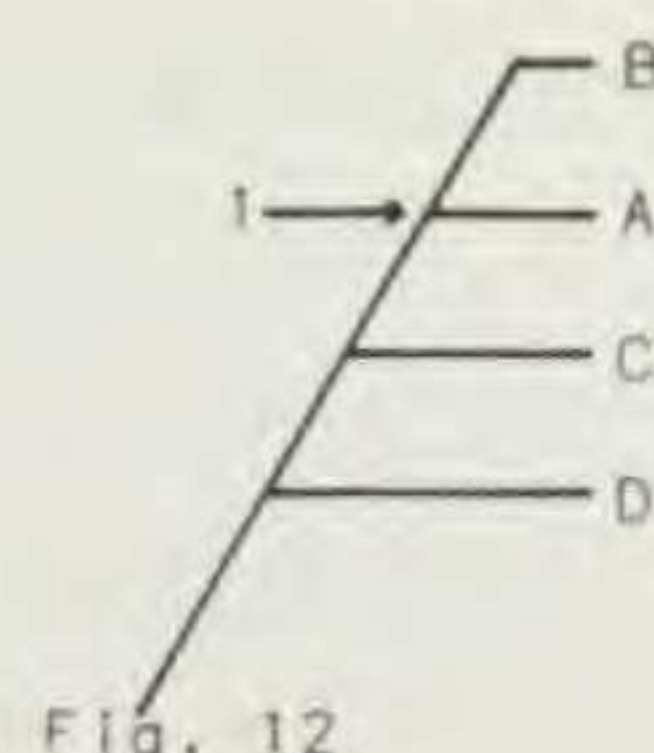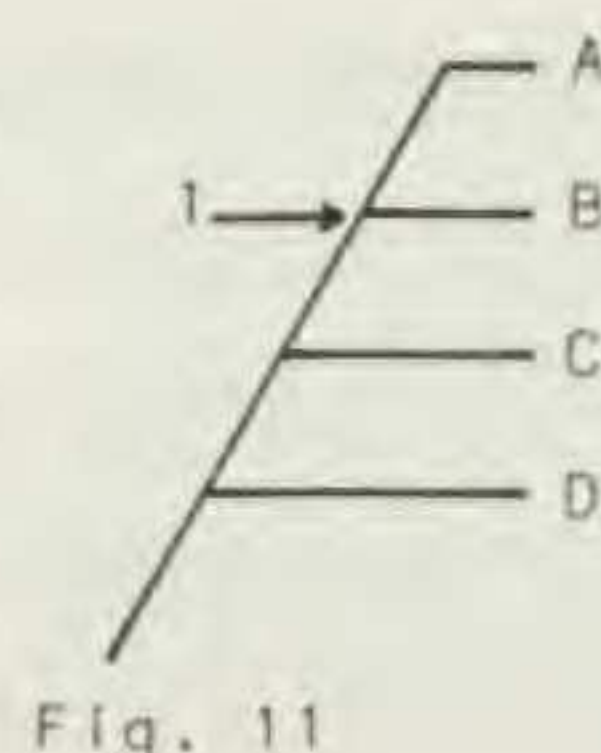

FIGURES 11–15. 11–12. Taxon cladograms of a hypothetical group of species in which the positions of species A and B are reversed by rotating the cladogram at node 1. Such a rotation does not change the informational content of the cladogram.—13. An area cladogram in which the relationships of areas outside of North America, Europe, and Asia have been indicated by a dashed line.—14–15. Area cladograms illustrating how three species occurring in eastern North America, NA(e), have been reduced to one area in Figure 15.

been reversed (Fig. 12). Such a reversal has absolutely no effect on the interpretation of the data presented. The statement "A and B are more closely related to one another than either is to C" is the same as the statement "B and A are more closely related to one another than either is to C." Put in another way, nodes in a cladogram may be rotated on their axes. As you will see, this rotation procedure is often helpful in detecting congruent distribution patterns.

At this point it is worthwhile to remember that the plants and animals we study are not obliged to fit precisely and neatly into either our classification systems or our distribution patterns. Any student of nature, even after a limited amount of experience, quickly recognizes the variation that is rampant in nature. This does not mean that biological patterns do not exist, for certainly they do. It does mean that while striving to detect patterns that are common to large groups of taxa, we must also accurately record the variability we observe in nature. Patterns exist because individual plant and animal species have not evolved independently of one another. Individual species are constituent members of larger biotas. These biotas have shared common elements in their histories and it is these common elements for which we are searching. With these thoughts in mind I have employed two methodological procedures that have assisted in discovering common distribution patterns between the biotas in North America, Europe, and northern Asia.

The first methodological procedure that I have

used was necessary because many taxa occur in disjunct areas other than those under consideration. For example, Li (1952) noted a number of temperate deciduous forest taxa that occur not only in eastern North America and northeastern Asia but also in more southern tropical areas such as the Philippines. Other taxa such as some caddisflies (Insecta: Trichoptera) occur in eastern North America, Europe, northeastern Asia, India, Africa, etc. In the cladograms used in this paper, the relationships of taxa and areas outside of NA, EU, and AS have been indicated by dashed lines (Fig. 13). It is felt that this method conveys all of the known data about the groups but allows one to perceive what the relationships are among the areas and taxa that occur in our three principal areas, NA, EU, and AS.

The second methodological procedure used in detecting distribution patterns was first employed by Rosen (1975, 1978). In this technique, identical areas that are juxtaposed to one another in a single monophyletic lineage are combined (Figs. 14, 15). When this combining method is used, the original data should always be presented so that other workers will have access to all the facts and so that any conclusions may be judged objectively.[5]

The last topic to be considered here is the accuracy of distribution records. What is meant by accuracy is the tendency that some biogeographers had in the past to list taxa as occurring in broad geographical areas, i.e., Asia, North America. We now know that many of the geographical areas formally recognized as single units are actually composed of two or more geographical subunits. These subunits have often had independent and therefore different histories. Even the relatively small island of Celebes is composed of at least two independent island masses that

only fused together a few million years ago. When summary cladograms of other workers have been used in this paper, the distribution of each taxon and lineage has been verified and determined as accurately as possible. This has sometimes led to conclusions that differ from those expressed by the original authors.

Using a cladistic methodology, including the methodological procedures just discussed, the distribution patterns of a number of north temperate, disjunct, monophyletic arthropod taxa have been analyzed. Let us consider these individual taxa, their taxon cladograms, and their area cladograms.

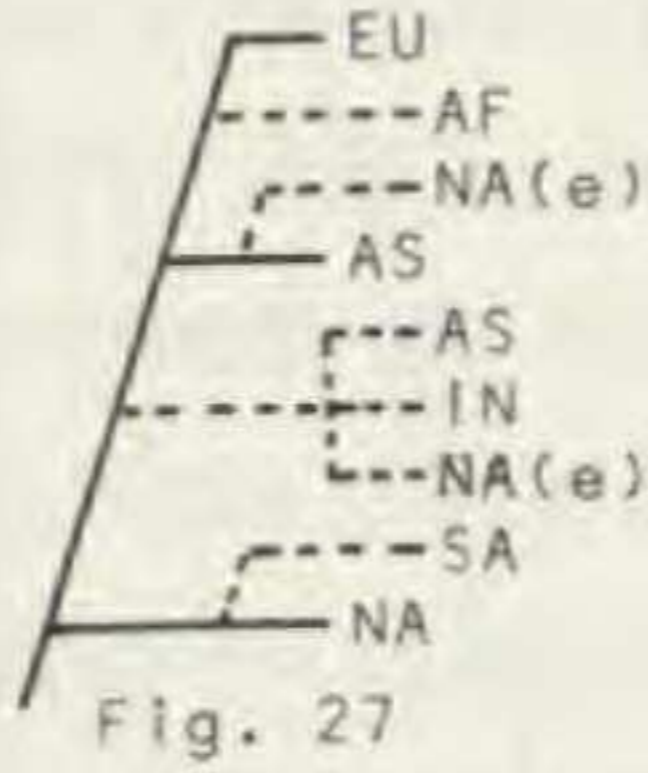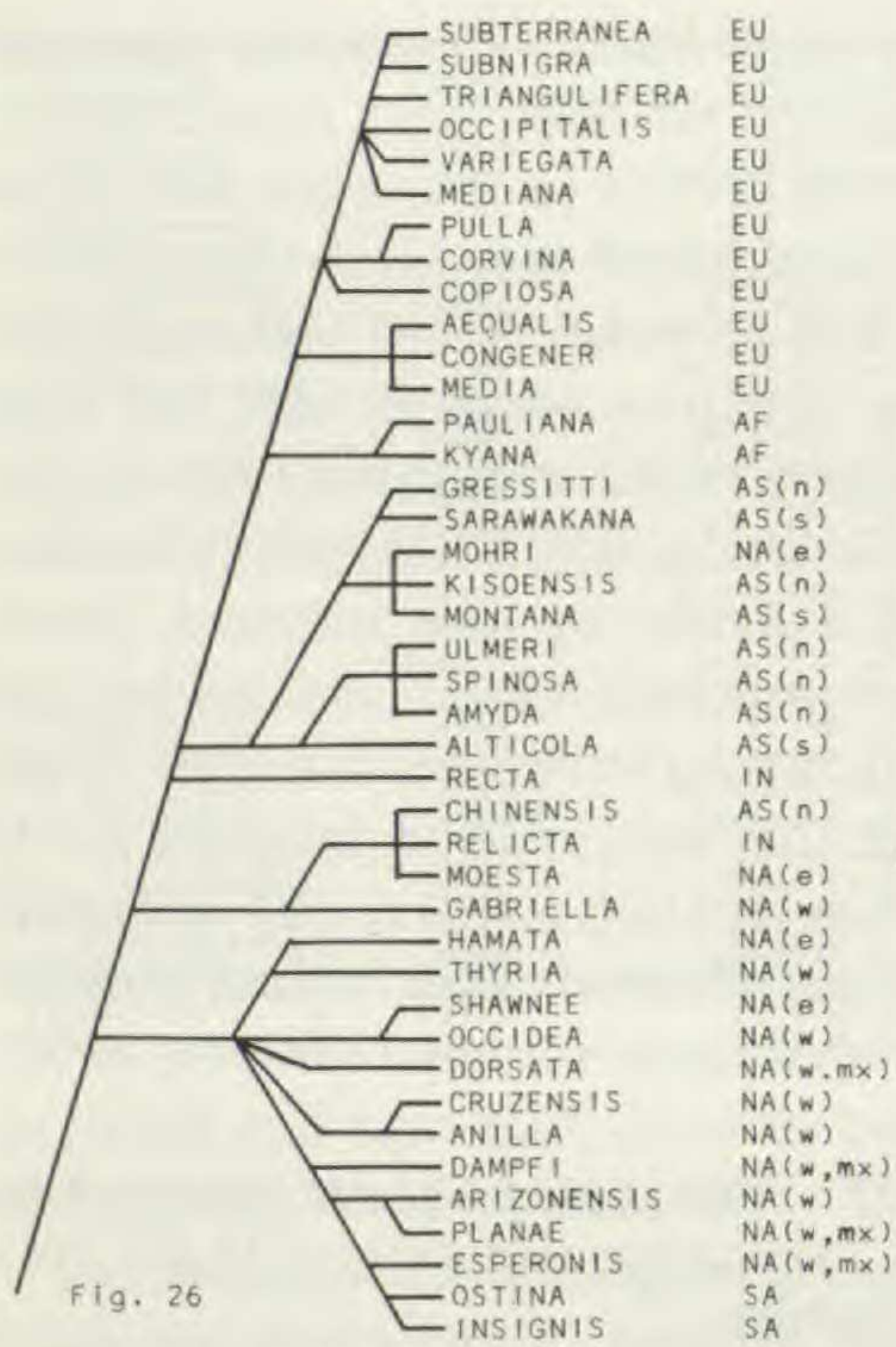### TAXON AND AREA RELATIONSHIPS AMONG DISJUNCT NORTH TEMPERATE ARTHROPOD GROUPS

A search of the literature revealed a number of arthropod taxa with distributions that might be informative about the relationships of temperate biotas and areas in North America, Europe, and northeastern Asia. These groups occur in three orders of insects: the caddisflies (Trichoptera), the leafhoppers (Homoptera), and the beetles (Coleoptera), and in one group of spiders (Araneae).

CADDISFLIES (INSECTA: TRICHOPTERA; GLOSSOSOMATIDAE, PHILOPOTAMIDAE, RHYACOPHILIDAE)

Caddisflies are a moderately large order of aquatic insects. The systematics and ecology of these organisms have attracted the attention of a number of highly competent entomologists for many years. One of the leading authorities of caddisfly systematics was H. H. Ross. Ross was especially interested in the basic taxonomy and biogeography of these insects.

Caddisfly taxa inhabit a wide range of aquatic habitats, but many taxa are characteristic of mountain regions throughout the world. Ross made a special study on the systematics of a number of mountain caddisfly taxa with worldwide distribution patterns and published the results in 1956. The phylogenetic diagrams that Ross presented for the mountain caddisfly taxa (Fig. 16) have been changed to taxon/area cladograms (Fig. 17). These cladograms, in turn, have been reduced to more simple cladograms (Figs. 18, 19) illustrating the area relationships between North America (NA) (east and west), Europe (EU), and Asia (AS). Four mountain caddisfly

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[5] At the first annual meeting of the Willi Hennig Society in 1980 Norman Platnick pointed out that Rosen's method of combining the same juxtaposed areas in a cladogram could have a negative result if the areas proved to be actually disjunct. Platnick believes that unless the combined areas represent the same natural areas of endemism (not disjunct), then one could argue that the "agreement" in different cladograms might result from chance alone. Perhaps Platnick's argument is true. However at our present level of knowledge it appears that there are both large (continents) and small (a mountain top) areas of endemism and that these areas of endemism have different levels of relationships (Allen, ms.). As long as the original, detailed data are presented accurately we will be able to return to the problem Platnick suggests exists if necessary.

Fig. 16

PRODUCTA	AS(n)	
UNINACULATA	NA(w)	
VETINA	NA(w)	
BELONA	NA(w)	
LAEVIS	EU	
VEPULSA	NA(w)	
NARVAE	AS(n)	
TRANSQUILLA	AS(n)	
KISOENSIS	AS(n)	
YUKII	AS(n)	
SIBIRICA	AS(n)	
MINORA	NA(e)	
MANISTEE	NA(e)	
BLARINA	NA(w)	
MELITA	NA(e)	
AMICIS	NA(w)	
ATRATA	NA(e)	
VALUMA	NA(w)	
PELLISA	NA(w)	
RICKERI	NA(w)	
DEPRESSA	AS(n)	
ABCHASICA	AS(n)	
VISOR	NA(w)	
OPHRYS	NA(w)	
VELORA	NA(w)	
OREIA	NA(w)	

Fig. 17

Fig. 18

Fig. 19

FIGURES 16–19. The caddisfly genus *Rhyacophila sibirica* group.—16. Original phylogenetic chart published by Ross (1956).—17. Taxon/area cladogram based on Ross.—18–19. Reduced area cladograms.

taxa discussed by Ross (1956) that have representatives in the north temperate areas are being considered here. The four taxa and their associated taxon/area cladograms are as follows: (1) *Rhyacophila sibirica* group (Figs. 16–19), branch 6 (Figs. 20–22); *Glossosoma* (Figs. 23–25); (3) *Wormaldia* (Figs. 26–27); (4) Agapetini (Figs. 28–30).

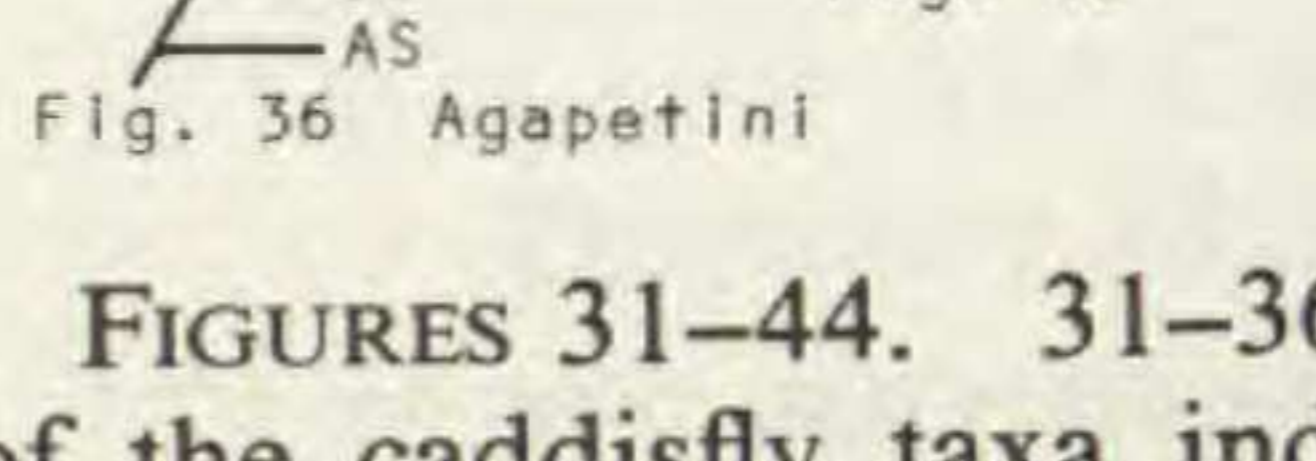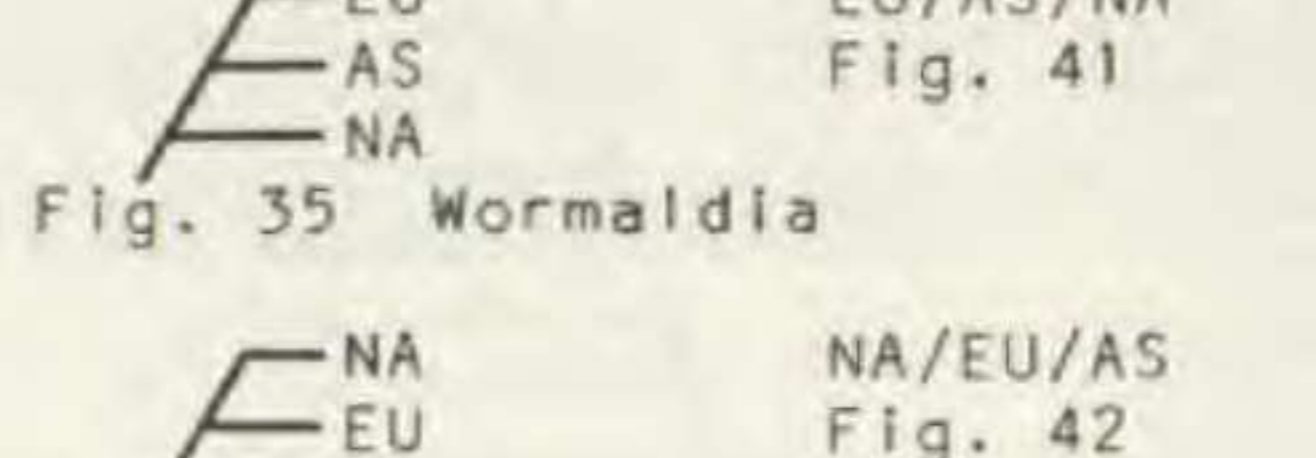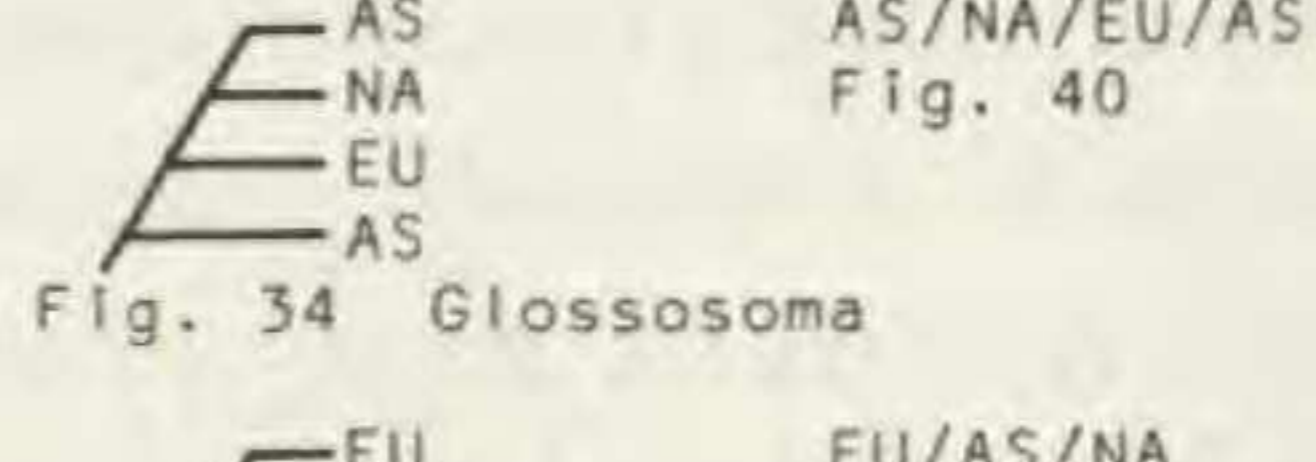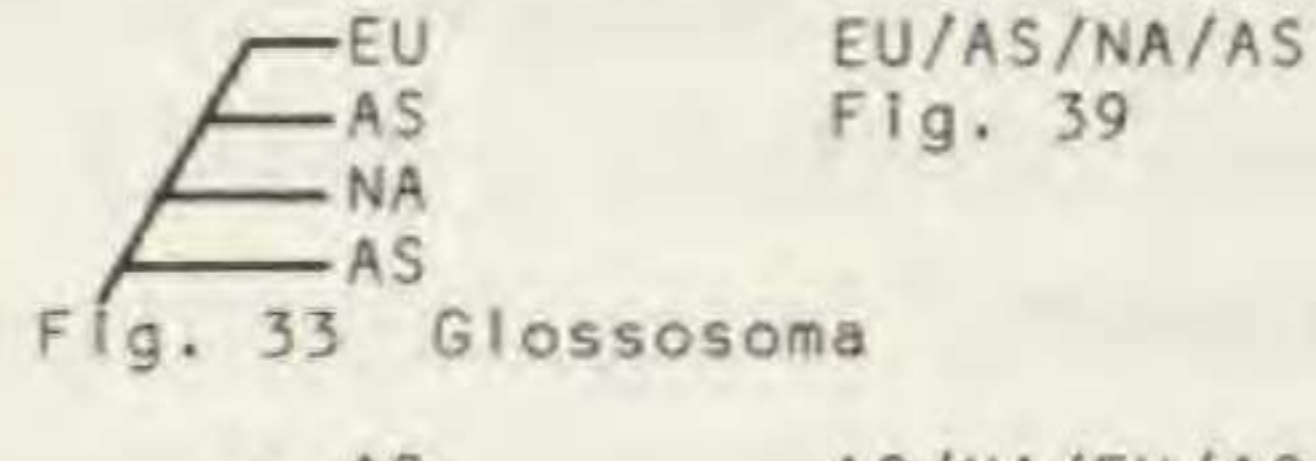When each of the reduced area cladograms representing the independent monophyletic lineages is considered (Figs. 31–36), two distribution patterns seem to be identical: the pattern in the *Rhyacophila sibirica* group (Figs. 31, 37) and the pattern in *Glossosoma* (Figs. 34, 40). We might now ask, "Are the other patterns in these north temperate caddisfly taxa radically different from one another?" When the area cladograms are considered (Figs. 31–36) the area sequences do seem to be different on the one hand, yet on the other hand there also appears to be some degree of congruence. Consider how the different patterns may be arranged in linear sequences (Figs. 37–42). Now consider how these linear sequences may be arranged so that the same areas correspond with one another (Fig. 43). This latter arrangement (Fig. 43) of the linear sequences in

LILLIPUNTA	AS(n)	
MINUTA	AS(n)	
ARGENTIPUNCTELLA	AS(s)	
DAVAO	AS(s)	
CASTANEA	IN	
SCISSA	IN	
group		
PEPINGENSIS	AS(n)	
MARCIDA	AS(n)	
PHILOPOTAMOIDES	EU	
PUBESCENS	EU	
TEDDYI	NA(e)	
CAROLINA	NA(e)	
FENESTRA	NA(e)	
LEDRA	NA(e)	
KIAMICHI	NA(e)	
SONOMA	NA(w)	
HYALINATA	NA(w)	
VOCALA	NA(w)	
CLAVALIS	EU(me)	
GLAREOSA	EU	
MYCTA	NA(e)	
NIGRITA	NA(e)	
CARPENTERI	NA(e)	
PARANTRA	NA(e)	
BANKSI	NA(e)	
VIBOX	NA(e)	
INVARIA	NA(e)	
KERNADA	NA(w)	
COLORADENSIS	NA(w)	
BIFILA	NA(w)	
RAYNERI	NA(w)	

Fig. 20

Fig. 21

Fig. 22

FIGURES 20–22. The caddisfly genus *Rhyacophila* branch 6.—20. Taxon/area cladogram.—21–22. Reduced area cladograms.

no way changes the original data but it does accentuate congruent areas and it notes those areas in which members of a monophyletic lineage do not occur. Perhaps we are seeing in each of the individual area cladograms a segment of a larger, more inclusive pattern (Fig. 44). Let us consider additional taxa.

LEAFHOPPERS (INSECTA: HOMOPTERA; CICADELLIDAE)

Because of his general interest in the evolution and biogeography of insects, H. H. Ross worked on a number of diverse groups. In addition to the caddisflies, leafhoppers, especially the genus *Empoasca* (Cicadellidae), were of interest to Ross. He published a number of papers dealing with

PYRENACIUM	EU	
PRIVATUM	EU	
BEAUMONTI	EU	
TIMURENSE	EU(me)	
ANALE	AS(n)	
CAPITACUM	EU	
MALAYANUM	AS(s)	
CAUDATUM	AS(n)	
ATRICHUM	AS(s)	
ASPERIGLOSSA	NA(w)	
MUROGLOSSA	AS(s)	
LIPOGLOSSA	AS(n)	
LIPOGLOSSA	AS(n)	
LIPOGLOSSA	AS(s)	
PROTOGLOSSA	AS(n)	
SINOGLOSSA	AS(s)	
DIPLOGLOSSA	EU	
SYNAFOPHORA	AS(n)	
DULKEJTI	AS(n)	
LIVIDUM	NA(e)	
USSURICUM	AS(n)	
VERDONA	NA(w)	
ALTAICUM	AS(n)	
RIPAEGLOSSA	NA(w)	

Fig. 23

Fig. 24

Fig. 25

FIGURES 23–25. The caddisfly genus *Glossosoma*.—23. Taxon/area cladogram.—24–25. Reduced area cladograms.

FIGURES 26–27. The caddisfly genus *Wormaldia.*—26. Taxon/area cladogram.—27. Reduced area cladogram.

FIGURES 31–44. 31–36. Reduced area cladograms of the caddisfly taxa indicated.—37–42. Linear sequential arrangements of the areas occurring in reduced area cladograms.—43. Comparison of the linear sequential arrangement patterns in six monophyletic caddisfly taxa.—44. A generalized distribution pattern suggested by comparison of the six monophyletic caddisfly taxa in Figure 43.

this genus. One of these papers is a taxonomic and biogeographic treatment of the empoascan subgenus *Kybos* (Ross, 1963).

Discussing the distribution of the subgenus *Kybos,* Ross said, "Of the 62 species of *Kybos* available for study, 49 are known only from North America, 13 from Europe. It would seem certain that species of this subgenus occur in Asia also, but currently none are available from that area, either through the avenues of specimens or descriptions giving details of male genitalia. When these distributions are plotted on the family tree for the subgenus, chart 1 [Fig. 46], it is remarkable that all of the known European species occur

in the large branch containing the *butleri* and *copula* groups."

Unknowingly, Ross alluded to the fact that *Kybos* is a north temperate taxon and that representatives might well occur in northeastern Asia. Ross had certainly seen many examples of this type of Northern Hemisphere distribution
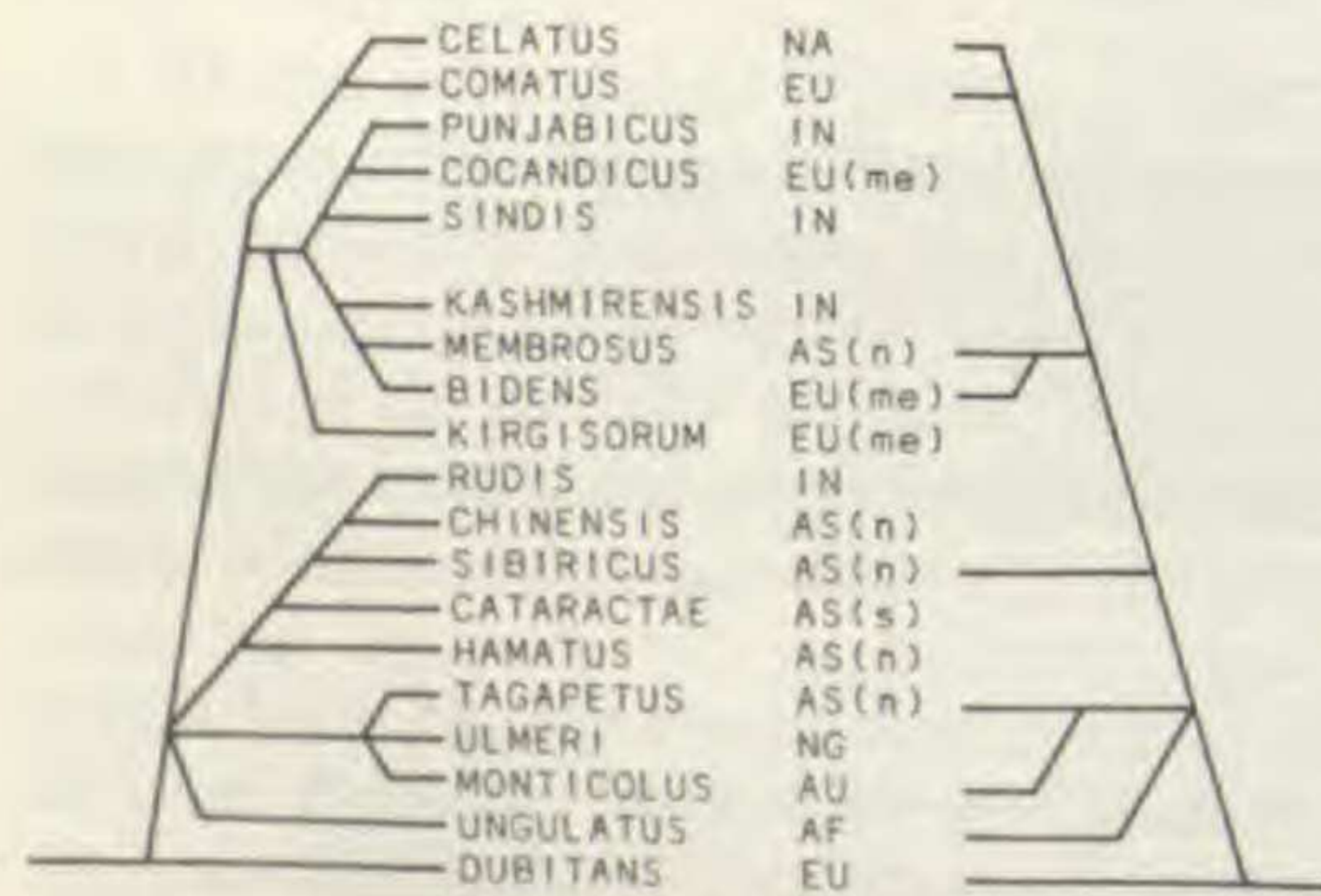
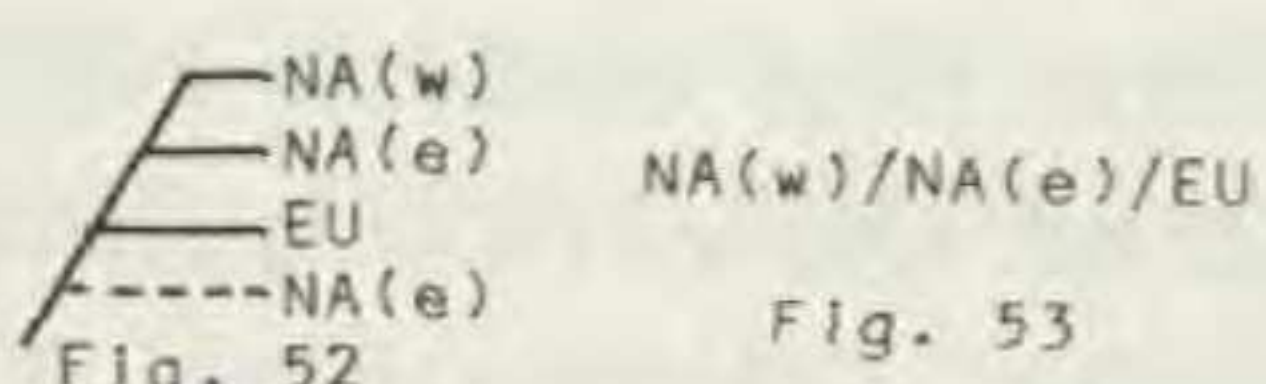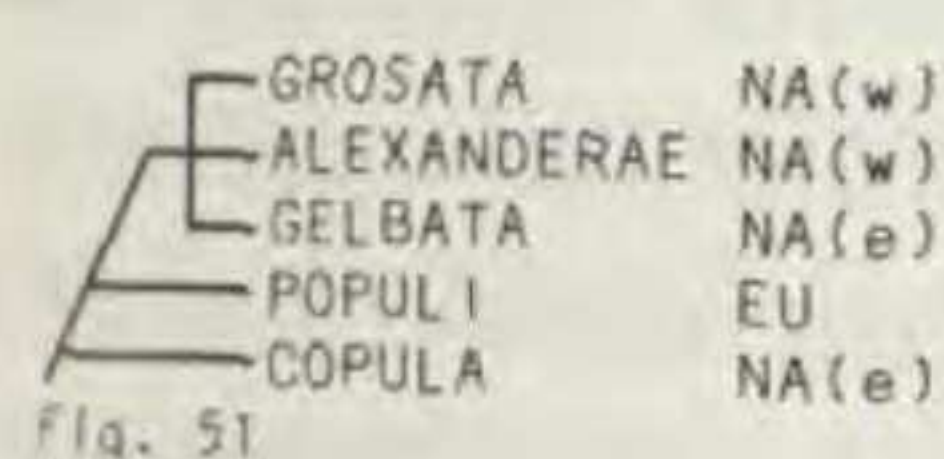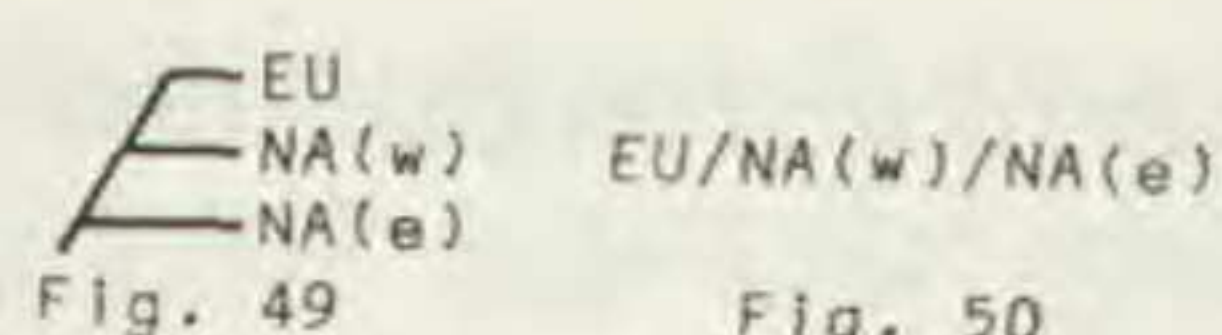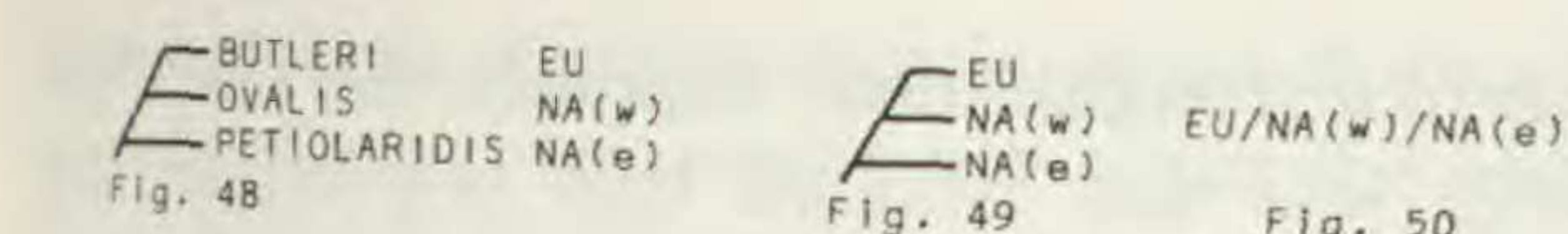FIGURES 28–30. The caddisfly tribe Agapetini.—28. Taxon/area cladogram.—29–30. Reduced area cladograms.
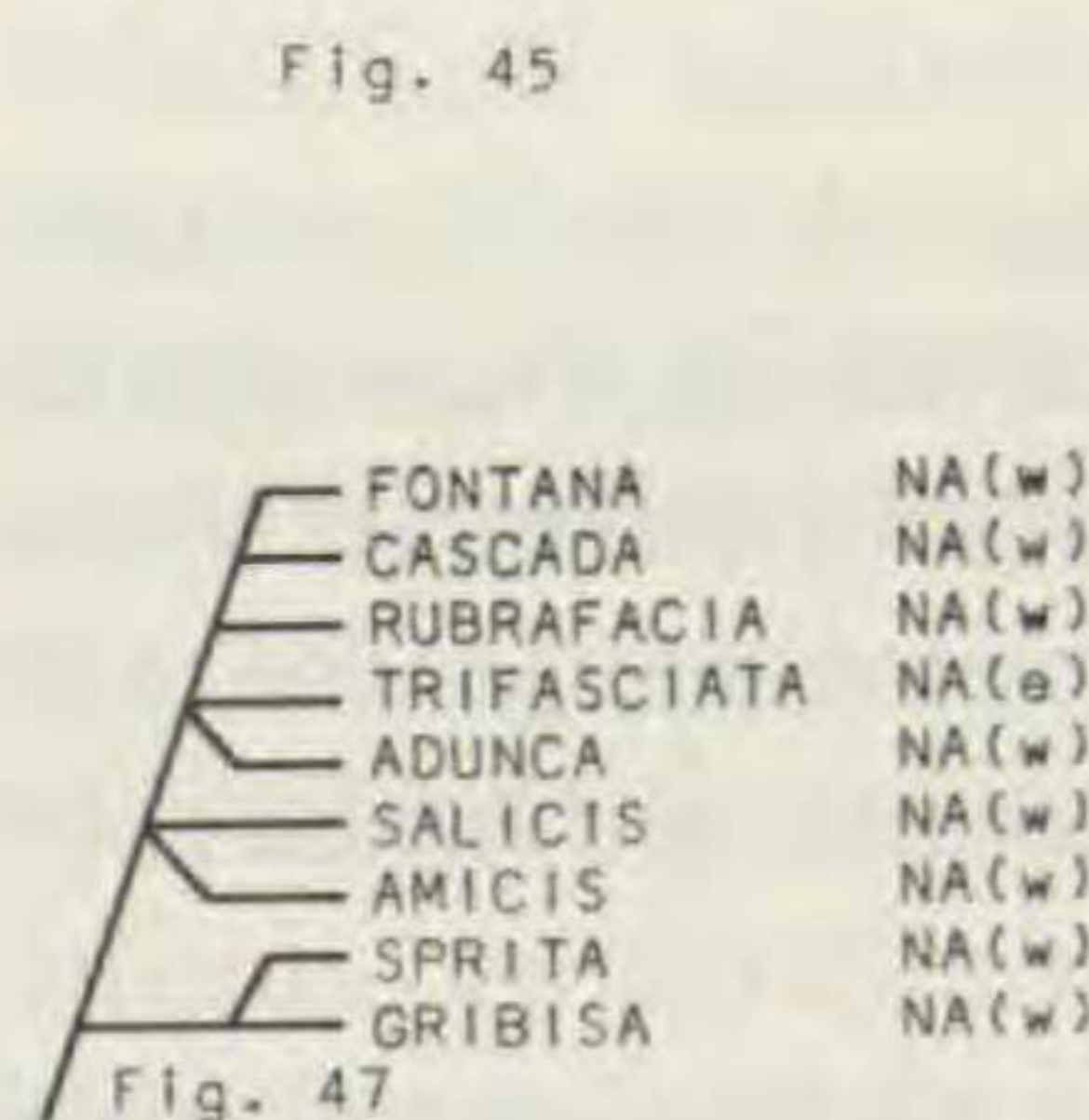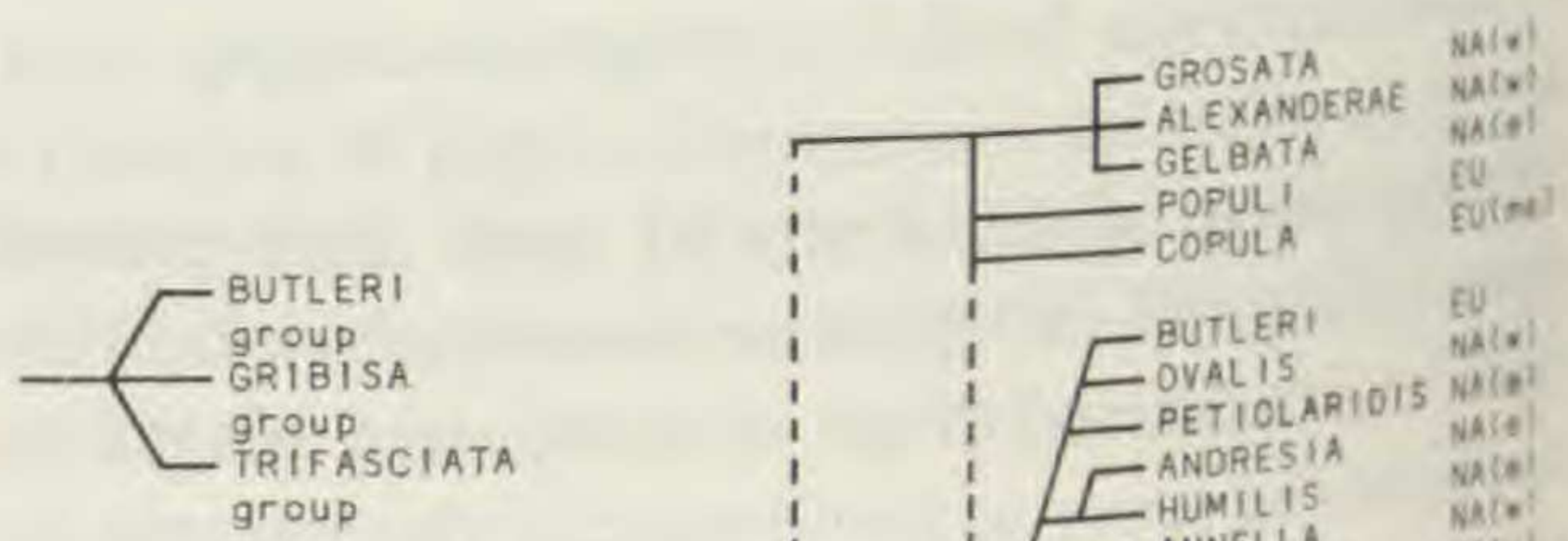
FIGURES 45–47. 45. A taxon cladogram showing an unresolved trichotomy existing between the three major groups in the leafhopper subgenus *Kybos.*—46–47. Taxon/area cladograms of the species taxa in the *butleri* (Fig. 46), *gribisa,* and *trifasciata* (Fig. 47) groups in the subgenus *Kybos.*

```
  ┌─BUTLERI      EU              ┌─EU
  ├─OVALIS       NA(w)          ┌┤NA(w)      EU/NA(w)/NA(e)
  └─PETIOLARIDIS NA(e)          └─NA(e)
   Fig. 48                       Fig. 49        Fig. 50
```

```
  ┌─GROSATA      NA(w)
  ┌┤─ALEXANDERAE NA(w)           ┌─NA(w)
  ││└─GELBATA    NA(e)          ┌┤NA(e)
  │├─POPULI      EU             ├┤EU        NA(w)/NA(e)/EU
  │└─COPULA      NA(e)          └───NA(e)
   Fig. 51                       Fig. 52        Fig. 53
```

```
  ┌─EXCAVA·     NA(e)
  │  group
  ├─SALICIS     NA(w)
  │  group
  ├─AMICIS      NA(w)            ┌─NA(w)
  │  group                     ┌┤NA(e)-
  ├─GRIBISA     NA(w)          └─EU         NA(w)/NA(e)/EU
  │  group
  └─VIRGATOR    EU               Fig. 55        Fig. 56
     group
   Fig. 54
```

```
  ┌─NEOMYAS        NA(e)          ┌─NA(e)
  ├─MYAS           EU(s)         ┌─EU
  ├─TRIGONOGNATHA  AS            ├─AS        NA(e)/EU/AS
  ├─XENION         EU(me)        ┌────EU
  └─ARISTOCHROA    AS            └────AS      Fig. 59
   Fig. 57                       Fig. 58
```

FIGURES 48–59. 48, 51, 54. Taxon/area cladograms of three lineages in the subgenus *Kybos.*—49, 52, 55. Reduced area cladograms of three *Kybos* lineages illustrated in Figures 48, 51, and 54.—50, 53, 56. Sequential linear arrangement of area cladograms of three *Kybos* lineages illustrated in Figures 49, 52, and 55.—57. Taxon/area cladogram of the genera in the ground beetle subtribe Myadi.—58. Reduced area cladogram of the subtribe Myadi.—59. Sequential linear arrangement of the reduced area cladogram of the subtribe Myadi.
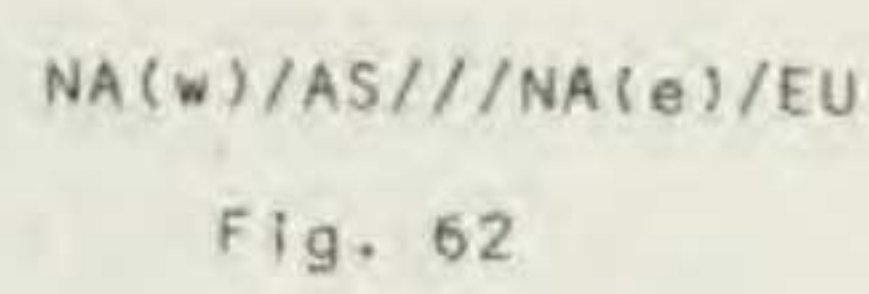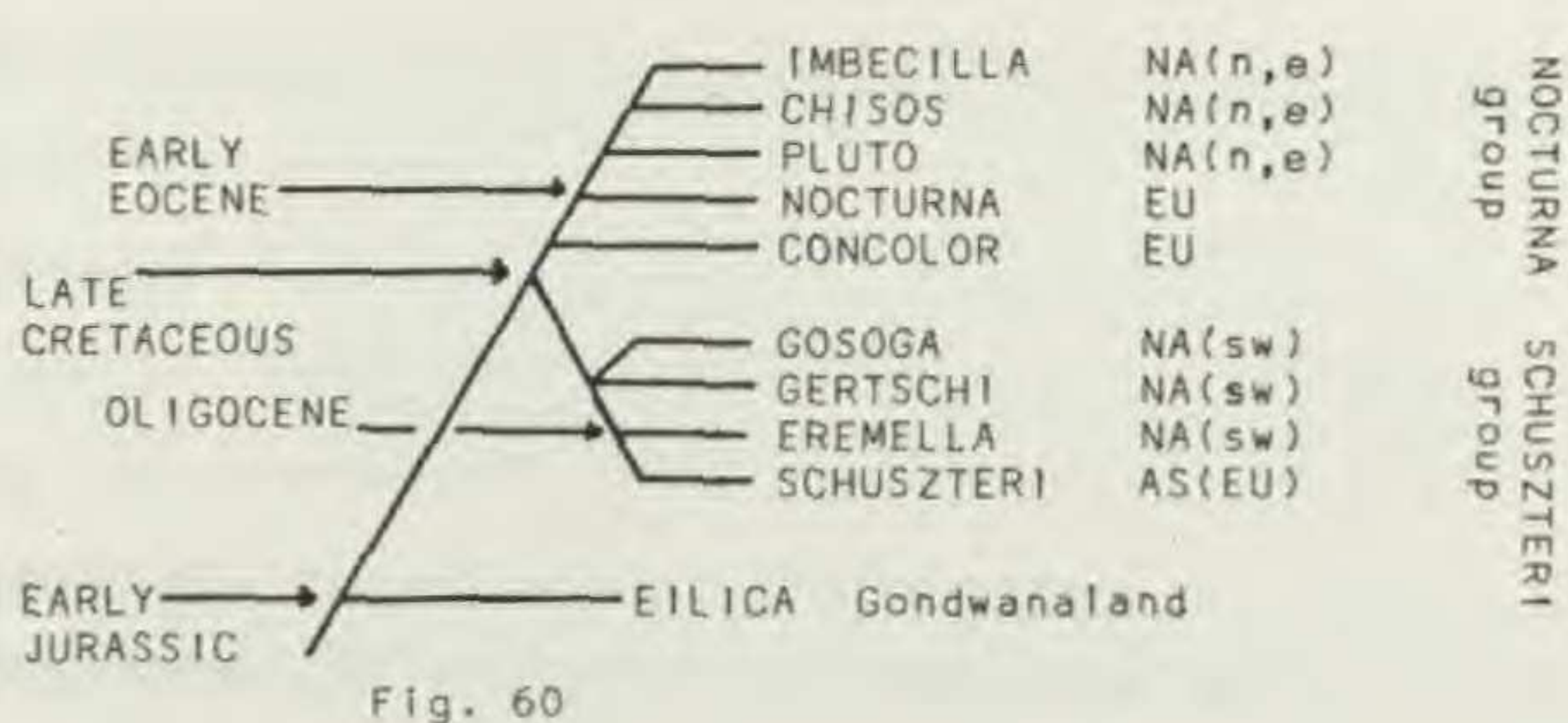
from his work with caddisflies. It will be interesting to see where any north Asian species fit in the cladogram should they be discovered in the future.

If the major species lineages in *Kybos* are determined and the distribution ranges are plotted against these lineages (Figs. 45–47), there appear to be three lineages (Figs. 48, 51, 54) that are informative about north temperate area relationships: *Kybos* lineage 1 containing *butleri* and two other species (Figs. 48–50); *Kybos* lineage 2 containing the *copula* lineage (Figs. 51–53); and *Kybos* lineage 3 containing the *trifasciata* lineage, plus the European species that occur in the major *butleri* group (Figs. 54–56). Before considering the possibility that these three leafhopper patterns (Figs. 50, 53, 56) are congruent with the caddisfly pattern (Fig. 44) let us examine patterns in two additional arthropod groups.

GROUND BEETLES
(INSECTA: COLEOPTERA; CARABIDAE)

The ground beetle family Carabidae is worldwide in distribution with a significant fauna in

```
                                   ┌── IMBECILLA   NA(n,e)   ┐ Z
                                   ├── CHISOS      NA(n,e)   │ O
  EARLY        ┌─────────────────►├── PLUTO       NA(n,e)   │ C
  EOCENE───────┤                  └── NOCTURNA    EU        │ T
  LATE─────────┤                      CONCOLOR    EU        │ U
  CRETACEOUS   │                                            │ R
                                   ┌── GOSOGA      NA(sw)    │ N A
  OLIGOCENE ───┤ ┌───────────────►├── GERTSCHI    NA(sw)    ┐
               └─┤                 ├── EREMELLA    NA(sw)    │ S
                 │                 └── SCHUSZTERI  AS(EU)    │ C
                                                            │ H
  EARLY ───────►├────────── EILICA  Gondwanaland            │ U
  JURASSIC                                                  │ S
           Fig. 60                                          │ Z
                                                              T
                                                              E
                                                              R
                                                              I
```

```
        ┌─EU
      ┌─┤ NA(e)
      │ └─NA(w)         NA(w)/AS///NA(e)/EU
  Fig. 61 └─NA(w)
           ─AS              Fig. 62
```

FIGURES 60–62. 60. Taxon/area cladogram of the spider genus *Callilepis.*—61. Reduced area cladogram of the genus *Callilepis.*—62. Sequential linear arrangement of the reduced area cladogram of the genus *Callilepis.*

North America, Europe, and northeastern Asia. A number of monophyletic taxa in this north temperate fauna have disjunct representatives in NA(e), EU, and AS. To date, only one taxon, the subtribe Myadi, has been objectively analyzed (Allen, 1980).

There are six genera in the subtribe Myadi: *Neomyas,* North America; *Myas,* Europe; *Xenion,* southern Europe; *Aristochroa,* Tibet-China; *Trigonognatha,* China, Japan, Korea, Formosa; and *Steropanus,* China. Specimens of *Steropanus* have not been available for study and therefore the genus is not discussed. A cladogram depicting the relationships of these taxa with their distributions has been constructed (Fig. 57). Unfortunately, there remains an unresolved trichotomy at the base of the cladogram, but this does not detract from the information content above this node (Fig. 58). We may see that in the Myadi, North America and Europe appear to have been more recently associated with one another than either area was with Asia (Figs. 57–59).

SPIDERS (ARANEAE: GNAPHOSIDAE)

Platnick (1975a, 1975b, 1976) has analyzed the cladistic and biogeographic relationships among species in the spider genus *Callilepis. Callilepis* is presently found in North America (east and west) and in Europe reaching east into northeastern Asia. This distribution pattern, at first glance, may not appear to be disjunct between Europe and Asia, but when the ranges of the individual species of *Callilepis* are plotted against the cladogram of species relationships and the *Callilepis*'s cladogram is reduced (Figs. 61, 62), a disjunct pattern becomes evident (Fig. 60). It

```
Glossosoma 1       EU/AS/NA(w)/-----/--/AS
Rhyacophila br. 6  EU/AS/-----/NA(e)
Myadi                          NA(e)/EU/AS
Glossosoma 2       AS/NA(w)/-----/EU/AS
Rhyacophila sib.gr.  AS/NA(w)/-----/EU/AS
Wormaldia          EU/AS/NA(w)/NA(e)
Agapetini                 NA(w)/NA(e)/EU/AS
Kybos 2                   NA(w)/NA(e)/EU
Kybos 3                   NA(w)/NA(e)/EU
```

FIGURE 63. A comparison of the linear sequential distributional patterns in nine monophyletic arthropod taxa.

is true that there are broad areas of sympatry in some taxa, for example *C. schuszteri* occurs in both Europe and Asia. This apparent sympatry may be due to dispersal at some point after the *C. schuszteri* lineage had been isolated and had evolved into a distinct species.

Now that we have studied a number of north temperate distribution patterns among several arthropod taxa, let us consider all of these patterns together.

SUMMARY OF DISTRIBUTION PATTERNS

We have now examined the distribution patterns in seven different arthropod taxa occurring in the temperate Northern Hemisphere. A total of eleven individual monophyletic lineages that have distinct, disjunct representatives in three or more north temperate areas (NA(e), NA(w); EU; AS) have been detected. Using the results of a cladistic analysis of these lineages we may arrange the individual patterns of these lineages in linear sequences and match the corresponding areas (Fig. 63).

The arrangement of the areas in linear sequences (Fig. 63) tells us that perhaps each individual lineage and sequence is a segment of a larger, more generalized pattern. The sequential arrangement of areas also brings to our attention areas not represented in a particular monophyletic lineage. But the sequencing of areas must be used in conjunction with the actual cladograms because phyletic events do not always occur in a precise sequential pattern.

Consider the cladograms for the spider genus *Callilepis* (Fig. 60) and the caddisfly tribe Agapetini (Fig. 28). The same areas (NA(e), NA(w); EU; AS) are represented in each cladogram but the relationships of the areas are different in each cladogram. In the Agapetini, the area relationships occur in a straight linear sequence: Asian forms were isolated first; European forms were isolated second; finally North American forms were isolated into eastern and western segments. In the genus *Callilepis*, area relationships do not

occur in a straight linear sequence: the *Callilepis* lineage was first isolated into two major segments, Asia plus western North America and Europe plus eastern North America. Species in each of these two major segments were subsequently isolated into Asian species related to western North American species and European species related to eastern North American species. Thus, the phyletic events depicted in cladograms tell us a great deal about area relationships and must be considered when analyzing area relationships.

In all of the taxa we have examined, the phyletic events depicted in the cladograms imply that ancient populations or parts of ancient populations have become separated and have subsequently evolved into distinct taxa, the allopatric speciation model. We might now ask how these taxa became isolated. Two possibilities have been suggested to account for the isolation of individuals and/or populations: (1) dispersal across preexisting barriers (oceans, mountains, etc.) and subsequent isolation and (2) the origin of barriers (opening of the North Atlantic) that divided ancient cosmopolitan populations, i.e., vicariance. In recent years, there have been biogeographers that have advocated both dispersal and vicariance explanations. Both of these types of explanations have been proposed in this symposium to explain the distribution of plants and animals (notably, Iltis as a proponent of dispersalism and McKenna and Allen as proponents of vicariance). It is not the purpose of this paper to give an account of this debate. I can only state that in my estimation the phenomenon of dispersal obviously does occur, but the resolution of whether a distribution pattern is due to dispersal or vicariance can be ascertained only after a cladistic analysis of the taxa involved and the correlation of this cladistic analysis with the geographic history of the areas in which the taxa occur (Platnick & Nelson, 1978). Hypotheses that attribute either a dispersal or vicariance explanation to an individual pattern can be corroborated or refuted based on the analysis of additional taxa. In this paper it has been shown that the taxon/area cladograms of nine independent monophyletic lineages seem to corroborate the hypothesis that the faunas of Europe and eastern North America have shared a more recent common biota with one another than either has shared with Asia (Fig. 63).

If we assume that at least some ancient cosmopolitan populations or parts of ancient pop-

ulations were divided and isolated during the earth's history, we might ask what the events were that led to division and isolation. In the taxa we have studied we are particularly interested in possible division events affecting the landmasses that are now found in the Northern Hemisphere. The first event relevant to understanding the history of north temperate taxa was the division of the supercontinent of Pangaea into a northern landmass, Laurasia, and a southern landmass, Gondwanaland, sometime in the Cretaceous. Raven and Axelrod (1974) suggest that the last possible date for the direct interchange of taxa between North America, Europe, and Africa was about 180 million years ago (Ma). From the Cretaceous to the present, many populations have displayed considerable east-west, north-south movements throughout the history of the north temperate areas (the work of Margaret B. Davis, this symposium, gives examples of recent movements of some plant species). The older fossil record is indicative of movement and strongly indicates that elements of the north temperate biota once existed in more northern latitudes than at present. It has been suggested (Chaney, 1947; Kendeigh, 1961) that the ancestors of the present-day temperate deciduous biota existed at high latitudes in a more or less continuous band around the circumference of the Northern Hemisphere. If this is true, then these biotas have been subject to a number of distinct geological events occurring in the Northern Hemisphere.

The fossil and geological record indicates that portions of the Northern Hemisphere have been periodically inundated by epicontinental seas. Two such epicontinental seas were the Midcontinental Seaway that divided North America into eastern and western sections and the Turgai Straits that divided Europe and Asia. These seaways were active in the Upper Cretaceous (100 Ma). Cox (1974) suggested that these seas divided an ancient dinosaur fauna into distinct groups, an Asiamerica Group and an Euramerica Group. The Euramerica area was divided in the Eocene (45 Ma) by the opening of the North Atlantic (Raven & Axelrod, 1974; Cox, 1974). The Asiamerica area was first severed in the Oligocene (40 Ma) (Cox, 1974; Colbert, 1973).

Concurrent with the Midcontinental Seaway (Upper Cretaceous) was the beginning of the orogenies that gave rise to parts of the western Cordilleran mountain system (Dunbar & Waage, 1969). This western mountain building began in the early Cretaceous and continued along the eastern border of the present-day Rockies, through the Paleocene, and died out by the Eocene. These early mountains were eroded, filling the intervening basins so that by the Oligocene this western area became a flat surface 2,000 to 3,000 feet high. This peneplained, elevated area was not high enough to create an eastern rain-shadow effect. Thus, during the Oligocene the eastern and western biotas of North America were reunited as the Midcontinental Seaway subsided. The European seaway, the Turgai Straits, also subsided and the biotas of Europe and Asia were also reunited.

During the Miocene the mountain areas of western North America again became active. Uplifting occurred along the entire Cordilleran range from Alaska into Middle America (Dunbar & Waage, 1969). In addition to this mountain building, climatic changes took place throughout the world. These events eventually led to the separation, once again, of North America into eastern and western biotas and the separation of Asian and European biotas. In the intervening areas separating these continental biotas, extensive grassland biomes began to develop.

The geological history of the Bering Straits after the Oligocene is one of repeated land connections and disjunctions between Siberia and North America (Colbert, 1973). The connections have provided opportunities for plants and animals to disperse and establish cosmopolitan populations. The disjunctions would have isolated segments of these cosmopolitan populations and provided opportunities for allopatric speciation to occur.

The geological events that have just been discussed have been correlated with phyletic events in nine of the area cladograms (Fig. 64) we have studied. (*Callilepis* and one of the *Kybos* lineages will be discussed separately.) We may see that there is an orderly, sequential occurrence of both phyletic and geological events through time. The connections and disjunctions of continents and continental parts at the different time intervals can be depicted schematically (Fig. 65), illustrating how different land areas were associated.

In the diagram showing the correlation of phyletic and geological events (Fig. 64), the Miocene mountain orogeny in western North America and the worldwide climatic changes occurring at this time are shown at two points in the cladograms. The occurrence of these Miocene events is consistent with the cladograms and the geological
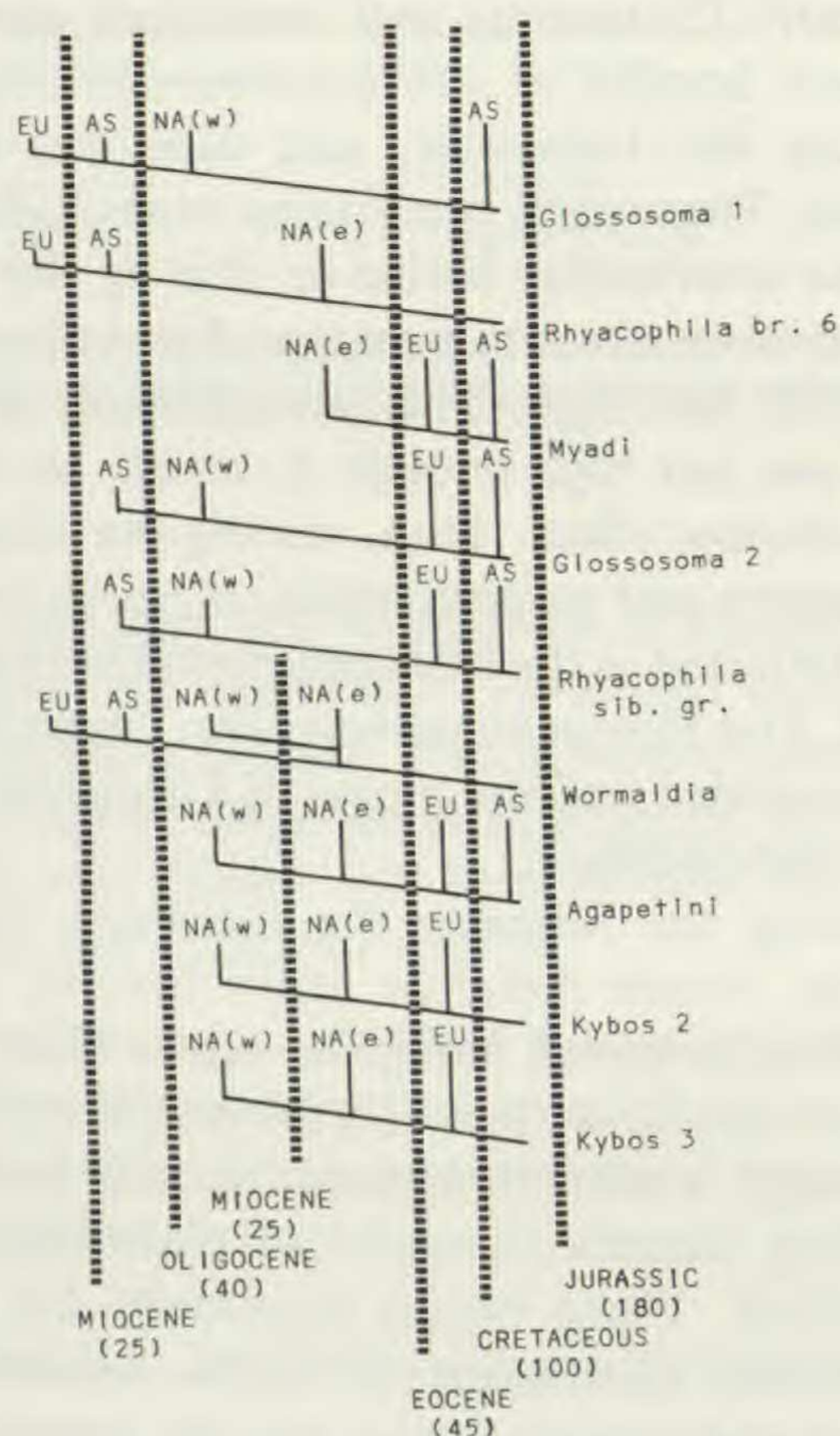
Fig. 64

FIGURE 64. The reduced area cladograms of nine monophyletic arthropod taxa superimposed on a geological time scale. It is implied that events occurring during the indicated geological periods would have divided and isolated ancient cosmopolitan populations at the points indicated on the cladograms.

history. In the two *Kybos* lineages and in the Agapetini lineage, North American populations were separated from Europe in the Eocene (45 Ma). The North American populations were subsequently divided into eastern and western segments in the Miocene (25 Ma). In these lineages (*Kybos* 1, 2, Agapetini), additional taxa have not been found in other areas. In the *Wormaldia* lineage, there was apparently a cosmopolitan population occurring in North America, Asia, and Europe. The North America and Asia-Europe connection was severed in the Oligocene (40 Ma). The now independent North American population was not divided into eastern and western lineages until the Miocene. The Asian and European cosmopolitan population of *Wormaldia* was also divided in the Miocene as were populations occurring in the *Glossosoma* 1 and *Rhyacophila* branch 6 lineages.

The *Callilepis* area cladogram is a double dichotomy (Fig. 61) that does not lend itself to inclusion with the linear cladograms of the other taxa. However, the area cladogram of the spider genus *Callilepis* may be correlated with four of
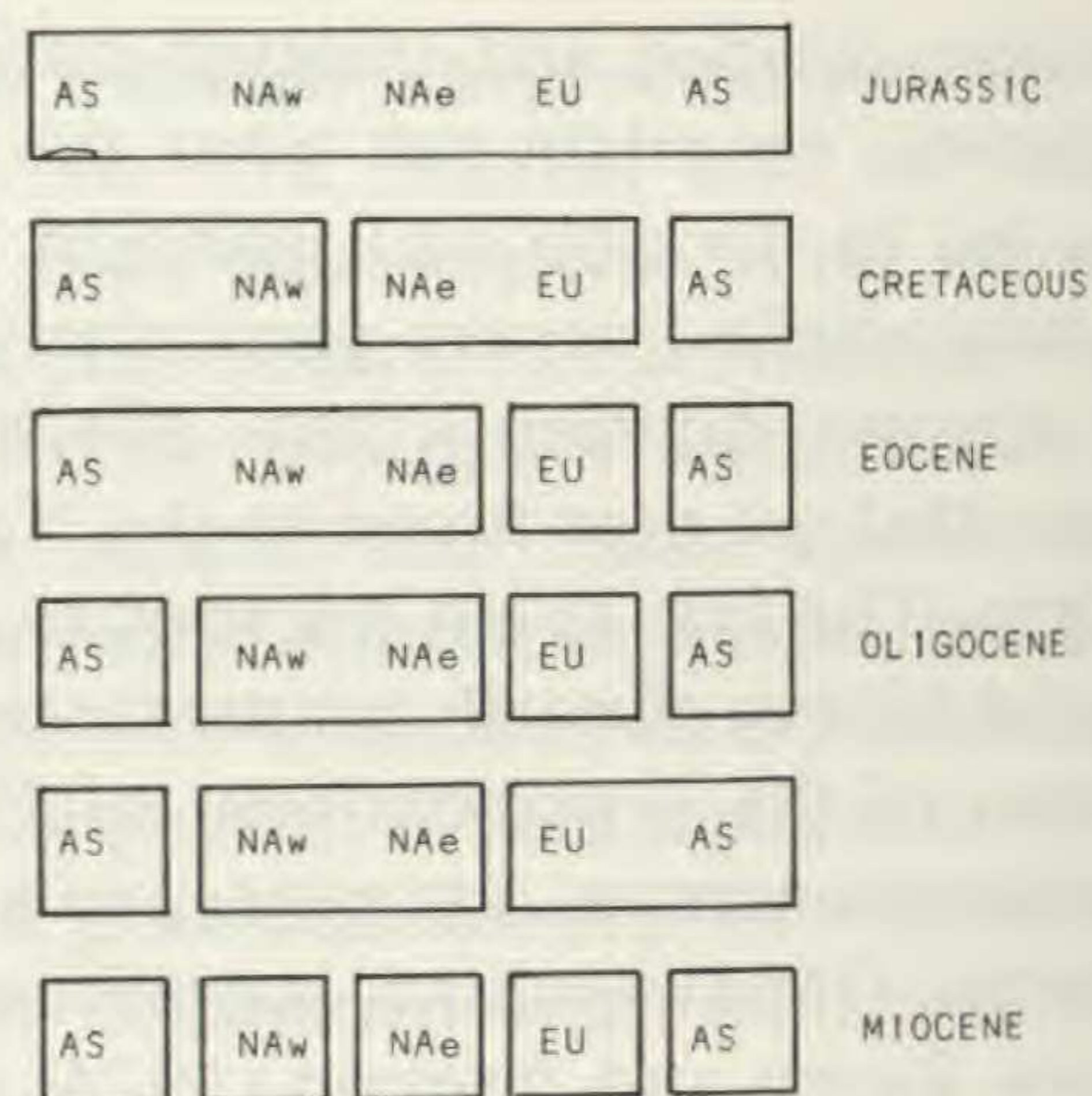

Fig. 65

FIGURE 65. A schematic diagram depicting the divisions and reassociations of North Temperate land masses during specific geological periods. These divisions and reassociations are based on information derived from cladograms illustrated in Figure 64.

the same geological events we have discussed (Fig. 60). *Callilepis* may represent a slightly different biogeographic pattern than the pattern exhibited by the other arthropod taxa we have studied. Since there appears to be a degree of sympatry among species in *Callilepis* it will be worthwhile to consider Platnick's (1976) discussion of the cladistic and biogeographic patterns of this genus in greater detail.

There are ten species in *Callilepis*. Their known distributions are indicated on the cladogram showing relationships among the ten species (Fig. 60). There are two species groups, the *nocturna* group and the *schuszteri* group. Both groups have representatives in North America, with the *nocturna* group having one species in Europe and Asia (*C. schuszteri*). At first, we might assume that a distinct pattern of population divisions (a vicariance pattern) is not evident since there are broad areas of sympatry. Platnick considered the sympatry to be dispersal "noise" and if the noise is eliminated a vicariance pattern emerges. He said, "If we assume that the presence of *C. schuszteri* in Europe is due to dispersal from Asia, the two groups of *Callilepis* can be seen as essentially vicariant on a global basis, with the *schuszteri* group occurring in southwestern North America and eastern Asia and the *nocturna* group occurring in Europe and northern and eastern North America."

Platnick next associated the two biotas, Euramerica and Asiamerica, with specific lineage divisions in the *Callilepis* cladogram (Fig. 60). These divisions correspond with the Late Cretaceous epicontinental seaways previously discussed. Fi-

nally, Platnick correlated the separation of Europe and America (45 Ma) with a separation of the *nocturna* group into European and eastern North American taxa.

The area pattern of relationships in the *butleri* lineage of the leafhopper subgenus *Kybos* (Fig. 49) is not congruent with the area patterns we have discussed thus far (Fig. 63). The *butleri* lineage indicates that a cosmopolitan population was first divided into an eastern population and a western North American-European population. Subsequently, the western North American and European population was divided. This sequence of events in the *butleri* lineage seems to represent a different biogeographic pattern. It is also possible that the cladistic relationships in the *butleri* lineage have been incorrectly determined. Whatever the case may be the *butleri* inconsistency has been noted and future workers may objectively determine the truth of the matter.

We may now conclude that of the eleven arthropod monophyletic lineages discussed only three biogeographic patterns were detected. The phyletic events depicted in the patterns were attributed to the same geological events and therefore both patterns resemble each other closely. We can say that there is a remarkable degree of congruency among the eleven cladograms. This latter statement takes on considerable more significance when the number of possible patterns that could occur are considered.

Since we only considered eleven monophyletic lineages in the summary (Figs. 63–64), the largest number of patterns we could have detected would have been eleven. We also considered only four areas (NA(e), NA(w); EU; AS). When four different areas are considered, there are two possible structurally different cladograms and 12 possible linear sequences for one of these cladogram types (Platnick & Nelson, 1978). Thus a total of 13 possible different patterns exist. The fact that only three biogeographic patterns were detected in eleven lineages indicates that individual lineages, which are members of larger biotas, have responded to historical events in a similar way. If this is true, then there may well be only a very limited number of cladistic and biogeographic patterns in nature that represent the evolutionary history of the world's biota. A great deal of work remains to be done if we are to detect and confirm the earth's evolutionary patterns. If we choose to search for these patterns using an objective, testable methodology, then this future work will

lead us to a more complete and accurate understanding of the evolutionary process.

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