

CHAPTER TWELVE

LOSS OF DISPERSIBILITY IN ISLAND ANIMALS

The most obvious loss of dispersibility in insular animals is the loss of flying ability in insects and birds whose ancestors were capable of flight when they immigrated to islands. Before proceeding with that conspicuous phenomenon, I would like to discuss some more subtle ways in which dispersibility can be lost in insular animals.

As an example of a "nonflying" animal that is nonetheless definitely capable of aerial dispersal, one may cite a remarkable range of dispersal abilities among spiders. In the genus *Pardosa*, Richter (1970) has rated populations of the species according to the percentages of individuals which, on the basis of their behavioral characteristics, are "potential aeronauts." These percentages range from a low of 0.05 percent in *P. lugubris* to a high of 65.00 percent in *P. palustris*. Richter finds a close correlation between low dispersal ability and preference for stable habitats. However, when he rated habitats as to their abundance or rarity, he found high dispersibility correlated with "rare" habitats. These findings are eminently acceptable on the basis that species of far-flung habitats of limited extent—like beach plants among angiosperms—have high dispersal capacity, and that these same habitats also tend to be unstable. Thereby, a selective advantage for high dispersibility is characteristic for species inhabiting unstable, dispersed habitats of limited extent. Such species would make good immigrants to islands—indeed they can be regarded as living on a series of ecological islands within continents. If such a species should migrate to an oceanic island and adapt to stable conditions (as are characteristic of most islands in prehuman times), one would expect a

loss of dispersibility. Available habitat is then "abundant" in a sense—the new island population is a solitary population, not one of many populations among which interchange can take place. This principle applies to high islands—atoll plants and animals remain vagile and form populations among which interchange occurs.

In carabid beetles, both Lindroth (1945–1949) and Boer (1970) believe that "species living in unstable habitats invest extensively in dispersal" (quoted from Richter, 1970), a concept in effect advanced somewhat earlier by Southwood (1962). The inverse seems obvious: the more stable the habitat, the less the pressure for dispersibility. Darlington (1943) stated this, in essence, when he said, "The principal function of flight is found to be to maintain sparse, unstable populations in large, unstable areas. In small, stable areas, where populations are dense and stable, flight presumably loses this function, permitting existence of flightless . . . Carabidae, especially geophiles."

These considerations also apply to various other animal groups. On the Hawaiian Islands, Perkins (1913) noted the remarkable tendency of *Achatinella* (Gastropoda) colonies to reside in a single tree over a period of months. Clarke and Murray (1969), noting that the *Partula* species of Moorea tend to remain isolated (although hybridization does occur), cited geographical barriers within the island but believed that other factors must be responsible for maintaining integrity of the species of these land shells. If *Partula* resembles *Achatinella* in its precinctiveness, lack of mobility may well provide the mechanism that could explain maintenance of species. Indeed, in *Achatinella* the numerous species, each restricted to a very few valleys, must have been produced and maintained by both geographical isolation and precinctiveness.

Dispersibility of plants and animals is subject to evolutionary modification. Once a population (other than that of a repetitively introduced beach species or the like) has been established on an oceanic island, the factors that favor precinctiveness are many, the factors that favor increased dispersibility are few and exceptional. Different groups and different islands will not provide identical pressures for precinctiveness. In extremely windy and cold subantarctic islands, precinctiveness will be favored for reasons different from those operative in deep forest of tropical islands. As Darlington stated (1943), "Whether or not flight is useful, and whether

or not wings atrophy, depends on a balance of factors very much more complex than Darwin guessed." I will attempt to assess which factors may be favored in which situations. Nevertheless, it appears to me that precinctiveness does operate in insular plants and animals and that we must consider flightlessness only one manifestation of it. It is entirely possible for an insect species capable of flight to be highly precinctive also, but there are only a few observations at present that note this (see, however, some examples below from subantarctic islands).

In the discussion that follows, continental areas are considered peripherally, and flightlessness is also briefly considered in chapter 14 in a discussion of the equatorial alpine biota. As Darlington (1943) compellingly showed for carabid beetles, flightlessness can be definitely characteristic of certain continental areas. Likewise, loss of dispersibility in plants is far from an exclusively insular phenomenon, as suggested in the preceding chapter. The majority of instances, in fact, occur on continents.

Flightless Birds

In my account of flightless birds on islands (1965, pp. 224-41), a listing of flightless birds and references to them (pp. 416-18) are given, together with illustrations and brief descriptions. Because most of these (other than the large continental ratites and the penguins) are endangered or extinct, the account of Greenway (1958), the I.U.C.N. Red Data Book (vol. 2, Aves), and the literature they cite are the most complete sources of material. Attention is called to De Beer's (1956) account on the evolution of the ratites. To my 1965 listing I can add that the Ascension Island rail (listed as "*Crecopsis* sp." in the I.U.C.N. Red Data Book) is now known from complete skeletal material (Olson, 1971), and can be added to the list of now-vanished insular Rallidae of the world. My mention of the flightless duck or teal might be amended to indicate that two subspecies are now recognized, *Anas aucklandica aucklandica* on the Auckland Islands and *A. a. nesiotis* on Campbell Island. Personal observations during my 1966 visit to Laysan Island show that the Laysan teal can, in fact, be frightened into flight rather easily, but the birds merely fly to

another portion of the lagoon. Geographically, they can still be said to be quite sedentary.

In reviewing my (1965) account of flightless birds, I find that several features become apparent. First, no truly arboreal birds or bird groups are in the list, with the exception of the flightless parrot (*Strigops habroptilus*) and the flightless wren (*Xenicus lyallii*), both of New Zealand—and these flightless representatives are, of course, terrestrial in their habits. The relatively abundant time available in New Zealand, as well as the absence of mammals, is undoubtedly a factor in the evolution of so many flightless birds there. The Mascarene dodos and solitaires are of obscure ancestry, but may well stem from nonarboreal birds.

To find that flightless birds are derived from groups that are ground-feeders is no surprise. We must make an exception, at first glance, for flightless waterbirds: the penguins, the giant auk (*Pinguinus impennis*), the Galápagos flightless cormorant (*Phalacrocorax harrisi*), and the flightless grebe of Lake Titicaca, *Rollandia micropteryx* (= *Centropelma micropteryx*). These are all analogous to ground-feeding birds, however, in that swimming (together with underwater diving) is all that is required, not flight. With these exceptions, flightless birds are descended from terrestrial-feeding bird groups, and these habits are merely maintained and heightened on islands. Another feature common to the flightless insular birds (other than the waterbirds mentioned) is their virtually omnivorous feeding habit. This is particularly true of rails. In view of the limited size of the islands on which many of the rails exist or once existed, broad food tolerances are necessary for survival of viable populations. Another feature Rallidae exemplifies is the tendency to fly not so much in long migratory patterns, but merely from one suitable feeding area to another. On islands, this would predispose them not to use flight as a tactic to any appreciable degree. During feeding per se in such terrestrial birds as rails, flight does not play a role, as it would for a frugivorous bird or nectarivorous bird. Flight does occur in Rallidae as an evasive mechanism where predation occurs.

The preadaptation of Rallidae to dispersal to islands, survival on islands, and evolution into flightlessness there becomes obvious from the preceding. Because they are somewhat migratory in their feeding habits and not territory-bound as passerine birds typically are, Rallidae are likely

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to occur as stragglers to islands, more so, one would expect, than passerine birds. On islands, they will survive because of their broad food tolerances. Their feeding at ground level or in shallow water continues. Flight to new feeding grounds is impossible because of oceanic distance. If an island can support a rail population at all (and evidently small islands can), the food supply can be exploited without resort to flight. The only further requisite for evolution into flightlessness is then the absence of predators. Even flight for evasive purposes may not be necessary. The flightless Tasmanian native hen (*Tribonyx mortieri*, of Rallidae) can run at speeds up to 30 mph, faster than can the Rallidae of Tasmania that are still capable of flight (Sharland, 1958). One cannot stress too strongly that of all natural methods of locomotion, flight is the most highly expensive of energy; therefore, in any condition under which flight is not a necessity for a volant organism, there will be a positive selective pressure for flightlessness.

The continental ratites (emus, ostriches) substitute rapidity of running for flight as an evasive mechanism. They are also able to use feet, legs, and beak defensively; the cassowary, in addition, can use its horned crest. Penguins, subject to predation by porpoises, use "underwater flight" as a means of escape. Survival of flightless birds has either depended on lack of predation or, where predation occurs, has involved compensatory evolution of evasive mechanisms other than flight. Although one tends to think of flightlessness as a retrogressive tendency, it can also be considered a new and even efficient adaptive mode that is possible under certain circumstances. One can cite exploitation of habitats in the fashion of large herbivores (dodos, moas, ratites) as features of efficient ground locomotion made possible by "release" from wing formation and maintenance.

Flightless Insects

Darlington (1943) views flightlessness in carabid beetles as an inevitable trend wherever flight is not of high selective value in order to maintain large, sparse, unstable populations over large, unstable areas. The smallness of occupiable area and the stability of the environment are, in his considerations, of prime importance. Going farther, Darlington cites an

instance in weevils where flightless individuals may, in fact, show better viability than winged individuals within a single species (Jackson, 1928), and tends to regard flightless insects as having "inherent superiority" due to "simplicity and vitality." One might wish for some physiological measures to demonstrate actual types of advantage in reduced-wing insects, other than the obvious one that an economy is involved if wings and even hapteres are lost. Spencer (1932) did show that vestigial-winged *Drosophila* mutants survived better under conditions of food and water deprivation than normal-winged populations. However, Lindroth (1945-1949), with the aid of some experimental work, contradicts the idea that flightlessness improves viability. Brinck (1948) would seem to agree with Darlington, for he states that "on oceanic islands, where the conditions occasionally become very unfavorable, a vestigial [flightless] type might even oust the normal." However, Brinck's discussion obviously favors the selective effect of wind pressure as operative in producing a high proportion of flightless insects on Tristan da Cunha. Darlington does not believe wind pressure is a factor in evolution of flightless insects, but the subantarctic insects may be an exception (see below). Tristan da Cunha has some of the aspects of a subantarctic island.

Perkins (1913) subscribed to the "disuse" theory to explain flightlessness in Hawaiian insects. Interestingly, a high proportion of *arboreal* Coleoptera are flightless in the Hawaiian Islands. Among instances Darlington cites where flight is useful in carabids are hydrophiles or arboreal species; species in areas likely to be flooded; species on low tropical islands; and species on dry lowlands of tropical islands. Small, low, tropical islands (e.g., coral platforms like the Cayman Islands) are, as Darlington notes, often recent, with no endemism. However, applying the considerations of MacArthur and Wilson (1963), one can say that extinction rate is high on a small, low island, so that influx of new stocks by a constant stream of immigrants is required to maintain a given number of species. In the case of carabids, fully winged, widespread, tropical species would presumably be the immigrants to such islands. If repetitive and continual immigration to a small low island occurs, even without extinction, new immigrants with wings would doubtless swamp out any winglessness, assuming (as seems likely) that brachyptery and aptery are the results of recessive genes.

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Darlington (1943) would explain lack of flightless carabids in tropical lowlands (insular and otherwise) by the fact that these dry areas, poorer in food resources, fall under the category of the "large and unstable areas" he designates as correlated with selective advantage for flying forms.

Darlington discounts altogether the possibility that wind pressure may exercise a selective force leading to flightlessness. His data on montane carabids demonstrate, in his opinion, no appreciable difference in flying versus flightless in exposed or protected situations, respectively. Wind pressure was claimed by Darwin to make flightlessness advantageous in insular insects, in that excessive numbers would be blown out to sea (on mountains, wind pressure would presumably blow insects to ecologically unsuitable locations according to the Darwinian reasoning, although Darwin did not comment on flightlessness in montane situations). An alternative explanation would be that where wind pressure is excessive, wings are disadvantageous because wind would tend to hinder flight during feeding. Darlington (1943) analyzed data for carabids of the Presidential Range, New Hampshire. His results show that when hydrophiles, non-resident, and arboreal species are excluded, 70 percent of the forest geophiles and 64 percent of the exposed-area geophiles above 3000-ft elevation are flightless. This he attributes to the geophilous habit and the concentrated area of suitable habitat—the latter related to the concept of precinctiveness that I have cited earlier. Flightless Carabidae for New Hampshire as a whole amount to 13 percent, so there is, without doubt, a much higher percentage in montane carabids in Darlington's data. Greenslade (1968) finds similar data in Argyll, Scotland, although the percentages are much less striking than in Darlington's data—and the number of species of carabids involved is relatively small also.

Whether wind pressure is a factor in winglessness has not been resolved, to judge from the literature. Downes (1962) noted reduction of mating flight in insects of far northern Canada. The experiments of L'Heritier, Neefs, and Teissier (1937) with brachypterous and normal-winged *Drosophila* races in culture dishes open to wind showed that normal-winged flies tended to be blown away, while the flightless flies had a low rate of attrition. This experiment, however, may well not be definitive in demonstrating the effect of wind.

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SUBANTARCTIC ISLAND INSECTS

Either insects of subantarctic islands add data to illuminate the question of wind pressure in relation to flightlessness, or else they form a special case. Gressitt (1970) says that Darlington's hypotheses "do not apply" to the subantarctic islands, and he also finds the models of MacArthur and Wilson (1963) inapplicable. Cold makes flying much more difficult for insects, and the subantarctic islands are exceptionally cold—cool even during the summer. This, together with the added "burden" of wind pressure, may prove a definitive selective pressure for flightlessness and eventually aptery (see the last portion of chapter 14 for a discussion of these points).

In any case, subantarctic and Antarctic insects have been the subject of intense study during the past decade. For references to biological work of all kinds on the "true" subantarctic islands, Gressitt's (1970) summary is invaluable. Somewhat more northern islands of the far south are summarized by Gressitt (1962, 1964), and Gressitt, Leech, and Wise (1963) have provided a summary for Antarctic entomology. Attention should be called to monographic papers, not cited here, which accompany Gressitt's papers (1962, 1964, 1970).

The comments of Gressitt (1962, 1964) and the rich base of data on which he operates are of especial significance to Antarctic entomology. In particular, the effect of climate—presumably strong winds and cold—is examined. Gressitt's data (1964, 1970) show the following degrees of flightlessness for insect faunas of subantarctic islands:

	<i>Total number of species</i>	<i>Percentage flightless</i>		<i>Total number of species</i>	<i>Percentage flightless</i>
Campbell I.	183	40	Kerguelen	26	85
Crozet Is.	36	89	South Georgia	16	75
Marion I.	18	89	Heard I.	9	100
Macquarie I.	20	55			

On Antarctica itself, only a single insect capable of flight is known (out of 20 land arthropods, mostly insects): a chironomid midge, *Parochlus steineni* (Gressitt, 1970). Gressitt's data are subdivided further than my table shows; he indicates various degrees of wing reduction from moderate to complete. The strong degree of flightlessness is evident. In addition,

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the degree of nonflying behavior in insects capable of flight is manifest in his observations. He cites, on Campbell I. (Gressitt, 1964), many species known to fly but never taken in trapping experiments. These include pyralid moths, geometrid moths, and an ichneumon wasp. The smaller wasp *Campoplex disjunctus* was, however, taken in nets. Gressitt states, "These species which were not trapped are weaker fliers than some of the types commonly caught in the nets, like calliphorid flies, muscids, and others, yet are stronger fliers than some which were taken abundantly in the nets, like the aphids, psychodids, sciarids, and others." According to Gressitt and Weber (1959), wingless or partially winged subantarctic insects as a whole may be termed "active," whereas winged species are "sluggish." The highly sedentary aspect of the far-southern insect fauna is strongly evident.

Lepidoptera are particularly interesting in respect to flightlessness. Lepidoptera, with few exceptions, have evolved flightlessness only on the subantarctic islands (Enderlein, 1909; Viette, 1948, 1952a, 1952b, 1954, 1959). This, together with the tendency for strong-flying insects not to fly during periods of high wind, suggests that extreme wind pressure may indeed be a factor in the evolution of the subantarctic fauna. The most important feature may not even be that an excessive number would be carried out to sea (although lack of flightless forms in nets would seem to offer support for this), but that there might be interference with locomotion by wind pressure on wings or that there would be loss of heat through wings during conditions of low temperatures.

Three Campbell Island flightless moths are shown here: *Tinearupa sorenseni* of the Hyponomeutidae (fig. 12.1); *Campbellana attenuata*, also of Hyponomeutidae (fig. 12.2); and *Exsilaracha graminea* of the Pyralidae (fig. 12.3). *Exsilaracha* is nearly twice as large as the others, and has a pronounced jumping habit that substitutes for flying (Munroe, 1964). *Exsilaracha* lives exclusively in grass tussocks, and its hopping habits resemble those of grasshoppers, according to Salmon and Bradley (1956). *Tinearupa* (fig. 12.1) is found on coastal rocks, where its coloring and markings form a perfect camouflage, according to these authors. Sorensen (quoted in Salmon and Bradley [1956]) finds that *Campbellana* is a tussock insect, also with grasshopperlike habits. Strong development of legs is

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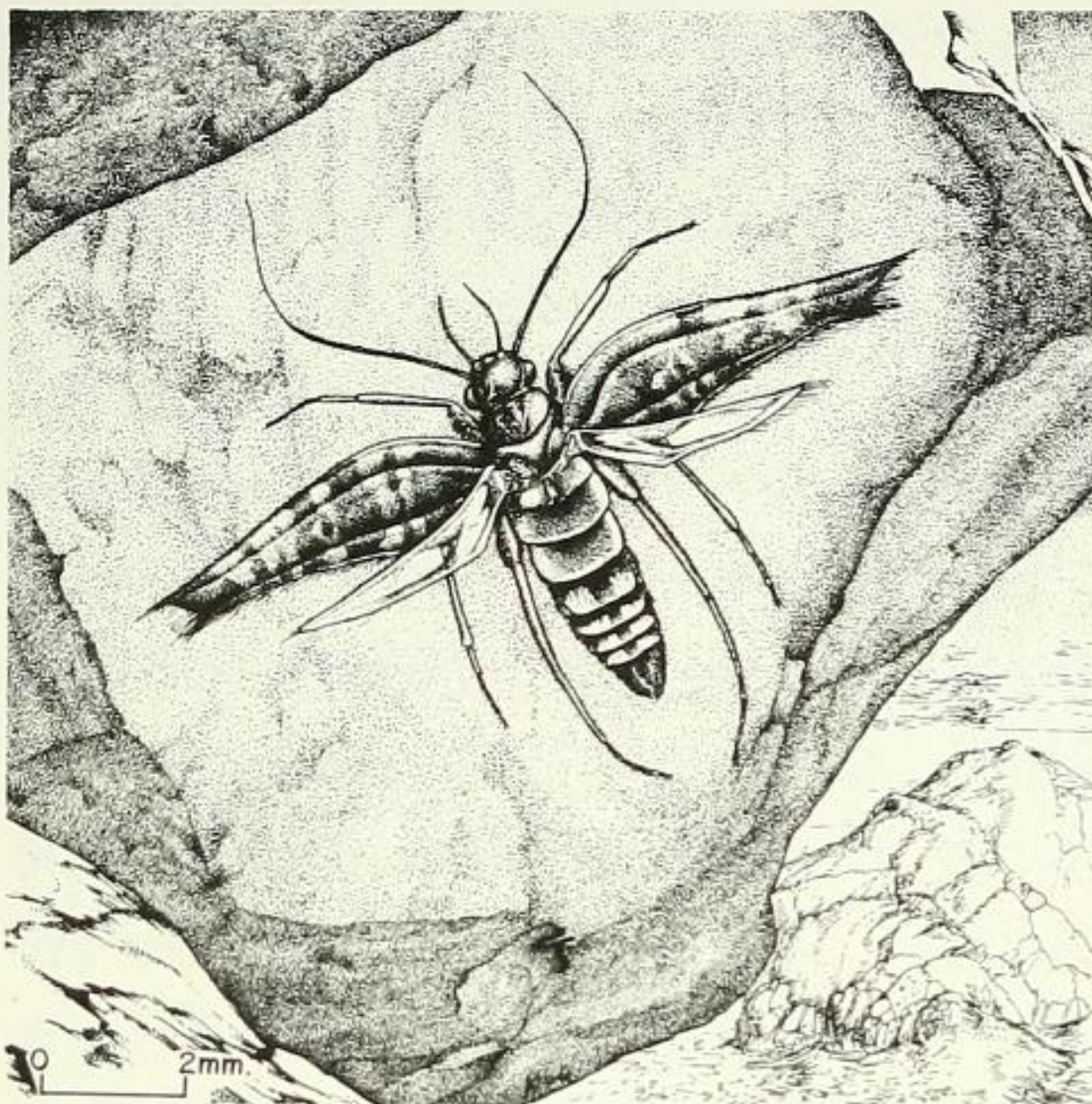


FIG. 12.1. *Tinearupa sorenseni*, a flightless moth from Campbell I.

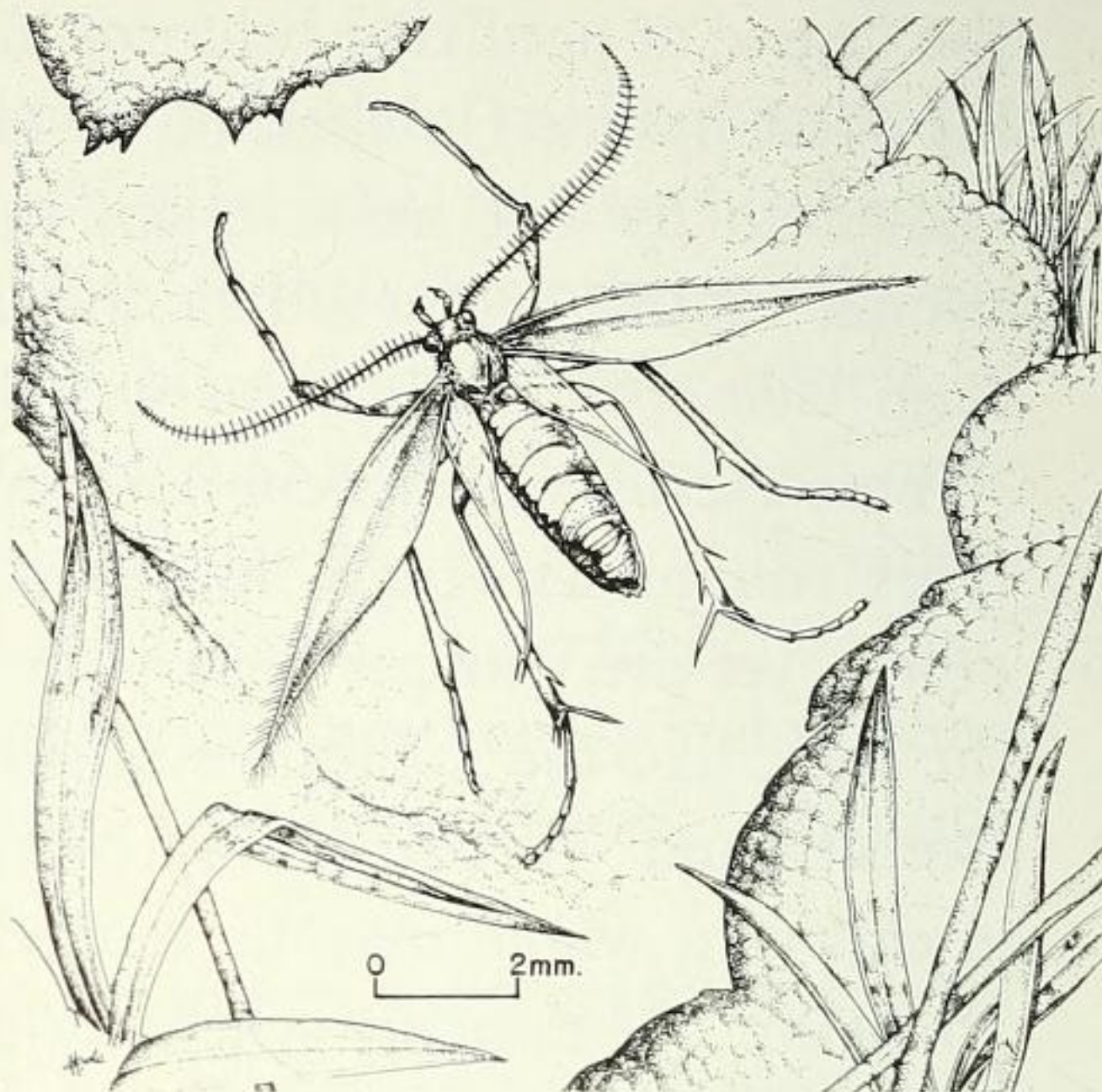


FIG. 12.2. *Campbellana attenuata*, a flightless moth from Campbell I.

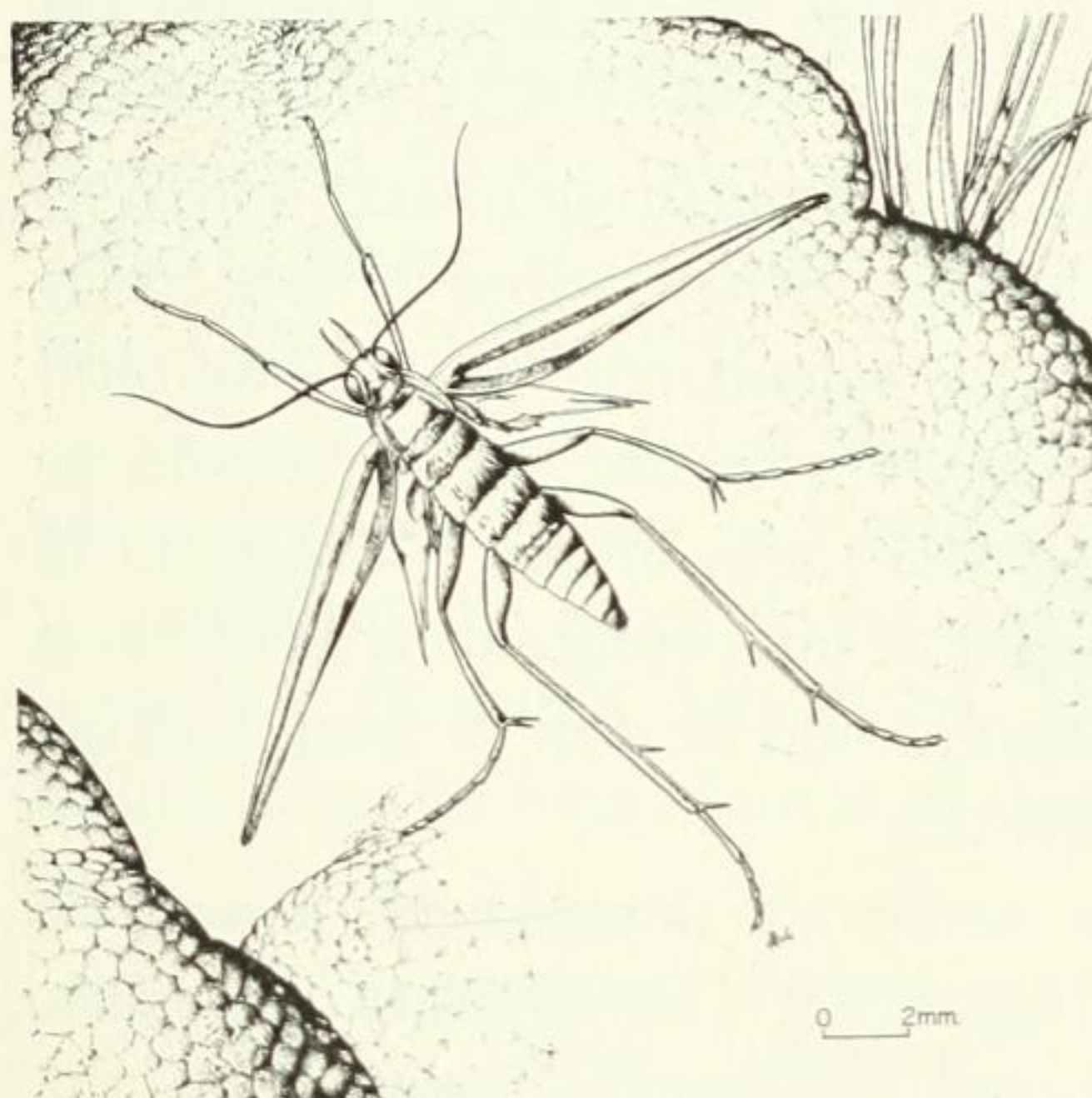


FIG. 12.3. *Exsilaracha graminea*, a flightless moth from Campbell I.

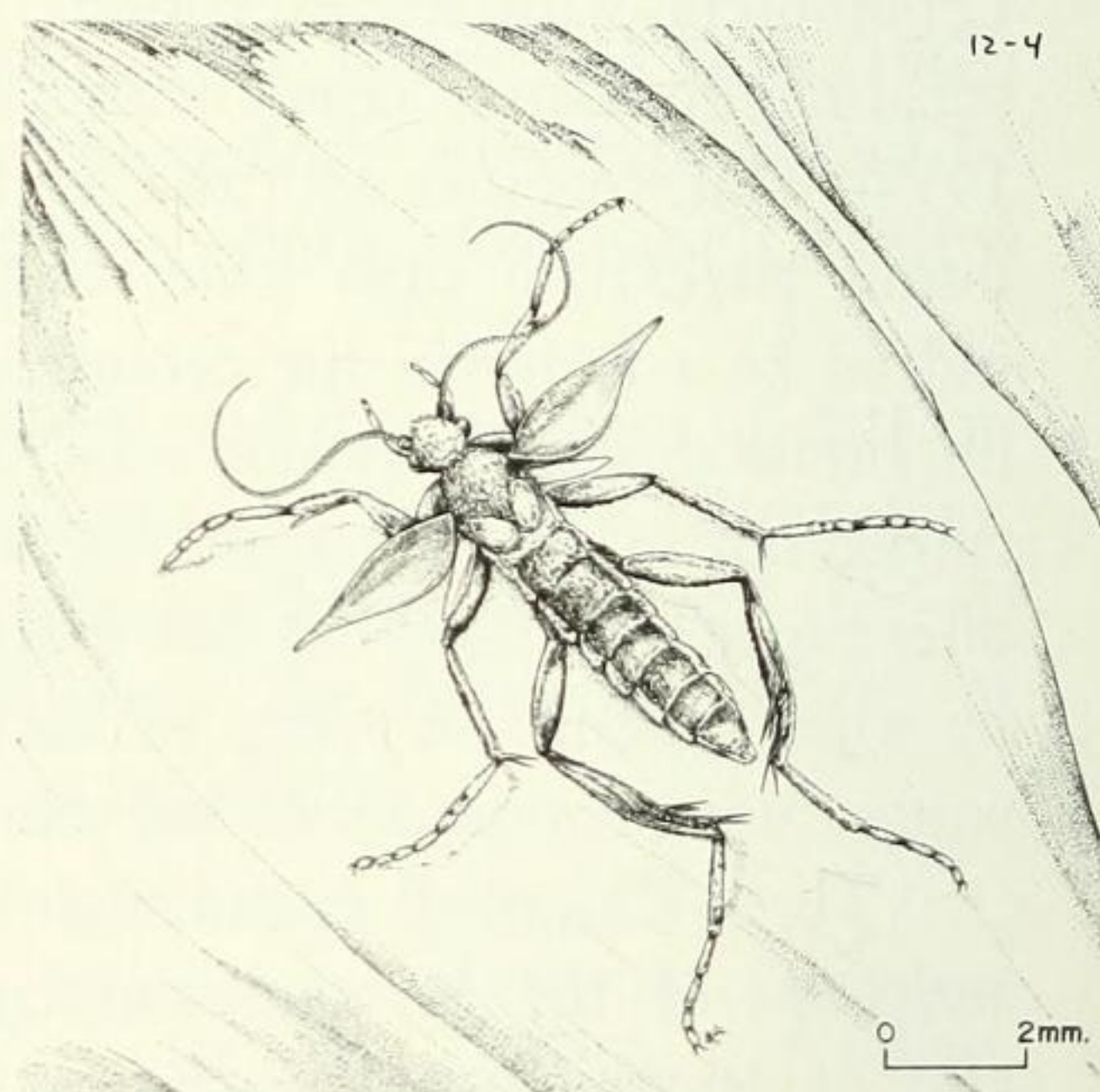


FIG. 12.4. *Pringleophaga kerguelensis*, a flightless moth from Kerguelen I. It is shown on a leaf of *Pringlea antiscorbutica*, the "Kerguelen cabbage."

evident in both *Exsilaracha* (fig. 12.3) and *Campbellana* (fig. 12.2). The abundance of flightless moths on Campbell Island may be related to the closeness to New Zealand, which could have served as an efficient source area for entry of moths into these southerly islands. Relative absence of moths from remote Macquarie Island is cited by Gressitt (1970) as a

reason why the proportion of flightless insects is lower there than one might expect on the basis of the extreme climate.

A curious feature of the Campbell Island moths is their tendency to sham death or seek refuge in tussocks or crevices despite the seeming lack of predatory birds—the pipit is the only insectivorous bird on Campbell Island (Gressitt, 1964).

One notable flightless moth on a remote subantarctic island is *Pringleophaga kerguelensis* on Kerguelen (fig. 12.4). As its generic name suggests, this insect's host plant is the curious Kerguelen "cabbage," *Pringlea antiscorbutica*. Comparison of many flightless moths of subantarctic islands shows remarkable similarity in that the wings are reduced by narrowing, although shortening is obviously involved as well. Extreme wing reduction is shown in the moth *Dimorphinoctua cunhaensis* of Tristan da Cunha (Viette, 1952a) and *Brachyapteragrotis patricei* of Amsterdam Island (for illustrations, see Carlquist, 1965).

A tendency noted by various authors is that in subantarctic moths the males have somewhat less wing reduction than females. For comparisons, see Viette (1948), Salmon and Bradley (1956) and Carlquist (1965, p. 222). This is also true in the one Hawaiian moth with flightless tendencies, *Hodegia apatela*. One is tempted to speculate that the males are more "expendable" than the females. Wind pressure alone might be a selective agent, but predation on males that are more conspicuous by virtue of longer wings might also be evoked. Field investigation of this dimorphism would, of course, be difficult yet very valuable.

In subantarctic Diptera, there is great variation in wing development, even within a single species. On Macquarie Island, the entire endemic species *Schoenophilus pedestris* (fig. 12.5) is flightless, yet some individuals have longer wings than others; there is no evident correlation with habits or habitats (Gressitt, 1964). *Schoenophilus pedestris* moves by hopping and tends to occur in tussock plants, such as *Colobanthus* (Kohn, 1962). Kohn compares *Schoenophilus* to a Hawaiian member of the same family, Dolichopodidae, in its wing reduction. A dolichopodid of Campbell Island, *Acropsilus borboroides*, has the ultimate in wing reduction: lack of wings and even halteres (Oldroyd, 1955).

Apataenus watsoni (Coelopidae) is another dipteran from Macquarie Island (fig. 12.6). It tends to be found under stones, particularly those

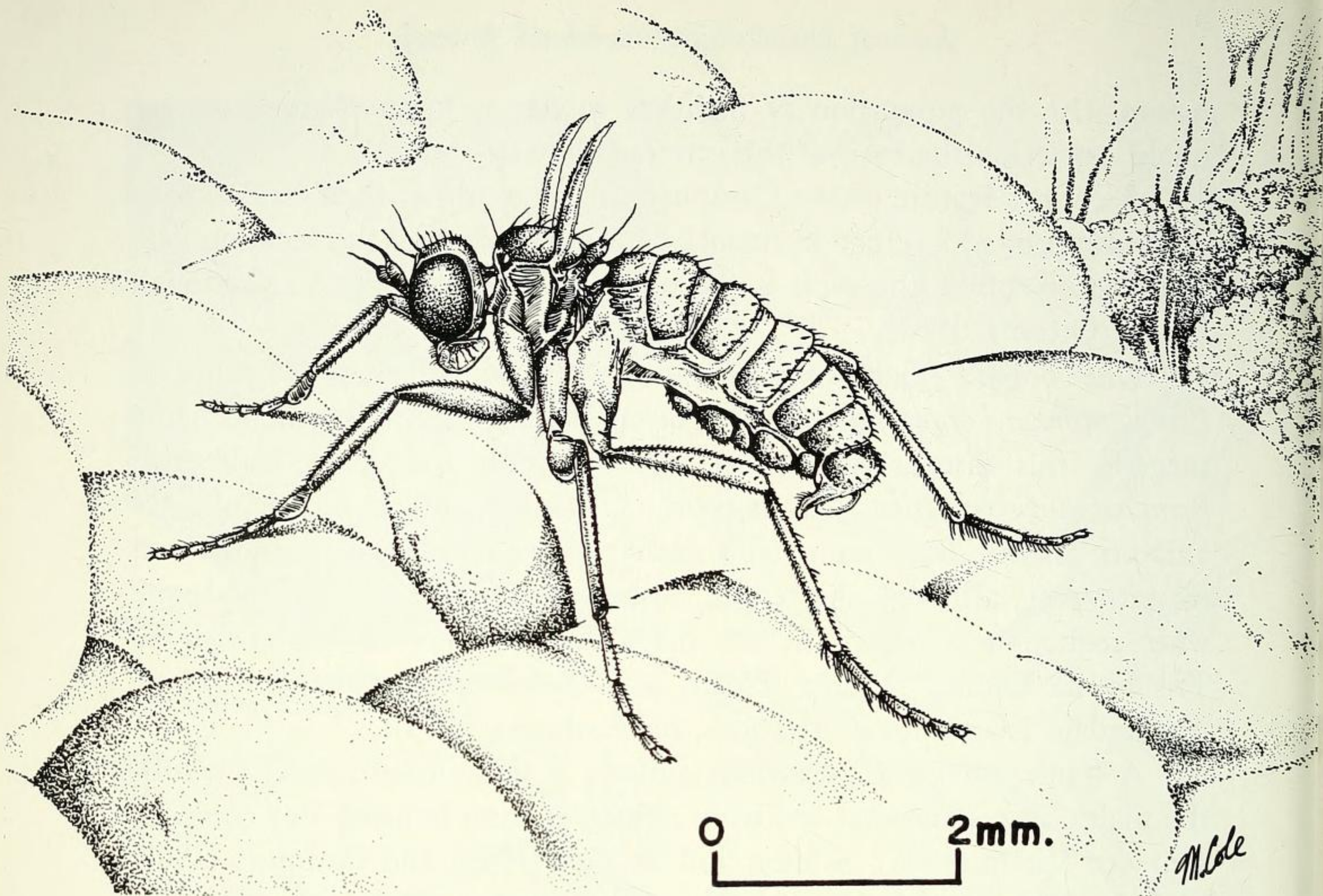


FIG. 12.5. *Schoenophilus pedestris* (Diptera: Dolichopodidae), from Macquarie I.

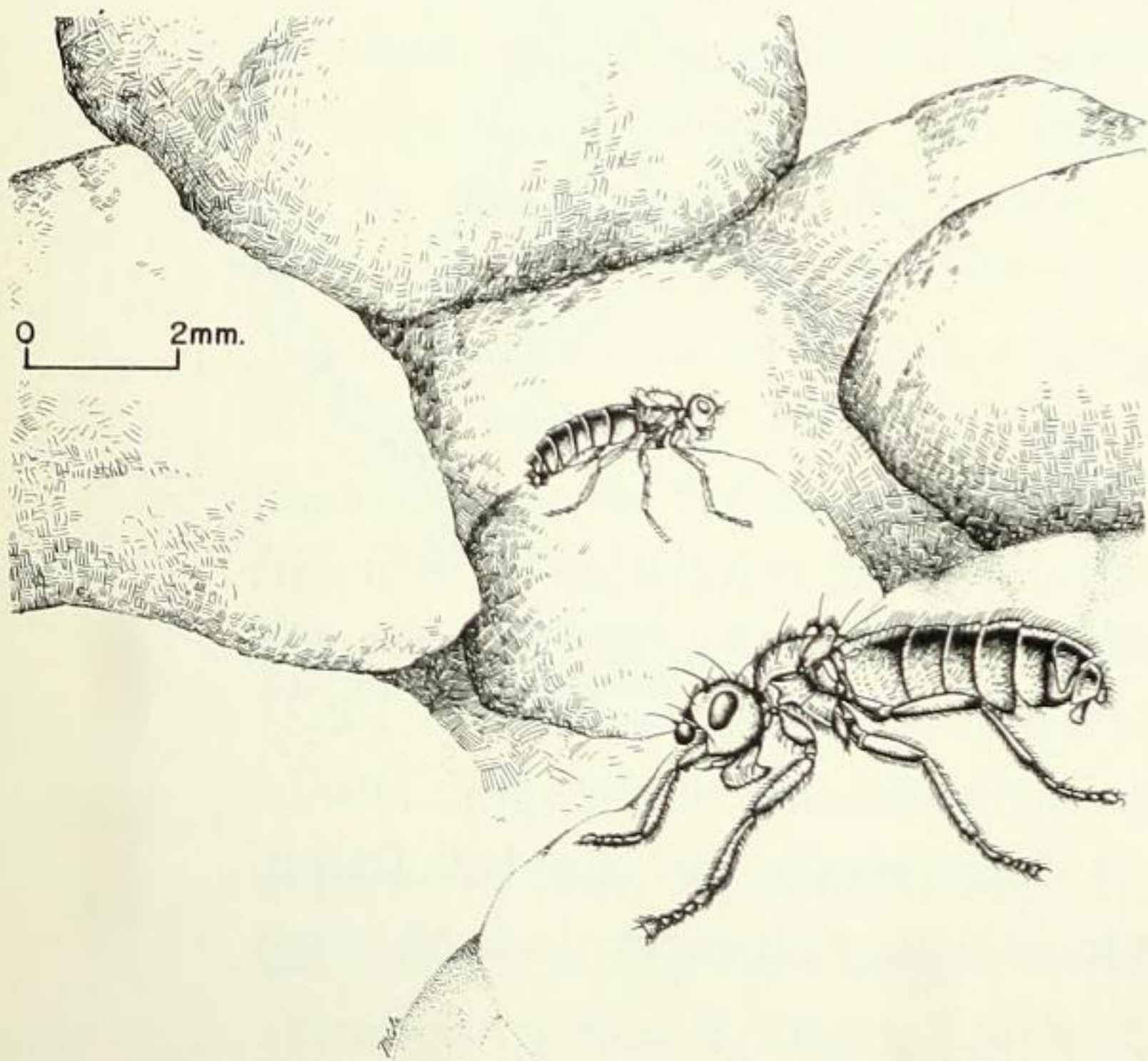


FIG. 12.6. *Apataenus watsoni* (Diptera: Coelopidae), from Macquarie I.

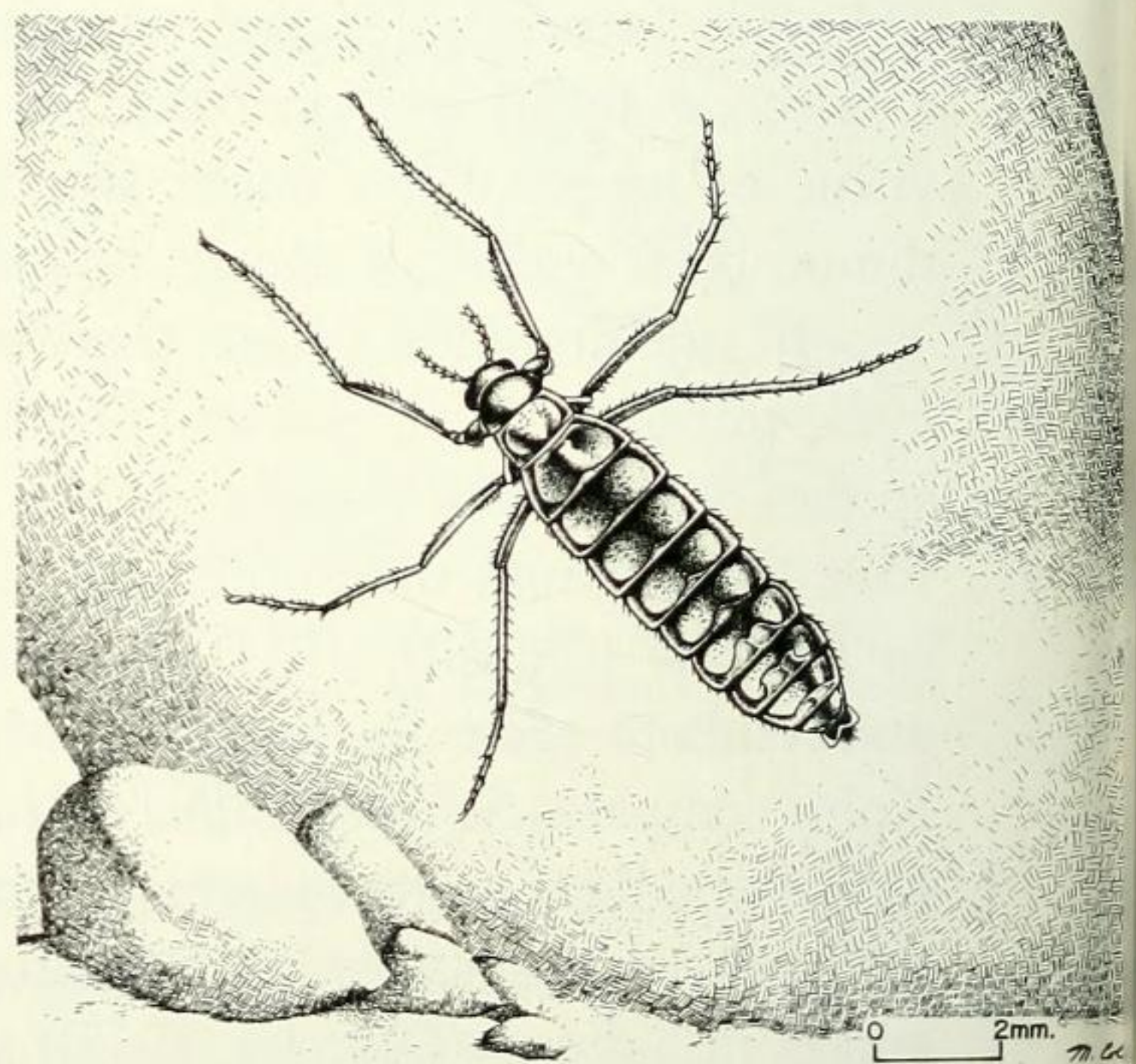


FIG. 12.7. *Belgica antarctica* (Diptera: Chironomidae), a flightless midge from the Antarctic mainland.

of bird rookeries (Hardy, 1962). Its wings may be up to half as long as the thorax. Extreme wing reduction is found in a midge from the Antarctic continent, *Belgica antarctica* of the Chironomidae (fig. 12.7). It occurs in penguin rookeries and can even be found on the penguins themselves (Gressitt, Leech, and Wise, 1963).

With respect to flightless Diptera of subantarctic islands, Seguy (1940) claimed several structural trends: robust pharynx, long malpighian tubules, reduced gastric coeca, short hind intestine, abundant adipose tissue; tough pupaia; adults with heavily sclerotized mouthparts, atrophied notopleural callus, small thorax, and reduced wing and leg muscles. However, Gressitt (1964) found that on Campbell Island an increase in leg size and musculature occurred with reduction in wing size. This is certainly obvious in his figures of the dipteran *Baeopterus robustus* and *Icaridion nasutum* (both of Coelopidae). The latter has no wings or halteres.

Kleidotoma subantarctica of the Encoilidae (fig. 12.8) is the first record of a cynipid wasp from any subantarctic island (Yoshimoto, 1964). It shows an interesting series in wing reduction, and one individual with fully developed wings has even been collected. *Kleidotoma subantarctica* is an endemic of Campbell Island. It lives on algae-covered rocks, to judge from collection data, but its feeding habits are as yet unknown (Yoshimoto, 1964).

Hymenoptera are not abundant in flightless species in areas other than the subantarctic islands, but they clearly occur with frequency on the far-southern islands. Various hymenopteran families are represented. *Antipodencyrtus procellosus* of Campbell Island (fig. 12.9) is a representative of Encyrtidae. It is evidently a parasite on a soft-bodied coccid of tussock grass (Kerrich, 1964). Occurrence of a parasite under the difficult conditions for establishment on subantarctic islands is interesting. Another curious feature of *Antipodencyrtus* is the presence of very long antenna branches.

Aucklandella flavomaculata (fig. 12.10) is an ichneumonid wasp discovered during an early survey of the subantarctic islands of New Zealand (Chilton, 1909). It occurs in Carnley Harbor of Auckland Island and may have a habitat similar to that of *Kleidotoma subantarctica*. There is another flightless ichneumonid on Campbell Island, *Gelis campbellensis*. Other flightless subantarctic Hymenoptera include two diapriids, *Antarc-*

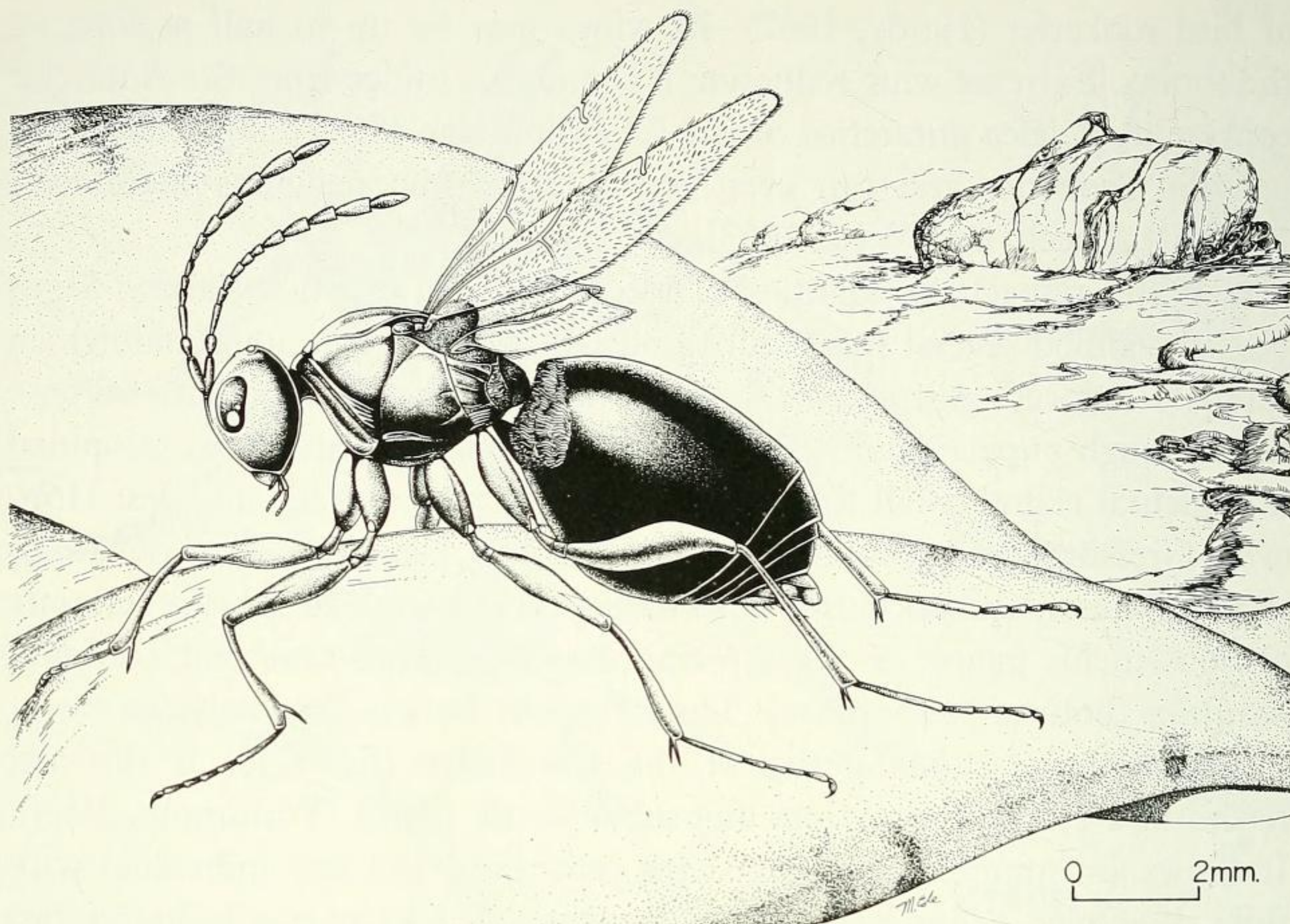


FIG. 12.8. *Kleidotoma subantarctica* (Eucolidae), a flightless hymenopteran from Campbell I.

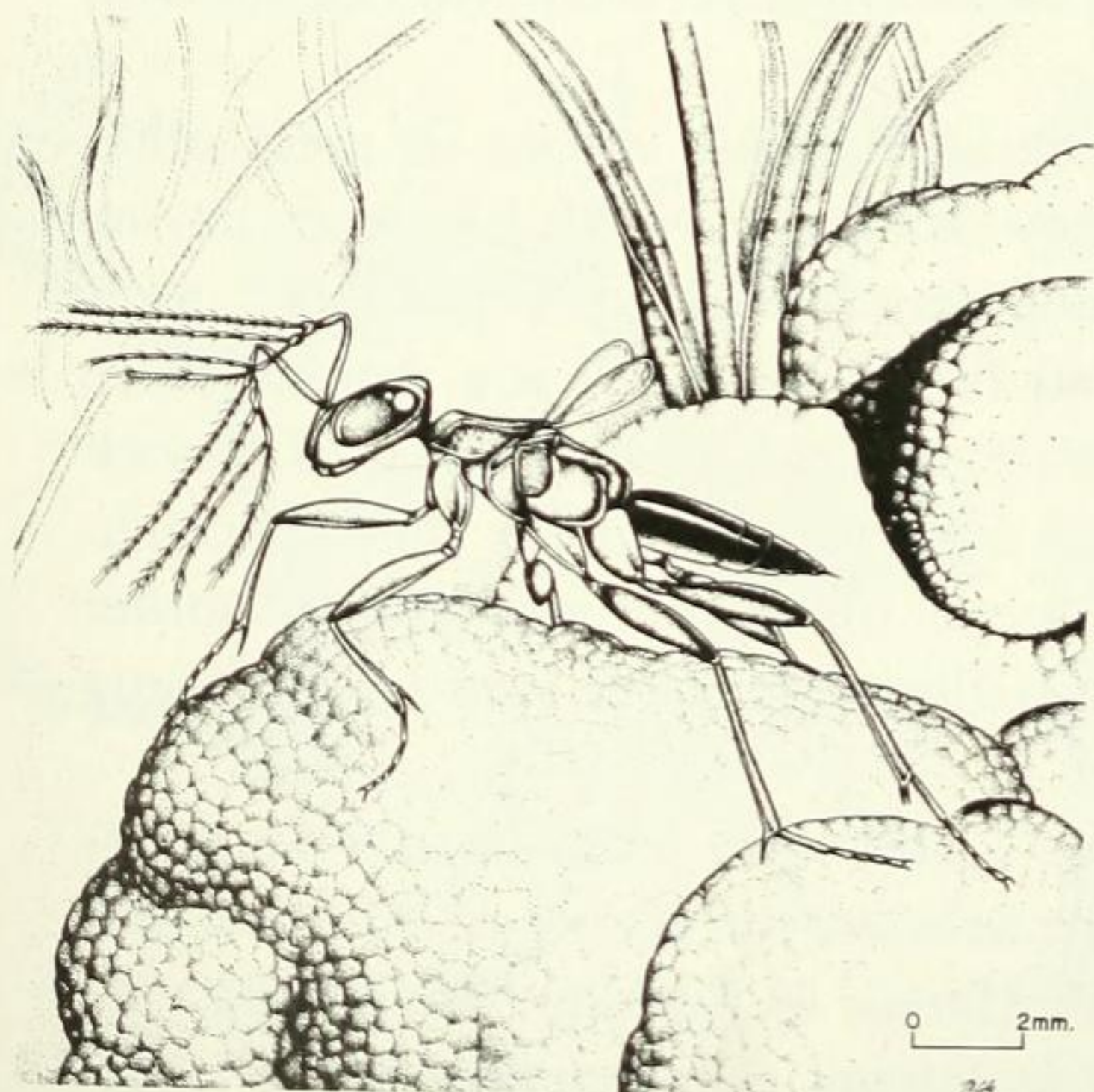


FIG. 12.9. *Antipodencyrtus procellosus* (Encyrtidae), a flightless hymenopteran of Campbell I.

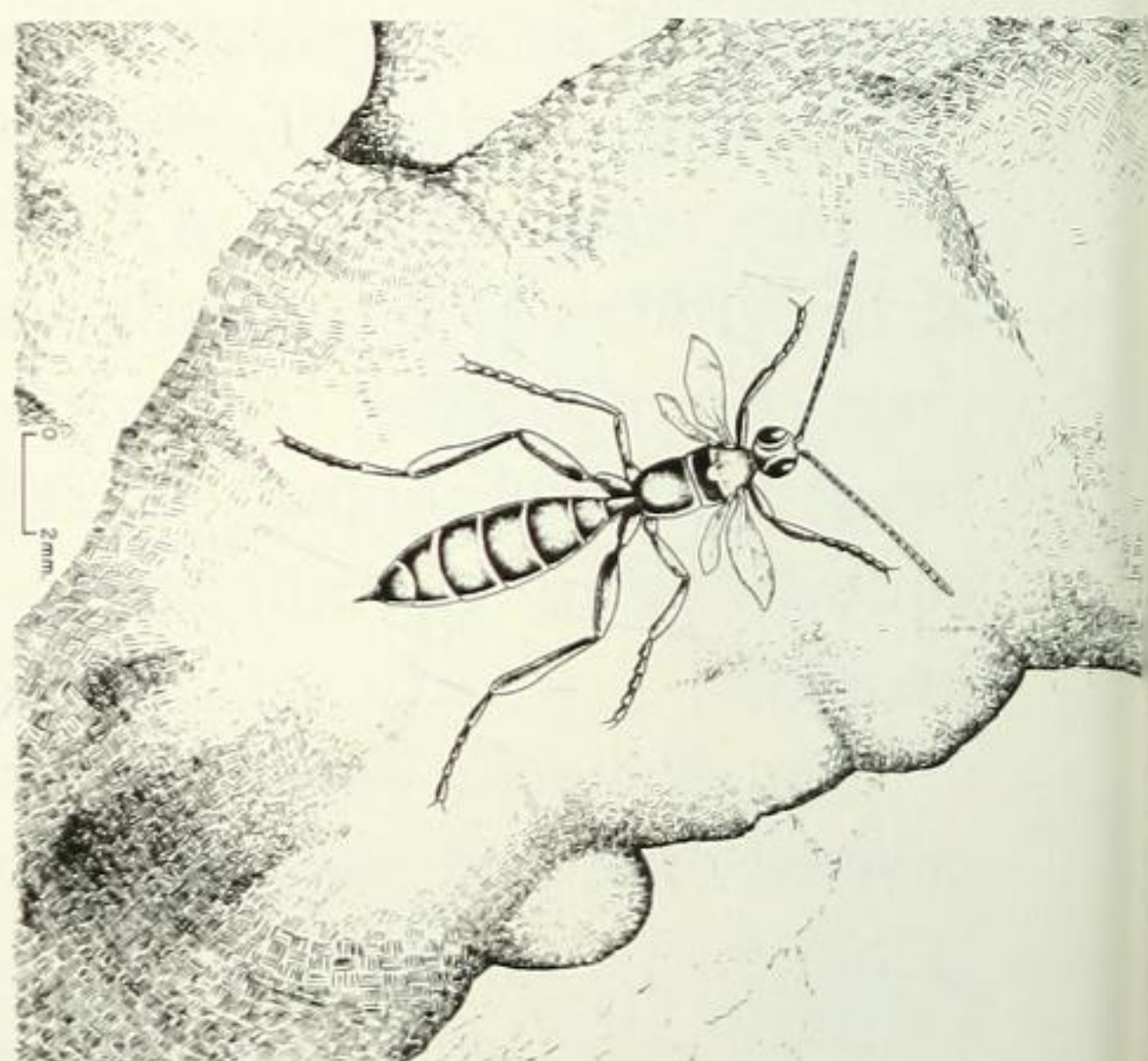


FIG. 12.10. *Aucklandella flavomaculata* (Ichneumonidae), a flightless hymenopteran from the Auckland Is.

topria latigaster of Macquarie Island, and a subspecies, *A. l. campbellana*, on Campbell Island (Gressitt, 1964).

Judging from insect groups that have flightless representatives in insular situations elsewhere in the world, one would not expect, a priori, that subantarctic islands would bear numerous flightless Lepidoptera, Hymenoptera, and Diptera, yet only a scattering of Coleoptera. Coleoptera are probably underrepresented because larger-bodied insects travel poorly over long distances and in cold wind currents—which also would account for the absence of Orthoptera and Neuroptera, and the paucity of Homoptera other than widespread aphids on the subantarctic islands. Interestingly, according to Beardsley (1964) the family Pseudococcidae of Homoptera is represented on subantarctic islands by several genera and species in which males are flightless and completely apterous (female winglessness would be expected in this family in any case).

An interesting feature of Coleoptera discussed by Brinck (1948) is the tendency for the ratio of carnivorous to phytophagous species to vary with habitat. Although the ratio is high in northern Europe, including some insular areas (7.53 in the Faeroe Is., 6.08 in the Shetland Is., 4.5 in Greenland, 3.05 in Norway), the proportion is lower farther south (1.17 on Corsica, 1.33 on Madeira, 2.14 on the Cape Verde Is.). However, subantarctic islands have an extraordinarily high number of phytophagous insects, so that the ratios are 0.17 on Tristan da Cunha and 0.12 on Kerguelen. The explanations for this are not at all clear, although Brinck (1948) offers a number of possibilities.

MADEIRAN AND OTHER ATLANTIC ISLAND INSECTS

Darwin, upon reading Wollaston's *Insecta Maderensia* (1854), was struck by the high proportion of flightless forms. As we have seen earlier, Darwin's explanation has seemingly been supplanted by Darlington's (1943) detailed and compelling considerations. However, assuming that precinctive populations and geophily are, as Darlington suggests, the most important factors in evolution of flightlessness of Coleoptera, it is interesting to review Wollaston's data to see how these factors operate on Madeira. Wollaston's work is of particular interest because he studied these species extensively in the field and dealt with their habits in great detail. Although Wollaston's monograph is outdated by subsequent faunistic

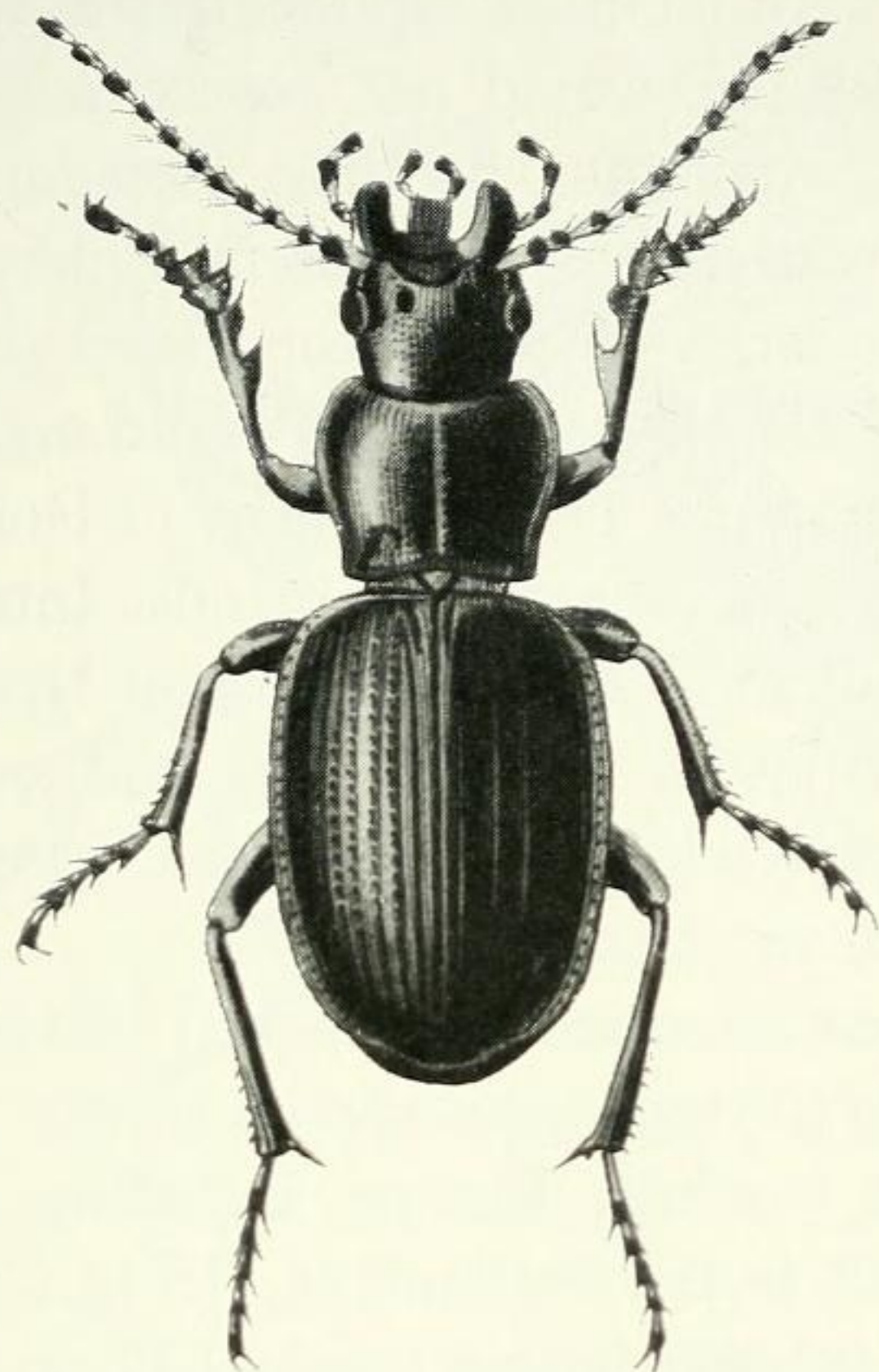


FIG. 12.11. *Eurygnathus latreillei*, male, a flightless carabid (Coleoptera) from Madeira (from Wollaston, 1854).

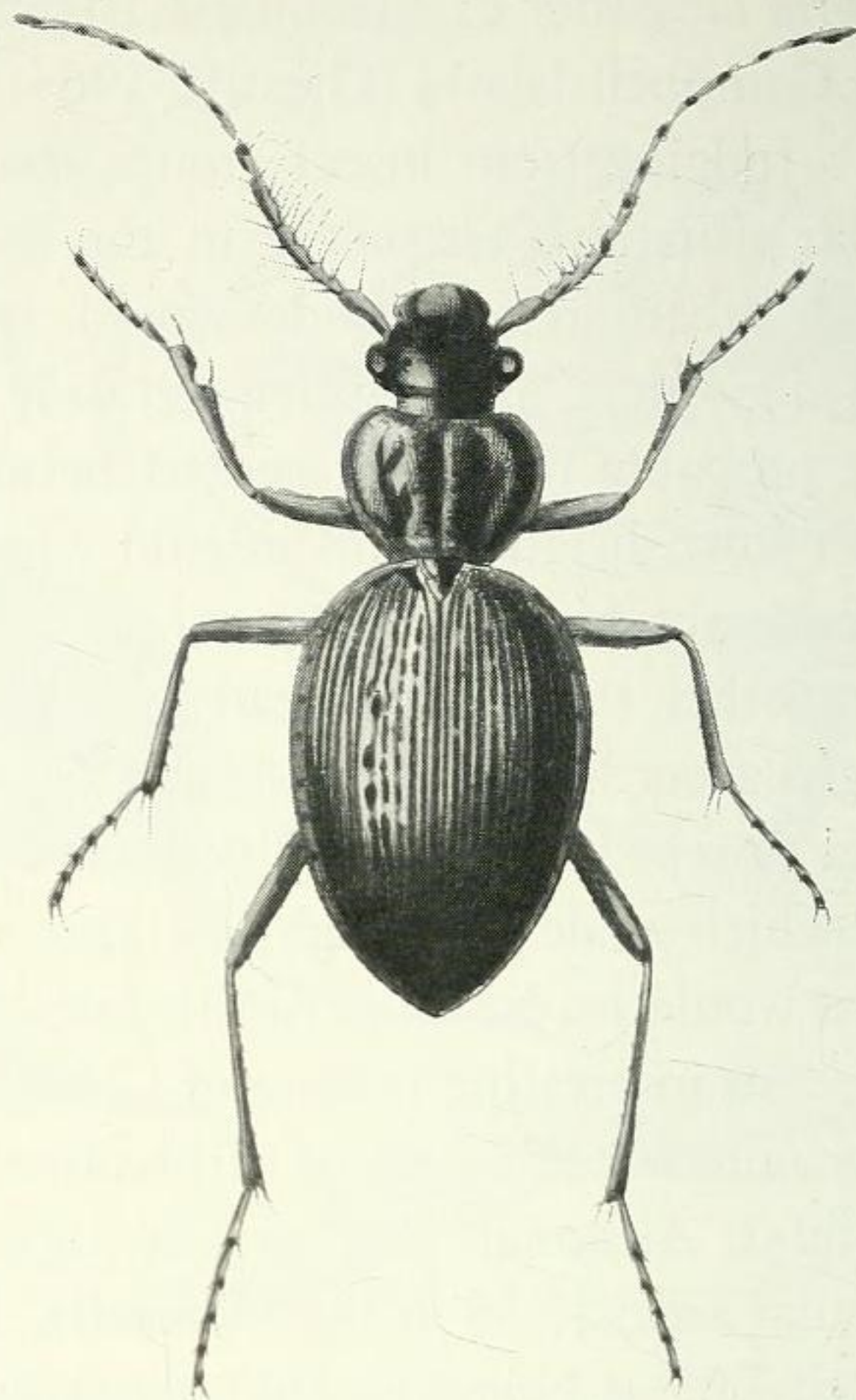


FIG. 12.12. *Loricera wollastoni*, a flightless carabid (Coleoptera) from Madeira (from Wollaston, 1854).

work, it can still be admired for its care to ecological detail. Indeed, such information would be perhaps impossible to secure today. For purposes of precise reference to Wollaston's volume, I am retaining his nomenclature.

Eurygnathus latreillei (fig. 12.11) is interesting to us for several reasons. Not only is this carabid beetle apterous, but its elytra are connate—or “soldered” as some have said—definitely canceling the power of flight. Its ancestors were, with little doubt, carabids capable of flight. In addition to this striking expression of flightlessness, *E. latreillei* exhibits different size tendencies in different localities. Although found beneath stones on the small islands of Porto Santo and on the Desertas (both offshore islet groups of Madeira), specimens on Deserta Grande are much larger than those on Porto Santo, according to Wollaston. This is also true of another carabid, *Olisthopus maderensis*, much larger on Deserta Grande than on Madeira itself. Wollaston erects a new genus, *Thalassophilus*, for a flight-

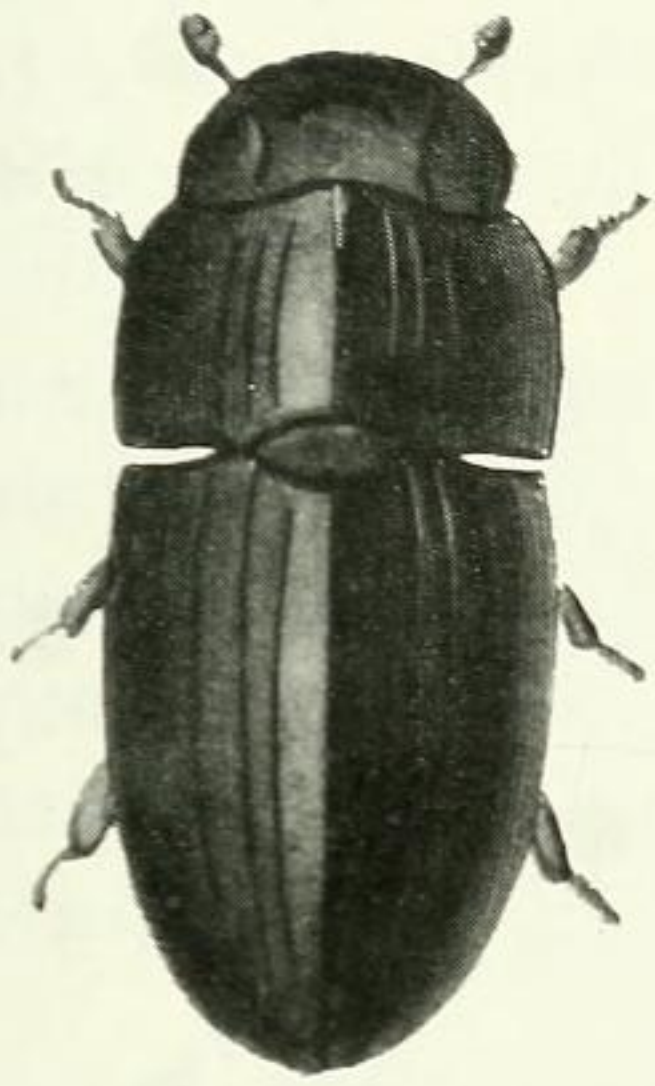


FIG. 12.13. *Cossyphodes wollastoni* (Colydiidae), a flightless and eyeless coleopteran from Madeira (from Wollaston, 1854).

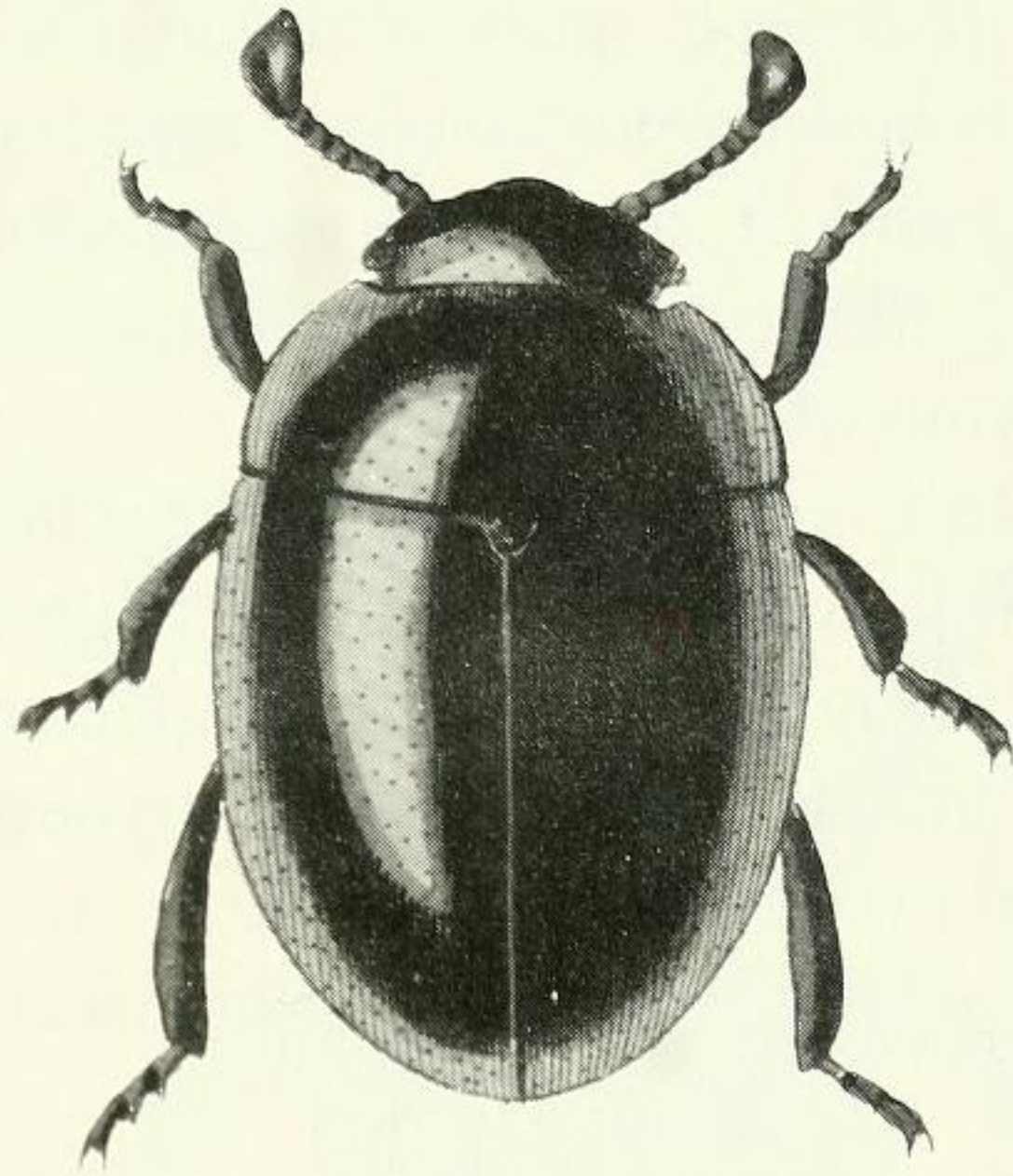


FIG. 12.14. *Cholovocera madaerae* (Coleoptera: Lathridiidae), a flightless beetle from Madeira (from Wollaston, 1854).

less reduced-wing carabid of gigantic size compared with its closest relative, *Aëpus. Bembidium obtusum*, a widespread species, attains a much greater size on Madeira than in Europe. Comments on gigantism on islands, which may be relevant to the preceding instances, will be found in chapter 15.

The carabid *Loricera wollastoni* (fig. 12.12) has vestigial wings but normal elytra. It lives chiefly under logs and leaves. Wollaston suggests that its peculiar antennae and long legs are virtually "supralimital" characteristics within the genus *Loricera*.

Another Madeiran carabid, *Harpalus vividus*, is wingless, with elytra connate to various degrees. Lowland and high-elevation populations have soldered elytra and are dull in color, whereas elytra are separate and body colors are brighter in mid-elevation populations.

Other families of Coleoptera on Madeira show flightlessness independently. *Tarphius* (Colydiidae) is an example, with reduced wings. Wollaston notes that *Tarphius* species are strictly nocturnal. Interestingly, Greenslade (1968) notes that nocturnalism and dark colors are much more common in Coleoptera with reduced wings, whereas diurnalism and brighter colors are commoner in normal-winged species. Another genus of Colydiidae, *Cossyphodes* (fig. 12.13), a Madeiran endemic, is interesting not merely in its winglessness and exceptional shape, but in its loss of

eyes. It feeds in nests of an ant, *Oecophora pusilla*. Although the legs of *Cossyphodes wollastoni* are apparently small in relation to body size and it is blind, it runs with exceptional velocity. Another endemic colydiad genus, *Pleiosoma*, is also wingless and occurs "in the very center of moist decaying wood."

In the family Lathridiadae, *Cholovocera maderae* (fig. 12.14) is notable in its vestigial wings. Although not blind, its eyes are much reduced, with many fewer facets than are characteristic for beetles. It is not surprising, therefore, that it, like *Cossyphodes*, is predatory in nests of ants. Reduced eyes of this type occur in an endemic Madeiran species of another ant-predaceous genus, *Metophthalmus*, which has European species as well.

In Ciidae, the Madeiran endemic species *Cis wollastoni* is exceptional for its genus by virtue of its large and elongated body. Among flightless curculionids, numerous Madeiran species could be cited, such as *Atlantis vespertinus* (fig. 12.15). Wollaston created this endemic genus for flightless species in which wings are absent and elytra firmly united. These features are also shared by another endemic curculionid genus that Wollaston named *Echinosoma*. *Echinosoma porcellus* (fig. 12.16) is exceptionally setose and has an unusual "robust" rounded form, yet it has delicate antennae. *Atlantis* lives beneath moss on trees and is strictly nocturnal. *Echinosoma* occurs beneath stones and logs.

LAKE BAIKAL INSECTS

Lake Baikal exhibits many insular features, as do other freshwater lakes (see chapter 9), so it is not surprising to find certain situations of flightlessness there among a family of aquatic caddis flies, Limnophilidae. In Lake Baikal, there are two endemic genera, *Baicalina* and *Thamastes*, while the only other genus of the tribe Baicalinini, *Radema*, lives in the Lena and other creeks that flow into Lake Baikal. Larvae of *Baicalina* and *Thamastes* live on the rocky bottom of the littoral of Lake Baikal, *Radema* larvae occur underwater in streams. As the water rises in spring and summer in Lake Baikal, adults formed from larvae occur at a distance from the newly expanded shoreline, toward which they swim in droves. Wings and legs of the three endemic caddis-fly genera are modified for swimming (Martynov, 1929, 1935). The wings are not capable of flight but are used



FIG. 12.15. *Atlantis vespertinus* (Coleoptera: Curculionidae), a flightless weevil from Madeira (from Wollaston, 1854).

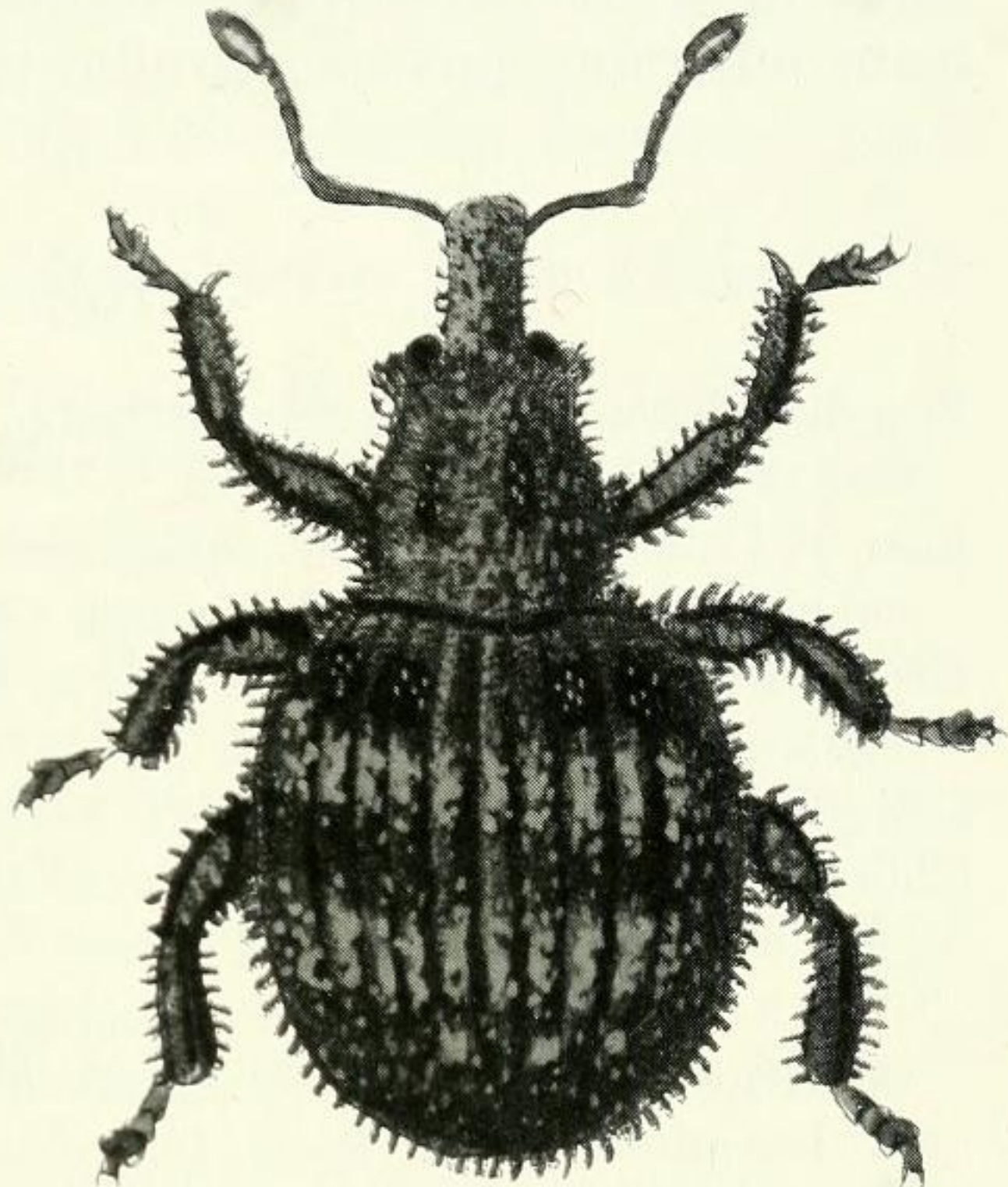


FIG. 12.16. *Echinostoma porcellus* (Coleoptera: Curculionidae), a flightless weevil from Madeira (from Wollaston, 1854).

as “paddles.” Kozhov (1963) attributes the wingless habit to the limited habitat available. He states that fully winged insects with a typical caddisfly life cycle would be bound to be driven far from the shore and could not have offspring. This is reminiscent of the Darwinian interpretation of the effect of wind pressure on insular insects. Certainly, at least precinctiveness and a limited stable habitat are involved. Lake Baikal is unusual in its low temperature, and larvae of the endemic limnophilid genera are adapted to this and might not survive under other temperature regimes.

NEW ZEALAND INSECTS

Among the many interesting flightless insects of the mainland islands of New Zealand, the wetas (Orthoptera) have received abundant comment because of their flightlessness, hopping habits, and adaptive radiation in wet recesses in caverns and forest situations (see chapter 7). Among hopping Orthoptera, the wetas are also unusual in their capability to regen-

erate appendages of near-normal size (Ramsay, 1964). Is this ability related to their total reliance on legs for locomotion, or does the relative longevity of the wetas (two years or longer) play a role? This is one of the many intriguing questions possibly related to loss of flight on insular areas.

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