Fauna of
New Zealand

Fauna of New Zealand
Number 19

Mantodea
(Insecta),
with a review of aspects of
functional morphology and biology*

G. W. Ramsay

DSIR Plant Protection
Mt Albert Research Centre
Private Bag, Auckland, New Zealand

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* Femoral brush, wing morphology, pterostigma, coloration, stridulation, acoustic sensitivity, defence behaviour, regeneration, predation, parasitism, pathology, and diet

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Front cover. The insects depicted are *Orthodera novaezealandiae*, female (above) and *Miomantis caffra*, female (below)

ABSTRACT

Orthodera novaezealandiae (Colenso) (Orthoderinae) and *Miomantis caffra* Saussure (Mantinae) are the only two species of mantid established in New Zealand. *O. novaezealandiae* is taxonomically very close to some populations of *O. ministralis* (Fabricius) in Australia, with which it has generally been regarded as synonymous; it is here reaffirmed as a distinct species. *M. caffra*, a southern African species, was discovered in New Zealand in 1978 and is now established around Auckland and spreading. The taxonomy and status of these species are outlined, and characters distinguishing between them in all life stages are tabulated and illustrated. Morphology and life history are described in detail, with particular attention to variation in wing venation and genital characters. The history of mantid classification is discussed, and several aspects of mantid morphology and biology are critically reviewed, from a worldwide perspective, in the light of a detailed examination of the New Zealand species. These are: (a) femoral brush; (b) wing morphology; (c) pterostigma; (d) coloration; (e) stridulation; (f) acoustic sensitivity; (g) defence behaviour; (h) regeneration; (i) predation (on mantids); (j) parasitism; (k) pathology; (l) diet. SEMs show details of the femoral brush, pterostigma, and cyclopean ear (acoustic receptor).

CHECKLIST OF TAXA

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ACKNOWLEDGMENTS

in valuable observations and useful information which have been incorporated into the present work.

Museum staff have co-operated with information about the mantid specimens under their care: Keith Wise and Rosemary Gilbert (Auckland Museum), Ron Ordish and Pamela Lovis (National Museum), Anthony Savill (Canterbury Museum), and Anthony Harris (Otago Museum). So too have many other entomologists: Don Cowley (Auckland University), George Gibbs (Victoria University), Peter Johns (Canterbury University), and Warwick Don (Otago University); in Auckland O. Green (MAF), R. Kleinpaste (MAF), and C. Green (DoC); in Rotorua M. Nuttall (FRI); in Wellington M.J. Meads (DSIR Ecology) and J.D. Tenquist (MAF); in Christchurch R.P. Macfarlane (DSIR Plant Protection); and in Otago G.F. McLaren (DSIR) and B.H. Patrick (DoC).

In the private sector, Mrs D. Melville (Auckland), Mrs J. St Paul (Waiheke Island), P.L. Wilding (Howick), Charles Reid (Auckland), Denis Gibb (Hamilton), Eddie McCutcheon and Frank Chambers (Taranaki), Ian McLellan (Westport), Jason Castle (Christchurch), and numerous other persons have supplied information. Mr Tom Davies of Haumoana, Hawkes Bay, has been particularly helpful in obtaining specimens from Colenso's type locality and soliciting other information. Miller Avenue School, Paeroa, and Wairoa College assisted in gathering information.

The librarians at DSIR's Mt Albert Research Centre – Jeanette Muggeridge, Bella Smith, Marleene Boyd, Jill Unwin, and Maria Pfeiffer – have always been most helpful with obtaining literature; and Pamela Gilbert (BMNH) has assisted with certain esoteric literature citations.

Persons overseas have also assisted in many ways: Dr J. Balderson and Dr K.H.L. Key (CSIRO, Canberra); the late Dr Max Beier (Naturhistorisches Museum, Vienna); Dr B. Hauser (Muséum d'Histoire Naturelle, Geneva); Dr A.P. Kaltenbach (Naturhistorisches Museum, Vienna), who first identified the New Zealand population of *Miomantis caffra*; Dr Graeme Lowe and Mrs J. Marshall (British Museum (Natural History)); Dr G.M. Nishida (Bishop Museum, Hawaii); Mr R.D. Pope (BMNH); and Prof. D.K.McE. Kevan (Lyman Entomological Museum, Macdonald College, McGill University, Canada), who has made many helpful comments about the functional morphology and biology section of this work. My wife Helen has patiently read through and commented on various drafts.

I greatly appreciate the skills of Paul Sutherland in the preparation and photography of specimens for SEM examination, and of Des Helmore in the preparation of some illustrations.

To all these persons I say a sincere 'Thank you!', and hope that the publication of this work will be some recompense for their efforts and support.

INTRODUCTION

Praying mantids have held a long-standing fascination and interest for mankind, and feature prominently in the traditions and mythology of some cultures – in Africa, Europe, China, and Japan, for instance; they appear in old African cave drawings, and on a Roman coin (K.M. Rudall, pers. comm.). They have been the subject of folk-tales and of dances; a ballet, 'Mantodea', choreographed by Vassili Sulich and first performed in Las Vegas in 1976, was presented during the 1984–86 seasons by the Royal New Zealand Ballet Company (Anon. 1985). The public perception of mantids as ferocious predators is also sometimes exploited in cartoons, for example 'The Preying Douglas' (Abacus 1986).

What are the biological realities underlying these images and perceptions?

Suborder Mantodea
Praying mantids are exopterygote insects, that is, their wings develop as external buds on the thorax of the nymph and increase in size at each moult. The wings are hinged through a series of sclerites and so can be folded along the body – a characteristic of the insect infraclass Neoptera. Mantids are moderate-sized to large insects with typical orthopteroid mouthparts (i.e., mandibles, maxillae, etc., developed for biting and chewing) and with large raptorial forelegs which have elongate, mobile coxae. All species are predaceous, capturing insects or spiders.

The head, which is not covered by the pronotum as it is in the Blattodea, is freely movable with large, globose or conical compound eyes and three ocelli; the ocelli are sometimes larger in males, and occasionally are lost in females. The antennae are slender and filiform, with numerous segments. The maxilla has five-segmented palps and the labium three-segmented palps.

The pronotum is usually elongate, narrow, and movably attached to the mesothorax. The femora and tibiae of the raptorial forelegs have rows of spines on their opposing surfaces, and the tibia terminates in a sharp, curved spur. The middle and hind legs are normal walking legs with no special modifications. All tarsi are five-segmented. There are two pairs of wings, which may be reduced or absent in females. At rest the wings are folded along the abdomen. The forewing is narrow and leathery, with a small anal lobe, and the hind wing is membranous with a narrow anterior blade and broad, fan-like anal lobe. The venation of both wings is characteristic in mantids, and is discussed in detail on pp. 36–41.

The dorsoventrally flattened abdomen comprises eleven segments including one or more reduced terminal segments. There is a pair of segmented cerci in both sexes. The

male genitalia are asymmetrical, the ninth sternum (subgenital plate) usually bearing a pair of styli. In the female the seventh sternum forms a cleft subgenital plate which surrounds the three pairs of small valves of the ovipositor.

The alimentary canal is relatively short and straight, with a large crop, a six-toothed or six-ribbed proventriculus, and eight mid-gut caeca. There are more than a hundred fine Malpighian tubules.

The diploid chromosome number ranges from 15 to 39, and the males are mostly XO, although in some genera the sex determination system is $X_1X_2 Y$.

The egg-case (ootheca) of mantids is unique. From 10 to 400 or more eggs are laid in a horny ootheca which may be enveloped in a lighter, spongy envelope also produced by the female's accessory glands. The ootheca, which has a characteristic form in each genus or species, is usually attached to surfaces such as stems, bark, or rocks, but is placed in the soil by members of some genera. The embryos form a pair of chitinous hatching threads (unique amongst arthropods) from which the newly emerged nymph is suspended during its first moult. The nymphs (miniature adults) increase in size at each moult, of which there are from five to nine, and the wing-pads, genitalia, and antennal segments increase proportionately at each stage. The wing pads do not reverse their orientation in the later nymphal stages, as they do in other orthopteroid insects such as the Gryllacridoidea, Tettigonioidea, Grylloidea, and Acridoidea.

The coloration of mantids tends to be cryptic, matching that of their preferred habitat – foliage, or bark, or the soil surface, and so on. Sometimes leaf-like expansions of the body and limbs are developed. Many species have bold, striking markings on the wings and forelegs which may serve to visually startle or warn would-be predators, but which may also attract prey in some instances.

The specialised raptorial forelegs of the Mantodea are not unique amongst insects. They occur in similar form amongst such diverse groups as the Mantispidae (Neuroptera), Emesinae (Reduviidae, Hemiptera), and Hemerodromiinae (Empididae, Diptera). Some of these are confused with mantids by the uninformed.

Other characters also distinguish the Mantodea: the possession by many species, if not all, of a forewing pterostigma or incipient pterostigma; the presence of a tympanate auditory organ in the mid-ventral longitudinal metathoracic groove of many species (Yager 1989); the presence of a femoral brush on the inner distal aspect of the fore femur; the articulation of the antenna with the head capsule comprising a long, rod-like mid-ventral projection of the antennal sclerite; the presence of anastomosing ridges alternating with teeth in the proventriculus; in the forewing, the presence of a proximal lobe bounded by the

peripheral vein leading to a weak cubital furrow; and in the hind wing the absence of the first vannal vein, except in primitive species, and the presence of an $r–cu_1$ cross-vein.

The distribution of Mantodea is essentially tropical to subtropical, with a few species in temperate regions (Beier 1939). The order comprises approximately 1800 species, organised into more than 320 genera and eight families.

General accounts of the Mantodea have been given by Sharp (1895), Chopard (1949), Beier (1964, 1968), Key (1970), Kaltenbach (1976), Richards & Davies (1977), and Brown (1982).

The close relationship and common origin of the Mantodea and Blattodea has long been acknowledged, and has been briefly summarised by Judd (1948). Characters in common are: presence of unpaired abdominal ganglia in the nervous system; similar external morphology, abdominal musculature, and abdominal appendages; scape articulation with the head capsule comprising a mid-ventral extension of the antennal sclerite; proventriculus conical, with eight tubular gastric caeca at its junction with the mid-gut; internal structure of the proventriculus almost identical; forewing Cu_2 characteristically curved, and branching of Cu_1 similar (Ragge 1955); arrangement of vannal veins of hind wing identical, except that $1V$ is lost in mantids (Ragge 1955).

Classification

Knowledge of the Mantodea is insufficiently advanced as yet for a definitive classification to have been produced; the system is still developing (Roy 1987a). In 1839, when Audinet-Serville produced his monograph on the Orthoptera, the mantids were placed in one family and classified according to the size and shape of the prothorax. In 1869 Saussure proposed a classification using prothorax characters and the shape of the eyes. He subsequently refined this (1870b), but then (1872a) developed another classification comprising two divisions: the Nudipèdes, in which all genera lacking extensions or expansions on the head, abdomen, and legs were included; and the Lobipèdes for the genera in which such expansions were present. Within each of these he recognised two main groupings, based in one on the shape of the pronotum at the point where the coxae are attached, and in the other on the shape of the antennae. Stål (1873) regarded these characters as being of secondary significance, and suggested that the structure of the raptorial leg, especially the tibia, was of prime importance. In 1877 he proposed an alternative classification in which the mantid genera were arranged in six subfamilies based on the form and structure of the raptorial legs and of the eyes.

The English orthopterologists Westwood (1889) and Wood-Mason (1889) uncritically accepted Stål's system.

Brunner von Wattenwyl (1893) examined both systems, pointed out various spurious generic associations that resulted, and proposed a new classification derived from the good points of both. He suggested that there are six main groups, distinguished firstly by characteristics of the raptorial legs and then by characters such as the shape of the pronotum, the form of the antennae, and whether or not the legs have lobes. This system was adopted by Sharp (1895) in his contribution to the 'Cambridge Natural History'. Kirby (1904), in the first volume of his 'Synonymic Catalogue of Orthoptera', arranged the mantids in one family comprising eight subfamilies. Giglio-Tos (1914, 1917b, 1919) developed these concepts of mantid classification, his work culminating in the 1927 'Das Tierreich' review in which he recognised 32 subfamilies within the single family Mantidae. Then Beier commenced his researches, and the system was changed yet again (Beier 1934a–c, 1935a–c). The Giglio-Tos system was unsatisfactory in that it resulted in a superficial association of unrelated groups and genera. For example, the orthoderinids were grouped with the eremiaphilids. In Beier's system, in which eight families were recognised, many of the Giglio-Tos groups were downgraded or merged with others, new subfamilies were recognised, and the old system was revamped to give a more natural classification, better reflecting phylogenetic relationships. This is the system presented in Beier's 1964 and 1968 reviews and which has been accepted by Richards & Davies (1977) and Brown (1982).

Chopard, in his 1949 'Traité de Zoologie' review, recognised thirteen families, with twelve subfamilies in the Mantidae. His system has not been adopted by more recent researchers. In the currently accepted system there are eight families, of which the Amorphoscelidae have two subfamilies, the Hymenopodidae three, the Mantidae twenty-one, and the Empusidae two. The bulk of the species are in subfamily Mantinae of the Mantidae. The large number of subfamilies is not satisfactory, and some – especially those with good diagnostic characters such as the Thespinae, Iridopteryginae, Sibyllinae, Orthoderinae, and Deroplatyinae – should be promoted to full family status (Roy 1987a). The New Zealand species belong in the family Mantidae, one in subfamily Orthoderinae, the other in Mantinae.

The cytology of praying mantids, especially their sex chromosome mechanism, may have some significance in the higher classification of the group (White 1951, 1965).

In general, mantid classification is based on the form of the raptorial forelegs and of the antennae, the shape of the pronotum and of the compound eyes, and colour. Male genital structure and details of wing venation are not used to any great extent, and female genital structure not at all.

Paulian (1957) illustrated the male genitalia of many of the Madagascan species he redescribed, and mentioned some wing characters, but did not use this information in identification keys or classification. Male genital characters were used by Beier (1955) to discriminate between the species of *Miomantis* in South Africa.

It is likely that the structure of both male and female genitalia – the shape of the hypophallus, pseudophallus, and so on; the shape of the ovipositor valves – will provide useful characters for higher categories of classification, as well as at the species level. The finer details of wing venation may be useful in this context as well. Regrettably such information is not available for most mantid species. In the present work all these structures are described and illustrated in detail, so that the information will be available for future reviews of mantid classification.

New Zealand's mantids

The New Zealand mantid fauna comprises two species only, one of them widespread and established probably long before human settlement, and the other a very recent introduction from South Africa with a restricted but expanding distribution in the north. The former, commonly known as 'praying mantis' *(Orthodera)*, was among the insects described from this country during the early days of settlement by Europeans. An ootheca collected by Dr Andrew Sinclair during 1841 at the Bay of Islands or Auckland or possibly on Great Barrier Island is mentioned by White & Doubleday (1843) and referred to by White (1845–1874). It is still in the British Museum (Natural History) collections, in London. Taylor (1855) stated that the mantis abounds, but may have been confusing phasmids with mantids.

The first nymphs and adults to be reported on were collected at Scinde Island (now Bluff Hill), Napier in 1878–79 and described by Colenso (1882). There was thus a gap of nearly 40 years from the time this species was first found in New Zealand until it was formally named. Potts (1884) found mantids in Canterbury in 1880, and Hutton (1897) stated that he had found them at Clyde in 1873–74. Hutton (in Potts 1884) had sent an adult female specimen to Wood-Mason – a world authority on Mantodea at that time – in Calcutta several years prior to 1883. Although Wood-Mason (1889a) identified it as *Orthodera ministralis* (Fabricius), he did in fact distinguish the New Zealand specimen from its Australian counterpart on morphological grounds (less dense reticulation of the forewing). *O. ministralis* is the name by which this taxon has been known in New Zealand ever since.

Elsewhere it has been regarded as a distinct species – Colenso's *O. novaezealandiae* – by such authorities as Giglio-Tos (1927) and Beier (1935b). Even though

morphologically *O. noveazealandiae* lies within the range of variation of *O. ministralis*, it is regarded as being distinct for the following reasons. The New Zealand population is relatively constant in its morphological features, whereas the Australian one is quite variable, and possibly comprises several taxa. Secondly, the New Zealand population is geographically isolated. Thirdly, the nominal separation is a convenient means of keeping information about the two populations distinct and conveniently accessible.

A single specimen of a second species was collected at Auckland some time before 1870 and described by Saussure (1870) as *Tenodera intermedia*. It is a large species (about 75 mm long), and has not been found again in this country. Probably it was a vagrant carried here by ship from northern Australia or New Guinea, where it occurs today. A third species, *Tenodera australasiae*, has been listed several times as occurring in New Zealand, but this is incorrect, and results from repetition of a mistaken record of Kirby (1904).

A fourth species, *Miomantis caffra* Saussure, known as the springbok mantis, was discovered in suburban Auckland in 1978. It was most likely introduced accidentally as a fertile ootheca on imported plants. It is now well established and expanding its area of distribution; it may even be displacing *O. novaezealandiae*, as *Tenodera sinensis* is possibly doing to *Stagmomantis carolina* in North America (Hurd 1985). *M. caffra* oothecae contain many more eggs than do those of *O. novaezealandiae*, and the emergence period is extended, so that predation on newly hatched nymphs is probably less severe and the chance of some of them encountering favourable conditions is greater. Also, the life cycle is not so rigidly seasonal – nymphs emerge unseasonally, and adult females survive the winter more frequently than is the case with *O. novaezealandiae*. On the other hand there may be some ecological separation, in that *M. caffra* tends to favour rank grass and weedy areas as well as shrubs and to hide beneath foliage, etc. (the abdomen of nymphs is curved), whereas *O. novaezealandiae* prefers shrubs and utilises the upper surfaces of foliage (abdomen of nymphs straight), often aligning itself to the sun.

Although by no means exhaustive, there is a certain amount of information available about the biology and distribution of mantids in New Zealand, not all of which is touched upon in this contribution. Three university degree projects have been produced, one of which has resulted in a publication; there is otherwise little biological information available:

• Ward (1969), "Aspects of reproduction in *Orthodera ministralis*", in which courtship, copulation, and other aspects of sexual behaviour such as the effect of light, time of day, influence of vision, and recognition of the sexes were studied. Oviposition, egg development, morphology of the female reproductive system, biochemistry of the ootheca, and the spermatophore are described also.

• Suckling (1978), "Laboratory studies of the praying mantid *Orthodera ministralis* (Fabricius)", in which predation, population density, shelter, availability of food, cannibalism, effect of temperature and humidity on the survival of immature stages, life history, and sexual dimorphism were studied.

• Craven (1982), "Pre-strike tactics and visual mediation in a praying mantis *(Orthodera ministralis)*". The effect of environmental factors such as light, background, and surroundings, and such aspects of behaviour as response to lures, distance from prey, approach to prey, movement and removal of prey, visual occlusion, and response to stimuli were studied. Also, the anatomy and functional organisation of the eye and the role of the eyes in mediating predatory behaviour were described or discussed.

The cytology of *O.novaezealandiae* has not been investigated, but White (1962, 1965) has studied the chromosomes of males of two species of *Orthodera*, including *O. gunnii*. The karyotype is distinguished by the large size of the equal arms of the Y chromosome. The New Zealand species is probably similar.

The most recent accounts of New Zealand mantid biology and ecology are those of Crosby (1984), Suckling (1984), and Castle (1988). Much remains to be discovered about praying mantids, especially the species present in New Zealand. They are fascinating insects to keep as pets, and are easy to rear (Meadows 1979, Heath 1980). Perhaps this study may stimulate further investigation.

Origin of *Orthodera novaezealandiae*. There is little doubt that the common New Zealand praying mantid *O. novaezealandiae* originated in Australia. The evidence can be interpreted to support the opinion that it is pre-European, as is probably also the case with several other New Zealand orthopteroid insects which have very close – if not conspecific – relatives in Australia: *Caedicia, Teleogryllus* (see Bigelow 1964), *Pteronemobius, Locusta, Phaulacridium*. The evidence is:

• The New Zealand population is relatively constant morphologically, which indicates that there was only one initial introduction or that, if multiple invasions occurred, all originated from a morphologically constant population.

• *Orthodera* prefers shrubland and open country rather than forest or grassland, and may not have been so widespread or abundant in pre-European times because of this. The clearance of lowland forest following European settlement, and the consequent increase in its preferred habitat, probably contributed to its spread and increase during the 1870s and 80s (see Thomson 1922).

Hutton (1897) was firmly of the opinion that it had been introduced into "... Auckland from Sydney, and into Otago from Tasmania or Victoria at the time of the commencement of the gold-diggings, when large quantities of hay were brought to Otago from Australia." He had not seen the mantid during his sojourn in the Auckland area (1866–70), although it was certainly present there about 1876. It was reported in Napier 1878–79 (Colenso 1882), Canterbury in 1880 (Potts 1884), and Nelson in 1886 (Hudson 1892).

O. novaezealandiae appears to have become widespread within a relatively short time, especially when compared with the recent spread of *Miomantis caffra*. Even after ten years, this latter species has still not fully colonised Northland and has not yet reached the Waikato. Even though the female is flightless, her numerous and indiscriminately laid eggs could be expected to be widely dispersed under present-day conditions. *O. novaezealandiae* was widely distributed from Auckland to Otago within thirty years. Certainly the female can fly, but she is not a strong flier, and does not readily take wing, so this is unlikely to be of great advantage in dispersal.

Hutton seems to have been persuaded by the sudden appearance and abundance (see Wood-Mason 1889a) of *O. novaezealandiae* during 1873–74 at Clyde, where it was regarded as a newcomer, its sudden and widespread appearance during the 1870s and 80s, his acceptance of its common identity with the Australian population, and the availability of means of dispersal from Australia. Wood-Mason (1889a) agreed with this view, even though he distinguished his New Zealand specimen from Australian material on morphological grounds. Frogatt (1907) also thought that this mantid could have been easily introduced from Australia on foliage. Tillyard (1926) stated that it appeared to have arrived in New Zealand with the earliest European settlers.

The evidence of Maori traditions and knowledge should be considered, though it is now fragmentary. Dall (1872; cited in Godley 1985) stated that with the Maori of the generation that is dying out, "every plant, every animal, every insect even that New Zealand knows has its proper name. The new generation has not acquired the knowledge ...".

Best (1908) states that "the old men who held full knowledge of the old customs, myths, and quaint beliefs have now passed away, and much interesting lore has died with them. ... The ritual pertaining to all work connected with the forest and its fauna was of a most extensive and pervading character. ... the bulk of such matter is lost." However, the fragments that have survived are interesting, and indicate that the Maori recognised the praying mantis.

Miller (1952) states that the "...distinction between the mantis and the stick-insect was of importance to the Maori; if *whe* alighted on a woman it was a sign of conception, and according to which kind of *whe* (mantis or stick-insect) it was known whether the child would be a male or a female."

It is also stated that the praying mantis is the material emblem of the god Te-Ihi-o-te-Rangi (corrected from Te-Ihi-o-te-Ra). This information is repeated by Kreuzer (1983), who also suggests that some Maori petroglyphs represent insects (though not, unfortunately, mantids). However, Wendy Pond (in prep.), in a review of Maori knowledge and language relating to the praying mantis, finds that the distinction between mantids and phasmids is not always clear. This applies to many people, of diverse races and cultures.

In the scientific literature mantids and phasmids have been grouped together as 'Gressoria', and numerous phasmid species were initially placed in the 'genus' *Mantis*. It was only in 1813 that Stoll divided the 'genus' *Mantis* into *Mantis* and *Phasma*. Pond (in prep.) has gathered together such fragments of Maori knowledge and perceptions of the praying mantis as survive, and finds little to confirm or reject the suggestion that this insect was present in New Zealand in pre-European times. On balance, taking into account the points discussed earlier and the indications of involvement of mantids in Maori tradition, it seems most likely that the praying mantis, *Orthodera novaezealandiae*, was present in New Zealand before European settlement began.

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DESCRIPTIONS

Family MANTIDAE

Diagnosis. Head broader than long. Eyes large; ocelli usually well developed in male only. Antennae filiform, sometimes ciliate or thickened but never bipectinate. Wings of male only rarely reduced or degenerate, of female often so. Prothorax several times longer than broad. Femur of raptorial leg always with ventral spines, at least distally; spines of inner (prolateral, anterior) row alternately long and short; tibia terminating in a strong claw, and with 2 rows of ventral spines, those of the outer (retrolateral, posterior) row separate from each other and erect or slanted, rarely reduced. Suranal plate sometimes elongate; cerci occasionally modified; styli usually present on male subgenital plate. Colour green or brown, never metallic nor with strong, bicoloured, transverse or spiral markings on forewing.

Remarks. The Mantidae are morphologically diverse, widely distributed geographically in subtropical and temperate regions, and comprise the bulk of the species of Mantodea. In the most recent revision (Beier 1968), twenty-one subfamilies are recognised. The two New Zealand subfamilies are easily separated by the shape of the pronotum, which is broad, more or less straight-sided, anteriorly truncate/sinuate, and slightly overlying the head in the Orthoderinae, and slender with a swollen/expanded area over the insertion of the foreleg coxae and a rounded anterior shape in the Mantinae. Also, the venation of the forewings is normal in the Mantinae but densely reticulate in the Orthoderinae.

Characters separating the two species are summarised in Table 1 (p. 12).

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Subfamily ORTHODERINAE

Diagnosis. Head plain, without extensions or ocellar tubercles; eyes rounded, occasionally slightly conical. Pronotum flat or roof-shaped, with a mid-dorsal longitudinal ridge, more or less parallel-sided, slightly widening anteriorly; anterior border truncate, sinuous, spanning most of posterior part of head, which it cradles and slightly overlies. Wings fully developed in both sexes; forewings (tegmina) with a dense network of veins, never with eye-spots or markings; hind wings membranous, clear. Raptorial femur with 4 discoidal and 4 outer spurs; walking legs normal, without apical expansion, cylindrical in cross-section. Suranal plate triangular, not elongate. Colour uniformly green.

Remarks. The distinctiveness of the Orthoderinae, based on the form of the pronotum, has long been recognised. Burmeister (1838) afforded the taxon equal status together with fourteen other genera, one of which (*Mantis*) comprised thirteen species groups.

In Saussure's 1869 system the Orthoderites are recognised as a subtribe of the tribe Mantii, while in his 1870a system the Orthoderii comprise one of the two divisions of his Nudipèdes, and have equal status with the Mantii. Stål (1877) did not recognise this distinctiveness, and included *Orthodera* in his subfamily "Eremophilidae". The family Orthoderidae was one of six recognised by Brunner von Wattenwyl (1893), but was not recognised as such by Kirby (1904), who included *Orthodera* along with seventeen other genera in the subfamily Eremiaphilinae. The assemblage of genera comprising this subfamily remained together in the Giglio-Tos (1927) system, in which the

Orthoderae were recognised as one of ten groups of the subfamily Eremiaphilinae. Beier (1935b), recognising the polyphyletic and superficial nature of this concept, redistributed the genera so that the Eremiaphilinae came to comprise two genera only, and the subfamily Orthoderinae was reinstated. Chopard (1949) gave the taxon family status as the Orthoderidae, but Beier (1968) still considered it to be a subfamily of the Mantidae. Although Roy (1987a) has also suggested that it should have familial status, along with several other subfamilies, this has yet to be effected.

The broad, parallel-sided pronotum and dense reticulation of the forewings (tegmina) are the main distinguishing features of Orthoderinae. The subfamily is restricted to Australasia, and comprises two genera only, *Orthodera* and *Orthoderina*. No tribal taxa are recognised.

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Genus *Orthodera* Burmeister

Orthodera Burmeister, 1838: 529. Type species *Orthodera prasina* Burmeister, 1838, by original designation; synonymised with *Mantis ministralis* Fabricius (1775, p. 277) by Westwood (1889, p. 2) and Wood-Mason (1889, p. 20).

Bolidena Blanchard, 1853: 356. Type species *Bolidena hobsonii* Blanchard, 1853, by original designation. Synonymised with *Orthodera* by Saussure (1872a, p. 15).

Diagnosis. Medium-sized, rather slender, uniformly green mantids. Head triangular; eyes prominent, projecting a little and slightly conical, but rounded; ocelli and antennae situated on upper edge of head, the ocelli on small elevations; antennae filiform; frons pentagonal, wider than high; vertex plain, without extensions. Pronotum almost flat, with a median longitudinal ridge; sides straight, mostly parallel but slightly diverging anteriorly; supracoxal swelling absent; anterior margin truncate, sinuous, cradling occiput of head; posterior margin likewise truncate, but laterally notched. Wings present in both sexes, well developed, extending beyond tip of abdomen; tegmina densely veined; hind wings hyaline. Raptorial legs strong; coxa with small denticles; femur deep, with 4 discoidal and 4 outer spines, the claw-furrow situated near middle of segment; tibia with 12–14 closely packed outer spines; middle and hind legs normal; middle metatarsus shorter than all other segments together, hind metatarsus equal to them. Suranal plate triangular, not elongate; cerci moderately long, simple. Sexual dimorphism slight.

The genus is restricted to Australasia, including Australia, New Zealand, New Guinea, and Timor.

Table 1 Characteristics of the two New Zealand mantid species

Orthodera novaezealandiae	*Miomantis caffra*
Adults (Fig. 1, 3, 4)	**Adults** (Fig. 2, 5, 6)
Sexual dimorphism slight	Sexual dimorphism strong
Colour constant, always green	Colour variable, green to pale brown
Pronotum broad, as wide as head, more or less straight-sided and with lateral carinae; head and pronotum together approximately 25% of body length	Pronotum narrower than head and with a node or swelling; lateral carinae absent; head and pronotum taking up approximately 35% of body length (less in male)
Females with power of flight; forewings similar in both sexes, elongate elliptical, completely covering abdomen in gravid individuals, with a dense network of fine veins in which the pigment is confined	Females without power of flight; forewing subfalcate, not fully covering abdomen of gravid individuals; venation normal; pigment present in both veins and membrane. Male forewing elongate, slender; costal area pigmented, remainder clear; venation normal
Hind wings similar in both sexes, clear	Female hind wing small, subfalcate when folded, sometimes coloured bright yellow. Male hind wing large, clear
Forelegs with inner surface of coxa uniformly yellow; femur with a conspicuous vivid blue patch on inner surface	Forelegs with 4–6 dark spots on inner surface of coxa; femur with 2 small, dark, proximal patches
Male genitalia: hypophallus left side with a blade-like expansion lacking teeth but with a sharp, dark, sclerotised apex at each end; pseudophallus a dark, sclerotised fold terminating in a strong distal spine; apophysis a blunt, parallel-sided, finger-like projection	Male genitalia: hypophallus left side forming a dark sclerotised knob with a cluster of approximately 7 sharp, recurved spines; pseudophallus a flat, dark, strongly sclerotised finger-like projection with 11–13 distal recurved teeth; apophysis a conical, tapered, finger-like projection
Ovipositor: dorsal valve acute, with a proximal dorsal shoulder; ventral valve slightly curved, with a ventral cusp; medial valve with a strong proximal dorsal shoulder, ventrodistally with trichoid sensilla	Ovipositor: dorsal valve blunt, without a dorsal proximal shoulder; ventral valve bent, with a ventral conical expansion; medial valve rounded, lacking a proximal dorsal shoulder and ventrodistal sensilla
Males rarely eaten by females during or after copulation; behaviour placid	Males usually eaten during or after copulation; behaviour aggressive
Nymphs	**Nymphs**
Emergence synchronised, nymphs of an ootheca usually hatching within a few days of each other	Emergence extended, nymphs emerging from ootheca over a 2–3-week period or longer, even into the following season
Colour green, with a strong dorsal longitudinal brown band; legs uniformly green; body straight; older nymphs uniformly bright green	Colour grey-brown, mottled; legs banded; abdomen strongly up-curved; older nymphs pale green or straw brown, often with strong longitudinal stripes, and legs banded
Oothecae (Fig. 7)	**Oothecae** (Fig. 8)
Slender, dark brown, with a pale, thin froth layer; sides ribbed, more or less straight; emergence apertures large, conspicuous, flat, covered by a distinct cream-coloured substance; commencing end irregular, rounded; terminating end smooth, sloped	Broad, pale brown; sides smooth, rounded, puffed; emergence apertures small, hidden beneath a central, rounded, pale-coloured strip; commencing end usually rounded; terminating end drawn out into a prominent pan-handle

Taxonomy. The species *ministralis* was established by Fabricius (1775; and redescribed in 1793) in genus *Mantis*, as also were *rubrocoxata* (Audinet-Serville, 1839), *gunnii* and *hobsonii* (le Guillou, 1841), and *novaezealandiae* (Colenso, 1882). Burmeister (1838) named *prasina* and created genus *Orthodera* for it. In 1853 Blanchard redescribed and illustrated *gunnii* and *hobsonii*, and transferred them to a new genus, *Bolidena*. Saussure (1872a) synonymised *Bolidena* with *Orthodera*, including *rubrocoxata* and *hobsonii* in it, and doubtfully placing *gunnii* in genus *Humbertiella*. He placed *ministralis*, also doubtfully, in *Paraoxypilus*. In 1872c and 1874 Saussure described the new species *Orthodera marginata*. Westwood (1889) and Wood-Mason (1889a) both list *ministralis* in *Orthodera*, the former retaining *gunnii* in *Humbertiella* and the latter describing the new species *burmeisteri*. Two further species, *laticollis* and *longicollis*, were described by Brancsik (1895, 1898). Kirby (1904) listed all these species in *Orthodera*, as well as *gunnii*. Giglio-Tos (1917a) described *australiana* and *gracilis*, and Werner (1933) *ministralis timorensis*. Thus there are thirteen specific and subspecific names available for *Orthodera* taxa.

Saussure (1872a) regarded *hobsonii* and *rubrocoxata* as synonyms of *prasina*, and both Westwood (1889) and Wood-Mason (1889a) included these and *prasina* as synonyms of *ministralis*, the former adding *marginata* as well, and the latter, having compared specimens with the types in the Banks collection, giving it status as a distinct species. Kirby (1904) listed *laticollis, prasina,* and *rubrocoxata* as synonyms of *ministralis, gunnii* as a synonym of *hobsonii*, and the other names as distinct species. Giglio-Tos (1927) presented a key to the species of *Orthodera*, and listed *prasina* only as a synonym of *ministralis*. He placed *hobsonii* and *laticollis* as synonyms of *rubrocoxata, longicollis* as a synonym of *burmeisteri*, and *marginata* as a synonym of *gunnii*. In all he recognised seven species – *ministralis, rubrocoxata, novaezealandiae, australiana, burmeisteri, gracilis,* and *gunnii*. This interpretation was accepted by Beier (1935b), who included the additional subspecies *ministralis timorensis*, and by Balderson (1984), listing the Australian nominal taxa. However, Tindale (1923), after examining 90 specimens, concluded that *ministralis* is extremely variable, and regarded *prasina, rubrocoxata, hobsonii, gunnii, laticollis, australiana,* and *gracilis* as synonyms of it. He would no doubt have included *novaezealandiae* also had he had access to New Zealand material, possibly regarding it as a subspecies as he did the Tasmanian *ministralis hobsonii*. He suggested that this wide-ranging species has not yet developed clearly defined races, and recognised only *marginata* and *burmeisteri* as distinct species, with *longicollis* a synonym of the latter. J. Balderson (1984, in litt.) states that the range

of variation is even greater than that indicated by Tindale, and that *gunnii* is the only distinct named species. He suggests that all the others should be included together as *O. ministralis*. Thus there are three different views, one admitting only two distinct taxa (Balderson), one four (Tindale), and the third eight taxa (Beier).

The extreme variability of *O. ministralis* and its wide distribution in suitable habitats over the whole of Australia (it is one of the most common and widespread Australian mantids: Froggatt 1907) make definition of the species difficult. J. Balderson (1984, in litt.) states that thorough reinvestigation of the genus is necessary. As a start, Balderson (1984) has traced the location of the type specimens for five of the names. The type specimens of three others (including *novaezealandiae*) have probably been lost or destroyed, and those of the remaining five will probably be located eventually. Detailed studies of the range of variation within local populations, and the use of modern integrated taxonomic techniques (Sakai 1980, Okuda & Sakai 1980, Terata & Sakai 1980, Kevan 1985b, Baccetti 1987) would certainly provide information of value in solving these problems.

Colenso (1882) described the New Zealand mantid as *Mantis novae-zealandiae*, and Hutton appended a description – without, however, assigning a generic or specific name – to a paper on its biology by Potts (1884). Hutton had sent a dried female specimen, probably collected at Clyde (CO) in 1874, to Wood-Mason for identification. Wood-Mason (1889a) identified it as *Orthodera ministralis* (Fabricius) after comparing it, along with three others from Swan River, Western Australia (*marginata?*), with the types in the Banks Collection. Hutton (1897) then synonymised *O. novaezealandiae* with *O. ministralis*, and subsequently all New Zealand authors have referred to the taxon by this latter name. However, Wood-Mason (1889a) himself mentioned that the New Zealand specimen differed from the Australian specimens (which included the types) in the less dense reticulation of its tegmina, and Westwood (1889), Kirby (1904), Giglio-Tos (1917a, 1921, 1927), Caudell (1927), and Beier (1935b) all regarded *O. novaezealandiae* of Colenso as a distinct and valid species. Giglio-Tos (1921) listed *O. prasina* of Brancsik (1895) and *Tenodera intermedia* of Hudson (1892) as synonyms of *O. novaezealandiae*. In 1927 he distinguished *novaezealandiae* from *australiana* Giglio-Tos by the greater length of the forewings; from *burmeisteri* Wood-Mason and *gracilis* Giglio-Tos by the fact that the posterior part of the pronotum (metazone) is considerably longer than the anterior part (prozone); and from *ministralis* (Fabricius) and *rubrocoxata* (Serville) by the pronotum being at least twice as long as the lateral pronotal carinae. Beier (1935b) accepted these conclusions, and recognised all the species.

In contrast to the Australian situation, New Zealand populations of this mantid do not vary greatly in the form of the pronotum, and in fact are relatively constant in all the characters used by Giglio-Tos (1927) for distinguishing the species. However, their pronotal proportions are less and their wing dimensions greater than those given by Giglio-Tos.

In this situation, where the geographically isolated New Zealand population is relatively constant in its morphological characteristics yet falls within the range of variation of the Australian population, and has long been recognised elsewhere as a distinct, valid species, it is expedient to continue to so regard it. This approach has the advantage of separating information about the species in New Zealand from that of the Australian species. In future, should information become available about the Australian taxa indicating that the New Zealand population cannot be regarded as distinct, then its reduction to synonymy would be a very simple matter.

Orthodera novaezealandiae (Colenso)

Figures 1, 3, 4, 7, 9–43

novae-zealandiae Colenso, 1882: 277 (*Mantis*). Westwood, 1889: 11 (*Mantis*). Kirby, 1904: 21 (*Orthodera*). Giglio-Tos, 1917a: 107; 1921: 33; 1927: 118 (*Orthodera*). Beier, 1935b: 2 (*Orthodera*).

novae-seelandiae (Colenso). Caudell, 1927: 19 (*Orthodera*).

ministralis (Fabricius). Wood-Mason, 1889a: 20 (*Orthodera*). Hutton, 1897: 242; 1904: 353 (*Orthodera*). Thomson, 1922: 268 (*Orthodera*). Tillyard, 1926: 93 (*Orthodera*). Wise, 1977: 37 (*Orthodera*).

intermedia Saussure. Hudson, 1892: 109 (*Tenodera*).

[The taxonomic history and current status of *O. novae-zealandiae* are discussed in detail under genus *Orthodera*.]

Both sexes uniformly bright green; antennae and occasionally vertex and top of eyes reddish brown; anterior (costal) border of forewing and, rarely, lateral rim of pronotum also reddish brown; middle (especially) and hind legs often with broad banding of darker colour.

Females usually slightly larger than males. Dimensions (mm; mean or modal dimension in parentheses):

	Head width	Wing length	Body length
Males:	4.5–5.0 (4.5)	27.0–30.0 (29.0)	35.5–40.0 (38.0)
Females:	5.0–6.5 (6.0)	23.0–31.0 (28.0)	34.0–46.0 (41.0)

Suckling (1978) found that the width of the head capsule is not closely correlated with other morphological measurements, but that there are highly significant differences between the sexes in all measurements.

Males more slender than females. Wings more than 3x longer than pronotum in males, less (approximately 2.5x) in females.

Head (Fig. 9, 10) in male relatively more angular, with ocelli larger, prominent, elevated, and antennae long, moniliform; in female less angular, with ocelli smaller, less elevated, and antennae shorter, finer, not moniliform. In both sexes frons deep, subquadrate, with a mid-dorsal point. (The slight sexual dimorphism was noted by Potts (1884) also.)

Pronotum. Dimensions (mm):

	Width	Length	Prozone length	Metazone length
Males:	4.0–4.25	8.0–8.75	3.0–3.25	5.0–5.5
	(4.0)	(8.5)	(3.25)	(5.25)
Females:	4.5–6.0	9.5–11.5	3.5–4.0	6.0–7.5
	(5.25)	(11.0)	(4.0)	(7.0)

Broad, with strong lateral punctate carinae and a sharp mid-dorsal ridge, apically grooved in prozone. Small tubercular denticles, each with a short, fine, subapical seta, scattered over dorsal surface, forming a dense fringe along margins of carinae and a double row along crest of dorsal ridge. Prozone and metazone demarcated by a distinct transverse suture which curves abruptly forwards halfway across pronotum on each side so that suture is U-shaped. Anterior border slightly arched forward; posterior border notched laterally, then strongly arched posteriorly. Sides almost parallel, slightly narrowing posteriorly, straight in male, slightly curved outwards in female, in which pronotum is distinctly narrowed towards posterior.

Legs (13 females and 12 males from widespread localities examined). Foreleg (Fig. 11) similar in both sexes. Coxa pale yellow or brown, with dorsal and ventral rows or concentrations of small, fine tubercles, each with a subapical seta. Femur green, with a conspicuous pigment patch (signal patch, eye spot, 'ear') on inner (anterior) surface comprising a dark or black triangular spot with bright turquoise or blue areas below and pink coloration above; an anterior ventral row of 14 strong spurs, alternately longer and shorter, separated by a strong tibial spur groove from the row of 4 discoidal spurs, the 3rd distalmost from the trochanter much larger than the other spurs, and with a proximal ventral row of approximately 8 small, setose tubercles preceding the discoidal spurs; posterior ventral margin with 4 large, widely spaced, equal spurs between which are approximately 10–12 setose tubercles/denticles, these also numerous on ventral surface; distally on inner surface an elliptical patch of dense, paddle-shaped setae occurs – the femoral brush; apically 2 small ventral spurs are present. Tibia with a ventral comb-like row of 10 or 11 spurs on inner margin, these gradually increasing in size distad to the large, curved terminal spur, and an outer row of 14 spurs also increasing in size distad. Tarsus attached

laterally, short, not extending beyond trochanter, 4-segmented; metatarsus as long as the other 3 tarsal segments together, somewhat bent proximally to compensate for lateral attachment.

Variation. The following variations in foreleg spur count are noted. Femur: 3 examples had 13 instead of 14 inner ventral spurs, 6 had 15 spurs, and 2 had 16; 2 examples had 3 instead of 4 discoidal setae; 1 example had 5 instead of 4 outer ventral spurs. There is a tendency for the apical ventral spurs to be reduced; in some instances they were very small, and in one were absent altogether. Tibia: 1 example had 15 spurs instead of 14 in the inner ventral row, 8 had 13, 2 had 12; in the outer ventral row, 5 examples had 9 spurs, 15 had 10, 9 had 12, and 1 had 13, instead of 11, of which there were 18 examples.

Middle leg normal. Inner surface of coxa and ventral surface of trochanter with longer trichoid sensilla. Femur with ventral surface curved and with a single apical spine on anterior side only. Tibia slender, distally forming a terminal cusp-shaped dorsal extension, and with a pair of ventral spines. Tarsus 4-segmented; metatarsus relatively shorter than that of foreleg.

Hind leg similar to middle leg. Coxa with short trichoid sensilla only. Femur and tibia identical with those of middle leg. Tarsus 4-segmented; metatarsus as long as the other 3 segments together. Trichoid setae arranged in approximately longitudinal rows on all segments.

Wings. In the following description the nomenclature of Snodgrass (1935) as interpreted by Smart (1956a) is used. Twenty-three forewings (8 female) and 22 hind wings (8 female) were used.

Forewing sclerotised, sexually dimorphic in shape and size, that of female tending to be proportionately slightly shorter, wider, and more pointed distally. Male forewing (Fig. 12) parallel-sided and broadly rounded distally, 29.0–30.0 mm long and 7.0–7.5 mm wide; female forewing (Fig. 13) slightly curved anteriorly and posteriorly, bluntly pointed distally, 27.5–30.5 mm long and 8.0–9.0 mm wide. Area between costal and subcostal veins broad, not expanded. Jugal lobe or jugum membranous, occupying proximal quarter of hind margin of forewing in both sexes, unexpanded, continuing outline of wing except proximally, where an additional membranous alular lobe is formed. In both sexes colour a uniform bright green except on costal region, which is usually pale reddish-brown. Pigment present in veins only; membrane transparent apart from a slight clouding caused by a diffuse scattering of reddish-brown droplets, particularly proximally and in costal area.

Venation. In both sexes, forewing (excepting jugal lobe) completely covered by a dense mesh of irregularly anastomosing veins, the archedictyon, to which green pigment is confined. Archedictyon strongly developed, often causing difficulty in distinguishing main veins, but finer and more dense in female than in male (Fig. 14, 15); archedictyon elongate obliquely forward and outward in area between costal and subcostal veins and more or less longitudinally over rest of remigium and vannus. Cross-veins not developed. Jugum with a reticulation of veins quite different in appearance to archedictyon of rest of wing. A small, very slender, irregular swelling, the 'pterostigma', lying parallel to and between medial and cubital veins at about one-third their length from base, within which veins appear disorganised and ill defined. A peripheral vein, continuous with costa, completely circumscribing remigium and vannus but not jugum; proximally this vein curves forward and around to merge with root of cubitus, forming a distinct, strong lobe encompassing roots of vannal veins and postcubitus. A short cubital furrow present. All main veins except subcosta and several vannals reaching border, and all veins elevated on upper surface.

Costa (*C*) slightly submarginal proximally, extending along anterior margin to wing apex, where it becomes peripheral vein. Subcosta (*Sc*) strong, proximally enlarged, extending for most of wing length and almost reaching costa distally, where it becomes part of archedictyon. Radius (*R*) the strongest, most convex forewing vein, proximally enlarged, lying very close to and running parallel to subcosta for three-quarters of its length, then diverging and forking into R and radial sector (*Rs*), both of which may then be further divided so that mostly 2 or 3 radial branches occur; distally pseudopectinate branches of R_1 sometimes formed by archedictyon. Media (*M*) weaker, not enlarged proximally, closely paralleling R over its proximal half and then diverging and bifurcating into *MA* and *MP*; *MA* often forking once more, to form 2 or 3 medial branches. Cubitus (*Cu*) also weaker than radius and not swollen proximally, forking near base into Cu_1 and Cu_2; Cu_1 further dividing into Cu_{1a} and Cu_{1b}, and both of these further forking so that cubitus usually forms 7 or 8 branches. Radial, medial, and cubital veins together usually produce 12 or 13 branches. Cu_2, which proximally forms rim of vannus, fuses with postcubitus (*Pcu*) at about two-thirds its length, then with 1st vannal (*1V*), the resulting single vein usually reaching border of wing. Vannal veins (*1V*, *2V*, *3V*, and *4V*) arising from a common root, and not associated with jugal lobe; *2V* shorter than *1V*, eventually becoming part of archedictyon; *3V* approximately half as long as *2V*, also merging with archedictyon distally; *4V* not always developed, sometimes separate from its root, short, less than half as long as *3V*. Pterostigma present but indistinct (see pp. 41–43).

Variation. Very considerable variation occurs in forewing venation, not only between different individuals but

also between the left and right wings of one individual. The following variations have been noted.

R is sometimes forked, and rarely one or both branches may divide yet again. Rs likewise is sometimes bifurcated, and the posterior branch may divide again. In one example Rs became merged with the archedictyon well before reaching the peripheral vein. The maximum number of radial branches is 4. There is one example of M failing to bifurcate and remaining single right to the peripheral vein. MA is often unforked, but in one instance divided twice. MP forked near the periphery in 2 examples, but the maximum of 3 medial branches is never exceeded. The primary bifurcation of M may be displaced distally. In one example MP merged with the archedictyon before reaching the peripheral vein. The anterior branch of Cu, Cu_{1a}, often develops only 2 branches, occasionally 4, and rarely 5; in one instance a branch of Cu_{1a} merged with the archedictyon before reaching the peripheral vein. Cu_{1b} likewise sometimes develops 4 branches, very rarely 5, or is undivided. The total number of cubital branches varies between 6 and 9 and the total number of radial, medial, and cubital branches between 10 and 15. Cu_2 rarely is fused with either Pcu or $1V$ only, or with $2V$ in addition to $1V$, or remains separate, possibly connected with Pcu by a cross-vein, and merges into the archedictyon. Sometimes the fused vein $Cu_2+Pcu+1V$ merges with the archedictyon before reaching the peripheral vein. Pu very rarely becomes part of the archedictyon before uniting with Cu_2. Rarely the separation of the vannal root into $3V$ and $2V+1V$ and into $2V$ and $1V$ is displaced slightly distally; when $1V$ fails to join with Cu_2+Pcu it becomes part of the archedictyon. In one instance $1V$ bifurcated, both branches uniting with Cu_2+Pcu. Sometimes $4V$ is absent, sometimes it is poorly formed, and often it is not connected with the root. Rarely $5V$ is present.

Hind wing. Sexual dimorphism apparent, female wings tending to be shorter, with distal lobe less pronounced than in male (Fig. 16, 17). Wing shape normal; remigium bluntly rounded distally; vannus large, greatly expanded, folding up like a fan when in resting position. Hind wings shorter than forewings, usually 25.0–26.0 mm long but varying between 23.5 mm and 27.5 mm, and 14 mm wide, varying between 12.5 mm and 15 mm. Jugum merged with vannus. Hindwings clear and membranous, with only the veins pigmented, green in costal area but often reddish brown elsewhere, especially on vannus.

Venation. Remnants of archedictyon apparent at apex in costal, radial, radial sector, and medial areas, and also in jugal area of vannus. A net of regular, simple cross-veins present between all veins. All veins reaching margin but peripheral vein not formed.

Costa (C) completely marginal, extending along anterior border to apex, where it becomes obsolete; costa basally enlarged to form a sclerite which articulates with axillary plates. Subcosta (Sc) strongly concave, gradually diverging distally from radius and usually becoming lost in archedictyon, forming a basal triangular plate which articulates with that of costa. Radius (R) strongly convex, usually simple and unforked, forming an elongate plate proximally from which a strong, convex cross-vein connection to cubitus arises. Media anterior (MA) usually arising from radius at level of cross-vein, mostly simple and unforked. Media posterior (MP) rather weak, arising from cross-vein, mostly simple and unforked. Cubitus (Cu) strong, dividing into Cu_1 and Cu_2 at its origin; Cu_1 slightly arched to meet cross-vein, then passing to border, usually forking twice to form 3 branches; Cu_2 simple, unforked. Postcubitus (Pcu) strong, undivided, slightly diverging from Cu_2 proximally then converging again. Vannal veins (V): $1V$ lost, as is normal in mantids (Smart 1956a); $2V$ forking 5 or 6 times to form 6 or 7 branches; $3V$ to $9V$ present, so total number of vannal veins typically 14; all vannal veins with a common root except for $8V$ and $9V$, which are shorter, weaker, and arise separately. Jugum recognisable by presence of a coarse reticulation of veins and an incipient jugal vein. Frequent cross-veins present between all veins, and incipient intercalary veins present between several of the vannal veins, though none complete or strong.

Variation. As with the forewing, considerable variation occurs not only between individuals but also between left and right sides of the same individual. The following variations have been noted.

Sc occasionally reaches and unites with C distally as well as branching into the archedictyon. R is sometimes forked, either at its very tip or further back, and in one or two instances several anterior pectinations can be recognised. MP occasionally forks once, either right at the border or further back; when the latter, either R or MA only is branched. MA usually branches off from the end of the elongate expanded basal plate of R (Fig. 18, 19), but sometimes MA and MP arise together from a common stem (Fig. 20), and in one example MA arose from the cross-vein. The common stem for MA/MP varies in its origin too, usually arising from the cross-vein itself, but in one example it arose from the radius near its junction with the cross-vein (Fig. 20). In another instance R formed a strong, oblique branch passing to MA which further on formed another oblique branch passing to MP, itself then forking twice to form 3 branches. In the example illustrated in Fig. 21 MA, arising a short distance along R, united with MP from the cross-vein to form a very short common stem, which soon forked into MA and MP again. Further on, at

approximately three-quarters of its length, *MA* united with *R* to form a relatively long common stem, which again divided into *R* and *MA*, but before doing so produced a strong, oblique branch which fused with *Sc*. In yet another example *MP* formed a strong oblique branch passing up to *MA*, which later forked. Once *MA* curved towards *MP*, forming a strong cross-vein before becoming obsolete, and being replaced by a branch of *MP* which forked at this point. There is one instance of *R*, *MA*, and *MP* each branching at their distal tip. Cu_1 sometimes forks 3 times to form 4 branches, some of which may reunite (Fig. 22), and rarely only once, to form 2 branches. Cu_2 and *Pcu* are constant. Occasionally *2V* forks 7 times to form 8 branches. In some specimens the number of vannal veins is reduced and *9V* is absent, while in others there is an increase and *10V* is present.

Nymphal wing pads (6th instar: 28 male and 10 female examples examined). These are invariably uniformly dense green in colour, except for the costal strip, which is often reddish brown or paler coloured. The pigment is distributed throughout the hypodermis. In shape the wing pads foreshadow the adult wings even to the extent that female nymphs can be distinguished from males by their slightly more pointed wing-pad outline (Fig. 23, 24). In both sexes a well developed anterior proximal shoulder is made conspicuous by its strong brown-red coloration. A very weak shoulder only is formed by the hind wing. Forewing approximately 7.0 mm long (maximum), and hind wing 6.0 mm (maximum) in both sexes. There is no apparent precursor to the pterostigma of the adult forewing. In general the arrangement of the tracheae of the wingpad is very similar to the venation of the adult wing, and the pattern of ridges on the upper surface of the wingpad reflects the arrangement of the tracheae beneath. Sometimes these ridges ('veins') are distinguished by colour as well.

Forewing tracheation (Fig. 25). Costal trachea absent; subcostal trachea strongly developed, pectinate, giving rise to a series of tracheoles, often forked, along its entire length. Radial trachea normal, dividing into R_1 and *Rs* distally, the latter sometimes forked, and R_1 pectinate distally. Medial trachea variable, forking into *MA* and *MP* at approximately two-thirds its length; *MA* mostly forking once, but *MP* remaining undivided, giving a total of 3 branches. Cubital trachea dividing near root; Cu_1 variable, forking into Cu_{1a} (which mostly has 1 fork) and Cu_{1b} (which usually has 2 or 3 forks); Cu_2 constant and curving to meet tracheal precursors of *Pcu* and *1V*; total *Cu* branches hence 6–8; postcubital trachea constant. Vannal root subtending 4 main tracheae; *4V* usually forking and branching, posterior limb of fork supplying jugal area. A network of fine tracheoles, precursor to archedictyon, present also.

Hind wing tracheation (Fig. 26). Costal trachea absent; subcostal trachea well developed, pectinate, giving rise to a series of tracheoles, some with fine branches, along its entire length which distally bend strongly towards apex, forming an incipient costal trachea. Radial trachea well developed, at about one-third its length giving off branch *MA*. Posterior medial trachea simple, unbranched, arising independently, so usually only 2 medial branches present. Cubital trachea dividing near base; Cu_1 in turn forking into Cu_{1a} (mostly forking into 2 branches) and Cu_{1b} (usually undivided); Cu_2 simple, undivided, failing to reach rim of wingpad; postcubital trachea undivided, constant, arising independently. Vannal tracheae: *2V* usually forking 5 times, and usually 7 other tracheae present, all arising from a common root; 4 posteriormost tracheae becoming successively shorter and weaker, arising from a common branch which forks 3 times, the posterior branches giving rise to fine tracheoles of jugal region. Tracheole precursors of cross-veins and incipient intercalary veins present, but conspicuous r–cu_2 cross-vein of adult wing not reflected by tracheation of nymphal wingpad. Subcostal, radial, and medial tracheae close together and parallel, especially proximally.

Variation. In the forewing the radial trachea may remain undivided or R_1 may fork also; the position of the initial R_1 / *Rs* fork varies, and may be very distal. *MA* is often unforked, and in one example forked twice; there are 5 instances of *MP* forking once. The cubital trachea is quite variable; Cu_{1a} may be undivided or fork twice (in one example 3 times), and Cu_{1b} may fork once or even 4 or 5 times, giving a variable total of mostly 6–8 branches, but sometimes only 5; in 3 examples a branch of Cu_{1a} is blind, extending only 25–65% of the distance to the rim of the pad; Cu_2 is constant, as is usual. *Pcu* occasionally weakens and fails to reach Cu_2 and join with it and with *1V*, but remains enclosed by these tracheae. In two examples *1V* failed to join *Pcu* and Cu_2 and continued independently to the rim of the pad. The number of vannal tracheae is constant except for the additional branch formed when *4V* forks; *4V* may also branch variously. Sometimes tracheae arising separately from the vannal root supply the jugal region, rather than branches from the posterior fork of *4V*. In the hindwing the medial tracheae are usually unbranched, but there is one example of *MA* forking almost terminally, 4 examples of *MP* forking, and one example of *MA* curving to unite with *MP* distally, resulting in 5 instances in which there were 3 rather than 2 medial branches. In a number of specimens the cubital *1a* trachea is undivided, and in one it forks twice. There are 2 instances of Cu_{1b} forking once, in one of which the posterior branch fails to reach the edge. In 3 examples Cu_2 is sufficiently

well developed to reach the rim of the wingpad. In a number of examples the cubital branches total only 2 or 3. The postcubital trachea is constant except in one specimen in which Cu_2 curves distally to join with it. The total number of vannal tracheae varies from 11 to 15, and the number of $2V$ forks from 3 to 6. There is one example of a $2V$ branch forking once and several examples of the posteriormost vannals forking twice instead of 3 times.

Abdomen. Normal, soft, slender in male, broader in female. Male with 9 tergal and 7 sternal plates, female with 9 and 5 respectively. Tergite IX forming a mid-dorsal posterior point in both sexes, and a weaker point on tergites VII and VIII in female. First sternite forming a strong spur between hind coxae in both sexes. Cerci slender, soft, tapering, circular in cross-section, clothed with long and short trichoid sensilla, comprising approximately 15 annulations or segments; segments becoming longer and better defined distally, extending for half their length beyond subgenital plate in male and for a quarter to one-third their length beyond ovipositor in female; proximal segment flattened dorsoventrally (semi-pedunculate) in both sexes. Suranal plate (Fig. 27, 28) similar in both sexes, wider than long, triangular, with a weak mid-dorsal crest apically, relatively wider and shallower in female, sparsely clothed with trichoid sensilla. Paraprocts soft, lightly sclerotised, subquadrate lobes, angular; distal border clothed with long trichoid sensilla. Subgenital plate in male (Fig. 29–31) convex, asymmetrical, subtriangular with curved sides, apically truncate to weakly emarginate, clothed with long and short trichoid sensilla; styli small. Subgenital plate in female (Fig. 32) strongly convex, posteriorly forming a narrow, tubular, bilobed sheath surrounding ovipositor; dorsally, sheath and distal rim of plate reflected inwards; groove separating plate from sheath well developed, emarginate, medially deep and strong; lobes contiguous for more than half their length; 2 semi-cusps formed at point where lobes separate; plate clothed with long and short trichoid sensilla.

Genitalia. *Male.* Hypophallus (Fig. 33) a large, sclerotised plate, convex but becoming concave on right-hand side, tapering slightly distally; right posterior angle rounded, with a group of weak, scale-like projections; posterior border concave; left posterior angle comprising a straight, blade-like expansion with sharp apices at each end, each darkly sclerotised and bearing numerous minute, acute, scale-like projections directed anteriorly; proximal apex pointed anteriorly also; scattered non-trichoid sensilla present on both dorsal and ventral surfaces but trichoid sensilla absent; integument covered by numerous weak, minute, scale-like structures terminating in one or several fine spines; on left side, and proximally on right side, integu-

ment smooth or with weak microscales. Left epiphallus (Fig. 34): titillator only lightly sclerotised; distal lobe folded over dorsally, short, rounded, with very short trichoid sensilla concentrated in apical area; integument generally covered by minute, sharp, scale-like projections; pseudophallus exposed, not enveloped by membranous folds, strongly sclerotised, darkly pigmented, comprising a humped ridge and deep saddle densely clothed with minute, scale-like projections, and terminating distally in a strong, weakly scaled spine. Right epiphallus (Fig. 35) a flat, elongate, triangular, curved, lightly sclerotised lobe distally folded ventrad, with numerous short trichoid sensilla concentrated distally and scattered on ventral surface, and non-trichoid sensilla present proximally on ventral surface; basal notch darkly pigmented, strongly sclerotised, comprising a flat ridge (sometimes with transverse folds), and a short, broad, parallel-sided projection, the apophysis; both apophysis and ridge densely clothed with recurved, scale-like projections; integument densely covered with numerous minute, scale-like spines.

Female. Ovipositor comprising 3 short, downward-curved pairs of valves which are soft and only lightly sclerotised. Ventral valve (Fig. 36) a slender, curved, gradually tapering arm with a ventral conical projection at two-thirds its length, a long dorsal groove, and a shorter distal groove causing apex to be bilobed; long, trichoid sensilla densely concentrated on all surfaces of ventral terminal lobe, which is unexpanded; upper inner lobe nude; all surfaces of ventral valve with concentrations of shorter, varied trichoid sensilla; integument with patches of microtrichia medially and dorsally and microscales ventrally, otherwise integument smooth. Dorsal valve (Fig. 37) scimitar-shaped, with a strong proximal dorsal shoulder and a pointed apex with a subapical lobe and a longitudinal groove or hollow; a conspicuous crest of very long, trichoid sensilla present dorsally, otherwise dorsal and outer surfaces clothed by numerous well developed, variable trichoid sensilla; ventral surface with a concentration of trichoid sensilla proximally and an area of dense, long microtrichia; integument generally forming minute, weak scales or tending to form weak microtrichia. Median valve (Fig. 38) flat, scimitar-shaped, with a strong, sharp, proximal dorsal shoulder, a truncate apex, and a strong, sharp ventral spur at about half length; a strong transverse, proximal dorsal bar present; upper third of valve comprising a thin blade with pectinate ridging, gradually tapering distally; sensilla absent except for a distal ventral row of 4 or 5 strong trichoid sensilla; integument densely clothed by minute scale-like structures and microtrichia; a darkly pigmented patch of strong integumental scales on lower surface of ventral tooth.

Type data. Syntypes: several nymphs and one adult from "Scinde Island" (=Bluff Hill), Napier (HB), New Zealand.
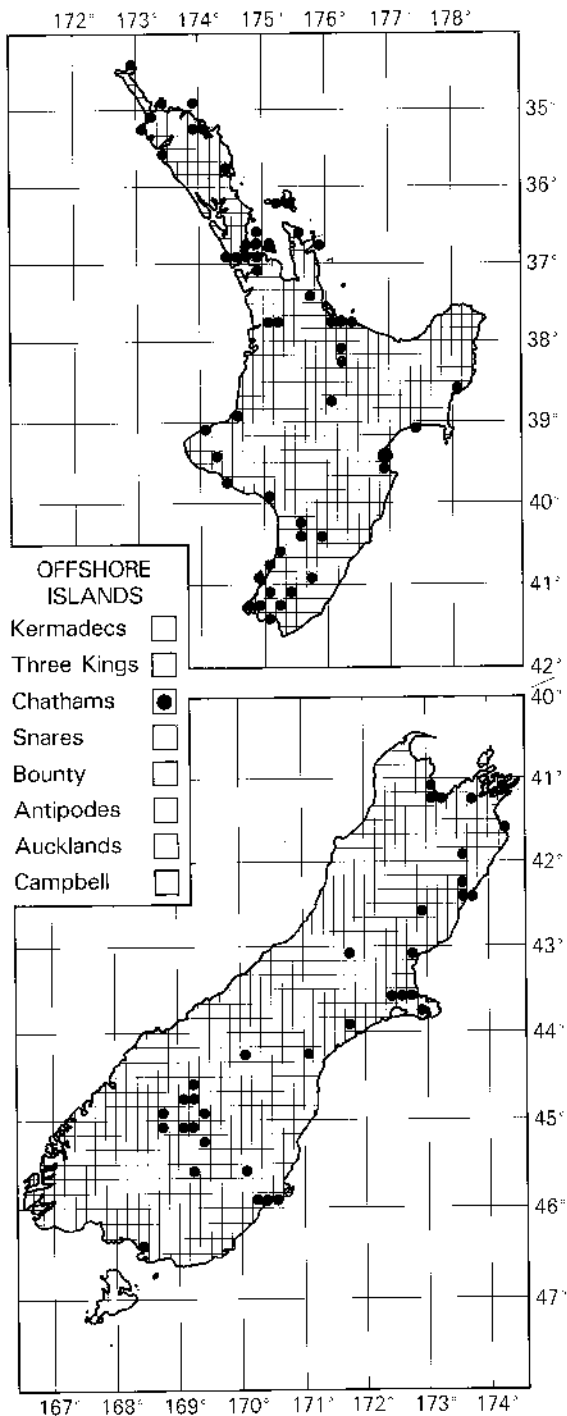
A search for the original specimens on which Colenso (1882) based his description of *Mantis novaezealandiae* has failed to locate them. Colenso stated that he had sent some nymphs preserved in spirits to the Colonial Museum, but no trace of them can be found. Therefore it must be presumed that they have been lost or destroyed, as well as the notional type specimen (an adult).

The type specimens of other species of relatively large orthopteroid insects – for example wetas (Stenopelmatidae) and stick insects (Phasmatidae) – described by Colenso mostly cannot be found; nor is there any trace of an insect collection (if such existed) attributable to Colenso in the Colenso Museum at Napier, or elsewhere.

In view of the fact that *O. novaezealandiae* is very similar to *O. ministralis*, designation of a **neotype** is justified on the grounds that it will facilitate future taxonomic study. An adult male collected at the type locality on 28 March 1987 by T.H. and J.M. Davies has been selected for this purpose and so labelled; it is deposited in the New Zealand Arthropod Collection, DSIR Plant Protection, Mt Albert Research Centre, Auckland. Three other specimens from the same series have been selected and designated as **paraneotypes:** a female with the same data as the neotype, and a pair collected from a privet hedge, Lighthouse Road, 9 April 1987.

The voucher material on which this study is based is also housed in NZAC.

Distribution (Map 1). *O. novaezealandiae* occurs only in New Zealand. It is present throughout the North Island in suitable habitats; published records are from Spirits Bay in the far north, through Northland, Auckland, Coromandel, Waikato, Taranaki (Thomson 1922), Hawkes Bay, and Wellington regions. In the South Island there are records from Nelson, Marlborough Sounds, Kaikoura, Amberley, the "Canterbury Lowlands" (Harrison & White 1969), Christchurch, Akaroa (Potts 1884, Johns 1986), Lincoln, Timaru, Oamaru, Dunedin, and Invercargill. The known western limits of its distribution are Hanmer (Johns *et al.* 1980), Cass (Burrows 1977), Clyde (Hutton 1897), Cromwell (Potts 1894), Alexandra, Hawea, Lake Wanaka, and Speargrass Flat near Queenstown, Lake Wakatipu. There are no records from Stewart Island or the west coast of the South Island. It is present on some offshore islands such as the Cavalli group (Roberts 1979), The Noises, and Waiheke (Bennett 1984) in the north; on Maud, Long, Motuara, and Pickersgill islands in the Marlborough Sounds (Meads 1976, Moeed & Meads 1987); and doubtfully on the Chathams (an ootheca was found on a beach, but no

OFFSHORE ISLANDS

Kermadecs	☐
Three Kings	☐
Chathams	⬛
Snares	☐
Bounty	☐
Antipodes	☐
Aucklands	☐
Campbell	☐

• **Map 1** Distribution of *Orthodera novaezealandiae* •

living insects were seen – Macfarlane 1979). It is not known from the Three Kings or from any of the Subantarctic Islands.

A computer file listing the distribution details of all specimens used in this study is held by DSIR Plant Protection, and may be accessed by contacting the Curator of the New Zealand Arthropod Collection at the address on p. iii.

Life history. The life cycle of *O. novaezealandiae* is univoltine: nymphs emerge in spring and mature in summer; adults mate and produce eggs in autumn, and die off at the onset of winter. The majority of the population is more or less at a similar stage at any particular time. Egg-laying commences in February (January according to Potts 1884, April according to Suckling 1978) and continues through to April and May, or as long as the females survive. In the laboratory females continue laying long after their sisters in the wild have died (Suckling 1978). Potts recorded that one female produced five or six oothecae; Suckling recorded two or more oothecae per female and, in one instance, five. This number is low in comparison with that of *Stagmomantis carolina*, for which Breland (1941b) found the average of eight captive females to be greater than seven, with a maximum of fourteen.

The earliest any first-instar nymphs have been found in the wild is May in Auckland (Bennett 1981) and mid August in Nelson (NN). However, also in Nelson E.W. Valentine (unpublished data) recorded that a few nymphs emerge in June and July, slightly more in August, and the vast majority during September and October, after which hatching ceases abruptly. Many appear during September, and some have been found as late as January.

Adults are present from February onwards. The earliest an adult has been seen is February, but they are not present in numbers until late February, and particularly during March, when they are most abundant. Their numbers start falling off in May, and most adults have disappeared by the beginning of June or earlier (first week of May on the Taieri Plains, Dunedin (DN) – A.C. Harris, pers. comm.). That this is the result of cooler temperatures is attested to by the fact that adults taken into the laboratory from the wild survive and produce more oothecae for some time after their siblings in the wild have disappeared (Suckling 1978). Males are the first to disappear, and a few females may overwinter and survive even up until the following November (Crosby 1984). Females begin producing oothecae during March, and continue for as long as they survive.

The interval from laying to hatching is normally 5–6 months. However, Suckling (1978) found the period to vary from only 35 days to 53 days for laboratory-reared specimens, and this is corroborated by Bennett (1981), who reported nymphs emerging after 73 days from an ootheca

laid in the laboratory in June. In general in the wild eggs laid during April do not hatch until September at the earliest, so development requires at least 150 days. An exception to this is the example of an overwintering female in Auckland which produced an ootheca between August and October from which the nymphs had emerged by November (Crosby 1984), a possible maximum of some 90 days only. Nymphs have been reported emerging in autumn (Crosby 1984).

The time taken for egg development in both New Zealand species is unusually long, but may be normal for species living in temperate climates.

In France and Europe the eggs of *Mantis religiosa* and *Ameles* sp. take approximately nine months before hatching (Fabre 1894, Sharp 1895), whereas in seven tropical species the period is short, varying from 13 to 51 days, with two species having a maximum of 31 days and one 25 days (Ene 1962, 1964, Kumar 1973). The same is true of Indian mantids, in which one species required 20 days to develop, a *Mantis* sp. 18 days, and *Schizocephala bicornis* 30 days (Wood-Mason 1878b). Adair (1914a), in Egypt, found that *Miomantis savignyi* required an average of 27.5 days (range 18–38), *Sphodromantis bioculata* 57 days (range 41–78), *Blepharis mendica* 34 days (range 30–40), and (in 1914b) *Mantis religiosa* an average of 33.75 days (range 31–51). Warmer temperatures accelerate development (Ene 1964), and Faure (1940) found the average incubation for a South African species to be 31 days in summer and 62 days in winter. Adair (1914b) found that *M. religiosa* eggs took 31–33 days to develop in early autumn and 48–51 days in early winter. *M. religiosa* thus exemplifies this very strongly when the subtropical data from Egypt are compared with the temperature data from the northern limits of its distribution – nine months. Further, since mantids are generally tropical / subtropical insects, it is not surprising that the time taken for egg development in species at the northern and southern extremes of mantid occurrence is unusually long.

It is probable that development of the egg of *O. novaezealandiae* is triggered by a temperature effect (see Zaslavski 1988), as all eggs of an ootheca usually hatch within a day or two of each other, although the oothecae themselves may be at different stages of development even in the same area. Suckling (1978) studied 150 oothecae of *O. novaezealandiae* in Palmerston North (WI–WN) and found that in 84 of them (56%) all the nymphs had emerged within 24 hours of each other; in another 28 (19%) all the nymphs had emerged within 3 days of each other; and in the remaining 38 (25%) the nymphs emerged within 11 days of each other. E.W. Valentine (unpublished data) found that in Nelson most oothecae had completely hatched within 3–4 days, the majority emerging on the same day from any one

ootheca. In a few instances the hatching period was extended to 11 or even 17 days.

Overwintering. In general, in temperate regions, mantids pass the winter in the egg stage (Gurney 1951). *Orthodera novaezealandiae* is no exception to this. However, in suitable places – probably localities with a warm microclimate – it is able to overwinter in the wild as nymphs and adults, as well as in the egg, the usual overwintering stage. Crosby (1984) found third-instar nymphs in May, fifth instars in late July, and sixth instars in September–October; adults developed from them in November. One of these, a male, was observed mating with an overwintered female from the preceding generation (usually only females overwinter). There are 16 records of adult mantids being found during June (including one from Stokes Valley (WN), two from Wellington (WN), and one from Te Puke (BP)), one for July, five for August (including one from Hamilton (WO)), two for September, two for October, and two for November – all from Auckland (AK), except as specified. Crosby (1984) concludes that it is likely that adults and nymphs of *O. novaezealandiae* regularly overwinter in Auckland in low numbers, and that this probably occurs in the wider Auckland region and in Northland (ND) also. Survival may be dependent on warm daytime temperatures, as at the southern limits of the species' range in New Zealand it thrives in Cromwell (CO), where the winter daytime temperatures are warm, but not in Dunedin or Southland (SL), where they are not.

Oothecae are laid on walls, fence posts, branches, twigs, and so on, in fact on any reasonably flat, firm surface, but are never squeezed into cracks or folds. Shelter does not appear to have much influence on the female's choice of oviposition site. Suckling (1978) examined 150 oothecae from the Palmerston North area and found that their dimensions were in the range 4.55–8.80 mm (usually 5.50–6.60 mm) high, 4.00–7.00 mm (usually 6.00–6.50 mm) wide, and 8.00–18.75 mm (usually 10.00–12.00 mm) long. Except for one example from Titirangi, Auckland which was 23.00 mm long, one example from Point Chevalier, Auckland, which was only 7.5 mm long, and the width dimension of 3.0 mm recorded by Ward (1969), the dimensions of the oothecae examined during this study and those of Ward (1969) fall within these limits. No malformed oothecae have been found, apart from one very small example, almost a fragment, which probably resulted from the mother being disturbed.

Oothecae (Fig. 7, 39, 40) are rich, dark brown with a thin surface layer of scattered, irregular-sized vesicles, rather like a thin, pale-coloured, dispersed, glistening foam. Orifices are closed by a thick, flat layer of fine, bright, cream-coloured foam which comprises the conspicuous stripe along the top of the ootheca. In some instances this may dis-

integrate before the nymphs emerge. The narrow shape is constant whatever the form of the surface on which the ootheca is laid – the sides with vertical sloped ribs, the commencing (posterior) end irregularly rounded, and the terminating (anterior) end sloped like the sides. The orifices are arranged mid-dorsally in two rows in a figure-of-eight configuration, and vary in number from 5 to 35 (commonly 15–25) (Suckling 1978), or from 8 to 30 (average 17) (Ward 1969). In the throat of each orifice a thin, flexible, transverse valve occurs; it is attached across the posterior wall at some distance down, almost at the level of the eggs, and completely seals off the egg chamber by passing upwards and fowards so that its border lies in close contact with the anterior wall. Such flaps or valves have been described or illustrated in the oothecae of various species of mantid on a number of occasions (Brongniart 1881, Fabre 1897, Giardina 1898, 1899, Kershaw 1910, Rau & Rau 1913, Williams & Buxton 1916, Chopard 1938 (pp. 197–199), Breland & Dobson 1947, Sharell 1971), and are probably a general characteristic of mantid oothecae of this type. Thus, access to each egg chamber is protected by this flap and by the plug of foam-like material filling the mouth of the orifice. The outer lip of each orifice is more or less horizontal.

Each orifice leads into a transverse egg-chamber containing a single row of eggs each contained in a membranous cell. The membrane of the cell is glistening and adheres to the egg-chamber wall and to the membrane of the contiguous cell. The posterior wall of each has a broad vertical strip of opaque pale-coloured material adhering to its inner surface which may serve to grip the egg. The egg-chambers of each side are offset in relation to each other, and each contains three eggs arranged vertically.

Suckling (1978) suggested that only two eggs were present within each egg chamber, and that there was no relationship between the number of eggs and the number of orifices. He found the number of eggs in each transverse row to vary between one and five. Ward (1969) also found only two eggs in each chamber. However, in the present study three was the usual number, and each transverse row, comprising two offset egg chambers, therefore had six eggs. Thus there is a direct relationship between the number of orifices, the number of egg chambers, and the number of eggs. Their arrangement is similar to that of *Stagmomantis carolina* (Johansson) described by Rau & Rau (1913).

The total number of eggs per ootheca is very variable. Suckling (1978) found this to be as high as 70 and as low as 5, with 20–40 most commonly present. Ward (1969) found the range to be 20–60, with an average of 40. E.W. Valentine (unpublished data) found in Nelson that the number of nymphs emerging from an ootheca varied from

2 to 65, but was mostly 24–45. This number is low when compared with that of *Miomantis caffra* (up to approx. 248) and very low in comparison with 325 recorded for *Sphodromantis lineola* (Burmeister) (Kumar 1973). It may indicate a lower mortality rate for *O. novaezealandiae*. Adair (1914a) reported between 54 and 102 nymphs emerging from a single ootheca of *Miomantis savignyi*, up to 436 in *Sphodromantis bioculata*, and between 32 and 88 in *Blepharis mendica*.

Although the form of the ootheca varies greatly in different mantid species, its structure is basically similar. It has been described for *Mantis religiosa* by Pagenstecher (1864), Brongniart (1881), Fabre (1897), and Giardina (1898, 1899); in *Gongylus gongyloides* by C.E. Williams (1904); in *Hierodula saussurii* by Kershaw (1910); in *Stagmomantis carolina* by Rau & Rau (1913); in *Miomantis savignyi*, *Fischeria baetica*, and *Sphodromantis bioculata* by Adair (1914a, b), who also illustrates those of *Empusa egena*, *Eremiaphila khamsin*, and *Mantis religiosa*; and in *Sphodromantis guttata* by Williams & Buxton (1916); as well, Shelford (1909) and Waterhouse (1913) have described mantid oothecae. The ootheca illustrated by Chopard (1938, p. 202, fig. 201) is not that of *Orthodera ministralis* and is misidentified.

The biochemistry of the ootheca of *Orthodera novaezealandiae* and *O. ministralis* has been studied by Giardina (1899), Hackman & Goldberg (1960), Rudall (1965), and Ward (1969). In 1955 Parker & Rudall described small, rectangular crystals adhering to or embedded in the protein membranes of which the mantis ootheca is formed. These crystals, each of which was embedded in a complicated protein envelope, were identified as being calcium citrate. Hackman & Goldberg (1960), working with oothecae of *O. ministralis* from Australia, denied the presence of calcium citrate crystals. However, Rudall (1965), working with their material and using their techniques, considered that they had dissolved the crystals before analysis, and went on to illustrate beautiful calcium citrate crystals present in the body-wall gland of reared female *O. novaezealandiae* from New Zealand. Identical crystals had been seen previously in oothecae of other mantids. Ward (1969) found that the ootheca material was not chitin, probably contained protein, and contained approximately 0.1% calcium.

The process of the formation of the ootheca in *Orthodera novaezealandiae* has been illustrated or described by Bandsma & Brandt (1963), Sharell (1971), and Castle (1988), and a detailed account of its production and of oviposition is given by Ward (1969). It is similar to that described by Pagenstecher (1864), Perrier (1870), Brongniart (1881), Fabre (1898), Giardina (1899), and Przibram (1907) for *Mantis religiosa*, by C.E. Williams (1904) for *Gongylus gongyloides*, by Kershaw (1910) for *Hierodula saussurii*, by Rau & Rau (1913) for *Stagmomantis carolina*, by Adair (1914a, b) for *Miomantis savignyi* and *Fischeria baetica*, and by Williams & Buxton (1916) for *Sphodromantis guttata*. The ootheca is formed from a substance secreted by large abdominal glands which hardens on exposure to the air. It is vacuolated and beaten into a froth by movements of the ovipositor blades. Regular cycles of abdominal movement occur as one group of eggs is deposited on one side and then another on the other. The method of formation of the orifice rim of flaps and the internal valve is obscure. The wings play no part in the process and the cerci monitor the surface being produced.

Eggs (Fig. 41, 42). Each egg, densely packed with yolk and with a soft, smooth, glistening chorion, is 4.5 mm long by 1.25 mm wide when freed from the ootheca and taking its natural form. It is subcylindrical to cigar-shaped, with the ventral surface almost straight, the dorsal curved, and each end rounded, with the anterior end slightly the narrower. The exochorion is smooth, structureless, and slightly thicker at the anterior pole; the endochorion is densely and finely granular, the granules appearing as rods in sectional view. The granules are refractive, vary in size and shape, and are uniformly distributed over the whole egg. Numerous small, clear patches are distributed amongst the granules, especially on the dorsal surface, where the granules are larger and stronger. In the mid-dorsal equatorial area a series of unidirectional, strongly refractive, dart-shaped structures occurs, each with longitudinal banding and pointed posteriorly. These are internal, and do not project above the surface. Other curved, rod-like structures shaped like nail clippings occur posterior to these.

After the nymphs have hatched the chorion becomes opaque and the darts are more conspicuous, appearing dark-coloured when viewed from certain angles. Their distribution ceases within a conspicuous mid-dorsal differentiation which is large (approx. 0.25 mm), circular, and brown in colour. It is a smooth, slightly elevated dome with a strong, central, cup-shaped crater – the micropyle – in which there are irregular, clear, refractive patches.

Beier (1968) described and illustrated the egg of *Hierodula crassa*, which is quite different from that of *Orthodera novaezealandiae* in being more complex, strongly tapered anteriorly, and dorsally concave, with a chitinous cap covering its anterior third, and, in particular, in having a transverse ring or furrow and a projecting, tongue-like columella. The micropyles are scattered at the anterior pole.

Embryo. The fully developed embryo is completely enclosed by an embryonic cuticle within the chorion. The abdominal part of this is clothed with numerous tiny, posteriorly directed scales, similar to those described by Williams & Buxton (1916) in various mantid embryos.

Anteriorly a strongly pigmented, dark brown or black cephalic cap (Fig. 43) protects the greatly enlarged and swollen vertex of the embryo. This is dome-shaped and, when flattened, subrhomboidal in outline. It is smooth and finely porose, and has a zone of strongly incised cellular patterning along its lateral borders; the median border of patterning is sharply defined. Dorsoposteriorly it is emarginate and has a caudal lobe or tail with a mid-dorsal ridge or fold and a line of refractive spots which extends forwards on the cap. Ventroposteriorly it is triangular, and is formed into a slender rod which, after hatching, comes to lie beneath the folded membranous clypeus and partly beneath the strong labrum. The labrum is spatulate, truncate anteriorly, and rounded posteriorly, with lateral and transverse apodemes and studded with strong, small, refractive, posteriorly directed scales. Together with the cephalic cap and ventral rod it may be part of the mechanism by which the pronymph escapes from the egg and ootheca. The embryo is very similar to that of *Sphodromantis guttata* (Thunb.) described and illustrated by Williams & Buxton (1916).

Hatching. The pronymph splits the egg chorion longitudinally at the anterior pole and squirms its way upwards, squeezing between the egg-chamber closing flap and the chamber wall, through the plug of foam-like material and out to the exterior of the ootheca. The embryonic cuticle is immediately moulted, and the first-instar nymph emerges. The process by which the pronymph escapes from the egg has been described for *Mantis religiosa* by Przibram (1907), for *Sphodromantis guttata* by Williams & Buxton (1916), and for *Miomantis paykullii* Stål by Kumar (1973). The part of the head between the eyes of the emerging nymph becomes distended like a balloon and filled with air. By means of continual upward movement (presumably contractions and pulsations distending the balloon) the pronymph eventually breaks out of the egg and squirms its way out of the ootheca. The labrum, ventral rod, and cephalic cap of the pronymph are no doubt important in this process.

The latter part of the emergence of *O. novaezealandiae* has been described and illustrated by Suckling (1978) and by Castle (1988), and takes from seven to ten or more minutes from the time the pronymph begins to emerge from the ootheca. The pronymph is attached to the ootheca by a pair of long, fine hatching filaments so that the cast-off embryonic cuticle with its cephalic shield remains attached after the nymph has emerged. The hatching filaments, which are unique to mantids, are produced by proliferations of cells of the embryonic cercus, and are attached to the inner surface of the chorion at the posterior pole of the egg. They are composed of alpha-chitin (Rudall 1962), and develop from a helical filament of thread-forming cells which transform into a syncytium and then secrete a sheath of chitin around themselves (Kenchington 1969, 1984). These were first described by Pawlowa (1896, cited in Williams & Buxton 1916).

Immature stages. The nymphs pass through six instars before becoming adult (Suckling 1978); in mantids generally the number of instars varies from six to nine (Beier 1968). Development takes from 3 to 6 months, and adults do not usually appear until mid February at the earliest. There is some evidence that development may be synchronous, despite variation in availability of food (Crosby 1984). However, first-instar nymphs occur from mid September through to January. In one instance, an ootheca laid on 25 April hatched on 26 October (183 days), the first stadium lasted 20 days, the second 19 days, the third 10 days, the fourth 11 days, the fifth 11 days, and the sixth 15 days, i.e., 86 days from hatching to adult, and 269 days from oviposition to adulthood (B. Tremain, pers. comm.).

First instars are 6.5 mm long and bright green in colour except for a broad, longitudinal, mid-dorsal dark brown band on the head and body which disappears after the first moult. The pronotum has the characteristic lateral expansions but is more strongly tapered than in the later stages. Also, there is a thin, pale longitudinal line passing mid-dorsally for the length of the body. It is at the crest of the pronotal ridge and causes the rest of the body to appear ridged also. Thereafter the nymphs are uniformly bright green except for a reddish-brown border on either side for the entire length of the body in some larger nymphs, which may also have a mid-ventral longitudinal white stripe on the abdomen, and the middle femora may be reddish brown.

As with all small mantid nymphs, especially the first instar, the head and eyes are proportionately much larger than the rest of the body. The lateral borders of the prothorax of the first-instar nymph are already slightly expanded, but not straight-sided as in the larger instars. There is a slight expansion above the attachment of the raptorial legs. The stance of the nymphs is characteristic, in that the body is held more or less straight rather than with the abdomen curled upwards (Sharell 1971).

Biological notes
Flight. Both males and females of *O. novaezealandiae* fly, but the females more reluctantly. During late summer and early autumn males are frequently attracted to lights at night, and can be found on the window panes of lighted rooms. They are also atracted to mercury vapour lamps, and will settle on light-trapping sheets or on walls in the vicinity of such a lamp (C. Green, pers. comm.).

Behaviour. *O. novaezealandiae* is a relatively placid species, not nearly as active and aggressive as *M. caffra*. Only rarely will it venture indoors, neither staying for long

nor laying oothecae there. It further differs from *M. caffra* in preferring to rest on the upper surface of leaves and twigs. Often several individuals can be found similarly oriented, presenting the maximum upper body surface area to the sun. *M. caffra* tends to hang upside down from twigs and leaves when at rest. This may explain why its body is so strongly curved, especially in the immature stages, gravity pulling the abdomen into a downward (dorsad) curve.

O. novaezealandiae may sometimes be observed with a captured housefly held in the raptorial forelegs. Occasionally two mantids will capture the same fly and proceed to devour it (Homewood 1978). An instance of deliberate piracy was observed by T.K. Crosby (pers. comm.). A female devouring a honeybee was stealthily approached from the left rear by another female, which gradually positioned itself to the front before grabbing the prey. In the ensuing fracas the mantids frequently struck at each other with their forelegs. The original owner failed to repossess its half-eaten prey, and eventually moved away. During this latter phase, which lasted some 10 minutes, the robbed mantid faced the aggressor with its forelegs folded but turned outwards to display the femoral colour patches. Its wings were slightly spread also. The aggressor held its prize with the left foreleg, which was extended at 'arm's length' to the side; the right foreleg was turned outwards to display the femoral colour patch. When the bee was first captured the pirate mantid was at least 1.5 m distant, and deliberately moved to challenge the captor for its prey.

Colour. The coloration of *O. novaezealandiae* is relatively constant. Apart from very rare instances of luteinism – bright yellow individuals – reported for this species (see p. 44), it is invariably a bright green, with little or no variation apart from amounts of a reddish-brown pigment which sometimes occur on the vertex, the lateral rims of the pronotum, the leading edge of the forewings, and on the middle and hind legs.

Interspecific mating. There have been several observations of males of this species mating with females of *M. caffra*. In one instance, at Parnell, Auckland, 5 April 1989, the pair were closely examined to ensure that copulation was actually taking place (D.I. Gardiner, D. Cowley, pers. comm.). Whether or not fertile eggs or parthenogenetic development resulted is unknown, but hybrids have never been found (Ramsay, in prep.).

Sex ratio. Even though few males of *O. novaezealandiae* are lost by sexual cannibalism, few of them survive through to late autumn and winter. Probably their lifespan is shorter than that of females. In contrast, all males of *M. caffra* disappear within a short period, probably as a result of sexual cannibalism.

Subfamily MANTINAE

Diagnosis. Head plain, without vertical processes and usually without ocellar tubercles. Eyes almost always rounded. Pronotum slender, elongate, mostly lacking lateral expansions or carinae and not parallel-sided (as a swollen node occurs above insertion of raptorial leg), anteriorly rounded, not cradling or overlying head. Wings developed in both sexes, exceptionally reduced or absent in male, and usually shortened in female, which has lost the power of flight; tegmina lacking eye spots or markings. Venation of forewings normal, without a dense network. Raptorial femur with 4 (rarely 3) discoidal and 4 (rarely 5) outer spines; walking legs normal, at most with a preapical expansion on femur; hind tibia circular in cross-section. Supra-anal plate wider than long. Cerci circular in cross-section. Colour variable, green to brown.

Remarks. This subfamily includes the bulk of the mantid species, some of which are diverse in size and form. It comprises more than 50 genera and almost 500 species, distributed through all warm and temperate regions of the world except southern South America. A definitive classification cannot yet be proposed. At present all these species are placed in only five tribes (Roy 1973), and until recently there were only three (Beier 1964). The five tribes are distinguished as follows.

Tribe MANTINI: raptorial leg femur with first discoidal spine shorter than the second, with four outer spines, the surface area between which is smooth, lacking teeth or denticles; if such are present, however, then only three discoidal spines are present (usually four). Occurs in all warmer regions of the world.

Tribe MIOMANTINI: raptorial leg femur with 1st discoidal spine shorter than the 2nd and with 4 outer spines on surface, between which are small spines or denticles. Occurs in tropical and subtropical regions of the Old World.

Tribe ARCHIMANTINI: raptorial leg femur with 1st discoidal spine as long as the second or longer; cerci even, uniformly rounded or compressed. Restricted to Australia.

Tribe POLYSPILOTINI: alternate dark and pale bands present on forewing, especially on discoidal area. Male genitalia – hypophallus forming along distal process directed to the right; apophysis of right epiphallus with a well differentiated anterior process. Occurs in tropical Africa.

Tribe PARAMANTINI: characterised by structure of male genitalia – hypophallus with a distal process terminating in a point and directed to the right; apophysis of right epiphallus without an anterior process. Occurs in tropical Africa.

The second species of New Zealand mantid is placed in the genus *Miomantis* of tribe Miomantini, which comprises 24 genera (Beier 1964).

Genus *Miomantis* Saussure

Miomantis Saussure, 1870b: 225. Type species *Mantis forficata* Stoll (1813, p. 4), by original designation; synonymised with *Mantis monarcha* Fabricius by Giglio-Tos (1927, p. 374).
Calidomantis Rehn, 1901: 271. New name for *Miomantis* (preoccupied). *Miomantis* revalidated by Giglio-Tos (1927, p. 358).

Diagnosis. Moderately small mantids, variably green/brown in color. Head broader than long, distinctly wider than pronotum, especially in female; ocelli and antennae inserted on anterior face, the ocelli without prominent tubercles or elevations and the antennae filiform; frons much wider than high, with corners more or less rounded; eyes rounded or conical but not projecting. Pronotum moderately slender, anteriorly rounded and narrower than posterior, with a flat, oval, weak supracoxal swelling, the disc, which in female is occasionally granular with serrated edges. Wings present in both sexes; in male well developed, hyaline, occasionally somewhat smoky, the tegmina having a longitudinal coloured stripe between costal and discoidal fields; in female somewhat shortened, variable in length, opaque, the tegmina with costal field at most half as wide as discoidal field. Raptorial legs strong; coxa longer than metazone of pronotum, with strongly developed denticles; femur moderately slender, with 4 discoidal and 4 outer teeth; ventral surface around outer teeth with several denticles; claw-furrow situated in proximal half of femur; tibia with 7 teeth in outer row. Middle and hind legs normal; middle metatarsus as long as other segments together, hind metatarsus longer. Suranal plate triangular, not elongate. Cerci moderately short, simple. Sexual dimorphism strong.

Remarks. *Miomantis* is a large genus comprising about 65 named species distributed in Egypt and eastern and southern Africa (Beier 1935c, Schoeman 1985, Roy 1987b). It is in urgent need of revision, as many of the species named by Giglio-Tos are based on colour only. Beier (1955) points out that the only certain way of distinguishing the species is by way of the structure and form of the male genitalia. *Miomantis caffra* was listed as a synonym of *M. monarcha* (Fabricius, 1793) by Beier (1935c), but was reinstated in 1955 on the basis of the structure and form

of the male genitalia. The taxonomic situation of *Miomantis* in South Africa may parallel that of *Orthodera* in Australia, in that there are a number of abundant, widespread, similar species.

New Zealand specimens were first identifed by Dr A. Kaltenbach (Naturhistorisches Museum, Vienna). Discovered as nymphs at New Lynn, Auckland, by a schoolboy, Richard Cuthbert, in February 1978, they have been referred to by O'Brien (1981). The species was reported as being established in New Zealand by Ramsay (1984).

Miomantis caffra Saussure

Figures 2, 5, 6, 8, 44–80

caffra Saussure, 1871: [?page]; 1872b: 309 (*Miomantis*). Rehn, 1927: 32 (*Calidomantis*). Beier, 1955: 261 (*Miomantis*).
monarcha (Fabricius). Giglio-Tos, 1927: 374 (*Miomantis*).

Female uniformly pale pastel green, occasionally pale greyish-brown or straw-coloured; forewings strongly pigmented, sometimes with costal vein white and other veins red/purple; pterostigma conspicuous, pale, glistening; hindwings bright yellow, becoming green anteriorly and at apex; dorsum of abdomen bright yellow anteriorly, at sides with two rows of white panels and sometimes a brown longitudinal band, all exposed only when abdomen is distended. Male also pale green, but metazone of pronotum tinged with pale reddish brown (no straw-coloured or brown variants seen; brown nymphs become green adults); forewings hyaline except for a band of green more or less extending for length of wing over radial and medial veins; radial vein pale-coloured, sometimes as a conspicuous white stripe; hindwings hyaline, with veins green. In both sexes, eyes with a conspicuous yellow band passing up from lateral angle of frons to top of eye, and sometimes middle and hind femora and all tarsi reddish-brown. One female had straw-green wings and pronotum and all legs tinged reddish-brown.

Females considerably larger than males. Dimensions (mm; mean or modal dimension in parentheses):

	Head width	Wing length	Body length (excl. wings)
Males:	4.5–6.0 (4.5)	27.0–34.0 (31.0)	36.5–43.0 (40.0)
Females:	6.0–7.0 (6.0)	18.0–25.0 (22.0)	32.0–50.0 (43.0)

Males slenderer than females. Wings much less than twice pronotum length in female, not completely covering abdomen in gravid females; in male 2–3× as long as pronotum and extending beyond tip of abdomen.

Head (Fig. 44, 45) triangular, in male more angular, shallower, and with eyes more pronounced; ocelli large, prominent, well developed; antennae 3x longer than pronotum. In female head deeper, triangular, with eyes less prominent and ocelli small, inconspicuous; antennae approximately as long as pronotum. In both sexes, frons shallow and arched mid-dorsally.

Pronotum. Dimensions (mm; mean or modal dimension in parentheses):

	Prozone length	Metazone length	Total length	Metazone width	Node width
Males:	3.0–4.0	6.5–9.0	9.5–13.0	1.5–1.75	2.5–2.75
	(3.5)	(7.5)	(11.0)	(1.75)	(2.75)
Females:	4.0–5.5	9.0–11.0	13.0–16.0	2.0–2.75	3.5–5.0
	(5.0)	(10.0)	(15.0)	(2.25)	(4.0)

Slender, much narrower than head, with a rounded swelling or node above attachment of coxae, comprising about one-third of total body length in female and one-quarter in male. Prozone arched anteriorly in lateral view, gradually widening towards node; anterior rim smooth, rounded; surface with a pattern of setate tubercles; lateral margins smooth in male, in female tuberculate-serrate; tubercles each with a small, subapical seta directed posterad; a short, mid-dorsal groove present anterior to suture; suture arched posteriorly, distinct, extending almost to lateral margins, where it turns abruptly forwards and becomes submarginal. Metazone lightly tuberculate, narrowing behind node, then gradually expanding posterad; lateral margins smooth in male, in female tuberculate-serrate, each tubercle with a subapical seta directed anterad on node and posterad behind this; posterior border smooth, rounded, slightly emarginate.

Legs (22 females and 4 males examined). Foreleg (Fig. 46, 47) similar in both sexes. Coxa same general colour as body, triangular in cross-section. In female, lower (posterior) coxal surface flat, with sharp, conspicuous margins each bearing a row of setate tubercles and with tubercles scattered on surface; upper (anterior) rim almost blade-like, comprising a row of strong, enlarged, setate tubercles/denticles alternating with 2 much smaller setate tubercles/denticles. In male, lower (posterior) coxal surface curved, with scattered setate tubercles/denticles distributed over surface only. In both sexes inner coxal surface with a linear series of 4–6 black spots. Femur with 2 dark pigment patches on inner surface, one proximal and the other nearby, at base of proximal discoidal seta, and a ventral anterior row of 13 (often 14) strong spurs, alternately long and short, separated by a strong groove housing tibial spur from 4 discoidal spurs, of which the 3rd distalmost from trochanter is much the largest; a proximal ventral row of approximately 6 setate tubercles/denticles lies proximal to row of discoidal setae; posterior (outer) ventral margin with 4 large, widely spaced, equal spurs between which are 1–3 small, setate tubercles/denticles; a few such also along anterior side of ventral surface of femur; distally on inner surface an elongate patch of paddle-shaped setae; apex with a pair of small, ventral spurs. Tibia with an inner, ventral, comb-like row of 13 (less commonly 14) spurs, these gradually increasing in size distad to a large, curved terminal spur, and an outer ventral row of 7 spurs, also gradually increasing in size distad. Tarsus inserted laterally, long, extending beyond trochanter when legs folded, 4-segmented; metatarsus longer than other 3 segments together, more or less straight. (See 'Regeneration', p. 50, and Fig. 48, 49, for details of abnormal morphology.)

Variation. The following variations in spur count were noted. Femur: one-third of the examples had 14 rather than 13 spurs in the anterior ventral row; the number of discoidal setae was constant; the spurs of the outer ventral edge in one example numbered 5 rather than 4; there is a tendency for the apical ventral spurs to be reduced – in several examples they were very small, and in one were absent. Tibia: half the examples had 14 rather than 13 spurs in the inner ventral row, and in one there were 15; in the outer row there was one instance of 6 spurs, 5 examples had 8, and one had 9 rather than the usual 7 spurs. Rehn (1927) remarked on the variation in number of the dark spots on the internal surface of the coxa and femur of the foreleg.

Middle leg. Normal inner surface of coxa and ventral surface of trochanter with stouter trichoid setae; flat outer surface of coxa with strong ribbed margins. Femur long, slender, with a ventral longitudinal ridge and a single, well developed anterior apical spine; trichoid setae more or less arranged in longitudinal rows. Tibia long, slender, with a strong, pointed expansion over insertion of tarsus and 2 strong, ventral apical spurs; trichoid setae in longitudinal rows. Tarsus 4-segmented; metatarsus relatively short, as long as the other 3 segments together, with trichoid setae arranged in strong rows.

Hind leg similar to middle leg. Coxal trichoid setae sparse. Femur and tibia identical; trichoid setae on all segments also the same. Tarsus 4-segmented; metatarsus considerably longer than the other 3 segments together.

Wings (22 examples, 8 of them males). As in the description of the wings of *Orthodera novaezealandiae*, the nomenclature of Snodgrass (1935) as interpreted by Smart (1956a) is used.

Both fore and hind wings strongly sexually dimorphic in colour, shape, size, and venation. Wings of female reduced in size, and ability to fly lost, although some non-gravid females do occasionally glide (D.I. Gardiner, pers. comm.).

Forewing sclerotised strongly in female, weakly in male. In both sexes a strong proximal lobe formed by peripheral vein, which curves upwards and around to merge with root of cubitus, encompassing postcubital vein and roots of

vannal veins. A strong furrow formed between roots of postcubitus and vannal veins and at root of cubitus.

Male forewing (Fig. 50) membranous, glossy, lacking pigmentation apart from a slender green band immediately behind radius in which not only the veins are pigmented but also the wing membrane, densely so in middle part of band. Veins mostly unpigmented or very pale-coloured apart from radius and costa, which are distally reddish-brown; media, which is strongly green in its proximal part; and cubital veins, which are pale green in the more distal area. Cross-veins and archedictyon strongly pigmented in colour band, where archedictyon is best developed. Forewing elongate, parallel-sided, slightly concave anteriorly, bluntly rounded distally, 28.0–31.0 mm long by 6.5–7.0 mm wide; costal area normal, unexpanded; jugum membranous, well developed, expanded beyond wing outline; alular lobe present. Pterostigma present but indistinct (see pp. 41–43).

Venation. In both sexes cross-veins numerous between all veins; in costal area cross-veins form pectinations. In female, archedictyon present distally in apical area, between radius and media, and weakly developed along posterior wing periphery; in male, a weak archedictyon present distally in area of subcosta, radius, and radial sector. Incipient intercalary veins recognisable between radius and medial and cubital (Ia) veins. Jugal lobe separated from rest of wing by peripheral vein, with reticulating veins only, i.e., with no direct association with vannal veins.

Costa (C) weakly submarginal proximally, extending almost to apex, where it becomes obsolete; peripheral vein obsolete in apical and distal areas, although a thin brown band is sometimes present. Subcosta (Sc) paralleling radius and gradually diverging to join costa distally. Radius (R) strong, forking distally into R_1 and radial sector (Rs). Media (M) forking to form media anterior (MA), which itself forks twice to form 3 MA branches, and media posterior (MP), which is usually undivided. Cubitus (Cu) forking proximally to form Cu_2, which never divides, and Cu_1, which forks to form Cu_{1a} and Cu_{1b}; Cu_{1a} forks once, and the anterior branch once again; Cu_{1b} forks only once, so that in total 6 cubital branches are formed. Postcubital (Pcu) joining with $1V$ to form a common stem which passes to peripheral vein. Vannal veins 4 in number: $2V$ joining peripheral vein, $3V$ not so, and $4V$ often very short. Pterostigma vague and indistinct, elongate, slender, overlying root of anterior branch of Cu_{1a}, sometimes extending to media (see section on pterostigma, p. 41).

Variation. The costa, subcosta, and radius do not vary. Rarely MA branches may have 1 or 2 additional forks or only 1 fork, and MP may fork once, the total number of M branches varying from 3 to 6. Cu_{1a} may have 1 or 3 forks,

or be undivided, while Cu_{1b} may be undivided or have 2 forks, the total number of Cu_1 branches varying from 3 to 6; in one example, the posterior branch of Cu_{1b} stopped well before the border; Cu_2 is constant. Pcu in one example united with Cu_2 instead of $1V$, and in both forewings of one specimen it remained separate right to the peripheral vein. The number of vannal veins is constant, but $4V$ is very short in some examples. The position of the pterostigma is relatively constant.

Female forewing (Fig. 51) sclerotised, with both veins and membrane densely pigmented and opaque, especially in anterior half of remigium. Colour varying from pale pastel green to straw brown; surface dull (?waxy layer present) apart from pterostigma and sometimes top surface of veins, which are glossy. Wing strongly arched anteriorly, slightly curved posteriorly; length 21.0–25.0 (23.0) mm, width 7.5–9.0 (8.5) mm; apex bluntly pointed; costal area expansive; jugal area membranous, distinct, but not protruding beyond wing outline; alular lobe present. Pterostigma strongly developed.

Venation. Costa (C) slightly submarginal proximally, extending along anterior border to apex, there becoming peripheral vein, which is sometimes weak or obsolete in apical area. Subcosta (Sc) variable, strong, paralleling radius to peripheral vein, sometimes diverging slightly and becoming part of archedictyon before peripheral vein is reached. Radius (R) the strongest vein, usually forking distally into R_1 and Rs but sometimes remaining undivided, variably associated with Sc and M in about half the examples studied. Media (M) usually forking at about half its length into MA and MP; MA usually forking once again, but MP remaining undivided; forking of M veins variable, but mostly 3 branches present. Cubital (Cu) forking into Cu_1 and Cu_2, the latter always remaining undivided while Cu_1 forks into Cu_{1a} and Cu_{1b}; these mostly each fork once again, but branching variable – mostly 5 branches present. Postcubital (Pcu) always undivided, usually becoming obsolete at approximately 85% of distance to margin. Vannal veins (V) mostly 4 in number, often only 3; $4V$ (when present) always very short; only $1V$ reaching border, curving behind Pcu to do so. Pterostigma a distinct, glossy, raised patch in centre of wing, usually occurring between branches of Cu_{1a} just distad of fork (see pp. 41–43, Fig. M16).

Variation. C is constant, but Sc sometimes diverges from R to become lost in the archedictyon or to unite with C, or curves to unite with R, forming a common stem which soon forks. R is sometimes undivided; in one example, Rs is forked. MA is unforked or forks twice; MP forks once or twice; the total number of M branches varies between 2 and 5. Cu_{2a} is sometimes undivided or forks twice, and Cu_{1b} is

sometimes undivided, the total number of branches varying between 5 and 7; in one example, one branch stopped some distance short of the border; Cu_2 is constant. The total number of $R+M+Cu$ branches varies from 8 to 13, but is mostly from 9 to 11. Pcu is relatively constant, but in 2 examples reaches and unites with the peripheral vein, and in one example curves to join $1V$, forming a common stem which reaches the peripheral vein. The V veins are relatively constant. The shape of the pterostigma is variable but its position is relatively constant, except for 2 instances of it lying between MP and Cu_{1a}.

Male hind wing (Fig. 52) well developed, flimsy, membranous, colourless apart from distal third of costal zone, where veins opaque and coloured pale green (veins otherwise colourless). Shape normal, slightly elongate; shorter than forewing, 25.0–28.0 mm long by 12.0–13.0 mm wide. Remigium bluntly pointed apically; vannus large, greatly expanded and folded like a fan when in resting position; jugum merged with vannus, recognisable only by presence of a faint, weak reticulation of veins.

Venation. Slight remnants of archedictyon present apically and on jugum. All main veins reaching wing margin; peripheral vein reduced to a brown line from apex to common stem of $Cu_{1b}+Cu_2$ along posterior margin.

Costa (C) completely marginal, extending along anterior border to apex, where it becomes weak and continuous with brown line of peripheral vein, enlarged proximally into a triangular plate which articulates with axillary sclerites. Subcosta (Sc) strongly concave proximally, closely paralleling radius and gradually diverging distally to join costa or merge with archedictyon. Radius (R) strongly convex proximally, the strongest hindwing vein, becoming straight and then slightly curved posteriorly at apex, proximally thickened, giving rise to media anterior and connecting with a strong, convex cross-vein from 1st cubital. Media anterior (MA) arising from radius just distad of cross-vein, closely paralleling radius, undivided, straight but becoming gradually curved posteriorly at apex. Media posterior (MP) arising from cross-vein, paralleling media anterior, undivided. Cubital (Cu) dividing at its origin; Cu_1 connecting with r–cu_1 cross-vein from radius, then continuing on, forking twice to form 3 branches (two anterior, one posterior); Cu_2 straight, undivided, then curving strongly to unite with the opposite-curving Cu_{1b}, forming a short common stem which meets margin; usually 5 cubital branches present. Postcubital (Pcu) straight, undivided, extending to margin. Vannal veins: $2V$ forking 3 or 4 times to form 4 or 5 branches; usually 6 other vannal veins present, with $7V$ and $8V$ separate from common proximal stem of all the others; number of vannal branches usually 11. Frequent cross-veins present between all veins; incipi-

ent intercalary veins present distally between radius, media anterior and posterior, anterior branch of 1st cubital, and vannals, but none of them strong or complete; indications of a weak incipient jugal vein sometimes apparent.

Variation. C, Sc, Pcu, and (with 2 exceptions) R are generally constant, but considerable variation is apparent in M and Cu. In one instance R and MA curved strongly together and united to form a common stem almost at the wing apex; and in another they joined at the very apex. There were 2 examples of fusion of MA and MP: in one a common root arose from the r–cu cross-vein, soon forking and uniting again to form a loop, the common stem later forking twice to produce 3 branches; in the other a common root arose from the radius at the usual MA position and soon forked into MA and MP, the latter forking later to give a strong, oblique cross-branch to Cu_{1a}. In two examples Cu_2 remained right to the wing margin, i.e., not uniting with Cu_{1b}. In another, Cu_{1b} became obsolete at 15% of its usual length, allowing the posterior branch of Cu_{1a} to curve posteriorly to meet the reverse-curved Cu_2 at the border. In yet another instance Cu_2 produced a short, obsolete branch curved to join Cu_{1b}. Once a total of only 3 cubital branches were present (Cu_{1a} failing to fork) and once only 4 (Cu_{1a} forking only once), instead of the usual 5. In one instance Pcu distally curved posterad to join the anterior branch of $2V$, producing a short common stem going to the border. In one specimen $2V$ forked 5 times on each hind wing and in another $3V$ and $4V$ had a common basal root, which however soon forked. The number of vannal branches is 10–12.

Female hind wing (Fig. 53) well developed, but reduced relative to that of male, shorter and more strongly curved apically, where it is bluntly pointed; costal area relatively broader; length 16.0–21.5 (20.0) mm, width 7.0–11.0 (10.0) mm; jugum merged with vannus, but recognisable by presence of a faint, weak reticulation of veins.

Venation similar to that of male. No two wings identical, even members of a pair. Remnants of archedictyon present at apex and in jugal areas only. All main veins reaching margin, although some becoming weak. Peripheral vein a faint, pigmented line only at apex and along posterodistal border of remigium, sometimes absent. Well developed cross-veins frequent on remigium, especially in proximal half, and in costal area; on vannus they are also frequent but weaker. Incipient intercalary veins present on vannus only, and a weak incipient jugal vein usually present.

Costa (C) completely marginal, extending along anterior border, becoming weak towards apex. Subcosta (Sc) strongly concave proximally, paralleling radius, from which it diverges only slightly distally, where it sometimes meets costa or more usually becomes part of archedictyon. Rad-

ius (*R*) strongly convex, sometimes enlarged proximally, gradually curved distally; *r–cu$_1$* cross-vein present proximally, convex. Media anterior (*MA*) often arising from radius near *r–cu$_1$* cross-vein, paralleling radius, variable. Media posterior (*MP*) arising from *r–cu$_1$* cross-vein, paralleling *MA*, variable. Cubital (*Cu*) dividing at its root; *Cu$_1$* joining *r–cu$_1$* cross-vein, then later forking, *Cu$_{1a}$* mostly forking once while *Cu$_{1b}$* continues undivided; *Cu$_2$* undivided; total number of cubital branches usually 4. Postcubital (*Pcu*) straight, undivided, unvariable. Vannal veins: *2V* forking 2 or 3 times to form 4 or 5 branches; 5 or 6 other vannals present, the last 2 unconnected with common root of the others; total number of vannal veins usually 10.

Variation. No two wings are identical, even members of a pair. Variations mostly involve *R, M,* and *Cu$_1$*, but *Cs* and *Cu$_2$* are also occasionally involved. In 2 examples *R* curved to fuse with *MA*, forming a short common terminal stem. In another (Fig. 54), described below, it fused with *M* to form a common stem which soon forked to give two branches, one passing to *Sc* and one which forked again. In yet another example *R* became obsolete at about 60% of its length and bent to join *Sc* (Fig. 55). In 11 of the 14 wings studied *M* is different. Mostly *MA* and *MP* arise separately, *MA* from the radius distal to the *r–cu$_1$* cross-vein, and *MP* from the cross-vein itself (Fig. 56). The origin of *MA* is usually close to the cross-vein, but in one instance is 25% of its length distad from it. In two examples *MA* and *MP* have a short common root (Fig. 57) arising from the cross-vein. In three examples *MA* commences as a short diagonal vein, passing obliquely to briefly fuse with *MP*, and then separating; in one of these *MA* very soon reunites with *MP* for a short distance (Fig. 58) before separating again, and in another (Fig. 54) *MA* is fused with *R* at about 65% of its length, forming a common stem which soon forks to give an anterior branch curving towards and uniting with *Sc*, and a posterior branch which soon forks again. (In this latter instance it is impossible to decide whether the distal anterior branch is a united *Sc+R* or *Sc* only, and whether the next two branches are *R* and *MA* or two branches of *MA*.) In two examples *M* failed to divide proximally; in one it forked at about half its length, the anterior branch uniting with *Sc* as *R* had already done; in the other (Fig. 59) *M* also forked at about half its length, giving an anterior branch which first has a strong cross-vein to *R* and then unites with it, and a posterior branch which later forks once. In another specimen (Fig. 60) *M* branches from *R* proximal to the *r–cu$_1$* cross-vein, uniting with *Cu*, which curves to meet it before the cross-vein, from which *MP* arises as usual. In only five instances does *MA* proceed unimpeded to the wing margin. There is one example in which the *r–cu$_1$* cross-vein is not formed at all (Fig. 61) and where both *MA*

and *MP* arise separately from *R*. Lastly, there is an instance of *MA+MP* curving to meet and forming a short common terminal stem. Despite this variation there are no examples of *MP* branching, and only two (one doubtful, depending on interpretation) of *MA* dividing. The cubital vein usually divides at its very root, so *Cu$_1$* and *Cu$_2$* are connected, but in one instance (Fig. 61) they arise quite separately, with the root of *Cu$_1$* attached to *R*. The number of *Cu$_{1a}$* forks varies from nil to two; *Cu$_{1b}$* is undivided except for a single instance in which it forks once. There is one example of *Cu$_{1b}$* ceasing shortly before the wing margin, and another of it uniting with the first posterior branch of *Cu$_{1a}$*. Apart from one instance of it dividing and then reuniting to form a loop (see Fig. 59), *Cu$_2$* is invariably simple and undivided. The total number of cubital branches is from three to five. *Pcu* is also invariable, in only one instance failing to reach the wing margin. The number of *2V* forks is from two to five, and with up to seven other veins the total number of vannal branches and veins is from nine to twelve.

Variation is also evident in the size and shape of the hind wing. In one example the costal border is notched distally, and in another pair the wings tend to be misshapen.

Nymphal wing pads (8 male and 2 female examples examined). In both sexes, colour variable from green to brown according to overall colour of nymph. In male, area above subcostal, radial, and medial tracheae often differentiated by a strongly coloured stripe; in female, this often paler-coloured; incipient veins also differentiated by stronger or paler pigmentation. Forewing pads completely without any shoulder development, and strongly sexually dimorphic in shape. In male, pad more or less parallel-sided and rounded apically, but in female arched anteriorly, with costal zone expanded, and bluntly pointed apically. Hindwing pads also sexually dimorphic, that of female with a proportionately larger costal zone, more strongly curved, and bluntly pointed apically. Male forewing pad 6.5 mm long (female 6.0 mm), hindwing pad 5.25 mm long (female 5.0 mm). No apparent precursor to pterostigma.

Forewing tracheation – male (Fig. 62). Costal trachea absent. Subcostal trachea strongly developed, pectinate, giving rise to a series of fine tracheoles. Radial trachea normal, dividing into *R$_1$* and *Rs* distally. Medial trachea variable, forking into *MA* and *MP* at about 65% of distance to rim; *MA* usually forking twice and *MP* remaining undivided, so that mostly 4 medial branches occur. Cubital trachea dividing near root; *Cu$_1$* variable, forking into *Cu$_{1a}$* (usually with 1 fork) and *Cu$_{1b}$* (mostly undivided); *Cu$_2$* undivided; total branches thus 4. Postcubital trachea normal but not reaching rim of pad. Vannal tracheae with 4 branches; *1V* longest, strongest; all branches giving off fine tracheole branches distally; *4V* smallest, finest, supplying

jugal region, sometimes forking. Tracheole precursors of cross-veins and incipient intercalary veins present.

Female (Fig. 63). Tracheation almost identical to that of male. Costal trachea not formed. Subcostal trachea strong, well developed, pectinate, giving off a row of long tracheoles, some forked or branched, over most of length. Radial trachea forking into R_1 and Rs. Medial trachea forking into MA, which has 1 fork, and MP, which may be forked or unforked. Cubital trachea forking near root; Cu_1 in turn forking into Cu_{1a} and Cu_{1b}, each either undivided or with 1 fork; Cu_2 undivided. Postcubital trachea normal, not reaching rim. Trachea $1V$ longer than postcubital; 3 smaller vannal tracheae present. Tracheole precursors to reticulum of adult wing present.

Hind wing tracheation – male (Fig. 64). Costal trachea absent. Subcostal trachea strong, pectinate, along its entire length giving off a series of fine tracheoles, these often forked, with tips bent towards apex. Radial trachea well developed, at approximately one-third of its length branching off medial anterior trachea. Medial posterior trachea simple, undivided, arising independently, so that 2 medial branches occur. Cubital trachea dividing near root; Cu_1 forking halfway along its length into Cu_{1a}, itself forking into 2 branches, and Cu_{1b}, which is undivided; Cu_2 undivided, so total number of branches usually 4. Postcubital trachea undivided. Trachea $2V$ usually with 3 forks; mostly 5 other vannal tracheae present, giving a total of 9; 2 posteriormost tracheae with a common root. Tracheole precursors of cross-veins and incipient intercalary veins present. Subcostal, radial, and medial anterior tracheae closely paralleling each other for entire length. MP arising apart, approaching R and then bending to give off MA before gradually diverging.

Female (Fig. 65). Costal trachea not formed. Subcostal strong, well developed, pectinate, giving off a row of fine tracheoles. Radial trachea strong, undivided, branching off MA at approximately 40% of its length to apex. Cubital trachea splitting proximally into Cu_1, which then forks into Cu_{1a} and Cu_{1b}, and Cu_2. Postcubital arising from root of cubital, extending to rim. Vannal veins totalling 11; $2V$ with 5 forks; 3 posteriormost veins arising from a common root. Tracheole precursors of cross-veins and incipient intercalary veins present.

Variation. Since so few specimens were available, especially of the female, the range of variation will doubtless be much greater than that described here. In the male forewing pads there were examples of R_1 forking terminally; a branch of MA forking terminally; a Cu_1 giving off a short, blind branch before forking into Cu_{1a} and Cu_{1b}; and Pcu arising as a short, blind branch of $1V$, which itself was forked. M divided into MA and MP at 50–60% of the

distance to the rim of the wing pad. There were examples of the medial anterior trachea forking only once or as many as three times, and of Cu_{1b} forking once or twice, the number of branches hence totalling from four to six. For the female only two wing pads were examined. MP was undivided on one and forked twice on the other, so the total number of medial branches was three and five respectively. The cubital branch totals were also three and five, as on one side Cu_{1a} and Cu_{1b} each forked once, whilst on the other they were undivided.

The male hindwing pad varied too. There were examples of trachea MA forking once distally or twice terminally; of MA and MP uniting for a short distance, then separating again (three examples); of Cu_1 forming a diverticulum before separating into Cu_{1a} and Cu_{1b}; of Cu_{1b} extending for only half its normal length; and of Cu_{1b} curving to join Cu_2 distally. There was one example with three medial branches instead of two. The number of cubital branches varied from three to seven. There were four examples of $2V$ having four forks instead of three, and the total number of vannal branches was more or less equally nine, ten, or eleven. In the female examples Cu_{1a} was undivided in one and single-forked in the other.

Abdomen normal, soft, parallel-sided in male, larger, broad, with curved sides in female. Male with 9 tergal and 7 sternal plates, female with 9 and 5 respectively. Tergites VII, VIII, and IX weakly ribbed mid-dorsally in female only; IX emarginate in both sexes. First sternite forming a strong spur behind hind coxae in male and a weak, blunt point only in female. Cerci slender, soft, tapering, circular in cross-section, with long and short trichoid sensilla in both sexes; cerci longer and stronger in male, comprising approximately 14–17 segments, these ill defined proximally, narrower and longer distally; in female cerci curved, no longer than and paralleling ovipositor, in male extending for approximately one-third of their length beyond subgenital plate; proximal segment flattened dorsoventrally (semi-pedunculate) in both sexes. Suranal plate (Fig. 66, 67) similar in both sexes, wider than long, deeply triangular, slightly irregular to crenulate in outline, more or less flat, well clothed with short and long trichoid sensilla, especially around margin. Subgenital plate in male (Fig. 68) convex, asymmetrical, longer than wide; sides curved; apex extending between strongly developed, tapered styli, truncate; subgenital plate and styli clothed with strong, long and short trichoid sensilla. Subgenital plate in female (Fig. 69) strongly convex, hemispherical, apically forming a bilobed sheath surrounding ovipositor; dorsally, plate and sheath reflected inwards; groove separating plate from sheath well developed, emarginate; lobes contiguous for less than half their length; point of separation of sheath

lobes not cusped; entire surface densely clothed in long and short trichoid sensilla.

Genitalia. *Male.* Hypophallus (Fig. 70) a large, more or less flat, subquadrate plate; left margin curved dorsally to encompass left epiphallus; distal border broadly pointed, with apex round; angle of left side forming a dark, sclerotised knob with a group of approximately 7 sharp, strong, recurved spines; angle of right side broadly rounded, without spines; integument ventrodistally well clothed with strong trichoid sensilla; left side dorsally with a group of non-trichoid sensilla and proximally with numerous microtrichia, otherwise generally smooth and featureless. Left epiphallus (Fig. 71): titillator slender, flat, its posterior projections distally truncate, round and strongly curved dorsally, lightly sclerotised, ventrally with a separate broad, rounded lobe and laterally on left side with an extension comprising 2 lobes, from between which pseudophallus emerges; a group of short trichoid sensilla present apically on titillator, and non-trichoid sensilla grouped on titillator neck and scattered on ventral lobe and proximal membranes; lateral pseudophallic lobes membranous, densely covered in fine, sharp microtrichia; integument otherwise smooth. Pseudophallus a strongly, darkly sclerotised, flat, blunt, finger-like projection with 11–13 strong, recurved spines; surface strongly wrinkled, with a cellular pattern. Right epiphallus (Fig. 72) a flat, more or less conical lobe curved to right; basal notch strongly, darkly sclerotised, densely covered with recurved microscales and comprising a flat ridge and a blunt, strongly developed, finger-like projection, the apophysis, which is slightly tapered and crenulate along its inner border; short trichoid sensilla grouped apically and scattered on dorsal surface and left lateral area of ventral surface, non-trichoid sensilla scattered along right lateral region of ventral surface; proximal membranes densely clothed with fine microtrichia, microspines, or microscales; integument otherwise smooth and featureless.

Female. Ovipositor comprising 3 short, downward-curved pairs of valves which are generally soft and lightly sclerotised but with some pigmented plates. Ventral valve (Fig. 73) a moderately slender, irregular-shaped rod with a proximal Y sclerotisation, a broad, ventral, conical extension at a little over half length, a strong longitudinal dorsal groove with slightly sclerotised rims, and a short distal groove separating the 2 terminal lobes – the inner smaller, nude, not enlarged, the outer well developed, enlarged, densely clothed with strong, trichoid sensilla on all surfaces; scattered concentrations of varied trichoid sensilla present on all surfaces of valve; integument smooth, often densely porose except for reticulated, sclerotised area along inner rim of dorsal groove and a proximodorsal patch of microtrichia. Dorsal valve (Fig. 74) slightly curved,

strongly arched dorsally but without proximal shoulder, apically truncate, with 2 lips associated with longitudinal groove or hollow; a median, longitudinal, bar-like sclerotisation for muscle attachment present; strong trichoid sensilla present along dorsal rim but not forming a crest, otherwise numerous scattered, varied trichoid sensilla present on all surfaces but absent on much of inner surface; integument with a proximoventral patch of strong, dense microtrichia and areas of dense, strong microscales; proximal two-thirds of valve generally tending to form microscales, distal third smooth but porose. Median valve (Fig. 75) flat, dorsally arched, without a proximal shoulder, rounded apically, and ventrally with a strong, blunt spur at about half length; a strong proximal, dorsal, transverse bar present; upper third of valve comprising a thin blade with finely crenulate margin and pectinate ridging, uniform in height but strongly tapered and rounded distally; 2 pigmented longitudinal plates present in lower half of valve and ventrally, as well as a median longitudinal thickening providing muscle attachment and extending an arm down to spur, which ventrally is strongly pigmented; sensilla absent; integument forming microtrichia or microscales over entire surface except apically, these particularly well developed and dense in a median longitudinal band on inner surface and ventrally, including spur.

Type data. **Holotype** male: South Africa, Natal (Brunner von Wattenwyl Collection, Naturhistorisches Museum, Vienna).

The voucher material on which this study is based is in the New Zealand Arthropod Collection, DSIR Plant Protection, Mt Albert Research Centre, Auckland.

Distribution (Map 2). *M. caffra* is a South African species which is gradually extending and consolidating its distribution in Auckland and the northern parts of New Zealand. It is now well established around metropolitan Auckland, eleven years after its initial discovery in the suburb of New Lynn, and has been reported from Green Bay, Glen Eden, Henderson, Massey, Te Atatu, Avondale, Mt Albert, Point Chevalier, Westmere, Herne Bay, Auckland City, Parnell, Remuera, Ellerslie, Glen Innes, Pakuranga, Glendowie, Howick, Onehunga, Mangere, Glenfield, Browns Bay, and Mairangi Bay. Beyond Auckland it has been found to the south at Takanini and Waiuku, and to the north at Campbell's Beach (Warkworth), Patana South (Whangarei), and Kaitaia. It has been reported from Paeroa and Morrinsville also.

No doubt its spread has been assisted by the deliberate dispersal of oothecae, but even so a pattern of gradual marginal increase is apparent. The limits to its distribution, actual and potential, are unknown, but since it is an adapt-

able species able to survive the Auckland winter more readily than *O. novaezealandiae* it may well eventually colonise a greater area of New Zealand than the latter species. Indeed, it may even be able to displace it, as in some areas it is now more frequently seen than *O. novaezealandiae*, which formerly was the more common.

A computer file listing the distribution details of all specimens used in this study is held by DSIR Plant Protection, and may be accessed by contacting the Curator of the New Zealand Arthropod Collection at the address on p. iii.

Life history. The life cycle is annual, but more flexible than it is with *Orthodera novaezealandiae*. Egg-laying commences in February, soon after the adult stage is reached, continues through April, and may run on into winter, in fact as long as the females survive (D.I. Gardiner, pers. comm.). Adult females often overwinter, but males have mostly disappeared well before the onset of winter, commonly being cannibalised by the female during copulation. In one instance an overwintering female captured in August lived through to January in captivity, producing several oothecae. Another female overwintering in captivity produced three oothecae during October. Nymphs may also overwinter.

The length of time from laying to hatching is not precisely known, but is probably similar to that for *O. novaezealandiae*, i.e., 5–6 months. There are no records of rapid development such as occasionally occurs with *O. novaezealandiae*. In the laboratory at Auckland nymphs emerge in spring, beginning in September and continuing through October and into November and December. Emergence from each ootheca is not simultaneous and synchronised as it is with *O. novaezealandiae*, but extends over the whole hatching period. In one example an ootheca which had commenced hatching in October produced three nymphs during the following April and May; and in several other instances, nymphs (usually only a few) emerged from an ootheca which had commenced hatching 12 months previously – some of the eggs had therefore remained viable for two successive seasons (D.I. Gardiner, pers. comm.).

The fact that emergence is spread over several months or even over two seasons, and that no examples of accelerated development are known in *M. caffra*, is unusual and suggests that temperature may not be a triggering factor in the development of its egg as it probably is with *O. novaezealandiae*. It seems that with many mantids, synchronised hatching is the usual state of affairs. An extreme example is mentioned by Heath (1980), who observed up to 300 nymphs of *Tenodera aridifolia sinensis* (Saussure) erupting from their egg-mass within approximately half an hour.

Up to 100 or more nymphs may emerge from a single ootheca. Most nymphs are fast-growing, and reach the adult stage by late January or early February; others are slower, and some much slower, not attaining the adult stage until August, September, or even October. The nymphs remain at the same instar (4th) during winter and then moult and pass rapidly through the 5th instar. In these examples the nymphal stage lasted almost a full year (D.I. Gardiner, pers. comm.). A fifth-instar female nymph was present in June and a fourth-instar male in October in laboratory culture; in the wild, first- and second-instar nymphs have been collected at the end of March, a first instar in June, and another in August. In culture females often live for 10 or more months from hatching; in the wild some may survive even longer.

Ootheca. Females are not particular about where they deposit their oothecae. These may be laid in corners or crevices or between folds, on leaves and twigs, on flat solid surfaces, or even on gauze, fabric, and so on, in fact anywhere – even in the wheel-bay of a car. As with *O. novaezealandiae*, shelter does not seem to be important. Malformed oothecae are sometimes produced, for example with eggs arranged irregularly, giving an irregular shape to the ootheca, or very small. In one instance the central opercular cover was not clearly differentiated, and was almost overtopped by the foamy material of the sides (C.T. Duval, pers. comm.). Each female produces several oothecae, in one instance as many as five. However, there is little data about this, and the total could be greater. Oothecae are quite variable in size, the length ranging from 9.0 mm to 31.0 mm (usually 16.0–26.0 mm) and the width from 5.0 mm to 14.0 mm (usually 10.0–12.0 mm). There is a projection 3.0–6.0 mm long from the posterior end of the ootheca as well.

The ootheca (Fig. 8, 76, 77) is a pale creamy brown, sometimes slightly greenish when first laid, with a longitudinal band overlying the orifice paler still. The surface has a felt-like appearance caused by the thick layer of fine foam from which it is made. In shape the ootheca is broad and rounded, rather like a braided loaf of bread. The commencing (posterior) end is irregularly rounded, and at the terminating (anterior) end a prominent dorsal projection rather like the spout of a teapot is formed. Oothecae are often misshapen, even twisted, to accommodate the form of the substrate. The thick outer layer of fine foam can be peeled back to reveal the strong, rigid wall of the ootheca beneath, which is strongly ribbed and dark brown in colour (purplish in fresh specimens). It is much wider than that of *O. novaezealandiae*, with curved, strongly bulging sides which arch upwards to form the serrated orifice crest (Fig. 76).

The orifices are arranged in a double row, but the figure-of-eight configuration so obvious in *O. novaezealandiae* is not apparent superficially because the upper rim of each orifice slopes strongly downwards and inwards. The number

of orifices varies from 10 to 62, but is most commonly between 40 and 50. The lateral outer rim of each orifice forms a strong, anteriorly slanting cusp. The inner borders are replaced by very well developed, rounded flaps which are thin, flexible, and pale in colour with a curved darker rim. Each commences at a lateral cusp and arches across the orifice band to the other side, sloping upwards and forwards in the process. The flap extends downwards for a considerable distance, overlying the posterior wall of the orifice throat and eventually fusing with it transversely just above the level of the eggs.

The flaps do not close off the entrance to the egg chamber as they do in *O. novaezealandiae* but are embedded in the ootheca foam right down to the level of the eggs. Internally the foam is coarse, but externally it is very fine. Thus, in this species the foam filling the neck of each orifice and embedding the flaps is the medium by which the egg chambers are sealed. This may be related to the wide time-spread of hatching in this species compared with *O. novaezealandiae*, in which hatching is more or less simultaneous, and where the dislodged egg chamber flap may no longer act as a barrier. The foam and enlarged flap of *M. caffra* could still be an obstacle, even though penetrated by one or more larvae.

Each orifice leads into an egg chamber which is transverse, containing a single row of eggs arranged vertically in the medial area and sloping inwards at the sides so as to be radial in cross-section (Fig. 76). Each egg is contained in a membranous cell, the membrane of which is thin and translucent when fresh but dull and opaque after the eggs have hatched. The membrane of each egg cell adheres to the egg chamber wall and to the membrane of the contiguous cell.

The chambers of each side are offset in relation to one another. Each contains from one to six eggs, depending on its position in the ootheca (Fig. 77). The very first chamber at each end contains one or two eggs only, but this immediately increases to three and then to four or five, the number sometimes being different on each side, and then reaches six on each side towards the middle. Because of the close packing of the eggs, their arrangement in transverse rows in egg chambers is not always obvious. Thus, there is a maximum of twelve eggs and a minimum of three in a transverse row. As with *O. novaezealandiae* there is a relationship between the number of eggs, the number of egg chambers, and the number of orifices.

No counts of the total number of eggs per ootheca have been made, but it can be estimated that if the average number of eggs in each egg chamber is taken as four then the total number will vary from 40 to 248, lying mostly between 160 and 200. These are probably conservative estimates, however. The mortality rate could be high, as

OFFSHORE
ISLANDS
Kermadecs
Three Kings
Chathams
Snares
Bounty
Antipodes
Aucklands
Campbell
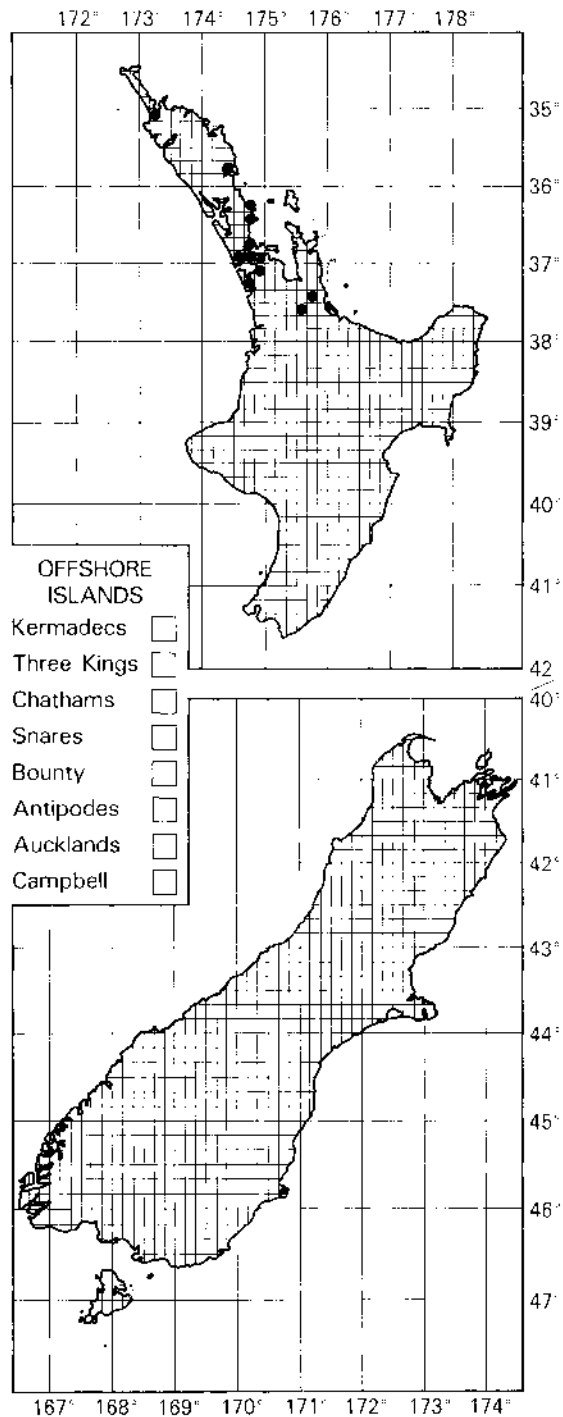
· **Map 2** Distribution of *Miomantis caffra* ·

Heath (1980) states that "in the wild probably only two out of two hundred [nymphs] from one egg mass will survive".

Egg (Fig. 78, 79). Densely packed with yolk; chorion smooth, soft, glistening, and transparent. Egg 3.5 mm long by 1.0 mm wide at top and 1.5 mm at bottom, curved pyriform in shape when freed from ootheca. Dorsal (anterior) pole rounded, bottom (posterior) pole slightly truncate. Exochorion smooth, structureless, thicker at anterior pole. Endochorion densely and finely granular, the granules appearing as rods in sectional view. Granules refractive, varying in size and shape, uniformly distributed over entire egg apart from numerous small, clear patches evenly distributed amongst them, the largest at anterior pole; granules largest, strongest, and darkest dorsally. At about one-third of length of egg from posterior pole, on dorsal surface, clear patches become larger, elongate, more or less unidirectional, and dart-shaped, pointing posterad. Darts structureless, not strongly refractive, and apparently not internal as they are in *O. novaezealandiae*. The curved rods present in *O. novaezealandiae* are lacking in *M. caffra*.

Chorion of mature, embryonate egg with a distinct circular micropyle, consisting of irregular refractive material and granules, behind patch of longitudinal darts. After hatching, chorion becomes pale-coloured and opaque, but otherwise unchanged. No pigmentation or elevation of micropyle or its surrounding area.

Thus the egg of *Miomantis caffra* is different from that of *Orthodera novaezealandiae* in its shape and the form of its micropyle. However, it is much more similar to that of the latter species than to the egg of *Hierodula crassa*, described by Beier (1968), in which the chorion forms a circumferential flange at one-third of the length of the egg from the anterior. Ventrally this arches forward in the shape of a tongue.

Embryo. Fully developed embryo enveloped by an embryonic cuticle within the chorion. Mesothoracic, metathoracic, and abdominal tergites densely clothed with small, posteriorly directed scales. Anteriorly a pale brown-pigmented, deep, bell-shaped cephalic cap present (Fig. 80), unlike that of *O. novaezealandiae* too deep to be flattened out; cap smooth, finely porose, with a lateral band of incised, strong cellular patterning with ill defined inner border as it extends medially and gradually fades away; dorsoposteriorly cap triangular, with a short caudal extension and fine, serrated mid-dorsal crest extending well forward; ventroposteriorly also cap triangular, formed into a slender, rod-like structure extending posteriorly which, after hatching, lies beneath the folded, compressed, membranous clypeus and partly beneath labrum. Labrum spatulate, truncate anteriorly, rounded posteriorly, with lateral and transverse apodemes and densely studded with small, strong, refractive, posteriorly directed scales.

Hatching. The pronymph splits the egg chorion longitudinally at the anterior pole. In both species pronymphs emerge through the orifices of the ootheca and remain suspended by their pair of hatching filaments while moulting takes place and the first-instar nymph emerges and escapes.

The cast-off embryonic cuticle with its conspicuous cephalic cap remains connected to the ootheca by the hatching filaments, which pass down through the orifice and attach to the chorion on the inside of the posterior pole of the egg, which remains in position at the bottom of the egg chamber. The hatching filaments are produced by the cerci of the pronymph.

The empty egg chorion is flimsy, and ends up more or less folded and compressed at the bottom of the egg chamber (cf. *O. novaezealandiae*). The balloon-like expansion of the vertex of newly emerged nymphs is transparent and pulsating, and is soon resorbed as the head assumes its normal shape. The surface of the expansion is sticky and will adhere to surfaces like glass if the nymph is unfortunate enough to fall so that the expansion contacts such a surface.

Immature stages. There are normally six instars, but sometimes – especially with large females – seven. The time taken to reach maturity, as for *O. novaezealandiae*, is up to 5 months, but must vary considerably, especially with overwintering nymphs.

First-instar nymphs 5.0–5.5 mm long, with head and thorax occupying more than half this length; head and eyes disproportionately large and well developed; abdomen strongly up-curved; colour greyish brown, with legs conspicuously banded alternately brown and white. Second instar nymphs more uniformly coloured, some pale green. Legs of all instars banded, but less conspicuously so with each successive moult. Abdomen more or less strongly upcurved in all instars. Older nymphs often longitudinally striped.

Green nymphs, both male and female, often have antennae, posterior half of pronotum, and middle and hind femora reddish brown. Abdomen often with a mid-dorsal, anterior, diamond-shaped brown patch surrounded by yellow or white, then a conspicuous mid-dorsal stripe which may expand on each segment. Dense, white, lateral stripes sometimes occur along the abdomen. Other nymphs are uniformly green except for the middle and hind femora and tarsi, which are dark brown-mottled, and the abdominal tergite behind the wing buds, which has very conspicuous brown and yellow coloration. Brown male nymphs are common, and usually have mid-dorsal and lateral longitudinal stripes of darker brown; brown nymphs may become green adults. The nymphs are very aggressive and capable of fast movement.

Biological notes

Flight. Males of *M. caffra* are not strong fliers, but are attracted to mercury vapour lamps. Unlike *O. novaezealandiae* they tend to settle only on foliage, and not in the open – on a light-trapping sheet, for instance (C. Green, pers. comm.).

Females cannot fly, but are able to spread their wings and glide, especially when not gravid (D.I. Gardiner, pers. comm.).

Behaviour. M. caffra is active and aggressive in comparison with *O. novaezealandiae*. Nymphs and adults will leap out at prey, and can move very rapidly. Adult female's will even attack and bite a handler's finger to the extent that pain is felt (D.I. Gardiner, B.G. Bennett, J. Cardis, pers. comm.). It seems quite content to live indoors, and will remain for some time near windows or in a conservatory area, provided an adequate food supply is available. Eggs may also be laid indoors.

This species seems to be displacing *O. novaezealandiae* in places where it is abundant. Perhaps its greater aggressiveness, higher reproductive potential, less seasonal life cycle, greater longevity, and ability to live in a wider variety of habitats contribute to this.

Colour. The colour of *M. caffra* varies greatly. Most commonly females are green in various shades, some almost bluish, and only very occasionally are straw-brown individuals found. However, during the 1989 summer numerous brown individuals, some almost red or pink, were reported, and one very pale, almost albino individual was seen in February 1990.

Males are also most commonly green, but brownish specimens were seen in 1989. The reason for this is unknown. It could possibly be caused by climatic factors, or perhaps be the result of the greater abundance of the species, the proportion of brown individuals remaining constant.

Interspecific mating. The mating of female *M. caffra* with male *O. novaezealandiae* was noted earlier (see p. 24, and Ramsay, in prep.*). The reciprocal mating of a female *O. novaezealandiae* with male *M. caffra* has not been observed.

Infertility. A considerable proportion of the oothecae of this species fail to hatch. This may reflect the fact that most if not all males are eaten during copulation, so that not all females are able to find a mate. (Females always seem to be more abundant than males anyway.) This is possibly a means of controlling population size.

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*Sex attraction, interspecific mating, parthenogenesis, and fertility of mantids. *New Zealand entomologist.*

SPECIES DELETED FROM THE N.Z. FAUNA

Tenodera intermedia Saussure, 1870

The type specimen, a female 85 mm long, was collected at Auckland some time before 1870. However, Hutton (1897) suggested that the locality data were incorrect, as no further specimens of this large insect had been found, despite the presence of keen observers. This is still the situation, so it must be presumed that the specimen was accidentally transported by ship and gained entry into New Zealand before any quarantine regulations were in force. Although not the first foreign insect to be intercepted in New Zealand, the type specimen of this species is probably the second (Kleinpaste 1983, 1984). Mantids are still being intercepted at New Zealand ports and points-of-entry (Richardson 1979, Keall 1981).

Descriptive details of the specimen, which was placed in the "Museum de Paris", are given by Saussure (1870b, c, 1871, 1872a, b), and of the species by Giglio-Tos (1912, 1927). It has been listed as a New Zealand species by Saussure (1870b, c, 1872a, b), Westwood (1889), Kirby (1904), Giglio-Tos (1912, 1927), Tindale (1923), and Beier (1935c). Hudson (1892) used this name for *Orthodera novaezealandiae* in his 'Manual of New Zealand Entomology', a misidentification which was recognised by Hutton (1897) and Giglio-Tos (1921). It is easily distinguished from the two New Zealand mantids by its much larger size (body length of males 80–86 mm, of females 85–92 mm); from *Orthodera* by its proportionately longer, slender, dorsally rounded pronotum; and from *Miomantis* in that the female is slenderer and the wings completely cover the abdomen, even when gravid, and by the attachment of the foreleg coxae at 20% of the pronotal length from the anterior, cf. 35% in *Miomantis*. The species is recorded from Australia (Queensland, Northern Territory) and New Guinea (Tindale 1923, Beier 1935c).

Tenodera australasiae (Leach, 1814)

There are no published reports of specimens of this species having been collected in New Zealand, and I do not know of it ever having been found here. The listings of Kirby (1904), Tindale (1923, 1924), and Pemberton (1952) could have resulted from a misinterpretation of the information in earlier works, in which the distribution was given as "New Holland; Tasmania; Papua; Ceram; New Caledonia; New Guinea" (Westwood 1889). It is widespread in Australia and Tasmania, New Guinea, and the Molucca Islands (Tindale 1923) and has established in Hawaii (Pemberton 1952). Beier (1935c) listed it from South Africa as well. It could possibly establish in New Zealand too, given the opportunity.

REVIEW OF ASPECTS OF
FUNCTIONAL MORPHOLOGY AND BIOLOGY

(a) Femoral brush

The presence of a dense patch of setae on the mediodistal part of each forefemur, known as the femoral brush, was first noted by Stål (1872), and was reported on by Wood-Mason (1876a–c, 1877). (The promised full account of this in the *Journal of the Asiatic Society of Bengal* (Wood-Mason 1877) was never published.) Wood-Mason (1876a,c) suggested that the femoral brush probably occurs universally throughout the Mantodea, as he had observed it in numerous species of at least 29 genera in six families and subfamilies. He also noted its presence in first-instar nymphs. It is shown in the illustrations of the forelegs of *Thesprotia filum, Amorphoscelis annulipes, Eremiaphila numida, Chaeteessa valida, Metallyticus splendidus,* and *Acanthomantis aurita* of Chopard (1938, p. 276), and *Archimantis latistyla* of Key (1970, p. 294).

Wood-Mason (1876b, 1877) reported that the femoral brush is used exclusively for keeping the compound eyes and ocelli clean. Shelford (1903) observed that "the forelegs are repeatedly rubbed over the eyes and top of the head [following a meal] much in the same way as the House-fly, after rubbing its fore tarsi together, passes its legs over its head". Faure (1940) stated that "the anterior end of the forefemur is manipulated by the mouth-parts, and presumably moistened, and then repeatedly passed over the eyes and the upper part of the head, with slow deliberate movements ... in the best feline manner". Chopard (1949), when describing the same habit, stated that the mantis moistens the femoral brush with saliva. Finally, Heath (1980) mentions that mantids always clean themselves after feeding by passing their forelegs over the surface of the head and then cleaning the forelegs with the mouthparts. Head grooming behaviour in *Sphodromantis lineola* has been described and analysed by Zack (1978), and the role of the interommatidial sensilla in its initiation has been investigated by Zack & Bacon (1981).

A femoral brush is present in the two New Zealand mantid species. Both Potts (1884) and Dixon (1938) mention that *O. novaezealandiae* is particular in cleaning its head after every meal, using its foreleg in a manner similar to that of a cat passing its paw over ears and eyes. *M. caffra* exhibits the same behaviour. The femoral brush (Fig. M1) comprises 100–200 feather- or paddle-shaped setae, the females usually having more such setae than the males. The setae are arranged in a dense, compact group (Fig. M2) and so orientated that their blades are directed distally and ventrally. In the proximal and dorsal areas of the group, the setae tend to be directed distally, becoming more and more ventral towards the distal and lower edges of the patch.

Each seta has a strong, cylindrical shaft or rachis on which proximally a short groove occurs, leading into a distinct pore (Fig. M3,5, 7). This has rounded lips, and is the moulting pore or ecdysial canal (Gnatz & Schmidt 1971, McIver 1975, Zacharuk 1985). It is constant in position on the exposed surface of the rachis near the base. A vane or blade is formed along the ventral sector of the rachis for about the distalmost three-quarters of its length. This vane is bluntly pointed apically, and especially when split at its margin gives the seta a feather-like appearance. In *M. caffra* the vane tends to be narrower and more sharply pointed, and is often twisted (Fig. M4,5). It is only rarely a little twisted in *O. novaezealandiae*. In both species the upper surface of the vane is transversely ribbed or wrinkled, but not always conspicuously so (Fig. M6). Each seta is oriented obliquely to the integument surface, and its insertion is shaped accordingly, having a strong, raised lip on the proximal side only (e.g., Fig. M7,8). In older specimens, transverse splits which may develop into notches occur in the vane (Fig. M8). In old specimens the vane becomes more and more tattered and parts are lost, so that eventually only the rachis may remain (Fig. M9,10).

(b) Wing morphology

Orthodera novaezealandiae. The dense, strongly developed archedictyon of the forewing is its most obvious characteristic. As a consequence of it, cross-veins are absent. The amount of variation is similar in each sex and mostly involves the radial, medial, and cubital veins. Both sexes are able to fly, and sexual dimorphism is slight, being apparent in size and shape but not venation, apart from minor differences in the archedictyon. The forewings combine the functions of flight and protection.

The hind wing of *O. novaezealandiae* is much more similar to that of other mantids than is the case with the forewing. Only remnants of the archedictyon are present and the cross-veins are normal. The amount of variation is similar in the two sexes and again usually involves the radial, medial, and cubital veins. Sexual dimorphism is slight also, and is limited to size and shape.

In general the nymphal wing pads reflect the adult condition except that the pigment is uniformly distributed in the hypodermis and not confined in a reticulum. Variation occurs in the tracheation of the nymphal wing pads just as it does with the venation of the adult wings. The second cubital trachea becomes weak distally and fails to reach the margin, and there is a tendency for this condition to develop with the postcubital also. As with the costal vein there is no separate tracheal precursor for the peripheral vein. However, the main veins of both wings each bifurcate terminally into two fine tracheoles, which could be regarded as precursors of the peripheral vein. Trachea *IV* of

the forewing curves strongly distally to meet the common stem of Cu_2 and Pcu, but does not necessarily unite with it. In several examples it then carries on parallel and contiguous with the stem for some distance. The constancy of the R, MA, and MP tracheae in the hindwing, in which MA without exception distinctly arises as a branch of R, is interesting in view of the different interpretations which have been put upon the vein here regarded as MA, the variation of the origin of the vein in the adult, and the absence of the conspicuous convex $r–cu_1$ cross-vein in the nymph. These three tracheae are very closely associated with the origin of MP, which is widely separated from that of $R+MA$ on the hindwing tracheal root, curves to meet and run parallel with $R+MA$, and is even always bent slightly to accommodate the MA branch where it separates from R.

Miomantis caffra. The forewings are distinguished by their strong sexual dimorphism, which reflects the inability of the female to fly. Although the female is larger and more robust than the male her wings are shorter, and have a different function – protection. To this end her forewing is more heavily sclerotised, strongly pigmented, opaque, covered by a waxy layer, and leaf-like. The costal region is expanded and the outline is curved, while posteriorly the jugal lobe conforms to the wing outline. In the male the costal region is normal and the wing outline is straight and much more elongate, while the jugal lobe is well developed and projects from the wing outline posteriorly. The surface of the female forewing is covered by a wax-like layer which causes it to appear dull and powdery (Fig. M16, M17, M20). Only the upper surfaces of the veins and pterostigma are glossy and free of this waxy material. The pterostigma is a strongly developed, very distinct, elevated patch. In the male the forewings are mainly transparent, membranous, and flimsy, their principal function being flight. They are glossy and lack the waxy surface layer of the female. The pterostigma is not as discrete nor as distinctive as in the female (Fig. M23).

The forewing venation too is strongly sexually dimorphic. In the female the postcubital vein (Pcu), although strong and retaining its identity, fails to reach the wing border, becoming obsolete at approximately 80% of the distance to the border. In the male it joins with the first vannal vein ($1V$) to form a common stem, which passes to the border. As well, one additional branch each of the medial and cubital veins usually occurs, and the vannal veins are more strongly developed.

A further distinction between the male and female forewing is in the degree of development of the jugum. In the female this does not extend beyond the general wing outline, whereas in the male it forms an expansion. In both it is separated from the wing by the peripheral vein, and has a reticulated archedictyon venation only.

The hind wings of *M. caffra* lack both the pterostigma and the waxy surface of the female forewing. The strong sexual dimorphism of the forewings is reflected in the hind wings, not only as regards their shape and size but also in venation. The female hind wing is much smaller, with more apical curvature, resulting in the veins being more strongly curved, and with venation that is both distinct and quite variable, although remaining basically very similar to that of the male. The male is characterised by the distal union of Cu_{1b} and Cu_2, which curve strongly towards each other and unite to form a short common terminal stem. In the female they remain discrete, and moreover $2V$ usually has one less division. The degree of development of the incipient intercalary veins is less in the female also. The female hind wing is further distinguished from that of the male by its relatively broader costal area. In both sexes, variation of the venation mostly involves the media and first cubital veins and, in the female, the radius also occasionally. The amount and frequency of variation is much greater in the female, in which no two wings are identical. This may be a result of the female being unable to fly, such that the hindwings have become almost functionless and may be in the early stages of atrophy and eventual loss.

The wing pads of the penultimate instar of *M. caffra* in general foreshadow the adult condition in their colour, shape, and tracheation, and in their strong sexual dimorphism. However, some interesting characteristics are not anticipated. For instance, sexually dimorphic characters of the adult wing venation such as the union of Pcu and $1V$ of the male forewing and the terminal union of Cu_{1b} and Cu_2 in the male hind wing are not foreshadowed in the tracheation of the nymphal wing pad (there was in fact one example of the latter, but this I am treating as a variation). There is a tendency for the diminished number of medial and cubital branches of the female as compared with the male wings to be reflected in the tracheation of the nymphal wing pads, but not (in the two examples studied) the diminished number of vannal branches or of forks of the second vannal vein. These may become apparent when more specimens are examined, but there is difficulty in ascertaining the actual number of forks in the proximal part of $2V$ because the beginning of the common vannal root and the beginning of $2V$ are always vague. Another point of distinction between the male and female hind wing pad is the wider spacing of the subcostal, radial, medial anterior, and medial posterior tracheae in the female, which results in MP being straight rather than bent to accommodate MA as it branches from the radius.

Discussion: New Zealand species. The strongest and most obvious distinguishing feature of the wings of *Orthodera novaezealandiae* is the tremendous development of the archedictyon and the absence of cross-veins in

the forewing. The shape of the wing, in which the costal area is not expanded, also serves to distinguish it from the female of *Miomantis caffra*, the only other species in New Zealand, in which the costal area is enlarged. Another characteristic is the slight degree of sexual dimorphism, apparent in the size and shape of the wings but not in their venation. The wings of the male are proportionately larger, which suggests that he is a stronger or more frequent flyer – borne out by the greater number of males attracted to light at night; but females also fly. The pterostigma – the small, elongate swelling between M and Cu_{1a} – is inconspicuous and not always clearly defined, but is constant in position and similar in both sexes of *O. novaezealandiae*. The surface of the wings is identical in both sexes, being glossy and generally lacking any covering layer.

The wings of *M. caffra* are characterised by their strong sexual dimorphism, especially in their, shape, size, and venation, which reflect the fact that only the male can fly. Probably as a result of this there is a greater degree of variation in the venation of the female wings, especially the hind wing, relatively strong development of the pterostigma in her forewing, and a waxy layer on its surface which is dull and powdery. In the male the pterostigma is very slender, variable, and ill defined, and the wing surface is glossy as it lacks the surface layer. The fact that the two most posterior vannal veins of the hind wing in both sexes are free and separate from the common root of the other veins may be characteristic also.

Another point of distinction concerns the pigmentation of the forewings. In *Orthodera* the bright green colour is present in the veins only; the membrane in between is generally clear. In female *Miomantis* pigment is present in the wing membrane as well as the veins.

The forewing venation of *O. novaezealandiae* is distinguished from that of *M. caffra* in that there is no sexual dimorphism, and Cu_2 unites first with Pcu and then with $1V$, whereas in *M. caffra* it is discrete to the wing margin in both sexes. It is very similar to that of *Sphodromantis*, illustrated by Ragge (1955), except that the vannals do not extend on to the jugum.

There are a number of points of distinction between the wings in *Miomantis* sp., illustrated by Smart (1956a), and in *M. caffra*. In the forewing of *Miomantis* sp. the costal area is narrow and Pcu fails to reach even halfway to the wing margin, whereas in *M. caffra* the costal area is slightly expanded and Pcu joins $1V$ in the male, and in the female the costal area is greatly expanded and Pcu extends at least 85% of the distance to the margin. In *Miomantis* sp. the subcosta becomes obsolete at about 65% of the distance to the apex, whereas in *M. caffra* it reaches the border at the apex, or very nearly so. Also, in *Miomantis* sp. R does not divide into R_1 and Rs as it does in *M. caffra*; and M and Cu

have one less branch each than in female *M. caffra* and two less than in males.

The hind wing of *O. novaezealandiae* is generally undistinguished, and lacks strong intercalary veins. It is most similar to that of *Mantoida* sp., in which MA and MP have a common root, arising at the junction of R and the $r–cu$ cross-vein. It is readily separated from that of *M. caffra* by its slight sexual dimorphism, identical venation in both sexes, the fact that Cu_{1b} and Cu_2 do not unite terminally as they do in the male of *caffra*, and by its greater number of $2V$ forks (5 or 6) and vannal veins (14).

In the hind wing of *Miomantis* sp. Sc is very reduced and present in the proximal half of the wing only. In *M. caffra* it joins C at about 85% of the distance to the apex in the male, and virtually reaches the apex in the female. In *Miomantis* sp. MP arises from the junction of R and $r–cu_2$ rather than from the cross-vein itself; Cu_1 forks once rather than twice, and Cu_{1b} does not unite distally with Cu_2 as it does in male *M. caffra*. Also $2V$ forks only twice (three or four times in male *M. caffra*, two or three times in females), and there are only three other vannals, of which the two posteriormost arise from the common vannal root, whereas in *M. caffra* there are six other vannals, and the two posteriormost are detached from the vannal root.

The wing differences between *Miomantis* sp. and *M. caffra* probably reflect the much smaller size of the former – forewing length approximately 9 mm, as against 28–31 mm (male) and 23 mm (female) in *caffra*. Certainly the greater reduction of Sc and Pcu and the diminished number of R, M, and Cu branches must be related to it. Also, the shape of the wing in *Miomantis* sp. suggests that the specimen illustrated could fly, and so was probably a male. If so, then the reduction of Pcu is not confined to the female as it is in *M. caffra*.

A point of similarity between the forewings of these two species is the fact that Cu_2 remains discrete and extends to the wing margin. The condition of this vein is similar in *Chaeteessa* and *Ameles*, but in *O. novaezealandiae*, *Mantis*, *Sphodromantis*, and *Archimantis* it either unites first with Pcu and then with $1V$ or is connected with Pcu by a very short cross-vein, as mentioned earlier.

The nymphal wing pads of *O. novaezealandiae* are characterised by their constant, uniformly bright green colour, the development of strong anterior shoulders on both wings (highly pigmented on the forewing), and the slight sexual dimorphism apparent in their shape. The wing pads of *M. caffra* nymphs have a diffuse, variable, and uneven pigmentation, completely lack anterior proximal shoulders, and are strongly sexually dimorphic in shape and size.

Discussion: general. The wings of the two species from New Zealand conform to the general condition in mantids described by Ragge (1955): forewing with costa

strong and well developed, extending the entire length of the wing, radius usually without anterior pectinate branches, and jugal lobe small, membranous, folded underneath when wings are flexed; hind wing with remigium supported by five parallel, generally unbranched veins (C, Sc, R, MA, and MP), and vannal lobe extensive.

Mantid wings are similar to those of the Blattodea, from which they are distinguished by several characters – inter alia, the lack of a cubital furrow on the forewing and of $1V$ on the hind wing. The subcosta of the blattid forewing is usually relatively short, and the radius is distally pectinate, having numerous anterior branches, unlike their equivalent in the Mantodea.

The cubital furrow of the forewing is usually considered to be absent in mantids (Ragge 1955). However, it occurs in a vestigial form in the two species studied here, and probably in most other species as well. In O. *novaezealandiae* and M. *caffra* a strong, distinct proximal lobe is present, bounded posteriorly by the peripheral vein, which curves forwards to enclose the roots of the vannals and postcubitals, and then curves to merge with the cubital root, where a short furrow occurs. Although it is not shown in the illustrations of Ragge (1955) and Smart (1956a), it nevertheless is probably present. It can be recognised in the illustration of *Archimantis latistyla* by Key (1970).

Smart (1956a) reinterpreted the venation of the mantid hind wing, suggesting that $1V$ had been lost and that the forking vannal vein is in fact $2V$. Vein $1V$ is present on the hind wings of blattids and the mantids *Chaeteessa* and *Metallyticus*. The vein interpreted as $1V$ by Ragge (1955) is regarded as being Pcu. There is no trace of this first vannal vein in the hind wing of nymphs and adults of O. *novaezealandiae* and M. *caffra*.

Another contentious problem concerning the venation of the mantid hind wing which was not properly resolved by Smart (1956a) concerns the interpretation of the veins regarded as Rs and M by Ragge (1955) and dubiously accepted as such by Smart. He questioned this interpretation, and pointed out certain unusual features of the veins in *Chaeteessa*: R_1 is more closely associated with M than with R at the wing base, and the forewing R is pectinate and does not form an Rs (the advanced hind wing condition is thus surprising). The furcation of R into R_1 and Rs is usually well away from the base in orthopteroid insects, and M usually has two distinct branches also. Smart suggested that the vein regarded as Rs in *Chaeteessa* is in fact MA, and that M is MP. Although this interpretation explains the unusual features just mentioned, Smart accepted Ragge's interpretation because "it fits" and because of supporting evidence from the tracheation of the nymphal wing pad, where the Rs/MA trachea invariably arises as a proximal branch of R.

However, R and M generally form a complex common root at the base of the hind wing, as is shown in the illustrations of Ragge and Smart, and of *Archimantis latistyla* by Key (1970). Only in *Sphodromantis viridis* (illustrated by Ragge) are the roots of R and M distinct, but even here they soon fuse. Also, Smart states that in *Chaeteessa* R and M appear to be " two veins in close apposition rather than a complete fusion into one large vein", although this is not shown as such in his illustration. In S. *viridis*, *Ameles heldreichi*, and *Mantoida* sp. a common root (which very soon furcates) branches off from R, and in *Mantis religiosa*, *Miomantis* sp., and *Chaeteessa* Rs/MA and M/MP branch from R independently but close together.

With both New Zealand mantids there is great variation as far as the origin of the hind wing veins Rs/MA' and M/MP' is concerned. Both may branch off from the radius, or both may arise from the r–cu cross-vein, or only M/MP' may arise from the cross-vein, or there may be a common root (which bifurcates) arising from the cross-vein, as in 25% of the O. *novaezealandiae* hind wings studied. It is therefore impossible to decide which is the normal condition. Perhaps this area of the wing is undergoing evolutionary change and has yet to stabilise.

The situation is further complicated by the development of a strong cross-vein, r–cu, also in the proximal basal area. It was first mentioned by Smart (1956a), who illustrated it in the hind wings of *Chaeteessa filiata*, *Mantis religiosa*, *Miomantis* sp., and *Mantoida* sp. Handlirsch (1930) had earlier depicted it in his illustration of the hind wing of *Gonypeta* sp., as had Beier (1935c) in illustrations of *Hierodula membranacea*, *Sphodromantis viridis*, *Dactylopteryx orientalis*, *Litaneutria obscura*, and *Ameles objecta*. It is not evident in Key's (1970) illustration of *Archimantis latifolia*, as the wing is not fully unfolded. No-one else has observed or illustrated it, possibly because of the confusion of interpretation resulting from the closeness or fusion of the roots of the main veins in this region. It is a constant feature in the wings of O. *novaezealandiae* and M. *caffra* (in only one out of 44 examples was it lacking), and its presence is probably a basic characteristic of the mantid hind wing.

Given this situation, it is difficult to see how the two veins immediately behind R can be regarded as anything other than MA and MP. However, the fact that in the tracheation of the nymphal wing pad Rs/MA invariably branches from R does not support this interpretation. Both Ragge and Smart observed this in the wing pads they studied, and it was probably the main reason behind their interpretations. Further, in all 48 hind wing pads studied of both New Zealand mantids there were no exceptions to this condition, despite variation in other wing pad tracheae.

Smart (1956a) questioned how much weight should be given to the tracheation of the nymphal wing pads in interpreting adult wing venation, and as a result of his experiments concluded that the "pattern of the tracheae is not immutable and cannot be regarded as fundamental in determining the pattern of the imaginal wing-venation". Further support for this is given by the fact that the r–cu_1 cross-vein has no nymphal tracheal precursor. So, although the origin of the tracheal precursor of MA as a branch of the radial trachea is a basic characteristic of the mantid wing pad, it does not necessarily follow that it should be regarded as Rs rather than MA. This unusual condition may be related to the fact that the venation of this area of the wing is apparently in a state of flux.

The forewing veins Cu_2, Pcu, and $1V$ have several character states which may be of value in higher classification. Cu_2 may retain its individual identity to the very border of the wing, as in $Gonypeta$ sp., $Metallyticus$ (Handlirsch 1930), $Ameles heldreichi$ (Ragge 1955), $Chaeteessa filiata$, $Mantoida$ sp., $Miomantis$ sp. (Smart 1956a), $Theopropus borneanus$, $Anabomistria werneri$, $Pseudocreobotra ocellata$ (Beier 1964), and $Miomantis caffra$. It may approach Pcu and connect via a short cross-vein before curving away again to the border, as in $Mantis religiosa$ (Smart 1956a). It may unite with Pcu only, as in $Stagmomantis carolina$ (Levereault 1936). It may join first with Pcu then with $1V$ to produce a common stem which proceeds to the border, as in $M. religiosa$ (Chopard 1949), $Sphodromantis viridis$ (Ragge 1955), $Archimantis latistyla$ (Key 1970), and $Orthodera novaezealandiae$. Or it may join with $2V$ as well, as in $Hierodula tenuidentata$ (Wood-Mason 1878), and again produce a common stem which passes to the border.

Pcu may retain its individuality to the very border, as in $Gonypeta$, $Metallyticus$, $Anabomistria$, $Pseudocreobotra$, and $Mantoida$. It may be shortened, as in $Ameles$, $Chaeteessa$, $Miomantis$ sp., and females of $M. caffra$. It may join with both Cu_2 and $1V$, as described above; or join with $1V$ only, as in $Theopropus$ and males of $M. caffra$. Or it may connect with Cu_2 via a short cross-vein, and then join with $1V$ to form a common branched stem which passes to the border, as in $M. religiosa$ (Smart 1956a).

Vein $1V$ may retain its identity to the very border, as in $Gonypeta$, $Metallyticus$, $Stagmomantis$, $Ameles$, $Chaeteessa$, $Miomantis$, $Anabomistria$, $Pseudocreobotra$, and females of $M. caffra$; or join Pcu, or Cu_2+Pcu, as described above.

The venation of the jugum has two character states. The vannals may extend over the peripheral vein and on to the jugum, as in $Hierodula$, $Stagmomantis$, $Ameles$, $Sphodromantis$, $Mantis$, and in $Iris oratoria$, $Alalomantis muta$, and $Stagmatoptera supplicaria$ as illustrated in Beier

(1935c) and Rehn (1911). Alternatively, they are contained within the vannal area by the peripheral vein and the jugum has its own reticulum of veins, as in $Gonypeta$, $Metallyticus$, $Chaeteessa$, $Mantoida$, $Miomantis$, $Theopropus$, $Anabomistria$, $Pseudocreobotra$, $Archimantis$, $Orthodera novaezealandiae$, and $Miomantis caffra$, as well as in the generalised mantid forewings of Giglio-Tos (1927) and Chopard (1951), and the majority of species illustrated in Beier (1935c).

With the hind wing too there are various character states. The presence of the r–cu_1 cross-vein is probably universal, despite the fact that it has hardly ever been reported. The situation with the main veins varies. M may commence independently and then divide into MA and MP branches, as in the forewing ($Sphodromantis$). MA and MP may have a common root which almost immediately divides ($Mantoida$ and variants of $O. novaezealandiae$). MA and MP may arise in close proximity to each other from R, as in $Metallyticus$, $Ameles$, $Chaeteessa$, $Mantis$, $Miomantis$ sp., $O. novaezealandiae$, $M. caffra$, and the majority of the species illustrated by Beier (1935c). They may arise from R, but widely separated, as in $Mantis religiosa$ (Chopard 1949). Or, MP may arise from the r–cu_1 cross-vein, as in $Gonypeta$. In the generalised mantid wing of Giglio-Tos (1927) MA and MP arise from R in close proximity to each other, and in that of Chopard (1951) they arise from R but widely separated.

Although the number of $2V$ branches varies intraspecifically, several character states can be recognised. Often illustrated, this vein is not often referred to. There are two branches in $Gonypeta$, eight in $Metallyticus$, three in $Chaeteessa$, five (Chopard) or six (Smart) in $Mantis$, two in $Miomantis$ sp., five in $Mantoida$, eight in $Sphodromantis$, three in $Ameles$, two in the generalised mantid wing of Giglio-Tos (1927) and four in that of Chopard (1951), six or seven in $O. novaezealandiae$, and four or five in $M. caffra$. The presence or absence of intercalary veins is also a character that should be considered. Among the species that have been illustrated they are shown in $Ameles$ as being distinct and strongly developed. There are indications that they may be strongly developed in some of the species illustrated by Beier (1935c). They are lacking in $O. novaezealandiae$ and $M. caffra$.

Wing venation characters are not usually recognised as being of value in the diagnosis of mantid species. Although this may be so in general, it could also result from a lack of detailed study of the wings, emphasis being placed on other characters. With $Miomantis caffra$ the condition of Pcu and the number of forewing vannals may be specific characters. Similarly with the hind wing, the terminal union of Cu_{1b} and Cu_2 in the male, the number of vannal veins, and the number of furcations in $2V$ may be of value. Size will

be important also, as small species may tend to have simplified venation, fewer vannals, and fewer $2V$ furcations.

Variation. Variation of venation within a species or population is not often reported. In the two species studied here it is common and widespread, and usually involves the radial, medial, and cubital veins and also the tracheation of the nymphal wing pads. Mantids have a tendency to disuse the power of flight (Smart 1956a). Once this has occurred and fully formed but reduced wings are still present, a trend towards even greater variation and the acquisition of other functions can be expected. This certainly seems to be so with the flightless female of *Miomantis caffra*, in which the wing variation is greatest; the forewing has a well developed pterostigma and a waxy coating which are probably associated with this loss of the power of flight, and the acquisition of new functions such as protection and camouflage.

Dimorphism. Although some degree of sexual dimorphism in the wings is probably common and widespread amongst the mantids, there is little information available about it. It is apparent in the nymphal wing buds as well, and is manifested in the size, shape, coloration, venation, and function of the wings. Loss of the power of flight in the female of *Miomantis caffra* is an important factor in the strong sexual dimorphism in the wings of this species. Sexual dimorphism in the venation, such as occurs here, has not previously been reported in mantids.

Diagnostic characters. There are several wing features which seem to be characteristic of mantids and which should be included in their definition. These are:
• the presence of the $r–cu_1$ cross-vein on the hind wing;
• the plasticity of the vein configuration around the roots of R and M in the hind wing; and
• the origin of the tracheal precursor of MA as a branch of R in the nymphal hind wing pad.

Other characters may be of value in understanding the higher classification of mantids. These include:
• the presence or absence of the archedictyon and cross-veins in the forewing;
• the condition of the postcubital vein on the forewing;
• the shape and venation of the jugal lobe of the forewing;
• the presence or absence of anterior shoulders on the nymphal wing pads.

(c) Pterostigma
The presence of a pterostigma has not usually been regarded as a general feature of the mantid forewing. When obvious it is a thickening or swelling, distinctly coloured and sometimes described as calloused, lying between the media and cubitus veins, more or less halfway along the wing. Illustrations of mantids in which the pterostigma is

indicated occur in such early works as those of DeGeer (1773), Stoll (1787–88), Palisot de Beauvois (1805), and Charpentier (1842), but attention was not drawn to this feature until Fischer (1853) clearly illustrated it for *Mantis religiosa* and *Empusa ?agena*, stating "in speciebus quibusdam macula cornea nitida apparet". Wood-Mason (1878b) depicted it on the forewing of *Hierodula tenuidentata* (=*H. simulacrum*) without referring to it in the text, and in 1878b described it in *H. (Rhombodera) butleri*, *H. (R.) fratricida*, *H. (R.) atricoxis*, and *Creobroter pictipennis*. In 1880 he mentioned it in *Choeradodis*. Brunner von Wattenwyl (1882) noted the pterostigma in mantids generally as "Dem Deckflügel der Mantodëen eigenthürmlich ist ein horniger Flecken, welcher der Vena radialis posterior etwas vor der Mitte gleichsam aufgetragen erscheint und dessen Hinterrand die Vena ulnaris anterior berührt." He illustrates this for a male *Hierodula bioculata* (=*Sphodromantis viridis*) and a female *Mantis religiosa*. Wood-Mason (1889a) described it in *Tarachodes insidiator* and *T. dissimulator*, and in 1889b referred to it in *Heterochaetula fissispinis* and the genera *Toxoderopsis*, *Toxodera*, and *Paratoxodera* (as well as *P. cornicollis*). In 1891 he depicted it on the forewing of the male of an *Iridopteryx* sp., and described it in *Ceratomantis saussurii*, *Pachymantis bicingulata*, *Theopompa taprobanarum*, and *T. septentrionum*. Redtenbacher (1889, 1890) mentioned "in der Mitte der Discoidalader ein glatter, horniger Fleck (Stigma)" in the mantid wing. Rau & Rau (1913) described a "highly pigmented and clearly defined spot which is very conspicuous in green-winged" *Stagmomantis carolina*. Chopard (1922) said of the mantidae generally "vers le milieu de l'élytre existe une tache calleuse oblonge, le stigma", which he illustrated, apparently after Wood-Mason (1891) but without acknowledgment. Giglio-Tos (1927) referred to its "presque constamment" occurrence and described and illustrated it as a thickening ("stigma") of the forewing. Lameere (1935) said of mantids "... un ptérostigma plus ou moins distinct se trouve près du bord antérieur." Chopard (1943, 1951) slightly modified the wording of his earlier (1922) statement, mainly by using "oblique" instead of "oblongue", and repeated the illustration. He also (1949) depicted it on the forewing of *Mantis religiosa* and stated that "Il existe toujours un pterostigma constitué par une tache calleuse, oblique ...". It was not mentioned by either Ragge (1955) or Smart (1956a, b) in their studies of mantid wing venation. Paulian (1957) referred to a "pterostigma souvent très visible, parfois indistinct" on the mantid forewing. Harz (1959, 1960) says "etwas vor der Mitte der Media befindet sich ein glanzender glatter Langsfleck, das Stigma", which he illustrates for *M. religiosa*. Beier (1964, 1968) described it as a thickened, often calloused and very conspicuous spot, the so-called stigma, implying – but not

Superfamily CHAETEESSOIDEA (see Kevan 1976–77, Vickery & Kevan 1983)

• **Family Chaeteessidae**

Chaeteessa (Westwood 1889; as *Haplophora*)

Superfamily MANTOIDEA (see Kevan 1976–77, Vickery & Kevan 1983)

• **Family Empusidae**

Subfamily Blepharodinae

Idolomantis (Westwood1889; as *Idolum*)

Subfamily Empusinae

Empusa (Fischer 1853, Paulian 1957)

• **Family Hymenopodidae**

Subfamily Acromantinae

Acanthops (Charpentier 1842, Westwood 1889), *Acontista* (Westwood 1889), *Ambivia* (Westwood 1889), *Catasigerpes* (Westwood 1889; as *Sigerpes*), *Creobroter* (Wood-Mason 1878b), *Epaphrodita* (Westwood 1889), *Phyllocrania* (Westwood 1889, Paulian 1957)

Subfamily Hymenopodinae

Callibia (Beier 1934a), *Pseudocreobotra* (Brunner von Wattenwyl 1897), *Theopropus* (Westwood 1889; as *Creobroter*)

Subfamily Oxypilinae

Ceratomantis (Wood-Mason 1891), *Pachymantis* (Wood-Mason 1891)

• **Family Mantidae**

Subfamily Amelinae

Ameles (Beier 1964, Bazyluk 1977), *Armene* (Kaltenbach 1976), *Campsomantis* (Westwood 1889; as *Hapalomantis*), *Dystacta* (Westwood 1889, Beier 1935c), *Gonypeta* (Westwood 1889, Beier 1935c), *Myrcinus* (Westwood 1889, Beier 1935c)

Subfamily Choeradodinae

Choeradodis (Stoll 1787–88, Wood-Mason 1880, Westwood 1889, Beier 1935b, 1964, 1968)

Subfamily Deroplatyinae

Brancsikia (Beier 1935c, Paulian 1957), *Deroplatys* (Westwood 1889)

Subfamily Iridopteryginae

Hapalopeza (Westwood 1889), *Iridopteryx* (Wood-Mason 1891), *Tylomantis* (Westwood 1889; as *Hapalomantis*)

Subfamily Liturgusinae

Humbertiella (Westwood 1889), *Majanga* (Paulian 1957), *Theopompa* (Wood-Mason 1891), *Theopompella* (Giglio-Tos 1921), *Theopompula* (Westwood 1889; as *Theopompa*)

Subfamily Mantinae

Alalomantis (Beier 1935c), *Cilnia* (Beier 1935c), *Heirodula* (*Heirodula*) (Stoll 1787–88, Wood-Mason 1878b, Westwood 1889, Brunner von Wattenwyl 1893, Beier 1935c), *Heirodula* (*Parheirodula*) (Tindale 1923), *Heirodula* (*Rhombodera*) (Westwood 1889, Beier 1935c), *Heirodula* (*Tamolanica*) (Brancsik 1898), *Isomantis* (Palisot de Beauvois 1807, Westwood 1889 (as *Stagmomantis*)), *Mantis* (Fischer 1853, Brunner von Wattenwyl 1882, 1893, Chopard 1949, Harz 1957, 1960, ?others), *Miomantis* (Heath 1980, herein), *Paracilnia* (Beier 1935c), *Polyspilota* (Westwood 1889, Paulian 1957), *Pseudempusa* (Brunner von Wattenwyl 1893, 1897, Rehn 1911), *Sphodromantis* (Brunner von Wattenwyl 1882 (as *Hierodula*), Beier 1935c, 1964, 1968, Kaltenbach 1976, Bazyluk 1977), *Sphodropoda* (Westwood 1889), *Sphodropoda* (*Ngawala*) (Tindale 1923), *Stagmomantis* (*Stagmomantis*) (Westwood 1889), *Stagmomantis* (*Stauromantis*) (Rau & Rau 1913, Beier 1935c), *Tarachomantis* (Saussure & Zehntner 1895 (as *Hierodula*), Paulian 1957), *Tenodera* (Brunner von Wattenwyl 1893), *Tisma* (Saussure & Zehntner 1895 (as *Hierodula*), Paulian 1957)

Subfamily Orthoderinae

Orthodera (herein)

Subfamily Oxyothespinae

Heterochaetula (Wood-Mason 1889b)

Subfamily Photininae

Coptopteryx (Westwood 1889)

Subfamily Tarachodinae

Galepsus (Paulian 1957), *Tarachodes* (Wood-Mason 1891)

Subfamily Toxoderinae

Paratoxodera (Wood-Mason 1889b), *Toxodera* (Wood-Mason 1889b), *Toxoderopsis* (Wood-Mason 1889b)

Subfamily Vatinae

Oxyopsis (Brancsik 1898), *Popa* (Paulian 1957), *Stagmatoptera* (DeGeer 1773, Stoll 1787–88, Palisot de Beauvois 1807, Westwood 1889, Brunner von Wattenwyl 1897 (as *Stagmomantis*), Rehn 1911)

stating – that it is a general feature of the mantid forewing. He reproduced the wing illustrations of *Chaeteessa* and *Mantoida* of Smart (1956a), in which no pterostigma is shown, although one is shown on the wing of the former species by Westwood (1889; as *Hoplophora*). Beier also gives illustrations of the wings of *Sphrodromantis* and *Ameles* from Ragge (1955), to which he added an indication of the presence of a pterostigma.

The pterostigma has been recorded or illustrated (but not necessarily mentioned in the text) in many mantid genera, including the 63 listed in Table 2 (classification after Beier 1968). In these 63 genera and subgenera (the list is provisional only) it is an obvious feature. Paulian (1957) recorded it in 23 of the 48 winged Madagascan mantids he redescribed, and noted it as being indistinct or absent in five. He did not mention it in the other 20 species. In one genus, *Tarachomantis*, it was present in eight species and indistinct in one.

It is present but indistinct in the males of both New Zealand species and in the female of *O. novaezealandiae*, and is most obvious in the female of *M. caffra*. In both sexes of *O. novaezealandiae* it is a slender, elongate, irregular swelling lying more or less parallel to the main veins and merging with them and with the archedictyon. The veins lose their identity within it (Fig. M11,12). In a few areas only the wing surface is covered by a thin, diffuse layer of a material that appears to be a wax (Fig. M13). This does not obscure the detail of the surface, which is covered by scale-like projections in a reticulate pattern, strongly developed on the veins and pterostigma but weaker on the wing membranes between the veins (Fig. M14). The scales tend to become elongate on the pterostigma (Fig. M15).

In *M. caffra* the pterostigma is more compact, better developed, and strongly sexually dimorphic. In the female it is a conspicuous, swollen, subelliptical spot, obvious because of its discreteness and paler colour. It is quite distinct from the wing veins (Fig. M16). The wing surface is covered by a well developed layer of material – probably wax – which obscures the surface structure of the integument (Fig. M17). The pterostigma itself is free of the wax and is covered over its entire surface by a series of rounded scales (Fig. M18,19) which are flatter and more dispersed than those of *O. novaezealandiae*. Only at the edge of the pterostigma does the wax layer begin (Fig. M20). The wing cells between the veins and the cross-veins show a pattern of fine, subparallel lines (possibly resulting from textural differences in the waxy layer) in some places (Fig. M21); elsewhere the lines radiate from the centre of the cell (Fig. M22). In some places the scales on the veins can be detected beneath the waxy layer (Fig. M23), whereas in others they are completely obscured. This waxy layer, which is well developed only in the female of *M. caffra*,

probably gives the forewings their pastel/powdery appearance.

In the male of *M. caffra* the pterostigma is much less distinct, irregularly shaped, and shorter and broader than it is in *O. novaezealandiae* (Fig. M23). The waxy layer is not present, and the surface scales are clearly visible on the pterostigma and veins (Fig. M24). Occasional trichoid sensilla are also present (Fig. M25). The surface of the integument between the veins and cross-veins is uniformly uneven, with a faint reticulation.

The pterostigma is probably a plesiomorphic character, as it apparently occurs in the most primitive of living mantids *(Chaeteessa)*, as illustrated by Westwood (1889). In either its well developed form or as a rudiment or vestige, it is probably present in most mantids. The fact that it is present in both sexes of both New Zealand mantids, but conspicuous only in the female of one, *M. caffra* (which is flightless), supports this suggestion. It is relatively constant in position, lying between the media and cubitus veins, and is perhaps best developed when the ability to fly has been lost. Its function and anatomy are unknown, but its surface structure suggests that it may comprise a merged confluence or proliferation of veins. Giglio-Tos (1927) suggested that because of its colour it can play an important role in the phenomenon of mimicry, but it is not always conspicuous even when present.

(d) Coloration

Colour polymorphism sometimes occurs in the Mantodea, in that certain species are dichroic – that is, they have two colour morphs, one green, the other brown or yellow. Such dichromatism occurs widely in other orthopteroid insects such as tettigoniids, acridoids, and phasmids (Chopard 1938, p. 449). It may be either genetically controlled or influenced by environmental factors such as diet (Okay 1953, Meyer 1979) in mantids, acridids, and phasmids or background (Eugene 1953, 1955a–c) in mantids and acridids. Nymphs have the capacity to change from one colour morph to the other, but the change is usually 'morphological' and permanent (Hinton 1960).

The colour itself results from the interaction of several pigments – a brown similar to insectorubin, a yellow which is usually a carotenoid, and a blue bilin, which is usually a tetrapyrrole (Okay 1948, 1953; Gilmour *et al.* 1970). Darker colours in the cuticle may be the result of a tanning process (Norris 1970). The green pigment is commonly insectoverdin, which is a mixture of a yellow and a blue chromoprotein (Przibram & Lederer 1933), mesobiliverdin and a yellow carotenoid, probably ß carotene (Meyer 1979), i.e., a protein conjugated with blue and yellow compounds (Cromartie 1959, Gilmour *et al.* 1970). Darker colour in an acridid *(Paulinia)* resulted from melanisation

of the cuticle, the melanin being produced because of unfavourable diet, which also caused hyperactivity, greater mortality, reduced growth rate, protracted life cycle, and reduced oviposition rates (Meyer 1979). The brown pigment may occur in large amounts in some green grasshoppers (*Locusta, Acrida*) overlain by blue so as to produce the green (Okay 1953).

According to Beier (1964) both colour morphs in mantids possess a green pigment in the epidermis which, in brown individuals, is obscured by brown pigment in the integument. This can be seen in the exuviae of brown or brown-marked nymphs, in which the dark markings are very obvious. Passama-Vuillaume (1962), however, suggested that the subcuticular layer of green pigment is absent in brown specimens.

In New Zealand *Miomantis caffra* has green and brown colour morphs, but the brown is much rarer than the green; this is also true of *Mantis religiosa* (see Okay 1953). In the immature stages dark markings are present, such as bands on the legs. This is particularly obvious in the exuviae of *M. caffra,* which mostly have conspicuous markings. *Orthodera novaezealandiae,* on the other hand, is always a uniform bright green, sometimes with a fine reddish-brown edging to the pronotum and the leading edge of the forewings, and sometimes with darker middle and hind legs. Further, its nymphal exuviae are always a very pale straw colour, completely lacking any pigment or markings except for the eyespot on the inner surface of each fore-femur, which persists as a variable, irregular group of dark brown patches. The green colour is quite constant except in very rare instances of luteinism, and then the colour is bright yellow (Bennett 1984).

Bright yellow nymphs and adults of *O. novaezealandiae* have been observed or collected at scattered localities in New Zealand, from Kaitaia (ND) in the north to Hawea (OL) in the south. Usually only single yellow individuals occur in a mantid population, and the colour abnormality may not be seen again in that population. However, the mantid population at the eastern end of Lake Hawea comprises many yellow individuals, and it is even possible that the yellow colour form may be replacing the original green form in that locality (A.C. Harris, pers. comm.).

The green pigment, insectoverdin, of both New Zealand species is probably similar to that of *Mantis religiosa,* in which it is a combination of a yellow carotenoid and blue bilin (Fox & Vevers 1960). The paler pastel colour of *M. caffra* in comparison with the bright green of *O. novaezealandiae* may be an effect of the waxy epicuticular layer present in the former species.

There can be no doubt that the colour morphs of New Zealand mantids are genetically mediated rather than the result of nutrition or environmental influences, as the

brown individuals of *M. caffra* and yellow individuals of *O. novaezealandiae* develop amongst populations of the green morph and have the same food and habitat preferences. In breeding experiments carried out with the yellow form of *O. novaezealandiae* (Bennett 1984), a yellow female mated with a normal green male produced yellow-green progeny which, when interbred, produced green, yellow-green, and yellow progeny. This is an example of luteinism rather than colour polymorphism, as the abnormal colour form probably results from a mutation by which the insect has lost the ability to synthesise the blue pigment.

It is interesting to consider that the propensity for luteinism to occur may be a characteristic of the New Zealand population of *Orthodera,* as it has not been reported in any of the Australian species of this genus.

(e) Stridulation

Mantids have often been regarded as mute insects, producing no sound and lacking acoustic sensitivity (Handlirsch 1930, Key 1970, Richards & Davies 1977). Recently, however, a sound receptor organ – the 'cyclopean ear' – has been reported from a mantid (Yager & Hoy 1986). This is said to have a protective function, and is apparently able to detect sounds emitted by predatory bats. Furthermore, some mantids do produce sounds, and their stridulation has been briefly summarised by Maldonado (1970).

The development of specialised stridulatory structures is very rare except in the empusid mantids. Vickery & Kevan (1983, 1986) state that a "true stridulatory mechanism [is] not developed although a rustling sound may be produced by vibration of the hind wings which may strike against [the] raised tegmina; some species when in a 'threatening' position may raise the abdomen and bend it forwards so that the cerci strike the tegminal veins and make an intermittent chirping sound". This is similar to the information presented by Chopard (1938, pp. 365–366) and Beier (1968), except that here the chirping sound is said to be produced by scraping the cerci over the longitudinal veins of the hindwing. These descriptions are based on information in Goureau (1835, 1841), Dufour (1841), Kirby & Spence (1858), Wood-Mason (1879), Fabre (1897), Coupin (1899), H.F. Atwood (in Slingerland 1900), Stäger (1928, 1941, 1950), Binet (1931), Judd (1950), Chopard (1951), Kevan (1955), and Edmunds (1972), who all describe this behaviour of *Mantis religiosa.*

Wood-Mason (1879) examined *M. religiosa* for the presence of specialised stridulatory structures. He found none, and suggested that the "rustling noise" produced by this species results either from a shuffling of its wings or from friction caused by the sides of the abdomen being moved rapidly up and down against the posterior inner margins of the hind wings and tegmina (forewings). He

found the wings and tegmina to be quite unmodified, lacking the submarginal file of other mantids he had examined (see below). This, too, is the condition of the tegmina of both species found in New Zealand, in which the costal vein of the tegmen is quite smooth on its dorsal, anterior, and ventral surfaces. Dufour (1841) indicated that a hissing sound was produced by species other than *Mantis religiosa*, and Stäger (1928) pointed out that any winged mantid is potentially capable of producing sound in this way. There are a number of examples: Wood-Mason (1878a) reported a hissing sound made by an Indian mantid, and Durrell (1956) observed a large mantid in Crete rustling its outspread wings as it swayed from side to side during a confrontation. Robinson (1969) observed *Angela guianensis* Rehn producing a brief burst of stridulation by moving the extended hindwings against the tegmina while under restraint. Edmunds (1972) reports that rustling or swishing sounds are produced by *Tenodera superstitiosa* (Fabricius), *Pseudocreobotra ocellata* (Palisot de Beauvois), and *Stenovates strachani* (Kirby), as well as by *M. religiosa*. Maldonado (1970) and Heath (1980) also describe *Stagmatoptera biocellata* Saussure producing a hissing sound by rubbing the abdomen against the hind wings.

The other mantids examined by Wood-Mason (1878a, b) for the presence of stridulatory structures were *Hierodula (H.) pustulifera* Wood-Mason, *H. (H.) tenuidentata* Saussure, *H. (H.) venosa* Olivier, *H. (Rhombodera) laticollis* Burmeister, *H. (Sphodromantis) gastrica* Saussure, *H. (Tamolanica) atricoxis* (Wood-Mason), *Sphodropoda (Ngwala) dentifrons* (Stål), and various empusids including *Gongylus gongyloides* (Linnaeus). He was looking for a rasp or file over which a scraper could rub, and discovered such a structure on the anterior margin of the forewings of all the species listed above except the first, and including "all the Empusidae". Initially, Wood-Mason (1878a) thought that this file on the leading edge of the forewing could be rubbed against the hindwing, but he then abandoned the idea and suggested that sound could be produced by the abdomen being scraped against the file. However, he could not find any abdominal structure developed for this purpose. Chopard (1938, p. 286) mentioned that sound could be produced by the rubbing of either the femur or the abdomen against the denticulate border of the forewing in *Sphodromantis* and *Gongylus*. Varley (1939) confirmed the presence of the series of sharp teeth (file) on the underside of the leading edge of each forewing in *Hierodula* and the Empusidae. He found that in the empusids *Idolum* and *Gongylus*, with wings in the resting position, this file is close to a ridge on the hind coxa which may act as the plectrum. With the forewings raised and their undersurface rotated outwards – the attitude adopted by *Empusa* in its startle-behaviour – the femur (as well as the coxa)

could rub against the file. Thus it seems probable that when this insect sways during startle-behaviour, the hind femur will rub against the forewing file to produce sound.

Williams (1904) and Willey (1918) described stridulation in *Gongylus gongyloides* in which a loud rasping sound was produced by rubbing the borders of the hind femora against the rim of the forewings. The mechanism, which is well developed in both sexes, comprises a finely serrate, thickened, sclerotised rim along the leading edge of each forewing. The border is slightly emarginate in the region of the hind femur so that the free movement of the limb is facilitated. The femur itself is smooth, and lacks any rough edges. Stridulation in *Idolomantis diabolicum* Saussure is similar, and has been described by Carpenter (1921) and Burtt (1943). The hind femur was drawn rapidly along the leading edge of the tegmen, the tegmina being slightly separated, and the abdomen moved up and down in time with the motion of the legs.

Another kind of stridulation has been described by Shelford (1903) in the mantid *Hestiasula sarawaca* Westwood (= *H. phyllopus* (Haan)). Here, the wings were rustled as the foretibiae snapped against their femora with clock-like regularity. Yet another mode of stridulation has been described in *Choeradodis rhombicollis* (Latreille), in which a distinct scraping noise is produced by movement of the raptorial limbs against the outer margins of the prothoracic shield (Robinson 1969). The upper margins of the forefemora bear rows of small spines able to strike the edge of the prothorax, which, because of its flattened form, may act as a sounding board.

Thus, although most mantids do not possess a specialised stridulatory mechanism, all winged species are potentially capable of producing a rustling sound either by means of moving the abdomen rapidly up and down between the upraised wings and thereby scraping their inner surfaces, or by the rubbing of the hindwings against the tegmina. All species of the Empusidae and some species of the Mantidae (*Hierodula* s.l., *Choeradodis*) and Hymenopodidae (*Hestiasula*) have developed specialised stridulatory mechanisms.

There are no records or observations of either of the New Zealand mantids stridulating.

Invariably, the stridulation of mantids is of a sound-threatening or intimidatory nature (Cott 1940) and associated with startle- or threat-display. Whether or not the 'cyclopean ear' can detect such sounds is unknown.

(f) Acoustic sensitivity

In general mantids have been considered to be unable to perceive or respond to sound, even though some were known to be able to stridulate. The means by which mantids may perceive sound does not conform with the various

methods described for other insects by Michelsen & Larsen (1985), who did not even mention mantids. Yager & Hoy (1986), however, showed that at least *Mantis religiosa* is sensitive to sound, and recorded extracellular neural responses in the ventral nerve cord associated with auditory stimulation. The sound-detecting organ – the midline metathoracic ear or cyclopean ear – is situated in a mid-ventral cleft of the metathorax, and comprises two tympana facing each other. Later, Yager & Hoy (1987, 1988) reported its presence in *Stagmomantis carolina*, in *Ameles heldreichi*, and in species of 177 different genera representing all the major groups of the Mantodea, and gave detailed morphological and anatomical descriptions. Of the species examined, it was found to be absent in *Eremiaphila brunneri* only.

The acoustic sensitivity of *M. religiosa* was in fact recognised as long ago as 1835 and 1841 by Goureau (also referred to by Varley 1939). Goureau kept a captive *M. religiosa* which he provoked with a feather in order to induce it to display by raising its wings, and to stridulate. He whistled at the same time as he did this. Eventually his mantid could be induced to respond to his whistling alone without any provocation with the feather. It would be interesting to see if this observation could be repeated and verified.

It has been widely believed that the New Zealand mantid *Orthodera novaezealandiae* has hearing organs situated on the inner surface of each raptorial forefemur, in the strongly pigmented purple patch or eye-spot (Potts 1884, Hudson 1892, Martin 1929, 1948, Dixon 1938, Paintin & Murdoch 1964, Miller 1971). This is not so, but the misconception remains deeply entrenched. However, Lowe (1987) established that *O. novaezealandiae* can perceive sound, and obtained a neural response to sound stimulation in the form of a transient burst of action potentials lasting for about one second in adults. There was no response in nymphs. He was unable to test insects in flight for any response to the sound, but suggested that there would be an ultrasonic sensitivity, perhaps leading to bat-avoidance behaviour.

The auditory receptor organ in both New Zealand mantids is morphologically not unlike that of *M. religiosa*, described by Yager & Hoy (1986, 1987). It comprises a longitudinal mid-ventral groove and cleft with associated structures, on the basisternal area of the metathoracic sternum (Matsuda 1970). In *O. novaezealandiae* the structure of the acoustic receptor organ is very similar in both sexes. The anterior groove is well developed, lightly sclerotised, and commences at a slightly elevated flat plate bearing trichoid sensilla. Its margins are ridges, almost carinae, which diverge slightly posteriorly and pass on either side of a transverse, triangular orifice. From this, a deep, narrow cleft extends posteriorly to the anterior bor-

der of the abdomen (Fig. M26). The posterior border of the orifice is formed by two lobes ("knobs" of Yager & Hoy 1987), which are compressed in the vertical plane, discrete, and demarcated laterally by a smooth, longitudinal, superficial hollow and internally by a deep groove. Anteriorly the integument is slightly reflected laterally into the groove so that each lobe has a thick, rounded rim (Fig. M27). Superficially the rim merges behind with the medial external border of the slit, while internally it demarcates the lobe until it merges with the walls and floor of the cleft. The walls are more or less flat, vertical, and parallel, with a broad, shallow depression subdivided by two longitudinal ridges. These begin close together near the anterior focal point of the lobe and gradually diverge, eventually merging with the smooth posterior wall of the lobe. The region enclosed between the ridges corresponds with the "elongated tear drop"-shaped tympanum described in *M. religiosa* by Yager & Hoy (1986, 1987). The areas above and below the ridges are likewise slightly concave. The tympanum is not otherwise differentiated.

Externally, the cleft is surrounded by a strongly convex, hemispherical area demarcated from the pre-episternal area of the metasternum (Matsuda 1970) by a deep, curved groove, and which bears approximately 12 relatively fine, long trichoid sensilla. The slit itself is about 1.5 mm long and gradually widens from 0.06 mm at the front to 0.12 mm towards the rear. At the orifice, the floor of the groove, now at its widest, passes internally beneath the lobes, narrows to form the deep floor of the cleft, and broadens again posteriorly to where the sternal apodemes (furcae) arise (Fig. M28); these are large, hollow, and horn-like. The floor then abruptly slopes to meet the transverse fold of the thoracic / abdominal intersegmental membrane.

Anteriorly, beneath the lobes, the integument of the floor is sclerotised and considerably thickened, especially in the region from which the slender, blade-like apodemes of the ventral longitudinal muscles of the metathorax arise. In section, the integument in this area can be seen to be laminate and the inner layers greatly thickened, so that there is an increase of approximately 3x in thickness (Fig. M28,29). Behind this the floor is membranous, apart from a weakly sclerotised, transverse band behind the sternal apodemes. Here the lateral angles of the floor are thickened in the sloping section, and there is a weak longitudinal ridge. In profile the external margin of the median wall of the cleft slopes posteriorly to meet the up-coming floor, just before it reaches the transverse fold of the intersegmental membrane (Fig. M28). Between the coxae the pre-episternal area of the metathoracic sternum narrows and forms two arms, one on each side of the swollen hemisphere of the acoustic receptor organ (Fig. M26). They too arch downwards to meet the transverse fold of the interseg-

mental membrane. They are broader in the female than in the male, and in both sexes they carry a patch of trichoid sensilla on their posterior part.

The surface of the rim of the lobes, the medial faces of the cleft, and the hemispherical convexities are all densely clothed with fine denticles, which in some areas are broad and blunt but in others slender and sharp (Fig. M27, 28, 30). They are often arranged in irregular rows, and occasionally microtrichia occur. The posterior internal third of the wall of the cleft is smooth (Fig. M28). Anteriorly, in the middle of the medial face of each lobe, there is a smooth subcircular area surrounded by smaller denticles and with a conspicuous thick, blunt horn in the centre (Fig. M31). Here the integument is thin and delicate; it is often damaged or split during preparation for scanning electron microscopy, and sometimes even exploded or blown out. The horn itself is bilaterally symmetrical in a plane occasionally vertical but usually oblique at approximately 45° extending upwards and posteriorly; it is subtriangular in profile. The inner surface is smooth, rounded, more or less vertical, and slightly curved; lateral and outer surfaces are sloped and botryoidal, with approximately five swellings on each side and a straight longitudinal groove along the line of symmetry. The horn, bifid distally (Fig. M32), is the unsocketed bifid conical sensillum of Yager & Hoy (1987).

There is slight sexual dimorphism in the cyclopean ear in *O. novaezealandiae*, as it is generally better developed in the male, being more strongly sclerotised, more strongly curved downwards posteriorly, and with the posterior arms of the metasternal plate more slender.

The cyclopean ear of *Miomantis caffra* is generally similar to that of *O. novaezealandiae* except that sexual dimorphism is great, the organ of the female being much less distinct than that of the male. Here it is less sclerotised than in *O. novaezealandiae*. The anterior groove is relatively longer and wider, and is more or less parallel-sided except anteriorly, where the sides curve together (Fig. M33). The floor of the groove is more intensely denticulate, and becomes lower posteriorly, where its lateral ridges are strongly developed and the throat of the orifice is deeper. Here too it is denticulate (Fig. M34), whereas in *O. novaezealandiae* the throat is shallow and smooth with longitudinal wrinkles (see Fig. M27). The posterior border of the orifice of male *M. caffra* is again formed by the anterior lobes of the cleft, which are similar in shape to those of the former species but are more intensely denticulate (Fig. M34). Their thick, rounded rims pass back and join the margins of the cleft and, laterally, they are demarcated from the metasternum by a superficial hollow and an internal groove. The median walls of the slit are similar to those of *O. novaezealandiae*. Two longitudinal ridges again commence together at the focal point of the lobe,

diverge slightly, and eventually merge with the median wall. The tympanum is normal (Fig. M35). The external border is considerably less strongly arched, and lacks a clearly differentiated rim. The external area surrounding the cleft, although swollen and convex, is narrower, not hemispherical, and has few or no trichoid sensilla. It is not demarcated from the metasternum anteriorly, but laterally there is a shallow groove. The posterior arms of the preepisternal region of the metasternum are membranous (Fig. M36).

The floor of the longitudinal cleft, although still strongly laminated (Fig. M37), is more or less uniform in thickness throughout its length (Fig. M35). The laminations are folded at the commencement of the thickening (Fig. M37). The floor is more or less unsclerotised (apart from the lateral angles which are thickened and provide support for the muscle apodemes, especially behind the sternal furcae) and lacks the strong, transverse thickening beneath the anterior lobes. It is considerably narrower and smaller than that of *O. novaezealandiae*. Posteriorly each thickened angle gives way to a fold, which immediately diverges laterally to merge with the intersegmental membrane between the metathorax and the first segment of the abdomen. These folds are not continuous medially as they are in *O. novaezealandiae*. The surface of the anterior lobes, the anterior half of the medial walls of the cleft, and the swollen external area are intensely denticulate.

The blunt horn is again present at the anteromedial focal point of each anterior lobe, lying at the centre of the subcircular area of smooth integument (Fig. M38). The angle of the plane of symmetry is the same as in *O. novaezealandiae*, but here the horn is less strongly developed and more tooth-like. Its anterior surface is rounded, curved and approximately perpendicular. Its posterior surface is flatter, more sloped, and sometimes has a slight longitudinal groove along the line of symmetry. It is bifid apically, and the basal three-quarters are swollen and more or less smooth (Fig. M39).

The cyclopean ear of the female *M. caffra* is somewhat vestigial and considerably less well differentiated than it is in the male. The anterior groove is much broader, with thick, rounded rims diverging in the anterior half and then becoming parallel. The orifice is not differentiated, and the longitudinal cleft, which is wide and not closed over except posteriorly (Fig. M40), is a continuation of the anterior groove. The anterior lobes are represented by elevated swellings which form low, rounded projections behind the rim of the anterior groove, and which are undeveloped in comparison with those of the male (Fig. M41). The vestige of the lobe lip is smooth, swollen, slightly raised, and has longitudinal wrinkles on its internal part. It forms an external ridge which passes slightly obliquely backwards

to merge with the integument surrounding the slit (Fig. M42, 43). The medial surface of the slit is not as flat as it is in the male, slopes outwards externally, and has only one longitudinal ridge or fold, the ventral ridge. This ridge commences in a concavity at the anterior and folds upwards, almost covering the tympanum (which thus lies mainly in a groove); posteriorly it merges with the medial surface.

The external area surrounding the cleft is neither differentiated nor demarcated, and only a few trichoid sensilla are present towards the anterior. The outer profile of the cleft is relatively flat and has no curvature, unlike that of the male. Between the cleft and the metacoxae the pre-episternal arms of the metasternum are broad and flat, becoming membranous and wrinkled laterally and posteriorly, where there is a group of trichoid sensilla. The floor of the anterior groove, which is denticulate, forms a weak, smooth, transverse ridge at the level of the vestigial lobes (Fig. M40, 41) and then curves deeply to become the floor of the cleft. It is narrow, completely sclerotised, greatly thickened for most of its length, and has the usual laminated structure (Fig. M44). It widens posteriorly in the region of the hollow sternal furcae, which are large, strong, and well developed. Behind them it is sclerotised and very narrow, forming a groove which slopes steeply to the posterior border of the metathorax and is virtually closed over by the medial walls of the cleft. At its posterior end the groove is continuous with the intersegmental, transverse groove between metathorax and abdomen. The surface of the vestigial lobes, the medial wall, and the anterior part of the area surrounding the cleft are denticulate; the denticles are blunter and less well developed in the female than in the male.

The tooth-like horn at the centre of the anterior focal point of the lobe is also reduced in the female. The subcircular smooth area surrounding the tooth is delicate (it was accidentally 'blown out' in one specimen during preparation), relatively reduced in area, and largely wrinkled (Fig. M45). The tooth itself is variable in form. It can be a small, irregular projection without symmetry or it can be a small, bifid structure with the same plane of symmetry as that of the male and similar to it except for its smaller size and less well differentiated form.

Yager & Hoy (1988) found sexual dimorphism in less than half (68) of the 179 genera that they examined. These were probably the more extreme instances as, considering the example of *O. novaezealandiae*, in which both sexes fly and have similar acoustic receptor organs, there is nonetheless a slight sexual dimorphism – related, no doubt, to the fact that the male is the stronger flier. It is likely that a degree of dimorphism occurs in all acoustically sensitive species except those in which both sexes fly equally strongly. In both New Zealand mantids the acoustic receptor organ

is better developed in the male, and in the flightless female *M. caffra* it is vestigial.

Yager (1989) reported that he had examined 330 of the 400 mantid genera, and had recorded physiological audiograms from 31 species in 29 genera. He identified five distinct types of metathoracic groove, of which only one was consistently associated with ultrasonic sensitivity, and found a strong correlation between the presence of long, presumably functional wings and the possession of ultrasonic hearing, both within sexually dimorphic species and among different taxa. This supports the contention of Yager & Hoy (1986) that the mechanism has evolved as a means of detecting predators (bats), especially while the insect is in flight and therefore most vulnerable.

The morphology, anatomy, and physiology of the cyclopean ear have been described by Yager & Hoy (1986, 1987). The tympana on either side of the mid-ventral cleft of the metasternum face each other, and are separated by less than 150 mm. The internal surface of each is backed by a stack of three large tracheal sacs which arise from the narrow branches of the main tracheal commissure of the first abdominal spiracles. The largest air sac has a small neural structure, the tympanal organ, associated with its anteromedial border. This tympanal organ is connected at one end to the tympanum by a long, narrow attachment process, and at the other end to the ventral wall (at some distance from the tympanum) by two ligamentous processes. It comprises 32 chordotonal sensilla, those associated with the tympanum attachment process being oriented at 180° to those associated with the ligamentous processes. Yager & Hoy also describe a single unsocketed conical hair surrounded by an area of smooth, very thin cuticle; this is the bifid tooth or horn previously mentioned.

Yager & Hoy (1986) found that *M. religiosa* hears best in the ultrasonic range, and suggested that flying mantids perceive the ultrasonic bisonar signals of insectivorous bats. Perhaps the species is sensitive also to the hissing sound that it produces itself, which may have an ultrasonic component. Possibly the functioning of the mantid cyclopean ear is even more complex than is suggested by Yager & Hoy (1987), in that the varying thickness of the floor of the cleft and the laminated structure of its integument, the strong, hollow posterior furcae which open off the cleft, the form of the lobes with their ridges and tympanum, the form of the lips of the orifice and anterior rim of the lobes, as well as the anterior sternal groove may all be involved. Further, the unsocketed conical bifid sensillum mentioned by Yager & Hoy (1987) as having a scolopophorous sensillum in each apex is probably also important in the auditory function. The fact that it is vestigial in the flightless female *M. caffra*, where the other acoustic receptor organ components are also vestigial, suggests this.

Information about the anatomy of the bifid horn, when available, will probably give insights into its function. It is unlikely to be two fused, modified sensilla, as each apex already contains a chordotonal sensillum. Rather, it is a special single sensory structure in its own right. It seems to have maximum differentiation in *O. novaezealandiae*. Here the strong bilateral symmetry, the regular botryoidal form, the more or less constant oblique orientation, and the central placement in the area of thinnest integument, in a position that seems in some way to be a focal point of the lobes of the cleft, all indicate its probable importance in sound perception.

Whatever the facts of the case, the acoustic sensory mechanism of mantids certainly has features seemingly unique amongst the insects (Yager & Hoy 1987) and the understanding of its structure and function presents a very interesting challenge.

(g) Defence behaviour

The various kinds of defensive or intimidatory behaviour exhibited by mantids have been described and reviewed by Adair (1914b), Varley (1939), Crane (1952), Robinson (1969), Maldonado (1970), and Edmunds (1972). Once discovered by a predator, mantids may attempt to escape by running or flying, by feigning death, or by adopting a dramatic or intimidatory posture which may involve sound-threat or flash-coloration − "floral simulation" (Sharp 1895), "l'attitude spectrale" (Fabre 1897), "frightening display" (Varley 1939), "warning or threatening display" (Cott 1940), "startle response" (Crane 1952), "deimatic response" (Maldonado 1970). Defensive behaviour is restricted to relatively few species, and is characterised by the unpredictability and rarity of its occurrence (Crane 1952). Sometimes, chemical defence − regurgitation of fluids from the mouth − occurs also. The deimatic response, involving stridulation and wing elevation, is particularly well documented for *Mantis religiosa* (Goureau 1835, 1841, Dufour 1841, Kirby & Spence 1858, Wood-Mason 1879, Fabre 1897, Stawell [n.d.], Coupin 1899, Atwood *in* Slingerland 1900, Stäger 1928, 1941, 1950, Chopard 1938, 1951, Judd 1950, Kevan 1955, Edmunds 1972). The startle response, without stridulation or wing elevation, has been described in *Mantis religiosa*, *Tenodera angustipennis*, and *T. aridifolia sinensis* by Kramer (1960). It has also been studied in *Stagmatoptera biocellata*, in which the wings are elevated, by Barrós-Pita (1974).

Both New Zealand species will run or fly (especially the males) when disturbed, and both will respond with an intimidatory or startle-display, in which the body is elevated to a steep angle and the raptorial legs are spread. This is sometimes associated with regurgitation of a dark fluid from the mouth. It has been seen in patches on the walls of the container of a captive mantid. An advanced male nymph was seen to initiate escape behaviour on several occasions by springing laterally a distance of about 40 cm (B.A. Holloway, pers. comm.).

Other defensive behaviour has also been observed, but only very rarely. On two occasions T.K. Crosby (pers. comm.) noticed two female *O. novaezealandiae* confronting each other, probably as a result of invasion of territory. (Female *Orthodera* and *Miomantis* tend to become territorial, especially later in the season, as has been reported for other mantids (McKinnon 1970).) The protagonists were face to face, in a 'stand-off' situation, and occasionally sparred. Their wings were loosely opened and the forelegs remained folded but were turned outwards to display the bright colour-patch or eye-spot on the inner surface of the femora. The mantids continued in this position for several minutes, until one or the other turned and walked away. No stridulation was observed. A third instance, also observed by T.K. Crosby (pers. comm.), involved a male, in the wild, deliberately approaching another and suddenly attacking from a distance of more than one body length away. The wings of both were spread and erected vertically. After a few seconds the attacking male retreated, folding its wings, while the other remained for about ten seconds with its wings erected and extending its forelegs, without, however, especially exposing the bright colour patches. Sharell (1971) also describes how a female *O. novaezealandiae*, when confronted, will open and raise the forelegs, thereby exposing the eye-spots, and simultaneously elevate the wings, but mentions that it does not very often assume this "spectral attitude". Jackson (1982) mentions that the eye-spot on the foreleg is "displayed when being offensive".

On several occasions two captive females of *M. caffra* in a single container have been observed displaying at each other. The protagonists faced each other with the prothorax elevated so as to be almost vertical, and the body flexed almost to a right-angle. The forelegs were either folded or gripped the substrate. The wings were partly opened, so as to expose the bright yellow hind wings, and at the height of the display were raised and extended so as to be vertical and parallel, as described for *Mantis religiosa*. With *M. caffra*, the abdomen remains stationary and there is no stridulation. The wings were raised, relaxed, and strongly raised again several times at the height of the display. Such confrontations lasted from several minutes to up to several hours, though with little activity for much of the time. Maldonado (1970) recorded a display that lasted for 6 hours, and stated that "the response was displayed as long as the stimulus [was present]". Such behaviour is rare with *M. caffra*. More commonly females of this species confront each other without extending their wings. They simply face

each other with the body more or less vertical and the forelegs elevated and extended. The stance is maintained for a few minutes up to half an hour. This behaviour has been observed both in captivity and in the wild (B.G. Bennett, N.A. Martin, pers. comm.).

(h) Regeneration

In mantids, regeneration of lost appendages – legs, antennae, and cerci – is a well known phenomenon (Przibram 1907, 1935, Meissner 1908a,b, Blackbourn 1921, Beier & Jaus 1933, Roberts 1937a, Chopard 1938, 1949, Beier 1964, 1968). Its extent depends on the stage at which the appendage is lost. If the loss occurs during the early instars then the regenerated appendage will virtually attain full size by the adult stage, except that in regenerated legs the tarsi will have four segments rather than five. If the loss occurs at a later stage, then the regenerated appendage will be correspondingly smaller.

Roberts (1937a) found loss of parts of limbs and their regeneration to be very frequent during her rearing of *Stagmomantis (Auromantis) limbata*. If the loss occurs during the first instar, then the nymph will usually die at ecdysis, as in *Tarachodes afzelii* (Ene 1964) and *Orthodera novaezealandiae* (J. Castle, pers. comm.). With regenerated antennae there are fewer annulations and longer-than-normal segments in between (Przibram 1935). Occasionally nymphs with regenerating appendages pass through additional ecdyses and the period of the nymphal stadia is increased (Przibram & Megusar 1912, Ene 1964). In *O. novaezealandiae* when appendages were regenerating the duration of the stadia was increased but no additional ecydyses occurred (J. Castle, pers. comm.).

Limb regeneration occurs in both New Zealand mantids, and has also been reported in *Orthodera ministralis* in Australia (Blackbourn 1921). Here an entire middle leg lost by a nymph during the second moult regenerated at the third moult into a small version of the normal limb. Portions of the raptorial and hind legs on one side of another specimen, distorted during the third ecdysis, were amputated and then regenerated as smaller portions of the limb, after the fourth moult (the hind leg) or after the fifth moult (the raptorial foreleg). Regeneration of limbs has been observed in *O. novaezealandiae* by J. Castle (pers. comm.), and there is one instance of it occurring in an adult male *Miomantis caffra* in which both raptorial legs were involved (Fig. 48, 49). The loss must have occurred during an early instar, as both tibiae were almost normal in size. The tarsi, however, were shorter than usual – one very much shorter, and with blunt claws – and had four rather than five segments.

Deliberate self-amputation – 'autotomy' – as a means of survival and escape has been once reported in *Stagmomantis carolina* (Guthrie 1933), but this should not be accepted without verification. It may refer to a phasmid rather than to a mantid (see p. 10, col. 2, para. 3). Two of the three common names included in the title cited refer to phasmids; and the behaviour of the insect, "in a state of quiescence with its feelers shielded by the fore-legs", and the fact that it was picked up by grasping the forelegs both suggest that a phasmid rather than a mantid was involved. Phasmids frequently rest with their antennae shielded by their extended forelegs, which it is natural to grip when one handles them. Finally, there have been no further reports of autotomy occurring in this or any other mantid species, whereas it is quite a common phenomenon with phasmaids. In any event, New Zealand mantids are not involved.

(i) Predation

Predation of mantid oothecae and their contents has not often been recorded. Williams (1904) recorded a small black ant in India boring beneath the ootheca of *Gongylus* and eating the contents. Kershaw (1910) noted that beetle larvae of a species of *Dermestes* destroy the whole interior of the oothecae of a Chinese mantis, *Hierodula saussurii*, and Rau & Rau (1913) reported oothecae of *Stagmomantis carolina* in Missouri and Illinois being attacked by a dermestid beetle, *Anthrenus* sp., and by the straw itch mite *Pyemotes tritici* (La Greze-Fossat & Montagne) (= *Pediculoides ventricosus* (Newport)). James (1959) observed oothecae of *Mantis religiosa* being chewed by the field cricket *Gryllus pennsylvanicus* Burmeister in Ontario, and Rivard (1965) mentions crickets and ants eating the oothecae.

Predation of oothecae has not been reported in New Zealand, but badly damaged oothecae of both mantid species are sometimes found. The damage could have been caused by insects, possibly Lepidoptera, Coleoptera, or Hymenoptera, all of which have been found attacking mantid oothecae. In four instances Lepidoptera had attacked oothecae of *M. caffra*: a tineid moth cocoon (pupa eaten out by mites) was present within a previous season's ootheca; a living larva of *Blastobasis tarda* Meyrick (Blastobasiidae) was found boring within a living ootheca; a case-moth (Psychidae) was observed feeding on the thick outer layer of a live ootheca, cleanly removing approximately a quarter of it and exposing the hard, reddish-brown layer within; and a living ootheca was partially devoured by the case-bearing larva of a small psychid moth – an undescribed adventive species locally known as the 'little log cabin' (J.S. Dugdale, pers. comm.).

There are two examples from the Coleoptera, both dermestid beetles. A *Trogoderma signatum* Sharp emerged from a previous season's ootheca, and a large larva of *Anthrenocerus australis* (Hope) was discovered actively

tunnelling in a *Miomantis* ootheca from which numerous nymphs were emerging. As for Hymenoptera, ants (*Pheidole variabilis* Mayr) have been observed chewing into the crest of a hatching *M. caffra* ootheca – three circular cavities, each 2–3 mm in diameter, had been created, and the walls of exit tunnels had been gnawed away to a depth of several millimetres. The same species has been seen attacking a previous season's ootheca. *Technomyrmex albipes* (Smith) has been recorded completely demolishing a *Miomantis* ootheca (D.I. Gardiner, pers. comm.). The thick, soft outer layer of the *M. caffra* ootheca is sometimes partly removed by ants, which gnaw circular cavities into it. Oothecae which appear 'moth-eaten' are probably the result of ant attack. Older weathered oothecae in this condition sometimes occur, occasionally very incomplete and with large holes, tunnels, chambers, or cavities gnawed into them. In some the chorion is still in place in each egg chamber, indicating that the ootheca had been attacked whilst still containing live eggs.

Several arthropod species which are not necessarily preying on mantid oothecae are nevertheless sometimes closely associated with them. For example, there are two instances of a neuropteran, *Cryptoscenea australiensis* Enderlein, pupating in an unoccupied cavity at one end of an *O. novaezealandiae* ootheca and later emerging. In another instance two specimens of the predatory rhodacarid mite *Caliphis novaezelandiae* (Womersley) were sheltering individually in deep cavities in the outer layer of an *M. caffra* ootheca, and in yet another a tydeid mite, *Tydeus lambi* Baker, sheltered amongst the exposed apertures of an ootheca. Acarid mites are also sometimes associated: *Caloglyphus rhizoglyphoides* (Zachvatkin 1937) and *Tyrophagus perniciosus* (Zachvatkin 1941) have been found on *O. novaezealandiae* oothecae, and a thriving colony of *Tyrophagus neiswanderi* (Johnston & Bruce 1965) was present within an injured *M. caffra* ootheca, feeding on dead and decaying eggs and embryos.

Several predators have been reported capturing and eating *O. novaezealandiae* nymphs and adults. Ants (*Iridomyrmex glaber* (Mayr) and *Pheidole ?variabilis* Mayr) have been observed showing great interest in living oothecae of both mantid species, and later on capturing, eating, and removing newly emerging nymphs (D.I. Gardiner, pers. comm.). This has also been noted by Fabre (1897, p. 332; translated by Teixeira de Mattos 1917, p. 121), James (1959), and Ross (1984). James observed two species of ant, *Formica lasioides* Emery and *Myrmica* sp., frequently examining oothecae that had been deposited near the ground, and capturing the emerging nymphs. The wasp *Polistes chinensis* has been observed picking off a group of recently emerged *M. caffra* nymphs, and would have devoured every one if allowed to (B.G. Bennett, pers.

comm.). On several occasions, spiders have been observed spinning webs around *O. novaezealandiae* oothecae about to hatch and capturing the emerging nymphs (T.K. Crosby & D.I. Gardiner, pers. comm.), and first instars and small nymphs of both species are often caught in spiders' webs. *M. caffra* nymphs of various sizes will capture and devour *O. novaezealandiae* nymphs in the wild. This has been observed quite often, but only once has an *O. novaezealandiae* nymph been observed with a captured *M. caffra* nymph (D.I. Gardiner, pers. comm.). There is one report of a German wasp, *Vespula germanica* (F.), capturing and dismembering an adult *O. novaezealandiae*; first the forelegs were removed at the coxo-femoral articulation, then the head was eaten (Gibbs 1983).

There are also reports of vertebrate predators: MacMillan (1981) records five *Orthodera* mantids being fed to nestlings by house sparrows (*Passer domesticus* (L.)), and Roach & Turbott (1953), Daniel (1979), and Daniel & Williams (1983) describe how a captive long-tailed bat (*Chalinolobus tuberculatus* Forster) readily accepted and ate a praying mantis, *O. novaezealandiae*. Whether or not bats capture such insects in the wild is not mentioned. Another mammal, the cat (*Felis catus* L.), has been reported capturing and eating this mantid at Clyde, CO (G.F. McLaren, pers. comm.).

For *M. caffra* there is very little information. Again, ants (*Pheidole ?variabilis* Mayr) have been observed capturing, eating, and carrying off newly emerging nymphs, and half-grown nymphs will capture and eat their own kind in the wild. Spiders too capture many small nymphs. There are instances of spiders spinning webs close to oothecae and capturing many of the newly emerged nymphs, and there is one example of a salticid spider (*Salticus* sp.) capturing and devouring a fifth-instar nymph (D.I. Gardiner & J.A. Berry, pers. comm.). Mismanaged capture of the German wasp may prove fatal if the wasp is able to sting its captor, as happened with an adult female *M. caffra* (D.I. Gardiner, pers. comm.). A house sparrow, *Passer domesticus* (L.), has been observed capturing and carrying off large nymphs (J.G. Charles, pers. comm.), and the Indian myna *Acridotheres tristis* (L.) has been seen hunting, capturing, and eating adult female mantids of this species (M. Lessiter, pers. comm.). Cats have been reported capturing and eating adult male *M. caffra* (J.A. Berry, pers. comm.).

In India, Williams (1904) reported large lizards capturing and feeding upon *Gongylus*, and in North America thirty-four species of birds, including the "English sparrow", have been found to feed on mantids, as have nine species of mammal (including the dog) and some reptiles (Gurney 1951). Rau & Rau (1913) reported "small red ants" attacking and dismembering mantid nymphs. Adair (1914b) described a captive mother *Blepharis mendica*

capturing and eating her emerging nymphs. Ene (1964) reports salticid spiders and large ants as attacking early-instar nymphs, and birds, skinks, and geckos preying upon the older nymphs. Key (1970) states that the active stages are subject to predation by birds, lizards, insectivorous mammals, and sphecid wasps, and Ross (1984) lists birds, monkeys, other small mammals such as skunks and opossums, and some reptiles as preying on mantids.

(j) Parasitism

The oothecae of New Zealand mantids are parasitised by several species of Hymenoptera. Valentine (1967) records three species – *Eupelmus antipoda* Ashmead (Eupelmidae) and *Podagrion* spp. A and B (Torymidae). It is now known that one of these latter two species is *Pachytomoides ?frater* Girault.

In Australia a number of species of hymenopterous parasite have been reared from oothecae of *Orthodera* (J. Balderson, pers. comm.), including in the family Eupelmidae possibly a second species each of *Eupelmus* and *Anastatus*, and in the Torymidae *Propachytomoides spilopterion* (Cameron), probably more than one species of *Podagrion*, and a *Pachytomoides* species. Other species will undoubtedly be found when the fauna is more thoroughly surveyed (J. Balderson, pers. comm.).

There is no information available about hymenopterous parasites of *Miomantis caffra* oothecae in southern Africa. However, in New Zealand two examples of a hymenopterous parasite larva have been found within their oothecae. Unfortunately further identification was not possible.

Beier (1964) lists thirty-one species of Hymenoptera and two of Diptera as parasites of the oothecae of nineteen different mantid species. Eleven different hymenopterous genera of the families Eupelmidae, Torymidae, Mymaridae, and Eulophidae are involved, as well as proctotrupoid and scelionid species. *Podagrion* alone contributes fifteen species, and *Anastatus* five; the remaining genera have only one or two species in each. Most species are host-specific as far as is known, but three species of *Podagrion* each parasitise hosts in two different genera. One of these three species parasitises two host species in each of two genera. One species of *Anastatus* and the single *Mantibaria* species each parasitise oothecae of mantid hosts belonging to three different genera. Ene (1962) reports eight chalcidoid and two other hymenopteran species, and Kumar (1973) a species of the family Eulophidae parasitising mantid oothecae; some of these were host-specific. The two species of Diptera mentioned by Beier which parasitise mantid oothecae, *Pseudogaurax signata* Lw. and *Gonispita* (=*Fiebrigella*) sp., belong to the family Chloropidae. Key (1970) suggests that these chloropids are not necessarily parasites but could be scavengers, and he

mentions that numerous *Botanobia tonnoiri* Malloch have been reared from the oothecae of *Tenodera australasiae* (Leach).

Information on the biology and life history of species of *Podagrion*, *Eupelmus*, and other genera in North America is given by Breland (1941a).

Three parasites of *Orthodera novaezealandiae* oothecae were found in a survey carried out in Nelson by E.W. Valentine between 1960 and 1966. His data show that out of 107 oothecae studied, 36 were parasitised, 57 were unparasitised, and 14 were infertile. Of the parasitised oothecae, 24 produced mantid nymphs as well as parasites, and the remaining 12 produced parasites only. In some of the latter examples the level of parasitism may have been as high as 100%, as the numbers of emerged parasites were relatively large. The actual numbers of parasites that emerged from each ootheca varied from several to as many as 61, and females always outnumbered males. Several dissected oothecae were found to contain dead mantid nymphs and immature parasites, as well as desiccated and rotten mantid eggs. Hymenopterous oothecal parasites have also been observed in Wellington by Sharell (1971), who illustrates a parasite pupa in situ within an ootheca, and in Christchurch by J. Castle (pers. comm.).

The adult wasps emerge from the oothecal apertures, boring their way through the internal closing layers and the foam plug, in which they make conspicuous round holes. Usually only one species is present in each parasitised ootheca, but in two instances both *Eupelmus* and *Podagrion* emerged from the same ootheca (E.W. Valentine, unpubl. data).

The New Zealand species of oothecal parasite are as follows (J.A. Berry, pers. comm.).

FAMILY MEGASPILIDAE

• *Dendrocerus ?carpenteri* (Curtis). Emerged from an *O. novaezealandiae* ootheca collected in Christchurch. The host record is unusual, as *Dendrocerus* species are almost always hyperparasites of Hemiptera, particularly aphids (A. Polaszek, pers. comm.).

FAMILY EUPELMIDAE

• *Eupelmus antipoda* Ashmead. Found in Christchurch, Nelson, and Auckland, and usually emerging in the spring at the same time as the mantid nymphs. It must survive through the summer until new oothecae are produced by its mantid host.

FAMILY TORYMIDAE

• *Podagrion* sp. Known from Canterbury (Rangiora), Nelson, and Auckland (Henderson, Lynfield). It emerges from the ootheca later than the mantid nymphs, and its emergence period is spread out from spring to summer.

• *Pachytomoides ?frater* Girault. Known from Nelson only. Also an autumn-emerging species.

The New Zealand mantid oothecal parasite fauna seems impoverished when compared with that of Australia. Further investigation will perhaps show that the three species are more widespread than the above evidence indicates, and that more species are present. That this is probably so is evidenced by the discovery of an *Orthodera* ootheca at Titirangi (AK) in which parasites had made circular emergence holes, four on one side, three on the other, all at a height about one-quarter up from the substrate.

Nymphs and adult mantids are also parasitised. An interesting example of endoparasitism has been reported by Brennan (1987), who described two fatalities in captive *O. novaezealandiae* which had been fed on the fly *Sarcophaga crassipalpis* (Miller). Apparently in both instances eggs or larvae from the fly survived ingestion by the mantid and continued to develop, eventually killing it. Whether or not the maggots reached maturity is not reported. Rosewall (1924) records ten fully grown maggots of *Sarcophaga* emerging from a dying *Stagmomantis carolina*, pupating in soil, and later emerging as adults. Shelford (1903) reported that a gordian worm, *Chordodes shipleyi* Camerano, is generally present in the fat body above the intestine of *Hierodula dyaka* and *Rhombodera basalis* in Borneo, and Ene (1964) found nematodes, Nematomorpha, and tachinid larvae as internal parasites of nymphs and adults of *Tarachodes afzelii* in West and Central Africa. Key (1970) mentions parasitism of Australian mantids by mites and mermithid nematodes.

(k) Pathology

There is very little information about diseases of mantids. Specimens found dead unseasonally, in good condition and obviously not senile or old, may have died as a result of wasp stings inflicted during a mismanaged attempt at capture. There is no record of fungal attack in New Zealand. Captive females of both species occasionally become egg-bound – said to result from insufficient humidity (Heath 1980). In one example of this, a large *Miomantis caffra* contained so many eggs that the pigmented hypodermis was rubbed away, exposing groups of parallel eggs which could be seen through the transparent integument. Ene (1964) reported that some unmated females did not oviposit, even though they were swollen with eggs. They became sluggish, and the terminal three or four abdominal segments turned black. Eventually the mantids died. No morphological abnormalities or disease-causing organisms could be found.

In one instance only, a nymph of *M. caffra* was observed to emerge backwards from the ootheca, managing to get its body free of the embryonic cuticle and ootheca. It died, however, because its head, the tips of its limbs, and the cephalic cap of the embryonic cuticle were held between the flap of the exit aperture and the foam material filling the apertures. This particular ootheca was irregular in shape and appeared to be rather disorganised, so perhaps the egg producing this individual had been laid upside down; 132 other nymphs emerged from the same ootheca.

(l) Diet

Mantids are wholly carnivorous and prey mostly upon live arthropods, especially insects. In captivity small nymphs devour aphids, *Drosophila* flies, and tetranychid mites (Rollinat 1926, Roeder 1936, Breland 1941a, Beier 1968, Suckling 1984). Larger specimens will capture and devour almost any insect, especially if it is not greatly larger than themselves. Chopard (1938) suggests that grasshoppers are the main prey of mantids in the wild. However, the species of prey most frequently captured will be those which are most abundant in the mantids' habitat. Marshall (1902) fed only Lepidoptera to various species of mantis in South Africa.

Stagmomantis carolina was reared by Rau & Rau (1913) on a diet of mayflies, lacewings, various species of cockroach, nymphs of grasshoppers and locusts, crickets, aphids, various species of beetles, various species of butterflies and moths (both caterpillars and adults), houseflies, honeybees, and ants. Both nymphs and adults were cannibalistic. Breland (1941a) reared this species on adult crickets, katydids, grasshoppers, squash bugs, butterflies, moths, caterpillars, American cockroaches, fairly large spiders, a centipede, and a scorpion. Williams & Buxton (1916) fed the nymphs of *Sphodromantis guttata* aphids, *Aleyrodes*, coniopterygids, cercopids, jassids, and small Diptera. Later they were fed houseflies (*Musca*), bluebottles (*Calliphora*), wasps, syrphids, small Heteroptera, grasshoppers, and butterflies. One nymph was seen to completely devour a fly that had been dead for some days, and another was observed biting pieces off dead hawthorn leaves. Cannibalism was also noted.

Didlake (1926) fed *Stagmomantis* and *Tenodera* (= *Paratenodera*) on "huge cockroaches and grasshoppers as large as the mantids", caterpillars, moths, stink-bugs, wasps (*Vespa*), and spiders. Nymphs were fed tiny leaf-hoppers, fruit-flies, small caterpillars, and, later, larger leaf-hoppers, flies, and caterpillars, as well as young grasshoppers. Hadden (1927) listed 29 species of grasshoppers, katydids, mantids, aphids, moths and butterflies, flies, and hymenopterans including the honey bee, as being eaten by *Tenodera* (= *Paratenodera*) in Hawaii. Thierolf (1928) fed captive *Tenodera* (= *Paratenodera*) grasshoppers, crickets, katydids, houseflies, horseflies, blister beetles, Japanese beetles, caterpillars, and honey bees. In the wild he observed this species to eat crickets, aphids, houseflies, caterpillars, butterflies, honey bees, wasps, and spiders. He

also analysed the stomach contents of 35 wild-caught mantids and found grasshoppers, Heteroptera, Lepidoptera including caterpillars, one coccinellid beetle, numerous honey bees, wasps, hornets, sawflies, ichneumons, flies, and spiders in them. Bromley (1932) fed specimens of this species ants, bumble bees, Diptera, Coleoptera, Lepidoptera, acridids, gryllids, and katydids. Its diet is also considered by Eisenberg *et al.* (1981), Bartley (1983), and Hurd & Eisenberg (1984). *Stagmomantis carolina* were kept on a diet of German cockroaches by Breland (1941b), and would eat or attempt to eat practically any living invertebrate that was introduced into their cage, provided it was not too large.

Roberts (1937a, b) reared *Stagmomantis limbata* and *Litaneutria minor* on a diet of aphids and various flies. Faure (1940) fed *Tarachodes maurus* pentatomids, lygaeids, reduviids, cockroaches, grasshoppers, noctuid moths, small bees, and Coleoptera including chrysomelids and malachiids. Mittelstaedt (1957) used *Calliphora* and *Lucilia* in his experiments with *Parastagmatoptera unipunctata*. Ene (1964) fed nymphs of *Tarachodes afzelii* on *Drosophila* flies, and, when larger, various microlepidoptera, mosquitoes and other Diptera, Trichoptera, Ephemeroptera, alate termites, and small Hemiptera.

Mantis religiosa was fed locusts (larger than itself), grasshoppers, katydids, large spiders, butterflies, dragonflies, large flies, bees, and other insects by Fabre (1897), who also observed the voraciousness of its appetite and its propensity for cannibalism. Rollinat (1926) fed this species aphids, houseflies, large bluebottle flies, crickets, small butterflies, bees, and wasps. Muthukrishnan (1987) reared it on mosquitoes and houseflies only. Atwood (in Slingerland 1900) records *M. religiosa* feeding in North America on spiders and grasshoppers. Hutchings (1934) listed caterpillars, flies, crickets, grasshoppers, and other insects as its prey and reported large numbers attracted to lights, where they fed on mayflies and other insects. Roeder (1936) found any insect not strongly negative to light to be suitable – all kinds of flies, grasshoppers, moths, caterpillars, and cockroaches, as well as mealworms fed by hand. James (1942, 1959) found *M. religiosa* nymphs to feed on chloropid flies, cicadellid leaf-hoppers, small Hymenoptera, and cricket nymphs in captivity; and adults to feed on three species of cricket, three species of grasshopper, cicadellid leaf-hoppers, muscid flies, and argiopid spiders in the field. Because of its propensity to capture crickets and grasshoppers the species was distributed as a biological control agent in Canada (McLeod 1962, Kevan 1990a).

Cannibalism involving both nymphs and adults occurs frequently in captive colonies of various species of mantid (Slingerland 1900, Rau & Rau 1913, Williams & Buxton

1916, Didlake 1926, Roeder 1936). Adair (1914b) observed a mother *Blepharis mendica* capturing and eating her newly emerged offspring. Matsura & Nakamura (1981) found that in captive colonies there was little cannibalism if prey density was kept high. They suggested that it was necessary to know the feeding conditions of the mantids (i.e., prey density) before the frequency of cannibalism in the wild could be estimated. James (1959) records cannibalism in *Mantis religiosa* in the wild.

Although captive mantids can be induced to eat vertebrates and vertebrate tissue as a substitute for their normal arthropod prey (Roeder 1936, Gurney 1951, Richards & Davies 1977, Heath 1980), and larger mantids have for long been known to attack and devour vertebrates (Plinius Secundus A.D. 77 – see Kevan 1985a, 1990b), there are few records of its occurrence in nature. Chopard (1938), Beier (1968), and Kevan (1985a and in press) have reviewed the situation; their observations are as follows.

Stagmomantis carolina attacked and devoured small frogs and a striped lizard three times its length (Burmeister 1838, p. 358; Zimmermann 1844, cited in Kevan 1985a); Zimmermann (1844) reported newts as experimental prey of this species, and Rau & Rau (1913) fed a small frog to it in captivity, which was partly eaten.

Coptopteryx argentina attacked and killed a small bird (Burmeister 1864) in Brazil. *Hierodula bipapilla* attacked and killed a sunbird in India (Browne 1899), and attacked and devoured a "crying tree-frog" in southern China (Frank 1930; Beier 1933, p. 332).

Tenodera aridifolia sinensis attacked a field mouse and a small frog in eastern U.S.A. (Bromley 1932), and was probably the species which captured a humming bird in California (described by Ross 1984). *Mantis religiosa* caught and ate a small lizard in central Europe (Tomala 1903, cited in Kevan 1985a), caught and ate a lizard in France (Mourgues 1909), and a small snake, three times its length, in eastern Canada (Vickery & Kevan 1983, Kevan 1985a).

Durrell (1956, ch. 13) gives a beautiful and entertaining account of an "exceptionally large female mantid" (11.5 cm long) in Crete attacking, and eventually falling victim to, a gecko. This might have been *Stagmomantis viridis*, which has been recorded as attacking small vertebrates in Israel.

Depending to some extent upon the degree of hunger, some food items may be rejected. Poulton (1902) found that various mantid species in South Africa invariably rejected acraeine Lepidoptera, and there was some evidence that these were not only distasteful but also unwholesome for the mantids. Rau & Rau (1913) noted that potato beetles, robber flies, stink bugs, bagworms removed from the cocoon, and very large grasshoppers were rejected.

Williams & Buxton (1916) observed some nymphs rejecting aphids; larger mantid nymphs would not eat caterpillars, and showed a strong dislike of tipulids and coccinellids. Faure (1940) recorded a noctuid caterpillar being rejected. Large size may be a factor in prey rejection with some species. Rau & Rau (1913) noted that very large grasshoppers were always rejected, and Faure (1940) indicated that big prey would not be attacked. However, Williams & Buxton (1916) suggested that some prey items might be rejected because they were unmanageable rather than unpalatable.

Some species have specialised prey preferences. Marshall (1902) found Lepidoptera to be a common prey of various mantids in South Africa; Shelford (1903) reported that *Metallyticus semiaeneus* feeds entirely on cockroaches, for the capture of which it is specialised both in habit and morphology; Williams (1904) found small Lepidoptera, especially a small skipper butterfly, to be the favourite prey of *Gongylus gongyloides* in India; Adair (1914b) states that grasshoppers are the natural food of *Blepharis mendica*, although they will eat flies; Faure (1940) considered pentatomids to be the main prey of *Tarachodes maurus* in South Africa; adult *Mantis religiosa* are considered to feed mainly on grasshoppers and crickets in Canada (McLeod 1962); *Paratenodera angustipennis* feeds mainly on grasshoppers in Japan (Matsura & Nagai 1983). In some situations the mantid seems to have an instinct for strategic positioning (Ross 1984) such as lying in wait at flowers, or may have developed specialised behaviour (e.g., *Metallyticus* – see above).

Moisture is also important. Williams & Buxton (1916) noted that all stages readily drank droplets of water, and Heath (1980) observed that when thirsty they will drink from a spoon of water, and that they will sometimes bend down and pass their mouthparts over the skin when being handled, as they can sense the presence of moisture there.

The mantid appetite is voracious – Zimmermann (in Burmeister 1838) states that a mantid will devour several dozen flies, several robust grasshoppers, several young frogs, and even a lizard three times its own size, all in a day. Barlow (1895) fed approximately seven flies per day to adult female *Hierodula bipapilla*. Slingerland (1900) recorded eleven Colorado beetles being eaten during one night, and Gurney (1951) ten adult German cockroaches within 2.5 hours, all by *Stagmomantis carolina*. Adair (1914a) fed an adult *Sphodromantis bioculata* up to 64 flies in one morning. Breland (1941a) fed one or two, sometimes more German cockroaches to adult females of this species daily but found that they were capable of consuming still more – one devoured ten German cockroaches, an egg-case, and portions of another within 2.5 hours.

Roberts (1937a) fed 1st- and 2nd-instar nymphs of *Stagmomantis limbata* two *Drosophila* each daily, 3rd instars four *Drosophila* each daily, 4th and 5th instars two horn flies, 6th and 7th instars two houseflies, 8th instars three houseflies, 9th instars four houseflies, and adults four or more houseflies and blowflies. Thus, in the course of its development an average female of this species would consume 96 *Drosophila*, 48 horn flies, 179 houseflies, and 464 blowflies – a total of 787 insects. With *Litaneutria minor*, Roberts (1937b) fed the 1st instar one aphid daily, the 2nd instar two aphids daily, the 3rd instar one *Drosophila*, the 4th instar two *Drosophila*, the 5th instar three *Drosophila*, the 6th instar one housefly, the 7th instar two houseflies, and the 8th instar one blowfly. Thus, an average female of this species would consume during her lifetime 40 aphids, 70 *Drosophila*, 43 houseflies, and 90 blowflies – a total of 243 insects.

Faure (1940) observed that *Tarachodes maurus* devoured six *Astylus* beetles within 3 hours. Matsura *et al.* (1975) found that the total food intake of *Paratenodera angustipennis* from the 4th instar to the final moult varied from 130 to 260 adult houseflies. Matsura & Nagai (1983), dealing with the same species, concluded that a female would capture on average one grasshopper every few days, although the rate was higher than two grasshoppers per day in some instances. Males consumed very much less prey than did females.

Mantids are probably adapted to starvation and fasting, which probably often occur during their life history (Rau & Rau 1913). *Tarachodes maurus* starved for 25 days recovered when fed again (Faure 1940). Matsura (1981) found that the average survival period for *Paratenodera angustipennis* under starvation conditions was shortest for 1st- and 2nd-instar nymphs (3–9 days) and longest for adult females (19–37 days). Adult males survived for only 11–21 days. Starvation causes a decrease in body weight, and after 5 days the individual metabolic rate begins to diminish (Matsura 1981).

Nutritional value also has an effect. Ene (1964) found that when nutrition was inadequate in *Tarachodes afzelii*, the result was prolongation of the nymphal stadia, an increase in the number of instars from seven in both sexes to nine in males and ten in females, and smaller-than-average adults.

With *Paratenodera angustipennis*, nymphs that consumed a greater amount of prey had larger body dimensions and shorter development times (Matsura *et al.* 1975). Further, these authors found that with females nutritional status determined the potential number of eggs, and, in the adult, the maturation of the ova. Muthukrishnan (1987) found temperature to be important with *M. religiosa*: at 27°C food consumption of females was higher than at

22°C, 32°C, and 37°C, and lifespan was shorter at the higher temperatures.

In summary, mantids prey upon the species of insect that are most abundant in their particular habitat; often only a few species are involved. Specialised prey preferences and habits which facilitate the capture of their prey sometimes occur. Captive mantids can be induced to devour almost any flesh, vertebrate and invertebrate, and will even attack and devour small living vertebrates. However, they have an overwhelming preference for arthropods, especially insects, and will eat almost any species, including their own.

New Zealand mantid species. Both conform to the general pattern. In captivity, *Orthodera* nymphs feed on aphids and minute flies (including *Drosophila*), and larger specimens on grasshoppers, cockroaches, houseflies, blowflies, wasps, butterflies, moths, spiders, and various larvae (Potts 1884, Martin 1929, 1948, Bandsma & Brandt 1961, 1963, Natusch 1967, Miller 1955, 1971, Child 1974, Hudson 1975, Homewood 1978, Craven 1982, Riley 1983, Suckling 1984). On one occasion approximately one-third of an earthworm was eaten (P.L. Wilding, pers. comm.). *Miomantis* nymphs have been fed on tetranychid mites and aphids, and on the numerous small Diptera, Hymenoptera, Hemiptera, and other insects obtained by sweep-netting rank vegetation. Older nymphs and adults will devour most insects as well as other arthropods – large gravid crickets (*Teleogryllus commodus*), bees (*Apis mellifera*), wasps (*Vespula germanica*), green shield bug (*Nezara viridula*), magpie moth adults (*Nyctemera annulata*), large spiders, and the long-legged house spider (*Pholcus*) (M. Lessiter & P.L. Wilding, pers. comm.). In another instance, however, green vegetable bugs were not captured and devoured when alternative prey was available. Perhaps whether or not this particular species is eaten reflects the extent of hunger of the mantid, as in the first case the vile-smelling green vegetable bug was devoured just as readily as other insects. Allen & Allen (1987) maintained a female on a diet of one earwig per day for 3 weeks, during which time two oothecae were produced.

In the wild, *O. novaezealandiae* nymphs have been observed feeding on aphids (C. Read, pers. comm.), and adults have been observed devouring German wasps, honey bees, a monarch butterfly larva (*Danaus plexippus*), a Fuller's rose weevil (*Asynonychus cervinus*), and a katydid (*Caedicia simplex*) (Gibbs 1983, Given 1984a, b; T.K. Crosby, C. Reid, pers. comm.). A long-tailed mealybug (*Pseudococcus longispinus*) was captured and rejected on one occasion, and females have been seen to avoid the paper wasp *Polistes chinensis* (T.K. Crosby, pers. comm.). *M. caffra* has been observed feeding on caterpillars, passion vine hoppers (*Scolypopa australis*), bees, flies, and white butterflies (*Pieris rapae*) (D.I. Gardiner, pers. comm.).

As so many potential prey species are present in the habitat of both New Zealand mantids, particular prey preferences do not develop often. With both species, however, there is a predilection for flies of all kinds. There are also several examples of individual specimens of *O. novaezealandiae* developing a preference for particular prey species that are common in their territories. In one example a female commonly preyed on the ant *Paratrechina vaga* (T.K. Crosby, pers. comm.), and in two other examples honey bees and German wasps were particularly sought after (T.K. Crosby & C. Read, pers. comm.). Not every attempt to capture German wasps was successful. Both species of New Zealand mantid can be induced to eat raw meat and swatted flies (P.L. Wilding, pers. comm.; Walsby 1984), and *M. caffra* will take canned processed meat pet food (D.I. Gardiner, Mrs Cardis, pers. comm.). In Australia *O. ministralis* has been reared on a diet of mosquitoes and houseflies (Blackbourn 1921).

The New Zealand mantids are every bit as voracious as other mantid species. Potts (1884) reported that *O. novaezealandiae* consumed fourteen small flies within a short space of time, and Walsby (1984) fed his captives six flies per day, but they would take up to twelve. Suckling (1984) fed *O. novaezealandiae* one large blowfly (*Calliphora vicina*) per day. In the wild this species will eat up to two German wasps per day (C. Read, pers. comm.). Up to 6.5 flies could be eaten by one female within 6 hours, though the average was 2–2.5 flies per female. Female mantids ate an average of 17.5 *Musca domestica* per specimen during 3 hours, with a maximum of 26. The extent of the appetite of *M. caffra* has not been determined, but there can be no doubt that it is very great indeed. It has been observed by a nest of a paper wasp, *Polistes chinensis*, which it completely cleared out (Mrs Nicholas, pers. comm.).

Moisture is a requirement of the New Zealand mantids. Potts (1884) noted that drinking occurs only rarely in *O. novaezealandiae*, and 1st-instar nymphs of *M. caffra* have been observed traversing the surface of leaves with their mouthparts to obtain droplets of moisture, and also biting into the epidermal cells, possibly for the same purpose (B.G. Bennett & C. Chalmers, pers. comm.).

Cannibalism has been recorded for the New Zealand mantids. It has been reported by Potts (1884), and Sharell (1971) observed it amongst newly hatched nymphs before they dispersed. It frequently occurs amongst captive specimens (Suckling 1984), and has been reported in the wild. C. Read (pers. comm.) observed a half-grown *Orthodera* nymph devouring another at Mt Wellington, Auckland. Adult female *O. novaezealandiae* have been observed devouring another female on two occasions, and an adult male (not associated with copulation) twice (T.K. Crosby, pers. comm.).

Miomantis nymphs have been seen capturing and eating *Orthodera* nymphs as well as their own kind, but an *Orthodera* nymph with a captured *Miomantis* nymph has been seen only once (D.I. Gardiner, pers. comm.). Suckling (1984) studied cannibalism in captive *O. novaezealandiae* and found that it diminished amongst 3rd- and 4th-instar nymphs in the presence of *Drosophila* flies, and significantly increased when the mantid density was greater. Further, he found that cannibalism by 4th-instar nymphs on 1st-instar nymphs was again reduced in the presence of *Drosophila* in a more complex environment, but increased significantly with a higher 1st-instar density. He concluded that cannibalism is unlikely to be an important mortality factor in the wild, as the population density of mantids is usually low.

Sexual cannibalism occurs infrequently in *O. novaezealandiae* (Ward 1969, Castle 1988), although Miller (1984) suggests otherwise. Only two instances of its occurrence in the wild were observed by T.K. Crosby (pers. comm.) over several years of observation. With *M. caffra*, in contrast, sexual cannibalism is very frequent, and probably explains the relative lack of males in collections, and why males disappear from the population so rapidly.

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ILLUSTRATIONS

(1)

(2)
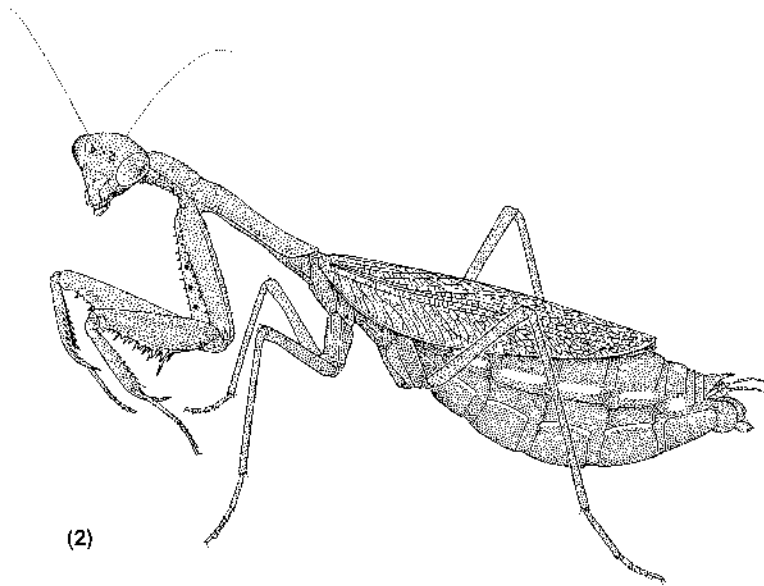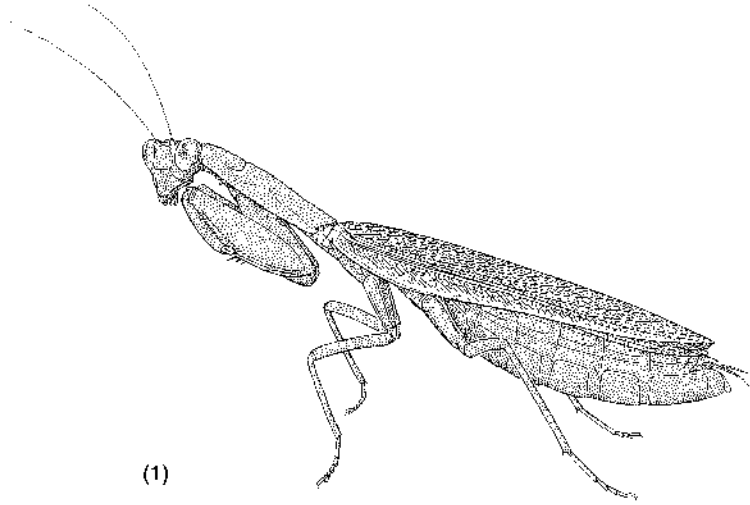
Figures 1 and 2 Habitus, lateral, adult female of (1) *Orthodera novaezealandiae*, (2) *Miomantis caffra* (x2).
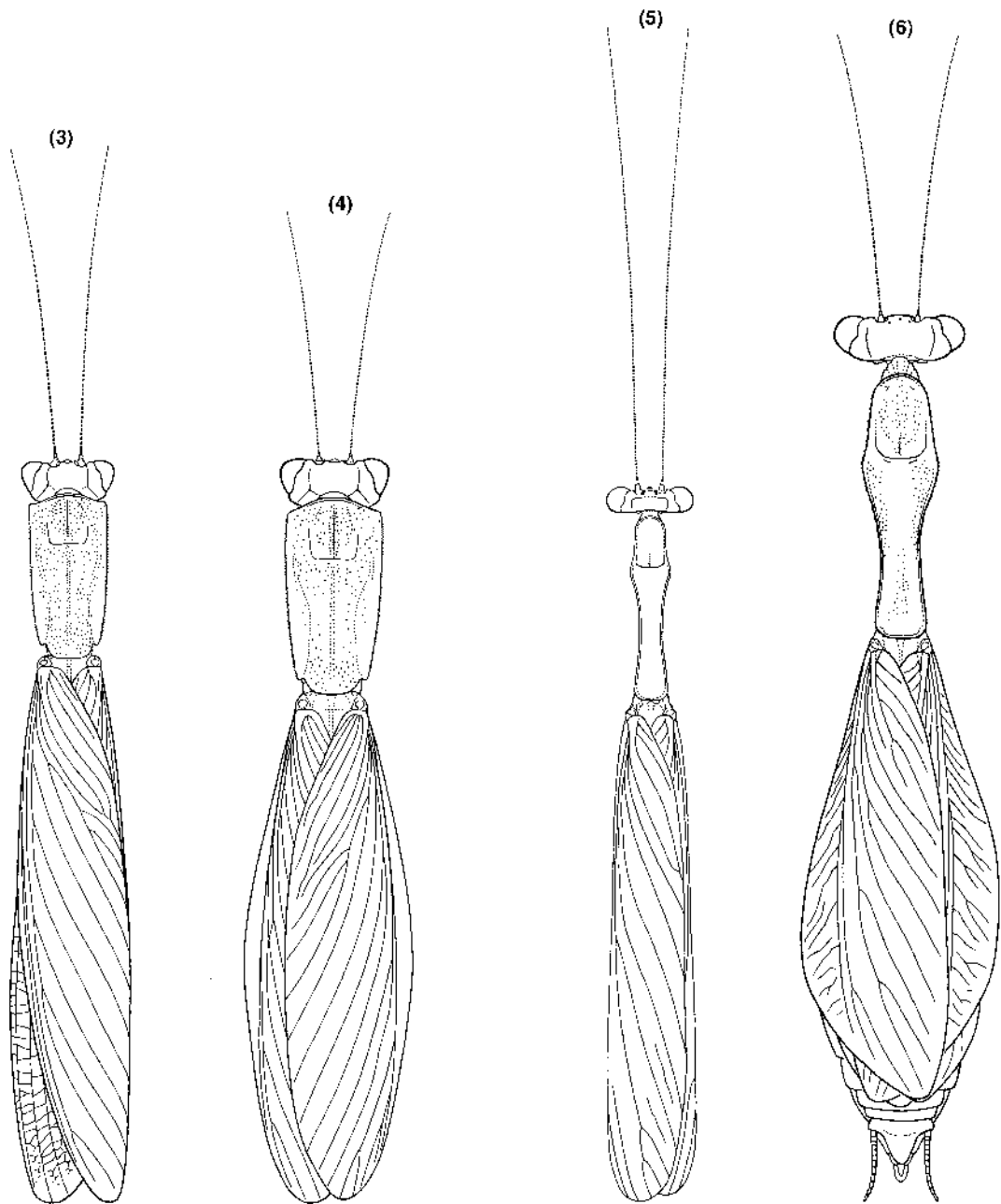
Figures 3–6 Habitus, dorsal, adult male and female of (3, 4) *O. novaezealandiae,* (5, 6) *M. caffra* (x2.6).
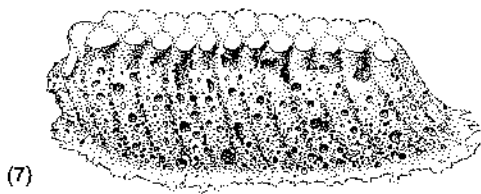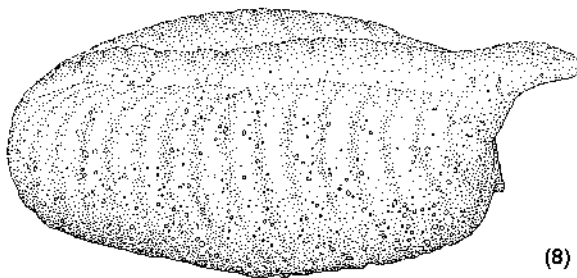
Figures 7 and 8 Habitus, laterodorsal, ootheca of
(7) *O. novaezealandiae*, (8) *M. caffra* (x3.25).

Figures 9–43 Morphological features of life stages of *Orthodera novaezealandiae*.

Fig. 9 and 10 Head, frontal, male and female (x10).　**Fig. 11** Foreleg, female, inner aspect (x4.8).
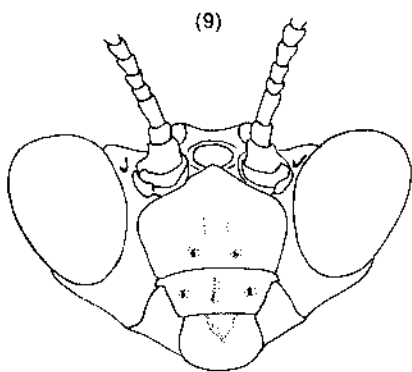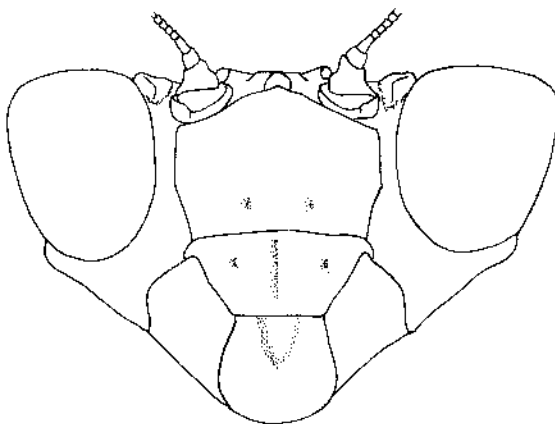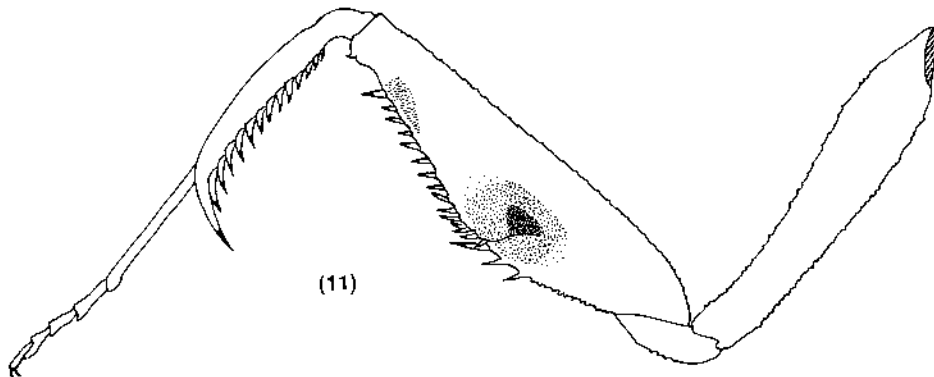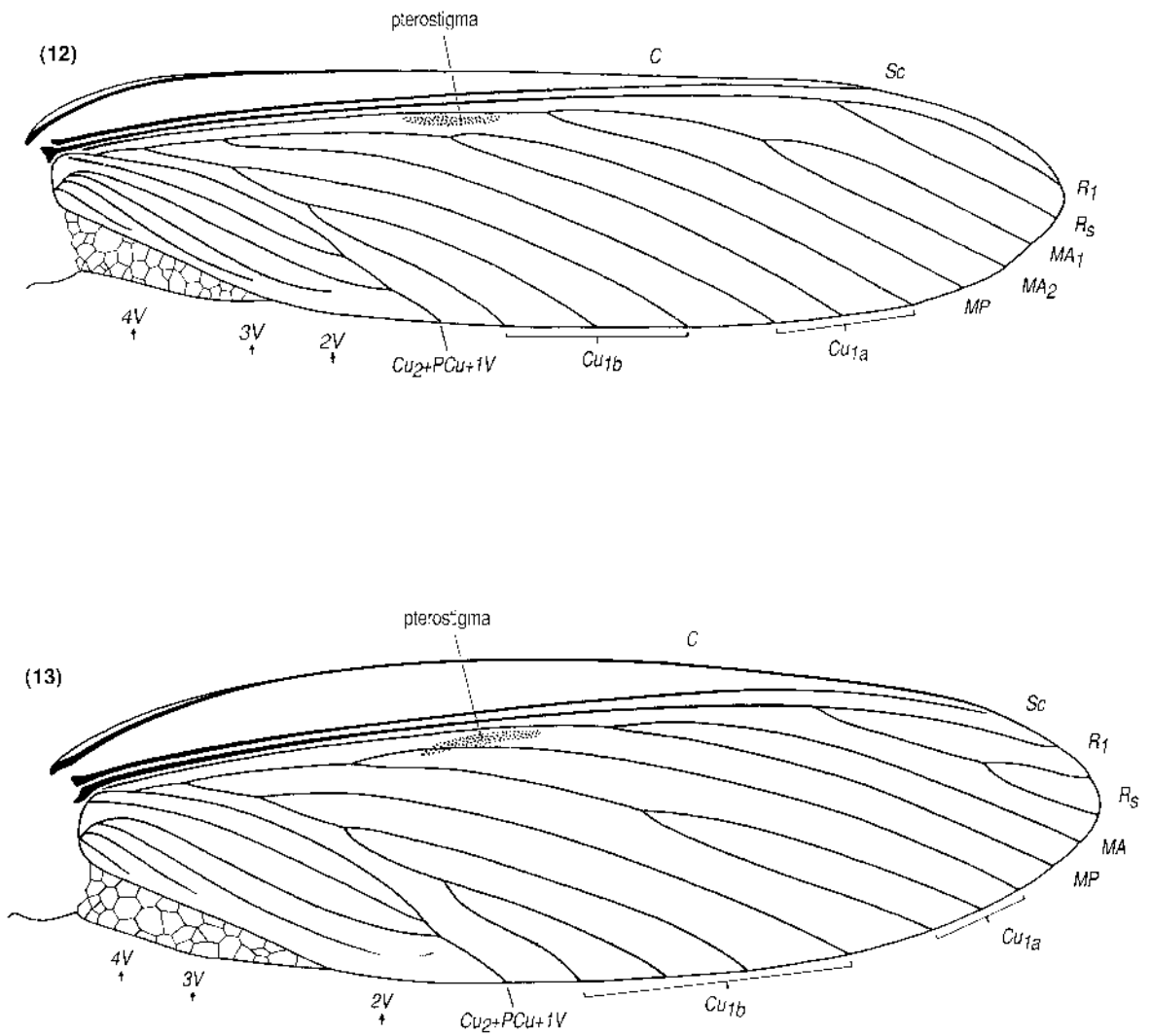
Fig. 12 and 13 Forewing, male and female (x4.8).　**Fig. 14 and 15** Archedictyon, male and female (x20).

distal

proximal

(15)

distal

proximal

(14)
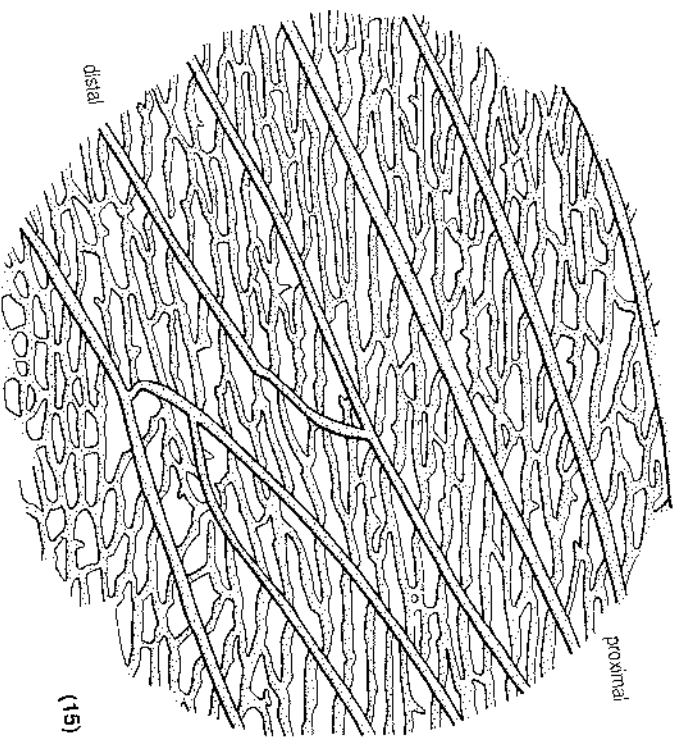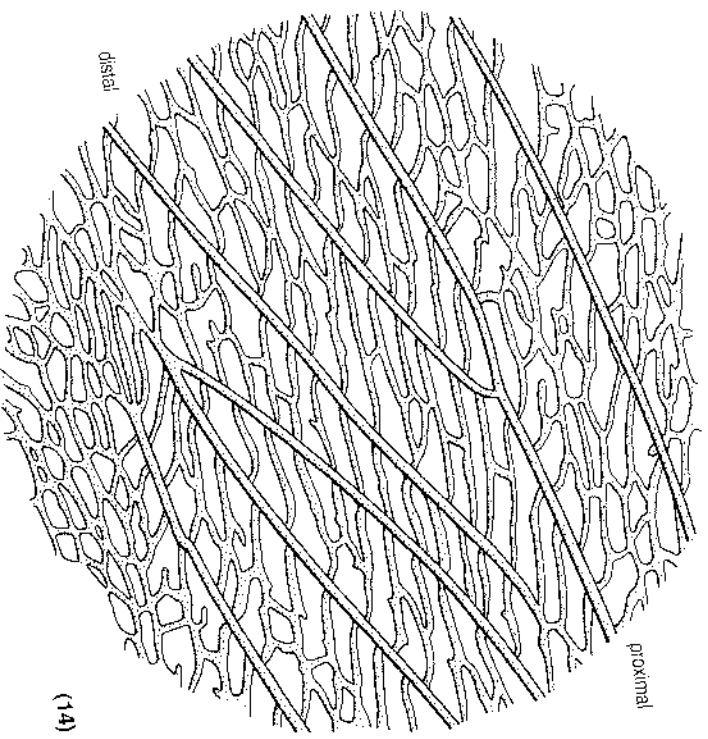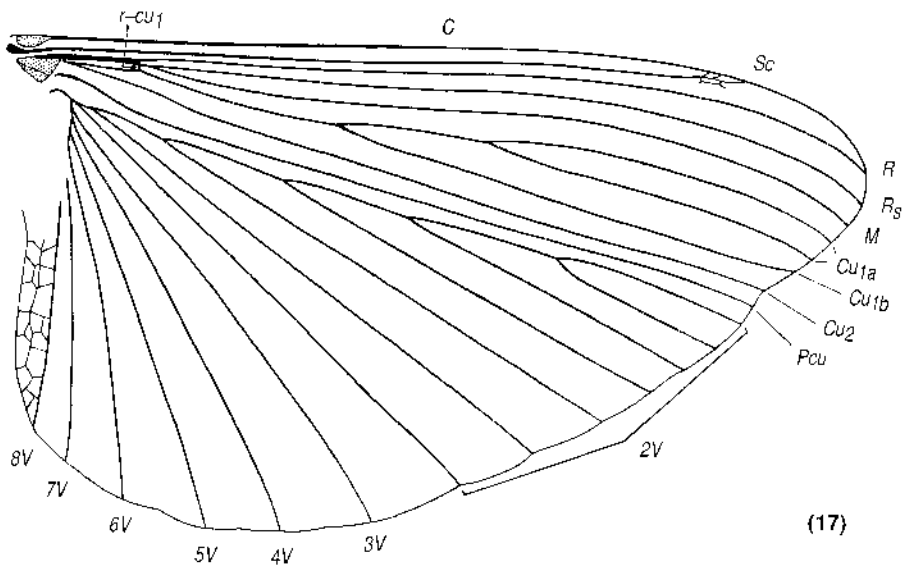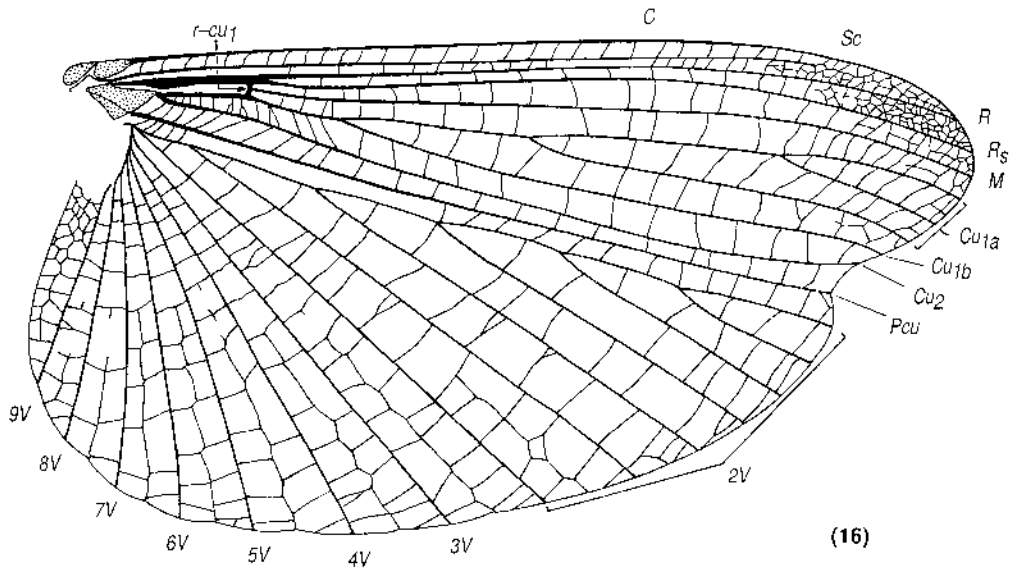
Fig. 16 and 17 Hind wing, male and female (x4.8).

(18)

R

MA

MP

Cu₁

r–cu₁

(19)

R

MA

MP

Cu₁

r–cu₁

(20)

R

MA

MP

Cu₁

r–cu₁

(21)

Sc   R   MA

r–cu₁

Cu₁

MP

(22)

Cu₁
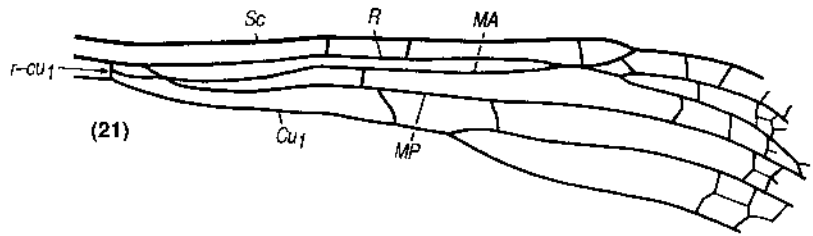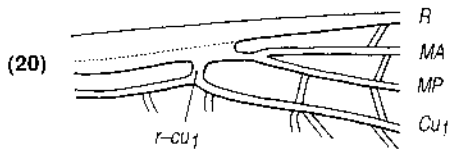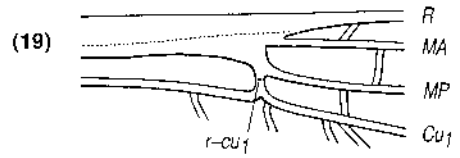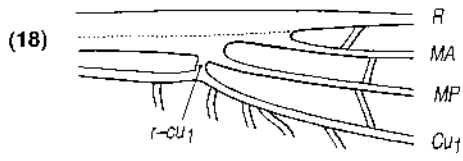
Fig. 18–22 Variation in hind wing venation, female (x8).

(23)

(24)

(25)

R

R_S

MA

(26)

(27)

(28)

(29)

(30)

(31)

(32)
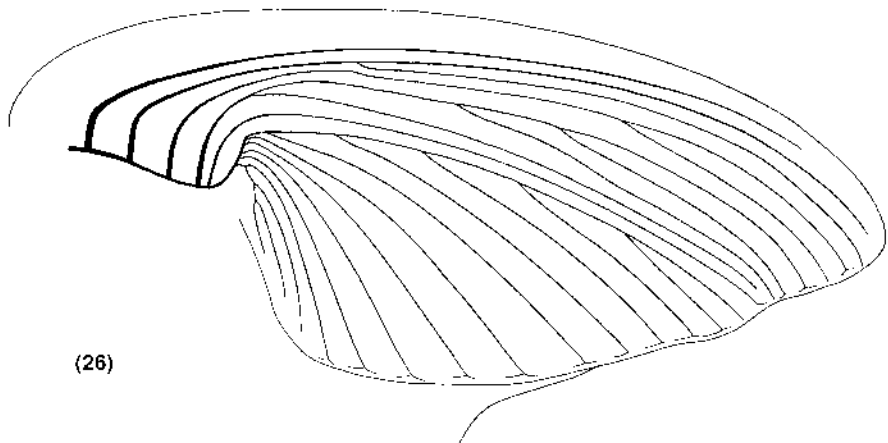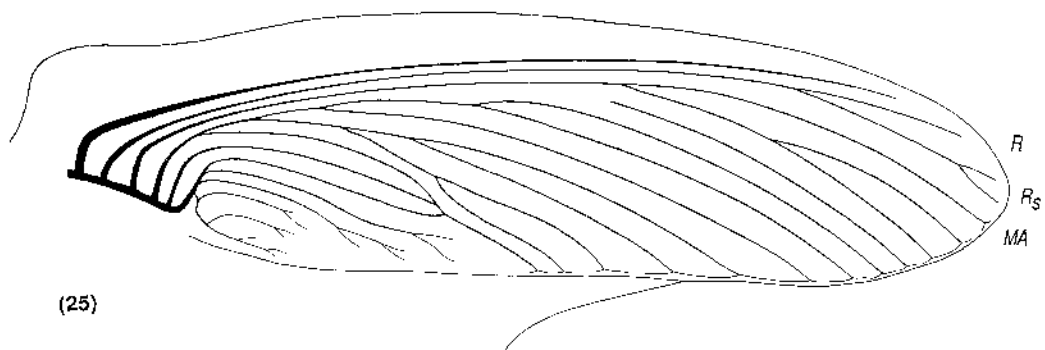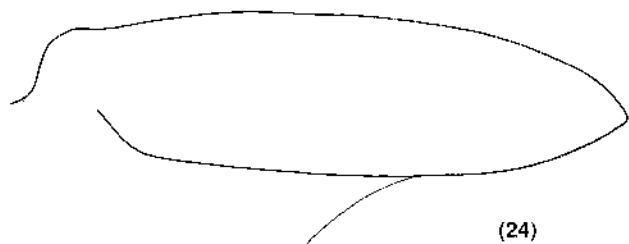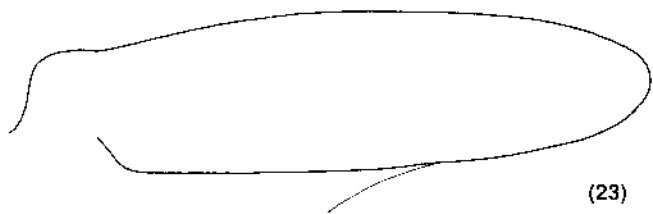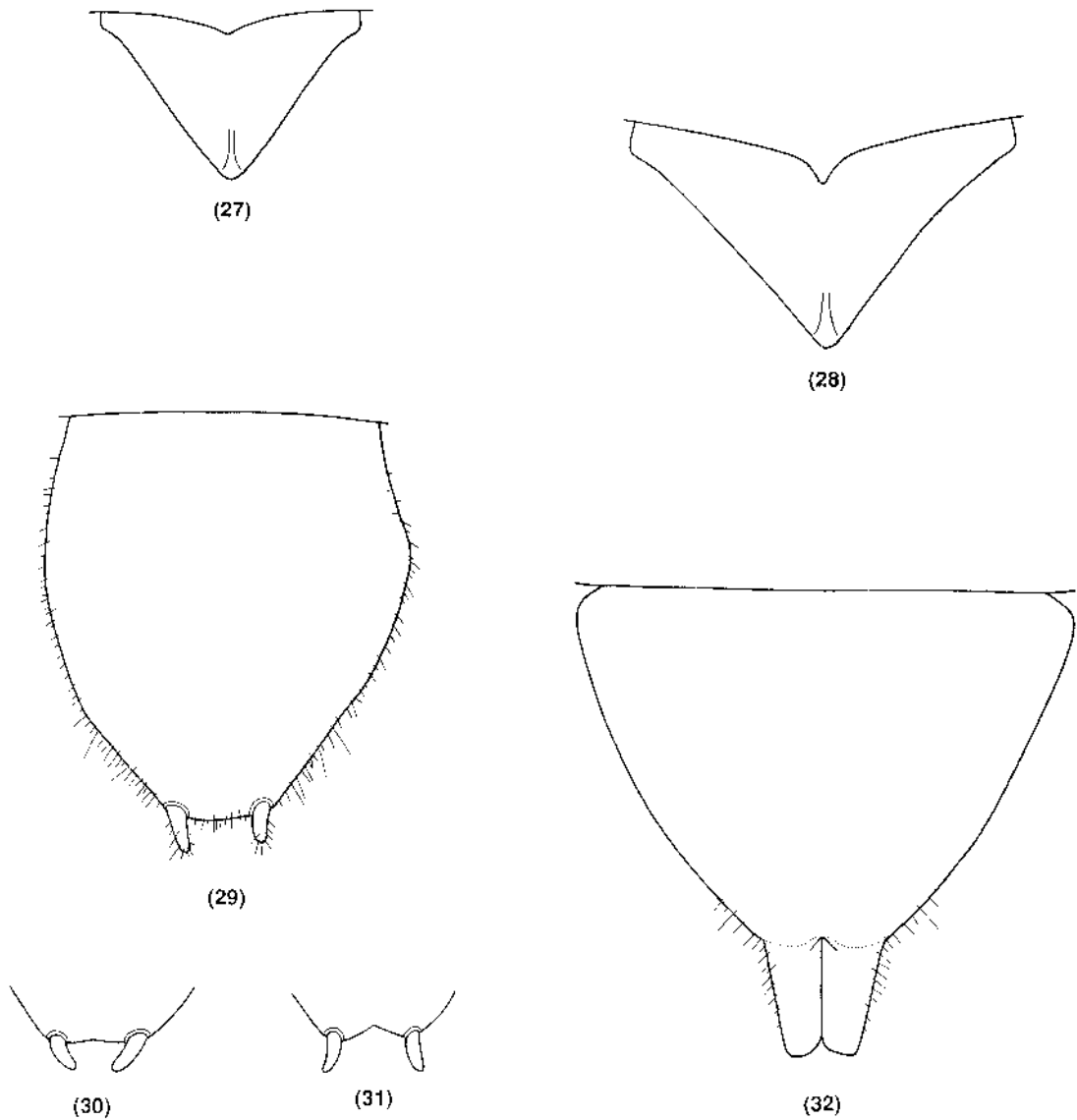
Fig. 23 and 24 Forewing pad, 6th instar, male and female (x18).
Fig. 25 and 26 Tracheation, fore and hind wing pad, 6th instar, male (x20).
Fig. 27 and 28 Suranal plate, dorsal, male and female (x20).   **Fig. 29–32** Subgenital plate, ventral, male (with variants of terminalia) and female (x20).

(33)

(34)

pseudophallus

titillator

(36)

(37)

apophysis

(35)

(38)

—76—
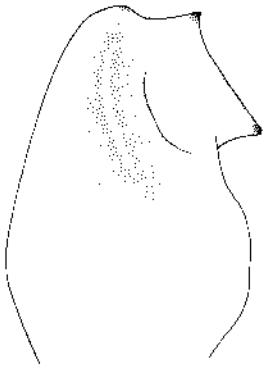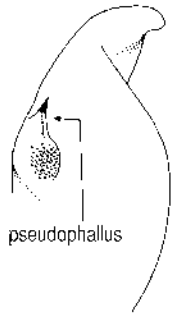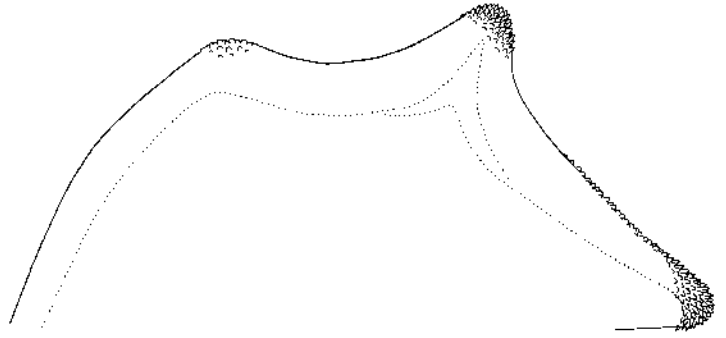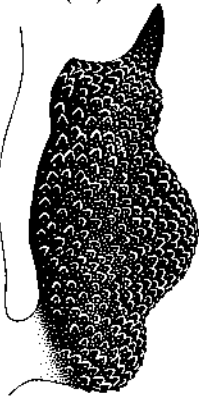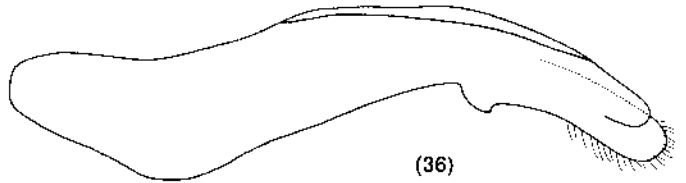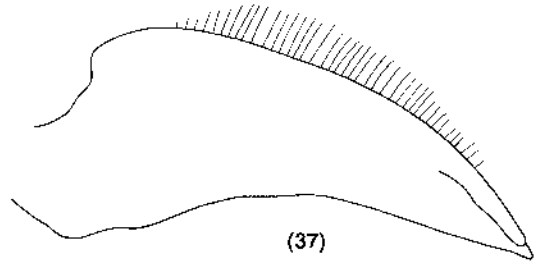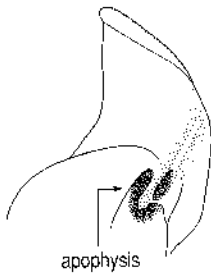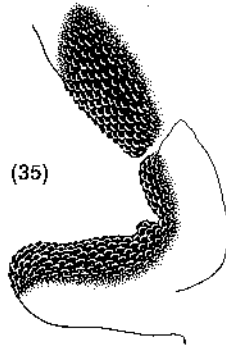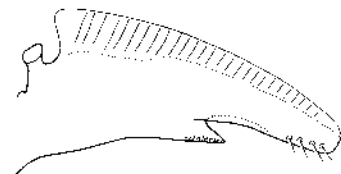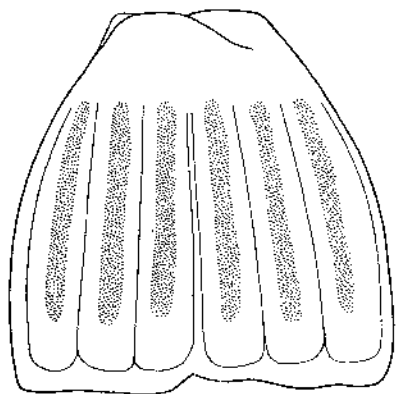
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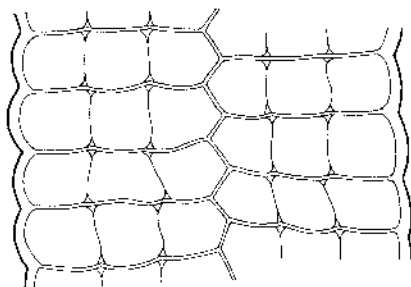
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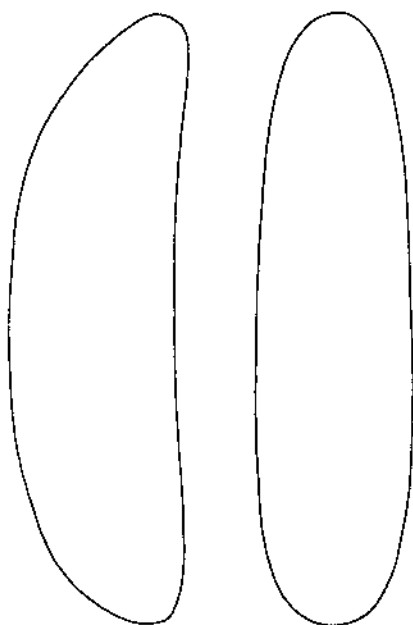
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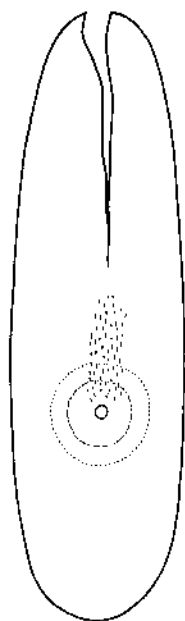
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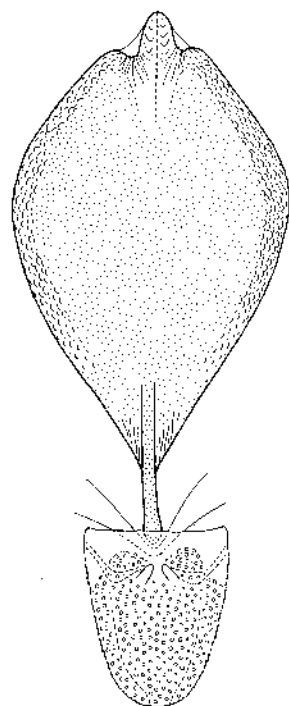
(43)

Fig. 33–35 Male genitalia: (33) hypophallus, ventral (x20), and detail of apical area (x65); (34) left epiphallus, dorsal / ventral (x20), and detail of pseudophallus (x65); (35) right epiphallus, dorsal (x20), and detail of apophysis (x65). **Fig. 36–38** Ovipositor, inner aspect: ventral, dorsal, and medial valve (x20). **Fig. 39 and 40** Ootheca, vertical and transverse section (x8). **Fig. 41 and 42** Egg, before and after hatching (x20). **Fig. 43** Embryo, cephalic plate (x65).

(44)

(47)

(48)

(45)

(49)

(46)
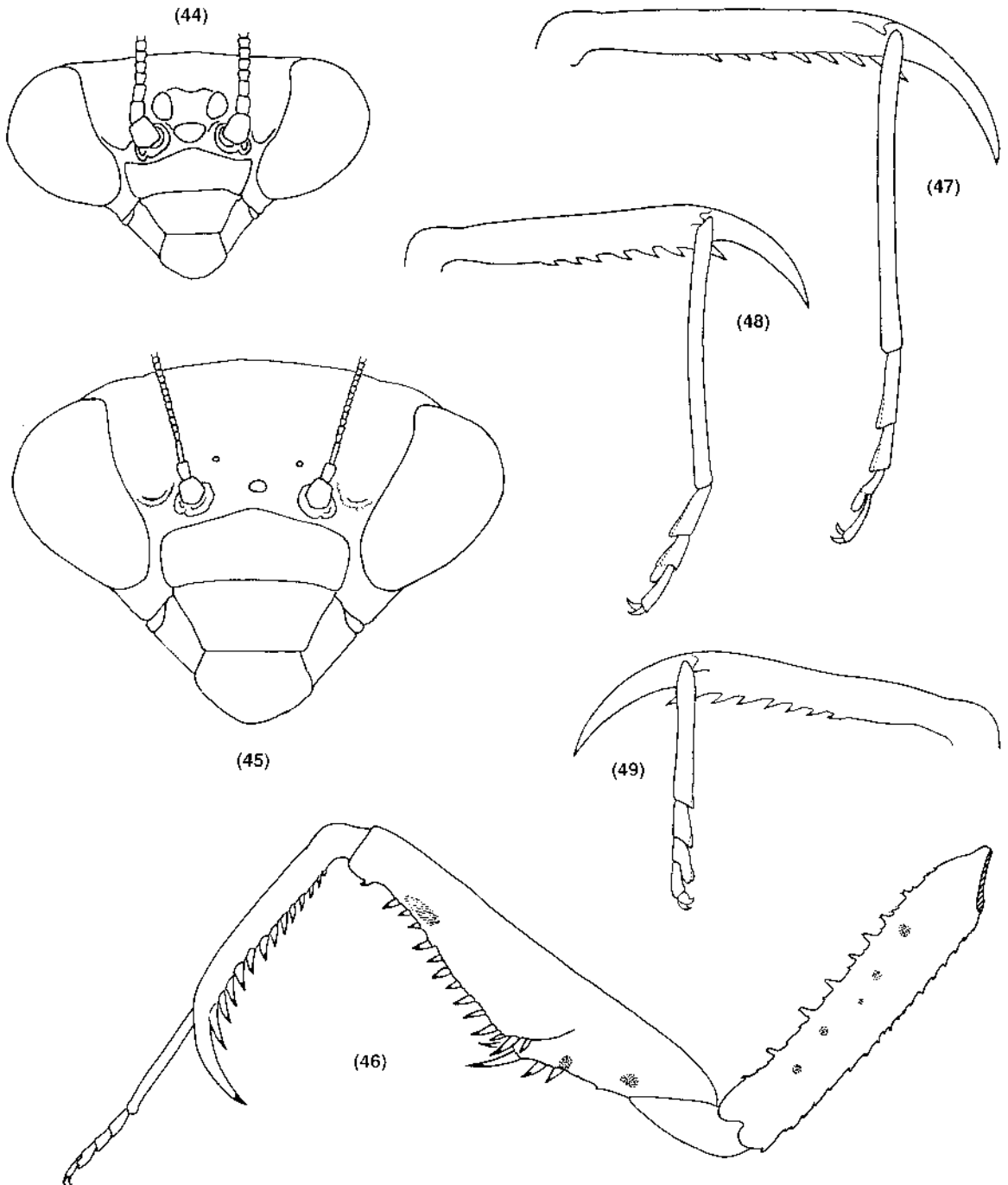
Figures 44–80 Morphological features of life stages of *Miomantis caffra*.

(50)

(51)

C

Sc

R₁

R_s

MA

MP

1V   *Cu₂*   *Cu₁ᵦ*   *Cu₁ₐ*

r–cu₁

(52)
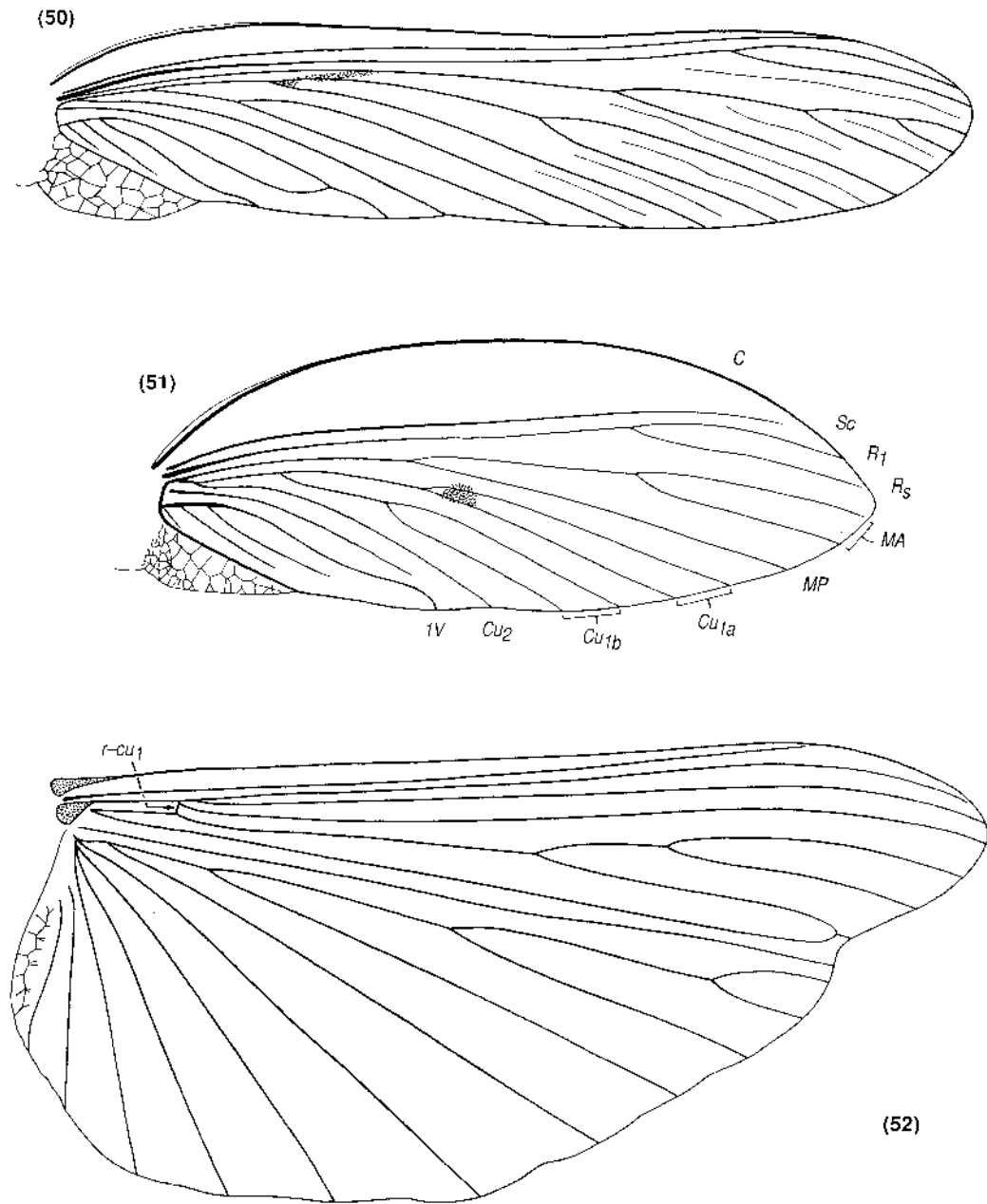
Fig. 44 and 45 Head, frontal, male and female (x10).   **Fig. 46** Foreleg, female, inner aspect (x4.8).
Fig. 47–49 Fore tibia + tarsus, male: (47) normal; (48, 49) regenerated, variants (x12).
Fig. 50 and 51 Forewing, male and female (x4.8).   **Fig. 52** Hind wing, male (x4.8).

(53)

R

MA

(54)

Sc

R

MA

MP

(55)

(56)

r–cu₁

r–cu₁

(57)

R

MA

MP

r–cu₁

Cu₁

(58)

Sc

R

M

Cu₁

Cu₂

Pcu

(59)

a

b

Cu₁

M₁

R

MA

MP

Cu₁

Cu₂

(60)

R

MA

MP

Cu₁

Cu₂

(61)
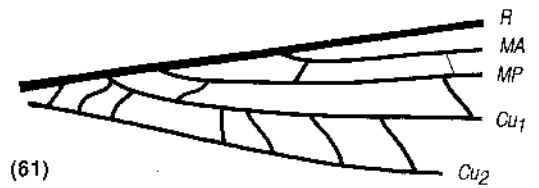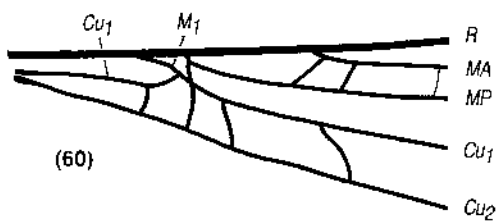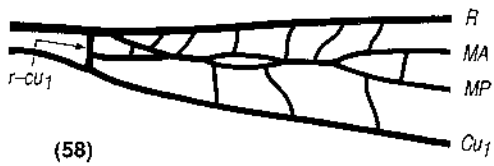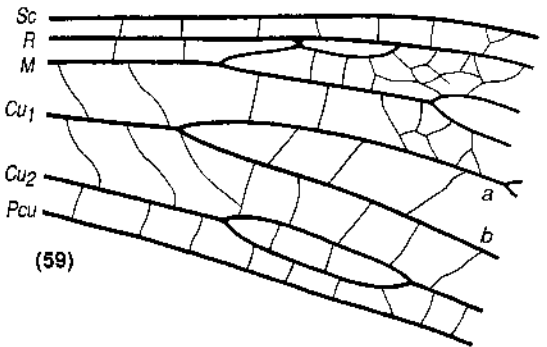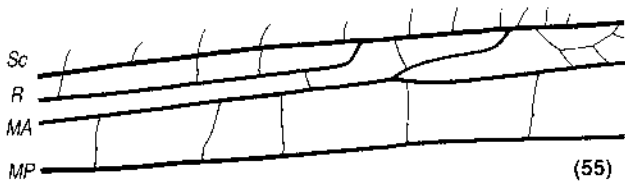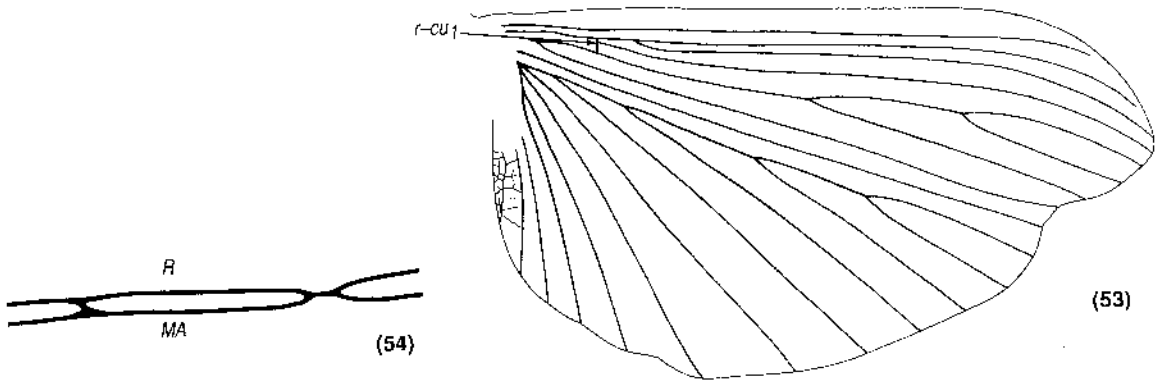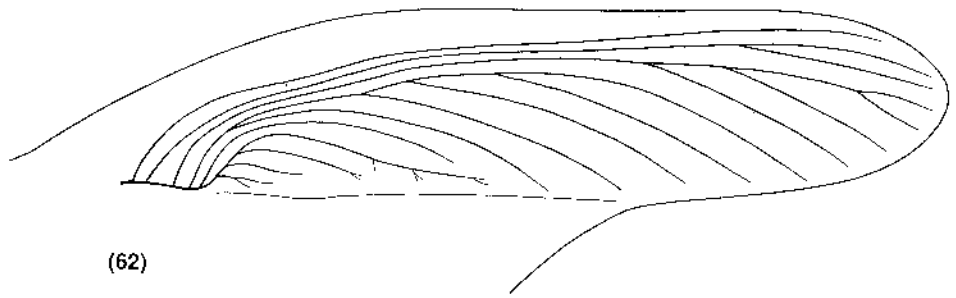
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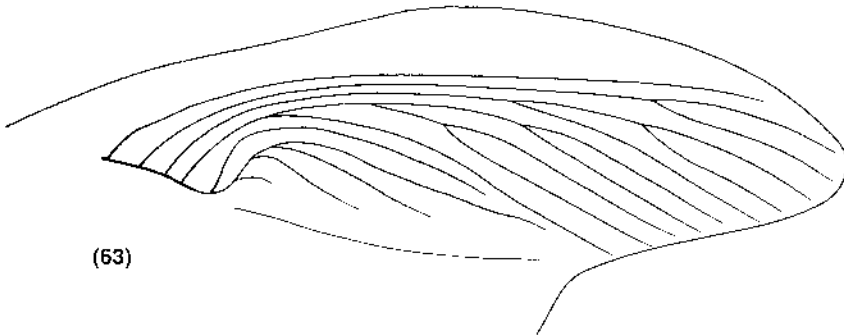
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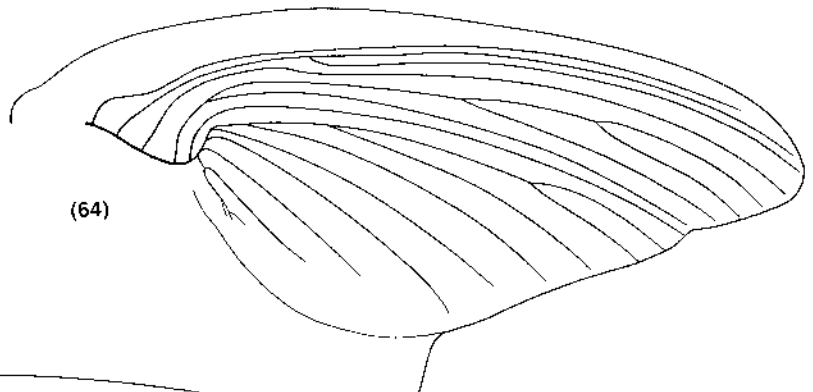
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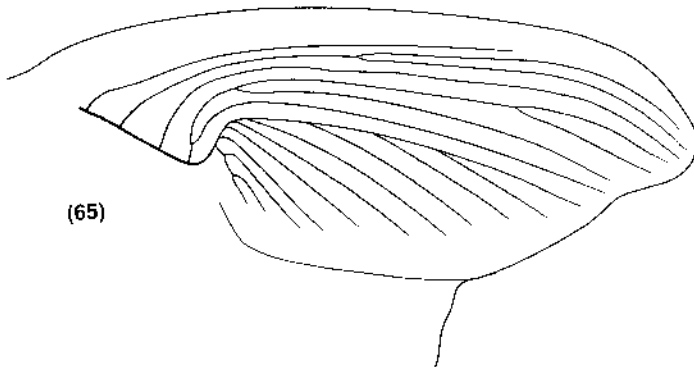
(65)

Fig. 53 Hind wing, female (x4.8).
Fig. 54–61 Variation in forewing venation,
female (x12).
Fig. 62–65 Tracheation of wing pads, 6th
instar: (62, 63) forewing, male and female;
(64, 65) hind wing, male and female (x20).

(67)

(69)

(66)

(68)

(70)
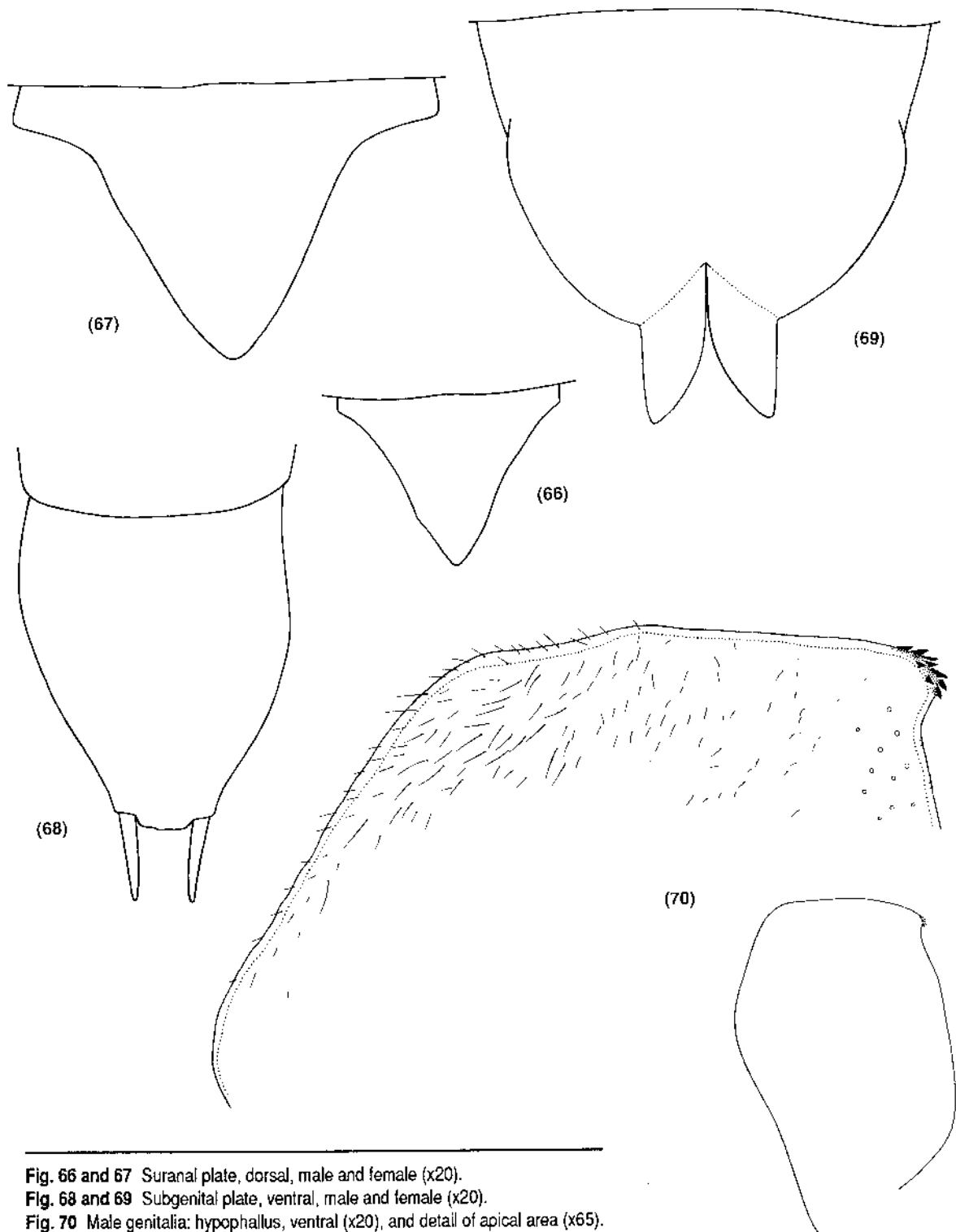
Fig. 66 and 67 Suranal plate, dorsal, male and female (x20).
Fig. 68 and 69 Subgenital plate, ventral, male and female (x20).
Fig. 70 Male genitalia: hypophallus, ventral (x20), and detail of apical area (x65).
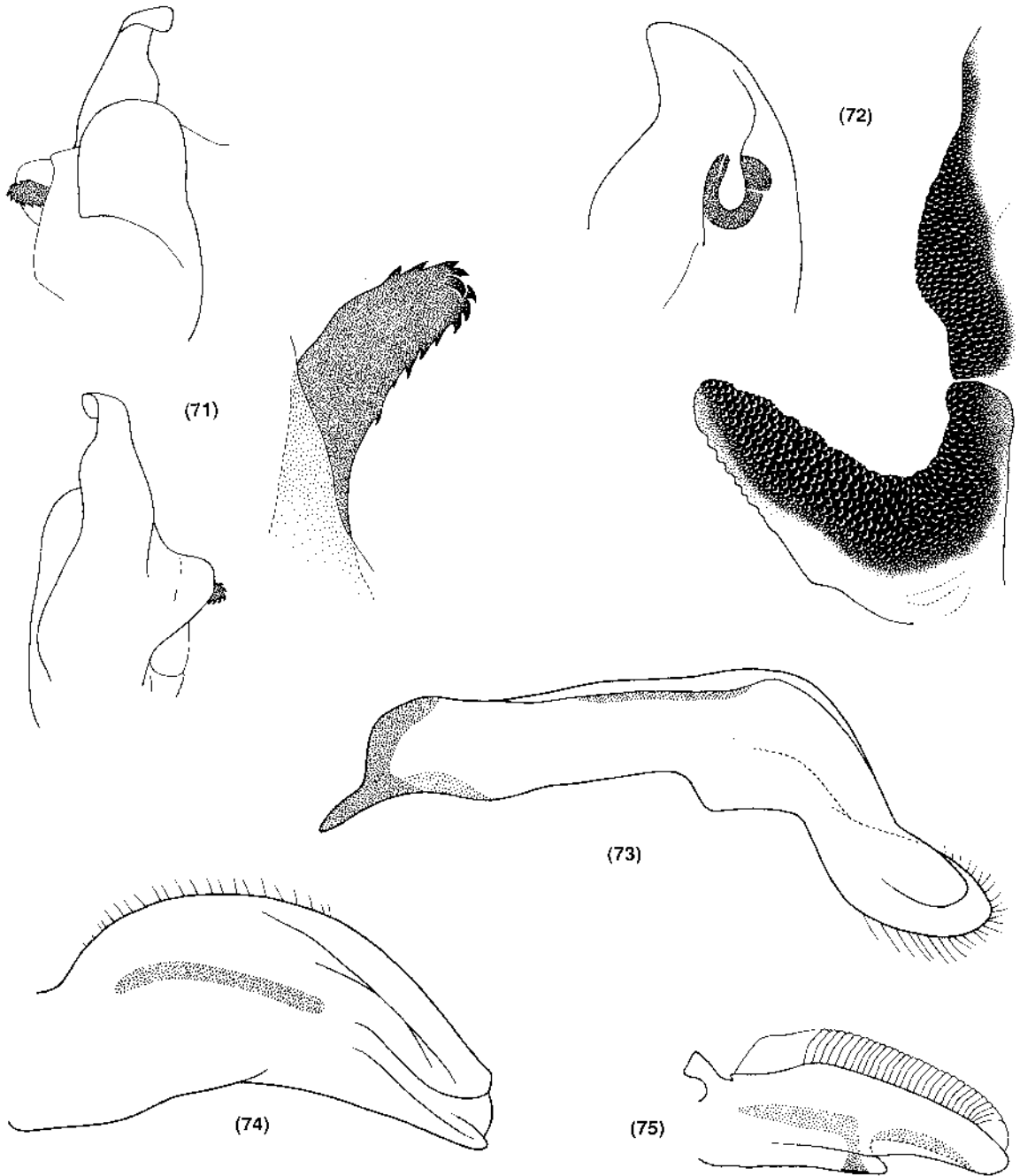
Fig. 71 and 72 Male genitalia: (71) left epiphallus, dorsal / ventral (x20), and detail of pseudophallus (x65); (72) right epiphallus, dorsal (x20), and detail of apophysis (x65).
Fig. 73–75 Ovipositor, inner aspect: ventral, dorsal, and medial valve (x20).

(76)

(77)

(78)

(79)

(80)
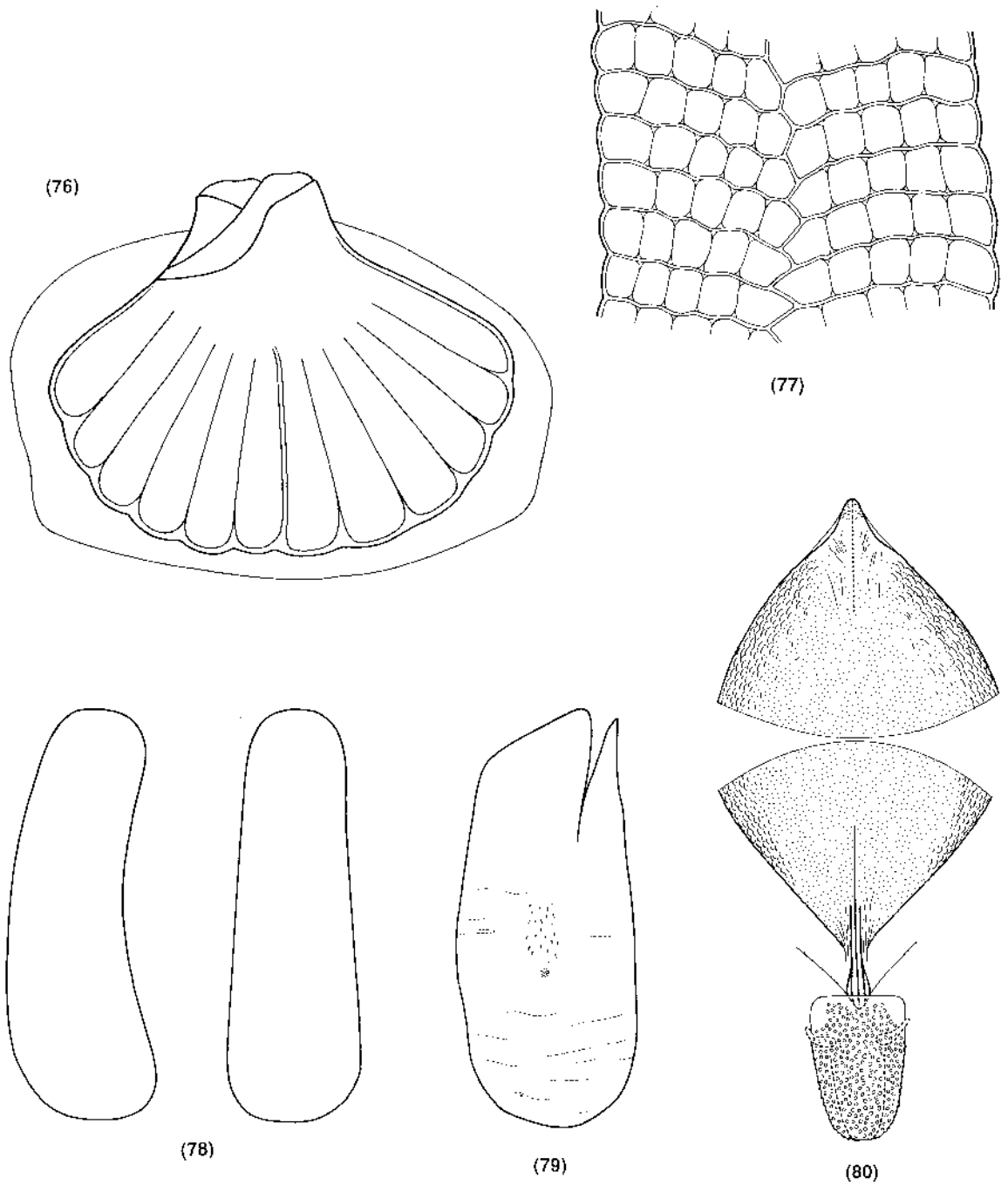
Fig. 76 and 77 Ootheca, vertical and transverse section (x8). **Fig. 78 and 79** Egg, before and after hatching (x20).
Fig. 80 Embryo, cephalic plate (x65).
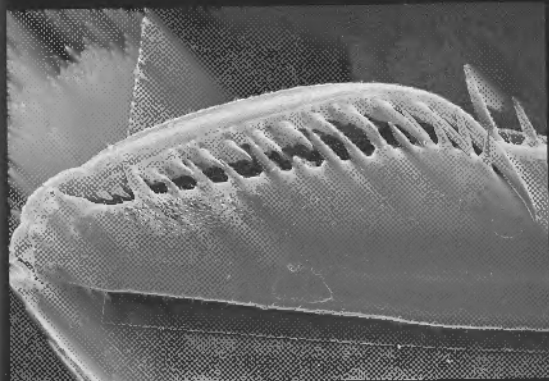
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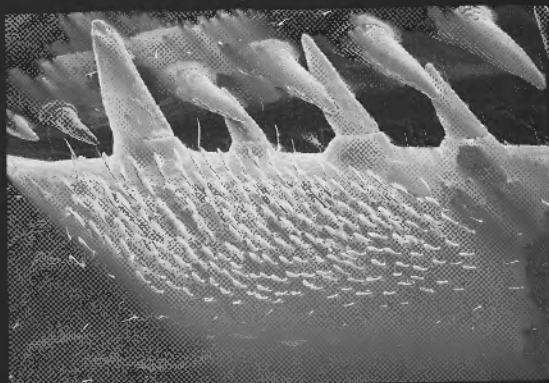
(M2)

Figures M1–5 Features of femoral brush.
M1–3 *Orthodera novaezealandiae*, female: inner surface of fore femur, showing (M1) position of brush, (M2) setal arrangement, and (M3) setal structure.
M4, 5 *Miomantis caffra*, male, setal structure.

(M3)

(M4)

(M5)

(M6)

(M7)

(M8)
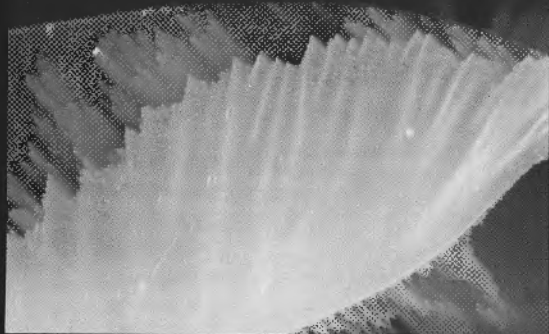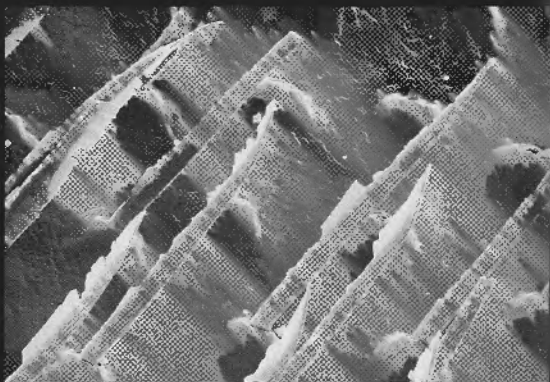
Figures M6–10 Features of femoral brush setae.
M6, 7 *O. novaezealandiae*: (M6) male, ribbing on blade;
(M7) female, moulting pore and setal insertion.
M8–10 Progressive wear in blade: (M8,9) *O. novaezea-landiae*, female, male; (M10) *M.caffra*, female.

(M9)

(M10)

(M11)
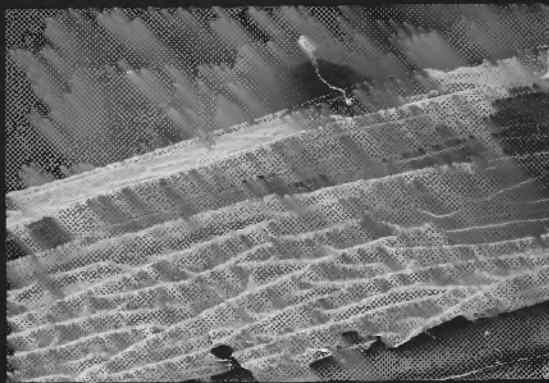
(M12)

Figures M11–15 Forewing, *O. novaezealandiae*.
M11, 12 Pterostigma, female and male.
M13 Reticulate pattern on cubital vein, female.
M14, 15 Male, surface detail of pterostigma.

(M13)

(M14)
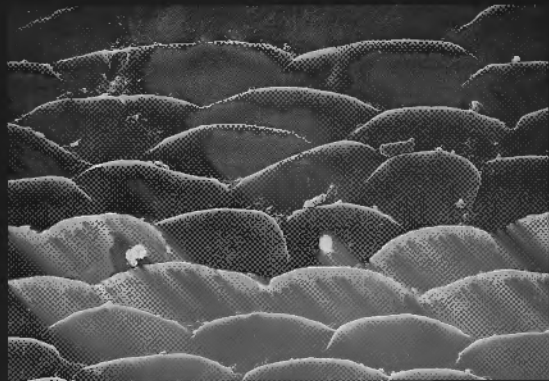
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(M16)
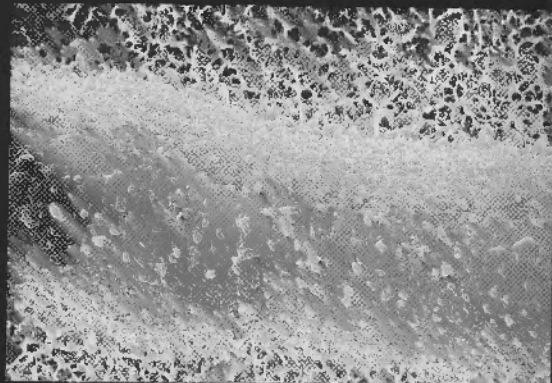
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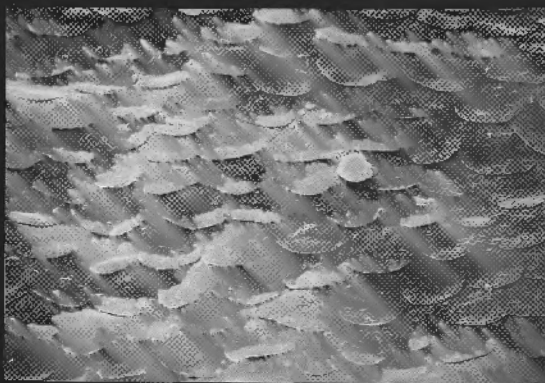
(M18)

Figures M16–20 Forewing, *M. caffra*, female.
M16 Pterostigma.
M17 Vein, showing 'waxy' coating.
M18, 19 Pterostigma, surface detail.
M20 Detail of pterostigma border.

(M19)

(M20)
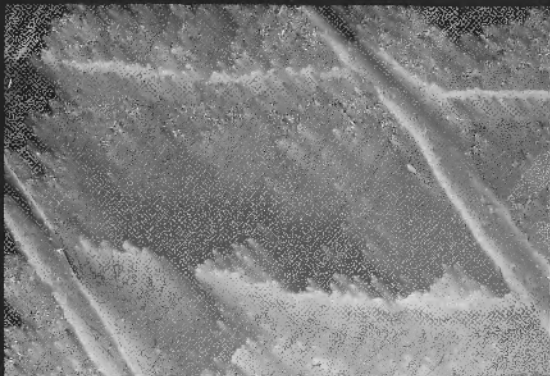
(M21)

(M22)

Figures M21–25 Forewing, *M. caffra.*
M21, 22 Female, showing 'waxy' surface, and structure in costal region.
M23–25 Male, pterostigma and surface structures.

(M23)

(M24)

(M25)

(M26)

(M27)

(M28)
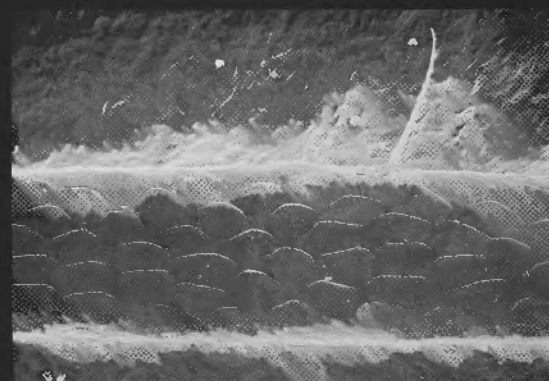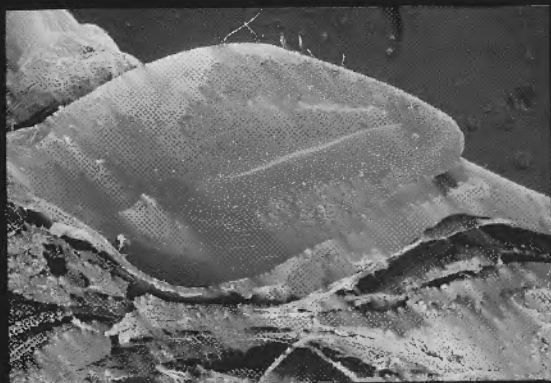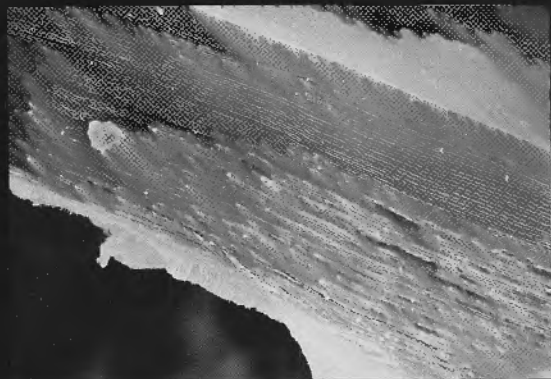
Figures M26–30 Cyclopean ear, *O. novaezealandiae*.
M26 Longitudinal groove, ventral, male.
M27 Detail of 'lips' of groove, male.
M28 Medial face of lobe, female.
M29 Laminate integument of floor of groove, male.
M30 Surface detail of lobe, medial face, female.

(M29)

(M30)
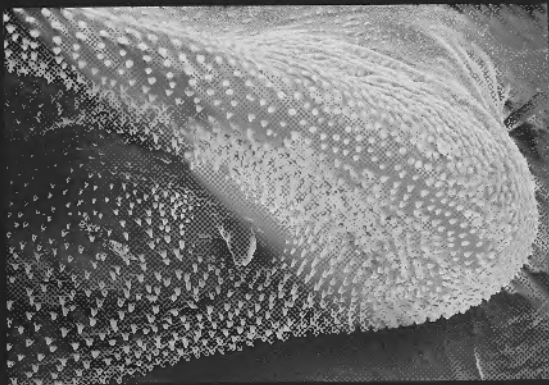
(M31)

(M32)

Figures M31–35 Cyclopean ear.
M31, 32 *O. novaezealandiae*, 'horn' at focal point on medial face of lobe, male and female.
M33–35 *M. caffra*, male: longitudinal groove, detail of 'lips' of groove, and medial face of lobe.
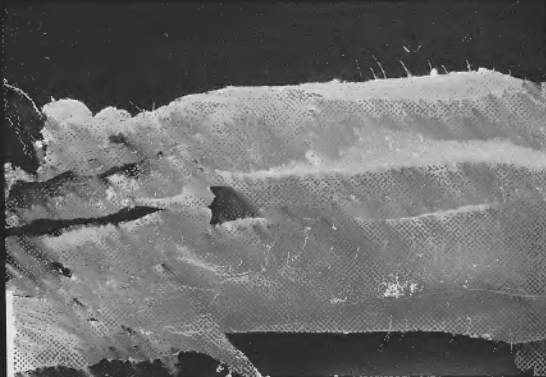
(M33)
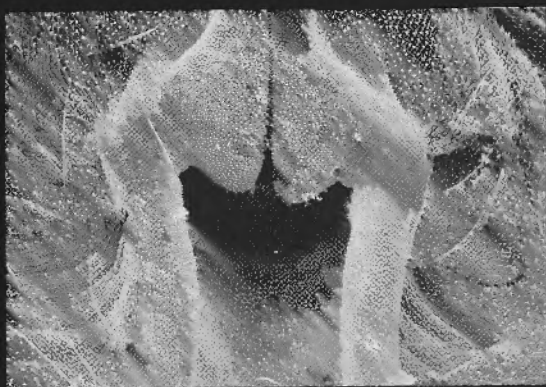
(M34)

(M35)

(M36)
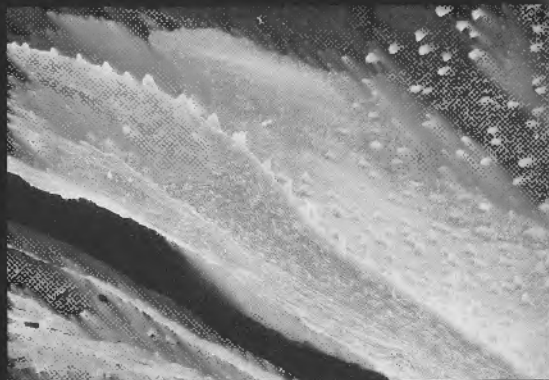
(M37)
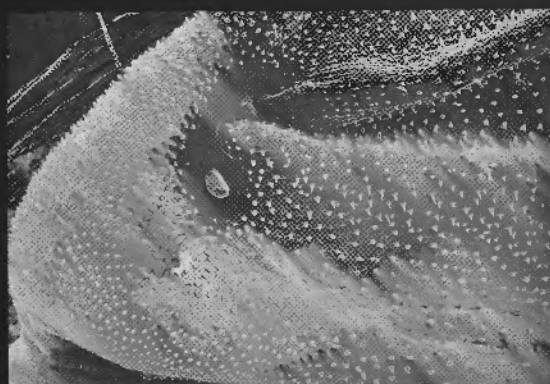
(M38)

Figures M36–40 Cyclopean ear, *M. caffra*.
M36 Lobes, ventral, male.
M37 Laminate integument of floor of groove, male.
M38, 39 'Horn' at focal point on medial face of lobe, male.
M40 Longitudinal groove, ventral, female.

(M39)

(M40)
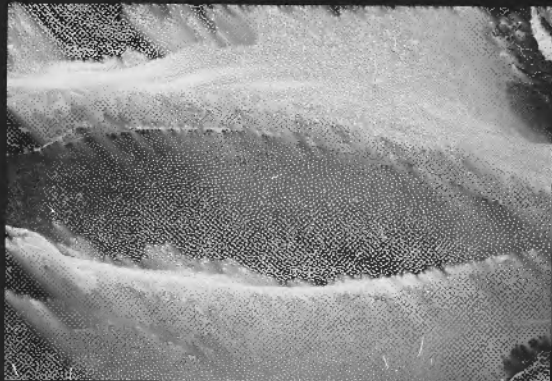
(M41)

(M42)

Figures M41–45 Cyclopean ear, *M. caffra*, female.
M41 Longitudinal groove, ventral.
M42 Medial face of lobe.
M43 Lobes, ventral.
M44 Laminate integument of floor of groove.
M45 'Horn' at focal point on medial face of lobe.

(M43)

(M44)

(M45)

TAXONOMIC INDEX

TAXON :

ALTITUDINAL
DISTRIBUTION

(MSL, mean sea level)
The range of altitude
for each scale division
may be set according
to need, but should be
in metric units.

OFFSHORE
ISLANDS

Kermadecs ☐
Three Kings ☐
Chathams ☐
Snares ☐
Bounty ☐
Antipodes ☐
Aucklands ☐
Campbell ☐

This proforma data sheet
may be photocopied as
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waived. Use the back
for data such as host
records.
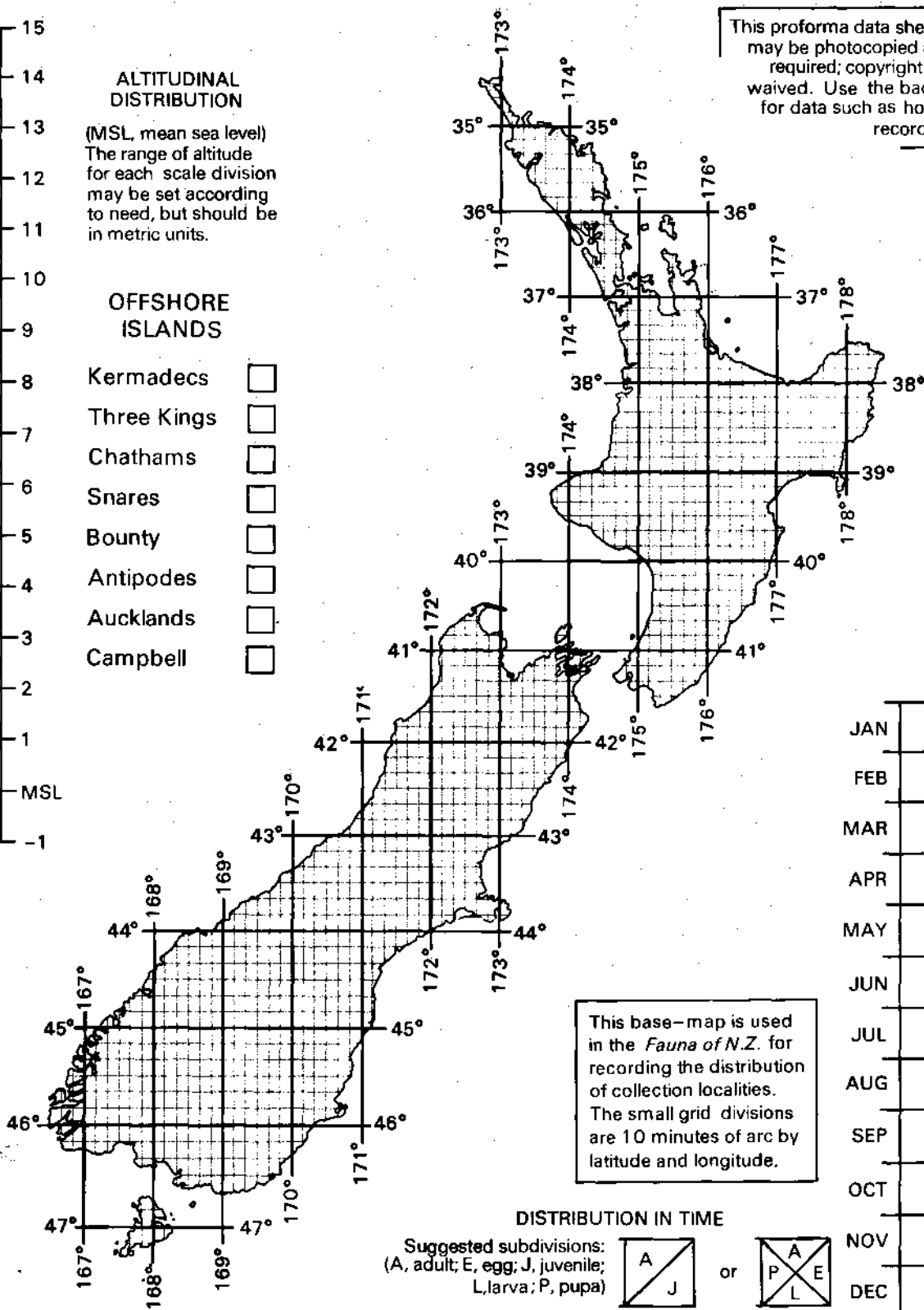
This base−map is used
in the *Fauna of N.Z.* for
recording the distribution
of collection localities.
The small grid divisions
are 10 minutes of arc by
latitude and longitude.

JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC

DISTRIBUTION IN TIME
Suggested subdivisions:
(A, adult; E, egg; J, juvenile;
L, larva; P, pupa)

A / J   or   A P × E L
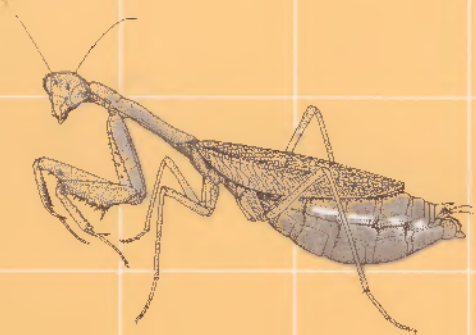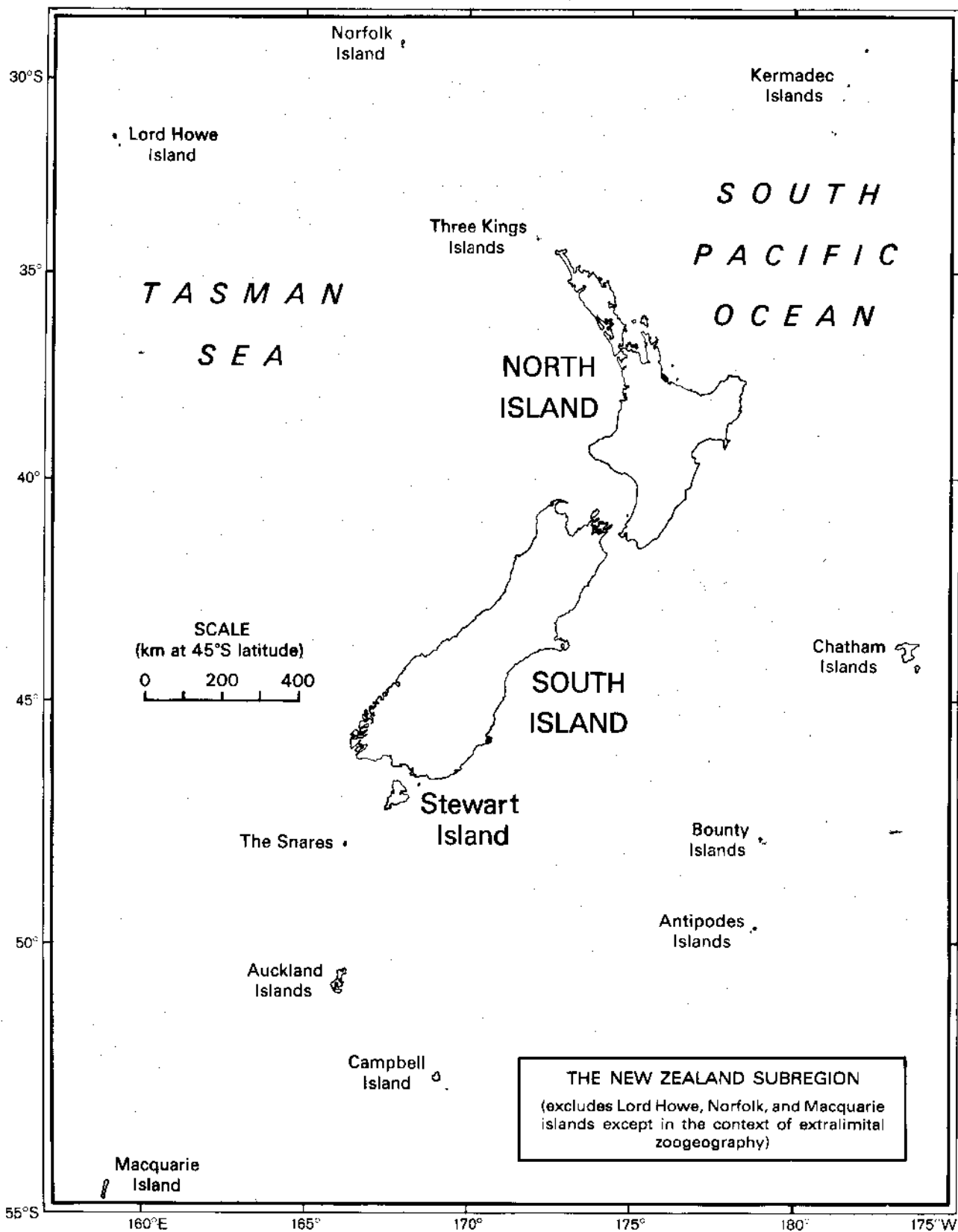
Fauna of New Zealand

Number 19

Mantodea (Insecta)

with a review of
aspects of functional
morphology and biology

G. W. Ramsay

30°S

Norfolk
Island

Kermadec
Islands

Lord Howe
island

S O U T H

P A C I F I C

35°

Three Kings
Islands

O C E A N

T A S M A N

NORTH

S E A

ISLAND

40°

SCALE
(km at 45°S latitude)

0   200   400

Chatham
Islands

45°

SOUTH

ISLAND

Stewart
Island

The Snares

Bounty
Islands

Antipodes
Islands

50°

Auckland
Islands

Campbell
Island

THE NEW ZEALAND SUBREGION

(excludes Lord Howe, Norfolk, and Macquarie
islands except in the context of extralimital
zoogeography)

Macquarie
Island

55°S

160°E   165°   170°   175°   180°   175°W

AK – Auckland

BP – Bay of Plenty

CL – Coromandel

GB – Gisborne

HB – Hawke's Bay

ND – Northland

RI – Rangitikei

TK – Taranaki

TO – Taupo

WA – Wairarapa

WI – Wanganui

WN – Wellington

WO – Waikato

BR – Buller

CO – Central Otago

DN – Dunedin

FD – Fiordland

KA – Kaikoura

MB – Marlborough

MC – Mid Canterbury

MK – Mackenzie

NC – North Canterbury

NN – Nelson

OL – Otago Lakes

SC – South Canterbury

SD – Marlborough Sounds

SL – Southland

WD – Westland

SI – Stewart Island
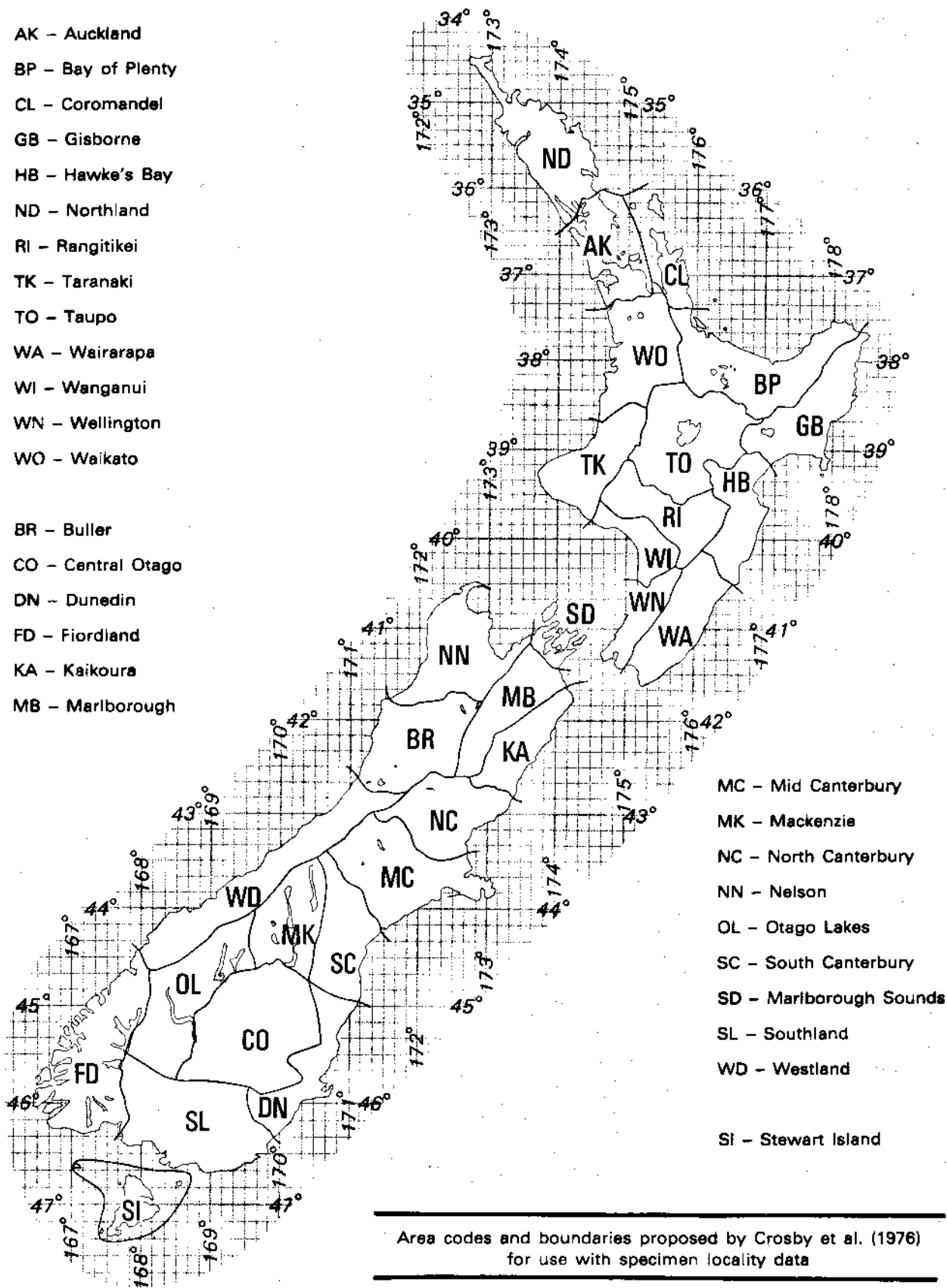
Area codes and boundaries proposed by Crosby et al. (1976)
for use with specimen locality data

Fauna of New Zealand

This series of refereed occasional publications has been established with two major objectives: to encourage those with expert knowledge of elements in the New Zealand fauna to publish concise yet comprehensive accounts; and to provide a means of identification accessible to the non-specialist. It will deal with non-marine invertebrates only, since the vertebrates are well documented, and marine forms are covered by the series 'Marine Fauna of New Zealand'.

Contributors should discuss their intentions with an appropriate member of the Fauna Advisory Group or with the Series Editor before commencing work (for names and addresses, see page ii). All necessary guidance will be given.

Persons wishing to receive issues of the 'Fauna' should address inquiries to the Publications Officer, DSIR Publishing, P.O. Box 9741, Wellington, New Zealand, who will maintain standing orders in three categories, as follows. 'A' – an invoice will be sent for each number, as soon after publication as possible. 'B' – essentially as for 'A', but invoices will be sent only for those numbers in a nominated field of interest (e.g., beetles only, mites only). 'C' – updated catalogues and order forms will be sent from time to time.

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CHECKLIST OF TAXA

INTRODUCTION

DESCRIPTIONS

REVIEW SECTIONS

ILLUSTRATIONS

IN PRINT

No. 1 Terebrantia (Insecta: Thysanoptera), by Laurence A. Mound & Annette K. Walker. Published 23 December 1982. 120 p. Price $29.95.*

No. 2 Osoriinae (Insecta: Coleoptera: Staphylinidae), by H. Pauline McColl. Published 23 December 1982. Second impression May 1983. 96 p. Price $18.60.*

No. 3 Anthribidae (Insecta: Coleoptera), by B. A. Holloway. Published 23 December 1982. Second impression February 1985. 272 p. Price $41.00.*

No. 4 Eriophyoidea except Eriophyinae (Arachnida: Acari), by D. C. M. Manson. Published 12 November 1984. 144 p. Price $29.95.*

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No. 12 Pompilidae (Insecta: Hymenoptera), by A. C. Harris. Published 13 November 1987. 160 p. Price $39.95.*

No. 13 Encyrtidae (Insecta: Hymenoptera), by J. S. Noyes. Published 9 May 1988. 192 p. Price $44.95.*

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No. 18 Chalcidoidea (Insecta: Hymenoptera) – introduction, and review of smaller families, by J. S. Noyes & E. W. Valentine. Published 2 August 1989. 96 p. Price $24.95.*

No. 19 Mantodea (Insecta), with a review of aspects of functional morphology and biology, by G. W. Ramsay. 96 p. Publication date and price to be announced.