Systematics of Sciadoceridae and Relatives With Descriptions of Two New Genera and Species From Canadian Amber and Erection of Family Ironomyiidae (Diptera: Phoroidea)

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Abstract   *Canad. Ent.* 98: 527–544 (1966)

The systematic relationships of Sciadoceridae and of the other families of the superfamily Phoroidea, i.e., Platypezidae, Ironomyiidae and Phoridae, are reviewed. A new family, Ironomyiidae, is proposed for *Ironomyia nigromaculata* White from Tasmania. Two fossil flies in Canadian (Cretaceous) amber, representing two new genera and species of Sciadoceridae, are described and figured. These constitute the first record of the family in North America. The supposed phylogenies of the families of the Phoroidea and of the genera and species of Sciadoceridae are outlined; the evolution and biogeography of the latter family is treated in detail. Keys to the families of the Phoroidea and to the genera and species of Sciadoceridae are provided.

Introduction

Study of some new collections of Canadian amber (McAlpine and Martin, in preparation) revealed two well-preserved fossils (Figs. 1, 2) of Sciadoceridae. These specimens, representing two new genera and species (Figs. 3–12), constitute the first record of the family in North America and increase the known species from three to five. Sciadocerids occupy a key position in the Phoroidea, one of the most primitive superfamilies of the cyclorrhaphous Diptera. Although "situated at an obscure point in the evolutionary plan of the Diptera" (Oldroyd 1964), this superfamily is exceptionally suitable for demonstrating how the elucidation of phylogenetic affinities can aid in solving systematic controversies (Hennig 1954, 1964). Within the Phoroidea, sciadocerids combine certain generalized features of primitive Platypezidae and important specialized characters of the Phoridae. The family is also peculiar in that its only living species occur in the southern extremities of Neotropical and Australian regions, while its fossil species are from Europe and North America (Fig. 24). As stated by Hennig (1964), Sciadoceridae and its relatives are emminently suitable for establishing the value of fossils for determining the geological age and occurrence of animal groups (Fig. 23).

Only two extant species of Sciadoceridae are known: *Sciadocera rufomaculata* White, "the most wonderful fly in the world" (Oldroyd 1964) from southeastern Australia, Tasmania and New Zealand, and *Archiphora patagonica* Schmitz from the southern tip of South America. In discussing the evolution and biogeography of dipterous groups with this type of distribution, Hennig (1960) surmised that they probably occurred in the Northern Continents during or prior to lower Oligocene times, whence representatives dispersed to the areas of the Southern Continents mentioned. Subsequent identification of the fossil species *Archiphora robusta* (Meunier) in Baltic amber (Hennig 1964) established that Sciadoceridae in fact did occur in Europe in the Oligocene epoch. The two new species in Cretaceous amber from Canada provide further probative evidence on the occurrence and evolution of these interesting animals.

Significantly these fossil sciadocerids fully confirm earlier conclusions on the evolution and biogeography of the family expressed by Hennig (Hennig 1954, 1964) and demonstrate that meaningful conclusions on such matters can be made even without the aid of fossils. The study of these fossils has also materially

contributed toward a clearer understanding of the relationships of the Phoroidea and its component groups (Fig. 23). This, in turn, has led to an improved system of classification for the group.

Taxonomy

Sciadoceridae belongs to the suborder Cyclorrhapha, the larvae of which lack a clearly differentiated head and pupate within the last larval skin, that is, in a true puparium; the adults in this suborder emerge through a slit in the puparium which usually detaches an anterodorsal cap. Within the Cyclorrhapha the family falls in the Aschiza, a natural group which also includes Lonchopteridae, Platypezidae, Phoridae, Syrphidae, Pipunculidae and, in the opinion of some authors, the Conopidae. The adults of all Aschiza lack a ptilinum and a frontal (= ptilinal) suture. Within the Aschiza Sciadoceridae belongs to the superfamily Phoroidea (= Hypocera), a monophyletic unit also containing Platypezidae and Phoridae (Hennig 1954, 1964).

The anomalous species *Ironomyia nigromaculata* White from Tasmania also belongs here. It was assigned first to the Empididae (White 1916), then transferred to the Platypezidae (Tonnoir 1925) and subsequently rejected from that family by Kessel (1952). As originally suggested by Tonnoir (*in* Fuller 1934) it represents a fourth family in the Phoroidea, and the new family Ironomyiidae is hereby proposed for it; *I. nigromaculata* is still the only known representative. The key below outlines the main characters for distinguishing this and the other families of the Phoroidea.

The family Sciadoceridae was proposed by Schmitz (1929) for the genera *Sciadocera* White and *Archiphora* Schmitz. *Sciadocera* was assigned first to Empididae (White 1916) and then to Platypezidae (Tonnoir 1923), and later to Phoridae (Tillyard 1926). Tonnoir (1926) treated it as the type genus of a new subfamily of Phoridae. Schmitz (1929) regarded it, along with *Archiphora* Schmitz, as representing a separate family between Platypezidae and Phoridae, "but on the whole more closely related to Platypezidae". Hardy (1946) placed it in the brachycerous family Dolichopodidae but this is unsatisfactory because *Sciadocera* is truly cyclorrhaphous. Hennig (1954, 1964) concurred with Schmitz on the rank and intermediate position of the family but, in agreement with Tonnoir (*in* Fuller 1934), he considered it more closely related to Phoridae than to Platypezidae. Our work shows that, in fact, Sciadoceridae is intermediate between Ironomyiidae and Phoridae, and that Ironomyiidae is intermediate between Sciadoceridae and Platypezidae (Fig. 23). The new genera and species described below fully justify Tonnoir's and Hennig's conclusions that Sciadoceridae is more closely related to Phoridae than to Platypezidae. The key to genera and species of Sciadoceridae outlines the most significant differences and similarities in all known members of the family.

Key to Families of Phoroidea

1. Subcosta complete and entirely free from r₁ (Figs. 13–16). Third antennal segment more or less triangular with a terminal arista; apex of second segment not deeply inserted into base of third. Compound eyes of male contiguous, and with upper and lower facets strongly differentiated .... **Platypezidae**
   Subcosta largely fused with r₁ (Figs. 17–22). Third antennal segment more or less oval with dorsal or subterminal arista (apical in *Ironomyia*); apex of second segment deeply inserted into base of third. Compound eyes of males not contiguous (narrowly separated in *Ironomyia*), and with upper and lower facets not differentiated 2

2. Stigma present; base and apex of subcosta free; r₄₊₅ ending in wing tip; veins r₁, r₂₊₃ and r₄₊₅ not distinctly stronger than the following veins (Fig. 17). Compound eyes of male narrowly separated. Arista terminal .... **Ironomyiidae**
   Stigma absent; apex of subcosta not free; r₄₊₅ ending well before wing tip; veins r₁, r₂₊₃ and r₄₊₅ distinctly stronger than following veins (Figs. 18–22). Compound eyes widely separated in both sexes. Arista usually dorsal or subdorsal (Figs. 5, 12) 3
3. Vein r₃ complete and entirely free from r₄₊₅; second basal cell present; roots of m₁ and m₂ not closely associated with r₄₊₅, i.e., their origins from stem of m₁₊₂ clearly evident (Figs. 18–21) .... **Sciadoceridae**
   Vein r₃ largely or entirely fused with r₄₊₅; second basal cell absent; stem of m₁₊₂ absent and m₁ and m₂ apparently, though not actually, arising obliquely from r₄₊₅ (Fig. 22) .... **Phoridae**

Key to Genera and Species of Sciadoceridae

1. Costa extending nearly to apex of wing; radial veins not compressed into basal half of wing (Figs. 18–20). Proscutellum developed (Fig. 6). Palpi little swollen (Figs. 3–5) 2
   Costa ending about middle of wing; radial veins very close together in basal half of wing (Figs. 10, 21). Proscutellum undeveloped (Fig. 11). Palpi distinctly swollen (Figs. 9, 12) .... *Prioriphora* new genus
   (Type species *P. canadambra* n. sp.; monobasic.)
2. Discal cell present (Figs. 18, 19). Mesopleuron bare (Fig. 9) 3
   Discal cell absent (Fig. 20). Mesopleuron bristled (Fig. 3) ....
   .... *Sciadophora* new genus
   (Type species *S. bostoni* n. sp.; monobasic.)
3. Common stem and bases of veins m₁ and m₂ obliterated (Fig. 19). Antero-basal half of wing without microtrichia. Hind metatarsus short and broad .... *Sciadocera* White (1916)
   (Type species *S. rufomaculata* White (1916) by monotypy; only species known.)
   Common stem and bases of m₁ and m₂ present (Fig. 18). Wing wholly covered with microtrichia. Hind metatarsus elongate (as in Figs. 3, 9) .... *Archiphora* Schmitz (1929)
   (Type species *A. patagonica* Schmitz by original designation; contains two species.) 4
4. Scutellum with two pairs of bristles (as in Figs. 6, 11); fossil species .... *A. robusta* (Meunier) (1905)
   Scutellum with one pair of bristles, the anterior pair missing; extant species .... *A. patagonica* Schmitz (1929)

Sciadophora new genus

Figs. 1, 3–8, 20

Head (Figs. 3–5) about twice as high as long, and about as wide as high. Compound eye bare. Frons with two pair of parafrontals, one pair of outer verticals, several pairs of interfrontals and one pair of ocellars; all these bristles reclinate. Postocular setae not very strong, uppermost two or three stronger and curved inwardly. Postverticals relatively strong, subparallel or slightly divergent. Third antennal segment oval. Arista dorsal, with very short pubescence, two basal segments elongate. Palpus small. Proboscis short and fleshy.

Mesonotum (Figs. 3, 6) coarsely setose, with an unpaired row of strong acrosticals, a similar but paired row of dorsocentrals, and laterally with a third row of strong bristles.
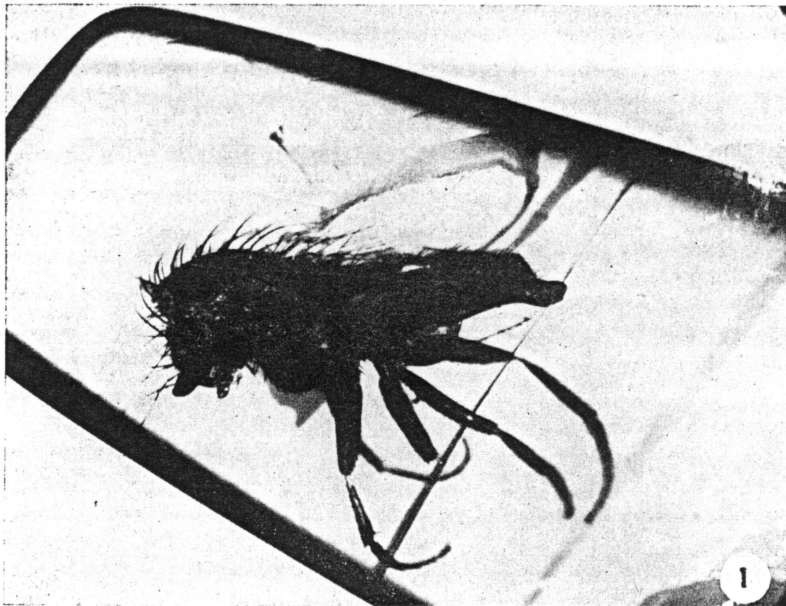
Fig. 1. Holotype of *Sciadophora bostoni* n. sp. as it appears in amber.

Proscutellum (Fig. 6) strongly developed. Scutellum large, with two pairs of bristles. Mesopleuron with one or more bristles (Fig. 3). Notopleuron with three bristles. Propleural bristles present.

Wing (Fig. 20) rather elongate. Axillary lobe moderately developed. Alula well developed, with strong setulae along all of margin. Costa ending slightly before apex of wing. Stem of m_{1+2} present, m_1 clearly joining m_2. Anal and discal cells absent. Second basal cell present.

Legs and tarsi (Fig. 3) simple. Femora without strong bristles. All tibiae uniformly setulose, with two small apical bristles on ventral side, without preapical dorsal bristles, and other bristles weak or absent. Basal tarsal segments of all tarsi elongate.

Abdominal terga 2–7 each with a row of relatively strong setae along posterior margin (Fig. 7).

Type species *Sciadophora bostoni* n. sp.

Sciadophora bostoni new species
Figs. 1, 3–8, 20

Holotype ♀. Length about 2.0 mm. Body and legs brownish, wings clear. Proportions of head as shown in Figs. 3–5. Frons slightly longer than wide; sides almost parallel; with three strong, lateroreclinate parafrontal bristles, the middle one arising slightly closer to the ventral one than to the dorsal one; with three mesoreclinate interfrontal bristles, the lowermost much longer and stronger than the upper two. Ocellar bristles lateroreclinate, almost as long and as strong as upper parafrontals. Postverticals moderately strong, almost parallel. Three postocular hairs behind uppermost parafrontal much stronger than remaining setulae in this series and curving mesad rather than laterad. Antenna a little longer than wide in side view, with acutely rounded apex. Arista bare; two basal segments subequal in length, each at least four times as long as their greatest diameter. Antennal grooves very shallow. Cheek with a strong vibrissa-like bristle preceded by a weaker one. Palpus orange, much smaller than third antennal segment; with about five short, black setulae at apex.

Mesonotum (Figs. 3, 6) abundantly and coarsely bristled. Acrostical bristles (probably eight) in a single row extending from anterior margin to prescutellar area. Dorsocentrals eight, extending from anterior margin to a point opposite hindmost acrostical, progressively longer and stronger toward rear of row. With a row of five equally strong bristles laterad
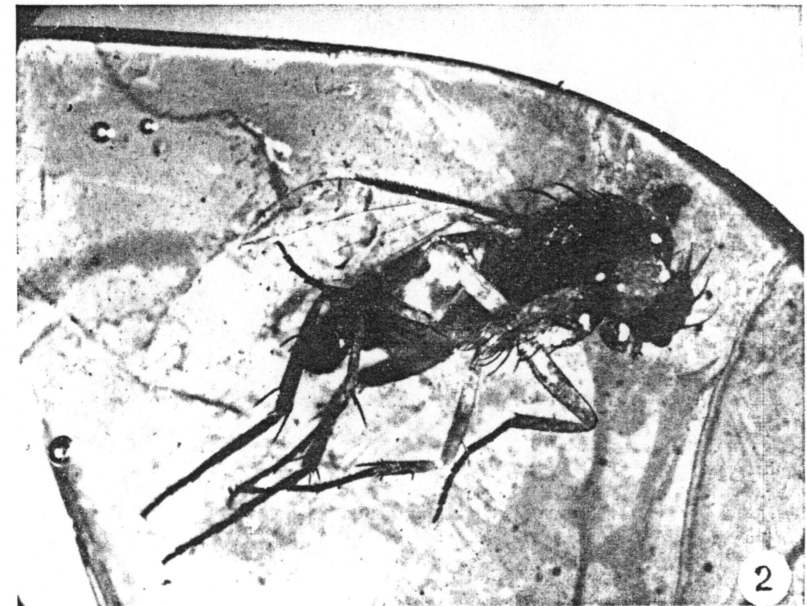
Fig. 2. Holotype of *Prioriphora canadambra* n. sp. as it appears in amber.

of dorsocentrals. With one humeral, one posthumeral, one supraalar and three notopleural bristles. Mesonotum and scutellum without fine hairs or setulae. Scutellum (Fig. 6) rather cordate from above, with four strong bristles. Proscutellum well developed. Mesopleuron with one strong bristle near middle of hind margin; with four or five smaller hairs along upper margin, the anteriormost hair directed anterodorsad over the mesothoracic spiracle (Fig. 3). Propleural bristle present. Sternopleuron and pteropleuron apparently bare.

Wing (Figs. 3, 20) about two and two-thirds times as long as wide; uniformly hyaline; microtrichia covering entire surface. Venation as illustrated. Axillary lobe well developed, with six or seven strong setulae along margin. Costa strongly setulose from a point distad of humeral cross vein to insertion of r_{1-5}. Second basal cell several times longer than wide. Halteres entirely brownish yellow.

Legs and tarsi (Fig. 3) entirely brown, rather uniformly setulose. Each tibia with one strong and one relatively small preapical ventral seta. Hind tibia with one small dorsal seta on basal third; otherwise all tibia without outstanding bristles. All metatarsi about as long as the combined lengths of the following three tarsal segments. Front and mid coxae with bristles on anterior surface.

Abdomen (Figs. 7, 8) rather flattened on dorsum, with a row of relatively strong bristles along posterior margin of each tergum. Last segment conical; appearing to be comprised of two parallel, somewhat blade-like lobes. Last two or three apparently strongly modified as shown in Fig. 8.

Holotype in amber (Fig. 1) collected from tailings at open pit coal measure near Medicine Hat, Alberta, by P. Boston in July, 1963. Type No. 9126, deposited in the C.N.C. by kind permission of Mr. P. Boston, Medicine Hat, Alberta.

Remarks. The amber was found associated with lignitic deposits from the Foremost Formation (Belly River Series, Upper Cretaceous). Radiometric dates obtained for the Bearpaw shales that occur immediately above the Foremost horizons at Medicine Hat range from 72 to 73 million years (Folinsbee et al. 1964). This establishes the upper limit for the age of the Foremost Formation at 73–74 million years (Folinsbee in lit.). According to Boston (in lit., quoting

from a letter from Dr. J. D. Campbell, Palaeontologist, Research Council of Alberta) "the Belly River group falls completely within the boundaries of the European Campanian epoch". The dates established by Kulp (1961) for the beginnings of the Campanian and Maestrichtian epochs are about 81 and 72 million years respectively. Thus, the holotype of *S. bostoni* is at least 73 million years old and this species undoubtedly existed before the close of the Campanian epoch.

We are extremely grateful to Mr. P. Boston, an amateur geologist and gem collector, for making this specimen and the related geological information available to us; it is a pleasure to name the species in his honour.

Prioriphora new genus
Figs. 2, 9–12, 21

Head (Figs. 9, 12) about two-thirds as long as high. Compound eye bare. Frons with one pair of each of following bristles: outer verticals, fronto-orbitals, anterior interfrontals, and ocellars; all these bristles reclinate. Postverticals very small and divergent as in *Sciadocera*. Postocular setae strong, uppermost two or three distinctly longer and curved inwardly. Antennal cavities rather weak. Third antennal segment oval. Arista dorsal with very short pubescence; two basal segments elongate. Palpus distinctly enlarged on apical half. Proboscis short and fleshy.

Mesonotum (Fig. 11) shortly setulose anteriorly, and with the following bristles: an unpaired row of acrosticals, a row of closely placed dorsocentrals, one humeral, one post-humeral, one strong postsupraalar preceded by a row of weaker ones, and one postintraalar. Proscutellum undeveloped. Scutellum rather small; with two pairs of bristles. Pleural sclerites (Fig. 9) bare except for two propleural setulae and three notopleural bristles.

Wing (Figs. 10, 21) relatively broadly oval. Axillary lobe not evident in holotype. Alula much as in *Sciadophora*. Costa ending near middle of anterior margin. Veins r_1, r_{2+3}, and r_{4+5} close together. Stem of m_{1+2} present, extreme base of m_1 atrophied. Anal and discal cells absent. Second basal cell small.

Legs (Fig. 9) with strong bristles. All coxae bristled anteriorly at apices. Mid femur with a strong anterior bristle. Preapical dorsal tibial bristle developed, at least on front and mid tibiae. Mid and hind tibiae with several bristles in addition to apical bristles. All metatarsi at least twice as long as following segment.

Abdominal terga uniformly and weakly setulose (Fig. 9).

Type species *Prioriphora canadambra* n. sp.

Prioriphora canadambra new species
Figs. 2, 9–12, 21

Holotype ♂. Length about 1.8 mm. Body dark brown, wings clear, and legs pale yellow.

Compound eye (Figs. 9, 12) bare, occupying almost entire side of head. Frons (Fig. 12) about as long as wide, sides almost parallel. All frontal bristles strong, outer verticals strongest. Parafrontal arising slightly closer to interfrontal than to outer vertical. Antenna entirely dark brown. Third segment about as long as wide. Arista with very short pubescence; two basal segments of arista subequal in length, each at least three or four times as long as their greatest diameter. Cheek narrower in width than greatest diameter of palpus, with one vibrissa-like genal bristle preceded by a row of smaller postocular setae. Palpus (Fig. 12) relatively elongate and distinctly swollen on apical half; strongly setulose apically, with one bristle much stronger than the others.

Mesonotum (Fig. 11) entirely brown; bristles relatively sparse and short; setulae sparse and depressed. Acrosticals, about 16, in a single row as illustrated. Dorsocentrals, about 17 in each of two rows, closely spaced and progressively longer and stronger toward rear of rows. Each side with one humeral, one posthumeral, two postalars, and three notopleural bristles. About seven, relatively weak, closely spaced supraalar bristles also present. Numerous fine setulae present in the presutural area between the dorsocentral row of bristles and the humerus. Scutellum shorter than broad; with four bristles, the apical pair more distant from each other than from the lateral ones. Proscutellum undeveloped. Propleuron with two weak bristles. Mesopleuron, sternopleuron and pteropleuron bare.

Wing (Figs. 10, 21) very phorid-like. Costa scarcely attaining middle of anterior margin. The first three longitudinal veins relatively thicker than in any other species of the family. Remaining veins relatively weaker than in other sciadocerids. Base of m, narrowly
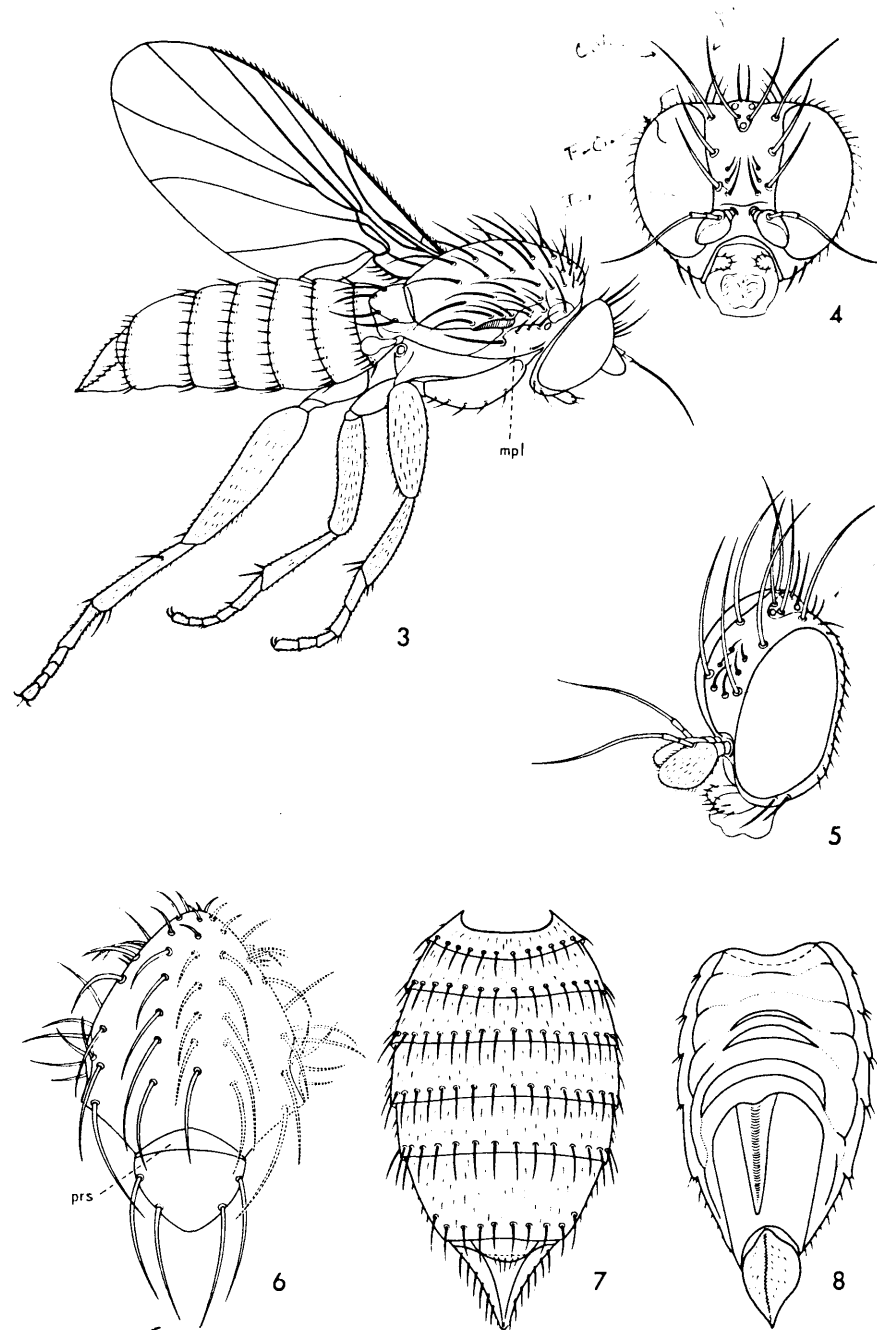
Figs. 3–8. *Sciadophora bostoni* n. sp.: 3, right lateral aspect; 4 and 5 anterior and antero-sinistral views, respectively, of head; 6, dorsal aspect of thorax; 7–8, dorsal and ventral views, respectively, of abdomen.

separated from m_2. Axillary angle probably rather poorly developed. Alula with about six setulae. Halteres entirely pale yellow.

All coxae strongly bristled at apices. Front and hind femur without strong bristles. Mid tibia with a single bristle near middle of anterior surface. All tibiae with dorsal, antero-lateral, and ventral bristles near apex (Fig. 9). Mid tibia with one dorsal and one postero-dorsal in middle. Hind tibia with one posterodorsal and two anterodorsals. Tarsi long and slender. All metatarsi about five times as long as wide; ventrally with five to seven evenly spaced, peg-like spines that stand out among numerous smaller setulae.

Abdomen (Fig. 9) rather slender; terga weakly setulose. Basal sterna apparently present, though not so distinct as figure indicates. Genitalia rather rectangular in side view.

Holotype in amber (Fig. 2) from Cedar Lake, Manitoba, collected August 1963, by J. E. H. Martin and J. F. McAlpine; type no. 9127 in the C.N.C.

Remarks. Because the amber at Cedar Lake was secondarily deposited there, its geological age is somewhat uncertain; it is widely believed to be Cretaceous (Carpenter *et al.* 1937; Holland 1951; Sanderson and Farr 1960; McAlpine and Martin, in preparation).

Evolution and Phylogeny

As implied in the introduction, changes that occurred during the evolution of the Phoroidea are strikingly displayed by its members and many step-by-step changes are revealed by comparing homologous characters in representative species. Several examples of such evolutionary morphoclines from primitive to specialized conditions are evident in the shape and venation of the wings (Figs. 13–22). As to be expected, no known single species embodies all the primitive char-acters of the original phoroid fly; likewise, none contains all the derived or specialized conditions that occur within the superfamily. Nevertheless it is possible to apprehend the primitive and derivitive conditions of many characters for this group and, by so doing, to conceive the appearance of the ancestor of the Phoroidea. The establishment of such a base-point is a useful preface for dis-cussing the evolution of the group.

In most respects the Platypezidae changed less from the ancestral conditions of the Phoroidea than any other group in the superfamily. Hennig (1954) showed that their wing venation (Figs. 13–16) is closest to the 'ground plan' of all the Phoroidea, and concluded it differed mainly by the absence of a costa behind the insertion of m_1, but even this is weakly present in at least one genus, that is, *Opetia* Meigen. Kessel (1948, 1952, 1960) postulated that the Platypezidae stemmed from the brachycerous family Empididae; he considered the following platypezid genera as the most primitive ones in the family: *Platypezina* Wahlgren, *Opetia* Meigen, *Microsania* Zetterstedt and *Melanderomyia* Kessel. By pooling the most primitive conditions of characters in these genera and also those of the annectant family, the Ironomyiidae, we deduced that the original phoroid fly had the following characters:

Size and general appearance similar in most respects to *Platypezina*, that is, rather small and slender, with arched mesonotum, and dark-brown or reddish-brown in colour.

Compound eyes close together in male, but slightly separated as in *Ironomyia;* upper and lower facets not or weakly differentiated. Frons of female with some bristles and some scattered interfrontal setulae, much as in *Platypezina*. Antenna rather elongate with a terminal arista; all segments, including third, hairy; very similar to that of *Opetia*.

Mesonotum moderately humped as in *Platypezina;* with numerous fine scattered hairs as in *Opetia* and *Ironomyia*; acrostical hairs not in distinct rows, or if so, weakly biserial; other mesonotal bristles relatively weakly differentiated from the hairs as in *Opetia*. Pro-scutellum (Fig. 6) developed as in *Opetia, Microsania, Ironomyia,* and *Sciadophora*. Scutellum with two or more pairs of weak bristles on the margins as in *Opetia* and *Ironomyia*. Pleural sclerites with weak bristles and hairs as in *Opetia*. Mesopleuron and pteropleuron with some setulae.
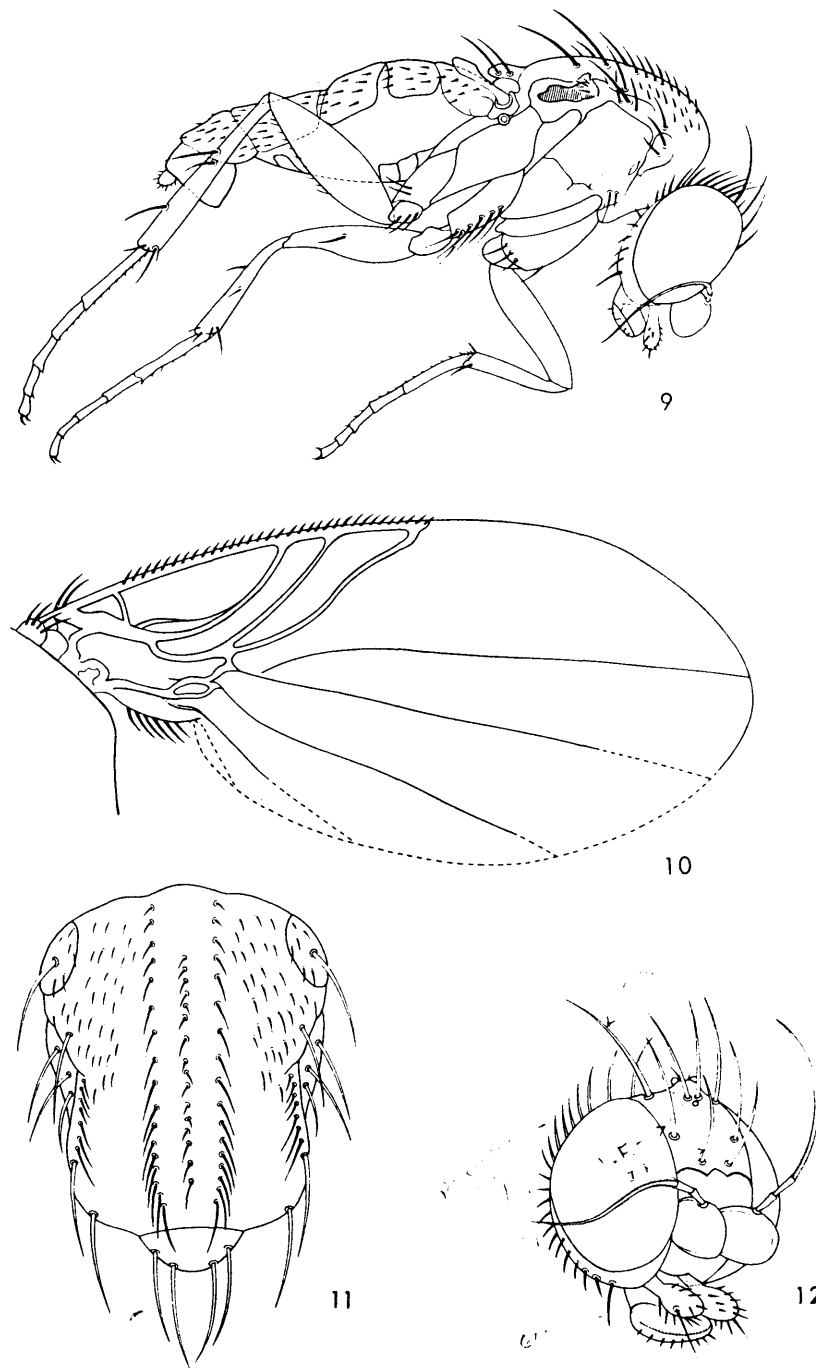
Figs. 9–12. *Prioriphora canadambra* n. sp.: 9, right lateral view, wing omitted; 10, dorsal aspect of right wing; 11, dorsal aspect of thorax; 12, anterodextral view of head.

Wing similar in shape to that of *Platypezina*, *Opetia* and *Microsania* (Figs. 13, 15, 16), that is, broad and with well-developed axillary lobe and alula. Venation similar to that of *Ironomyia* (Fig. 17) except subcosta entirely free as in *Platypezina* (Fig. 13) and costa continued weakly around margin of wing as in *Opetia* (Fig. 15). Wing membrane uniformly covered with microtrichia. Stigma (Figs. 13, 17) well developed. Calyptrae dusky with brownish margins and fringes. Halteres dark brown or black.

Legs moderately long, slender and simple as in *Platypezina*, *Opetia*, *Microsania* and *Sciadophora* (Fig. 3); entirely setulose, and with few strong bristles as in the genera mentioned. Hind metatarsus in both sexes longer than the following segment as in *Opetia*, *Microsania* and *Platypezina*, and perhaps slightly swollen, especially in males.

Abdomen simple as in *Opetia* and *Ironomyia*; terga and sterna with scattered, weak hairs. Male genitalia directed posteroventrad as in *Opetia*, *Ironomyia* and *Melanderomyia*.
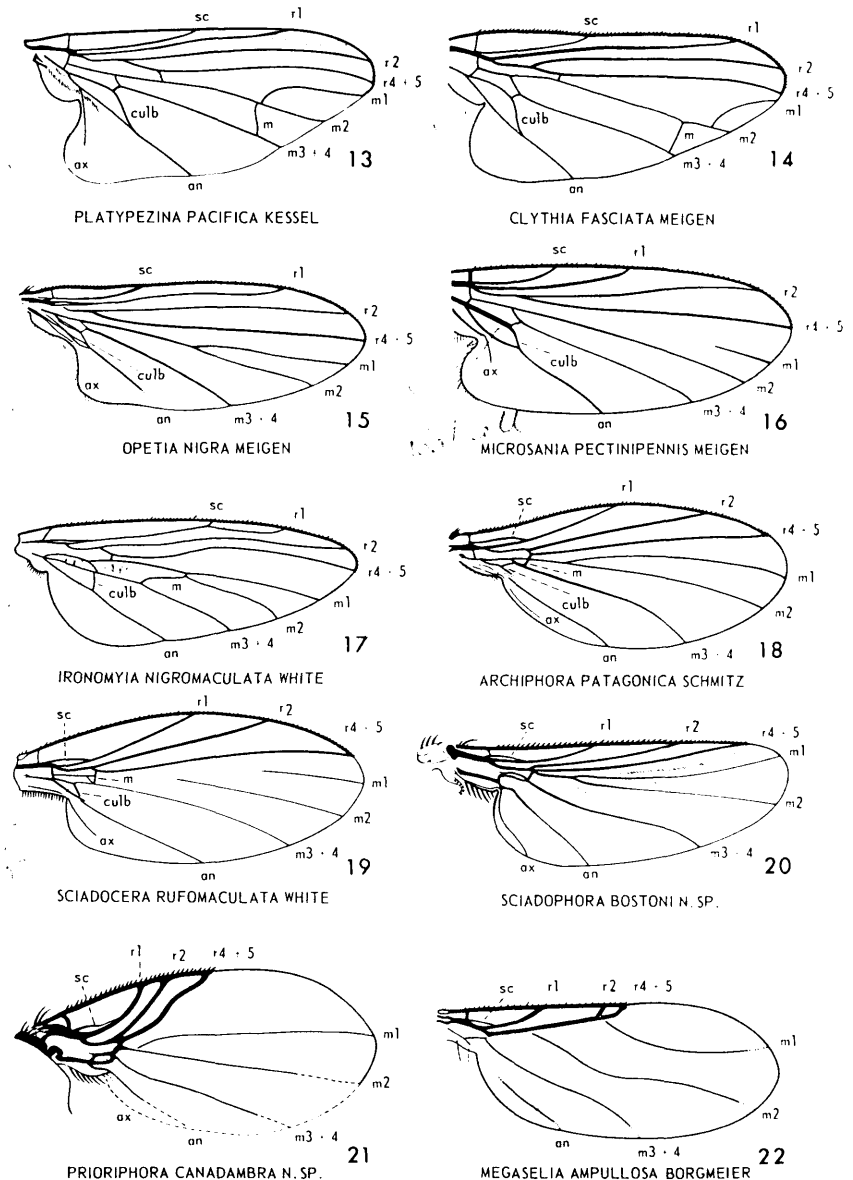
Among various empidids examined, those agreeing most closely with the above conditions belong to the genera *Gloma* Meigen and *Oreogeton* Schiner. These genera may be descendants of the evolutionary branch which led to the primordial platypezid.

Morphological evidence from the Phoroidea indicates that at least two lines descended from a primitive platypezid-like fly with the above characters (Fig. 23). One line retained empidid-like antennae and a completely free subcosta; in addition, the radial veins remained scarcely stronger than the other veins and did not become crowded toward the base of the wing (Fig. 13). This line led to the Platypezidae. The following specializations within it are particularly significant: the compound eyes of the males became or remained contiguous, the hind metatarsi became shortened and dilated, and the furcation of vein m_1 and m_2 and the hind crossvein became shifted distad from the middle of the wing. Kessel (1952, 1960) provided details on the evolution and phylogeny of all the genera of the Platypezidae.

In the other line the antennae became muscid-like, and the subcosta became partially fused with r_1 (Fig. 17). The furcation of wing vein m_{1+2} and the posterior crossvein became shifted toward the base of the wing (Fig. 17). These changes occur in all remaining members of the Phoroidea.

The most primitive descendant of the latter line is *Ironomyia nigromaculata* White. In this unique species, as in primitive Platypezidae, the proscutellum is well developed, the stigma of the wing is retained, and the apex as well as the base of the subcosta is free. Unlike the Platypezidae, however, the eyes of the male are not contiguous; nevertheless they are close together. Derivatively, the discal cell is much shorter than in typical platypezid wings (Fig. 17), presaging its gradual disappearance in annectant, more highly specialized groups (Figs. 18–20); the posterior end of the posterior crossvein (m) came to lie closer to the base of the wing than does its anterior end, whereas this vein is oppositely aligned in the Platypezidae (Fig. 13). The middle portion of the subcosta became fused with r_1, whereas it remained completely free in Platypezidae.

Morphologically *I. nigromaculata* represents a basic step from the Platypezidae toward the Sciadoceridae. From this standpoint it is difficult to imagine a better

PLATYPEZINA PACIFICA KESSEL 13

CLYTHIA FASCIATA MEIGEN 14

OPETIA NIGRA MEIGEN 15

MICROSANIA PECTINIPENNIS MEIGEN 16

IRONOMYIA NIGROMACULATA WHITE 17

ARCHIPHORA PATAGONICA SCHMITZ 18

SCIADOCERA RUFOMACULATA WHITE 19

SCIADOPHORA BOSTONI N. SP. 20

PRIORIPHORA CANADAMBRA N. SP. 21

MEGASELIA AMPULLOSA BORGMEIER 22

Figs. 13–22. Wings of Phoroidea. 13, *Platypezina pacifica* Kessel (redrawn from Kessel 1948); 14, *Clythia fasciata* Meigen (redrawn from Hennig 1954); 15, *Opetia nigra* Meigen (redrawn from Schmitz 1929); 16, *Microsania pectinipennis* Meigen (redrawn from Hennig 1954); 17, *Ironomyia nigromaculata* White (redrawn from Tonnoir 1925); 18, *Archiphora patagonica* Schmitz (redrawn from Schmitz 1929); 19, *Sciadocera rufomaculata* White (redrawn from Hennig 1964); 20, *Sciadophora bostoni* n. sp.; 21, *Prioriphora canadambra* n. sp.; 22, *Megaselia ampullosa* Borgmeier (redrawn from Borgmeier 1961).

qualified "connecting link" between these two families, for even if we did not know *I. nigromaculata* we would have to postulate the existence of a species with the same combination of characters to account for the changes from the Platypezidae to the Sciadoceridae. Evidently it is a little-changed descendant of the second line that evolved from the ancestor of the Phoroidea. As such, its systematic rank is equivalent to those of Sciadoceridae, Platypezidae and Phoridae, and consequently the new family Ironomyiidae must be erected for it (see above).

The more highly specialized branch leading to the Sciadoceridae plus the Phoridae changed as follows: the stigma of the wing was lost (Figs. 18–21), the subcosta became fused with r_1 on its apical two-thirds or more (Figs. 18–21), the posterior crossvein and the furcation point of m_{1+2} became shifted farther toward the base of the wing (Figs. 18, 20, 21), veins r_1, r_{2+3}, and r_{4+5} became relatively stronger than the remaining veins and their apical insertions in the costa became crowded toward the base of the wing (Figs. 18–21), the axillary lobe of the wing became less prominent; the male frons became almost as wide as in the female (Figs. 4, 12), and the arista was moved to a subapical dorsal position (Figs. 5, 12). All these relatively specialized conditions occur in the five known species of Sciadoceridae and in most Phoridae. The more primitive family, the Sciadoceridae, probably descended directly from this branch.

Guided by Hennig's work (Hennig 1954, 1964) we deduced the primitive and specialized conditions of about 20 characters of the Sciadoceridae. The relative conditions of these characters and their distributions among the genera and species are shown in Table I; sharing of specialized characters ("synapomorphy" of Hennig) is indicated by stippling.

As evinced by differences in wing venation and in characters of the antenna in known sciadocerids, this family evolved along two main lines (Fig. 23). One branch retained a small discal cell and an anal cell (Figs. 18, 19), and the arista, at least in the males, remained in a subapical dorsal position. The genera *Archiphora* and *Sciadocera* evolved from this branch.

In the other line, both the anal cell and the discal cell were lost through reduction and fusion of pertinent veins in the base of the wing (Figs. 20, 21), and the arista became shifted farther dorsad on the third antennal segment. This line led to the genera *Sciadophora* and *Prioriphora*. Hennig (1964) presented two plausible interpretations of the evolution of *Archiphora patagonica* Schmitz, *A. robusta* (Meunier), and *Sciadocera rufomaculata* White. The more probable of the two is that *robusta* and *patagonica* are sister descendants of an unknown ancestor which in turn had a sister-branch relationship with the line leading to *rufomaculata* (Fig. 23). If this interpretation is correct the evolution of these three species can be explained as follows.

The line leading to *patagonica* and *robusta* retained the bases of veins m_{1+2} and m_1, and simple, elongate hind metatarsi (Figs. 3, 9). Derivatively, the axillary lobe of the wing and the anal cell became somewhat reduced and the finer setulae of the mesonotum and the pleural sclerites were reduced or lost. Eventually this line split into two lines. The more primitive one, leading to the fossil species *robusta*, retained four bristles on the scutellum; the more specialized one, leading to the extant species *patagonica*, lost one pair of scutellar bristles.

In the line which led to *S. rufomaculata*, the axillary lobe of the wing and the anal cell remained relatively large (Fig. 19). Derivatively, the microtrichiae disappeared from the base of the wing, the bases of veins m_{1+2} and m_1 disappeared, and the hind metatarsus became relatively short and broad (paralleling a similar condition in many Platypezidae).

TABLE I: PRIMITIVE AND DERIVITIVE CONDITIONS OF 20 CHARACTERS IN THE SCIADOCERIDAE, AND THEIR DISTRIBUTIONS AMONG KNOWN SPECIES

	BOSTONI (SCIADOPHORA)	CANADAMBRA (PRIORIPHORA)	ROBUSTA	PATAGONICA (ARCHIPHORA)	RUFOMACULATA (SCIADOCERA)
Mesonotum with few (+), many (−) strong bristles	−	+	+	+	+
Anterior crossvein present (+), absent (−)	−	+	+	+	+
Discal cell present (+), absent (−)	−	−	+	+	+
Anal cell present (+) , absent (−)	−	−	−+	−+	+
Arista subapical (+), dorsal (−)	−	−	−	−+	+
Mesonotum with (+), without (−) scattered setulae	−	+	−	−	−
Pteropleuron with (+), without (−) setulae	−	−	+	−	−
Mesopleuron with (+), without (−) setulae	+	−	−	−	−
Fronto-orbitals two pairs (+), one pair (−)	+	−	−	−	−
Frons with (+), without (−) inter frontal hairs	+	−	−	−	−
Axillary lobe well developed (+), weakly developed (−)	+	−	−	−	+
Tibial bristles few, weak (+), several, strong (−)	+	−	−	+	+
M1 joining m2 (+), not joining m2 (−)	+	−	+	+	−
Alular lobe well developed (+), weak (−)	+	+	+	−	−
Wing entirely microtrichose (+), partially so (−)	+	+	+	+	−
Base of m1 + 2 present (+), absent (−)	+	+	+	+	−
Hind metatarsus elongate (+) short (−)	+	+	+	+	−
R4 + 5 inserted near wing tip (+), far from wing tip (−)	+	−	+	+	+
Palpus simple (+), enlarged apically (−)	+	−	+	+	+
Proscutellum present (+), absent (−)	+	−	+	+	+
Scutellar bristles, two pairs (+), one pair (−)	+	+	+	−	+

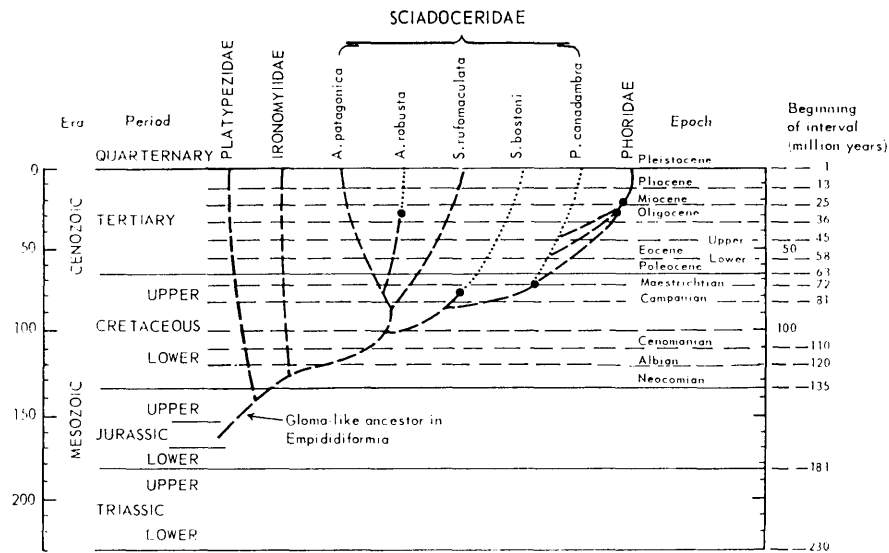+ = Primitive condition

− = Derivitive condition

TABLE I.

Fig. 23. Supposed phylogenies of known species of Sciadoceridae and of the other families of the Phoroidea superimposed on Kulp's (1961) geological scale (Santonian, Coniacian, Turonian and Aptian epochs of the Cretaceous period omitted).

Returning to the second main branch of the Sciadoceridae, differences between *Sciadophora bostoni* and *Prioriphora canadambra* show that it became divided into at least two lines (Fig. 23). The line leading to *S. bostoni* retained a relatively typical sciadocerid wing venation (Fig. 20), that is, with the branches of r not excessively crowded together in the wing base and r_{4+5} inserted in the costa near the wing tip. It also retained a proscutellum (Fig. 6) and relatively slender, simple legs (Fig. 3). In addition, some hairs were retained on the frontal vitta (Fig. 5) and on the mesopleuron (Fig. 3). Derivatively, the base of wing vein m_{1+2} became shifted forward so that it appears to arise from r_{4+5} (Fig. 20); also, it developed very strong bristles on the mesopleuron and mesonotum, but it lost all the scattered, fine, setulae on the latter (Fig. 6). This line seems to have been relatively unsuccessful, for the fossil species *bostoni* is the only descendant known.

The branch leading to *Prioriphora* retained numerous setulae on the mesonotum (Fig. 11), but changed in many other respects: the wing venation changed strongly toward the conditions typical for the Phoridae, that is, the branches of r became strongly shifted into the base of the wing and r_{4+5} became inserted in the costa near the middle of the wing; the branches of m were shifted basad and forward so that the axes of m_1, m_2, and m_{3+4} form a strong angle with the branches of r (Figs. 10, 21). The proscutellum was lost and the scutellum became smaller in size (Fig. 11). The legs became somewhat stouter, and the whole body assumed a more phorid-like appearance (Fig. 9).

This line seems to have been extremely successful, for unquestionably it is the base from which the large family Phoridae arose. This is not to say that *Prioriphora canadambra* is *the* ancestor of the Phoridae, but simply that phorids descended from some representative of the *Prioriphora* line. Since the oldest true phorids known are Oligocene in age (Schmitz 1941), the Phoridae probably arose from a geologically younger descendant of *Prioriphora* than *P. canadambra*.
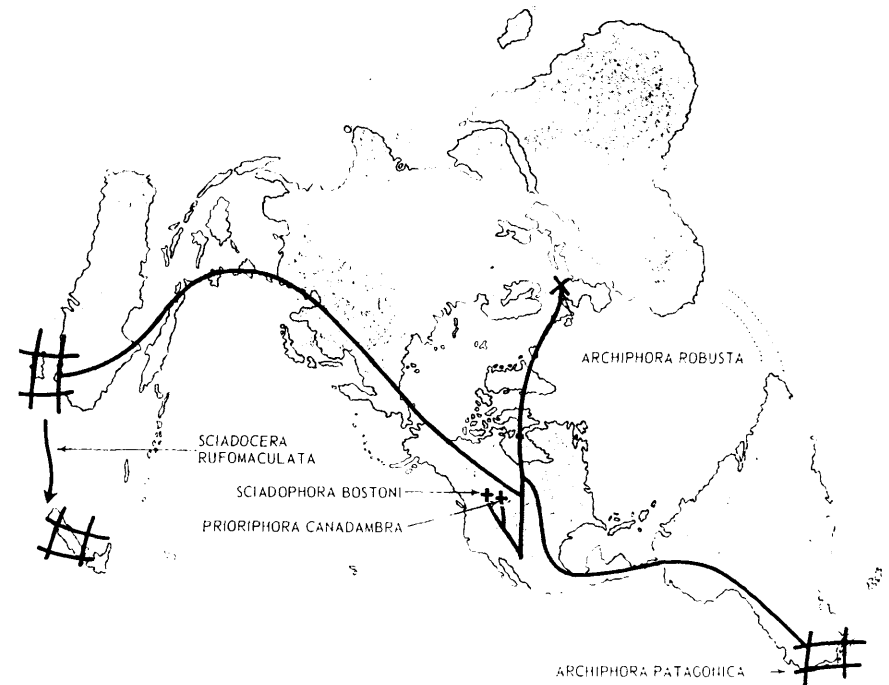
Fig. 24. Phylogenetic dispersal chart of the Sciadoceridae on a north polar projection of the world. Principal land masses of Cretaceous period (redrawn from Termier and Termier 1952) indicated by stippled areas.

The final evolutionary step toward the Phoridae included additional fusion and reduction in the length of wing vein r_3 and the loss of the second basal cell (Fig. 22). In addition, the coxae and femora became stouter and the body acquired the stockier habitus of typical phorids.

Temporal Origin of the Sciadoceridae

The occurrence of fossil sciadocerids in Canadian amber proves the family has existed continuously for at least 73–80 million years. Geological ages given for the formations believed to be the source of the fossil-bearing fragments (Upper Cretaceous formations in Alberta and Saskatchewan) range from 63 ($\pm$ 2) million years at the end of the Cretaceous period to 81 ($\pm$ 3) at the beginning of the Campanian epoch (Kulp 1961; Folinsbee *et al.* 1960). The supposed relationships of all known Sciadoceridae (Fig. 23) indicate that the two genera represented in Canadian amber arose after *Archiphora* and *Sciadocera*. Since *P. canadambra* is one of the oldest fossil sciadocerids known and also the most highly specialized member of the family, the family likely underwent a relatively long period of evolution prior to Upper Cretaceous times. Thus, the Sciadoceridae could not have originated much more recently than late in the Lower Cretaceous period.

The presence of *Archiphora robusta* (Meunier), a species not greatly different from *A. patagonica* Schmitz, proves that the genus *Archiphora* had already evolved by Oligocene times. The phyletic relationships of *Sciadocera rufomaculata* White to species of *Archiphora* indicate an equally early or earlier origin

for that genus. Thus, the four known genera probably originated in late Lower or Mid Cretaceous times (Fig. 23).

If these conclusions concerning the age of the Sciadoceridae are correct, the Ironomyiidae and the Platypezidae, both of which are distinctly more primitive than the Sciadoceridae, must have arisen at an even earlier time — certainly not more recently than the Lower Cretaceous and perhaps as early as the Jurassic period (Fig. 23).

Zoogeography

Data on the zoogeography of the Sciadoceridae are meagre. Two living species belonging to distinct genera are known: one in the southern tip of South America and the other in southeastern Australia, Tasmania and New Zealand (Fig. 24). Three fossil species belonging to three genera are known: one of the Oligocene period from Europe belonging to the same genus as the extant species from South America, and two of the Cretaceous period from Canada. The absolute age of the fossil species and the supposed relationships of all species indicate their genera arose in the Cretaceous period. If they arose in the Cretaceous they undoubtedly dispersed then. The family occurred on the Northern Continents from Upper Cretaceous to Oligocene times; some descendants reached South America, others reached Australia, Tasmania and New Zealand.

The relatively close affinity between the two species of *Archiphora* suggests that this genus dispersed at a time when North America, South America and Eurasia were interconnected by land. The sister-group relationship between *Sciadocera* and *Archiphora* indicates that their common ancestor occurred on a land mass that was interconnected with Europe, Australia and South America. Ecological characteristics of the family (Hennig 1964) suggest that it has always lived under subtropical or temperate conditions.

All these prerequisites prevailed during Cretaceous times (see Termier and Termier 1952), the period established for the origin of the family. During the Upper Cretaceous the Australian zoogeographic region became permanently separated from the Asiatic continent, and further evolution in many groups represented there was therefore restricted to lines that reached there prior to the Tertiary. At the same time, land connections between North and South America were relatively constant, followed by long periods of isolation during the Tertiary (Miskimen 1961).

The following explanation of the zoogeography of the Sciadoceridae is based on the fact that the fossil record and the supposed relationships of known species harmonize better with one set of paleogeographic findings than they do with any other set. Alternative explanations exist and are not ruled out, but the one given here seems the most plausible at this time. We offer it not as a definite and final conclusion, but as a working hypothesis to be tested against further discoveries.

The family Sciadoceridae probably arose on the ancient "North Atlantic Continent" (Fig. 24). The size, stability, geography, bioclimatology and the dispersal opportunities provided, this relatively large, stable land mass would seem to have afforded a suitable place of origin. Paleogeographic maps of the world (e.g., Termier and Termier 1952) show that much of what is now northeastern North America (including Greenland) probably remained above sea level from Pre-Cambrian times until the present. For long intervals, during the Jurassic and Cretaceous periods in particular, it was probably connected with western Eurasia across the North Atlantic, with eastern Eurasia via the Beringian arc, and with South America by "Terre Caraibe". At the same time Australia was joined, or

virtually so, with southeastern Asia by means of "Sundaland" and "Philippinia". During the Cretaceous the climate and bioecology on the North Atlantic Continent offered rich and varied habitats ranging from subtropical in the south to more temperate conditions in the extreme north.

When one superimposes the family tree of the Sciadoceridae on a map of the Cretaceous world one may easily visualize the possible, even probable, dispersal of the family to the parts of the world in which it is known to occur (Fig. 24). The place of origin could possibly have been Asia rather than the North Atlantic Continent, but the absence of representatives in Africa, Madagascar and central Asia and the increased difficulties for known lines to reach their present destinations seriously weakens this argument. The dispersal across the tropics of a group adapted to temperate or subtropical conditions might also be questioned, but north–south mountain chains existed at that time and provided subtropical and even temperate avenues across the tropical zone to South America and to Australia.

The occurrence of *Sciadocera rufomaculata* in Australia, Tasmania and New Zealand indicates that these populations of this species have not been separated very long, or that they are interbreeding more or less continuously. Because the immature stages can live in decaying flesh (Fuller 1934), the species probably was introduced into Tasmania and New Zealand from Australia or outlying islands in relatively recent times, likely through the agency of man, birds and (or) rafting. Tonnoir (1926) believed it reached New Zealand as a "migrant" from the north, possibly by way of Lord Howe Island (Solomon Islds.), New Caledonia, and (or) Norfolk Island. He discounted the possibility that man introduced it into New Zealand because "it is a rather localized species, found in native bush only". But, at that time it was not known that the species lives in decomposing flesh — a rather common attribute of flies that followed man.

If the zoogeography of the Sciadoceridae is correctly interpreted, this family is an insect group which was relatively widespread in the late Mesozoic and early Tertiary times, following which it suffered severe range restriction and became confined to its present southern continental habitats.

References

Borgmeier, Rev. T. 1961. Weitere Beitraege zur Kenntnis der neotropischen Phoriden, nebst Beschreibung einiger Dohrniphora-Arten aus der indo-australischen Region (Diptera, Phoridae). *Stud. Ent.* 4: 1–112.

Carpenter, F. M., J. W. Folsom, E. O. Essig, A. C. Kinsey, C. T. Brues, M. W. Boesel and H. E. Ewing. 1937. Insects and arachnids from Canadian amber. *Univ. Toronto Stud. Geol. Ser.* 40: 7–62.

Folinsbee, R. E., H. Baadsgaard and J. Lipson. 1960. Potassium–Argon time scale. *Rep. Int. Geol. Congr.* XXI Session, Norden, 1960. Pt. III: 7–17.

Folinsbee, R. E., H. Baadsgaard, G. L. Cumming and J. Nascimbene. 1964. Radiometric dating of the Bearpaw Sea. *Bull. Amer. Ass. Petroleum Geol.* 48: 525.

Fuller, M. E., *with a foreword by* A. L. Tonnoir. 1934. The early stages of *Sciadocera rufomaculata* White (Dipt. Phoridae). *Proc. Linn. Soc. N.S.W.* 59: 9–15.

Hardy, G. H. 1946. Miscellaneous notes on Australian Diptera. XII. *Proc. Linn. Soc. N.S.W.* 71: 65–71.

Hennig, W. 1954. Flügelgeäder und System der Dipteren unter Berücksichtigung der aus dem Mesozoikum beschreibenen Fossilien. *Beitr. Ent.* 4: 245–388.

Hennig, W. 1960. Die Dipteren-Fauna von Neuseeland als systematisches und tiergeographisches Problem. *Beitr. Ent.* 10: 221–329.

Hennig, W. 1964. Die Dipteren-Familie Sciadoceridae in Baltischen Bernstein (Diptera: Cyclorrhapha Aschiza). *Stuttgarter Beitr. Naturk.* 127: 1–10.

Holland, G. P. 1951. Insects in Canadian amber. *Div. Ent. News Lett. Sci. Serv. Canad. Dep. Agric.*, Dec. 1951: 1–2.

Kessel, E. L. 1948. A review of the genus *Platypezina* Wahlgren, announcement of its presence in the New World, and description of a new species (Diptera: Clythiidae). *Wasmann Collect.* 7: 47–64.

Kessel, E. L. 1952. A key to the genera of Clythiidae (Diptera). *Wasmann J. Biol.* 10: 201–204.

Kessel, E. L. 1960. The systematic positions of *Platycnema* Zetterstedt and *Melanderomyia*, new genus, together with the description of the latter (Diptera: Platypezidae). *Wasmann J. Biol.* 18: 87–101.

Kulp, J. L. 1961. Geologic time scale. *Science* 133: 1105–1114.

Meunier, F. 1905. Contribution à la faune des Acalyptéres Agromyzinae de l'ambre. *Ann. Soc. sci. Brux.* 29: 89–94.

Miskimen, G. W. 1961. Zoogeography of the Coleopterous family Chaulignathidae. *System. Zool.* 10: 140–153.

Oldroyd, H. 1964. The natural history of flies. Weidenfeld and Nicolson. London. 324 pp.

Sanderson, M. W., and T. H. Farr. 1960. Amber with insect and plant inclusions from the Dominican Republic. *Science* 131: 1313.

Schmitz, H. 1929. Sciadoceridae and Phoridae. *Diptera Patagonia and S. Chile* 6: 1–42.

Schmitz, H. 1941. 33 Phoridae *in* E. Lindner (ed.), *Flieg. pal. Reg.* 141: 64–99.

Termier, H., and G. Termier. 1952. Histoire geologique de la biosphere. Masson and Cie, Editeurs. Paris.

Tillyard, R. J. 1926. The Insects of Australia and New Zealand. Angus Robertson, Ltd., Sydney, Aust. 560 pp.

Tonnoir, A. L. 1923. Aperçu sur la Faune diptérienne de la Nouvelle Zelande. *Bull. (Ann.) Soc. ent. Belg.* 5: 91–100.

Tonnoir, A. L. 1925. Australian Platypezidae (Diptera). *Rec. Aust. Mus.* 14: 306–312.

Tonnoir, A. L. 1926. A new and primitive subfamily of the Phoridae (Dipt.). *Rec. Canterbury [N.Z.] Mus.* 3 (1): 32–39.

White, A. 1916 (1917). The Diptera-Brachycera of Tasmania, Part III. Families Asilidae. Bombyliidae, Empidae, Dolichopodidae, and Phoridae. *Pap. Proc. roy. Soc.* for Year 1915. pp. 148–266.

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