

The subgenus *Scaptodrosophila* (Diptera: Drosophilidae)

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ABSTRACT. Four major subgenera, *Drosophila*, *Sophophora*, *Hirtodrosophila* and *Scaptodrosophila*, and several minor subgenera, have been recognized in the genus *Drosophila*. The hitherto little studied subgenus *Scaptodrosophila*, possessing a complicated synonymy, contains 144 named species, or about 11% of the total described in the genus; it is likely that many more *Scaptodrosophila* species await discovery. *Scaptodrosophila* probably originated in tropical Asia, and the greatest *Scaptodrosophila* faunas occur in Asia, south-east Asia, New Guinea, Australia and Africa, with very few species in north and south America and Europe. *Scaptodrosophila* species usually possess a pair of prescutellar bristles, a propleural bristle, and three large subequal sternopleural bristles; other morphological features are more variable. Ecological information concerning the majority of *Scaptodrosophila* species is scanty or absent, but known feeding or breeding sites include tree sap, fungi, fruit, flowers and leaf litter; larvae of at least one species are gall forming in plant tissues. The establishment of species groups is complicated by lack of detailed knowledge of many species, but six groups containing four or more species are recognized.

Introduction

Drosophila is a large, complex and cosmopolitan genus known to contain in excess of 1300 described species; more species are continually being described and many more almost certainly await discovery.

Although a confused indication of a subgeneric classification of the genus *Drosophila* first appeared in Duda (1924a), the first attempts to establish a rational subgeneric classification were made by Sturtevant (1939, 1942), who sought to create what would in the terminology of present-day systematic theorists be designated an 'Evolutionary' classification ('...it is desirable that there be

available a satisfactory arrangement of the species into some scheme of classification that can be taken as indicating their degree of genetic relationship' Sturtevant, 1939). Sturtevant recognized six subgenera, *Drosophila*, *Sophophora*, *Hirtodrosophila*, *Pholadoris*, *Dorsilopha* and *Phloridosa*. Sturtevant made some reference in constructing his classification to the work of Duda, who certainly described numerous species of Drosophilidae. However, several of the genera originally established by Duda (1923) are now regarded as not sufficiently different from *Drosophila* to warrant more than subgeneric rank, and Duda himself reduced many of his original genera to subgeneric status.

Since Sturtevant's work on subgeneric classification in *Drosophila* further new subgenera have been added for a small number of aberrant groups so that the total number of

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subgenera now recognized stands at at least nine (cf. Throckmorton, 1975). The validity of certain of the 'minor' subgenera is in dispute and it is likely that some may subsequently be consolidated with other subgenera in the course of any future thoroughgoing revision. Four subgenera, however, *Drosophila*, *Sophophora*, *Hirtodrosophila* and *Pholadoris* in Sturtevant's original designation, each contain a substantial number of species and are generally regarded as representing major bursts of speciation.

The subgenus variously termed *Scaptodrosophila*, *Paradrosophila*, *Pugiodrosophila*, *Xiphidiochaeta*, *Spuriostyloptera* and *Tanygastrella* (part) by Duda, and *Pholadoris* by Sturtevant, is probably the least well understood of the major *Drosophila* subgenera. This paper considers the status of this subgenus and the distributions and relationships of its members.

The number of species of *Scaptodrosophila* now described is close to 150. Table 1 lists species described to date which have been included in *Scaptodrosophila* or its synonyms by their authors, or which have proved on examination of their types to be *Scaptodrosophila*, or which, as far as may be determined from the published descriptions, should be included in this subgenus. The list of *Scaptodrosophila* species will certainly continue to grow; several further Australian species as yet undescribed are also known, and the number of species yet to be found on a world basis may be considerable. Given that intensive collecting of the type (based on the Australian experience) most likely to yield *Scaptodrosophila* species (see below) has not been carried out over much of Africa or south-east Asia and New Guinea — areas already known to harbour moderate numbers of *Scaptodrosophila* species — one is inclined to speculate that the latter areas may contain undetected, and possibly rather substantial, faunas.

As is evident from Table 1, the world distribution of *Scaptodrosophila* species is highly uneven: there are major faunas in the Ethiopian, Oriental and Australian biogeographic zones, while few species occur in the Palearctic, Nearctic and Neotropical zones. Throckmorton (1975) suggested tropical Asia as the region of origin of *Scaptodrosophila*,

with subsequent substantial expansions into Africa and Australia, and much smaller radiations into the remaining areas of the world.

Very little is known of the ecology of most species. Of the few species the life histories of which are known in any detail, Throckmorton (1975) reported feeding or breeding sites as including tree sap, palm sap, fungi, fruit and flowers. The flower-breeding species in particular occupy highly specialized habitats. Three species collected in, and probably breeding in, flowers (*aterrima*, *ebena* and *pseudoebenea*) have been reported from Africa, two are known from Australia (*anthemon* and a new species breeding in flowers of *Hibiscus splendens* and *H. heterophyllus*), and one (*scaptomyzoidea*) has been reported from south-east Asia (Okada, 1975). In addition to species which actually breed in flowers, a greater number has been collected by sweeping flowers of various plants under conditions of high humidity. The larvae of one species (*notha*) of Australia and New Guinea are known to gall the stems of the bracken *Pteridium aquilinum* (A. A. Kirk, personal communication). Larvae of another Australian species (*inornata*) have been recovered from eucalypt leaf litter in the crowns of tree ferns on which they were shown in laboratory studies to feed (S. Kuhnell, unpublished).

Many *Scaptodrosophila* species are known from single or a few localities only. Two species (*neozelandica* and *kirki*) are restricted to endemic forests of the North Island of New Zealand and are the only endemic *Drosophila* species of New Zealand (Harrison, 1959), a region famous for its depauperate flora and fauna (given the dependence of *Drosophila* species diversity on plant species diversity the lack of the former is not unexpected). Few *Scaptodrosophila* species are, in fact, widespread in occurrence, and none is included amongst the eight cosmopolitan species of the genus *Drosophila*. The apparently specialized ecological requirements of *Scaptodrosophila* species presumably explain their restricted occurrence since the cosmopolitans feed and breed in garbage. Interestingly, *bryani*, one of the more widespread *Scaptodrosophila* species, has apparently adapted to some extent to garbage

TABLE 1. Species described, or which should evidently be included, in *Scaptodrosophila*. Full references to original species descriptions are given in the catalogues of Wheeler (1959) and Wheeler & Hamilton (1972) except for species marked below with an asterisk; references for the original descriptions of these species are included in the bibliography accompanying this paper. Synonyms and replacement names in *Scaptodrosophila* are indicated in square brackets.

Species	Distribution
<i>adelphe</i> * Bock, 1976	Australia
<i>adyukru</i> Burla, 1954	Africa
<i>agamse</i> Burla, 1954	Africa
<i>akaju</i> Burla, 1954	Africa
<i>albifrontata</i> Malloch, 1934	Samoa
<i>albostrigata</i> Malloch, 1924	Australia
<i>altera</i> * Bock, 1976	Australia
<i>alternata</i> de Meijere, 1911	Java; Sumatra; Nepal
<i>angusta</i> de Meijere, 1915	Satellite Is.
<i>anthonom</i> * Bock, 1976	Australia
<i>anyi</i> Burla, 1954	Africa
<i>aterrima</i> Duda, 1940	Africa
[<i>austratica</i> Duda, 1923 = <i>obsoleta</i> ; Bock, 1976]	
[<i>baeomyia</i> Wheeler, 1949 = <i>latifasciaeformis</i> ; Wheeler, 1959]	
<i>bambuphila</i> Gupta, 1971	India
<i>bangi</i> Burla, 1954	Africa
<i>barkeri</i> * Bock, 1976	Australia
<i>baseogrisea</i> Duda, 1924	Sumatra
<i>bistriata</i> de Meijere, 1911	Java
<i>brooksae</i> Pipkin, 1961	U.S.A.
<i>brunnea</i> de meijere, 1911	Asia
<i>brunneipennis</i> Malloch, 1923	Australia
<i>bryani</i> Malloch, 1934	Samoa; Australia; southeast Asia
<i>caliginosa</i> Lamb, 1914	Africa; Seychelles
<i>cancellata</i> Mather, 1956	Australia
<i>chandraprabhiana</i> Gupta & Ray-Chaudhuri, 1970	India
<i>collessi</i> * Bock, 1976	Australia
<i>compressiceps</i> Duda, 1923	Taiwan
<i>concolor</i> * Bock, 1976	Australia
<i>convexa</i> Malloch, 1934	Samoa
<i>crocata</i> * Bock, 1976	Australia
<i>decipiens</i> Duda, 1923	Taiwan
<i>aestexa</i> Duda, 1924	Europe
<i>dibi</i> Burla, 1954	Africa
<i>dichromos</i> * Bock, 1976	Australia
<i>divergens</i> * (Duda, 1924b)	Taiwan
<i>dorsata</i> Duda, 1924a	Taiwan; Japan; Vietnam
<i>dorsocentralis</i> Okada, 1965	Japan
<i>ebenea</i> Graber, 1957	Africa
<i>ebonata</i> Parshad & Duggal, 1966	India
<i>ehrmanae</i> * Parsons & Bock, 1977	Australia
<i>eluta</i> Wheeler & Takada, 1964	Australia; Micronesia
<i>enigma</i> Malloch, 1927	Australia
<i>eoundo</i> * Tsacas & Chassagnard, 1976	Africa
<i>excepta</i> Malloch, 1934	Samoa
<i>exemplar</i> * Bock, 1976	Australia
<i>fimbriata</i> * Bock, 1976	Australia
<i>finitima</i> Lamb, 1914	Africa; Seychelles
<i>flavipes</i> (Harrison, 1954)	Samoa
<i>flavissima</i> Duda, 1929	Buru
<i>framire</i> Burla, 1954	Africa
<i>fumida</i> Mather, 1960	Australia
<i>fuscithorax</i> Malloch, 1924	Australia
<i>fuscopalpis</i> Wheeler & Takada, 1964	Micronesia
<i>fuscovittata</i> Harrison, 1954	Fiji; Samoa
<i>gauca</i> * Bock, 1976	Australia

Table 1. *Continued*

Species	Distribution
<i>grossfieldi</i> * Bock, 1976	Australia
[<i>guyenoti</i> Burla, 1948 = <i>deflexa</i> ; Herting, 1953]	
<i>hypopygialis</i> (Duda, 1924)	Sumatra
<i>inornata</i> Malloch, 1923	Australia
<i>insolita</i> * Bock, 1976	Australia
[<i>interrupta</i> (Duda, 1923) = <i>lativittata</i> ; Bock, 1976]	
<i>jacunda</i> Lamb, 1914	Seychelles
<i>kirki</i> Harrison, 1959	New Zealand
[<i>kitazawi</i> Okada, 1964 = <i>bryani</i> ; Okada, 1965]	
<i>kyushuensis</i> * Tsacas & Chassagnard, 1976	Japan
<i>lambi</i> Duda, 1940	Africa; Seychelles
<i>latifascia</i> de Meijere, 1914	Java
<i>latifasciaeformis</i> Duda, 1940	Africa; North and South America
<i>latifshahi</i> Gupta & Ray-Chaudhuri, 1970	India
<i>lativittata</i> Malloch, 1923	Australia
<i>lebanonensis</i> Wheeler, 1949 (2 subspp.)	Lebanon; Israel; U.S.A.
[<i>levis</i> Mather, 1955 = <i>bryani</i> ; Mather, 1957]	
<i>louisae</i> * Parsons & Bock, 1977	Australia
<i>lugens</i> Duda, 1926	Sumatra
<i>lurida</i> * Walker, 1860	Southeast Asia; New Guinea*
[<i>maculosa</i> : Mather, 1955 = <i>novamaculosa</i> ; Mather, 1956]	
<i>mania</i> * Bock, 1976	Australia
<i>marginata</i> Duda, 1924a	Nepal; Taiwan
<i>marjoryae</i> Harrison, 1954	Samoa; Tonga; Niue
<i>mbettie</i> Burla, 1954	Africa
<i>medleri</i> * Tsacas & Chassagnard, 1976	Africa
<i>megagenys</i> * Bock, 1976	Australia
<i>meijerei</i> Wheeler, 1959	Java; Sumatra; India
<i>metaxa</i> * Bock, 1976	Australia
<i>minima</i> Okada, 1966	Nepal; India
<i>minimeta</i> * Bock, 1976	Australia
<i>minnamurrae</i> * Bock, 1976	Australia
[<i>mirim</i> Dobzhansky & Pavan, 1943 = <i>latifasciaeformis</i> ; Wheeler, 1959]	
<i>moenae</i> Wheeler & Takada, 1964	Micronesia
<i>mokonfim</i> Burla, 1954	Africa
<i>momortica</i> Graber, 1957	Africa
<i>moronu</i> Burla, 1954	Africa
<i>mulgravei</i> * Bock, 1976	Australia
<i>multipunctata</i> (Duda, 1923)	Taiwan
<i>neozelandica</i> Harrison, 1959	New Zealand
<i>nicholsoni</i> Malloch, 1927	Australia
[<i>nigra</i> : de Meijere, 1911 = <i>meijerei</i> ; Wheeler, 1959]	
[<i>nigrocolor</i> : de Meijere, 1911 = <i>meijerei</i> ; Wheeler, 1959]	
<i>nigrifrons</i> Malloch, 1934	Samoa
<i>nigrofemorata</i> Duda, 1926	Sumatra
<i>nimia</i> * Bock, 1976	Australia
[<i>nitens</i> Buzzati, 1943 = <i>rufifrons</i> ; Herting, 1953]	
<i>nitidithorax</i> Malloch, 1927	Australia
<i>notha</i> * Bock, 1976	Australia
<i>novamaculosa</i> Mather, 1956	Australia
<i>novoguineensis</i> (Duda, 1923)	New Guinea; Australia
[<i>novopaca</i> Mather, 1956 = <i>subnitida</i> ; Bock, 1976]	
<i>nublada</i> Wheeler & Kambysellis, 1966	Samoa
<i>obsoleta</i> Malloch, 1923	Australia
<i>oncera</i> * Bock, 1976	Australia
[<i>opaca</i> : Mather, 1955 = <i>subnitida</i> ; Bock, 1976]	
<i>oralis</i> (Duda, 1923)	Taiwan
<i>palauana</i> Wheeler & Takada, 1964	Micronesia
<i>pallipes</i> Lamb, 1914	Seychelles
<i>parabrunnea</i> * Tsacas & Chassagnard, 1976	Java; Sumatra

Table 1. Continued

Species	Distribution
<i>paratriangulata</i> Gupta & Ray-Chaudhuri, 1970	India
<i>parsonsi</i> * Grossfield, 1976	Australia
<i>pattersoni</i> Pipkin, 1956	Lebanon
<i>pictipennis</i> Kertész, 1901	New Guinea; Australia
<i>pilicrus</i> Duda, 1926	Sumatra; Nepal
<i>pleurovittata</i> Harrison, 1954	Samoa
<i>pressobrunnea</i> * Tsacas & Chassagnard, 1976	Sumatra
<i>pseudoebenea</i> Graber, 1957	Africa
<i>pugionata</i> de Meijere, 1915	Satellite Is.; ?Africa
<i>pumilio</i> de Meijere, 1908	Java; Sumatra
<i>puncticeps</i> Okada, 1956	Japan; Korea
[<i>punctipennis</i> van de Wulp, 1886 = <i>lurida</i> ; Wheeler, 1969]	
<i>pusio</i> Duda, 1923	New Guinea
<i>quadriradiata</i> (Duda, 1923)	New Guinea; Java
<i>quadristriata</i> * (Duda, 1923)	New Guinea
<i>rhabdote</i> * Bock, 1976	Australia
<i>rhipister</i> * Bock, 1976	Australia
<i>rufifrons</i> Loew, 1873	Europe
<i>rufuloventer</i> Lamb, 1914	Africa; Seychelles
<i>saba</i> Burla, 1954	Africa
<i>samoensis</i> Harrison, 1954	Samoa
<i>scaptomyzoidea</i> * (Duda, 1923)	Southeast Asia; Australia
<i>scutellimargo</i> Duda, 1923	Taiwan
<i>scutellaris</i> Duda, 1929	Buru (Indonesia)
<i>senfo</i> Burla, 1954	Africa
<i>setifera</i> Wheeler & Takada, 1964	Micronesia
<i>silvalineata</i> Gupta & Ray-Chaudhuri, 1970	India
<i>simplex</i> de Meijere, 1914	Java; Taiwan
<i>sinape</i> * Bock, 1976	Australia
<i>specensis</i> * Bock, 1976	Australia
<i>stonei</i> Pipkin, 1956	Lebanon
<i>stramineipes</i> (Malloch, 1934)	Samoa
<i>strigifrons</i> de Meijere, 1914	Java
<i>subacuticornis</i> Duda, 1924a	Taiwan
<i>subtilis</i> Kikkawa & Peng, 1938	Japan
<i>sumatrensis</i> Duda, 1926	Sumatra
<i>sydneyensis</i> Malloch, 1927	Australia
<i>throckmortoni</i> * Okada, 1973	Japan
<i>triangulifer</i> Lamb, 1914	Africa; Seychelles
<i>triseta</i> de Meijere, 1911	Java; Sumatra
<i>uebe</i> Burla, 1954	Africa
<i>victoria</i> Sturtevant, 1942	N. America; ?S. America

breeding since it is common in northern Australia in suitable 'backyard' habitats (compost heaps, etc.), while two further Australian species (*enigma* and *lativittata*) appear to have increased their ranges within historical times in association with the establishment of orchards.

Presumably also because of their specialized ecological requirements, few *Scaptodrosophila* species (e.g. the Australian *inornata*) may be collected in quite substantial numbers, they have rarely been bred in the

laboratory and indeed are often difficult to keep alive. One exception to this generalization is the relatively small group of species feeding naturally on decaying fruits; such species are culturable with relative ease although if the larvae are not given sand in which to pupate the yield of adults is small.

The traditional method of collection of *Drosophila* species is by baiting with fermented fruits. Experience in Australia has shown that this method yields few *Scaptodrosophila* species; baiting with rotting edible

mushrooms is also successful to a limited extent in collection of *Scaptodrosophila* species, and frequently yields species not attracted to fruit, but the majority of species is not attracted to any known baits and has only been collected by sweeping foliage and leaf litter.

Subgenus *Scaptodrosophila* Duda

Scaptodrosophila Duda, 1923: 37. Type-species *Scaptodrosophila scaptomyzoidea* Duda, 1923, by monotypy; type locality New Guinea.

Paradrosophila Duda, 1923: 43. Type-species *Drosophila pictipennis* Kertész, 1901, by subsequent designation; type locality New Guinea.

• *Spuriostyloptera* Duda, 1923: 38, **syn.nov.**
Type-species *Spuriostyloptera multipunctata* Duda, 1923, by present designation; type locality Taiwan.

Pugiodrosophila Duda, 1924a: 203. Type-species *Drosophila pugionata* de Meijere, by monotypy; type locality Simalur, south-east Asia.

• *Tanygastrella* Duda, 1924b: 254, **syn.nov.**
Type-species *Tanygastrella hypopygialis* Duda, 1924, by present designation; type locality Sumatra.

Xiphidiochaeta Duda, 1925: 200. Improper replacement name for *Pugiodrosophila*.

Pholadoris Sturtevant, 1942: 28. Type-species *Drosophila victoria* Sturtevant, by original designation; type locality U.S.A.

The subgenus *Pholadoris* was established by Sturtevant (1942) with the following diagnostic features: 'shining dark species; prescutellars present; a V-shaped shining bristle-bearing area on front; egg filaments 6-8; posterior Malpighian tubes apposed at distal ends; testis short, not coiled; ventral receptacle short, not coiled or kinky; skipping larvae.' Sturtevant included only two described species in this subgenus at the time of its establishment (*coracina* Kikkawa and Peng from Japan and *victoria* Sturtevant from U.S.A.) but indicated that several undescribed species were also included. Of the external diagnostic characters listed for this subgenus by Sturtevant, the most conspicuous is the presence of a pair of hypertrophied pre-

scutellar acrostichal bristles (i.e., the 'pre-scutellar bristles') between the posterior dorsocentrals and just anterior to the scutellar margin; this feature is otherwise absent in members of the subfamily Drosophilinae although it is characteristic of the stenanine genera (*Stegana*, *Leucophenga*, *Amiota*, *Cacoxenus*, etc.). As discussed further below, other characters not listed by Sturtevant are also diagnostic of members of this subgenus while some of those originally included now seem of lesser importance.

Prior to Sturtevant's work, Duda had described numbers of Oriental and a few Australian drosophilid species with pre-scutellar bristles. Many of these species clearly fall within the limits of the genus *Drosophila* as it is now recognized, but Duda's original conception of generic limits and the criteria on which new genera should be erected differed from those of all other workers, at least in the field of drosophilid taxonomy. In particular, Duda frequently separated into different genera species differing by only one or a few minor characters. A rather extensive multiplicity of drosophilid genera (later reduced to subgenera) was consequently created by Duda, and the problems faced by later taxonomists in revising his works were complicated by the fact that he neither defined and summarized the diagnostic features of new genera as he established them nor designated type-species, but merely introduced a new generic name in combination with a specific name in the description of a new species.

Duda (1923) introduced the generic name *Scaptodrosophila* for a single male of a new New Guinea species, *S.scaptomyzoidea* (further specimens of this species have subsequently been found in Micronesia, south-east Asia and Australia: Wheeler & Takada, 1964; Okada, 1975; Bock, 1976). Only one further species was described by Duda in this genus, *Scaptodrosophila divergens* (Duda, 1924b) from Taiwan (this species apparently awaits rediscovery). Apart from well-developed pre-scutellar bristles, the species were characterized by high costal indices and weak anal veins (costal index = ratio of second to third costal sections of wing).

Later in the same paper in which *Scaptodrosophila* was established, Duda described

a number of species under the generic name *Paradrosophila*. The original rationale for separating *Scaptodrosophila* and *Paradrosophila* at the generic level was apparently (although never explicitly stated by Duda) the lower costal indices and stronger anal veins of species of the latter; the *Paradrosophila* species were also characterized by prescutellar bristles. *Paradrosophila* was included in Duda's key to subgenera of *Drosophila* (Duda, 1924a), and it became evident to Duda later (1926) that generic or subgeneric separation of *Scaptodrosophila* and *Paradrosophila* was questionable on the basis of such minor differences as those emphasized above. Duda was evidently forced to this conclusion by the large number of species he had by then examined and the integrations between the *Scaptodrosophila* and *Paradrosophila* extremes. *Scaptodrosophila scaptomyzoidea* was included in a key to Sumatran species under the heading *Paradrosophila* (Duda, 1926), although Duda never published a formal statement that he considered the two taxa to be identical. *Scaptodrosophila*, however, has priority within the paper in which the two genera were initially established, and is now considered the senior synonym (Bock, 1976).

It is clear that the species variously referred to by Duda as *Scaptodrosophila* or *Paradrosophila*, and those by Sturtevant as *Phaladoris*, are members of the same basic radiation (cf. Throckmorton, 1975). The principal feature of these species emphasized by both authors is the presence of a pair of prescutellar bristles, a character as noted above not found in other members of the genus *Drosophila*. Duda (1924a) subsequently established yet another subgenus for a single species with this character, *Drosophila (Pugiodrosophila) pugionata* de Meijere, because this species possessed unusually long proclinate orbital bristles and the anterior reclinate orbitals were unusually close to the posterior reclinate orbitals. Apart from the fact that such minor characters hardly seem sufficient to warrant subgeneric separation, the feature emphasized by Duda as sufficient to warrant creation of a new subgenus is a sexual dimorphism peculiar to males; females of *D. pugionata* possess the 'normal' unhyper-trophied proclinate orbital bristles and are

quite undistinguished from other species of *Scaptodrosophila*, or for that matter of the genus *Drosophila*, in this respect. *Pugiodrosophila* (together with its improperly substituted replacement name *Xiphidiochaeta* Duda, 1925) were synonymized with *Scaptodrosophila* by Wheeler & Takada (1964).

Duda (1923) established a further genus, *Spuriostyloptera*, for two species with prescutellar bristles, *S. multipunctata* (Taiwan) and *S. quadristriata* (New Guinea). Both of these species possess a relatively deep distal costal incision with blackening of the costa immediately before the incision and therefore resemble *Mycodrosophila* species in this respect, although Duda noted that they otherwise resembled *Paradrosophila*. Examination of Duda's specimens has revealed that they are clearly members of the subgenus *Scaptodrosophila* as the group is now understood. They are atypical only with respect to the above-mentioned usually deep distal costal incision and blackening, which resembles that occurring in *Mycodrosophila* species although the development of this character in the latter is considerably greater.

Finally, Duda (1924b) introduced the generic name *Tanygastrella* for two further species from Java and Sumatra, viz, *T. gracilis* and *T. hypopygialis*. The feature Duda then regarded as of sufficient importance to warrant erection of a new genus was that the abdomens of these species are unusually narrow; he later remarked (Duda, 1926) that *Tanygastrella* was worthy of 'at the most' subgeneric rank. The former species, renamed *Drosophila eugracilis* (Bock & Wheeler, 1972) because 'gracilis' was preoccupied in the genus, is known to be widespread in south-east Asia and neighbouring areas and is a member of the *melanogaster* species group. (The narrow abdomen noted by Duda is a further sexual dimorphism restricted to males.) The latter species, *hypopygialis*, is evidently unknown apart from the three original specimens (in Amsterdam) on which the description was based, but examination of the holotype has revealed that the species is clearly a *Scaptodrosophila*. One of the original *Tanygastrella* species is therefore a member of the subgenus *Sophophora* while the other is a member of the subgenus *Scaptodrosophila*.

Subgeneric diagnosis

Species of the genus *Drosophila* are divided into subgenera on the basis of variations with respect to a number of presumably rather fundamental characteristics, mostly of external morphology although some internal features have also been used.

Most of the species now included in *Scaptodrosophila* are distinguished by possession of three principal features: a pair of large prescutellar bristles; a tiny propleural bristle (at the base of each foreleg); and three large subequal sternopleural bristles. All of these features are unique to members of this subgenus, and are discussed in more detail under the appropriate headings below together with other features of diagnostic or other significance.

Head

The second oral bristle is large in *Drosophila* and *Sophophora* but small in *Hirtodrosophila* and *Scaptodrosophila*. (It is also small in the members of most other drosophilid genera.) In the subgenus *Scaptodrosophila* there appear to be very few exceptions to this generalization; Duda (1923) described one species, *oralis* (from Taiwan) which possesses about six strong oral bristles (vibrissae) but this species must be regarded as highly aberrant.

Sturtevant included the character 'V-shaped shining bristle-bearing area on front' as typical of members of the subgenus. Many times the original number of species known to Sturtevant have now been discovered and the character still appears to be quite general with the exception of the 'shining'; many species possess microchaetae over a wide area of the front.

The carina is highly variable, ranging from a mere vestige (*inornata* species group) to exceedingly large (e.g. *brunneipennis*) and including all intermediate stages.

The arista is probably more variable within *Scaptodrosophila* than within any of the other subgenera. At one extreme is *nicholsoni*, the arista of which consists only of the axis plus one long dorsal branch; at the opposite extreme are several species (e.g. *brunnea*)

with large multibranching aristae. Between these extremes are species with large aristae containing few branches, and small aristae containing few or more numerous short rays.

Thorax

The prescutellar bristles range in size from conspicuously large — as large as the anterior dorsocentrals — to very small, i.e. barely distinguishable from acrostichal hairs. Typically, the prescutellars are about half the length of the anterior dorsocentrals or longer.

While most *Scaptodrosophila* species possess a pair of propleural bristles, this feature is not invariably present. The size of the bristle when present is always quite small compared to the other major thoracic bristles, being about the width of an acrostichal hair but usually longer. Typically, the propleural bristle is larger in the larger species and smaller in the smaller species. All members of the Australian *inornata* species group (*q.v.*) lack propleural bristles.

In members of all four of the major subgenera, *Drosophila*, *Sophophora*, *Hirtodrosophila* and *Scaptodrosophila*, the posterior sternopleural bristle is large. In *Drosophila*, *Sophophora* and *Scaptodrosophila* the anterior sternopleural is also usually large, although larger in *Scaptodrosophila* than in *Drosophila* or *Sophophora*. In *Scaptodrosophila* only, the middle sternopleural is also generally large, i.e. almost as large as the other two sternopleurals. The arrangement of these three bristles is also slightly different in most *Scaptodrosophila* species compared to those of the other subgenera in that the middle sternopleural is often almost directly above the posterior one (hence sometimes termed 'upper' rather than 'middle' sternopleural, although the former term is not consistent with the terminology applicable to species of the other subgenera). In a few *Scaptodrosophila* species, however, (e.g. *eluta*), the anterior and middle sternopleurals are considerably smaller than the posterior one, and in several other species (e.g. *albostrigata* and *fumida*) the middle sternopleural is minute (cf. members of the steganine genera) while the anterior and posterior ones are large.

The anterior scutellar bristles are long and divergent in most *Scaptodrosophila* species. In only a few species the anterior scutellars are short (e.g. *bryani*) or convergent, and in members of the other subgenera they are generally convergent.

Wing indices are highly variable in *Scaptodrosophila*. The costal index (ratio of second to third costal sections) ranges from about 1.0 to greater than 4.

Abdomen

Abdominal coloration and pattern varies widely in the subgenus. In some species the abdomens are of uniform coloration. In others the tergites possess uninterrupted posterior bands, while yet others have tergites with bands interrupted in the midline. (Examples of species amongst the Australian fauna in all of the above categories are given in Bock, 1976.) The type of abdominal banding is generally given in the case of subgenera *Drosophila* and *Sophophora* as diagnostic at the subgeneric level (bands continuous in *Sophophora*, usually interrupted in *Drosophila*), and this raises the question of the degree of heterogeneity of *Scaptodrosophila* if the banding pattern is otherwise reliable in separating two subgenera, although in the case of the subgenus *Drosophila* there are certainly at least a few species (*rubida*, *sulfurigeraster*) with continuous abdominal bands closely related to others (in the *immigrans* species group) having interrupted bands.

General coloration

Sturtevant's original diagnosis 'shining dark species' can no longer be regarded as valid. Body colour is widely variable, ranging from pale yellow species to shiny black species and including various intermediates, patterned and unpatterned. Many species are of uniform or near-uniform coloration, others are spotted or striped. Two species, *fumida* and *pictipennis*, possess patterned wings, a character not otherwise present in *Scaptodrosophila* although many other species of the genus have marked wing patterning (cf. the Hawaiian species). Several *Scaptodrosophila* species,

however, possess wings with a general brownish tinge.

Internal morphology and larvae

The several internal characters listed by Sturtevant as diagnostic of *Scaptodrosophila* cannot now be regarded as reliable in the absence of further work: far too few of the known species — fewer than 5% — have been examined for internal anatomy. Few species have been bred in the laboratory. Thus while more than four egg filaments are usually stated to be characteristic of *Scaptodrosophila* species, the character should be regarded with caution. The eggs of a recently discovered new Australian species breeding in the flowers of endemic *Hibiscus* species lack egg filaments. Similarly, the larvae of *Scaptodrosophila* species are also usually stated to 'skip' (that is, to be capable of jumping or springing movements after coiling their bodies into semi-loops) but the universality of this characteristic is a long way from demonstration. The habit does, however, suggest the possibility of separate larval and pupation sites; in laboratory cultures where the larvae are given the opportunity to pupate in sand outside the culture bottle they usually leave the bottle and bury in the sand before pupation. Regrettably, little ecological information is available about most species.

In summary, most species included in *Scaptodrosophila* possess the three principal distinguishing features of clearly differentiated prescutellar bristles, propleural bristles, and three large subequal sternopleurals; other features common to members of the subgenus are also shared by members of one or more other subgenera, or are more widely variable within *Scaptodrosophila*. A few species retained in *Scaptodrosophila* lack one or even two of the three main diagnostic characters; the aberrant species are included in the subgenus as they appear to be merely offshoots of the main *Scaptodrosophila* radiations. One is reluctant to characterize any taxon by a series of 'usualies', but in the present case there seems no escape from diagnosing *Scaptodrosophila* species as 'usually' possessing prescutellars, propleurals and three large subequal sternopleurals.

Species groupings

The recognition of distinct phylogenetic lineages (species groups) within the subgenus *Scaptodrosophila* is substantially hindered by the fact that knowledge of many of the species is very fragmentary; nevertheless it is possible to discern several rather discrete groups of species and these are considered below.

1. *The victorta species group*. Reviewed by Pipkin (1961), the group includes six species (*victoria*, *brooksae*, *pattersoni*, *stonei*, *lebanonensis* and *rufifrons*) of Palaearctic and Nearctic distribution; the species are difficult to collect by baiting. Two subspecies of *D. lebanonensis* have been recognized, the nominate occurring in Lebanon and Israel, and *D. lebanonensis casteeli* occurring in the western United States. It is probable that *D. throckmortoni*, a Japanese species closely resembling *D. rufifrons*, should also be included in this group.

2. *The inornata species group*. Discussed in greater detail by Parsons & Bock (1978), the *inornata* group comprises seven species (*inornata*, *rhabdote*, *obsoleta*, *grossfieldi*, *collessi*, *nicholsoni* and *fuscithorax*) of southern and, in the case of *obsoleta*, upland regions of northern Australia. Morphologically, members of the group are quite distinctive and are characterized by reduced arista (axis plus one dorsal ray only in *nicholsoni*), vestigial carina, absence of propleural bristle and weakly developed prescutellars. Members of the group have been collected in large numbers in southern Australian forests and sedge habitats but have very rarely been found at baits.

3. *The brunnea species group*. The *brunnea* group was established by Tsacas & Chassagnard (1976) to include seven species (*brunnea*, *parabrunnea*, *pressobrunnea*, *kyushuensis* and *scutellimargo* in the *brunnea* subgroup, and *eoundo* and *medleri* in the *eoundo* subgroup) of Asian and African distribution. To this group may be added the Australian *rhipister* which is clearly closely allied to members of the *brunnea* complex. Several of the *brunnea* group species are extremely similar morphology; thus by detailed examination of male genitalia, Tsacas and Chassagnard were able to separate three

species (*brunnea*, *parabrunnea* and *pressobrunnea*) from the series considered to represent one species only (*brunnea*) by de Meijere.

4. *The coracina species group*. The *coracina* group was established by Mather (1955) to include the Japanese *coracina* and the Australian *cancellata*, *enigma*, *lativittata* and *subnitida*. Three other Australian species, *novamaculosa*, *nitidithorax* and *spencensis*, with male genitalia very similar to those of the preceding species, are quite obviously members of the same group. All of these species are attracted to fermented fruit baits – an exceptional situation within the subgenus as noted above. At least two of the Australian species (*enigma* and *lativittata*) appear to have extended their ranges within historical times (i.e. within the last hundred years) in association with the establishment of orchards.

5. *The barkeri species group, new group*. Bock (1976) described seven Australian species (*barkeri*, *exemplar*, *minnamurrae*, *sinape*, *concolor*, *mulgravei* and *nimia*) all distinguished by plain brown or yellowish coloration and lack of fully developed claspers in the male external genitalia; a further species (*louisae*) with similar characteristics was added by Parsons & Bock (1977). These eight species comprise a group that has evolved in eastern Australia; no Asian relatives are known. Several of the species are restricted to southeastern Australia, while others are northern. None has been collected by baiting with the exception of a single individual of *D. concolor* found in Townsville, northern Australia (Bock, 1978). Individuals of *D. barkeri* and *D. louisae* have been collected in moderate numbers in southeastern Australia by sweeping.

6. *The brunneipennis species group, new group*. Bock (1976) described three large Australian species (*brunneipennis*, *notha* and *adelphe*) with brownish wings and very large carinas. A fourth similar species (*ehrmannae*) was described by Parsons & Bock (1977). These four species comprise a group the members of which are known from southeastern Australia and, in the case of *D. notha*, from New Guinea. As discussed above, larvae of the latter species are known to gall the stems of bracken.

The species included in the above six groups represent a total of 42, or 29% of the 144 species listed in Table 1. At various times, reference has been made to other monotypic 'species groups' in *Scaptodrosophila*, but it is arguable whether anything is gained by such designations. Many of the remaining species are in fact (at least in external morphology) quite distinctive and not obviously related closely enough to any other species to permit recognition of species groups consisting of several members. Until sufficient additional information (on external morphology, ecology, distributions, polytene chromosomal relationships, etc.) is gained to permit a clearer insight into intraspecific relationships amongst the latter species, it seems preferable to defer further groupings.

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