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PSYCHODIDAE (DIPTERA, NEMATOCERA) OF THE SUBANTARCTIC ISLANDS, WITH OBSERVATIONS ON THE INCIDENCE OF PARTHENOGENESIS

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Abstract. Adults of *Psychoda* are small, fragile, weak-flying Diptera that seem ill-adapted to life on subantarctic islands; but 2 fully-winged forms, *surcoufi* and *parthenogenetica*, are established there. Of these, *parthenogenetica* is the most widespread subantarctic dipteran, being known from 5 of the 6 islands that can, by strict climatic definition, be included in this group, and being absent only from the coldest, Heard I. It is suggested that the survival of *Psychoda* in the subantarctic would greatly depend upon its cryptic behavior, and that success or failure also depends upon low temperature-thresholds of development and other physiological attributes. In addition, the wide distribution of *parthenogenetica* is especially related to its parthenogenesis, a phenomenon which appears to be disproportionately common among free-living subantarctic insects: M.J.D. White estimates that bisexual genetic systems in animals may outnumber parthenogenetic systems by over a thousand to one, but on subantarctic islands the incidence of parthenogenesis among free-living insects may be as high as 15% (South Georgia), 13% (Macquarie), and 10.7% (Kerguelen). All but one of the forms involved are Diptera Nematocera.

As a consequence of rigorous climatic conditions and the screening effect on potential immigrants of the vast expanses of the southern oceans, subantarctic islands have extremely limited biotas and simple ecosystems and food webs: a few forms may abound, but most habitats are relatively unexploited and many niches are vacant (Gressitt 1970). Diptera are the predominant free-living pterygotes and, as in Coleoptera (Gressitt 1961), groups of Diptera that inhabit plant debris should be among those that are especially successful on such islands. The larvae of many Psychodidae have this habit, especially in *Psychoda*. In this paper I discuss the distribution of *Psychoda* in the subantarctic in relation to behavioral and physiological attributes and briefly compare the fauna with that of warmer islands. The *Psychoda* species involved are *parthenogenetica* Tonnoir, present on almost all subantarctic islands, and *alternata* Say and *surcoufi* Tonnoir, found on Macquarie alone.

The islands classified by Wace (1965) as subantarctic are in a zone whose northern boundary is formed by the southernmost limit of trees and woody shrubs, and whose

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southern boundary is formed by the southern limit of closed phanerogamic communities. These islands are the Crozets, Marion, Macquarie, Kerguelen, South Georgia and Heard, between 46° and 55°S latitude (Fig. 1), on which the mean temperature of the warmest month is less than 8.5 °C. According to Wace (1969: 220), they are characterized by "cool wet isothermal climates . . . and almost continuous and strong westerly winds."

Table 1, constructed from data in Gressitt (1970), shows that, excluding Collembola, Mallophaga, Anoplura and Siphonaptera, the number of insect species known from the islands ranges from 38 on the Crozets to 9 on Heard, this variation being correlated with the severity of the climate, as determined by position relative to the Antarctic Convergence (Gressitt 1970). Heard's very small fauna, the only one in this zone that does not include psychodids, is related to its more southerly position, exceptionally rigorous conditions, and high degree of ice cover. Macquarie, $\frac{1}{3}$ the size, lower and even further south, but still actually north of the Convergence and thus considerably warmer, has $2.6\times$ the number of species. The largest fauna is on the Crozets, which are warmest.

Among subantarctic insects, a high proportion of pterygotes are secondarily flightless, their wings being more or less reduced, sometimes to structures little larger than halteres. As Gressitt (1970: 362) points out, most flightless subantarctic Diptera also show behavioral adaptations, often with halteres, antennae, and eyes reduced, as well as wings. Such features occur in diverse unrelated genera and represent adaptations to special conditions on the islands, perhaps primarily low temperatures and exceptional windiness, both of which severely limit the opportunities for flight. In total, 42% of subantarctic Diptera are flightless (Gressitt 1970: Table 11), but the psychodids show no sign of wing reduction or other differences from mainland populations. Two flightless, brachypterous species, *Psychoda acutipennis* Tonnoir and *P. brachyptera* Quate, do, however, occur on some other cold and exposed islands in the southern oceans (Campbell, Bounty, Antipodes). That no such species are known from the subantarctic suggests that populations of any psychodid capable of giving rise to a brachypterous form have been short-lived. *Psychoda parthenogenetica* may have the physiological but not the genetic capacity to persist (see below), and most other common species in likely southern source areas would be more warm-adapted than *parthenogenetica* and thus excluded from the subantarctic.

BIOLOGY OF *PSYCHODA*

Larvae of most *Psychoda* feed at lower trophic levels in diverse decomposing plant materials and dung. Such materials abound on the islands, so there seems to be no reason why larvae that can develop at low temperatures should not thrive in a subantarctic environment. On the other hand, adult *Psychoda* are small, fragile, weak-flying insects that at first sight seem ill-adapted to the tempestuous conditions of subantarctic life. However, they are also short-legged and fold the wings over the abdomen in a tectiform position. This enables them to avoid boisterous conditions

TABLE 1. Data for climate and insects of subantarctic islands, extracted from Gressitt (1970: Tables 1, 7, 11). Collembola, Mallophaga, Anoplura, and Siphonaptera are excluded. Islands ordered according to mean monthly temperatures, which correspond in general with degrees of exposure and environmental rigor.

	RANGE OF MEAN MONTHLY TEMPS. (°C)		NO. OF INSECT SPP.	SECONDARY WING REDUCTION OR LOSS IN GROUPS THAT ARE NORMALLY WINGED (%)
	MIN.	MAX.		
Crozets	3	8+	38	87
Marion	3	7.9	19	84
Macquarie	3	7	23	47.8
Kerguelen	2	7.8	28	78.6
S Georgia	-3	+6	20	60
Heard	-2	+4	9	100

by sheltering in tiny crevices that would be impenetrable if the wings were held horizontally, as they are in many psychodids (Duckhouse 1966). Recently I have observed that in some *Psychoda*, including *penicillata* Satchell, the fly achieves maximum cover by *backing* into its shelter with a shuffling motion, so that the narrow end of the body goes into the deepest, and often narrowest, part of the crevice. It thus penetrates further than if it had entered head first. Moreover, as a result of this behavior the fly's eyes and antennae face outwards, and if disturbed it can emerge and take flight with great rapidity. Small size may also be adaptive to this habit (Duckhouse 1978), but, as graphically shown by Darlington (1937), the dislodging effect of wind is proportionate to the ratio of surface area to weight, and hence much greater for a smaller animal. Presumably this dislodging effect would be increased further by a covering of long hair, as in *Psychoda*, so it is likely that the survival of this genus in the subantarctic would greatly depend upon its cryptic behavior.

DISPERSAL OF PSYCHODIDAE

In discussing the psychodids of Micronesia, Quate (1958) concludes that some forms may have reached the islands as a result of human activity, including the transport of fruits and vegetables on ships. He adds that other means of dispersal cannot be discounted and mentions the study of aerial plankton by Glick (1957), who caught a female *Psychoda alternata* at 305 m over Texas, USA. Hardy & Milne (1938) also trapped *Psychoda phalaenoides* L. at 76–107 m over Hull, U.K., while unidentified psychodids have been recorded in aerial plankton collected over land by Glick (1939) and White (1970), and at sea by Yoshimoto et al. (1962) and Yoshimoto & Gressitt (1963).

Psychoda is represented by a substantial fauna of apparent endemics on many remote islands. On such islands it is usually the dominant genus of Psychodidae, and I believe that both this fact and the high degree of sympatry seen in continental areas are directly related to its capacity for aerial dispersal.

OCCURRENCE OF *PSYCHODA ALTERNATA* ON MACQUARIE

Psychoda alternata has a virtually cosmopolitan distribution. It also has unspecialized breeding habits, being recorded from freshwater mudflats, fig compost, decaying vegetables, piles of seaweed in the littoral zone, and a wide range of more or less foul places including bacteria beds of sewage purification works, drains, septic tanks, and manure heaps. On all subantarctic islands, seal wallows and other apparently suitable breeding places occur, so that at first sight the presence of this species on Macquarie, recorded by Quate (1962) as a single male from *Pleurophyllum* litter at Hasselborough Bay, would not be surprising. But it is unknown from any other subantarctic island, and even from the somewhat warmer islands of Auckland or Campbell. Watson (1967) lists it with species that are "probably not established residents" of Macquarie. Gressitt (1970) omits it from his list of subantarctic arthropods, and *alternata* is indeed unlikely to breed in the subantarctic under natural conditions: Lloyd (1937) found that the fully favorable temperature range for all stages is about 16–25 °C. He showed that effective mating occurs infrequently at 5 °C but that mating and egg laying are normal at 8 °C. However, few eggs hatched at 7–8 °C, and even when they were transferred after 10 days to a more favorable temperature, the egg mortality was very great. Moreover, young larvae at 7.5 °C usually died: only 1 brood in 8 survived the early larval stage at this temperature, producing just 5 male flies, and even at 8–9 °C there was heavy juvenile mortality. Compare this with the range of mean monthly temperatures on Macquarie, which is 3–7 °C (Gressitt 1970), and with Law & Burstall's (1956) observation that the highest recorded temperature is 11.5 °C. Thus, unless such physiological characteristics vary, the island is too cool for *alternata*. Possibly Quate's specimen came from the nearby research station, where breeding could have occurred under warmer conditions, or it may have fallen into the collection during sorting in a warmer climate.

BIOLOGY OF *PSYCHODA SURCOUFI*

Duckhouse (1966) shows that *P. surcoufi* occurs in New Zealand and southern Australia (as *spatulata* Satchell) and in southern South America (as *subimmaculata* Tonnoir). In the subantarctic it is only known from Macquarie. However, since it also occurs on Campbell and Antipodes (Quate 1964, as *spatulata*) and the Aucklands (Duckhouse 1971), it appears to have some capacity for life on cold and exposed islands.

Satchell (1947a) reared *surcoufi* from cow dung but found that in the laboratory it also bred readily on decaying leaves, decaying hay, and *Phormidium*. In Australia I have reared it from such materials as cow dung, compost heaps, and soggy decomposing leaves and inflorescences held between the branches of a Californian Laurel (*Umbellularia californica*). Thus, it has varied breeding habits that should facilitate colonization and aid dispersal through the agency of man.

Unfortunately, except for Satchell's (1947b) observation that in *surcoufi* the life-

cycle at 20 °C is completed in 15 days, there are no physiological data for this species. However, it appears to be more cool adapted than *alternata*. In Australia, both species occur in the south but *alternata* alone is recorded from the tropics, where it abounds. Similarly, *alternata* is common on many subtropical and tropical islands, while *surcoufi* has only been recorded from St Helena (Duckhouse 1976). Watson (1967) says that on Macquarie, *surcoufi* occurs in grassland and herbfield from the coast to 600 ft [183 m], keeping to the ground on cold and windy days under *Stilbocarpa* and in tussocks of *Poa*.

BIOLOGY OF *PSYCHODA PARTHENOGENETICA*

This form was described as a subspecies of *Psychoda severini* Tonnoir by Tonnoir (1940) but regarded as a separate species by Duckhouse (1962). Salamanna (1975) later maintained that *parthenogenetica* was a form of *severini*, mainly on the grounds that Sará (1950) and he could find no morphological differences and that he himself had taken male *severini* in early spring from a place where only females had been collected previously. He does not say how he excludes the possibility that the same habitat was colonized separately, by *parthenogenetica* first and later by *severini*. Salamanna also considers that the laboratory observations of Mirouse (1942), who observed only females over 5 generations, provide insufficient grounds for concluding that *parthenogenetica* is thelytokous (obligatorily parthenogenetic). But Lloyd (1937) noted, after a long series of field observations and laboratory experiments including the full range of temperatures which this species can survive, that he had found no males "in nature or in culture." Tonnoir (1940) also failed to produce males experimentally, and I have collected none in the Southern Hemisphere. Such forms are often polyploid. Indeed, White (1973) notes that 7 of the 12 thelytokous Diptera that have been studied cytologically are triploids. More recently, Troiano (1978) has shown that *parthenogenetica* from Italy is also triploid, and thus incapable of bisexual reproduction.

Whether *parthenogenetica* is a separate species or a form or biotype of *severini* is a philosophical rather than an experimentally determinable question, but in order to avoid using the same name for a form so distinct in biology and distribution I shall continue to regard it as a separate species. The lack of morphological differences between *severini* and *parthenogenetica* claimed by Sará and Salamanna would not really affect the issue because many otherwise distinctive *Psychoda* species have females that are virtually inseparable.

Overall, *parthenogenetica* is not cosmopolitan as described by Satchell (1950b), Salamanna (1980), and others, but is restricted in Europe, Africa, Japan, Australia, and New Zealand to beyond latitude 33°, north and south. Wagner (1982) lists a single female from Karst Spring in the Ghab rift valley, Syria, but until checked this should be regarded as a dubious record. Vaillant & Botosaneanu (1966) say it also occurs in Brazil, but they give no details and there are no other records for the tropics or

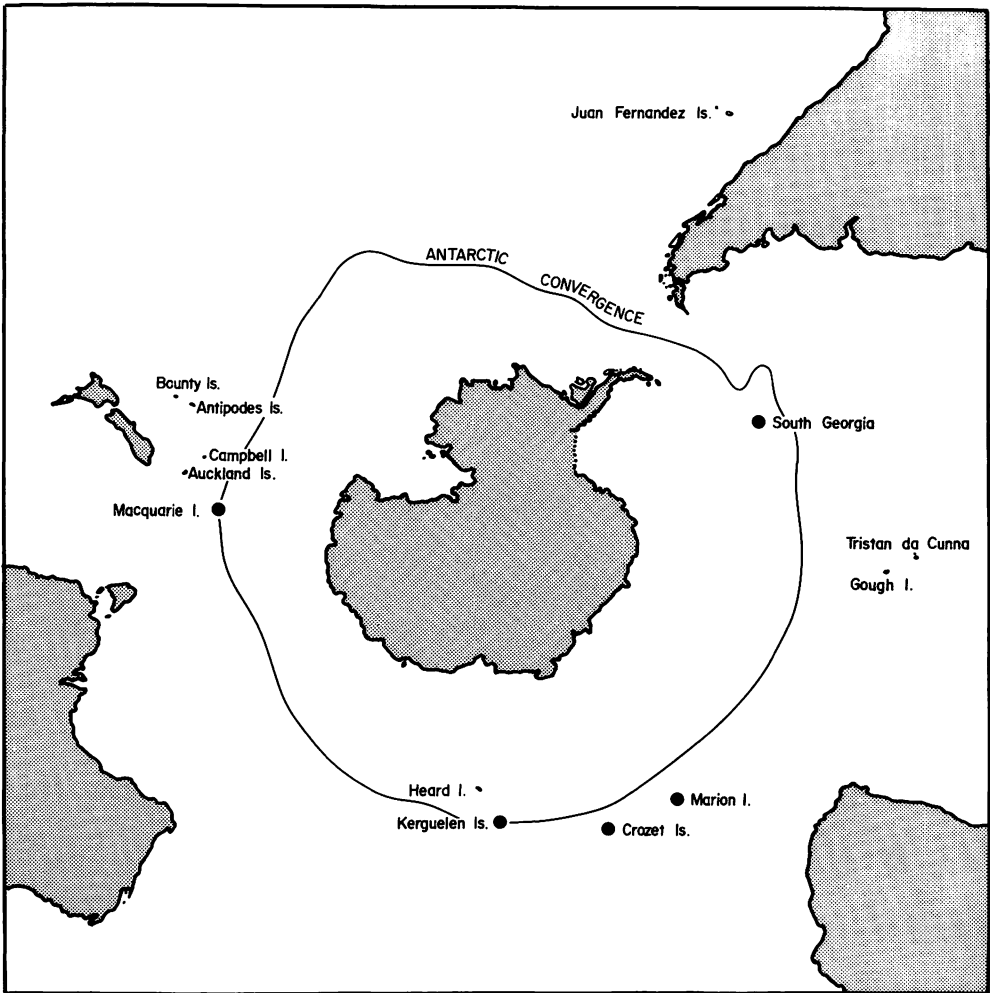


FIG. 1. Distribution of *Psychoda parthenogenetica* in the subantarctic: islands on which it occurs are indicated by closed circles.

subtropics. If it does occur in the tropics, I would expect that it is at high altitudes. Despite much collecting, the only islands where *parthenogenetica* has been found are Juan Fernandez (Satchell 1952), the Azores (Nielsen 1964), Campbell (Quate 1964, as *severini*), possibly Gough I (Holdgate 1965, as *severini*), and 5 of the subantarctic islands (Fig. 1). It is thus extraordinarily well represented in the subantarctic, but as yet unknown from the Arctic or subarctic. Vaillant & Joost (1983) say that it occurs "on the Antarctic Continent"; however, they give no details, and in view of the reproductive physiology of this species, it does not seem possible, unless in heated

buildings. Rounsevell (1979) earlier recorded an unidentified psychodid from a botanical collection made in Antarctica but presumed that it was a contaminant.

Arranged in order of progressively less harsh conditions, the subantarctic islands from which *parthenogenetica* has been collected are South Georgia (Duckhouse 1970), Kerguelen (Womersley 1937), Macquarie (Quate 1962, as *severini*; Watson 1967), Crozets (Duckhouse 1971, see Appendix) and Marion (Séguy 1971, as "*Pericoma* sp."²). It is absent from Heard, coldest and most ice-bound of the islands—possibly because the prevailing temperatures fall below what Lloyd (1937) describes as its "fully-favourable temperature zone" (6–20 °C). On South Georgia it must be close to its physiological limits.

Quate's records of *severini* for Macquarie should be read as *parthenogenetica* because his 38 specimens were all female, and those from Macquarie that I saw were also female. Moreover, Quate was accustomed to refer loosely to this taxon as *severini* [see, for example, his (1964) reference to Satchell's (1950) record for *parthenogenetica* in New Zealand as "*severini*"].

Psychoda parthenogenetica is particularly successful as a subantarctic insect, having a higher rate of colonization than any other dipteran. It is recorded from 5 of the 6 subantarctic islands. The next commonest dipterans are the ephyrid *Amalopteryx maritima* Eaton on Heard, Kerguelen, and Crozets³ and the coelopid *Apetaenus litoralis* Eaton on Marion, Kerguelen, and Crozets. However, the ephyrid occurs on Heard, the coldest of the islands, while *parthenogenetica* does not. Moreover, the ephyrid and the coelopid have strongly reduced wings and each occurs on a group of "adjacent" islands, so their more restricted distributions could be regarded as evidence of a degree of success in avoiding being swept away rather than the result of poorer adaptation to subantarctic conditions. Gressitt (1964: 572–76) shows that in strong and sudden winds, large numbers of insects may be caught up and carried over the water. There are no observations on the flying behavior of *parthenogenetica* in the subantarctic, but it is probably similar to that of *surcoufi*.

Apart from statistics of presence and absence, it appears that *Apetaenus litoralis* and *Amalopteryx maritima* are endemic to the subantarctic islands and have been on them long enough to have evolved their peculiar characteristics. The lack of recognizable peculiarities in subantarctic *parthenogenetica* is not evidence for recent immigration, because this form would have a severely limited capacity for evolutionary change. Nevertheless, it is also as a consequence of their limited capacity to evolve and adapt that thelytokous forms probably always persist for a relatively short time.

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2. Séguy's specimens of *parthenogenetica*, which I have examined, were identified as *Pericoma* sp. (Séguy 1971). In the same paper Séguy also recorded *Clogmia albipunctata* (Williston) from Marion, but in view of its known tropical and subtropical distribution, it is unlikely that it occurs on this island. I have not been able to trace the material.
 3. Harrison (1970) also lists *maritima* for Macquarie, but Gressitt (1970: 332) omits it from his table.

Although *parthenogenetica* could probably have reached the islands entirely by airborne dispersal, Watson (1967) notes that on Macquarie it was collected only from habitats around the Isthmus, the northern peninsula, and slopes and gullies between Nuggets Point and the Isthmus. Since the research station is in this region, it is possible that it was introduced.

The success of *parthenogenetica* in the subantarctic is probably related to the following. (1) Its parthenogenetic habits, which deprive it of the advantages of recombination but theoretically enable it to become established through the entry of a single individual into any favorable niche. Parthenogenesis also confers the advantage that all individuals lay eggs, presumably allowing a higher reproductive rate and helping to counter the effects of high mortality in rigorous environments.⁴ It means that the population density can be exceedingly low because there is no need for individuals to find each other as in bisexual species; and it allows the existing combination of genes, apparently so successful in the subantarctic, to be perpetuated without disruption through segregation and recombination (White 1973). (2) Its cryptic habits (see above). (3) Its ability to breed in almost any moist decaying vegetable matter or dung. As breeding places, Satchell (1947a) mentions rotten carrots and mangolds, refuse left in disused farm troughs, household drains, the bacteria beds of sewage purification plants, freshwater mudflats, and chicken, horse and cow dung; but not stacked dung (Satchell 1947b), probably, I think, because of the heat produced during decomposition. (4) Its high winter survival rate and ability to continue development in all but the coldest weather (Satchell 1947b), which is related to the low temperature thresholds of development of all stages, but especially the larvae (Lloyd 1937). Satchell's (1947b) observations showed that in England, adults of *parthenogenetica* reach peak abundance in spring and decline through summer to autumn. In temperate Australia I find this species is sometimes common in cooler seasons but always absent in summer. Watson (1967) collected adults on Macquarie in all months, mainly from piles of sheep dung and among decaying litter beneath *Stilbocarpa*. He says there is probably no seasonal variation in the life cycle. Lloyd (1937) shows that the fully favorable temperature range for *parthenogenetica* is only 6–20 °C, compared with 16–25 °C for the warm adapted *alternata*. In *parthenogenetica*, thresholds of development are also considerably lower for all stages, and eggs, pupae, and to a lesser extent larvae, have high thermal constants, which means that relatively long periods are spent in these stages. On the other hand, the thermal constant for maturation is relatively low, which should mean that eggs can be more quickly laid, thus reducing the span of the hazardous period between emergence and oviposition (Table 2) [see Wigglesworth (1972) for criticism of the concept of thermal summation employed by Lloyd].

4. Downes (1964) shows that the thelytokous arctic simuliid, *Gymnopsis* sp., lays less than a tenth the number of eggs produced by more southern bisexual species.

TABLE 2. Development in *Psychoda parthenogenetica* and *P. alternata*; data from Lloyd (1937). Columns 2-5 give theoretical thresholds of development (first figure) and thermal constants (in parentheses).

	MATURATION	INCUBATION	LARVAL GROWTH	PUPATION	RANGE OF FULLY FAVORABLE TEMPS (°C)
<i>Psychoda parthenogenetica</i>	0.2 (35)	2.2 (48)	0.6 (353)	1.5 (77)	6-20
<i>P. alternata</i> (9s)	2.0 (46)	5.9 (20)	5.5 (244)	7.7 (31)	16-25

Like parthenogenetic forms in other groups, *parthenogenetica* is ecologically versatile, with a distribution extending far beyond that of related bisexual forms. White (1973) says such distributions probably occur because every individual reaching a new locality is capable of founding a colony rather than because parthenogenetic forms are more hardy. He also suggests that apparent ecological versatility may simply reflect the presence of many genetically different biotypes adapted to different ecological niches. However, in Europe *parthenogenetica* is versatile in breeding habits even within restricted localities, and this versatility in combination with the physiological features demonstrated by Lloyd seems to account for its known distribution. Nonetheless, the possibility remains that it may represent more than 1 biotype and that not all biotypes are triploid.

PARTHENOGENESIS IN THE SUBANTARCTIC

Whether parthenogenetic forms are more hardy or not, Downes (1962) regards parthenogenesis as one of the most striking phenomena among arctic insects and notes its occurrence in arctic Chironomidae, simuliids including 2 of the most northern species known (*Gymnopsis* sp. and *Prosimulium ursinum* Edwards), 1 of the 2 most northern mayflies (*Baetis feminum* McDunnough), and the most northern caddis fly (*Apatania zonella* Zetterstedt). Similarly, Suomolainen (1950) shows that in certain weevils and the psychid moth *Solenobia*, polyploid parthenogenetic forms occur in recently glaciated areas while corresponding diploid sexual forms remain in presumed ice-age refugia; and Hodkinson (1978) finds strong circumstantial evidence that certain psyllids are parthenogenetic over parts of their ranges, particularly in arctic and alpine/tundra regions. What has not been remarked is that in proportion to its small fauna the subantarctic may support an even higher proportion of parthenogenetic species or biotypes than the Arctic. Besides *parthenogenetica*, these include the chironomids *Haliryus macquariensis* Brundin and *Smittia* sp. on Macquarie (Brundin 1962), and the sciarid *Bradysia* sp. on South Georgia. Further probable examples are subantarctic populations of *Limnophyes pusillus* Eaton, *Haliryus amphibius* Eaton on Kerguelen (Brundin 1962), and the thysanopteran *Anaphothrips secticornis* (Trybom) on South Georgia.

White (1973) estimates that bisexual genetic systems in animals may outnumber parthenogenetic systems by over a thousand to one, but I calculate that on the subantarctic islands the incidence of parthenogenesis in insects, excluding Collembola, Mallophaga, Anoplura, and Siphonaptera, may be as high as 15% of recorded species (S Georgia), 13% (Macquarie), 10.7% (Kerguelen) and 10.5% (Marion). All but one of the forms involved are Diptera Nematocera.

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APPENDIX

COLLECTION DATA FOR *PSYCHODA PARTHENOGENETICA* TONNOIR ON
THE CROZET ISLANDS

All specimens: CROZET IS: POSSESSION I: Baie du Navire, Dr L. Davies. Nearly all gravid. *Tullgren extracted*: 3♀, *Poa* tussock, 7.II.1968; 2♀, *Deschampsia* tussock, 9.II.1968; 1♀, Base, moss and fern, 14.II.1968; 6♀, Base, moss and fern, 14.II.1968; 6♀, Base, moss, 17.II.1968; 10♀, Base, moss cushions, stony area, 20.III.1968; 16♀, Base, *Acaena* grass peat, 22.III.1968; 8♀, Base, *Deschampsia*, stony area, 19.II.1968 and 2-7.IV.1968; 6♀, *Deschampsia* tussock, 10.IV.1968; 1♀, nr Teleferique, 10.IV.1968. *Netted*: 2♀, Riviere du Camp, 28.I.1968; 1♀, nr Riviere du Camp, 28.I.1968.