

Dr Hubbard,  
with compliments.  
Robin Wootton.

# The Evolution of Insects in Fresh Water Ecosystems

ROBIN J. WOOTTON

The palaeontology of fresh water systems is of great interest in evolutionary studies. In providing the situation probably for the origin and certainly for the early radiation of both crossopterygian and actinopterygian bony fish, the fresh water habitat played a crucial role in the development of all the major vertebrate groups; and fresh or brackish waters may well have provided the pathway to land colonisation for several groups of invertebrates: among them the Arachnida, the pulmonate Gastropoda and the oligochaete annelids. That, despite this interest, rather little is known of the nature and functioning of fresh water palaeoecosystems is due in particular to the gaps in our knowledge of the invertebrate component. Fresh water Gastropoda are patchily recorded from the Lower Carboniferous onwards; Bivalvia from the Devonian. Of arthropods, fresh water Ostracoda are plentiful, if discontinuous, from the Upper Carboniferous; brackish water forms from the Silurian; and Conchostraca from the Ordovician. Fresh water Eurypterida occur, rather uncommonly, from the Middle Devonian to the Coal measures, and Merostomata from the Silurian to the Lower Permian. The remaining fresh water groups, apart from the insects, occur not at all, or as odd specimens only, before the Tertiary; and one can only guess at the existence not only of abundant Protozoa and various worm-like forms, but also of arthropods with skeletons too delicate for preservation, as well as animals of many types inhabiting regions where fossilisation was not taking place.

The insects, which are of such importance in most modern fresh water ecosystems, provide a special case. The juvenile stages of many insects are flimsy—some indeed being no more liable to preservation than annelids—and fossils are correspondingly rare. Except in the Orders Hemiptera and Coleoptera, however, the adults of aquatic insect species are themselves terrestrial; and the wings, and sometimes the bodies occur in many beds from the Middle Devonian onwards, although there is no direct unequivocal evidence of aquatic habit before the Lower Permian. It is therefore sometimes possible to establish the presence of an insect group at a particular horizon and locality from adults, even when circumstances do not favour the preservation of the aquatic juvenile stages. This permits a more complete

picture of the distribution in time of aquatic insect groups than is available for any other fresh water invertebrate class. The time-ranges of all insect orders have been summarised, in some cases down to the level of superfamily, by Crowson *et al.* (1967); and further information is available in Rohdendorf (ed.) 1962, and Rohdendorf 1969. This paper will review in more detail the occurrence as fossils of aquatic insect groups; and will explore some of the implications on the structure of ancient fresh water ecosystems.

#### THE DISTRIBUTION OF AQUATIC INSECT GROUPS IN TIME

Riek (1971) has revived the theory that insects originated in water from fully aquatic forms; and the view that Pterygota, at least, arose from insects with aquatic juvenile stages still gains support from time to time. The weight of evidence and opinion, however, favours terrestrial origin for both Insecta and Pterygota (see Sharov 1966 for references to earlier work; and of subsequent papers, e.g. Sharov 1971, Smart 1971). The fact that relatively primitive orders in each of the divisions Palaeoptera, Polyneoptera and Oligoneoptera have aquatic larvae today appears less significant when the fossil record is examined. Thus Odonata and the Ephemeroptera are the *only* Palaeoptera which are known to have had aquatic juveniles. Nymphs of the Palaeozoic Orders Palaeodictyoptera and Megasecoptera are known, and show no evidence of aquatic adaptation (Rolfé 1967, Carpenter and Richardson 1968, Sharov 1971, Wootton in press). Plecoptera seem to have arisen from within a bewildering complex of Palaeozoic protorthopteroid forms, many of which were certainly terrestrial. There is no reason to suppose that the mecopteroid common ancestors of Trichoptera and modern Mecoptera had aquatic larvae. It is possible, on the contrary, that the survival of these orders whose adult structure is relatively primitive may result from the successful exploitation by their larvae of the possibilities of fresh water, where rather few higher groups are competing.

It is unsafe, therefore, to assume that any insect order was necessarily primarily aquatic; and for this reason the first recorded members of groups which are predominantly aquatic for some or all of their lives cannot themselves be assumed to have been so in the absence of direct morphological evidence, or unless they are known to be derived from another aquatic group with no fully terrestrial forms intervening. Similarly, no extinct insect group can be assumed to have lived in fresh water unless demonstrably aquatic fossils exist. The converse is also true: there may well have been lines, among the protorthopteroid complex for example, whose nymphs were aquatic, but which are known to us from adult fragments only.

With three isolated Devonian exceptions, insects are unknown before the Namurian. They were then already diverse, with palaeopterous and polyneopterous orders dominant throughout the Upper Carboniferous. From this period only two specimens are recorded which belong to orders typically having aquatic nymphs. The fore wing *Erasipteron larischi* Pruvost 1934 has been reexamined by Kukalova (1964) and confirmed in the Odonata—the only specimen of the Suborder Eomeganisoptera Rohdendorf; and *Triplosoba pulchella*

Brongniart 1893, from the Stephanian of Commentry, France, has been redescribed by Carpenter (1963) and remains the only member of the Suborder Protephemeroptera Handlirsch (O. Ephemeroptera). In neither case can the nymph be proved to be aquatic; and the same is true of the entire extinct Order Protodonata. These are dragonfly-like forms, often very large, and are known from the Upper Carboniferous of the USA and Europe, the Permian of the USA and USSR, the Trias of France, and the Lias of Central Asia. Their evident relationship to Odonata has led many authors to assume that their nymphs were aquatic—but none is known.

Abundant Lower Permian insects occur in rich beds in the USA, USSR and Czechoslovakia, and it is clear that several groups of insects were by then in fresh water. The aquatic orders will be considered one by one throughout their time-range.

A. *Odonata*. The most recent comprehensive review of the classification and phylogeny which takes account of fossil forms is that of Fraser (1957). Rohdendorf (1962) gives a later summary; and Pritykina (1968) describes important Jurassic material. Nymphs are unknown before the Mesozoic; but by the Middle Trias the coenagrionoid and anisozygopteran lines had separated, indicating that the aquatic habit, the nymphal mask, and other features common to both lines had arisen by then—and one suspects long before.

The Lower Permian dragonflies belong to the extinct Suborders Protanisoptera Carpenter and Protozygoptera Tillyard. The former disappear without issue in the Upper Permian; but the latter merge into the Zygoptera. Fraser (1957) cites *Permagrion falklandicum* Tillyard 1928, a coenagrionoid from the Upper Permian of the Falkland Islands, as the first true zygopteran; but the Permian saw extensive radiation of damselfly-like forms, and Rohdendorf's measure (1962) of incorporating the Protozygoptera in the Zygoptera is probably a useful simplification of a confused situation. Among the many zygopteran lines arising in the Upper Permian, Trias, and Jurassic, the Agrionoidea appear first in the Middle Jurassic of Karatau, Kazakhstan (Pritykina 1968). The Anisozygoptera appear first in the Middle Trias of Ipswich, Queensland, and are prominent in the Jurassic; but they dwindled following the spread of the Anisoptera, which arose from them. The first recorded anisopteran is *Liassogomphus* (F. Liassogomphidae) from the Upper Lias of Britain and Germany. Gomphidae, Petaluridae, and the extinct Aktassiidae occur at Karatau (Pritykina 1968); Gomphidae and Petaluridae in the Solnhofen lithographic stone at Eichstätt, Bavaria (Upper Jurassic). The extinct Aeshnidiidae are known from the Upper Jurassic of England and Solnhofen and the Cretaceous of Queensland. They appear to be related to the Cordulegasteridae, and are treated by Fraser (1957) as a subfamily. A libelluloid forewing has been found in the Upper Jurassic of Spain (Wootton, unpublished observation); and although Aeshnidae are unknown before the Miocene it seems probable that most, if not all modern families had appeared by the end of the Mesozoic.

B. *Ephemeroptera*. The mayflies have been reclassified by Edmunds and Traver (1954), Demoulin (1958), and Tshernova (1969); the last taking account of all fossil material, including many important discoveries of the last decade. Demoulin (1969, 1971, and other

papers referred to in these) has drawn further conclusions on mayfly classification and phylogeny from the new material.

Three families of Ephemeroptera occur in Lower Permian beds: the Protereismatidae in the USA, Czechoslovakia and the USSR; the Misthodotidae in the USA and USSR; and the Eudoteridae in the USA. These families have traditionally been linked—in the Suborder Permoplecoptera Tillyard by most authors, and in the Superfamily Protereismatoidea by Tshernova (1969)—on the grounds of general similarity, including the fact that fore and hind wings were similar in size and detail. Tshernova (1965) has shown that adult Misthodotidae had large and apparently fully functional mouthparts; and has described a nymph of the family, with nine pairs of foliate gills, and whose strong legs and short hairless tails lead her to conclude a crawling habit in running water. Kukalova too (1968) has described Lower Permian nymphs, from Oklahoma and Moravia, placing all but one in the Protereismatidae. These are well-preserved, and show several interesting features, including gills on nine abdominal segments, postero-laterally directed wing pads, and on one nymph powerful mandibles. Demoulin (1970) has referred these nymphs on evidence of venation to the little-known Order Archodonata, but this may be unjustified. It seems clear that the nymphs of Ephemeroptera were fully aquatic by the Lower Permian.

Some of the primitive characters of the Lower Permian families appear in later forms. *Phthartus* (Middle Permian of Russia) and *Mesoplecopteron* (Trias of France) are nymphs with divergent wing pads and more than seven gill pairs; and the Mesephemeridae (Upper Permian of Russia and Upper Jurassic of Solnhofen, Germany) have homonomous wings.

A range of more modern forms is known from the Jurassic, but their interpretation is controversial. The extant Siphonuridae are represented by adults and nymphs of *Stackelbergisca sibirica* from the Lower or Middle Jurassic of Siberia (Tshernova 1967) whose adults are compared by Demoulin (1968) with the living genus *Siphuriscus* (nymphs unknown). The Aenigmephemeridae—one fore wing fragment from the Middle Jurassic of Karatau, USSR (Tshernova 1968)—and the Hexagenitidae—adults and nymphs variously known from the Upper Jurassic of Siberia and Solnhofen—seem to be related on the one hand to Siphonuridae (Demoulin 1967, Tshernova 1967) and on the other perhaps to Oligoneurioidea (Demoulin 1967, 1971), in which superfamily Tshernova includes *Mesoneta* whose nymphs, from the Lias of Siberia, are regarded by Demoulin (1968, 1969) as Ametropodidae. *Epeoromimus*, similarly known from the Lias of Siberia, is believed by Tshernova (1969) to lie close to Heptageniidae, by Demoulin (1969) to be an artificial genus, two species of which are Siphonuridae and one a baetid. *Mesobaetis* (Lias of Siberia) has also been regarded as a baetid (Demoulin 1968), but Tshernova (1970) includes it in the Leptophlebiidae. Bactidae are otherwise known from the Cretaceous (Tshernova 1970). Ephemeroid-like nymphs occur in Upper Jurassic beds at Montsech, Spain (Wootton, unpublished observation). *Turfanella tingi* Ping, from the Upper Jurassic of Sinkiang, may be the abdomen of an ephemereid nymph. No other families are recorded before the Tertiary, when the majority of modern families are present in the Baltic Amber (Eocene, or Lower or Middle Oligocene).

C. *Plecoptera*. Illies (1965) has reviewed the fossil records of Plecoptera and has discussed the phylogeny of the group. Little needs to be added here. To summarise. Palaeoperlidae: a fore wing and a nymph from the Lower Permian of Siberia—the only specimens of the family. Perlopsidae Martynov: a fore wing and a nymph from the Lower Permian of the Urals, likewise the only specimens. Taeniopterygidae: four species, including one nymph, from the Lower Permian of Siberia; seven species, including two known only from nymphs so that synonymy is a possibility, from the Lower and Middle Jurassic of Siberia; three species from the Lower Cretaceous of China, two of which are known from nymphs only. Hypoperlidae Martynov: one species from the Lower Permian of the Urals, and one from the Upper Permian of Sojana, Russia; the only known specimens. Eustheniidae: one species from the Upper Permian of New South Wales, and another from the Middle Trias of Queensland. Perlidae: one species from the Lower Cretaceous of China. Nineteenth Century studies on the Baltic amber (Eocene, or Lower or Middle Oligocene) provide the first records of Perlodidae, Leuctridae and Nemouridae, as well as further Perlidae and Taeniopterygiidae; and a leuctrid is recorded from the Upper Oligocene of Rott, Germany.

D. *Aquatic Protorthoptera*. The life histories of almost all Protorthoptera (in the sense of Carpenter 1966, and nearly synonymous with Protoblattodea, not Protorthoptera, in Sharov 1968) are unknown. Some may well have had aquatic nymphs; and there is evidence that this was true of the Family Lemmatophoridae Sellards, known from the Lower Permian of the USA, the Urals, and Czechoslovakia. Carpenter (1935), has described nymphs of this family from Kansas. They superficially resemble those of Plecoptera, but appear to have nine pairs of abdominal gills.

E. *Aquatic Heteroptera*. Y. A. Popov is preparing a monograph on the evolution of water-bugs, but this is not yet in print. Published time ranges of the families of Hydrocorisae are as follows: Naucoridae, Notonectidae, Corixidae from the Middle Jurassic (Karatau) (Popov 1968 and earlier papers) to the present day; Nepidae and Belostomatidae from the Upper Jurassic (Solnhofen) (nineteenth-century records, confirmed by Becker-Migdisova 1962) to the present day; and the extinct Notonectid-like Scaphocoridae from the Middle Jurassic of Karatau only (Popov 1968). In a summary of his conclusions, Popov (1971) refers to two other families neither of which has been described at the time of going to press: the Jurassic Stygeonepidae, swimming forms related to the Nepidae and Belostomatidae; and the Cretaceous Mesotrephidae, related to Scaphocoridae, Helotrephidae and Pleidae, and more distantly to Notonectidae. In this paper he derives all Hydrocorisae from hypothetical littoral proto-ochterid-like forms, and supposes that the Nepoidea arose and became fully aquatic in the Lower Trias; and the corixoid, naucoroid and notonectoid lines followed suit in the Upper Trias. His phylogenetic conclusions agree broadly with those of Parsons (1965), formed from morphological study of extant Hydrocorisae.

Of Amphibicorisae: Gerridae, Veliidae and Hydrometridae are all recorded from the Oligocene of Europe; but the earliest known member of the group may be *Karanabis kiritshenkoi* Becker-Migdisova from the Middle Jurassic of Karatau, Kazakhstan, which

Popov (1968) believes to have gerrid and veliid affinity, rather than nabid as was first supposed (Becker-Migdisova 1962).

F. *Megaloptera*. The genus *Permosialis*, with 16 species recorded from the various Lower and Upper Permian localities in the USSR, is the only pre-Tertiary representative of this Order. One larva, from the Upper Permian of Kargala, has been described (Sharov 1953). Corydalidae and Sialidae both occur in the Baltic amber (Eocene, or Lower or Middle Oligocene).

G. *Neuroptera*. Osmylidae and Sisyridae are both present in Baltic amber.

H. *Coleoptera*. Fossil beetles are notoriously difficult to interpret, and, with the exception of the Archostemata, pre-Tertiary material has had little recent attention.

*Angaragabus jurassicus* and *Liadytes avus*, respectively a larva and an adult from the Lias of Siberia, may well be Dytiscidae (Ponomarenko 1963); and dytiscid or hydrophilid-like forms are known from the Upper Jurassic of Solnhofen (Handlirsch 1908). In addition many specimens of larvae of *Coptoclava longipoda*, the only species of the family Coptoclavidae Ponomarenko, have been found in Upper Jurassic beds in Siberia, Mongolia and China. These were large, swimming, evidently predaceous forms, apparently Hydra-dephaga (Ponomarenko, 1961).

Gyrinidae and Hydrophilidae are recorded from the Oligocene of Europe, and one haliplid from the Miocene of Germany. Nearly all the records date from the last century, and have not been restudied.

I. *Trichoptera*. The Trichoptera are an ancient Order. Martynova (1958) has described *Microptysma sibiricum* from the Lower Permian of the Kuznetsk Basin, Siberia, and *Microptysmodes uralicus* from the Upper Permian of the Urals, placing them in a distinct Suborder, the Permotrichoptera (F. Microptysmatidae). Of Annulipalpia, Cladochoristidae are restricted to the Upper Permian and Triassic of Australia, Prorhyacophilidae to the Australian Upper Trias. Necrotauliidae extend from the Upper Trias to the Cretaceous, and are particularly numerous in the Lias of Europe. Two other Jurassic families are based on single wings; one of which — *Dysoneura trifurcata* from Karatau — is thought by Sukaczewa (1968) to be close to Phryganeidae, Limnophilidae and Sericostomatidae, and hence a member of the Integripalpia. All remaining families appear for the first time in the Baltic Amber, with the following exceptions. Limnophilidae are recorded from the Miocene of Europe, North America and the USSR. Plectrotarsidae, Beraeidae, Philanisidae, Helicophidae and Philorheithridae are unknown as fossils. Larval cases, mostly of uncertain family, but providing evidence of Integripalpia, have been found in the Upper Jurassic of Siberia and the Cretaceous of Czechoslovakia, and recently of Minnesota (Lewis 1970) as well as in various Tertiary localities.

J. *Diptera*. Rohdendorf (1964) has reviewed in detail the fossil history and evolution of flies. In this Order, where an aquatic way of life has arisen independently several times, the difficulty of determining the larval habit of fossil species known only from adult material is often insuperable; and fossil larvae are almost unknown.

The earliest certain Diptera come from Upper Triassic beds in Central Asia, near lake Issyk-Kul. Rohdendorf has assigned them to 18 families in 14 superfamilies and three infra-orders; and such diversity clearly indicates some previous history. Among the Issyk-Kul flies are all the fossil members of Rohdendorf's Suborder Archidiptera, in which he also includes the extant *Nymphomyia alba* Tokunaga, a part archaic, part specialised fly whose larva seems to live in fast streams. This, however, is only doubtful evidence that the Triassic Archidiptera did likewise. The remaining species from this locality are all Tipulomorpha (equals Tipuloidea + Culicoidea of Oldroyd 1970) or Bibionomorpha; and it may be assumed that any aquatic forms are among the former.

Not all Tipulomorpha, though, are aquatic. Within the Tipulidae themselves occur fully aquatic and fully terrestrial larvae, as well as forms which inhabit semi-liquid decaying organic material—the habitat which some authors (e.g. Oldroyd 1964) believe to be primitive for dipterous larvae. The larval habitats of most of the Issyk-Kul Diptera is hence uncertain; but some are more likely to have been aquatic than others, notably the Architendipedidae, which show clear resemblance to Chironomidae. Also present are Architipulidae, whose larval habit is unknown, but which are thought by Rohdendorf (1964) to be ancestral to Tipulidae, Limoniidae and Trichoceridae. This family is plentiful in the Lias of Dobbertin, Germany; where also occur the Eoptychopteridae, which Rohdendorf believes ancestral to Culicidae and Chaoboridae; and the genus *Eolimnobia* which may be close to the ancestry of Ptychopteridae.

The outstanding Jurassic locality for Diptera, however, is Karatau, Kazakhstan (Middle Jurassic), whence are recorded the dixid-like *Dixamima*; *Tanyderophryne*, linked by Rohdendorf with the Psychodidae, Nemopalpidae and Phlebotomidae; *Protendipes*, a chironomid-like genus; and the pupae *Eopodonomus* and *Pachyneuronympha*—both chironomoid in form.

Some Brachycera, including the extant families Rhagionidae and Nemestrinidae, occur in Jurassic beds. No modern brachyceran family seems to be primarily aquatic, however; and the larval habits of the Mesozoic forms are unknown.

Ceratopogonidae and orthocladiine Chironomidae (Boesel 1937), and Stratiomyiidae, Empidae and Dolichopodidae (McAlpine and Martin, 1968) are known in Cretaceous amber in Canada. Tipulidae, Limoniidae, Ptychopteridae, Psychodidae, Culicidae, Dixidae, Simuliidae and Tabanidae all appear for the first time in the Tertiary—mainly in Baltic amber, where also are found chironomine, tanypodine and orthocladiine Chironomidae. It is nearly certain, however, that most of the modern aquatic families of Diptera were established in Cretaceous times. Dumbleton (1963) believes on zoogeographical grounds that Simuliidae and Blepharoceridae (the latter being unknown as fossils) have occupied New Zealand since the Cretaceous, and that they have changed little since.

## THE PROGRESSIVE EMERGENCE OF AQUATIC LIFE-MODES

No pre-Tertiary aquatic vascular plants are known. While this does not disprove their existence, it seems probable that the principal sources of plant food available to Palaeozoic and Mesozoic insects were algae, floating and encrusting; and plant debris, mainly of terrestrial origin, with associated decomposing microorganisms. Aquatic angiosperms may have arisen in the Cretaceous, and became widespread in the Tertiary; but living higher water-plants appear to be relatively unimportant as insect food today. Animal food, including insects and other small invertebrates, and also fish-fry, would have been available throughout to predatory and scavenging insects.

In determining how and when these various food-sources became exploited by insects it is necessary to refer to modern forms. The food and feeding-habits of many aquatic insects, especially those inhabiting running waters, have been reviewed by Hynes (1970). Hickin (1967) discusses the food of Trichoptera, and Oliver (1971) that of Chironomidae. The following summary is drawn in the main from these authors, who should be consulted for other references.

Algae are an important food-source for many insect groups. Corixidae, some eclyonurid mayflies, and a few genera of Plecoptera and Trichoptera scrape encrusting algae from stones or water plants. Simuliidae; Culicidae; some mayflies—*Tricorythrus*, *Isonychia*, *Murphyella*; and some Trichoptera—*Brachycentrus*, *Oligoplectrium*—filter algae directly from water together with other organic drift. Diatoms are an important food for most Chironomidae, which filter them in various ways, using nets or salivary secretion; or ingest them directly from the substrate. Many net-building Trichoptera—e.g. Hydropsychidae and Philopotamidae—ingest algal drift; and diatoms are also a major component of the food of many case-building caddises (Ross 1964).

Plant debris is consumed by a variety of insects. Many Plecoptera-Filipalpia, Trichoptera-Integripalpia, and some elminthid beetles chew large fragments; and finely-divided debris is taken by the drift-filtering groups already mentioned, and also by substrate-feeding representatives of most aquatic insect orders. It is seldom clear to what extent debris-feeders are deriving nourishment from associated decomposing microorganisms.

Living animals form the main, or at least a significant part of the diet of many groups. Odonata; some Ephemeroptera; perlid, perlodid and eustheniid Plecoptera; Rhyacophilidae and a variety of other Trichoptera; nepid and naucorid Heteroptera; and the larvae of some Diptera, notably Tabanidae and some Stratiomyiidae, are bottom-living predators which catch their food directly. Polycentropid Trichoptera net animals in running water. Of swimming forms, Hydradephaga and aquatic hydrophilid beetle larvae; notonectoid, nepid and naucorid Heteroptera; Chaoboridae; and tanypodine and a few chironomine and diamesiine Chironomidae, are habitually predaceous. Finally gyrid beetles, and of Heteroptera Notonectidae, Gelastocoridae, and all the Amphibicorisae, exploit the supply of terrestrial insects caught in the surface film.

Figure 5.1 shows the times of emergence among insects of some of these modes of life, as indicated by the first appearance as fossils either of groups which follow them today or of



CARBONIFEROUS	PERMIAN	TRIASSIC	JURASSIC	CRETACEOUS	TERTIARY
			Surface-film predators -----X		
			Pelagic predators -----X	?-----	Pelagic direct drift-filterers -----X
			Pelagic algal feeders -----X		
	Crawling benthic predators -----X		Benthic direct algal and debris feeders -----X	?-----	Benthic direct drift-filterers -----X
			Burrowing direct algal and debris feeders -----X	?-----	Benthic net drift-filterers -----X
				?-----	Benthic net-predators -----X

Fig. 5.1 The emergence of various modes of life in aquatic insects. A cross indicates the first clear fossil evidence; a broken line the period within which the habit probably arose.

forms whose morphology provides clear evidence of the habit. The broken lines are speculative, and indicate the probable true periods of origin of each habit.

Crawling predators, in the form of Odonata nymphs, may well have been present in the Upper Carboniferous; and by the Lower Permian (Leonardian) several insect groups were clearly occupied in this way. Indeed it may well be that the great majority of early aquatic insects were at least partly predaceous. We may assume that the Odonata were always wholly so. Kukulova's protreismatid ephemeropteran Nymph 1 has large prognathous mandibles (Kukulova 1968); and it is perhaps significant that most of the extant predatory mayflies belong to the archaic Family Siphonuridae (Edmunds 1957, Tshernova 1970). Among Plecoptera the Eustheniidae, which date from the Upper Permian and are by far the most primitive extant members of the Order, are predaceous forms (Hynes 1964). Megaloptera have probably always been so, and the Upper Permian nymph of *Permosialis* has large mandibles (Sharov 1953). The most primitive families of modern Trichoptera are likewise predatory; and the venation of early fossil forms appears closer to that of the carnivorous Rhyacophilidae than to other extant families.

All the above orders are represented in the Lower Permian, and some tentative conclusions may be drawn about their habitats. Plecoptera have always been predominantly

rheobiontic, and early Trichoptera too probably lived in running water (Ross 1963). The same was almost certainly true of Megaloptera; and the scarcity of fossils of all three orders supports the view that they lived in eroding rather than depositing situations. The habitats of Permian Odonata and Ephemeroptera are perhaps less certain; but there is evidence that these too may have been running-water forms. Permian Odonata are rare, and no nymphs are known. The nymphs of Midco, Oklahoma, from which locality came *Protereisma* nymph no. 1 (Kukalova 1968), were thought by Carpenter (1947) to have been washed down by streams. The lake at Obora (Moravia) where the remainder of Kukalova's nymphs were fossilised, similarly derived much of its insect fauna from streams (Kukalova 1963). Tshernova considers on morphological grounds that the nymph of *Misthodotes sharovi* was a running-water form (Tshernova 1965).

The Lemmatophoridae (Protorthoptera), so abundant in the Lower Permian beds of Kansas, Oklahoma and Moravia are represented, in Kansas at least, by nymphs as well as adults; and were therefore probably lacustrine. Those of Obora (Moravia) however, are believed by Kukalova (1964) to include both stream and river-dwelling species. No nymphs have been described from Obora. Their food is unknown.

The Upper Permian and Triassic saw the radiation of each of these orders, with the exception of Protorthoptera and possibly of Megaloptera. The Ephemeroptera are known to have extended their range with respect to both habit and habitat. *Mesoneta*, from the Lias of Siberia, was not obviously adapted for fast waters (Meshkova 1961); and the Liassic *Epeoromimus* and Upper Jurassic *Ephemeropsis* are thought on morphological evidence to have had swimming nymphs inhabiting still water (Tshernova 1961, 1970). The appearance of burrowing forms, probably feeding on algae and detritus, in the Upper Jurassic of Spain, represents a further extension of habit. One may assume that algal- and detritus-feeding, which predominate in Ephemeroptera today, had been developing in the Order since the Permian; and the same happened with Plecoptera, although predation has continued to be the principal method of feeding in several families. Trichoptera, with the development of the Integripalpia, progressively colonised slow-moving and still waters; and algal-feeding, detritus-feeding and omnivorous forms arose. Ross (1964) believes that case-building caddises arose directly from free-living forms and independently from net-makers. The last are unknown before the Tertiary, but their habitat would not favour fossilisation, and they may be far older.

Adephagous and polyphagous beetles and heteropterous bugs probably arose in the Upper Permian; and their colonisation of fresh water in the Mesozoic led to the appearance for the first time in Jurassic strata of a variety of actively swimming predatory adults and juveniles: Dytiscidae, Belostomatidae, Notonectoidea and Naucoroidea; and the surface-feeding Gerridae and Gyrinidae. The specialised swimming, algal-feeding Corixidae were also present; and Nepidae joined the benthic predators.

The most significant Mesozoic addition, however, were the Diptera. The presence of orthoclaadiine Chironomidae in the Cretaceous indicates that the rise of the family to its present immensely important status in aquatic ecosystems was underway. Today Orthoclaadiinae probably ingest algae and detritus directly from the substrate (Oliver 1971).

Brundin (1966) believes that Chironomidae initially arose in fast montane streams, and spread from there to slow-moving and still waters. The chironomid pupae in the Jurassic Karatau lake (Kazakhstan) were probably carried there by streams (Hecker 1965), and they, and the existence of chironomoids in the Trias hint that benthic, detritus-feeding Diptera were present in the mid-Mesozoic. The presence of Tanypodinae in Baltic amber marks the appearance of the predatory habit within the Chironomidae, and that of Chironominae the appearance of benthic indirect drift-filtering. Evidence for direct fast-water drift-filtering comes with the Simuliidae, and for surface-filtering in still and moving water with the Culicidae—both in Baltic amber. These families were probably present in the Cretaceous, and their modes of life may well have been established in their Jurassic precursors.

#### CONCLUSIONS

The history of aquatic insects, like that of terrestrial forms, demonstrates the peculiar versatility of the Class in drawing upon a remarkable variety of food-sources. Many of the ways of life available to insects were exploited from the first by other groups. Ostracoda devoured the phytoplankton. Gastropods fed on encrusting and filamentous algae. Bivalves were benthic drift filter-feeders. Conchostraca, if we may deduce from the habits of modern estheriids, burrowed in mud, feeding on organic detritus; as also may annelids of which we have no record. Xiphosura, where they occurred, were probably general scavengers and omnivores, like present-day Limulida. Eurypterida, fish and aquatic Amphibia and reptiles were at first mainly carnivores, occupying the higher trophic levels. As small predators, feeding predominantly on primary consumers, insects may however have had few competitors in other groups; and it is suggested that this was their most important early role. Progressively, however, they developed the morphological and behavioural equipment to exploit a wider range of food-sources, and came to comprise a great variety of macro- and micro-feeders operating at all levels, from within the substrate to the top of the surface film. At the same time most of the major groups were extending their habitat-ranges. Many lines appear to have originated in streams and rivers, only later spreading to lakes. The overall consequence of these trends has been a continual increase in the contribution of insects to the total energy flux through aquatic ecosystems. In this increase all groups have played their part; but the radiation and expansion of the Diptera in late Mesozoic times appears to have been of supreme importance.

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