ON THE BIOLOGY AND ZOOGEOGRAPHY OF AUSTRALIAN LYGAEIDAE (HEMIPTERA: HETEROPTERA) WITH SPECIAL REFERENCE TO THE SOUTHWEST FAUNA*

JAMES A. SLATER

Section of Systematic and Evolutionary Biology, University of Connecticut, Storrs, Connecticut, U.S.A.

Abstract

Bassian, Eyrean, relict, and recent Oriental elements of the lygacid fauna of southwest Western Australia are discussed. Host plant relationships of Lygacidae of this area are summarised. An account is given of wing polymorphism in Australian lygacids, and a classification of the major types of fore wings is proposed.

Introduction

During December, 1971, and January, 1972, I had the opportunity to make intensive collections and observations on the Australian lygaeid fauna. The work was concentrated primarily in the southwest but supplemented with some field work in South Australia and Queensland.

The southwest Australian fauna is of considerable zoogeographic importance and the present paper attempts to interpret the implications of this fauna relative to the rest of the Australian fauna.

Very little has been reported in the literature concerning the biology of any of the Western Australian Lygaeidae and it is hoped that the present contribution will stimulate interest in this most striking and important lygaeid assemblage.

Full synonymic and bibliographical references to most of the genera and species were given by Slater (1964).

Zoogeography

Fourteen subfamilies of Lygaeidae have representatives in Australia: Lygaeinae, Orsillinae, Ischnorhynchinae, Cyminae, Cryptorhamphinae, Blissinae, Slaterellinae, Geocorinae, Oxycareninae, Artheneinae, Pachygronthinae, Heterogastrinae, Henicocorinae and Rhyparochrominae. Of these the Henicocorinae, Cryptorhamphinae and Slaterellinae are Australian endemics. The other subfamilies are widespread (all but the Artheneinae and Heterogastrinae occur in all major zoogeographic regions), but most have endemic Australian genera.

Lygaeinae.—Chiefly of Oriental or Papuan derivation and with many taxa essentially confined to the Torresian subregion. However *Brachylygaeus* Gross is southern and endemic and *Melanerythrus* Stål is almost so (also reported from Fiji).

Orsillinae.—The ubiquitous and widespread genus *Nysius* is characteristic. It is world wide in distribution. There are 3 endemic genera in south and western Australia, *Austronysius* Ashlock, *Eurynysius* Ashlock and *Lepionysius* Ashlock, the latter representing a separate monotypic tribe.

Ischnorhynchinae.—Three of the 5 genera are endemic (Koscocrompus Scudder, Creocrompus Scudder, Crompus Stål). The relationships are complex, sharing on the one hand Eastern Hemisphere relationships but also apparently affinites with the Chilean genus Polychisme Kirkaldy.

Cyminae.—There are no endemic genera but the affinites of *Cymus novaeze*landiae Woodward as discussed below are indicative of a very old isolated taxon in southwest Australia.

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Blissinae.—The fauna has a Torresian component exemplified by *Dentisblissus* Slater, *Macropes* Motschulsky and *Iphicrates* Distant (the latter extending down the east coast to Tasmania) and an isolated endemic component probably associated with aridity exemplified by *Australodemus* Slater and *Heinsius* Distant. The presence of the peculiar *Ischnodemus sordidus* Slater in the southwest corner is zoogeographically perplexing.

Geocorinae.—The situation is not well understood but the fauna is dominated by species of such widespread genera as *Geocoris* Fallen and *Germalus* Stål. *Stylogeocoris* Montandon is endemic but possibly recently derived.

Oxycareninae.—A recent element represented only by 3 species of the genus *Oxycarenus* Fieber which is numerous and widespread throughout the tropics and subtropics of the Old World.

Artheneinae.—Represented only by the isolated endemic Dilompus Scudder.

Pachygronthinae.—The distribution is typical of so much of the Australian lygaeid fauna with a recent invading Torresian fauna in the northeast best illustrated by *Pachygrontha* Germar and *Opistholeptus* Bergroth and endemics in the southwest (*Darwinocoris* Slater and *Magninus* Distant).

Heterogastrinae.—This is entirely a Torresian element in the Australian fauna that has entered from the north in relatively recent time and is still essentially tropical in distribution.

Rhyparochrominae.—Eleven tribes have representatives in Australia: Udeocorini, Targaremini, Plinthisini, Lethaeini, Ozophorini, Antillocorini, Rhyparochromini, Drymini, Cleradini, Myodochini and Stygnocorini.

Of these the Udeocorini are heavily concentrated in southern Australia. The Targaremini have a restricted distribution largely in Australia and New Zealand (extensive radiation) but are also found in New Caledonia, the Philippines, Japan and the Solomons. The Stygnocorini have a striking austral element in southern Africa, New Zealand, southeast Australia and Madagascar but also a Palearctic element. The Lethaeini and Antillocorini occur in all major faunal regions but are largely tropical and subtropical. The Plinthisini also occur in all faunal regions but there is an extensive radiation in South Africa and southern Australia. The Drymini are abundant in the Old World tropics and subtropics. They occur in other zoogeo-graphic areas but are almost or completely absent in the Neotropics. The Rhyparo-chromini are chiefly Eastern Hemisphere and abundant in the Palearctic. The Myodochini are most diverse in the Neotropics but have taxa in all of the major faunal regions of the world. The Cleradini are a very specialized blood feeding group chiefly Old World Tropical and the Ozophorini have a peculiar largely "fringing" distribution in the tropics and subtropics of both hemispheres (Slater 1972b).

In Australia the Udeocorini, Targaremini, Stygnocorini and elements of the Plinthisini and Lethaeini appear to represent a largely Bassian and/or Eyrean element in that they are concentrated in the south, are represented by many endemic genera or "species groups" and appear to represent the "ancient" elements of the rhyparochromine fauna.

The southwest Australian lygaeid fauna is of particular interest because of the isolation of the area, the number of endemic Australian genera and species involved and the high degree of endemicity present among the host plants.

While it is certainly premature to attempt a definitive zoogeographic analysis of the southwestern Australian lygaeid fauna certain generalizations seem to be warranted.

Serventy and Whittell (1967) note that the bird fauna of southwestern Australia "cannot be classified as a simple zoo-geographical region, neither as a uniform portion of the Eyrean subregion . . . nor as a peculiar region on its own . . . It is a district occupied by an *intermingling* of two faunas, the Eyrean and the Bassian."

Horton (1973) recognizes a "southwestern" region allied to his Eyrean and Kosciuskan (= Bassian largely). (This author states that Serventy and Whittell 1961

in the second edition have recognized the southwest corner as a separate region. I have not seen this edition but they do not do this in the 1967 fourth edition—as quoted above.)

It is not my intent here to enter the discussion of Australian faunal subregions. The discussion of Keast (1961) is particularly informative in this regard. (See also Mackerras (1970), Munroe (1965) and Gressitt (1958) for general zoogeographic summaries.)

To a considerable extent the lygaeid fauna of southwestern Australia shows what is probably the same intermingling of Bassian and Eyrean elements as does the bird fauna. There are a number of species, particularly in the Rhyparochrominae, that occur only in southeast and southwest Australia. It is probably an oversimplification to view such species as representing a "Bassian element" in a strict sense since this term is often used as representing species of mesic habitats and many of these rhyparochromine species occur in relatively dry areas. However, it is possible that the so-called Eyrean fauna of Australia is chiefly the result of the subtraction of less xeric tolerant taxa. The significance of this theory for the Lygaeidae is that there is a definite southwest-southeast faunal element that can be construed to be disjunct at present due to climatic deterioration since (or during) the Pleistocene and down faulting of the Great Australian Bight. The fact that most of these disjunct elements are conspecific in the southwest and southeast indicates either recent separation or that there is still gene flow existing between the two areas. This is not really unlikely for many Lygaeidae, although it may be for birds, since many of the insects presumably have strong dispersal ability, and since many of them have the ability to live in dry places and utilize a variety of seeds the Nullarbor Plain may not be a strong barrier in some years.

There are other elements of the southwest Australian lygaeid fauna that are perhaps even more interesting. There appears to be an extremely old isolated southwest Australian faunal component that is often endemic at the generic level, is definitely mesic and does not have close relatives in the rest of Australia. Presumably this faunal component was more widespread in Australia in the Pleistocene and earlier and remains now as a remnant only in the southwest corner, although why it is not represented in the southeast is not clear. This element is well illustrated by the genus Magninus Distant, a pachygronthine, related to and perhaps ancestral to the tropicopolitan genus Pachygrontha Germar. Magninus is known only from southwest Australia but the tribe to which it belongs is otherwise absent in Australia except for a few species of *Pachygrontha* in northern Queensland that are conspecific with or closely related to New Guinea populations and obviously represent a recent tropical element in the Australian fauna. Ischnodemus sordidus Slater is perhaps even more isolated. It is known only from the south coast of southwest Australia and is the only species of the genus found anywhere in Australia. The pachygronthine genus Darwinocoris Slater also is confined to southwest Australia. It represents a different tribe from Magninus that does have other genera in eastern Australia but they are not closely related to Darwinocoris which is quite isolated morphologically in the subfamily. All three of these taxa inhabit mesic environments and breed on sedges or restios. It seems reasonably certain that these species represent a very old isolated fauna that has been greatly reduced in distribution by climatic deterioration. Keast (1961) points out the presence of extensive fresh water lakes in the interior of Australia in the Tertiary and at least four climatic "oscillations" corresponding to glacial advances and retreats in the Northern Hemisphere. Austronysius Ashlock and Stylogeocoris Montandon may also represent elements of this fauna.

The situation relative to *Cymus novaezelandiae* Woodward may be somewhat different although similar. This also is a mesic adapted insect (sedge feeder). It has been found only in southwest Australia and New Zealand. If this species actually is absent from southeast Australia it must represent a very old, Antarctic, cool-adapted component of the southwest Australian lygaeid fauna that presumably would illustrate a continental drift relationship (see Mackerras 1970). This faunal component in the Lygaeidae is usually composed of genera with related species found in southeastern Australia and New Zealand such as *Regatarma* Woodward and and *Tomocoris* Woodward of the tribe Targaremini.

The flightless species of *Plinthisus* Stephens (all species are undescribed) may also include species that will ultimately prove to belong to this old endemic southwest element, but if so it must be due to rather different selective habitat factors, for this complex tends to be dry adapted and its limitation to southern Australia would seem to reflect limited powers of dispersal rather than range restriction due to climatic deterioration.

The whole question of the significance of the distribution of this *Plinthisus* complex and that of the xeric adapted Lethaeini genera *Coleocoris* Gross and *Carabocoris* Gross is intriguing. *Coleocoris* species are known only from western and southern Australia and Thursday Island. Despite their presence on Thursday Island these species show obvious morphological adaptations for xeric conditions. Such taxa may well truly represent the Eyrean element in the fauna but only more careful collecting will allow any meaningful understanding of this faunal component.

There is a recent "invading" element exemplified by species of *Dieuches* Dohrn, *Remaudiereana* Hoberlandt, *Spilostethus* Stål, *Cymodema* Spinola and probably *Germalus* Stål and *Stenophyella* Horvath. These genera and many of the species are Oriental and are represented in Australia chiefly in the northern or Torresian subregion. In southwestern Australia they are usually found in disturbed ruderal areas rather than in those habitats where endemic vegetation is dominant.

Habitats

The southwest Australian lygaeid fauna occupies the usual wide range of ecological habitats typical of the family such as Cyminae and Pachygronthini on sedges and rushes, Rhyparochrominae in seed litter, etc. However the overall picture is considerably modified by the fact that southwest Australia is an area of winter rainfall and a subsequently dry summer period, and by its isolated position that results in the poor representation or absence of certain tribes and subfamilies which may or may not have been replaced ecologically by other taxa.

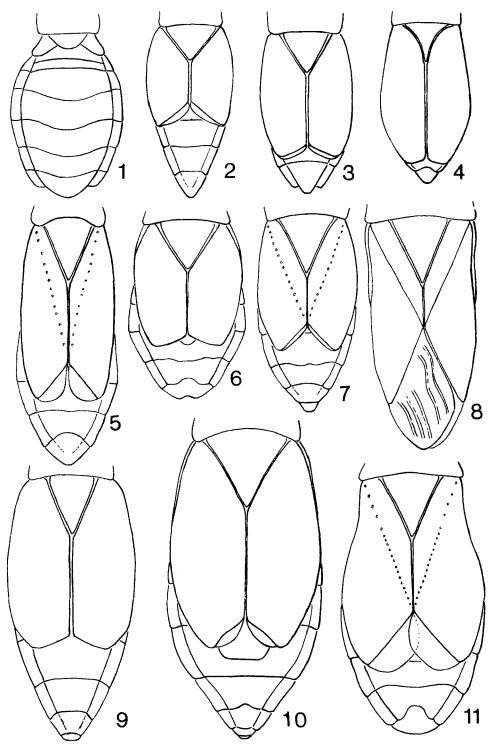
Wing polymorphism

One of the striking features of the west Australian lygaeid fauna is the large number of species exhibiting wing polymorphism (Table 8). The reduction of wings is a well known phenomenon in the Lygaeidae and occurs frequently in many, if not most, other families of Heteroptera. Sweet (1964) has reviewed the situation in detail and the general phenomenon will not be discussed further here except to point out that there appears to be a definite correlation of the presence of brachyptery in lygaeids to the relative permanency of habitat, especially xerosere habitats which generally represent a low biomass productivity.

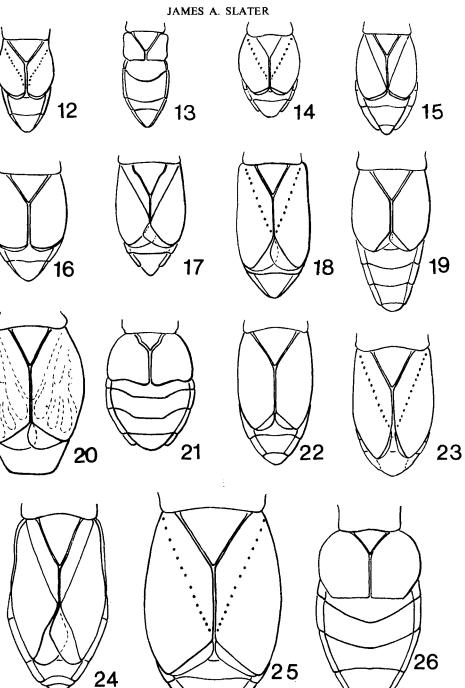
Slater (1972a) has suggested that the proportion of species showing wing polymorphism in an area may also be indicative of the stability of an area in terms of evolutionary time as well as those of relatively short term ecological stability, and that in relatively ancient groups there will be more species with flightless morphs than in more recently arriving taxa.

There has been a tendency to call all types of wing modification in the Heteroptera "brachyptery" if it involves a reduction of the hind wing, a modification of the forewing and a subsequent loss of flight ability. In the Lygaeidae the term is usually applied to any modification of the nature of the forewing from a "normal" condition of macroptery where the clavus and corium are distinct and the membrane well developed and nearly attaining or exceeding the end of the abdomen, often whether or not the hind wing is greatly reduced. This tendency masks very important differences in the types of wing modification involved and these differences often appear to be significant to an understanding of the ecology of the particular species or higher taxon and thus to an understanding of the selective factors involved in the production of the wing polymorphism.

While one would expect intermediate conditions of wing modification, and this does occur, it is surprising that such a large proportion of the Lygaeidae can be placed in no more than five categories, and that for the most part these categories



FIGS. 1-11.—Dorsal view of: (1) Nympholethaeus papuensis Woodward, micropter, (2) Cryptocoris fasciata Gross, coleopteroid (from Gross 1962), (3) Myocara nr. acuminatum (Dallas), coleopteroid, (4) Coleocoris ocellatus Gross, coleopteroid, (5) Euander multicoloratus (Distant), coleopteroid, (6) Porander scudderi Gross, coleopteroid, (7) Udeocoris scudderi Gross, coleopteroid, (8) Euander lacertosus (Erichson), macropter, (9) Fontejus sidnicus (Stål), coleopteroid, (10) F. westraliensis Gross, coleopteroid, (11) F. nr. collaris Stål, coleopteroid.



FIGS. 12-26.—Dorsal view of: (12) Tomocoris minutus Woodward, brachypter (from Woodward 1955), (13) T. minutus Woodward, staphylinoid (from Woodward 1955), (14) Regatarma tasmaniensis Woodward, coleopteroid (from Woodward 1956), (15) Brachydrymus lateabundans Gross, brachypter (from Gross 1965), (16) Tomocoris philippinensis Woodward, coleopteroid (from Woodward 1963), (17) Lamproceps ? sp. (Western Australia), brachypter, (18) Austroxestus carnarvoni Woodward, coleopteroid (from Woodward 1962), (19) Tomocoris scutellaris Woodward, brachypter (from Woodward, coleopteroid (from Woodward 1962), (19) Tomocoris scutellaris Woodward, brachypter (from Woodward, coleopteroid (from Woodward 1962), (19) Tomocoris scutellaris Woodward, brachypter (from Woodward, coleopteroid, (20) Henicocoris monteithi Woodward, coleopteroid (from Woodward 1968), (21) Plinthisus sp. (Swan River, Western Australia), staphylinoid, (22) Exomyocara australicum Slater and Woodward, coleopteroid, (23) Tomocoroides fijianus Woodward, coleopteroid (from Woodward 1963), (24) Ethaltomarus australicus Slater and Woodward, submacropter, (25) Plinthisus nr. timeoides (Distant), coleopteroid, (26) Tomocoris australiensis Woodward, staphylinoid (from Woodward 1955).

are applicable in most other heteropterous families as well. I suggest the following classification of major types of front wings be considered as an aid to greater precision in discussing wing modifications in the Heteroptera.

I. Aptery.—In this condition the front wings are entirely absent. There are no known examples of this in the Lygaeidae although some Type II conditions approach total loss. True aptery is widespread in the Aradidae.

II. **Microptery** (Fig. 1).—In this condition the wings are reduced to small pads usually widely separated from each other, leaving the abdomen exposed mesally with the clavus and corium fused and the membrane either absent or represented by a small flap. In extreme microptery the metanotum and the posterior portion of the mesonotum may be exposed.

III. Staphylinoidy (Figs. 13, 21, 26).—In this condition the fore wings have the clavus and corium indistinguishably fused into a coriaceous pad, and the wings meet each other evenly along the midline for their entire length, are evenly truncate across the posterior end and usually cover only the first 3 abdominal terga. This condition results in the anterior half of the abdomen being completely covered by the wings, and the posterior half exposed. This condition is so widespread that it appears it probably has a functional significance rather than being only an intermediate stage leading to microptery.

IV. Coleoptery (Figs. 2-7, 9-11, 14, 16, 18, 20, 22, 23, 25). — In this condition the total length of the wing may or may not be reduced but in either case the coriaceous portion is not reduced but lengthened. The clavus and corium are fused and frequently the former is considerably enlarged along the midline. The two wings do not overlap but meet along the midline like the elytra of Coleoptera. At least 3 subtypes can be recognized.

A. In which the clavus and corium form a single coriaceous wing cover that meets the opposite cover evenly down the midline, the "claval commissure" being elongated and the membrane reduced to a small flap, thus leaving the posterior abdominal segments exposed.

B. In which the corium extends posteriorly laterally to reach or nearly reach the end of the abdomen and the membrane is represented by only a small mesal flap that does not reach posteriorly beyond the end of the elongated lateral portion of the corium.

C. In which the fore wing completely covers or nearly covers the abdomen and consists of an undifferentiated coriaceous cover meeting down the midline and appears as the wing of a typical beetle. No membrane remnant remains.

V. **Brachyptery** (Figs. 12, 15, 17, 19).—A condition in which the clavus and corium are either distinctly separate or fused, and may be shorter than they are in the macropter. The membrane is much reduced, usually reaching onto the third abdominal tergum and generally with only the inner portion of one membrane overlapping the inner portion of the other.

VI. Submacroptery (Fig. 24).—In this condition the clavus and corium are usually clearly differentiated by a claval suture and appear the same as in the completely macropterous condition. The membrane is generally well developed and has veins but is shortened relative to the macropter, leaving the posterior abdominal tergum (7) exposed. In some cases the veins are absent and frequently the membrane is more distinctly tapered than it is in macropters. The hind wing may be either much reduced or well developed.

VII. Macroptery (Fig. 8).—The "typical" or "unmodified" wing condition with the clavus and corium distinct, the membrane well developed and usually covering the abdomen with the membrane of one wing completely overlapping that of the other. The hind wing is always well developed.

In Australia wing polymorphism occurs in many subfamilies: Lygaeinae (Brachylygaeus Gross), Orsillinae (Lepionysius Ashlock), Blissinae (Australodemus

Slater) and Pachygronthinae (*Darwinocoris*) but is best illustrated in the most diverse and largest subfamily, the Rhyparochrominae, of which the majority of species are ground litter living seed predators. When one examines the various tribes of Australian Rhyparochrominae it becomes readily apparent that there are great differences in the proportions of polymorphic genera and species and that there is a strong correlation with the distribution and presumed antiquity of the various taxa as well as differences in the nature of the wing modifications in relation to habitat. Darlington (1961) in a very important paper on Australian insect relationships comments on the high proportion of flightless carabid beetles in the Australian fauna (45%; 75% of geophile species). He notes that this is not true of the New Guinea fauna, that "many of the [Australian] species belong to wholly flightless genera or even flightless tribes that have evidently been in Australia a long time. Derivatives of old Australian flightless groups dominate the flightless ground-living carabid fauna . . ." He also notes a change between Australia and New Guinea in the relative dominance of different tribes. This seems consistent with the situation particularly in rhyparochromine Lygaeidae. An analysis of wing polymorphism in Australian rhyparochromines therefore seems especially desirable.

Wing polymorphism in Udeocorini

The percentage of polymorphic taxa in the Udeocorini is especially instructive. In southwestern Australia members of the Udeocorini make up a dominant element in the rhyparochromine fauna and appear to replace ecologically recognizable "types" of other parts of the world. This seems to be happening in South Australia as well. Pooling of data from personal collecting and from Gross (1962) indicates (Table 1) that of 14 species of Udeocorini representing 7 genera all but 2 species (14%) are known to show wing modifications. One of these, *Telocoris vittata*

Species	Modified wings	Macropters	Distribution*
Fontejus westraliensis Gross	8	0	WA
Fontejus sidnicus (Stål)	2	0	WA
Fontejus collaris (Stål)	2	1	WA
Porander scudderi Gross	26	3	ACT, NSW, SA, T, V
Zygocoris tindalei Gross	12	0	SA
Cryptocoris fasciata Gross	3	0	SA
Udeocoris scudderi Gross	45	10	WA
Udeocoris rolandi (Distant)	35	15	SA
Udeocoris nigroaeneus (Erichson)	36	63	WA
Euander cicero Gross	6	0	ACT, NSW
Euander torquatus (Erichson)	45	1	ACT, T, V
Euander multicoloratus (Distant)	9	4	WA
Euander lacertosus (Erichson)	0	21	WA
Telocoris vittata (Distant)	0	4?	NT, N-WA, Q
	229	122	

TABLE I WING MODIFICATION IN THE UDEOCORINI

*On this and the following tables the abbreviations are: WA—Western Australia; NSW—New South Wales; SA—South Australia; T—Tasmania; V—Victoria; ACT—Australian Capital Territory; Q—Queensland; NT—Northern Territory; N-WA—Northern Western Australia.

(Distant) which I have not seen, is noted by Gross (1962) as having a lethaeine habitus. The other, *Euander lacertosus* (Erichson), is a characteristic udeocorine and is reported as destructive to strawberries, probably indicating a species of temporary habitats, which would suggest strong selection against the flightless morph. The situation in *Udeocoris nigroaeneus* (Erichson) is very instructive, as will be discussed in detail in a forthcoming paper, as it seems to indicate selective pressure away from the flightless morph in recent years due to habitat disturbance by man.

All of the other Australian udeocorine species are predominantly coleopteroid. The species I have personally studied in Western Australia are all associated with relatively exposed dry hot xerosere type habitats. This appears to have a marked effect on the type of wing polymorphism exhibited. These species all show coleoptery in that while the membrane is reduced to a small flap leaving the posterior abdominal segments exposed, the clavus and corium are not reduced but frequently actually elongated. While the clavus and corium are always fused in these species, in some cases the rows of punctures that border the claval suture in macropters remain, so that it is possible to ascertain the former position of the claval suture. Such examples show that the clavus is greatly elongated mesally in these coleopteroid forms, which results in a beetle-like hemelytron with the two wings meeting evenly along the midline for their entire lengths. The predominance of this type of wing modification rather than a strong overall shortening of the wing is presumably an adaptation to hot xeric conditions and produces an insulating air space between the wings and the dorsal surface of the abdomen.

The Udeocorini appear to be a very old dry-adapted element in the Australian fauna. While they have what at present appears to be a Bassian distribution they may equally well be considered to represent an Eyrean element that has attained its present distribution by retreat from the "dead center" by post Pleistocene climatic deterioration.

Wing polymorphism in Targaremini

The Targaremini are known in Australia from only 2 genera and 4 species (see Table 2). These species are represented only by individuals with reduced wings and the expression of wing modification varies from species with only reduced membranes to those with very much shortened and reduced wings which cover only the anterior segments of the abdomen. However, this information is somewhat misleading for the Targaremini, as Dr T. E. Woodward (*in litt.*) informs me that he has species from Queensland of Hebrolethaeus Scudder, Lethaeaster Breddin and Sylvacligenes Scudder represented by numerous specimens all of which are macropterous. I would suggest that this indicates that even in the Targaremini two faunal elements exist, an older one represented by Tomocoris Woodward and Regatarma Woodward and more recent invading elements represented by the three macropterous genera noted above. However, the targaremine distribution is complex (Hebrolethaeus and Sylvacligenes are otherwise known only from New Caledonia) and probably cladistic analysis is needed before the zoogeographic picture can be reasonably understood. In contrast to the Udeocorini the Targaremini appear to be associated with relatively mesic forest and woodland habitats, sometimes with Nothofagus forests. They appear to represent an ancient forest litter group, and because they do not occur in xeric open habitats there has been no selection for "coleoptery" but rather for proportionally decreasing length of wings as selection for the flightless morph proceeds in evolutionary time.

Species	Modified wings	Macropters	Area
Tomocoris australiensis Woodward	6	0	0
Tomocoris minutus Woodward	9 (3 submacropt.)	0	ò
Tomocoris scutellaris Woodward	3 (submacropt.)	0	ò
Regatarma tasmaniensis Woodward	9	0	Ť

TABLE 2

WING MODIFICATION IN THE TARGAREMINI

Wing polymorphism in Plinthisini

Almost the entire Australian fauna is undescribed, but it consists of 2 quite distinct elements. One is composed of very small black or brown species, all of which are known only in the staphylinoid condition with the scutellum reduced and the hemelytra consisting of 2 undifferentiated coriaceous pads which are evenly or nearly

evenly truncate posteriorly, leaving the posterior half to two-thirds of the abdomen exposed. All but 2 of the known Australian species belong to this element, and while most of them are known from one or a very few collecting sites it is evident that they are concentrated in the southern and particularly the southwestern part of the continent.

The second element consists of species that occur in the macropterous condition. One of these has been collected only in Queensland and no brachypters are known. The second species is very widely distributed in Australia and occurs in New Zealand as well. These 2 species are very closely related to, if not conspecific with, wide ranging species in other faunal regions. In *Plinthisus* nr. *tineoides* (Distant) while submacroptery is very common, the nature of the wing modification (Fig. 25) is much less extreme than in those species (Fig. 21) where only staphylinoids are known in that the claval suture is evident, a distinct membrane is present and the degree of wing reduction is less extensive.

What appears to be represented by the Australian Plinthisini is 2 faunal components, one representing very ancient forms concentrated in the Bassian subregion and probably with many, if not all, species completely lacking a macropterous morph. This element represents the old "endemic" *Plinthisus* complex in Australia and has its closest relatives in the Cape area of South Africa. The second element has very close relatives in the Orient and its presence in Australia presumably represents a relatively recent invasion and colonization from the north, presumably by macropters crossing water barriers, possibly even subsequent to the Pleistocene.

Species	Modified wings	Macropters
Plinthisus nr. tineoides (Distant)		
W. Australia	20	6
S. Australia	58	36
Tasmania	24	4
Victoria	4	4
Queensland	1	104
Torres Strait	0	2
Totals	107	156
(New Zealand)	(16)	(8)
Plinthisus sp. nr. ptilioides Puton	0	12(+)
Plinthisus sp.	2 2	0
Plinthisus sp.	2	0
Plinthisus sp.	10	0
Plinthisus sp.	1	0
Plinthisus sp.	4	0
Plinthisus sp.	1	0
Plinthisus sp.	22	0
Plinthisus sp.	5	0
Plinthisus sp.	8	0
Plinthisus sp.	5	0
Plinthisus sp.	4	0
Subtotal	64	12
Total	171	168

I ABLE 3						
WING	MODIFICATION	IN	THE	PLINTHISINI		

Wing polymorphism in Lethaeini

In the Australian lethaeine fauna the situation is similar to that found in the Plinthisini but is more complex. There is what I consider to be an old endemic or ancient element exemplified by *Coleocoris, Carabocoris, Myocara* Bergroth and *Exomyocara* Slater and Woodward, and a second very recent element confined largely to the Northern Territory and Queensland (*Neolethaeus* Distant).

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Coleocoris and Carabocoris are known only as coleopteroids (Fig. 4) (probably there is no macropterous morph) and the wing modification is as fine an example of coleoptery as exists in the Lygaeidae. In these species the hemelytra cover almost the entire abdomen as a pair of completely coriaceous, convex, beetle-like wings that meet along the midline for their entire length. There is no actual shortening of the fore wing but rather it has become a hard shell-like covering. Presumably this is an adaptation for living in hot dry habitats. *Myocara* exhibits the type of coleoptery (Fig. 3) so commonly seen in the Udeocorini (Dr Woodward *in litt.* informs me that there is a number of undescribed Australian species). All of the above 3 genera are endemic in Australia.

Noteolethaeus Woodward and Slater is a rather special case (see Table 4). All of the southwestern Australian specimens (7) are macropterous whereas 26 of the 32 known eastern Australian specimens are coleopteroid. While this is really an inadequate sample it suggests that *Noteolethaeus* is not one of the really old endemic elements in Australia and at least raises the possibility that it may have reached Western Australia very recently.

Species of *Neolethaeus* which occur in the north and east are known only as macropters and are almost certainly relatively recent components of the Australian fauna.

Species	Modified wings	Macropters	Distribution
Coleocoris ocellatus Gross	86	0	WA
Coleocoris triplagiatus Gross	9	0	SA
Coleocoris lineatus Gross	1	0	(Thursday I.)
Carabocoris biplagiatus Gross	3	0	WA
Mvocara nr. acuminatum (Dallas)	12	0	WA
Exomvocara trispinosum Slater and			
Woodward	28	0	WA
Exomyocara submuticum Slater and			
Woodward	8	0	Q, V
Noteolethaeus armstrongi Woodward			
and Slater (E. Aust.)	26	6	Q
Noteolethaeus armstrongi (W. Aust.)	0	7	WA
Austroxestus carnarvoni Woodward	1	1	0
Neolethaeus tenebrosus (Distant)	0	29	NT, Q
Neolethaeus australiensis Woodward	0	19	NT, Q
Neolethaeus cantrelli Woodward	0	4	Q
Total	174	66	

WING MODIFICATION IN THE LETINEIN	WING	MODIFICATION	IN THE	LETHAEINI
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Wing polymorphism in Stygnocorini

Members of this interesting tribe have only recently been known to be present in Australia (although an endemic New Zealand genus has been known for many years). Thus far only 2 genera are known (Table 5), *Tasmanicola* Slater and Sweet and at least one undescribed genus related to a South African group. Although few specimens exist in collections both genera show an advanced form of coleoptery. They are known only from the southeastern portion of Australia and are associated with cool mesic conditions. Despite the fact that stygnocorines occur in the Palearctic the relationship of the Australian fauna is not with this section of the Stygnocorini but rather with South African genera which are cool mesic adapted and associated with the flora of the Cape subregion (Slater and Sweet 1970). There seems little doubt that the stygnocorine Australian fauna represents an old Bassian element.

Wing polymorphism in Ozophorini

Only 2 Australian species of *Ethaltomarus* Scudder are known. The genus also occurs in tropical Africa. The material is predominantly sub-macropterous (Table 5, Fig. 24), although a macropter is known. The wing reduction is essentially a shortening of the membrane but little or no modification of the other parts of the fore wing.

TABLE 5

Species	Modified wings	Macropters	Distribution
Stygnocorini			
Tasmanicola truganinae Slater and Sweet	2	2	Τ, V
N. g., n. sp. Antillocorini	1	0	Т
Botocudo nr. ornatulus (Bergroth) Ozophorini	0	110	WA
Ethaltomarus australicus Slater and Woodward s.f. Henicocorinae	35 (submacropt.)	1	WA
Henicocoris monteithi Woodward	8	0	v

WING MODIFICATION IN VARIOUS LYGAEID TAXA

As previously noted the Ozophorini have in general a peculiar somewhat "peripheral" world distribution (see Slater 1972b), but obviously strong dispersal ability which makes their position difficult to interpret. However, on present evidence I would not consider the Australian species to represent one of the old endemic components of the Australian fauna.

Wing polymorphism in Rhyparochromini

This large tribe is abundant and diverse in the Palearctic with numerous Old World tropical representatives. It is obvious that it represents a relatively recent element in Australia. Not only is it largely a Torresian component with most species confined to the northern and northeastern parts of Australia but the great majority of the Australian species are entirely macropterous. None represent endemic genera and where wing reduction occurs (2 species) it is not of a highly specialized nature, but submacroptery, with only the membrane reduced.

There seems little doubt that the entire Rhyparochromini fauna has reached Australia from the Orient relatively recently.

Species	Modified wings	Macropters	Distribution	
Dieuches notatus (Dallas)	101 (submacropt.)	0	ACT, NSW, N-WA, Q SA, T, V	
Dieuches nudus Gross and Scudder	22 (submacropt.)	0	NT, SA, WA, V, Q	
Dieuches grandicus Gross and Scudder	0	4	Torres Strait, Q	
Dieuches consanguineus Distant	0	26	Torres Strait, NT, Q	
Dieuches obscuripes (Walker)	0	10(+)	Torres Strait	
Dieuches oceanicus (Distant)	0	23	Torres Strait, N-WA, NT, Q, SA	
Dieuches hirsutus Gross and Scudder	0	.2	Q, NT, WA	
Dieuches breviceps Eyles	0	.2 3	WA, Q	
Dieuches scutellatus Distant	0	24(+)	NT, Q, SA, WA	
Dieuches curvus Eyles	0	239	NT, Q	
Dieuches distanti Bergroth	0	7()	WA, NT	
Dieuches maculicollis (Walker)	0	29	ACT, NSW, Q, SA, V	
Dieuches membranaceus Eyles	0	2	Q	
Elasmolomus sordidus (Fabricius)	0	21	NT	
<i>Elasmolomus v-album</i> (Stål)	0	3	NT, N-Q, N-WA	
Elasmolomus papuanus (Distant)	0	1	N-Q	
Narbo biplagiatus (Walker)	0	4(+)	NSW, Q	
Poeantius australopictus Gross				
and Scudder	I	8	NT, N-WA, Q	
Quiobbesus australis (Distant)	0	2(+)	NT. Q	
	124	408		

TABLE 6 WING MODIFICATION IN THE RHYPAROCHROMINI

Wing polymorphism in Drymini

The situation in this tribe in Australia is more complex than that of the Rhyparochromini. On the one hand the 2 tribes closely resemble each other in showing a very small percentage of species with reduced or modified wings. On the other hand the majority of genera of Australian Drymini are endemic to Australia (or to Australia and New Zealand) (9 of 11) and a considerable number of genera and species are present in the southern parts of the continent although 13 of 17 species occur in Queensland or the Northern Territory (Table 7). Thus the distribution is not typically Torresian as is the case in the Rhyparochromini. The Drymini might then seem to contradict the general thesis that the older elements in the Australian rhyparochromine fauna show a high degree of wing polymorphism while the more recent elements do not. Actually this may not be so. The Drymini is a very complex and relatively poorly understood taxon and it may well be that many of the genera now thought to be endemic actually are not. If this is so then they must represent a relatively

Species	Modified wings	Macropters	Distribution
Brachydrymus lateabundans Gross	10	0	NSW, T. NT, Q. V
Isopeltus australis (Bergroth)	0	152	NSW, Q, SA, T, V, WA
Isopeltus obscurus Gross	0	5	Q
Isopeltus tenuicornis Gross	0	1	Q
Brentiscerus major Gross	0	22	NSW, Q, V
Brentiscerus pallidus Gross	0	2	Q
Brentiscerus triocellatus Gross	0	8	ò
Brentiscerus diffusus Gross	0	2	ò
Austrodrymus flindersi Gross	0	17	SA, WA
Pseudodrymus florestalis Gross	0	15	Q, WA
Retrodrymus abundans Gross	0	23	T, V
Gastrodomorpha enigmatica Gross	0	1	v
Paradrymus exilirostris Bergroth	0	11	NSW, Q, SA, V
Megadrymus terraereginae Gross	0	3	ò
Scolopostethus forticornis Gross	0	17	SA, V
Appolonius territorialis Gross	0	2	NT
Appolonius robustus Gross	0	3	Q
	10	284	

TABLE 7 WING MODIFICATION IN THE DRYMINI

TABLE 8

	Тс	otal	Modified wings	Modified wings	% Species only known as non-	% Species majority of indi- viduals non-	% Genera showing non-
Tribe	genera	species	% Individuals	% Species	macropters	macropters	macroptery
Targaremini	2	4	100	100	100	100	100
Ozophorini	1	1	97	100	0	100	100
Lethaeini	7	11	70	73	55	55	86
Udeocorini	7	14	68	86	35	78	86
Stygnocorini	2	2	60	100	50	50	100
Plinthisini	1	13	51	92	84	92	100
Rhyparochromini	5	18	43	11	11	11	40
Drymini	11	17	3	6	6	6	9
Antillocorini	1	1	0	0	0	0	0
Myodochini	No dat	a, proba	bly all macrop	ters			
Cleradini	No dat	a, proba	bly all macrop	ters			

recent element from the Orient. However, even if the Drymini are an element old enough for generic endemism to have been reached, the lack of wing polymorphism can be conceived of as being the result of the presence of a group of intermediate age plus one living in habitats where the seed crop is markedly irregular, thus militating against the development of a flightless morph. Actually we know very little about the habits of most of the Australian Drymini. What is known in general indicates that they tend to be associated with "forest edge," shaded, open woodland conditions. The 2 southwestern Australian species of Drymini (*Isopeltus australis* (Bergroth), *Austrodrymus flindersi* Gross) are completely macropterous but both occur with predominantly coleopteroid specimens of other taxa although they are usually found close to the base of the host plants in the most shaded and mesic part of the habitat. *I. australis* is a characteristic ground bug of open woodlands.

I believe the Drymini are best viewed as a group of intermediate age in Australia, adapted to at least moderately mesic conditions and possibly replacing the old Targaremini either by direct competition or by better adaptation to relatively dry woodland conditions in contrast to wet humid, moss-rich mesic habitats which appear to be favored by the known Australian Targaremini.

Wing polymorphism in other Australian subfamilies of Lygaeidae

Henicocorinae.—This recently described subfamily is known from 78 specimens, all with a coleopteroid tendency (Fig. 20). The only known species occurs in moist *Nothofagus* habitats (Woodward 1968). The importance of coleoptery in *Henicocoris* Woodward is in its apparent relationship to the Idiostolidae, also associated with *Nothofagus* forest and with a South American-Australian distribution. Idiostolids certainly are an extremely old element and generally macropterous, although Shaefer and Wilcox (1969) note reduction in the membrane in 4 specimens of the South American *Idiostolus insularis* Berg. The wing modification in *Henicocoris* apparently illustrates the ability of forest living mesic habitat species of very old endemic groups to become flightless and it is similar to the situation illustrated by the Targaremini.

Orsillinae.—In Western Australia *Lepionysius grossi* Ashlock has the wings reduced to small flap-like pads (microptery) in most cases (14 of 15 specimens). Ashlock (1967) notes that wing polymorphism occurs in representatives of 8 genera (all 4 tribes) and that it occurs chiefly in species living on islands (*Hudsona* Evans, *Nesocryptias* Kirkaldy, *Robinsonocoris* Kormilev and *Nysius* Dallas) and on mountains (*Coleonysius* Ashlock, *Oreonysius* Usinger).

There is reduction to microptery in *Lepionysius* Ashlock, *Hudsona* and *Nithecus* Horvath. The other genera show various degrees of coleoptery rather than wing shortening which in *Coleonysius* results in a completely coriaceous beetle-like shell being formed.

Lygaeinae.—The majority of Lygaeinae occur above the ground on herbaceous plants and are macropterous. Wing reduction is associated with the development of ground litter living habits. It occurs in Australia in *Brachylygaeus* Gross and in Palearctic, Oriental and Ethiopian genera such as *Apterola* Mulsant and Rey, *Stenaptula* Seidenstucker, *Lygaeosoma* Spinola and *Karachicoris* Štys (see Slater and Sperry 1973, Štys 1972).

Pachygronthinae. —All of the species of the subfamily whose habits are known are plant feeders living well above the ground level. The Australian genera are mostly endemic or nearly so. Two of these, *Stenophlegyas* Slater and *Darwinocoris* Slater (both endemic), exhibit the most extreme reduction of the fore wings of any member of the subfamily. *Stenophyella* Horvath, which is chiefly Australian, frequently is submacropterous with only the membrane somewhat reduced. This latter condition occurs in some species of *Opistholeptus* Bergroth and *Cymophyes* Fieber in the Palearctic and Ethiopian regions. However, the only other microptery in the subfamily which approaches in degree that of the Australian genera is in the Western Hemisphere genus *Phlegyas* Stål. **Blissinae.**—Wing polymorphism is widespread in this subfamily, occurring in many genera. It may take the form of only moderate reduction of the membrane or extreme microptery may be exhibited wherein the fore wings are reduced to minute scale like pads. Interestingly coleoptery is never exhibited. Among the Australian genera *Australodemus* Slater and Sweet (endemic) and *Dimorphopterus* Stål (widespread in the Eastern Hemisphere) both have extremely reduced wings.

Subfamilies such as the Artheneinae, Geocorinae, Heterogastrinae and Oxycareninae in Australia are either completely or largely represented by macropters, lending I believe, additional evidence to that from the taxonomic relationships that these subfamilies are relatively recent additions to the Australian lygaeid fauna.

Host plant relationships of southwestern Australian Lygaeidae

The family Lygaeidae shows great diversity in feeding habits, for while the majority of species feed on mature plant seeds other utilize sap (Blissinae, many Lygaeinae, etc.). Others are predatory (Geocorinae) and a few suck vertebrate blood (Cleradini). It is becoming increasingly evident that within a given lygaeid taxon there is considerable food plant specialization. For example the Cyminae and Pachygronthini are largely restricted to Cyperales and Juncales, the Blissinae to monocots, the Heterogastrinae to Moraceae, Labiatae and Urticaceae, the Teracrini to grasses etc. It therefore seems particularly interesting to relate the Western Australian species of Lygaeidae to their host plants in view of the isolated nature of the flora and fauna.

The southwest Australian Cyminae in general show the same restriction to Cyperaceae as is general for the subfamily throughout the world. However one species of Ontiscus Stål utilizes a species of Restionaceae as a host. This may have implications for plant taxonomists as Hutchinson (1959) considers the Restionaceae to be a member of the order Juncales (directly ancestral to the Cyperales) whereas Takhtajan (1969) considers them to represent an independent order, the Restionales, ancestral to the Graminales and removed from the Juncales-Cyperales phyletic line. This may represent a secondary adaptation by Ontiscus to the Restionaceae as another species of Ontiscus breeds on Cyperaceae in Western Australia. A parallel case exists in the Pachygronthinae where species in the tribe Pachygronthini breed on sedges while those of the Teracrini utilize grasses. In Western Australia however the endemic monotypic teracrine Darwinocoris breeds on a species of Restionaceae. I would suggest that taken together with the fact that species of the South African Cape endemic blissine genus Capodemus Slater and Sweet utilize Cyperaceae, Gramineae and Restionaceae these lygaeid feeding data raise the possibility that the Cyperales, Graminales and Restionales may be more closely related than Takhtajan's (1969) classification indicates.

Given the radiation and diversity of the Myrtaceae in Australia it is not surprising that they are utilized as host plants by many Western Australian lygaeids. The fallen seeds of species of *Hypocalymma* serve as one of the favorite food sources of a large seed-litter lygaeid assemblage. Adults and nymphs of 4 genera and 5 species of Udeocorini, 2 species of Lethaeini (2 genera), a species of Plinthisini, a drymine, and an orsilline as well as numerous adults of an antillocorine and an ozophorine have been taken in seed litter of species of *Hypocalymma* and frequently large populations of several species occur together. The ischnorhynchine genus *Crompus* Stål frequently occurs in numbers on the flower heads of *Agonis* and *Kunzea*.

The family Epacridaceae, particularly *Leucopogon*, is also a favored seed source for litter living lygacids, many of the same species that utilize *Hypocalymma* also occurring below these plants. The antillocorine *Botocudo* nr. *ornatulus* definitely breeds here.

Complete plant relationships are given in Table 9 and under the accounts of the individual species in a forthcoming paper.

TABLE 9

HOST PLANT RELATIONSHIPS OF SOUTHWEST AUSTRALIAN LYGAEIDAE

Crompus opacus Lepionysius grossi Cryptorhamphus orbus Plinthisus nr. tineoides	a (many) anl al
Lepionysius grossi Cryptorhamphus orbus	anl
Cryptorhamphus orbus	
Plinthisus sp. n. Exomyocara australicum Coleocoris ocellatus Botocudo sp. nr. ornatulus Isopeltus australis Ethaltomarus australis Udeocoris nigroaeneus Porander scudderi Remaudiereana sp.	an anl anl anl al anl al(2) anl anl al(1)
Botocudo sp. Isopeltus australis	al anl
Cryptorhamphus orbus Cymus novaezelandiae Plinthisus nr. tineoides Coleocoris ocellatus Isopeltus australis Udeocoris nigroaeneus Euander lacertosus Fontejus nr. sidnicus	al al anl anl anl anl nl
Cryptorhamphus orhus Plinthisus nr. tineoides Coleocoris ocellatus Euander multicoloratus	al al(3) anl anl
Crompus opacus	a (many)
Coleocoris ocellatus Udeocoris nigroaeneus	ani al
Austronysius sericus	a(1)
Nysius vinitor	a
Cryptorhamphus orbus Coleocoris ocellatus Austrodrymus flindersi Euander lacertosus Fontejus westraliensis	al anl al ani al
Cryptorhamphus orbus Plinthisus sp. n. Coleocoris ocellatus Austrodrymus flindersi Euander lacertosus Fontejus westraliensis	al al anl al anl anl
Coleocoris ocellatus Isopeltus australis	al(2) al
Coleocoris ocellatus Botocudo sp. Euander multicoloratus Porander scudderi	anł anl anl anl
Lepionysius grossi	anl
	Coleocoris ocellatus Isopeltus australis Coleocoris ocellatus Botocudo sp. Euander multicoloratus Porander scudderi

AUSTRALIAN LYGAEIDAE

TABLE 9 (Con.)

Plant	Lygacidae recorded	Status*
Leucopogon tamariscinus R.Br.	Euander lacertosus Fontejus collaris Fontejus westraliensis	anl anl nl(1)
Leucopogon unilateralis Stschegl.	Lepionysius grossi Plinthisus sp. n. Botocudo sp. Isopeltus australis Euander lacertosus Euander multicoloratus Porander scudderi	anl al anl al nl (many) al anl
Andersonia caerulea R.Br.	Lepionysius grossi Plinthisus sp. n. Euander multicoloratus	al(1) al anl
Andersonia sprengelioides R.Br.	Fontejus collaris	al(1)
CHENOPODIACEAE		
Arthrocnemum halocnemoides? var. pterygospermum Black	Nysius vinitor Cryptorhamphus orbus Udeocoris scudderi	anl al anl
THYMELEACEAE		
Pimelea argentia R.Br.	Udeocoris nigroaeneus	anl
MORACEAE		
Ficus sp.	Udeocoris nigroaeneus	al
AMARANTHACEAE		
Ptilotus polystachyus (Gaud.) F. Muell.	Germalus sp. Udeocoris scudderi	an anl
RESTIONACEAE		
Lyginia tenax (Labill.) G. A. Gardn.	Ontiscus brevipilus	a (many)
Leptocarpus coangustatus Nees	Darwinocoris australicus	an
CYPERACEAE		
Lepidosperma angustatus R.Br.	Ontiscus obscurus	an
Mesomelaena stygia (R.Br.) Nees	Ontiscus obscurus	an
Tetrariopsis octandra (Necs) C. B. Clarke	Cryptorhamphus orbus	al
Cyperus tenuiflorus Rottb.	Cymodema basicornis Cymus novaezelandiae	an a (many)
GRAMINEAE		
Ehrharta brevifolia Schrad.	Stenophyella macreta Noteolethaeus armstrongi	an anl
Spartochloa scirpoides (Steud.) C. E. Hubbard	Nysius vinitor Cryptorhamphus orbus Plinthisus sp. n. Lamproceps sp.? Myocara nr. acuminatum	al al al al(1) anl

*a —adults on plant an —adults & nymphs on plant al – adults in seed litter anl —adults & nymphs in seed litter nl —nymphs in seed litter

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