

FROM FIELD STUDIES TO TAXONOMY

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ABSTRACT

Starting from the misconception that taxonomy was yesterday's science, only of use in serving the needs of proper sciences such as ecology, the author discovered from experience that ecology was fundamentally more dependent upon taxonomy than he had been led to believe. In pursuing taxonomy as a means to an ecological end, it was discovered that taxonomy was a challenging science in its own right. Furthermore, hypotheses regarding the evolution of behavioural and ecological diversity can be tested by being mapped onto phylogenetic reconstructions (cladograms) produced by the application of the methods of phylogenetic systematics, thus removing such speculations from the limbo of just-so-stories. The coming together of taxonomy and ecology restores the important phylogenetic component to the sphere of ecological explanation. It thereby promises exciting new prospects for comparative biology and the study of biodiversity.

This paper reviews aspects of my experience as an ecologist turned taxonomist, who is now trying to use phylogenetic systematics to illuminate ecological relationships between flies and other organisms. In drawing upon my own experience I aim to convey a perception of taxonomy as a challenging, mainstream science. Central to my experience is a conviction that field data are of inescapable importance, if a taxonomist is to correctly interpret data derived from the study of preserved specimens in the laboratory or museum. The reader interested in the general principles of taxonomy should refer to one of the standard texts (e.g. Mayr & Ashlock, 1991).

In 1962, I left Cambridge University with a shiny new degree, a passion for field studies and a prejudice that taxonomy was yesterday's science only useful, today, in enabling the ecologist to name specimens. I felt myself fortunate to have landed a job as Assistant Warden at Flatford Mill Field Centre, with a prime responsibility for teaching field zoology. I quickly discovered that many insect larvae, commonly encountered in the local freshwater habitats, could not be named unless reared to the adult stage. Many adult insects, not to mention mites and other invertebrates, could not be named with the literature available in the Centre's library. Indeed, it was often the most abundant creatures that could not be named beyond the order or family level. The ecology we were teaching was, as a consequence, strangely distorted by these taxonomic impediments. It was as though a sociologist had arbitrarily decided to exclude from his detailed investigations all people whose names begin with J, M, S or W and all children under the age of eleven with brown eyes!

To compound these deficiencies in the available taxonomic literature, many identification keys seemed to be poorly constructed or perversely obscure at critical points. I am pleased to say that the FSC's AIDGAP Project has subsequently led the way in trying to remedy this situation (see Tilling, 1987). At the time, I remained entrenched in the view that taxonomy was only a means to an end—namely the advancement of the knowledge of the ecology of organisms.

The one note I published, relating to work carried out at Flatford, was concerned with the larval diet and a parasitoid of a snail-eating fly (Disney, 1964). This was the beginning of a growing interest in Diptera (flies, midges and gnats) and their interactions with other organisms. When I left, in order to marry, I was persuaded to follow up this interest as a medical entomologist in tropical rainforest.

In Belize (British Honduras), I rapidly discovered that many species were unknown to science (e.g. Disney, 1969a). Furthermore the recognition of species and, even more so, the names applied to them, were subject to shifts of opinion. For example, a common man-biting sandfly, in terms of the characters employed in the published literature, was intermediate between a species known from Texas and one known from Panama and South America. Specimens from Belize completely bridged the gap. In consequence, I proposed the synonymy of the Texan species with the southern species (Disney, 1968b). Subsequently the Texan species was resurrected on the basis of an entirely new set of characters (Young & Perkins, 1984). Taxonomy was more evidently, than I had supposed, like any other science. It advanced by proposing the most probable hypothesis to explain the available evidence. When challenged by new evidence the hypothesis was modified or replaced.

With regard to the species of sandfly which was demonstrated to be the vector of Dermal Leishmaniasis in Yucatan (Disney, 1968a), its name has undergone a change of generic name, and also of its specific epithet, twice. The change of generic name resulted from revisionary work on the genera of Psychodidae. The changes of specific epithet resulted from a synonym problem on the first occasion. On the second occasion the status of the Yucatan subspecies was questioned and it was raised to the specific level (Fairchild & Theodor, 1971). Indeed the whole business of subspecies seemed to me much more subjective than I had realised. With the mammal specimens I collected in Belize, I discovered, by sending skins and skulls to four different museums, that the subspecies was related to the expert rather than to the specimen. I tested this hypothesis by laying a line of numbered traps for cotton rats and then splitting the catch into two series on the basis of whether they had been caught in odd or even numbered traps. Sure enough, the two series were assigned to different subspecies by two leading specialists!

Other taxonomic problems with the mammals were manifested as a result of rearing some rodents in the lab. One rare 'species' in the literature proved to be the juveniles of a common climbing rat, its characteristic shortened rostrum being a juvenile feature. Even more striking was the raising of the young of a rice rat on a patent rabbit food from Miami. This atypical diet caused the fur to turn a more ginger colour than usual. Although my notes indicated that the skins and skulls of these specimens were the progeny of a specimen with a different code number, the identifier overlooked this and assigned the mother and her offspring to different species!

Another lesson of my days in Belize was the realisation of the pervasiveness of man's impact on even remote ecosystems. I quickly learned to recognise secondary forest that had suffered the effects of the selective elimination of species by fire, leaving a relatively high frequency of fire-resistant species such as cohune palms. I only gradually realised that even apparently 'undisturbed' high forest had evidently been disturbed in the past. For example, I selected a remote and truly natural-looking piece of high forest for a small mammal survey. After half a day cutting a trail about one kilometre in length, we encountered a limestone formation with a vertical-drop entrance to a cave. Next day we returned with ropes and torches, to investigate this 'unknown' cave in 'undisturbed' forest. In it we found copious Mayan pottery, dating from around 900 A.D.!

Today, there is, perhaps, a tendency to over-emphasise the impact man has had on landscapes and their ecosystems. These impacts are real enough. However, elements of continuity abound also (e.g. Rackham, 1986). The principal lesson for a taxonomist is the extent to which man is aiding the spread of alien species. Most ecosystems now contain non-native species, whose establishment seems to be favoured by the disturbance of habitats. In Belize, the rats found in buildings provided a striking example. Murie (1935) and Laurie (1953) reported the normal domestic species to be a rice rat (*Oryzomys couesi*). In the 1960's, however, the black rat (*Rattus rattus*) had displaced it; but in the main port the latter was being displaced by the brown rat (*R. norvegicus*), which was beginning to move inland on lorries carrying supplies from the port (Disney, 1968a).

On moving to Cameroon, I discovered that, even in a medically important and well studied group (the simuliid blackflies), there were taxonomic problems. Surprisingly, there were problems with the specific status of the main vector of River Blindness (Onchocerciasis). Was it a single species or a species complex? (e.g. Dunbar, 1969, Disney, 1970). The latter has proved to be the case (e.g. Crosskey, 1990, Molyneux, 1992), although the number of sibling species in the complex is still in dispute.

One task I had been given was to resolve the identity of a secondary vector of Onchocerciasis. Duke (1962) had reported small numbers of a strange blackfly species to be regularly biting man in Cameroon, but the initial, provisional, identification had been rejected (Lewis & Crosskey, 1962). It was clear that the males (which do not bite) and pupae were required in order to solve this problem. I started by searching rivers, within 40 km of the lab, for unknown blackfly pupae. Five species new to science were found (Lewis & Disney, 1970, 1972, Garms & Disney, 1974), but none gave rise to Duke's fly when reared through to the adult stage in the lab. Despite the report of a previous survey which failed to find any phoretic blackflies, that is species whose larvae attach to mayfly nymphs or river crabs, I turned to a survey of these two groups. A known species was found on crabs (Disney, 1971d). On mayfly nymphs, a known species (Disney, 1971b) was found on a new species of *Elassoneuria* (Gillies, 1974), a new species on *Baetis* nymphs (Lewis & Disney, 1970, Disney, 1971c) and two species (one new) on *Afronurus* (Lewis & Disney, 1970, Disney, 1971c). However, Duke's fly had not been procured. I concluded that its larvae must live in association with some other group of organisms. This proved to be the case, the novel hosts being a family of prawns—the Atyidae (Disney, 1969b). Furthermore, there was not only the larvae of Duke's fly, duly named *Simulium dukei* (Lewis et al., 1969), but also another new species (Lewis & Disney, 1969). The two species showed an interesting niche separation, the larvae of Duke's fly being in the gill chambers but those of the other species being attached to the bases of the head appendages (Disney, 1971a).

It seemed that whatever one investigated as an ecologist, one ran into new species. Another example was the investigation of the natural enemies of the larvae of the main blackfly vector of Onchocerciasis. The larvae of two species of fly were evidently voracious predators of the early instar blackfly larvae. On being reared to the adult stage, these proved to be two new species of *Drosophila* (Tsacas & Disney, 1974). These were related to a known species, whose larvae had been obtained in water but were thought to have been immersed by a sudden rise in river level. Examination of the gut contents of some of these larvae, preserved in the Natural History Museum in London, showed that they had been feeding on the eggs and early instar larvae of blackflies and also chironomids (non-biting midges) (Disney, 1975c).

It needs to be emphasised that it was not just small insects that were unknown to science. Four of the species of fish, collected incidentally while I was using traps to sample rivers for the blackfly larvae which live on river crabs, proved to be new to science (Trewavas, 1974). One of these was a major item in the diet of one village! My assistants were regularly eating fish unknown to science!

At Malham Tarn Field Centre, I embarked on a study of the larvae of meniscus midges (Dixidae). I had been intrigued by these larvae when I was at Flatford and had subsequently collected and reared some in Cameroon (Disney, 1974a). I embarked on a key to these larvae as an aid to their study, as the Malham Tarn Nature Reserve was evidently home to more than half the British species. Writing the key entailed rearing every sort of larva through to the adult stage, in order to identify the species. Furthermore, on sorting through old collections from my Flatford days, I found I had a series of a species new to the British List (Disney, 1974b). My project on a key to larvae for my own use turned into a handbook on the larvae, pupae and adults of the British species, published by the Freshwater Biological Association (Disney, 1975b). I have recently added another species to the British List, previously recorded from the south of France and Greece (Disney, 1992b). This addition gives impetus to the idea of doing an improved and updated edition of my dixid handbook sometime in the not too distant future.

I continued to teach myself about Diptera (flies, midges and gnats) while at Malham Tarn, and seized every opportunity to add to knowledge of their larval ecology. Whenever possible, I reared out unfamiliar larvae. For example, I reared out the larvae of a scathophagid I found mining the stems of the docks growing in my garden (Disney, 1976b). These rearings included the larvae of a scuttle fly (Phoridae) I found to be feeding on slug eggs (Disney, 1977). However, my concentration on Phoridae dates from 28 March 1974, when I found a student preparing to jettison some sciarid midge larvae she had collected from the surface of peat on the fen complex at Malham Tarn. Her stated reason for her proposed action was that she could not find the larvae in the book! I therefore took charge of the larvae and installed them in a rearing container. In due course adult sciarids emerged, but then a phorid species started emerging also. Investigation revealed that many of the midge larvae had been parasitised by a scuttle fly larva. Furthermore the host larva was permitted to spin its pupal cocoon before being killed by the phorid larva, who purloined the cocoon for its own use (Disney, 1976a). This was clearly no case of facultative parasitism. The sophistication of the synchronisation was reminiscent of the parasitic Hymenoptera, such as ichneumonids or braconids. There was evidently more to scuttle fly biology than I had been led to believe by general works of reference. I therefore decided to concentrate on these small, common, but unobtrusive flies (Fig. 1).

As I struggled with the taxonomy of the scuttle flies, collected at Malham Tarn and elsewhere, I quickly started turning up species new to the British List and often new to science as well (e.g. Disney, 1979b). Thus, I found I had become embarked on a new, two-volume, handbook on the more than 300 species of British Phoridae: in due course to be published by the Royal Entomological Society (Disney, 1983a, 1989a). As with my keys to Dixidae, no such handbook can ever be definitive. One can only write a key to the species known to occur in Britain. Such a key then becomes a tool for the discovery of additions to the British List. Thus two additions were made to volume I of my handbook (Disney, 1984, 1986a), and subsequently included in an appendix to volume II. Since publication of the latter volume, another species has been added (Disney, 1991b), some

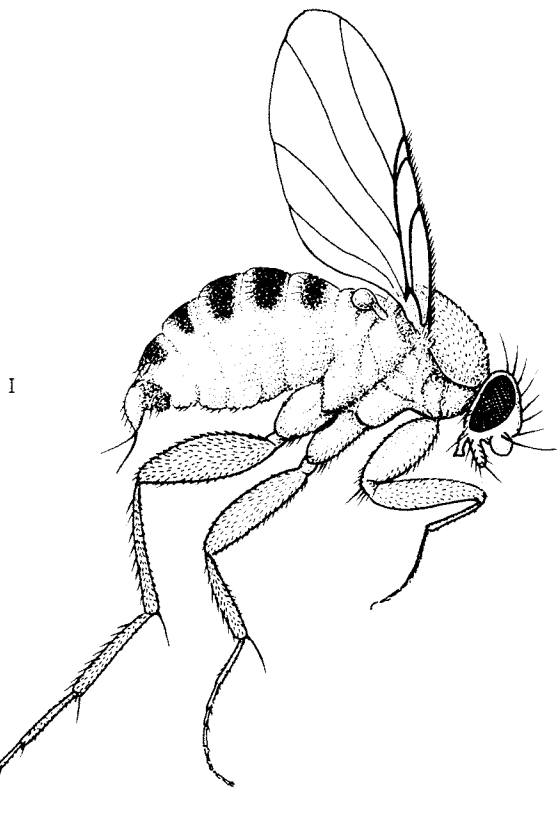


FIG. 1.

A typical scuttle fly, *Megaselia scalaris*, male. (scale bar=0.1 mm) (Drawn by J. W. Rodford).

new synonyms proposed, the name of one species changed, a previously unknown female (omitted from volume I) described; and revisionary notes given on the recognition of some poorly known species, in the light of freshly-available further specimens (Disney, 1993b). There are also some only partly resolved problems with certain species complexes. The pioneering use of some internal characters, such as the form of a gland/valve mechanism in the female crop or the number of rectal papillae (Disney, 1987, 1989a), has sorted out some problems but posed others (e.g. Disney, 1991a). No key can ever be definitive. Man is transporting species around the world in ship's cargoes and in aircraft. We know of four exotic phorid species which have become established in Britain. Furthermore climatic change is likely to lead to changes in the distribution of species. Perhaps the recently added dixid species represents such a case. Other species may be extinct in Britain. A number of species were included in my handbook on the basis of single specimens in museums, all of them collected early this century. Only one of these has subsequently been collected, in some woods in North Yorkshire (Disney, 1991b). Negative evidence is seldom easy to interpret. The confidence with which estimates of current rates of species extinctions were being proclaimed at the 1992 Earth Summit Conference in Rio de Janeiro was incredible. We probably only know of the existence of

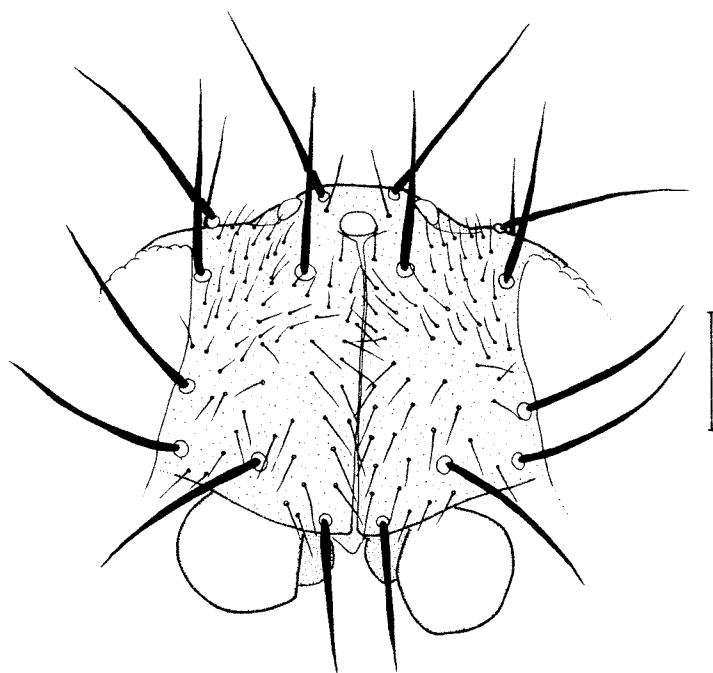


FIG. 2.

The frontal region of the head of a scuttle fly, *Megaselia biarticulata*. (Scale bar=0.1 mm).

about one tenth of the species on this planet (Stork, 1988, May, 1989, Hodkinson & Casson, 1991). We are even more ignorant with regard to the existing population levels and current distributions of most of the species which are known to science. The cause of conservation is not served by proclaiming wild estimates of rates of extinction, as though they were precise measurements. I would regard all such estimates as being far less soundly based than the notoriously unreliable predictions of the economic advisers to the British Government since the Second World War!

As soon as word got around that I was working on the taxonomy of Phoridae, I started receiving requests to identify exotic specimens. These often proved to be not only species but also genera new to science (e.g. Disney, 1979a). Because Britain has the best documented fauna in the world, an aspiration to produce a definitive key is not entirely aiming at the unattainable. The difficulties of attempting a definitive key are, however, much more obvious when one confronts exotic faunas. For example, I published a key to the peculiar females of the South East Asian genus *Rhynchomicropteron*, when describing two new species (Disney, 1981a). This allowed Papp (1982) to recognise a further three new species. I subsequently had another two species to add and so took the opportunity to produce a revised key (Disney, 1990b). Scarcely had this been published when I was sent a further new species (Disney, 1992d).

The often bizarre morphology of some of the exotic phorids set me thinking about their evolution. I had been interested in the evolution of the bizarre ever since speculating on the evolution of some striking associations between Diptera and other arthropods I had come across in the tropics (Disney, 1975a). However my interest had been revived by my reading of Hennig's (1966) classic *Phylogenetic Systematics*. I started looking at the

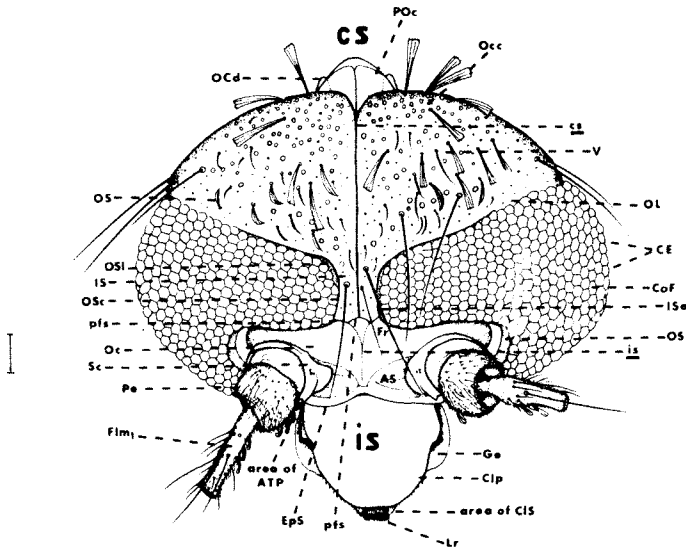


FIG. 3.

The frontal region of a mosquito's head, showing the longitudinal suture running from the top (cs) to a point between the bases of the antennae (is). (Scale bar=0.1 mm). (From Harbach & Knight, 1980).

morphology of the exotic Phoridae, I was being sent, with a new perspective. Furthermore I stuck my neck out when describing a striking new species from Nigeria. I proposed that the median furrow on the frons of some Phoridae (Fig. 2) should be interpreted as an ancestral feature, homologous with the anterior part of the epicranial suture in a mosquito (Fig. 3) or a fungus gnat (Disney, 1981b). I went on to homologise it with the frontal vitta of higher flies, such as *Drosophila* (Fig. 4) and its invaginated lower part with the ptilinum (a balloon-like structure employed by higher Diptera in escaping from their puparium) (Disney, 1988b). More recently, I have reinterpreted the peculiar frons of an African genus of phorids (Fig. 5) as being a case of independent evolution of a ptilinum by a group that is supposed to lack one (Disney, 1991c).

A species I was sent from India, as a routine request for the identification of a pest, really set me thinking. The larvae live in the root nodules of the chickpea (*Cicer arietinum*), an important crop of semi-arid regions. I was sent larvae, pupae and a good series of reared adults. The latter not only showed considerable sexual dimorphism but there were two sorts of female. One sort had abbreviated wings and no eyes, while the other had fully developed wings and eyes. If these flies had not been in a reared series then the sighted females would have been placed in the cosmopolitan genus *Metopina*, the blind females in the Brazilian genus *Typhlophorina* (only known from the females of a single species) and the males would have been assigned to a new genus! It was clear, however, that all three segregates belonged to a single species with two female morphs. It was named *Metopina ciceri* and the genus *Typhlophorina* was synonymised with *Metopina* (Disney, 1988a). This polymorphism prompted the suggestion that two 'species' in the genus *Adelopteromyia*, whose females live together in the same nests of the same army ant species in Central America, may be different morphs of a single species (Disney & Kistner, 1989b). One morph is essentially a smaller version of the other, allowing

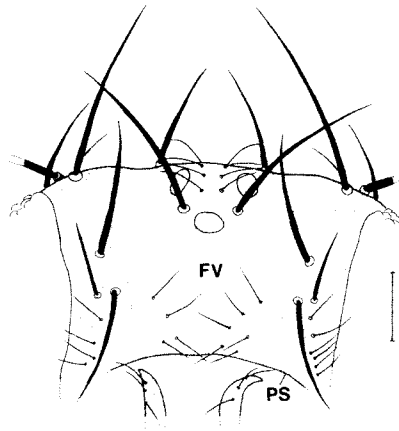


FIG. 4.

The frontal region of the head of a fruit fly, *Drosophila melanogaster*. (FV=frontal vitta, PS=ptilinal suture). (Scale bar=0.1 mm).

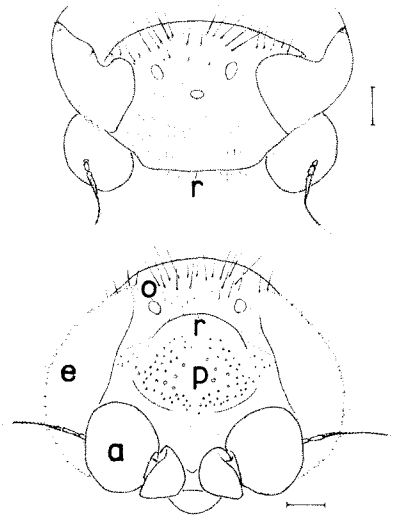


FIG. 5.

The head of *Aemignatistes foxcolatus* viewed from above and from in front. (a=antenna, e=eye, o=posterior ocellus, p= ptilinum, r=post-ptilinal ridge). (Scale bars=0.1 mm).

for allometric effects (i.e. changes in shape linked to changes in size), but with abbreviated wings. This hypothesis, however, remains to be tested by the rearing out of adults. These two cases serve to underline the taxonomic value of reared series with ecological data.

Hennig's book led me to take a closer interest in taxonomy as a science worth pursuing for its own sake. My new enthusiasm for this caused teachers visiting Malham Tarn Field Centre to persuade me to write a synopsis of the taxonomist's tasks (Disney, 1983b). While taxonomy involves much, often somewhat tedious, descriptive work, it is far from

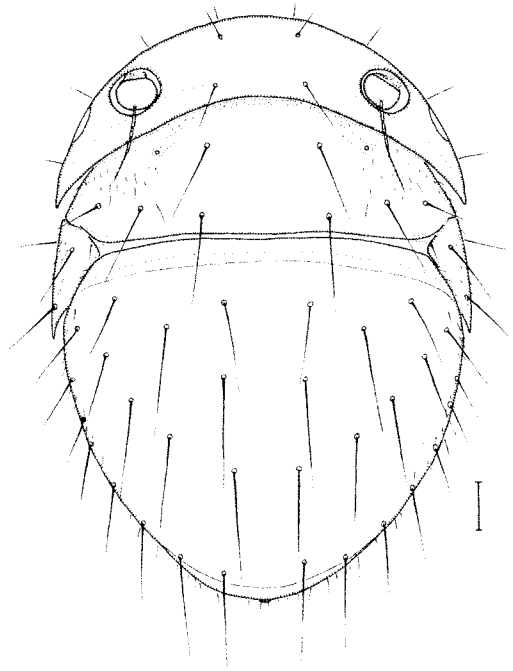


FIG. 6.

A female *Thaumatoxena andreinii* viewed from above, showing rudimentary wings and the antennae sunk into pits. (Scale bar = 0.1 mm).

being “merely descriptive”. It probably generates more hypotheses per unit effort than any other field of biology. Every identification of a specimen is an hypothesis, every designation of a new species or a new synonym is an hypothesis, every assignment of a species to a genus is an hypothesis based upon an edifice of interlocking hypotheses grounded in a developing theoretical framework—which in my case is in terms of theories regarding the evolution of flies in general and of scuttle flies in particular. In order to illustrate this perception I outline two examples of the way taxonomy is advanced, or hindered, by competing hypotheses.

The two examples concern Phoridae associated with termites. I have taken an interest in scuttle flies associated with termites ever since my discovery in 1985, while on study leave in Sulawesi, of two new species which con termites into following them away from their colony. The fly then renders the termite comatose and lays an egg in it. Its larva then consumes the living termite from within (Disney, 1986b). My two examples, however, concern two different subfamilies of aberrant scuttle flies, whose females live in termite nests in Africa or South East Asia.

My first example concerns the extraordinary African genus *Thaumatoxena* (Fig. 6). Breddin & Börner (1904) first described these remarkable insects, but thought they were a new suborder of bugs (Hemiptera). They proposed that their species had larger, flightless, females and similar, but smaller, males. Silvestri (1906) argued that these insects were aberrant flies not bugs. Furthermore he suggested they might be related to scuttle flies. This was quickly accepted; but a twenty year controversy ensued before most entomologists agreed with Schmitz (1929) that these flies are an aberrant subfamily of

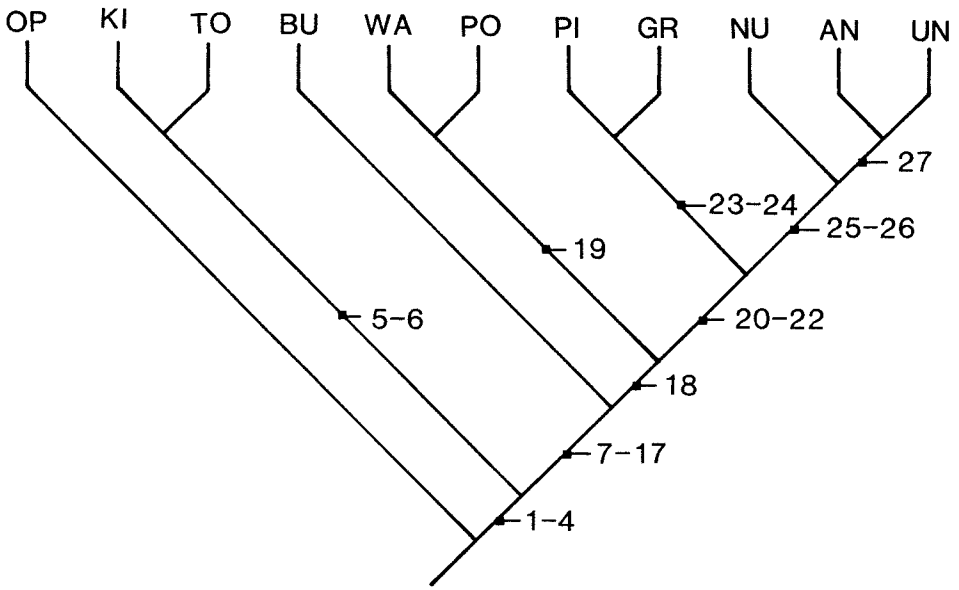


Fig. 7.

A cladogram depicting the postulated phylogenetic affinities of the two species of *Palpiclavina* (KI and TO) and eight species of *Thaumatoxena* (BU to UN) and their relationship (in terms of recency of common origin) with the rest of the Phoridae (OP), based upon 27 postulated derived character states (apomorphies). Character states 1-4 are those novelties which define the Thaumatoxeninae as a monophyletic group, assuming their common possession represents a unique common origin.

Phoridae, but a few authors (e.g. Grassé, 1986) persisted in treating them as a distinct family. Just as the consensus on these flies had become established in the textbooks, Edwards & Schmitz (1939) reported that a mating pair had been observed in East Africa. However, in an attempt to catch them the male had escaped by flying away! Re-examination of Breddin & Börner's 'male' specimens revealed that they were in fact females of another species. Until a winged male could be caught the discussion of the affinities of *Thaumatoxena* with respect to the rest of the Phoridae remained in the realms of speculation.

It was then pointed out that the Oriental genus *Palpiclavina* had been incorrectly assigned to the subfamily Metopininae and it was proposed, instead, that they showed affinity with *Thaumatoxena*. Thus the genus was transferred to the same subfamily (Disney & Kistner, 1989a). However the males of *Palpiclavina* were still unknown. Nevertheless the females are not as aberrant as those of *Thaumatoxena*, and this allowed exclusion of the Thaumatoxeninae from the Metopininae section of the family. To take matters further we needed males.

I was then sent the scuttle flies from an environmental study in Zimbabwe. The collection included some peculiar males which were consistently associated with *Thaumatoxena* females. Furthermore I was sent the same males and females caught in association in Botswana. The description of the males (Disney, 1992a) allowed recognition of the missing males of *Palpiclavina* from specimens collected in Thailand and the Philippines. These males have allowed a proposal regarding the nature of the linkage between the Thaumatoxeninae and the rest of the Phoridae (Fig. 7) (Disney & Kistner, 1992), as well as confirming beyond doubt that these flies are indeed Phoridae and not

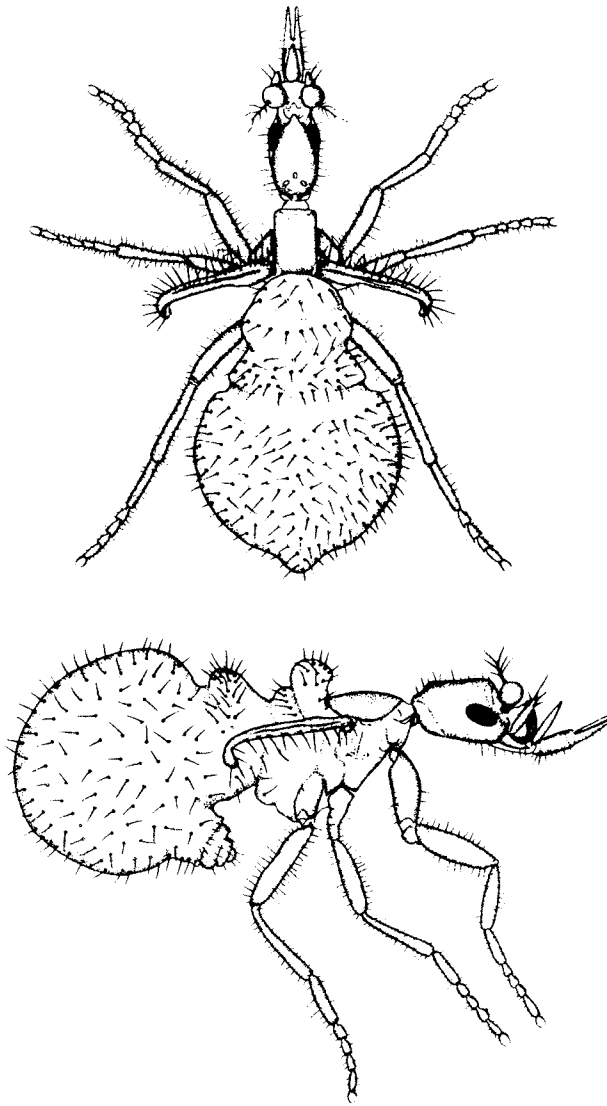


FIG. 8.

A mature termitoxeniine female, *Termitophilomyia gracilis*, viewed from above and from the side. (Drawn by V. Branco, from Stuckenberg, 1974).

a separate family. The Thaumatoxeninae are not only a monophyletic group, as deduced from a study of their morphology, but an integrated ecological group in that they are restricted to the nests of a single termite genus, *Macrotermes*. *Palpiclavina* females have been observed ovipositing onto their host termites (Disney & Kistner, 1989a).

My second example concerns the status of some highly aberrant flies belonging to the genus *Termitoxenia* and related genera. Publications in the last twenty years have treated these as a distinct Infraorder of the Diptera, as a family within the Superfamily Phoroidea or as a subfamily of the Phoridae. One's preference is determined by one's interpretations

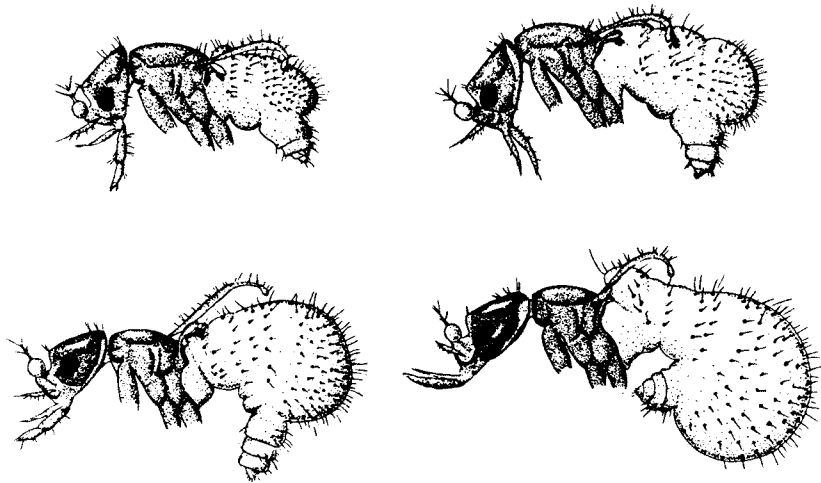


FIG. 9.

Stages in the post-emergence development of a female termitoxeniine, *Termitophylomyia gracilis*, from a stenogastric stage (top left) to a mature physogastric stage (bottom right). (The legs are omitted—see Fig. 8). (From Mergelsberg, 1935).

of various peculiar features of these flies. I reproduce below a, slightly amended, recent account of this particular case (Disney, 1992c); having been encouraged to offer it to a wider audience than my entomological colleagues.

These flies (Fig. 8) were first described by Wasmann (1900), from females found in termite nests. He originally described some small specimens of two species as males, but in a postscript added in proof he reported that these possessed both ovaries and a “testis”. He proposed that these were hermaphrodites (see below). There are now more than 50 species of Termitoxeniinae known from the Afrotropical and Oriental Regions. Following his initial paper, Wasmann (e.g. 1902, 1913) proceeded to advance a set of interpretative hypotheses based primarily on the study of preserved material:—

1. Free-living larval stages have been dispensed with, the adults emerging direct from the relatively enormous eggs (the Ametabolism Theory).
2. The freshly emerged adults are Stenogastric but they proceed to develop into Physogastric forms (Fig. 9), associated with the production of outsize eggs.
3. The flies are flightless throughout their lives.
4. The flies are confined to termite nests, only leaving these when attached to alate (flying stage) termites by means of special appendages (“die Appendices thoracales”).
5. There are no separate males but the apparent ‘females’ are protandrous hermaphrodites (functioning first as males and then as females).

The Ametabolism Theory became generally accepted (e.g. Lundbeck, 1922). However, Kemner (1922, 1926) disposed of it by discovering larvae. These free-living larvae only last from a few minutes to a few hours and, in some species, they do not feed (Franssen, 1933, Bridarolli, 1937, 1940). Surprisingly, the theory continued to be repeated in later works (e.g. Séguy, 1955, Oldroyd, 1964, Rohdendorf, 1974). There is no evidence of any adult hatching straight from the egg. The theory was only advanced to explain the failure to find larvae. The discovery of, albeit very short-lived, free-living larvae should have eliminated the theory once and for all.

The post-emergence development from stenogastric to physogastric adults was firmly established by Mergelsberg (1935). Furthermore he cited a one-line observation by Kemner (1932) to the effect that in the youngest stenogastrics the anus is directed rearwards. This observation, however, has been persistently ignored by most authors. Indeed the fact that the anus was directed rearwards in the subsequently discovered phorid genus *Alamira* was regarded as an important difference between the Alamirinae and Wasmann's flies (Schmitz, 1951).

Nevertheless, Schmitz was so struck by the resemblances between the Alamirinae and Wasmann's flies that he rejected his former, strongly-held, opinion that the latter belonged to a separate family (e.g. Schmitz, 1929, 1940) and he demoted Wasmann's flies to the subfamily Termitoxeniinae, within the family Phoridae (Schmitz, 1951, 1952). Rohdendorf (1974), however, overlooked Schmitz's papers and placed the family Termitoxeniidae in a separate Infraorder from the Phoridae. Others (e.g. Grassé, 1986) referred to *Alamira* and Schmitz's paper of 1952, but rejected his demotion of Wasmann's flies to a subfamily, while accepting the phorid subfamily Alamirinae and their resemblance to the 'Termitoxeniidae'.

Wasmann's hypotheses 3 and 4 relate to the lack of wings in his flies. However, the 'thoracic appendages' were convincingly homologised with wings, albeit reduced, by Kemner (1937). Nevertheless, the flies continued to be regarded as being always flightless and as possessing vestigial wing rudiments only. Schmitz (1951) subsequently emphasised that the bases of the wings in the fully-winged *Alamira* females were very similar to the wing 'rudiments' of Termitoxeniinae. Then it was pointed out that at least some Alamirinae are prone to shedding their wing membranes, leaving behind wing stumps as opposed to rudiments (Disney & Peterson, 1982). Thus at least some adult Alamirinae evidently had a flying stage followed by a flightless stage.

The last, and most surprising, of Wasmann's hypotheses, the hermaphrodite theory, was grounded on the complete failure to find any males in any of the termite nests excavated. It came to focus, however, on the interpretation of a sperm-filled sac, and its duct. One school of thought (e.g. Wasmann, 1900, 1913; Assmuth, 1913) interpreted this sac as an unpaired testis and its vas deferens. The rival school (e.g. Bugnion, 1913; Silvestri, 1920) regarded it as being a spermatheca (a sperm storage sac in a female) with its duct. The Wasmann school tended to triumph when the work of Franssen (1933) and then of Mergelsberg (1935) in particular seemed to overwhelm the opposition with a mass of detailed anatomical observations.

Mergelsberg, however, failed to find any evidence of spermatogenesis in the so-called testis of his stenogastric adults. He was obliged to postulate that this must be completed in the pupal stage. In support of this hypothesis he reported that sperm was always most abundant in the youngest stenogastrics examined. In particular, he reported this to be the case for some young stenogastrics fixed only a few hours after emergence from pupae collected in the field by Franssen. Reichensperger (1936) declared this to be the key observation ("der Schlussstein") of the whole theory. Likewise Schmitz (1940) regarded this as providing convincing support for Mergelsberg's hypothesis. Unfortunately the speculation started to be treated as an observation. One reason for this was an error and muddle in the later editions of Imms' famous textbook of entomology (e.g. Richards & Davies, 1977). The error was to misconstrue Schmitz's comment that both the sac with mature sperm and the ovaries were to be found in the same individuals of "den allerjüngsten Stadien". It is clear that Schmitz was referring to the youngest stenogastric

adults only, and did not intend the pupae to be covered by this statement. The muddle was to correctly list Schmitz (1940) in the bibliography but to cite this in the text as "Wasmann (1940)" in error. Readers, unaware that Wasmann had died in 1931, could be forgiven for thinking that this phantom paper of Wasmann's had been omitted from the bibliography in error. Thus the myth was born that Wasmann had found both sperm and ovaries in the same individual pupae.

Some authors (e.g. Kistner, 1982, Ferrar, 1987) remained sceptical with regard to the hermaphroditism theory. Others (e.g. Grassé, 1986) accepted it for some genera but not for those differently interpreted by Bugnion and Silvestri. However leading specialists (e.g. Borgmeier, 1964) and most textbooks sided with Wasmann.

The first challenge to the theory based on new data, or rather on new interpretations of old data, was made when attention was drawn to two awkward facts (Disney, 1989b).

A. Mergelsberg (1935) had shown that the so-called vas deferens had a cuticular intima. At the time the full significance of this was not apparent. Subsequent advance in knowledge regarding which structures develop from ectoderm and which from mesoderm, now allow us to generalise that "presence or absence of a cuticular intima indicates the origin" (Davey, 1985). The spermathecal duct is invariably ectodermal in origin while the insect vas deferens is of mesodermal origin, with only the ejaculatory duct being ectodermal. Thus we can now conclude that Mergelsberg's own data do not support his hypothesis that the duct from the sperm-filled sac is a vas deferens.

B. The undoubted phorid genus *Perissa*, only known in the male sex, had been incorrectly assigned to the subfamily Metopininae by Borgmeier. In reviewing its affinities I was led, by a process of elimination, to conclude that the genus was the most likely candidate for being the missing males of the Alamirinae or the Termitoxeniinae.

I was then sent collections from Zimbabwe, by Dr Colin Tingle, which served to confirm that *Perissa* were indeed the hitherto missing males of the Alamirinae (Disney, 1990a). I went further by commenting that the parallels between the Alamirinae and Termitoxeniinae "are so remarkable that they suggest the hypothesis that the Alamirinae is paraphyletic, by virtue of the exclusion of the Termitoxeniinae" (a paraphyletic group being an incomplete monophyletic group, by virtue of the exclusion of some species. A monophyletic group is an ancestral species plus **all** its descendants).

Shortly after the publication of this 1990 paper, I received a request from Meg. Cumming to identify some tiny flies she had observed arriving at a termite mound in her garden in Harare, Zimbabwe. Her material included male flies caught in copula with fully-winged females as they arrived together at the termite mound. On arrival the females dropped onto the wall of the mound, ascended to an air vent and entered. They then paused while the wing membranes were shed, before they proceeded into the depths of the nest. These females proved to be stenogastric Termitoxeniinae, belonging to one of Wasmann's original species. The anus of these flies is directed rearwards (Fig. 10). The males, however, proved to be Alamirinae! Furthermore Meg. Cumming had acquired a copy of a paper on collecting methods for insect surveys (Disney *et al.*, 1982) and decided to set out some water traps in her garden. The abdomens of some females procured in a water trap, set near the termite mound, had become distended by the uptake of water. This induced a deflection of the anus ventrally (Fig. 10). Apart from still retaining their wing membranes, these flies are indistinguishable from Mergelsberg's early-stage stenogastrics (Fig. 9).

These new data forced the conclusion that the "Alamirinae" represent the early, flying-stage, stenogastric females plus the hitherto missing males of the Termitoxeniinae

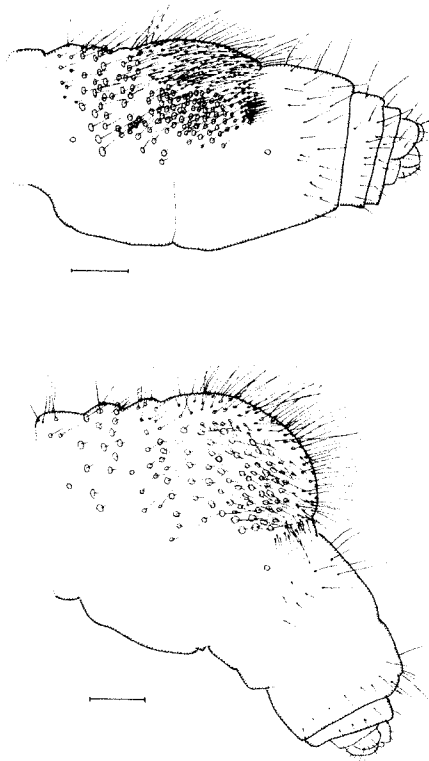


FIG. 10.

Left faces of the abdomens of the flying-stage females of *Termitophilomyia braunsi*. Above, a specimen caught at the entrance to a termite mound. Below, a specimen caught in a water trap set near the termite mound. (Scale bars=0.1 mm).

(Disney & Cumming, 1992). The males of eight species of Termitoxeniinae are now known (Disney, 1993a).

In conclusion only one of Wasmann's five hypotheses has survived, namely the post-emergence change from the stenogastric to the physogastric state in the females. This is probably an adaptation by which free-living larvae, which are very vulnerable to attack by soldier termites, are suppressed through the device of producing relatively enormous eggs. These not only have an incubation period of weeks, rather than days, but being as large, or slightly larger than, their host's eggs are treated as termite eggs by the host workers. Indeed, the latter groom and 'handle' these eggs as if they were their own.

Wasmann's theories stimulated much research. They also served to curtail certain lines of enquiry by insisting that the females were always flightless and were resident in termite mounds throughout their lives. The failure to procure the non-resident males in the termite mounds not only caused them not to be associated with their females, when caught elsewhere, but gave rise to the extraordinary hermaphroditism theory. The latter is the only case claimed for endopterygote insects and is incompatible with our current understanding of the mechanisms of sex determination in Cyclorrhaphan ('higher') Diptera. The theory also caused these undoubted phorids to be placed in a separate family, and even in a separate infraorder by one author. It will be interesting to see how long it takes to eliminate Wasmann's erroneous theories from textbooks. Wasmann's

flies, however, will continue to intrigue entomologists and merit much more research. Indeed David Kistner and myself are now embarking on a taxonomic revision and phylogenetic analysis of these extraordinary flies, along with a critical compilation of all the termite host records for the different species. When we have produced a cladogram for the Termitoxeniinae, comparable to that reproduced as Fig. 7, for the much smaller subfamily of the Thaumatoxeninae, we plan to map the host data onto it. In this way we hope to unravel the pathways of evolution which have given rise to the present pattern of ecological radiation.

As rightly emphasised by Brooks & McLennan (1991), the revolution initiated by Hennig is providing the methodology for transforming our "Just-So Story" speculations on the evolution of ecological and behavioural diversity into truly testable hypotheses. Having started in ecology, I moved into taxonomy without ever abandoning my primary interest. Now, through the methodology of phylogenetic systematics, I am gradually being able to bring an evolutionary perspective to bear upon ecological data, thus helping to redeem the latter from being an untidy accumulation of facts only imperfectly ordered into meaningful patterns. Too much ecology lacks a phylogenetic perspective. Ecology and taxonomy are coming together again in an ever more fruitful relationship. Comparative biology has once again become a challenging field for research.

However, the world's biodiversity is being rapidly depleted by pollution and habitat destruction and most species remain unknown to science. Every species which goes extinct represents a loss of phylogenetic information and a depletion of ecological diversity. Taxonomy is not only a challenging science. The documentation of the world's fauna and flora is an urgent task, particularly with regard to insect faunas (Wheeler, 1990). That is why I have devoted so much of my energies to contributing to an inventory of the world's fauna, even if my chosen field is a group of small flies unfamiliar to most people. These scuttle flies, however, just happen to represent the family of insects thought to possess the greatest variety of lifestyles—a family that by any reckoning must be considered one of the most remarkable products of evolution.

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