

A SYNOPSIS OF THE TAXONOMIST'S TASKS, WITH PARTICULAR ATTENTION TO PHYLOGENETIC CLADISM

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ABSTRACT

In view of the widespread ignorance of taxonomic endeavour, even among those familiar with the use of identification keys, a synopsis of the taxonomist's tasks is presented. Topics touched upon include recognition of species, problems of nomenclature, the problems and controversy surrounding the grouping of species into higher taxa, an exposition of phylogenetic cladism as the most reliable method of discovering natural (monophyletic) groups, the assignment of these groups to categories of the Linnaean System, key construction, and the collation of biological information for particular species.

INTRODUCTION

STUDENTS on courses in field biology regularly use identification keys written by taxonomists for the non-specialist. Such keys are an indispensable tool for ecologists. Indeed it has been recognised (NERC, 1976) that a lack of suitable keys to certain groups of organisms is a serious impediment to ecological advance. An additional impediment is that many existing keys are poorly constructed or over-technical, so that the novice is unable to make progress with any degree of confidence. The latter problem has prompted the AIDGAP project (Aids to Identification in Difficult Groups of Animals and Plants).^{*} Other sources of confusion and irritation are the apparently arbitrary changes in the scientific names of familiar species, and, even more confusing, radical changes in the way species are grouped together into a classification system. Enquiry as to what justifies the latter reveals a hotbed of controversy between different schools of taxonomy—Phenetics versus Gradism versus Cladism (with Phylogenetic versus Transformed Cladism). Furthermore, a smokescreen of jargon, not to mention a propensity to write in polysyllabic prose of singular opacity, adds to the onlooker's exasperation. It is thus perhaps not surprising to find ecologists who entertain an ambivalent attitude towards the science of taxonomy. On the one hand they allow their exasperation with a poorly constructed key or an irritating change in nomenclature to engender a contempt for taxonomy as a science. On the other hand they welcome the publication of each new identification key or monograph.

Taxonomy is the branch of biology concerned with describing the diversity of organisms and the ordering of this diversity into a system of classification. This classification is the necessary system of reference for all branches of biology.

This paper aims to provide no more than an introductory synopsis of the tasks of the taxonomist. It deliberately draws its illustrative examples from personal experience. This is partly to give them more immediacy, partly as a device by which I may limit the field, and partly because I am a largely self-taught taxonomist and it is the problems I have actually encountered that have led me to explore the principles involved.

To answer the question as to why I consider such a synopsis worthwhile I would

^{*} Information about the AIDGAP project may be obtained from The AIDGAP Project Co-ordinator, Leonard Wills Field Centre, Nettlecombe Court, Williton, Taunton, Somerset TA4 4HT.

reply, firstly, that I have often wished that I had had such a synopsis to guide me in my reading as I moved from being an applied ecologist (medical entomologist) to being a taxonomist. Secondly, it is evident that the education system at all levels tends either totally to neglect taxonomy or else to treat it in a most cursory manner. In the latter case the furious debates leading to growing acceptance of Hennigian (Phylogenetic) Cladistics are either ignored or presented in a manner that seems almost designed to create confusion. If history endorses the opinion that Hennig should be bracketed with Darwin and Mendel, then such neglect is extraordinary if not actually perverse.

If this synopsis achieves nothing more than to make the reader want to delve more deeply into the matters briefly touched upon, I shall be content. I hope, however, that it will lead to greater understanding of the taxonomist's role. I dare to hope that it may lead to greater respect for taxonomy and of the research which underlies an identification key.

In my experience a taxonomist finds himself involved in five distinct tasks. These are summarised below.

TASK I. RECOGNITION OF SPECIES

We cannot discuss the recognition of species until we have an acceptable definition of a species. The biological species concept ("groups of inter-breeding natural populations that are reproductively isolated from other such groups") is a useful working definition for most species in practice. There are, however, groups of species in which the "isolation" is not 100 per cent. Furthermore, the application of the biological concept to asexually reproducing species is impossible. The modern understanding is grounded in an evolutionary perspective. Today a species is understood as being the highest level taxon (= a group of related organisms) which may evolve. It may be defined more precisely thus: A species "is a single lineage of ancestor-descendant populations which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate" (Wiley, 1981, modified from Simpson, 1961).

In practice most species are recognised by the use of diagnostic morphological characteristics. These characters are features found to be useful by those who have studied the groups in question. There are two principal sources of error that have arisen from this classic approach to species recognition. Firstly, some species exist in a variety of distinctive forms (polymorphism) which may be erroneously assigned to separate species on the basis of morphological criteria alone. Secondly, two or three closely related species may be indistinguishable using the morphological criteria traditional for the group. These separate (sibling) species may, therefore, be erroneously assigned to a single species.

The unravelling of polymorphism or sibling-species problems may involve a range of evidence in addition to traditional morphological analysis. However, these problems always start with entities defined according to traditional morphological criteria. One either has a series of morphological segregates whose status is in question (are they separate species or morphs of a polymorphic species?) or a single morphological segregate that for some reason (behavioural or ecological differences between populations perhaps) one suspects may represent more than one species. Additional evidence includes results of breeding experiments, examination of chromosomes to determine their number and morphology (or even banding

patterns), electrophoretic analysis of structural enzymes, amino acid sequence analysis, immunological analysis, behavioural analysis, comparisons of songs, ecological relations, parasites, and basic natural history data. In fact the good taxonomist welcomes any comparative data he can get hold of.

Having established the existence of sibling species (a species complex) it is worth re-examining samples of each species for evidence of morphological difference. Even if no clear-cut morphological distinctions are found one will normally discover evidence of morphological divergence in statistical terms. That is to say, if one plots variation graphs for a quantifiable morphological character they will be different even though they overlap (Fig. 1).

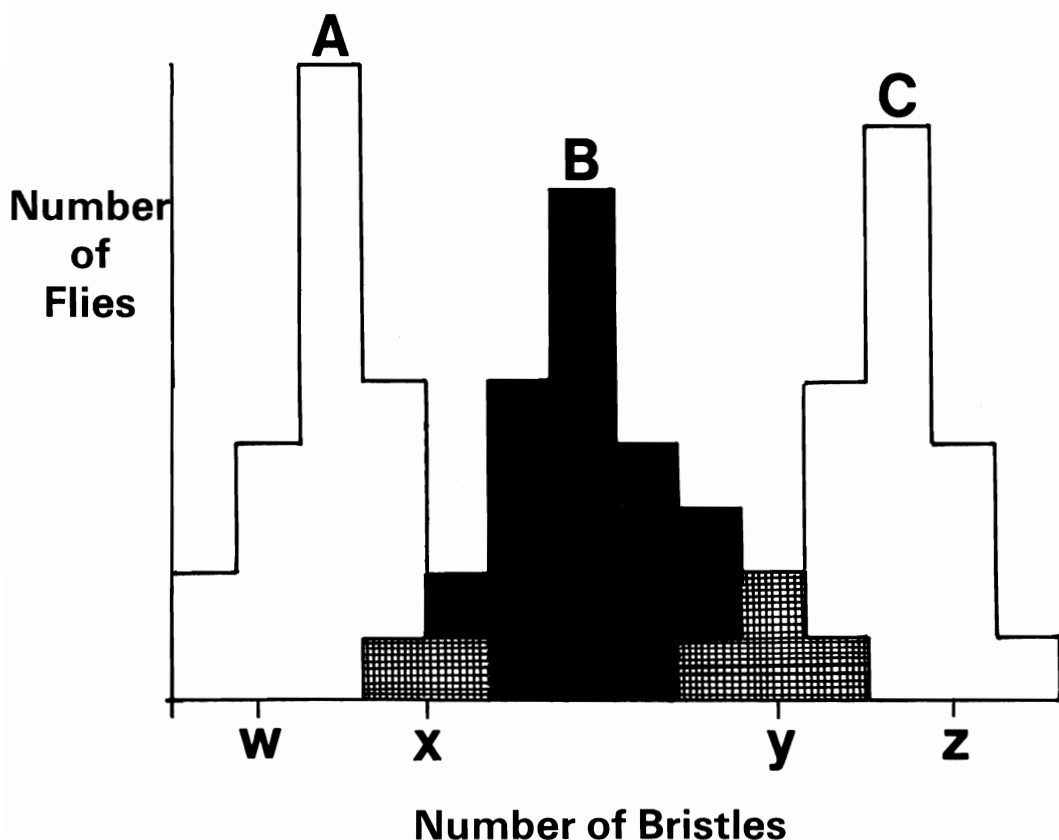


FIG. 1.

Variation plots for the number of bristles on the mesopleuron recorded for large samples from populations of three sibling species (A, B and C). Specimens with w bristles clearly belong to species A. Likewise specimens with z bristles clearly belong to species C. Specimens with x bristles belong to species A or B, likewise specimens with y bristles could belong to B or C.

Newly-described species are still frequently established by the splitting of a previously recognised "species" on the basis of morphological criteria alone. This is perhaps most likely to occur when a novel technique leads to examination of features not previously considered. For example in my studies of Phoridae (scuttle flies) I have made a break with tradition by switching from micro-pinned specimens

to specimens preserved in fluid and subsequently mounted on slides and examined under the compound microscope. In this way I found that there were two species of *Gymnophora*, initially recognised as such from details of the male genitalia, which both keyed out to *G. quartomollis* in the existing literature. In pinned specimens the male genitalia tend to be concealed by retraction into the tip of the abdomen. In slide-mounts these same genitalia can be nicely displayed by gentle pressure on the coverslip at the time of mounting. The newly recognised species, *G. healeyae* Disney (1980b), can be readily separated from *G. quartomollis* in the female sex by details of abdominal glands (probably pheromone glands) not visible in pinned specimens but clearly discernible on a slide-mounted specimen.

In the above example the newly recognised species was indeed a species new to science. However the discovery that two species key out at the same point in an existing key may only reflect the deficiencies of the key. Thus I found that I had two other species which both keyed out to *Gymnophora arcuata*. In this case the newly recognised species was already known, *G. integralis*, but not previously recorded from Britain (Disney, 1981d).

Species may also be abolished. Two species of scuttle fly belonging to the genus *Conicera*, *C. tibialis* and *C. fallens*, were for a long time separated on the basis of the ratio length of tibia to length of tarsus of the front legs. Having procured a large sample of these flies in a single trap over 24 hours, I plotted out the ratios for the whole sample (Fig. 2). This plot looked suspiciously like variation in a single species. In view of this I borrowed type material (i.e. the original specimens used when the species were first described) of both species and made detailed comparisons of genitalia and other features. I concluded that "*C. fallens*" was not a valid species (Disney, 1981b). Furthermore the plot reveals why "*C. fallens*" was comparatively rare. The definition for "*C. fallens*" placed it well away from the mean for the ratio in question. Consequently "*C. fallens*" is by definition a rarer variant. More detailed discussion of species-recognition problems can be found in numerous texts (e.g. Cain, 1963; Mayr, 1969; Crowson, 1970; Wiley, 1981).

TASK 2. SOLVING PROBLEMS OF NOMENCLATURE

A name may have to be changed for a number of reasons. It may have to be discarded if it is found to infringe the rule of priority. This rule declares that the first validly published name for a species takes precedence over any names subsequently given to the species.

An original name may have been overlooked by a subsequent worker, particularly if it had been published in an obscure journal in the last century or earlier. Sometimes a new name is proposed because of ignorance. Males and females have frequently been assigned to separate species before further information, such as catching a pair mating, revealed the error. Sometimes it may be a failure to appreciate the range of variation within a species, as in the case of "*Conicera fallens*" cited above.

Sometimes a new, but redundant, name may have been proposed because the original description of the species or genus is misleading. For example, in a paper (Disney, 1981a) on the genus *Rhynchomicropteron*, I explained why I had originally assigned the species *R. beaveri* (Disney) to a different genus. Annandale (1912) erected the genus *Rhynchomicropteron* on the basis of a single specimen of a single species. His description clearly states that the species possessed halteres and he even

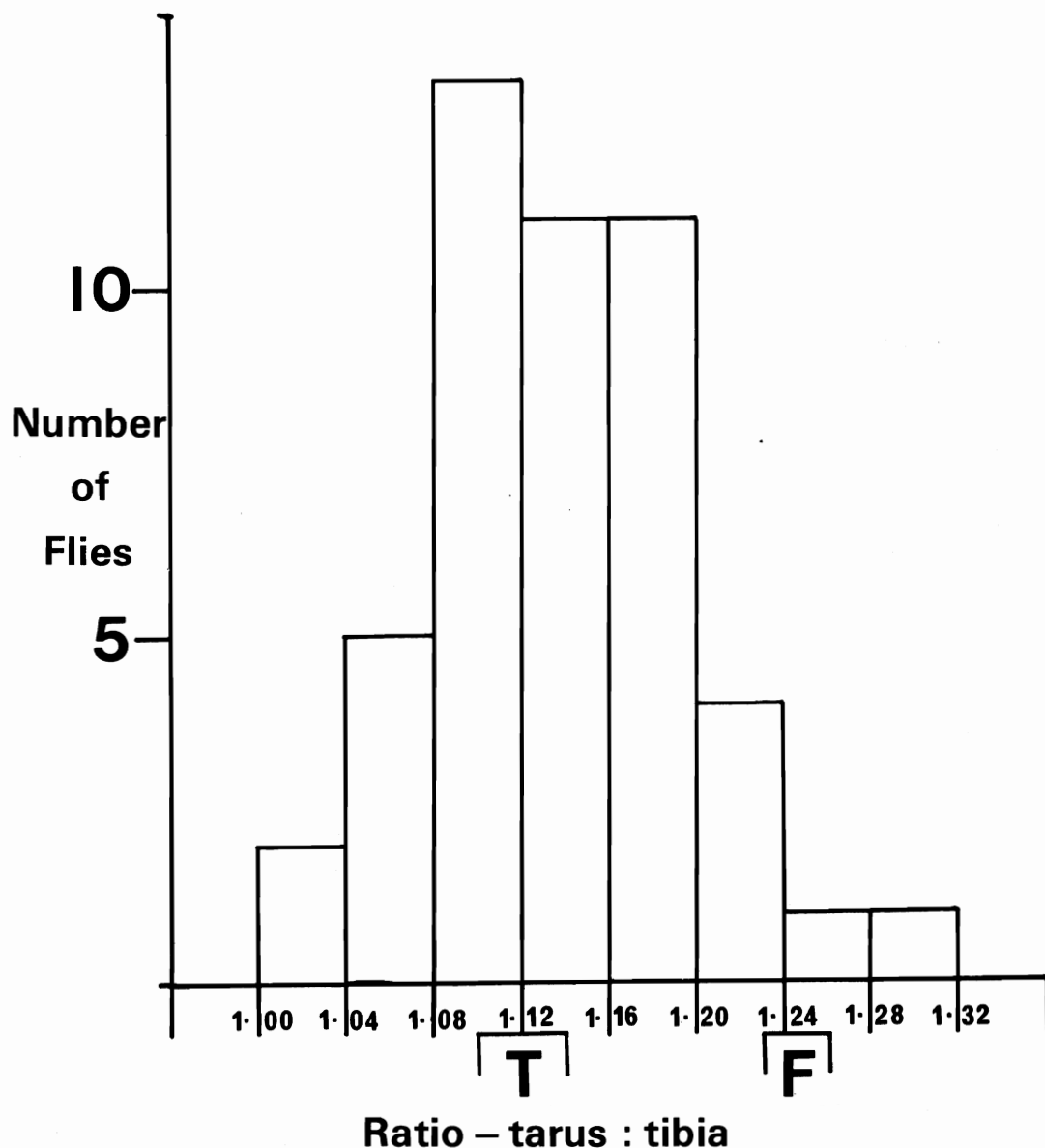


FIG. 2.

Frequency histogram for ratio of foretarsus to foretibia for a sample of 48 males of *Conicera tibialis*. T = ratios for *C. tibialis* given in previous literature. F = ratios for "*C. fallens*" given in literature.

illustrates this feature. However when I managed to borrow Annandale's specimen from India, and remounted it on a slide, I discovered the 'halter' illustrated by Annandale was, in fact, a piece of detritus! The species, like *R. beaveri*, has lost the halteres completely during evolution. There were other errors in Annandale's description, probably the result of a failure to examine such a small insect (<2 mm long) as a slide-mounted specimen under a compound microscope.

A nomenclatural muddle may involve a combination of errors and become quite a detective game to unravel. For example, I was sent a series of specimens, of both

sexes, of a species in the tropical genus *Chonocephalus*, from a hothouse in Middlesex. There is marked sexual dimorphism in this genus and some species have been described on the basis of females alone and some on the basis of males alone. The consequence is that the genus is in what we call a "taxonomic mess". Examination of the Middlesex specimens suggested that the females belonged to *C. jamaicensis* (described in 1915), but the males appeared to belong to *C. punctifascia* (described in 1935). However, subsequent to the published keys and descriptions, Prado (1976) had established the latter species as a synonym of *C. jamaicensis*. In addition Borgmeier (1963) had raised the possibility that *C. jamaicensis* might itself be a synonym of *C. heymonsi* (described in 1913) which itself might be a synonym of *C. depressus* (described in 1912). In view of this I started to tackle this confused situation by borrowing a series of *C. jamaicensis* and "*C. punctifascia*" from a museum in Washington. The first surprise was to discover two species in the series of "*punctifascia*"! One of these proved to be an undescribed species from Panama (Disney, 1980a). It was clear from examination of the rest of the series that Prado's synonymising of "*punctifascia*" with *jamaicensis* was correct and that this was the species from Middlesex. I then borrowed the type material of *C. heymonsi* from a museum in East Berlin. After mounting the specimens on slides I was able to establish that "*C. jamaicensis*" was indeed a synonym of *C. heymonsi*. I then attempted to procure the type material of *C. depressus* from a museum in Amsterdam. However, they reported the specimens to be lost. I discovered, however, that there were specimens in a museum in Bonn from the type-locality. Furthermore one was labelled "mit Type verglichen!" in the handwriting of the late Fr. Schmitz (the great Jesuit authority on scuttle flies). On examining these specimens it became clear that there were two significant characters, not mentioned in the original description, which served to distinguish *C. depressus* from *C. heymonsi*. I was thus able to report (Disney, 1981c) that the correct name for the specimens from Middlesex is *Chonocephalus heymonsi*.

A second reason for changes of name is when species are transferred from one genus to another. During my revisionary studies of the British Phoridae, I became increasingly dubious about the validity of the genus *Citrago*. There were certain species in the related genus *Triphleba* that bridged the gap between the two genera. I then found that one species, *T. gracilis*, showed a range of variation such that some specimens keyed to *Citrago* and others to *Triphleba* in the same key to genera. In particular wing vein 3 was forked in some specimens, was unforked in others, but in most exhibited an intermediate state. I looked at the matter in detail and concluded that the genus *Citrago* must be abolished and all the species transferred to *Triphleba*. In the case of *Citrago citreiformis* this was simply a matter of changing the name to *Triphleba citreiformis*. However in the case of *Citrago collini* (described in 1955) it was not so simple—there already was a *Triphleba collini* (described in 1943). In this case I was obliged to drop the name "*collini*", since it had become a "consequent secondary homonym" and proposed a new name—*Triphleba smithi* (Disney, 1982).

A third reason for name changes is when a taxonomist raises subgenera, or even species groups, to the generic level. This change of name due to change of rank is clearly a decision based purely on opinion. It is my contention that such changes are only acceptable if the opinion is likely to meet with the approval of other competent taxonomists. There are a number of taxonomists who do not support this view. The relation between classification and assignment of rank is discussed below.

Finally it needs to be emphasised that the significance of type specimens (i.e. the actual specimens on which the original descriptions of species were based) is solely in terms of the resolution of nomenclatural problems. It is not necessary for a type-specimen to be in any other way "typical". If a "species" is subsequently recognised as being two species in fact, as was the case of *Gymnophora quartomollis* cited above, then the segregate that includes the type specimen of the original "species" is the segregate that carries that name. The segregate which excludes the type specimen requires a new name. Unfortunately there are still a few taxonomists around who have not grasped this simple point. Thus the paper by Maia and Oliveira (1979), in which a numerical criterion for choosing the holotype specimen is suggested, is an excellent illustration of the principle that mathematics is an admirable means of elucidating the consequences of a premise, but it may tell you nothing about the truth (or in this case the falsehood) of that premise.

For more detailed information on nomenclatural problems, and the role of type-specimens, the reader is referred to the standard texts (e.g. Simpson, 1961; Mayr, 1969; Crowson, 1970; Wiley, 1981). In addition the excellent little book by Jeffrey (1977) is warmly recommended.

TASK 3. CORRECT CLASSIFICATION

Any assemblage of objects can be classified in a number of ways depending on the criteria chosen by the classifier. If the characters employed are selected entirely without restriction then a classification of organisms would be likely to resemble an interminable network. Biologists, however, prefer criteria that give rise to a hierarchical system of classification—that is species are grouped into taxa that are themselves grouped into taxa of higher rank and so on. This preference is not founded upon whim. On the contrary, ever since Aristotle, biologists have been committed to the view that there is a "natural" classification to be discovered which is found to be hierarchical. While the naming of the categories is a matter of arbitrary choice the taxa in question are, in principle, natural entities. Classification should not be confused with categorisation. Categorisation is concerned with the assignment of a rank, and an appropriate name, to a particular group proposed or discovered by a taxonomist. The ranks employed by biologists are those recognised in an expanded Linnaean System such as:

Kingdom
Phylum
Subphylum
Class
Subclass
Order
Suborder
Superfamily
Family
Subfamily
Tribe
Genus
Subgenus
Species

The problems associated with categorisation are touched on below. First we need

to consider the problems associated with how one discovers a “natural” classification.

All classifications are based on studies of the distribution of character states in different species. If the “correct” characters are selected, a natural classification will emerge from such studies. Taxonomists face the problem, therefore, of justifying the criteria used to select the “correct” characters.

The first school of taxonomy committed to the search for a “natural” classification begins with Aristotle. It reached a high degree of sophistication, prior to the acceptance of the theory of evolution in the work of the TYPOLOGICAL schools of taxonomy. It was recognised that if the “correct” characters are selected the resulting classification will reveal numerous resemblances between members of a group in terms of characters not considered. The explanation was sought in terms of characters associated with the “essence” of the organism contrasted with other characters. However, whilst there is merit in the idea of series of characters more-or-less strongly correlated with each other (and with other characters subsequently examined), typology leaves unresolved the question of what happens if two sets of imperfectly correlated characters for the same series of organisms produce contradictory groupings. In other words it only partially solves the problem of specifying the criteria by which one recognises the “correct” characters.

With the acceptance of the theory of evolution, one is provided with an explanation for the existence of “natural” groups of species that tend to be ordered into a hierarchical system. On top of this one immediately perceives that the criterion required for the selection of the “correct” characters is simply to choose those which are indicative of an evolutionary relationship. However this raises two questions. What is meant by “evolutionary relationship”? and what happens when different characters “indicating” such relationship produce different answers? Both questions have generated much controversy. Indeed the controversy has been so fierce that there has been the re-emergence of classifications NOT based on inferred evolutionary relationships. These can be grouped under two headings—Phenetics and Transformed Cladism. These are treated below.

Evolutionary (Phylogenetic) Classification

Most taxonomists interpret the word “natural” in terms of evolutionary relationship. The significant controversy of recent years has been between two schools both committed to this viewpoint. Whilst labels are always a problem in such controversies, it does help to simplify a complex series of debates if we can classify the contestants. The two principal viewpoints are upheld by the “Gradists” (“traditionalists”, “evolutionary typologists”) on the one hand and the “Phylogenetic Cladists” (“classic cladists”, “Hennigian cladists”) on the other. Whilst it is evident that Phylogenetic Cladism has been steadily gaining acceptance, even if there is still some resistance from gradists, many textbooks are written from the viewpoint of gradism; so it is important to understand both viewpoints. There are also ingenious, but unconvincing, attempts to synthesise the two approaches, that by Mayr (1981) being the best argued. However it seems that the only true synthesis has been the incorporation of the many valid elements of Gradism into the new system of Phylogenetic Cladism.

The following discussion introduces a number of terms and concepts. The novice may need to read parts more than once in order to follow the arguments.

It is not an exaggeration to say that Phylogenetic Cladists and Gradists are divided by different definitions of the same concept. The key concept is MONOPHYLY. This has been defined by a leading gradist (Simpson, 1961) thus: "Monophyly is the derivation of a taxon through one or more lineages (temporal successions of ancestral-descendant populations) from one immediately ancestral taxon of the same or lower rank". A leading cladist (Wiley, 1981) has concisely expressed Hennig's (1966) refined definition thus: "*A monophyletic group is a group of species that includes an ancestral species (known or hypothesised) and all of its descendants.*" (This definition rests on the assumption that evolution is always divergent. However it is occasionally reticulate—as in the case of a new species resulting from fertile, polyploid hybrids between TWO ancestral species. In fact such reticulate evolution has been not uncommon in several lineages of flowering plants. Such anomalies have been readily accommodated by phylogenetic cladism—e.g. Wiley, 1981.) The phylogenetic cladist claims that only taxa that are monophyletic in Hennig's sense can be regarded as "natural" taxa. The gradist, on the other hand, may exclude from a taxon a subordinate group that has evolved to a different evolutionary grade. In order to grasp the significance of these niceties of definition we need to consider how we classify character states. After all it is from the study of character states that we infer evolutionary relationships. An example of what is meant by a "character state" was cited above. In the genus *Triphleba* vein 3 occurs in three states—forked, unforked, or intermediate.

There are essentially two types of character we need to consider. Firstly there are characters that resemble each other in different species. Secondly there are characters that differ in different species but which we have reason to believe are related by evolutionary transformation from one condition to the other (as in the transformation from fin to arm in our own evolutionary history).

Characters may resemble each other because of similarity of function even though their evolutionary history (and basic structure) has been (is) different. Such characters are said to be *analogues* (e.g. the fins of whales and of trout). On the other hand characters may resemble each other because they are derived from the same ancestral condition in the same ancestor. Such characters are *homologues* or *homologies*. Only homologous characters can be used for inferring evolutionary relationship. However evolution is all about the appearance of novelty; characters becoming transformed during evolution into new character states. Thus most character states we hypothesise are homologous differ in appearance in the organisms concerned. For example in Fig. 3 the typical pointed glossa in the proboscis of a scuttle fly is represented by the state of this character we observe in *Megaselia scalaris* (Fig. 3c). This contrasts with the expanded, spinose, tip observed in the Brazilian species *M. megaglossa* (Fig. 3b).

The above relatively straightforward situation is complicated by the frequent occurrence in evolution of convergent or parallel transformations in related groups of organisms. These can give rise to "pseudo-homologies" or what are termed *homoplasies*. In homoplasies (as opposed to analogues) there is a basic structural similarity. For example the unforked vein 3 observed in some species of *Triphleba*, has arisen independently within several other genera of Phoridae (e.g. in *Megaselia* and *Borophaga*), and so it must be treated as a homoplasy—at least at the level of considering the affinities of these genera.

The establishment of a transformation series as being a sequence of homologies

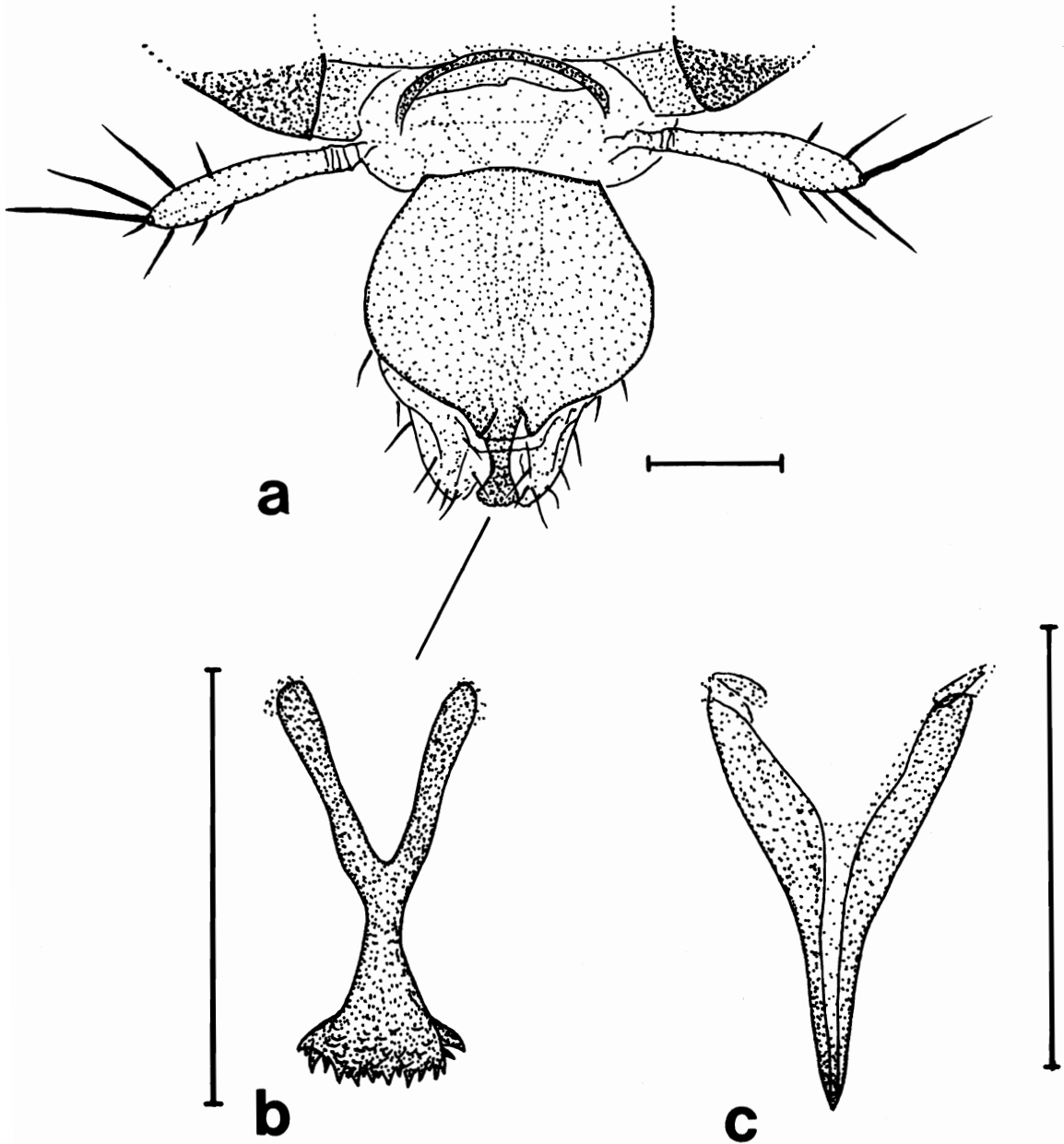


FIG. 3.

An example of two states of a character that form a transformation sequence. a. Proboscis and palps of *Megaselia megaglossa* Disney; b. The glossa of same enlarged; c. the glossa of *M. scalaris* (Loew) enlarged (Scale lines = 0.1 mm). (Originally published in Disney, 1982. *Zeitschrift für angewandte Zoologie* 68: 415-418, 1981).

as opposed to being a counterfeit sequence, of homoplasies, is sometimes far from easy. In fact it is wise to remind oneself that any proposed transformation sequence of homologies is essentially an hypothesis. There is, however, one important principle: the principle of congruence. That is to say, if one is considering the relative merits of several proposed transformation series then a sequence put

forward on the basis of two, or more, independent lines of evidence is to be preferred to those based on a single line of evidence. For example in attempting to homologue the wing veins of two families of flies one can consider separately the positional relationships of the veins as well as the convexity of the individual veins. In the wings of primitive flies there is a sequence in which the longitudinal veins are dorsally convex then ventrally convex in an alternating sequence. Thus if evidence from the sequence of veins in terms of being dorsally or ventrally convex is congruent with the positional relationships of the veins then one's proposed homologies are considered to be more soundly-based than if they had been derived from only one of these separate lines of evidence.

These fundamental concepts are illustrated in Fig. 4. Five taxa (P, Q, R, S and T) possess characters— b''' , c'' , or d' , d'' or d''' (all of which resemble each other). All of these character states were derived from a in the manner indicated. The following are homologies within their respective transformation series: a , c' and c'' ; a , c' and d''' ; and a , b' and d'' ; a , b' , b'' and d' ; and a , b' , b'' and b''' . In Q, R and S d' and d'' are homoplasies due to parallelism, but d''' is a homoplasy due to convergence. The important difference is that d' and d'' are derived from b , but independently (from b' and b''). By contrast d''' is derived from c .

Having clarified the fundamental way in which we classify character states we need to consider homologies further. In Fig. 4 character state a is ancestral to both b' and c' . The terms used to express these relationships are PLESIOMORPHIC for the ancestral state and APOMORPHIC for the derived state. Thus a is the plesiomorphic state with respect to b' and c' . The latter are apomorphies of a . c' is plesiomorphic with respect to d''' . Likewise b' is plesiomorphic with respect to d'' .

The use of the curious terms plesiomorphic and apomorphic has two advantages. Firstly, the alternative terms have been used in a variety of ways by different authors and so have lost precision of meaning. Secondly, the terms (proposed by Hennig)

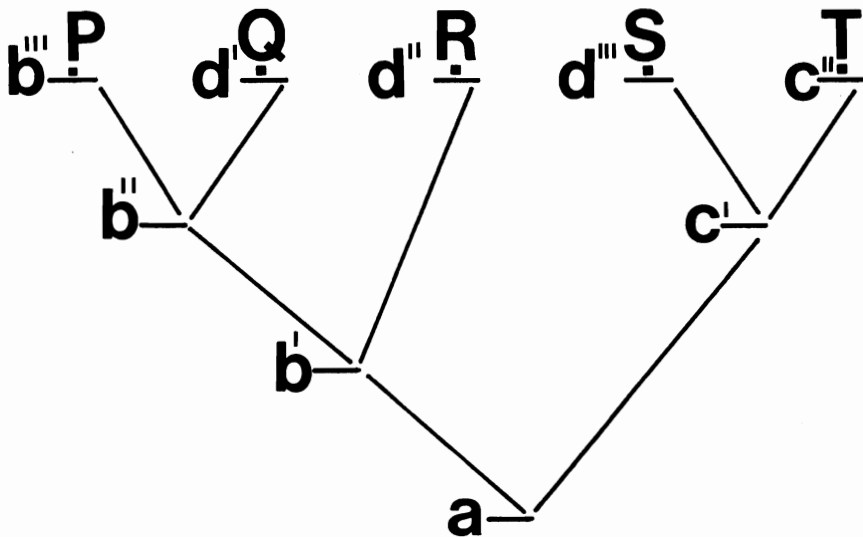


FIG. 4.

Diagram to illustrate the origin of character states (b''' , d' , d'' , d''' and c'') in taxa P–T from ancestral state (a). See text for discussion.

can be very usefully compounded—for example: synapomorphies (= shared derived characters), symplesiomorphies (= shared ancestral characters), autapomorphies (= derived characters unique to a taxon).

The fundamental postulate of phylogenetic cladism, as propounded in the classic works of Hennig (e.g. 1966), is that monophyletic groups are recognised solely on the basis of synapomorphies. That is to say, it is the possession of shared apomorphic character states that enable us to identify monophyletic taxa (as defined by Hennig).

When we examine classifications proposed by gradists we find that they, like phylogenetic cladists, reject groups based on homoplasies. However, their groups include not only those based on synapomorphic homologies but also groups based on symplesiomorphies (shared plesiomorphic character states). These situations are illustrated in Fig. 5 which is termed a cladogram. It portrays the way species are related in terms of recency of common origin, as inferred from postulated synapomorphies. Each dichotomy gives rise to two clades where there was one before. (In the cladogram illustrated, taxa A–F are related as indicated based on

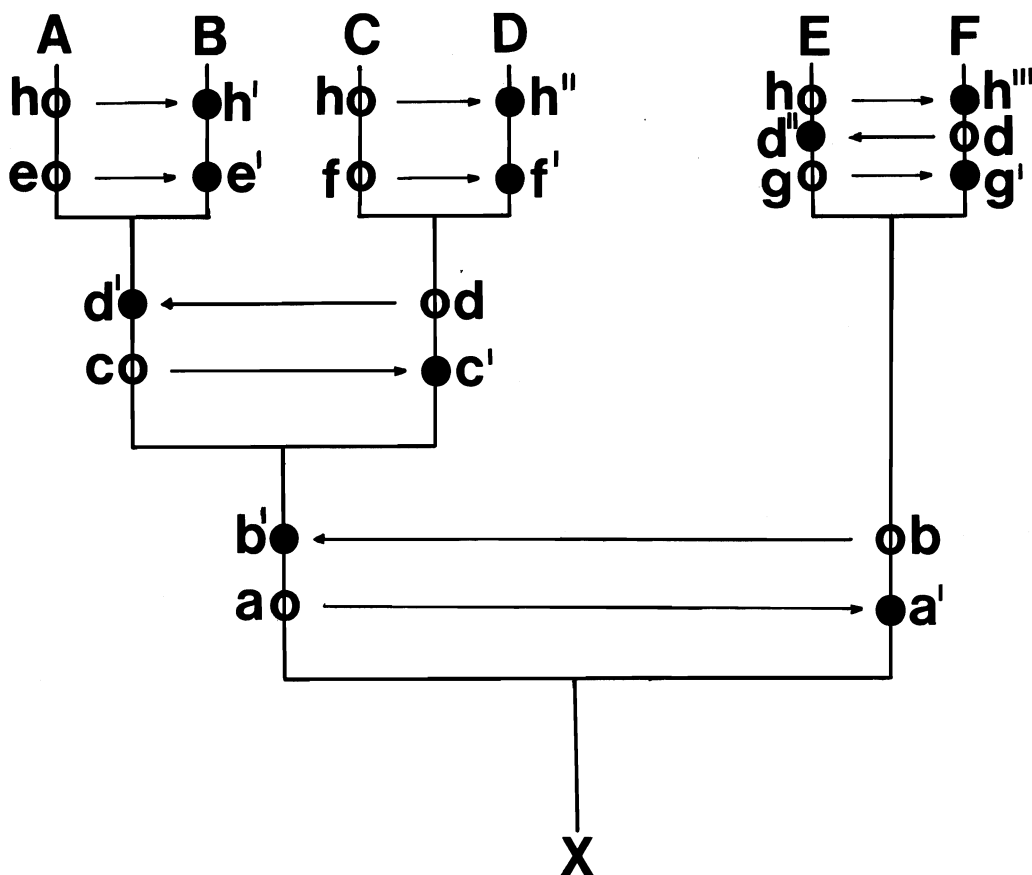


FIG. 5.

Cladogram showing the affinities of the species X and A–F based on synapomorphies and autapomorphies. Black circles = apomorphic states. Open circles = plesiomorphous states. a–h''' = characters. The following taxa are monophyletic: ABCDEF, ABCD, AB, CD, EF. ACE is a paraphyletic taxon based on the symplesiomorphy of character h. If h' , h'' and h''' show homoplasious resemblance (due to parallel evolution) then BDF would be a polyphyletic taxon. See text for details.

postulated synapomorphies). That is to say at least two synapomorphies (a' and b') separate ABCD from EF. Likewise at least two synapomorphies (c' and d') separate AB from CD. In addition at least one taxon of each pair (AB, CD, or EF) possesses at least one autapomorphy (e.g. e' , f' or g'). In Fig. 5 the character h is plesiomorphic, but is independently modified (to h' , h'' or h''') in B, D and F. If the end result was that h' , h'' and h''' were very similar this homoplasy could be mistaken for homology. The result might be the designation of a polyphyletic group BDF, proposed as a natural taxon in error. The error lies in the treatment of the homoplastic resemblance between h' , h'' and h''' as a synapomorphy. If however ACE are grouped together, on the grounds that they share the character h then a *paraphyletic* group is the result. A paraphyletic group is thus seen to be based on symplesiomorphy, which does indeed indicate evolutionary affinity. A, C and E are all descended from the same ancestral species X. However, by excluding species B, D and F from the taxon ACE not *all* the descendants of X have been included in the taxon. Thus taxon ACE is not monophyletic in the strict cladistic sense of the term.

Gradist classifications, apart from errors due to misinterpreted homoplasies, are compounded of groupings based on both symplesiomorphies and synapomorphies. It was the major contribution of Hennig (a distinguished German entomologist), whose views are best summarised in the classic revision in English (1966) of his original German text, to clarify these distinctions and to demonstrate the illegitimacy of paraphyletic groups. Much controversy followed. Hennig vigorously answered his critics. His last, posthumous, defence is to be found in the English (revised) version of his book on *Insect Phylogeny* (Hennig, 1981). Detailed discussion of the subject is to be found in Wiley (1981).

While it is now evident that paraphyletic groups can be no part of a proper natural classification it should not be denied that they can be a useful shorthand for referring to those taxa within a monophyletic group that are at the same evolutionary grade. For example the concepts "fish" and "reptile" are still useful concepts (in certain contexts) even if they are not monophyletic groups, but paraphyletic groups created by the exclusion of some taxa (within the same, larger, monophyletic taxon). In the case of the reptiles, for example, the birds have been excluded.

It is now being generally accepted that the correct classification, that is the defensible natural classification, is based on monophyletic taxa founded on synapomorphies, I do not propose to devote further space at this point to alternative, discredited, approaches. It is more valuable to consider the application of the Hennigian method to actual problems.

It is apparent from the above discussion that the fundamental problems in classification are the recognition of homologies and the determination of the apomorphic character state in each transformation sequence. The principal source of evidence is derived from comparative morphology (using this term in the broadest possible sense—embracing the sequence of amino acids in proteins for example). In practice transformation sequences are frequently discovered by this approach. However, the problem of polarity is often left unresolved. That is to say studies of comparative morphology may reveal a transformation sequence of a character in two states, A and B (e.g. Fig. 3b and 3c). Providing the sequence is indeed one of homologies, and not a false one based on homoplasies, there remains the question as to whether evolution was from A to B or from B to A. Other evidence

can help resolve such problems.

One of the major aids to the recognition of the apomorphic state is OUT-GROUP comparison. Given two characters that are homologous within the monophyletic group under consideration it will frequently be found that one character is restricted to the group of species under consideration whereas the other is also found in the most closely related group of species (the sister group). The former character is, therefore, the apomorphic condition. For example, out-group comparison indicates that an expanded and spinose glossa (Fig. 3b) is apomorphic with respect to a simple glossa (Fig. 3c) in the genus *Megaselia*.

A second important aid is the use of correlations between different character states. However, it needs to be certain that the correlations are between homologies and not homoplasies. A number of workers have attempted to resolve homology/homoplasy problems and polarity problems simultaneously by the use of correlations and the principle of parsimony. The basic idea is that one constructs a matrix of possible apomorphic character states against taxa. Regardless of which are based on homoplasy and which are based on homology, one treats all character states found in two or more taxa as though they were synapomorphies. One then proceeds to generate all possible cladograms that selections of these candidate synapomorphies allow. It is then argued that the cladogram incorporating the largest selection of these "candidate synapomorphies" is likely to be the "correct" one for the taxa in the original matrix. In effect one is recognising the synapomorphies retrospectively. The assumption is that true synapomorphies (based on homology) are likely to be more frequent in one's data matrix than pseudo-synapomorphies (based on symplesiomorphy or homoplasy). This might be true for a matrix that included all possible candidate synapomorphies. In practice one's data set tends to be more of a "lucky dip" sample. This fact, combined with growing recognition of the frequency of convergent and parallel evolution in many groups of organisms, renders the whole procedure somewhat unreliable. There is an inescapable element of circular argument involved. A more rewarding approach is the attempt to resolve the status of unresolved shared homologous character states by the determination of which coincide (at least in part) with established synapomorphies for some of the taxa under consideration. Indeed the correlation of a sequence whose polarity is known with one whose sequence is unknown frequently provides more reliable evidence. For example in several lines of Phoridae there has been a reduction and then loss of wings. There can be no case for arguing that this sequence went the other way as out-group comparisons indicate that the ancestral Phoridae were fully winged. Also in the Phoridae we find a repeated sequence of a fully developed median furrow on the frons (i.e. the part of the head above the antennae and between the eyes), a short median furrow (at the anterior end only) and no median furrow. This sequence correlates with the reduction and loss of wings so as to indicate that the absence of a median furrow is the apomorphic state.

It has just been noted that the end point of a transformation series, in this case the loss of wings in some scuttle flies, may prove to be an occurrence that has taken place several times independently within the group under consideration. Hence the character "absence of wings" must be treated as a homoplasy when considering the group (in this case a family) as a whole. However within a particular clade (which might be a genus) the loss of wings may have only occurred once. In this case the character (absence of wings) becomes a legitimate synapomorphy when one is

attempting to resolve relationships within this particular clade. For example in Fig. 5 d' and d'' are homoplasies, but d' is a legitimate synapomorphy that enables us to recognise the monophyletic group AB within the clade ABCD. Those who attempt to identify synapomorphies retrospectively, by seeking the most parsimonious cladogram that can be produced from a particular matrix of candidate synapomorphies (see above), tend to find themselves in frequent error with these character states that are illegitimate homoplasies at one level but legitimate synapomorphies at a subordinate level.

Other sources of evidence, for the resolution of polarity problems, are derived from the comparison of older fossils, younger fossils and recent species. With some groups of organisms (e.g. marine molluscs) good fossil sequences may occur. With many groups fossils occur so infrequently that any sequence of fossils is primarily a construct of the mind and so the sequence of appearances of particular characters may be more an expression of ignorance than of evolutionary history. Other evidence has been derived from the sequence of appearance of characters during development (ontogeny); and the spatial sequence of characters in a group of species whose geographical distribution patterns appear to reflect the evolutionary history of speciation. For detailed discussions of the use of such evidence the reader is referred to standard texts (e.g. Hennig, 1966; Wiley, 1981).

In the above example, I cited two cases where a character in question was the absence of a structure (no wings or no median furrow). Some authors have argued that the lack of something is not a character. For example Patterson (1980) asks the rhetorical question "How can absence of something characterise a group?" We can reply readily—it can if, and only if, the absence of the something in question represents the apomorphic state. The absence of feathers in reptiles is a plesiomorphic condition with respect to their presence in birds. In fact the group Reptilia is a paraphyletic group analogous to the now universally rejected paraphyletic group Pisces. Reptilia are defined (by gradists) as amniotes that lack fur, feathers or milk. In this case the absences are all plesiomorphic states. It is because they are plesiomorphies, rather than absences, that they are illegitimate characters.

Let us conclude this section by applying the Hennigian method to an actual group of species. The meniscus midges (Dixidae) of Britain are known in the larval, pupal and adult stages (Disney, 1975). If we consider the fourteen British species we must start by producing a table in which we list characters against species and enter the presence of the apomorphic state of each character in the table (Table 1). Each one of these entries represents an hypothesis. They are, in this case, based on comparative morphology, plus out-group comparisons (with the rest of the Culicoidea). This table serves two purposes. Firstly, it compels the author to expose his assumptions to public scrutiny. Secondly, it provides the data for the construction of the cladogram.

To construct the cladogram in Fig. 6, I started by selecting, from the table, pairs of species that were linked by at least one apomorphy unique to that pair. I then picked out apomorphies that united a single species to any of these pairs. I then picked out apomorphies that united any two clusters already formed. In this manner I gradually arrive at Fig. 6. I must confess my original table also contained some tentative apomorphies. For example the presence of clouds of dark pigment on the wings. However this character conflicted with five other characters (1, 6, 9, 11 and 12), which in fact segregate the species of *Dixa* from the species of *Dixella*. I

Table 1. *The postulated apomorphic character states for the British Dixidae*

Character states (illustrated in Disney, 1975)		Species											
a = apomorphic state		<i>Dixa</i>	<i>Dixa</i>	<i>Dixa</i>	<i>Dixa</i>	<i>Dixa</i>	<i>Dixa</i>	<i>Dixa</i>	<i>Dixella</i>	<i>Dixella</i>	<i>Dixella</i>	<i>Dixella</i>	<i>Dixella</i>
		<i>dilatata</i>	<i>maculata</i>	<i>nebulosa</i>	<i>nebulosa</i>	<i>nubilipennis</i>	<i>puberula</i>	<i>submaculata</i>	<i>aestivialis</i>	<i>amphibia</i>	<i>altica</i>	<i>autumnalis</i>	<i>atricornis</i>
<i>Larvae</i>													
1. Dorsal crowns of setae on abdomen		a	a	a	a	a	a	a	-	-	-	-	-
2. 6 crowns of setae (as opposed to 5)		-	a	-	a	-	a	a	-	-	-	-	-
3. No ventral comb on venter of abdominal segment 7		-	-	-	-	-	a	-	-	-	-	-	-
4. Basal plate with serrated expansion in median posterior region		-	-	-	-	-	-	-	-	a	-	-	-
5. Caudal appendage elongated		-	-	-	-	-	-	-	-	-	-	-	-
6. Posterior paddles almost as long as caudal appendage		a	a	a	a	a	a	a	-	-	-	-	a
7. Basal plate shortened		-	-	-	-	-	a	-	-	-	-	-	-
8. Dorsal crowns partly reduced		-	-	-	-	-	a	-	-	-	-	-	-
<i>Pupae</i>													
9. Caudal lobes elongated		a	a	a	a	a	a	a	-	-	-	-	-
10. Rim of respiratory trumpet with deep emargination		-	-	-	-	-	-	-	-	a	-	-	-
<i>Adults</i>													
11. Flagellar segments of antenna elongated		-	-	-	-	-	-	-	a	a	a	a	a
12. Apical process of male coxite elongated		-	-	-	-	-	-	-	a	a	a	a	a
13. Curved spine on tergite 9 of male abdomen		-	a	-	a	-	-	-	-	-	-	-	-
14. Robust median process on male coxite		-	a	-	-	-	-	-	-	-	-	-	-
15. Apical process of male coxite bifid		-	-	-	-	-	-	-	a	-	-	-	-
16. Sternite 9 of female abdomen broad and complex		-	a	-	a	-	-	a	-	-	-	-	-
17. Atrial cavity of female with distinct insula		-	-	-	-	-	-	-	-	-	-	-	-
18. Atrial cavity of female with sclerotised hinge-teeth		-	-	-	-	-	-	-	-	a	-	-	-
19. Male styles angled		-	-	-	-	-	-	-	-	-	-	-	-
20. Apical process of male coxite expanded distally		-	-	-	-	-	-	-	-	-	-	-	a
21. Apical process of male coxite longer than style		-	-	-	-	-	-	-	-	-	a	-	-
22. Cercus of female with lobe developed from base		-	-	-	-	-	-	-	-	-	-	-	-
23. Forks R_{2+3} and M_{1+2} clouded		-	-	-	a	-	-	-	-	-	-	-	-

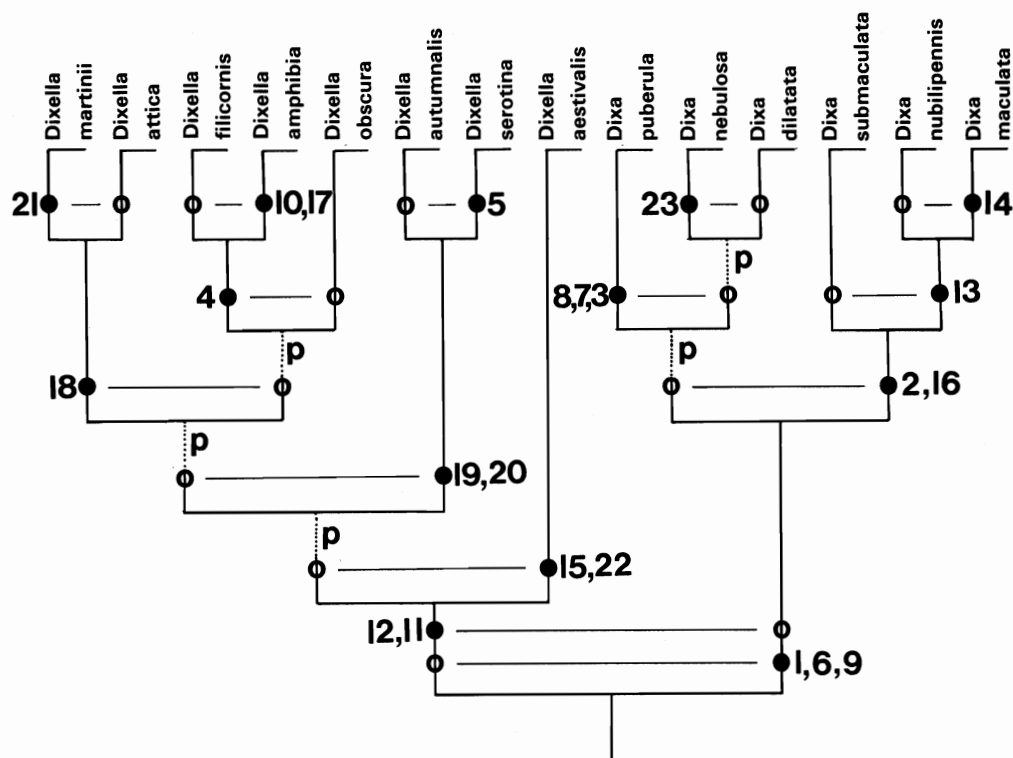


FIG. 6.

Cladogram showing the affinities of the British Meniscus Midges (Dixidae) based on the synapomorphies and autapomorphies postulated in Table I. The numbers refer to the characters in Table I. *D. martinii* and *D. maculata* are distinguished by adding their third letters. p = residual paraphyletic group (see text).

concluded that the wing clouds were either a plesiomorphic condition or if apomorphic then they were homoplasies (parallel transformations).

It is immediately apparent from Fig. 6 that the cladogram for British Dixidae based on Table 1 has only partially resolved the relationships between the species. A number of groupings (indicated by a "p" against the base of the clade in question) are what we might term residual paraphyletic groups. They are those we are left with when we have separated out the monophyletic groups based on our postulated synapomorphies. The reason for this "gradist contamination" is lack of data. Only the basal dichotomy is established on synapomorphies for both clades. The residual paraphyletic groups indicate those parts of the cladogram that would be most likely to benefit from further research.

It is easy for a phylogenetic cladist to pour scorn on gradism when discussing cladograms for theoretical taxa. As soon as one starts trying to construct cladograms for real taxa one finds oneself confronted by residual paraphyletic groups. The important point is that these are only to be accepted as provisional groupings. One's aspiration must be that future research will reveal additional synapomorphies that will either confirm or refute such groups, so that we eventually achieve a cladogram based exclusively on synapomorphies.

If anyone chooses to disagree with any of the monophyletic groups proposed in Fig. 6 it will need to be by refutation of some (all?) of the hypotheses presented in

Table 1. In fact, Contini (1965) has suggested that a sibling species of *D. puberula* (or possibly only a variety of this species) should be placed in a separate genus, *Palaeodixa*, and be regarded as being ancestral to the genus *Dixa*. In other words in my hypotheses 3, 7 and 8, I am suggesting a reversed polarity to that implied by Contini. The most important of these is hypothesis 3—the lack of the comb on segment 7 of the larva. During development in other species this is the last to develop of the three ventral combs. I am suggesting, therefore, that in *D. puberula* (and related species) the third comb has failed to develop but was present in its ancestors. Contini on the other hand is suggesting that the ancestral species had two combs and the third was added during evolution. This hypothesis implies an additional hypothesis—that the running-water *Dixa* species were ancestral to the still-water *Dixella* species. I suspect that the reverse was the case. I am certainly unconvinced by the hypothesis put forward by Contini, which seems to me to present an over-rigid application of the 'law' of recapitulation. If he is correct, however, then he is excluding *D. puberula* from my monophyletic group *puberula/nebulosa/dilata/submaculata/nubilipennis/maculata* on the basis of the hypothesis that possession of 3 ventral combs is a synapomorphy. I may be mistaken, but by laying out my views in Table 1 and Fig. 6 I have been forced to expose my speculations (which are based on acceptable principles) to scrutiny and thereby clearly reveal where further investigation (as opposed to speculation) needs to be directed. Clearly all my residual paraphyletic groups (in Fig. 6) merit further research in order to discover additional synapomorphies.

Non-Evolutionary Classifications

PHENETICS

Phenetics was founded on the belief that it is not possible to discover the evolutionary affinities of species with any degree of certainty. The attempt was made, therefore, to classify organisms solely on the basis of analysis of the degree of similarity between different species. The analyses employed for this purpose utilise entirely acceptable statistical procedures. However, the latter should not obscure the difficulties inherent in the notion of overall similarity. It is not clear precisely what such a notion might mean when applied to whole organisms as opposed to isolated parts. The concept becomes even more elusive of definition when applied to species (which are made up of populations of varied individuals). Apart from these theoretical objections, which have been discussed in detail by several authors (e.g. Hennig, 1966; Crowson, 1970; Griffiths, 1972), there are experimental refutations of the consistency of the results of phenetic analysis when more and more characters are progressively considered (e.g. see Wiley, 1981). It must be concluded that phenetics is a further example of ingenious mathematics on a foundation of false premise. While some of the statistical procedures developed by Pheneticists are of lasting value there are now few taxonomists who believe phenetic analysis will lead to the discovery of natural taxa.

The fact that phenetic analysis sometimes produces classifications largely congruent with those produced by phylogenetic cladism is readily explained. The characters employed may be synapomorphies or partly correlated with such characters. In particular some plesiomorphic characters may be partly correlated with some apomorphic states (e.g. those associated with the synapomorphies 1, 6 and 9 or with 11 and 12 in Fig. 6). It is when symplesiomorphies or homoplasies are

not so correlated that phenetic classification deviates from that resulting from a phylogenetic cladistic analysis.

The frequency of partial congruence between the results of phenetic analysis and phylogenetic cladistic analysis means the former may be a useful means of performing a preliminary sorting of a complex of similar species. This then needs adjusting by critical phylogenetic cladistic analysis. This does not mean, as has been argued by some (e.g. Moss and Hendrickson, 1973), that phenetics is the primary tool of taxonomy. It may be a "primary" tool only in the limited sense of serving as a preliminary tool that *may* prove useful for handling large numbers of similar species. If it serves as a useful means of rendering a large taxon manageable, by breaking it down into convenient phenetic units as a prelude to conducting a critical cladistic analysis, then it can obviously be defended on these pragmatic grounds. The only theoretical justification remains the probability of *partial* congruence with the results of a cladistic analysis.

TRANSFORMED CLADISM

Transformed cladism is an attempt to produce a clasitic (divergent or hierarchical) classification without recourse to evolutionary concepts. In particular it redefines the cladistic concept of apomorphy in non-evolutionary terms.

The surprising aspect of transformed cladism is that anyone should want to produce a non-evolutionary classification in the first place. Charig (1981) has provided a succinct criticism of Patterson's (1980) exposition of transformed cladism and has correctly pointed out that it is 'essentially typological'. The motivation for wishing to revert to typology, albeit dressed up in new cladistic clothing, seems to have derived from two quite distinct sources. Firstly some American advocates seem motivated by a desire to escape the attention of creationists, or even to find accommodation with them, by discarding the evolutionary perspective (and justification) of a cladistic classification. "Creation science", however, has no place in the field of scientific endeavour (e.g. see Ruse, 1982). The more serious motivation is derived, it seems, from an over-zealous adherence to the earlier views of the philosopher Popper on the status of evolution as a "proper" scientific theory (e.g. Patterson, 1978). However, it is the inadequacy of Popper's views when confronted with historical sciences that is at fault (e.g. see comment by Disney, 1979, on Patterson's position). A more reliable insight into the nature of scientific endeavours such as phylogenetic reconstruction is provided by writers such as Arber (1954).

A legacy of Popper's earlier views on the nature of science has been a desire to discover a classification independent of the theory of evolution in order to provide an independent means of testing that theory. Transformed cladism, however, finds itself lurching between the confused assumptions of phenetics on the one hand and the elusiveness of a non-evolutionary criterion for the selection of the characters to be given preference (if a cladistic, as opposed to a network, classification is to be produced) on the other. For example, Patterson (1982) has advocated as the necessary criterion a non-evolutionary concept of apomorphy based on von Baer's dictum—in development the general characters appear before the special characters. However, in advocating this as the "one apparently foolproof method" Patterson has transformed a tendency, encapsulated in a dictum, into a "law". It is not, however, a law in the sense that it allows no exceptions. The number of exceptions to von Baer's Law are legion: for example, the specialised larval

characters of many aquatic midges and mosquitoes when compared with their more generalised equivalents in the pupae and adults.

Categorisation

The procedures to be employed when deciding to which rank a particular natural (i.e. monophyletic) taxon should be assigned (whether the taxon in question should be treated as a species-group, subgenus, genus, or whatever) has been, and still is, a matter of dispute. The problem essentially springs from the desire of some to ensure that a genus in a family of beetles is in some sense "equivalent" to a genus in a family of snails. The only serious suggestion proposed as to what might be meant by "equivalent" in this context is in terms of equivalent time since the origin of the groups in question. Ingenious proposals have been made along these lines. However, they necessarily rest upon the assumption of approximately similar rates of evolution in different groups of organisms. The evidence suggests that such an assumption is untenable; but this is not easy to prove. Whilst the rates of evolution in different transformation series of particular character states can be, and have been, measured, it is not clear whether any real meaning can be attached to the concept of the rate of evolution of a whole organism. Until someone, therefore, can suggest a meaningful notion of equivalence that can be measured in some way, it seems best to adopt a utilitarian approach to the problem of categorisation.

Most biologists want a reference system of named categories (species, genera, families, etc.) based on the Linnaean System, which are stable, and which are readily characterised or at least readily keyed out in an identification key. If one applies these criteria then one will certainly render genera in one group non-equivalent to genera in another group. Also genera, families, etc., will vary in terms of the number of species they include. However, the usefulness of such a system of reference far outweighs the disadvantages, or presumed disadvantages, perceived by those who oppose a flouting of the principle of equivalence.

We can summarise by saying that a natural taxon is discovered but a category is imposed. The assignment of a particular rank to a taxon is an essentially arbitrary choice largely determined by a history of the understanding of the group in question but modified by the demands of usefulness. With regard to the latter it has been suggested (Disney, 1981e) "that morphological characters that meet the requirements of a properly constructed dichotomous key should characterise the difference between genera". However, it needs emphasising that a genus may not be easily characterised by a single character, owing to variation within it resulting from accumulated apomorphies subsequent to its origin. The ideal is that a genus be easily characterised, and therefore easily keyed. However, there will be situations where it may be necessary to key out different species-groups at different points in a generic key. If, however, it is necessary to key out each species separately then the generic concept cannot be regarded as useful!

If the ideal is that a genus be readily characterised then it is clear that the discovery of undescribed species may erode the value of the characters used to characterise two related genera. In other words it may become necessary to abolish a genus if it can no longer be characterised. In the example mentioned above, the genus *Citrigo* was clearly distinguished from *Triphleba*, by the condition of vein 2. In *Citrigo* it was absent. In *Triphleba* it was present as a forking of vein 3. However some species were found to have the base of vein 2 missing. Then it was found that one

such species, *T. gracilis*, showed variation from vein 2 being complete to it being absent altogether. The latter specimens were thus within the genus *Citrigo* as defined in the literature. Re-examination of the justification for the genus *Citrigo* in the light of this evidence forced the conclusion that the genus could not be characterised, and so it was abolished (Disney, 1982). By contrast the genera *Dixella* and *Dixa* are readily characterised in the larvae, pupae, and adults (e.g. by characters 1, 6, 9, 11 and 12 in Table 1 and Fig. 6).

For a more detailed discussion of categorisation see Wiley (1981).

TASK 4. KEY CONSTRUCTION

A key is a device to help a non-specialist assign a specimen to its correct taxon and an agreed name. A variety of key designs has been devised. The most generally used are the familiar dichotomous keys. A good key, of whatever design, leads the user to the correct answer, with a high degree of confidence, by the shortest possible route. In the light of this assertion it is evident that many published keys do not score very highly! One of the commonest reasons for bad keys is a confusion between classification and identification. A key that slavishly tries to key out specimens in the evolutionary sequence (i.e. as one systematically ascends a cladogram) is almost guaranteed to generate cumbersome couplets).

A key demands clear characterisation of the taxa to be keyed. Thus a good key may employ large numbers of plesiomorphic or homoplastic characters which are useless when trying to construct the classification of the group. Also a good key does not necessarily key out all species of a genus at a single couplet. If one species, or species-group, is readily characterised by a particular character it may prove better to key it out separately. Synapomorphy is the secret of sound classification whereas clear characterisation is the essence of a good key.

A second common fault in keys is the assumption that the user is familiar with the whole group, whereas he probably has only a single specimen in front of him. Statements like "normal" mean nothing to the novice. Likewise, a common fault with some specialists is to alternate couplets based on one sex only.

The specialist who is not guilty of the above faults may still write a difficult key, because what he, from familiarity, perceives as clear distinctions may appear obscure to the uninitiated. Thus the AIDGAP practice of only publishing keys after drafts have been tried out on non-specialists is to be highly recommended.

For further information on key construction the reader is referred to the standard texts (e.g. Crowson, 1970; Wiley, 1981). In addition the small book by Pankhurst (1978) is warmly recommended.

TASK 5. COLLATION OF BIOLOGICAL INFORMATION

The collating of the known biological information on particular species is not exclusively the job of taxonomists. Nevertheless the inclusion of biological information has always been a traditional task undertaken by taxonomists when producing monographic revisions. It is, however, a task that can only be accomplished successfully by someone familiar with the history of taxonomists' understanding of the group under consideration. There is a growing tendency for erroneous information to be propagated by those who fail to accommodate this simple fact. For example, Alford (1975) states, among other things, that the scuttle fly *Gymnoptera vitripennis* breeds in bumblebee (*Bombus*) nests and also that the same species has

been reared from an exhumed human corpse. He gives proper citations of the literature for these claims. Both claims are without foundation. The species *G. vitripennis* was named by Meigen in 1830. A century later Schmitz (1933) realised that two species were being confused under the name *G. vitripennis*. The second species he named *G. longicostalis*. Re-examination of published observations and supporting museum specimens, as well as subsequent observations, indicates that hard evidence so far only exists for *G. longicostalis* breeding in *Bombus* nests. *G. vitripennis* is the species characteristic of wasp (*Vespula*) nests. Alford's citation of *G. vitripennis* from a human corpse was based on specimens deposited in the British Museum (Natural History) in 1921. However re-examination of these specimens revealed that they had been misidentified—they really belonged to the coffin-fly (*Conicera tibialis*) (Colyer, 1954).

Apart from the obvious moral to be drawn from the above example there is an additional one that needs emphasis. Anyone investigating the ecology or basic natural history of a species belonging to a group which is not extremely well known should deposit some specimens in a properly curated museum. If this is not done, a subsequent taxonomic revision may necessitate the disregarding of valuable observations because of uncertainties as to which species was being investigated.

Some reviewers have been known to collate information on "two" different species, one of which is an established synonym of the other. An example would be invidious!

Sound taxonomy is not only the foundation for major biological disciplines such as ecology, but it is also the primary system of reference for all biology. A biological education should include an understanding of the taxonomist's tasks. A philosophy of science which does not embrace taxonomy is defective.

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GLOSSARY

While the majority of the terms are explained in the text the following glossary is provided for quick reference.

Analogue. A character in one taxon that resembles a character in another because of a similarity of function and despite the fact that the basic structures and evolutionary histories of the two characters are different.

Apomorphy. The derived state of the character in a pair of homologous states of the character.

Autapomorphy. An apomorphic character state unique to a single taxon in the group of taxa under consideration.

Categorisation. The assigning of a named rank in the Linnaean System to a taxon.

Character. Any feature or property of an organism used by a taxonomist when describing a taxon.

Character State. A particular stage in a transformation sequence whereby a character evolves into something different.

Clade. One of the branches resulting from a dichotomy in a cladogram. (*Klados* is the Greek for a branch.)

Cladism. Schools of taxonomy concerned with producing classifications based on cladograms.

Cladistics. The practice of cladism.

Cladogram. A diagram portraying the affinities of taxa by means of a dichotomous tree (e.g. Figs. 5 and 6).

Classic Cladism. See phylogenetic cladism.

Classification. The ordering of species into higher taxa.

Convergent Evolution. The evolution of similar character states in distantly related, or unrelated, taxa starting from different character states.

Creation Science. A system of explanation that utilises a literal interpretation of Genesis as an authority for selecting which scientific facts are to be admitted as legitimate evidence. It specifically rejects Occam's Razor (see below). It also rejects the Theory of Evolution.

Essence. The essential attributes of an organism that typological schools of taxonomy seek to define. The notion of the "essence" survived the advent of the Theory of Evolution in the refined concept of the evolutionary grade (see below).

Evolutionary Classification. A classification based on inferred evolutionary relationships.

Genus (plural genera). The first obligatory rank above the species level in the Linnaean System. A generic name not only applies to a particular group of related species but itself constitutes the first word in the scientific name of each of the included species.

Grade. The general evolutionary level of organisation exhibited by an organism (e.g. the fish grade observed in at least two evolutionary lines of vertebrates).

Gradism. The school of taxonomy, committed to Evolutionary Classification, which combines both paraphyletic taxa as well as strictly monophyletic taxa into a single system.

Hennigian Cladism. See Phylogenetic Cladism.

Homology (Homologue). A character state is a homology of another character state when they both form part of the same evolutionary transformation sequence. They will always have the same basic structure. They may not have the same function and do not necessarily resemble each other.

Homonym. A name given to a taxon that is not "available", as another taxon already bears the same name. The discovery of a homonym necessitates a replacement name.

Homoplasy. A character in one taxon that resembles a character in another and has the same basic structure but a different evolutionary history (ie the resemblance is due to parallel or convergent evolution).

Linnaean System. The system of ranks, proposed by Linnaeus, used for the categorisation of taxa.

Monophyletic Group. A group of species that includes an ancestral species (known or hypothesised) and all of its descendants. In practice it is recognised by the discovery of synapomorphies.

Morphology. Strictly speaking morphology is the study of the external forms of organisms. It is used more generally to refer to all structural features of organisms.

Natural Classification. Classification based on the natural affinities of the taxa rather than some arbitrarily imposed criteria.

Occam's Razor. The principle that the preferred scientific explanation is the one that accommodates all the relevant facts, makes the fewest assumptions and incorporates the fewest explanatory entities. Modern science is founded on the assumption that one will progress in the direction of truth more certainly by the systematic application of Occam's Razor than by any other approach that has been advocated.

Out-group. An additional, but related, monophyletic taxon that is examined in the course of cladistic analysis in order to determine which of two homologous character states may be inferred to be apomorphic. The closer the affinity of the out-group to the taxon under consideration the more reliance can be placed on one's inference.

Parallel Evolution. The evolution of similar character states independently in related taxa even though starting from equivalent character states. The homoplasies most likely to be confused with homologies.

Paraphyletic Group. A taxon based on symplesiomorphy, therefore it does not necessarily include *all* the descendants of the ancestral species.

Phenetics. The clustering of species by statistical procedures which treat a limited selection of characters as being of equal weight. The resulting classification is a function of the characters selected. A different selection is likely to produce a different classification. Network classifications are more likely to emerge from phenetic analysis than are cladistic classifications.

Phylogenetic Cladism. Classification based on the recognition of monophyletic groups, which will each constitute a clade in a single cladogram. It rejects both paraphyletic and polyphyletic groups.

Phylogenetic Classification. See Evolutionary Classification.

Plesiomorphy. The ancestral state of the character in a pair of homologous states of the character.

Polarity. In a transformation sequence of homologous character states the polarity is the direction taken by evolution.

Polymorphism. The occurrence of distinct forms within a single species.

Polyphyletic group. A taxon based on homoplasies rather than homologies.

Rank. A category (such as genus or family) in the Linnaean System.

Reticulate evolution. The evolution of a new species from two, rather than one, ancestral species (e.g. the appearance of a fertile polyploid hybrid produced by two plant species).

Sibling Species. Closely related species that look alike.

Speciation. The appearance of a new species during evolution.

Species. The highest level taxon, in the Linnaean System, that is able to undergo evolution. More precisely, it is a single lineage of ancestor-descendant populations which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate.

Species Group. A group of closely related species within a subgenus.

Subgenus. A group of closely related species within a genus.

Symplesiomorphy. The occurrence of a plesiomorphy common to some of the taxa under consideration.

Synapomorphy. The occurrence of an apomorphy common to some of the taxa under consideration.

Synonym. A name applied to a taxon other than the one by which it should properly be known.

Taxon (plural taxa). A group of organisms recognised by a taxonomist, regardless of their rank.

Transformation Sequence (or series). A sequence of two or more homologous character states (i.e. the individual states represent different stages in the evolution of the character in question).

Transformed Cladism. A form of phenetics in which certain characters are given preference in order to generate a cladistic, as opposed to a network, classification. The criterion for choosing the preferred characters, however, deliberately disregards any inferred evolutionary significance these characters might be considered to possess.

Type. The specimen that bears the name originally conferred upon the species that includes it. If the "species" is subsequently recognised to be two then the segregate including the type retains the original name.

Type-locality. The locality from which the type of a species was originally collected.

Type-material. The type specimen plus any other specimens considered when the species was originally described and named.

Typology. Classification based on the selection of characters related to the "essence" (see above) of each species.

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BOOK REVIEWS

Insects on Nettles B. N. K. Davis

Grasshoppers Valerie K. Brown

Solitary Wasps Peter F. Yeo and Sarah A. Corbet

Insects and Thistles Margaret Redfern

All published by Cambridge University Press: Naturalists' Handbooks series. 65p. Hardcover £8.00. Paperback £2.95.

Insects on Nettles

An introductory section on the British nettles is followed by a series of keys that should allow identification to species level in most insect groups likely to be encountered. Beginners are warned against the possibility of finding casual visitors which are not included in these keys. Although most characters used in the keys are illustrated and described in the glossary, some do need $\times 20$ magnification and are difficult for the beginner. The final chapters dealing with the biology of the insect fauna and including practical advice on field methods round off this comprehensive introduction to nettle communities.

Grasshoppers

Bush crickets (Tettigoniidae) are included with the true grasshoppers (Acrididae) in this extremely useful book. A taxonomic introduction is followed by details of the life history and of courtship, mating and oviposition behaviour. A further section covers morphological and behavioural adaptations and their significance to population dynamics and distribution patterns. The key to adult is based on characters visible with aid of a hand lens, and the identifications can be checked against the known national and habitat distribution patterns.

Solitary Wasps

In attempting to cover the complex and diverse subject matter in the limited space available, the authors have concentrated on arousing interest in their chosen group. Inevitably some aspects of the biology are only briefly mentioned, whilst others are not included at all. A variety of keys is offered, one of which is based on behavioural characters, useful for anyone attempting identification in the field. Some of the more complicated morphological characters in the species key may cause difficulty, particularly where there is no accompanying illustration, but on the whole a determined person with $\times 20$ magnification should be able to make the system work.

Insects and Thistles

Introductory chapters reviewing our knowledge of insect communities on thistles in Britain are followed by sections on their potential for biological control of the hosts (which are a serious problem in North America). Keys to identification with numerous line drawings and colour plates occupy half of the book. The morphological characters used for identification should be visible under a conventional microscope. This book, in particular, will be very useful to students (and their teachers) seeking a suitable biological project. For many of those outlined here the fieldwork would take an afternoon.

ALL THE BOOKS include full lists of references and are well illustrated with both line drawings and colour plates. The editors have launched a valuable series of books that will be particularly useful for people seeking new avenues for biological exploration. Although many will think twice about paying £8 for a 65-page book the paperbacks are certainly recommended at £2.95.

S. M. TILLING