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Review of the carrion beetles of Australia and New Guinea (Coleoptera: Silphidae)

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Abstract Keys, distribution maps and bionomic summaries are given for the five described species of large carrion beetles (Silphidae) known from Australia and the island of New Guinea. The genera *Nicrophorus* Fabricius and *Diamesus* Hope entered Australasia from the north. The Australasian genus *Ptomaphila* Kirby and Spence has three species and these show a southern or trans-Antarctic sister-group relationship to *Oxelytrum* Gistel of the Neotropical Region. The Australian species are mostly distributed in forest or scrub habitat within 300 km from the coastline. A phylogeny of *Ptomaphila* indicates that *P. ovata* Portevin of New Guinea is most plesiotypic, that *P. perlata* Kraatz of eastern Australia is intermediate, and that *P. lacrymosa* (Schreibers) of southern Australia is most apotypic.

Key words biogeography, bionomics, phylogeny, taxonomy.

INTRODUCTION

The world fauna of Silphidae, commonly known as the large carrion beetles, is composed of approximately 175 species in 15 genera. The family is predominantly Holarctic in distribution and abundance, with a total of five species in three genera being known from Australia and the island of New Guinea. The world fauna of Silphidae was last reviewed by Portevin (1926), and the Australian fauna by Lawrence and Britton (1994). No species in the Australasian fauna has had its natural history studied in detail.

I have had the opportunity to undertake five extensive periods of field work to sample the scavenging beetles of Australia and New Guinea and to study collections of them in the major museums in these and other countries. The purpose of the present paper is to summarise the distribution and bionomics of the species of Silphidae of Australia and New Guinea, to reconstruct the phylogeny of the genus *Ptomaphila* Kirby and Spence, and to stimulate additional investigations on their field biology and natural history.

All species in Australia are mostly collected less than 300 km from the coastline. Presumably the dryness of the continental interior limits their distribution in this direction.

Silphids are not known to occur on the major Pacific islands of New Zealand, Fiji, and New Caledonia and my field work in these places did not find them. One species of *Ptomaphila* does occur on Lord Howe Island (see following). *Zeanecrophilus* Newton, with two species in New Zealand (reported as *Necrophilus* Latreille in older literature), has been previously considered to belong to the family Silphidae but is now placed in the family Agyrtidae, and is more closely allied with the family Leiodidae than to the Silphidae (Newton 1997). Some species remain to be described from islands in the Indo-Malesian Archipelago, and this will be done by Derek Sikes.

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MATERIALS AND METHODS

Material was borrowed from or studied in all large Australian museums and several other foreign collections of Australian insects. Information on historical collectors and collections of Australian insects is in Musgrave (1932). The collections and the curators who allowed study of the collections under their care are: AMSA, The Australian Museum, Sydney, C.N. Smithers; ANIC, Australian National Insect Collection, CSIRO, Canberra, J.F. Lawrence; BMNH, The Natural History Museum, London, England, M. Bacchus; BPBM, Bernice P Bishop Museum, Honolulu, Hawaii, USA, G.A. Samuelson; CMNC, Canadian Museum of Nature, Aylmer, Quebec, Canada, R.S. Anderson; CNCI, Canadian National Collection of Insects, Agriculture Canada, Ottawa, Ontario, Canada, A. Smetana; FMNH, Division of Insects, Field Museum, Chicago, Illinois, USA, A.F. Newton and M.K. Thayer; MNHN, National Collection of Insects, Museum National d'Histoire Naturelle, Paris, France, N. Berti; MVMA, Museum Victoria, Melbourne, A. Neboiss; NTMA, Northern Territory Science Museum and Art Gallery, Darwin, Northern Territory, G. Brown; QMBA, Queensland Museum, Brisbane, G. Monteith; SAMA, South Australian Museum, Adelaide, E.G. Matthews; TPNG, Central Reference Insect Collection, Department of Primary Industry, Konedobu NCD, Papua New Guinea, J. Stibbick; UQBA, Department of Entomology, University of Queensland, Brisbane, G. Monteith; WAMP, Western Australia Museum, Perth, T. Houston.

In my field work, I collected extensively at roadside carrion and with carrion-baited pitfall traps in both closed and open canopy forests. This was generally within 200 km

of the eastern coastline from Cooktown, Queensland, through to Melbourne, Victoria; from Perth to Albany in Western Australia; and in the Darwin and Kakadu National Park areas of the Northern Territory. Most of my specimens are in CMNC, ANIC, or the author's collection. Additional material has been contributed to the study by: Olga Kukal, Halifax, Nova Scotia, Canada; A.F. Newton and Margaret Thayer, now of the Field Museum, Chicago, Illinois, USA; and Henry and Anne Howden, Ottawa, Ontario, Canada.

Full specimen label data are not reported here but are available from the author. The available label data have been summarised into generalisations about the geographical and elevational distribution of the species, the ways they have been collected, the seasonality of adult activity, and apparent habitat associations.

A phylogenetic analysis of the three species of *Ptomaphila* was by standard methods of outgroup comparison. Data on characters of the female genitalia were from direct observation and illustrations in Arnett (1944). The data set was analysed by McClade 3.1 (Maddison & Maddison 1992).

RESULTS

Key to subfamilies of Australasian Silphidae

1 Antenna seemingly of 10 segments, second antennal segment small, indistinct, hidden in tip of first antennal segment; epistomal suture present; elytra without raised longitudinal carinae or tubercles; elytra usually with irregular red or orange spots, elytra short, truncate, exposing 3 or 4 abdominal tergites; fifth abdominal tergite with stridulatory files on dorsum ..... Subfamily Nicrophorinae

– Antenna clearly of 11 segments, second antennal segment large, distinct, not hidden in tip of first antennal segment; epistomal suture absent; elytra with raised longitudinal carinae or tubercules; elytra with or without coloured areas, elytra long, usually not truncate (but short and exposing 3–4 abdominal tergites in *Diamesus*); fifth abdominal tergite lacking stridulatory files ..... Subfamily Silphinae

Subfamily Nicrophorinae

The subfamily contains the Asian genera *Eonecrophorus* Kurosawa and *Ptomascopus* Kraatz, and the widely distributed genus *Nicrophorus* Fabricius. Only *Nicrophorus* occurs in the Australasian region.

Nicrophorus Fabricius 1775

Nicrophorus, with approximately 82 species worldwide, is mostly north temperate and Holarctic in distribution. One or more lineages have followed the highlands of Mexico and Central America southward into the Andes Mountains of South America and speciated there (Anderson & Peck 1985), and one species occurs in the mountains of Algeria in Africa. At least one lineage has crossed Wallace's Line and speciated in the islands of the Indo-Malesian archipelago (Table l). Only *N. heurni* Portevin occurs on the large island of New Guinea proper, but *N. kieticus* Mroczowski occurs on the island of Bougainville, which is politically a part of Papua New Guinea. There are no new data on the latter species. There is no evidence that the genus has ever crossed the climatic dry zone bordering Torres Strait (Walker 1972) from New Guinea onto the Australian continent.

Nicrophorus heurni Portevin (Figs 2,10)

Nicrophorus heurni Portevin 1926: 211.

Type locality. North-west New Guinea, Doormanpad Camp, headwaters of the Mamberamo River, 1410 m elevation. Type specimen seen; in MNHN. Paratypes are in Berlin and MNHN.

Distribution. Upland forests of the island of New Guinea, in both Irian Jaya and Papua New Guinea halves (Fig. 10).

Bionomics. I have seen 206 specimens. Their label data indicate that adults have been collected at elevations from 480 m to 2750 m. Collections are from all months of the year and are from carrion or human-dung baited pitfall traps or from mercury-vapour and ultraviolet light traps. Habitat data are few but all collections seem to come from lower and upper elevation montane rainforest.

Table 1 List of Indo-Malesian species of *Nicrophorus**

Species	Distribution
N. nepalensis Hope 1831	South-east Asia, Indonesia (Sumatra, Java, Borneo, Flores), northern Philippines (Luzon, Palawan) (Mroczkowski 1966)
N. distinctus Grouvelle 1885	Indonesia: Sulawesi; lowland localities
N. insularis Grouvelle 1893	Indonesia: Java, Sumatra
N. podagricus Portevin 1920	Indonesia: Borneo, Celebes
N. heurni Portevin 1926	New Guinea
N. benguetensis Arnett 1946	Philippines: Luzon
N. apo Arnett 1950	Philippines: Mindanao
N. kieticus Mroczowski 1959	Papua New Guinea: Bougainville Island; lowland localities
N. sp. n.	Indonesia: Flores
N. sp. n.	Indonesia: Sumatra
N. sp. n.	Indonesia: Sulawesi; highland localities
N. sp. n.	Solomon Islands; highland localities

*For undescribed species see Hanski and Krikken 1991 and Hanski & Niemelä 1990.

Subfamily Silphinae

Key to tribes of Australasian Silphinae

1 Pronotum coarsely punctate, lateral margins not flattened, not of lighter colour; elytra short, truncate, normally 3 or 4 abdominal segments exposed; with one raised outer costa and two flat inner costae; hindfemora robust, often greatly expanded ....Tribe Necrodini

– Pronotum finely punctate, lateral margins flattened and of lighter colour; elytra long, normally covering all but last abdominal segment; elytral costae broken into a series of three rows of tubercules or pustules; hindfemora thin, not expanded ..... Tribe Silphini

Tribe Necrodini

Diamesus Hope 1840

The genus contains only two species, *D. bimaculatus* Portevin of Taiwan and the following species.

Diamesus osculans (Vigors) (Figs 1,11)

Silpha osculans Vigors 1825: 537.

Type locality. 'India Orientali', type specimen seen, in BMNH, with printed label 'Madras Major Sale'.

Distribution. The species is distributed from Sri Lanka and southern India to Vietnam and through Malaysia, Thailand, Sumatra, Java, Borneo, the Philippines and New Britain (Arnett 1950; Mroczkowski 1966). It is widely distributed in New Guinea and in Australia from north-eastern Western Australia, eastward along the north coast and down the east coast to southern New South Wales (Fig. 11). It seems strange that Portevin (1926) gave no Australian records for the species because MNHN has eastern Australia specimens collected by von Mueller in 1896 (unnamed locality) and in 1917 in Normanton, Queensland.

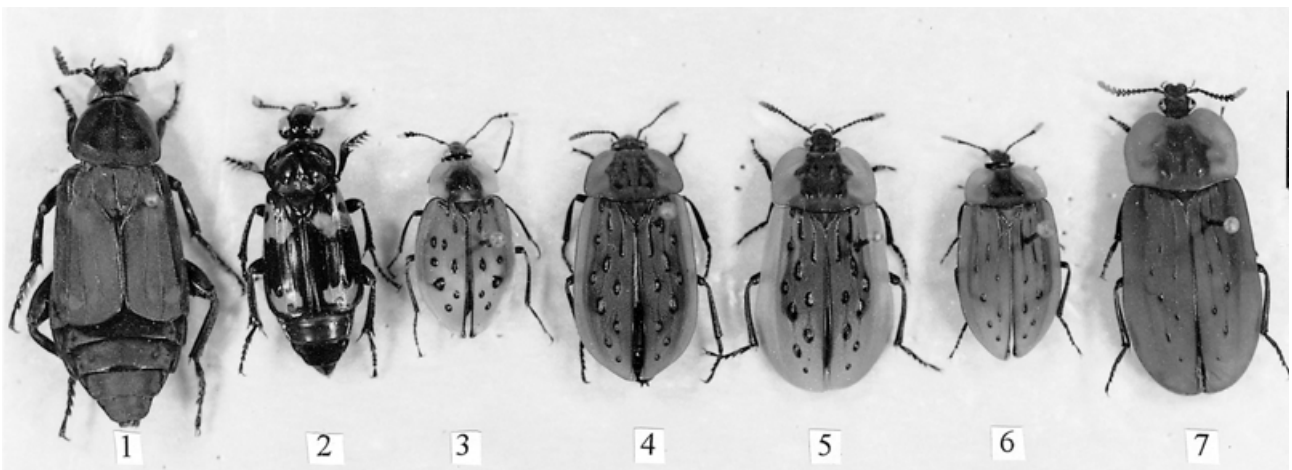
The seeming absence of early records may be the reason that Tillyard (1926) stated that the species was introduced into northern Queensland, but he gives no details or evidence. It seems unlikely that the species was introduced by human action, but it also seems strange that there are no records of this large beetle from the early or mid 1800s. Most Australian records date from 1950 and later but there is another record from Cairns in 1909 and Sydney in 1925. The tolerance of the species for open habitats suggests that it could have easily crossed the continental-shelf land-bridge of the Torres Straits from New Guinea to Queensland at times of low sea levels in the Pleistocene (Walker 1972).

Bionomics. I have seen 412 specimens from New Guinea and 135 from Australia. The species has been collected from sea level to 1500 m in New Guinea in every month of the year. Some collections are from carrion but most are from mercury-vapor lights or black-light traps. Habitats are mostly rainforest but some collections are from disturbed or secondary open and closed canopy forest sites. In Australia collections are from sea level up to 250 m. Specimens have been taken in every month except September and October and all are from carrion or carrion baits or ultraviolet or mercury-vapor light traps. Habitats are pastures, open sclerophyll forest, wet sclerophyll forest, and rainforest. Williams (1981) presents records from New South Wales and notes that adults make a high pitched sound in flight.

Tribe Silphini

Genus *Ptomaphila* Kirby and Spence 1828

The genus is known only from Australia and New Guinea and contains three species. It is most closely related to *Oxelytrum* Gistel of the Neotropics, with which it shares such apomorphic characters as a costate elytron, a longitudinally striate swelling on the intersegmental membranes between abdominal tergites 7 and 8 (possibly a stridulatory structure), and long hairs near the apical callus on the elytral underside



Figs 1–7. Habitus photographs of species of Silphidae occurring in Australia and New Guinea: **(1)** *Diamesus osculans*; **(2)** *Nicrophorus heurni*; **(3)** *Ptomaphila ovata*; **(4)** female *Ptomaphila perlata*; **(5)** male *Ptomaphila perlata*; **(6)** female *Ptomaphila lacrymosa*; **(7)** male *Ptomaphila lacrymosa*. Bar =10 mm.

(Anderson & Peck 1985). The genus is characterised by the apomorphic characters of the elytral apex bearing a flange, the head lacking a frontal chevron, a tuberculate elytron and an extremely wide elytral epipleuron (Anderson & Peck 1985).

Key to species of *Ptomaphila*

1 Last three antennal segments not of the same colour, basal two segments greyish or blackish, terminal segment yellow-orange; New Guinea .... *ovata* Portevin

– Last three antennal segments of the same yellow–orange colour; Australia 2

2 Elytral carinal tubercules more prominent, higher, broader (Fig. 8); elytral lateral margins lighter in colour than elytral disc, yellow–orange in colour; occipital carina entire ..... *lacrymosa* (Schreibers)

– Elytral carinal tubercules less distinct, lower, narrow-elongate (Fig. 9); elytral lateral margins not lighter in colour than elytral disc; occipital carina emarginate in middle ..... *perlata* Kraatz

Ptomaphila ovata Portevin (Figs 3,12,16)

Ptomaphila ovata Portevin 1926: 210.

Type locality. North-western New Guinea, headwaters of the Mamberamo River, Doormanpad Camp, 1410 m elevation. Type specimen seen, in MNHN. Paratypes are in Berlin and MNHN.

Distribution. Known only from Irian Jaya and Papua New Guinea (Fig. 12).

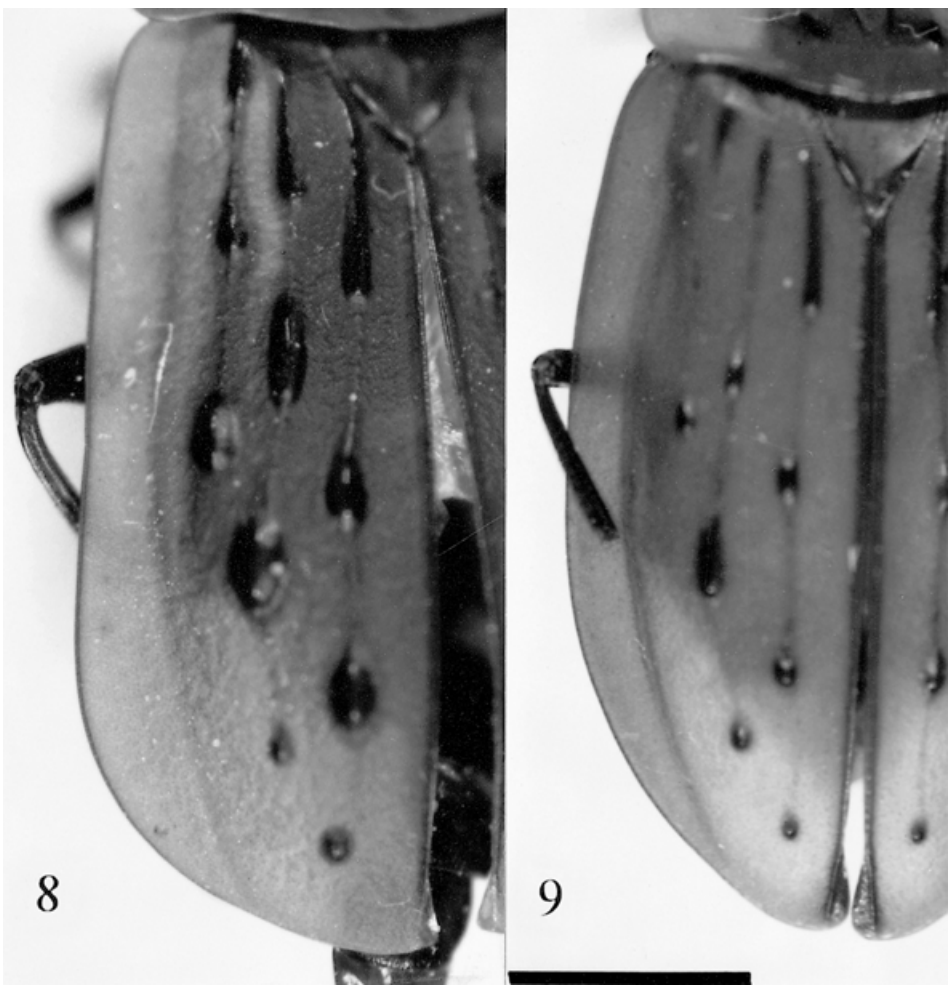
Bionomics. I have seen 66 specimens. Adults have been collected from 1400 m to 2850 m elevation and in every month of the year except February to April. The collections come from carrion and human-dung baited pitfall traps or mercury-vapor and ultraviolet light traps. The habitats are all upper elevation montane rainforest.

Ptomaphila perlata Kraatz (Figs 4,5,9,13,17)

Ptomaphila perlata Kraatz 1876: 356.

Type locality. Not given. Type specimen not seen, in Institut für Pflanzenschatzforschung, Eberswalde, Germany.

Distribution. The species occurs in eastern Australia from Gippsland, Victoria, north to the Lockerbie Scrub of Cape York Peninsula, Queensland (Fig. 13). There is also a population on Lord Howe Island. The earliest records from Lord Howe Island are from 1962 and 1966 (in AMSA). I found it on Lord Howe Island in abundance in 1980 following a National Park conservation campaign that shot many feral pigs and left their bodies in the forests. It seems unlikely that



Figs 8,9. Left elytra of *Ptomaphila* spp.: **(8)** *P. lacrymosa*; **(9)** *P. perlata*. Bar = 5 mm.

humans would either intentionally or accidentally introduce this insect to the island, so it presumably was a natural colonisation.

Bionomics. I have seen 371 specimens. The species is apparently less abundant than *P. lacrymosa*. Adults have been collected from sea level up to 1560 m elevation at the summit of Mt Bellenden Ker in Queensland. They have been taken in all months of the year except March. All collections are from carrion baits or carrion such as pigs and rats or at lights. They occur in rainforests, temperate rainforests, and wet sclerophyll forests.

Ptomaphila lacrymosa (Schreibers) (Figs 6,7,8,14,18)

Silpha lacrymosa Schreibers 1802: 194.

Type locality. 'Nova Hollandia.' Type specimen not seen, in Naturhistorisches Museum Wien, Vienna, Austria. New Holland was a vague term generally applied in the late 1700s to the whole continent of Australia. The specimens were collected by John Francillon, a British doctor, probably in south-eastern New South Wales and in the vicinity of Sydney. Some parts of his collection are now in BMNH and the Oxford Museum.

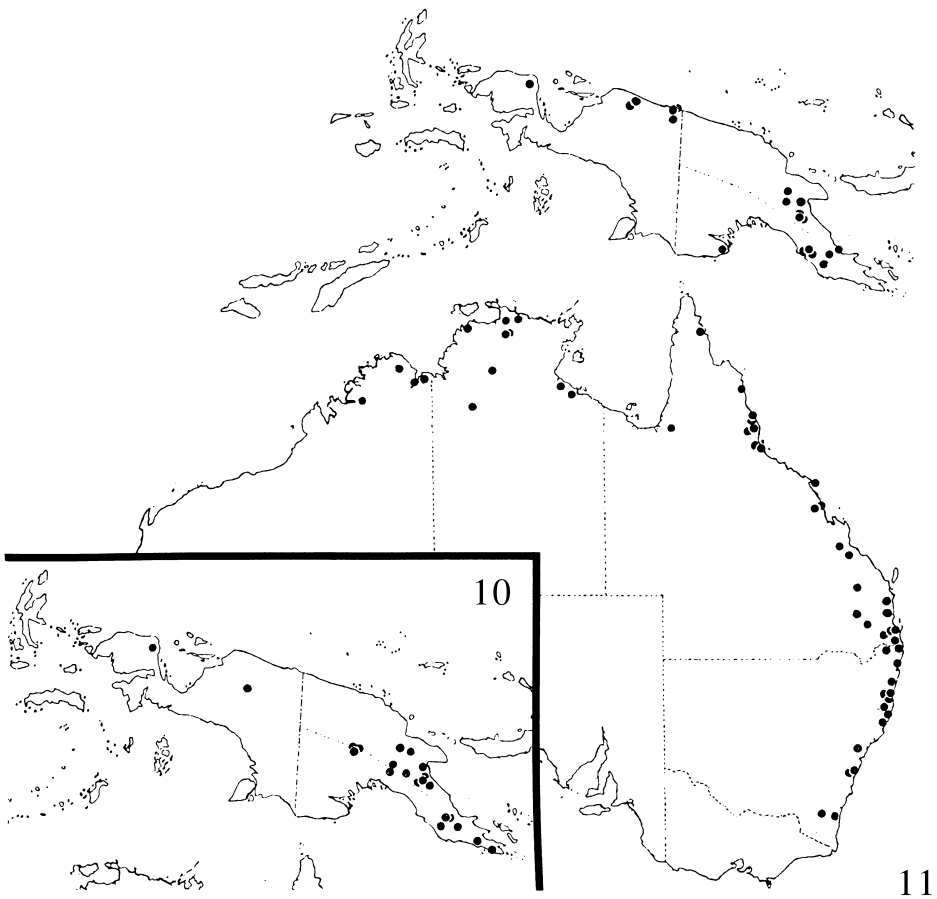
Distribution. The species occurs in the southern half of Australia. In the east it ranges from south-eastern Queensland, through New South Wales and Victoria, and west to the Eyre Peninsula of South Australia and throughout Tasmania. There is an apparent range disjunction across the Nullarbor Plain. In Western Australia, it ranges from near Esperance then west and north to near Northampton (Fig. 14).

Bionomics. I have seen 640 specimens. Adults have been collected from sea level to 1330 m on Mt Buffalo, Victoria. They have been taken in all months of the year. Most collections are from carrion baits or carrion, including dead sea birds, or at lights and light traps. Adults have been observed to feed on maggots on vertebrate carcasses. They occur in a variety of habitats including *Nothofagus* forests, temperate rainforests, wet sclerophyll forest, open *Eucalyptus* woodland and coastal heath.

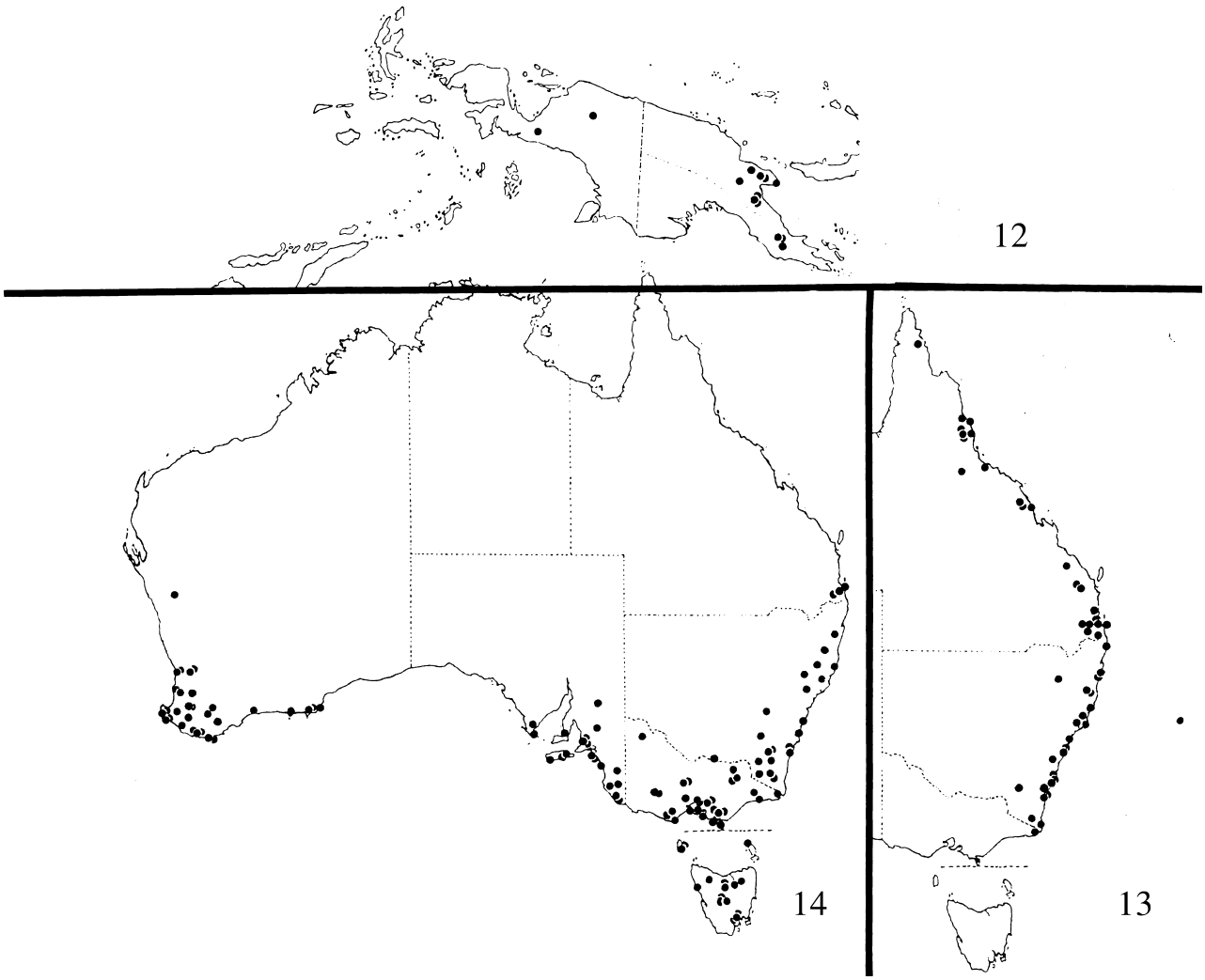
DISCUSSION

Phylogeny of *Ptomaphila*

Oxelytrum is the likely sister group of *Ptomaphila* (Anderson & Peck 1985) and this is used as an outgroup for phylogenetic interpretation of characters. No informative characters were found on the male aedeagus of either genus. Several characters of the female genitalia were found to be informative, as well as various external structures. Female genitalia have been used previously in a study of silphids only by Arnett (1944). Female genitalia of *Ptomaphila* were compared with *Oxelytrum cayennense* (Stürm) (Fig. 15) and



Figs 10,11. Distributions of Australasian Silphidae: **(10)** *Nicrophorus heurni*; **(11)** *Diamesus osculans*.

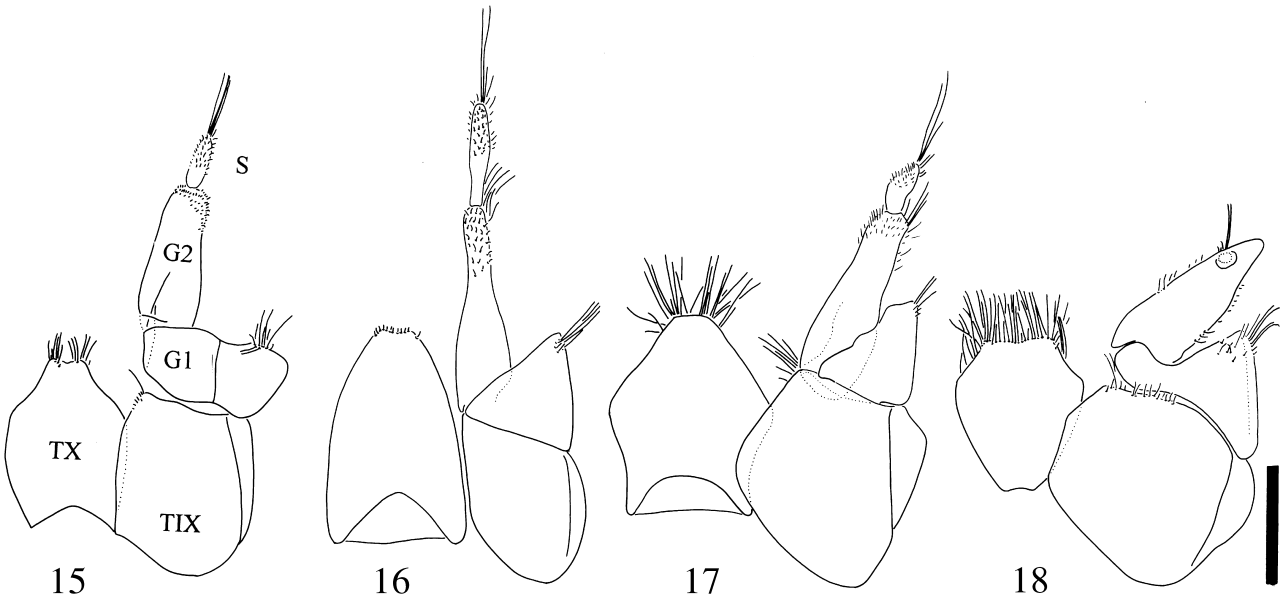


Figs 12–14. Distributions of Australasian Silphidae: **(12)** *Ptomaphila ovata*; **(13)** *Ptomaphila perlata*; **(14)** *Ptomaphila lacrymosa*.

Table 2 Analysis of character transformations in the species of *Ptomaphila**

Character	*O. cayennense*; outgroup	*P. ovata*	*P. perlata*	*P. lacrymosa*
1. Frontal chevron	Present, 1	Absent, 0	Absent, 0	Absent, 0
2. Occipital carina	Entire, 0	Emarginate, 1	Emarginate, 1	Emarginate, 1
3. Antennal club segments	All dark, 0	XI yellowish, 1	IX–XI yellowish, 2	IX–XI yellowish, 2
4. Pronotum hind-angles	Obtuse, 0	Rounded, 1	Rounded, 1	Rounded, 1
5. Pronotum costae elevated	Present, 0	Absent, 1	Absent, 1	Absent, 1
6. Elytral carinae	Tricostate, 0	Tuberculate, 1	Tuberculate, 1	Tuberculate, 1
7. Elytral epipleuron	Narrow, 0	Wide, 1	Wide, 1	Wide, 1
8. Apical elytral undersurface hairs	Present, 1	Absent, 0	Absent, 0	Absent, 0
9. Elytral tip colour	Dark, 0	Yellowish, 1	Dark, 0	Dark, 0
10. Elytral apical flange	Absent, 0	Present, 1	Present, 1	Present,1
11. Colour of elytral sides,	Dark as disc, 0	Dark as disc, 0	Dark as disc, 0	Lighter than disc, 1
12. Male hind-coxae	With tubercles, 1	Without tubercles, 0	Without tubercles, 0	Without tubercles, 0
13. Elytral surface	Coarsely punctate, 1	Finely punctate, 0	Finely punctate, 0	Finely punctate, 0
14. Female tergum 10 setae	Long, 1	Short, 0	Long, 1	Long, 1
15. Female tergum 9 setae	Present, 0	Absent, 1	Present, 0	Absent, 1
16. Female gonocoxite l setae	Lateral, 0	Lateral, 0	Lateral, 0	Inner, 1
17. Gonocoxite 2 shape	Elongate, 0	Elongate, 0	Shorter, 1	Scoop shaped, 2
18. Gonocoxite 2 sclerotisation	Thin, 0	Thin, 0	Thin, 0	Thickened, fossorial, 1
19. Female gonostylus shape	Elongate, 0	Elongate, 0	Shorter, 1	Much reduced, 2
20. Gonostylus setae	Long, 0	Long, 0	Long, 0	Short, 1
21. Gonostylus position	Terminal, 0	Terminal, 0	Terminal, 0	Lateral, 1

**Oxelytrum cayennense* was used as an outgroup. Character transformations: 0, plesiotypic; 1 and 2 apotypic.



Figs 15–18. Female genitalia of *Oxelytrum* and *Ptomaphila*: **(15)** *O. cayennense*; **(16)** *P. ovata*; **(17)** *P. perlata*; **(18)** *P. lacrymosa*. TIX, tergum 9; TX, tergum 10; G1, gonocoxite 1; G2, gonocoxite 2; S, stylus. Bar = 1 mm.

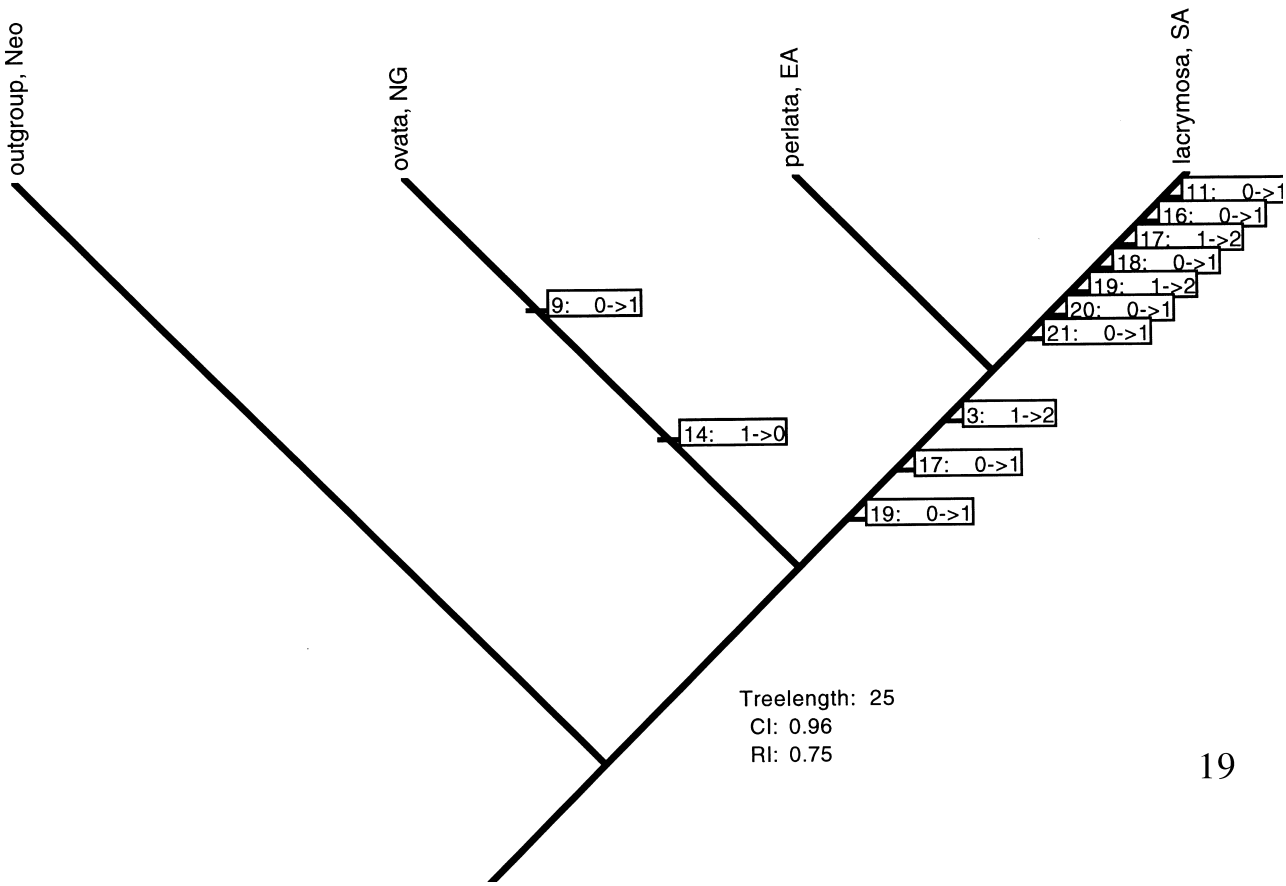


Fig. 19. Maximum parsimony cladogram of phylogenetic relationships of Australasian species of *Ptomaphila*. Data from Table 2. Outgroup representative: *Oxelytrum cayennense*. Geographical areas: Neo, Neotropical; NG, New Guinea; EA, eastern Australia; SA, southern Australia.

O. discicolle (Brulé) (in Arnett 1944; Fig. 5). Informative characters and hypotheses of character transformations are presented in Table 2. Characters 3, 15, 17, and 19 are the only shared derived states that are neither unistate nor autapomorphic. The maximum parsimony phylogenetic relationships of the species are shown in Fig. 19.

Ptomaphila ovata is the most plesiomorphic. *Ptomaphila perlata* and *P. lacrymosa* are sister species. *Ptomaphila lacrymosa* is the most derived, especially in characters of the female genitalia, which are highly modified for digging during oviposition.

Zoogeography of Australasian Silphidae

The fauna is composed of two components. The first probably entered Australasia from the north and in fairly recent times sometime after the northern edge of the Australian Plate joined the southern margin of the Asian Plate. *Nicrophorus* and *Diamesus* then followed the Indo-Malesian island chain across Wallace's line into Australasia. *Nicrophorus* has speciated in the uplands of several islands along the chain (Table 1).

The second is an ancient Gondwanaland component. The ancestor of *Ptomaphila* probably became separated from that of *Oxelytron* at the time of the separation of Gondwanaland when the Australian Plate separated from the South American Plate. *Ptomaphila ovata* of New Guinea seems least changed from the ancestral condition. The more derived sister pair of *P. lacrymosa* and *P. perlata* probably speciated in Australia, but the extrinsic isolating mechanism that helped to separate them is not obvious. The digging modifications of the ovipositor of *P. lacrymosa* may have helped it to colonise the more temperate climates of southern Australia. The range disjunction of *P. lacrymosa* across the Nullarbor Plain is a frequent biogeographic pattern and is usually related to Pleistocene aridity severing the once, more continuous forest corridor across the southern margin of the continent.

Prospects

Opportunities remain for the detailed study of ecology and natural history of all Australian species of Silphidae. Field studies could be modelled after those of Anderson (1982), Beninger and Peck (1992), Ratcliffe (1972) or Sikes (1996) on species in the Nearctic fauna. Where the ranges of the Australian species overlap, all species may occur in the same local habitat. If they divide resources through elevation, habitat preferences or have some seasonal partitioning of activity, as found in other silphids, remains to be learned (Anderson 1982; Hanski & Niemelä 1990). The larvae of all species remain undescribed.

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