The Nymphal Taxonomy and Systematics of Western Palaearctic Lygaeid Bugs (Hemiptera, Heteroptera, Lygaeidae), with Special Reference to the British Fauna

Volume 1

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Abstract

The nymphal taxonomy and systematics of Western Palaearctic lygaeid bugs (Hemiptera, Heteroptera, Lygaeidae), with special reference to the British fauna.

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Fifth instar nymphs of 80 of the 111 West Palaearctic lygaeid genera and 88 of the 90 British and Channel Island species are described and keyed. For the British fauna, 37 characters per specimen, of up to a maximum of ten specimens per species, are measured and 51 representative species are illustrated. The arrangement of spines on the prothoracic femur; the lateral view of the sterna showing sutures; spiracle and trichobothria position; the dorsal abdominal gland apertures and evaporative areas; are figured for British species and representative West Palaearctic genera. Systematic relationships, as suggested by the study of nymphal morphology, are investigated and the nomenclature and species representation in British and West Palaearctic checklists is updated. Published descriptions of nymphal Lygaeidae and all specimens held in the Liverpool Museum lygaeid collection are catalogued.

British lygaeid species distributions are mapped by ten kilometre national-grid squares. They are interpreted in geographical space and time and are discussed in relation to the ecology and biogeography of the Palaearctic and world lygaeid fauna.
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Lygaeid bugs are found throughout the world. The majority of the 3,000 known species are cryptically coloured, ground dwelling and feed upon mature seeds. Sweet (1960) suggested that an appropriate and satisfying name for the Lygaeidae would be "the seed bugs". This he maintained would give the family concept a biological as well as morphological unity.

Of the 17 subfamilies, only the Geocorinae are definitely predacious, whilst members of the Cleradini and a single drymine, are unique in being haematophagous. One other subfamily, the laminaphilous Blissinae, is phytophagous but not seed feeding.

Species of Blissinae, the Chinch bugs, are economically important pests of cultivated crops, as are members of the Orsillinae, Oxycareninae and Rhyparochrominae. The Nearctic Oncopeltus fasciatus (Dallas) is frequently used for physiological and toxicological experiments, whilst observations on Hawaiian Orsillinae have provided a classic study on evolutionary radiation on islands.

Slater (1964a) in his 'Catalogue of the Lygaeidae of the World', stressed that "this family with its great diversity of form, habitat, feeding behaviour and distribution appeared to offer an unusually fertile field for investigation". He pointed out that the basic bionomics of the vast majority of lygaeids were still unknown.
2. Objectives

The primary aims of this study were to:-

1) Provide detailed comparative descriptions of the fifth instar of nymphs of the 111 Western Palaearctic Lygaeidae genera.

2) Provide detailed comparative descriptions of the fifth instar of nymphs of the 90 British and Channel Island Lygaeidae species.

3) Produce taxonomic keys for British species and Western Palaearctic subfamilies, tribes and genera.

4) Investigate systematic relationships within the group, as suggested by the study of nymphal morphology.

5) Study patterns of distribution of the British species and relate this to West Palaearctic and world lygaeid biogeography.

6) Update nomenclature and species representation in British and West Palaearctic lygaeid checklists.

7) Catalogue all descriptions of nymphal Lygaeidae.

9) Establish a well curated and documented research collection at Liverpool Museum.
3. Introduction

3.1 The Study of Immature Insects

McGavin (1979) reviewed the reasons for studying immature insects. These are briefly summarised as follows:

Characters of immature stages are as valuable as those of adults for taxonomic and systematic study. Studies of immature stages may confirm or call into question phylogenetic hypotheses based on adult characters, thus defining congruent or incongruent groups (Van Emden, 1957).

Adults in general show greater morphological differentiation than immatures and are more suitable for species identification. However, morphological characters of immature stages can be more important for broad classification such as defining higher categories (Van Emden, 1955). Immature stages support the primary division of the Coleoptera, Diptera and Hymenoptera and are as important as adult characters in the subdivision of the Odonata and Neuroptera.

Comparative studies of immature forms are valuable in attempts to correlate ontogeny with phylogeny.

Taxonomic knowledge of immature stages is important for quantitative ecological research.

It has become obvious during this present study that knowledge of immature stages is of particular importance for site survey work, by substantiating the breeding presence of species at particular sites, so aiding the conservation of rare species.

3.2 Immature Lygaeidae - Role of Taxonomic Studies

Slater (1964a) considered that the systematic description and integration into the classification of the immature stages of Lygaeidae is in need of much investigation. The little work accomplished indicates that the characters of the immature stages are often very important in classification. Collectors and Museums, he suggested,
"should make every effort to obtain and associate these stages with the adults". His views are supported by other workers. For instance, nymphal morphology proved as useful as that of the adults in taxonomic studies on Australian and New Zealand Lygaeidae (Malipatil, 1975, 1977a, 1977b, 1977c; Woodward, 1977; Malipatil, 1978a), whilst the lack of nymphal material hindered the re-evaluation of the Lethaeini (Ashlock, 1964). Puchkov (1958a), in a study of lygaeid nymphs in the European part of the former USSR, noted a number of nymphal characters that confirmed or refuted the naturalness of the taxonomic groupings and, to a certain extent, the affinities between the species that composed them. The classification categories of the Lygaeidae must, in the future, be based in part upon nymphal material, before we can hope to have a truly mature classification (Slater & Sweet, 1961).

Nymphal taxonomy is thus playing an increasingly significant role in systematic and phylogenetic studies on the Lygaeidae. Slater & Sweet (1961) proposed modifications in the tribal classification of the Rhyparochrominae and Puchkov (1958a) divided it into three subfamilies, on the basis of nymphal evidence. In the Cleradine complex, characters of immature forms proved decisive for the tribal classification of Sweet (1967), whilst Ashlock (1964) used nymphal characters to suggest that members of the rhyparochromine tribe Targaremini are only distantly related to the Lethaeini and Antillocorini. Slater's (1952a) study of nymphal Cyminae indicated that the subfamily, as constituted, was not a natural assemblage of genera and species, and he provisionally proposed the removal of Kleidocerys Stephens. In a further study, Slater (1963) concluded that the Cyminae occupy an isolated position with respect to the rest of the Nearctic Lygaeidae. He considered that nymphal characters substantiated the distinction, at subfamily level, of the Ischnorhynchinae from the Cyminae.

At a lower taxonomic level there are numerous examples of the influence of nymphal studies on lygaeid taxonomy and these are cited in the systematic discussion. For instance, the unplaced genus Prostemmaidea Reuter was assigned to the Megalonotini once a nymph was discovered (Chopra & Rustagi,
1982). Apparently similar *Ischnodemus* Fieber adults were found to have markedly different nymphs, making it improbable that only one species was involved (Slater, 1987a), whilst adult and immature *Capodemus* Slater & Sweet are distinguished by different sets of characters (Slater & Sweet, 1972).

3.3 Taxonomic Studies on Immature Lygaeidae

Lygaeid nymphal identification and descriptive work is summarised in this section and details of all published information are systematically tabulated in Appendix 1. This indicates the priorities for future work, by highlighting the inadequacies in current systematic and geographical representation, and also places this study in context.

3.3.1 Identification Keys

A limited number of keys have been produced, providing a basic framework for more detailed investigations:

The Heteroptera are hemimetabolous and normally pass through five nymphal instars. Gulde (1919), studying pentatomid nymphs, first recognised the simple relationship between nymphal wing-bud development and instar. The numerous instar identification errors by early workers (e.g. Collett, 1927; Jordan, 1935) are documented by Puchkov (1958a), who emphasised that among the large number of descriptions in Butler (1923) there was a near absence of reference to the nymphal stages. Dolling (1991) and Southwood (1956a), adapting the earlier work of Slater (1951), key out the Heteroptera instars, whilst single species instar keys for *Heterogaster urticae* (Fabricius) and *Lachnophoroides thompsoni* Woodward have been produced (Servadei, 1951; Woodward, 1977). Characters used in all of these keys are discussed further in the section on nymphal morphology.

Kirkaldy (1908a) first constructed a key to Heteroptera families, based on the characters of the nymphs. Jordan (1951) produced a nymphal key to Heteropteran families in Germany. Nymphs for the British Heteropteran families were
artificially keyed out in Leston and Scudder (1956) but no attempt was made to indicate phylogenetic relationships. This key was later improved by Dolling (1991). Nymphs of 41 North American (North of Mexico) heteropteran families were included in Herring & Ashlock (1971), replacing earlier works on selected families (Lawson, 1959). Subsequently, the nymphs of North American Heteroptera have also been keyed to family by DeCourcey (1971) and Slater & Baranowski (1978a).

DeCourcey (1971) provided keys to the subfamilies of Nearctic Lygaeidae. Slater & Sweet's (1961) earlier classification of the Lygaeidae, distinguished nine subfamilies and seven rhyparochromine tribes, whilst Sweet's (1967) classification of the Rhyparochrominae, included a tribal key to adults and late instars.

Puchkov (1958a, 1969) originally provided keys to 56 of the 75 genera listed for the former European USSR, which were later modified to incorporate nine additional genera and 86 species. These are the most important works in relation to the present study, but unfortunately the latter (Puchkov, 1969) has not been translated from its original Ukrainian. Slater (1951) produced an initial generic key to Mid-Western Lygaeidae, a work extended in geographical scope and species coverage by Sweet & Slater's (1961) key to the 53 Nearctic genera.

Slater later (1952a, 1963) developed keys to some final instar North American Cymini and Ninini and included incomplete keys to Cymus Hahn, whilst Ledvinka (1970) keyed out four European Cymus species which occur in Britain. Immature Pachygronthinae genera and species were treated by Slater, (1952b, 1966) and Baranowski & Slater (1982). Malipatil (1978a) added to Slater's (1976a) separation of immature South-West Australian Lygaeidae and seventeen species of South African Lygaeinae were keyed by Slater & Sperry (1973).

The immature stages of the Blissinae have received more attention than those of other lygaeid subfamilies. Keys to final instars are published for three genera and six former European USSR species; the Blissus leucopterus (Say)

Recent works on the identification of species include:- a key to Hemipteran nymphs (including Lygaeidae) injurious to crops (Puchkov & Puchkova, 1956); keys to four *Heterogaster* Schilling species found in the old European USSR (Puchkov, 1959); South African *Heterogastrinae* (Slater, 1971a); six Florida *Ozophora* Uhler (Slater & Baranowski, 1983); four Australian *Ontiscus* Stål (Malipatil, 1977a) and work on the Hawaiian *Orsillinae* (Usinger, 1942).

All 277 lygaeid species featured in keys are listed in Appendix 1 and their family distribution is summarised in Table 1.

### 3.3.2 Descriptions of Nymphs of Lygaeid Species - 'World-wide'

A total of 351 species, just 18% of the world fauna and 128 species, 30% of the West Palaearctic fauna, are described in the literature, together with whole animal drawings for 180 world and 80 West Palaearctic species. The frequency distribution of these studies across subfamilies is summarised in Table 1. Only the Blissinae, Oxycareninae, Artheneinae and Pachygronthinae with 20% species coverage and the Cyminae with 30% have been studied in detail. The Ischnorhynchinae, Geocorinae and Heterogastrinae are particularly poorly represented with under 10% of their species described and no nymphs are known for Cryptorhamphinae, Slaterellinae, Psamminae, Bledionotinae and Henicocorinae.

Many early descriptions of lygaeid nymphs, listed in Appendix 1, have little scientific value. They are brief, lack measurements and rely upon general colouration. The work of Malipatil, Slater and others is, however, very thorough and Puchkov's (1969) account of the Ukrainian fauna contains 63 full animal drawings with brief generic and species descriptions.
Within the Blissinae, nymphs of 69 species are described, including 33 South African species (Slater & Wilcox, 1973a, 1973b). Six economically important *Blissus* Burmeister species were discussed by Leonard (1968) and Mailloux & Streu (1981), while Slater et al. (1969) gave an account of six species from Thailand and Indonesia. All instars of *Ischnodemus oblongus* (Fabricius) and *I. fulvipes* (Degeer) were described by Baranowski (1979). Slater & Brailovsky (1983) described the fifth instar nymphs of five *Toonglasa* Distant species from Mexico and their later (1986a) study of *Riggiella lucida* Slater & Brailovsky nymphs, clearly indicated that earlier conclusions on phylogenetic relationships in Slater (1979), were incorrect.

The nymphs of Lygaeinae are relatively well studied. Slater & Sperry (1973) described 17 South African species from eight genera. The Oriental subspecies of *Spilostethus pandurus* (Scopoli) (Bhattacherjee, 1959; Hamid & Ahmed, 1972) and other single species, are well documented (Dhamdhere & Rawat, 1967; Roy et al., 1989; Mukhopadhyay et al., 1990).

In the Orsillinae, 12 Hawaiian species were described by Usinger (1942). Slater & Ashlock (1980) gave an account of two South African *Camptocoris* Puton species, while Wheeler (1984) reviewed the behaviour and immature stages of arboreal North American *Belonochilus numenius* (Say). Sixteen cymine species were described by Slater (1952a, 1963, 1976a) and Malipatil (1977a, 1978a, 1978b) figured two Australian *Ontiscus* and one New Zealand *Cymus* species, and Hamid (1971a) separated the instars for three North American *Cymus* species.

In the Oxycareninae, the nymph of *Barberocoris myrmecoides* Slater & Sweet and nymphs of three South African *Oxycarenus* Fieber and one *Leptodemus* Reuter species, are known (Slater & Sweet, 1970a; Slater 1972a). Seidenstücker & Josifov (1961) briefly commented on the nymph of *Auchenodes joakimoffi* Seidenstücker & Josifov while Aukema (1976) figured *Oxycarenus modestus* (Fallén).

The artheneine *Nothochromus maoricus* Slater et al. is
described (Malipatil, 1977b), together with four African Heterogaster Schilling (Slater, 1971a) and 13 Pachygronthinae (Slater, 1952b, 1966, 1976a; Baranowski & Slater, 1982). A total of 46 Australasian species are known (Malipatil, 1975; Slater, 1976a; Malipatil, 1977a; 1977b; 1978a, 1978b).

Ozophora, with 12 species described, have received considerable attention (Slater & Baranowski, 1978b; Slater & O'Donnell, 1979; Slater & Baranowski, 1983; Slater, 1987b) but the remainder of the Rhyparochrominae are poorly studied. Malipatil (1975, 1978a) described 18 Australasian species, adding to the earlier work of Slater (1976a). Within the Lethaeini, the immatures of one Austroxestus Woodward, one Cistalia Stål species, two Trinidadian Lipostemmata Berg restricted to an aquatic fern, and two Cryphula Stål species, are characterised (Woodward, 1962; Slater & Baranowski, 1973; Baranowski & Bennett, 1979; Baranowski & Slater, 1979). In addition, two antillocorine Bathydema Uhler and two stygnocorine Notiocola Slater & Sweet species, were depicted by Slater & Sweet (1970b) and Slater et al. (1977). Indian Prostemmidea Reuter were confirmed within the Megalonotini, once nymphs were found (Chopra & Rustagi, 1982). Finally, nymphs of the zoophagous Mizaldus nidulus Slater & Carayon were described by Slater & Carayon (1963).

3.3.3 Descriptions of Nymphs of British Lygaeid Species

There is little information on the immature stages of British Lygaeidae and, although 61 species have been described, with varying adequacy, much of this work is by overseas workers (cited above), using non-British material. The majority require redescription, in a consistent style. The only detailed work by a British author was on the bionomies of five Rhyparochrominae species (Eyles, 1962, 1963a). Butler (1923) included short but incomplete descriptions of 39 Lygaeidae. These descriptions were vague and usually not accompanied by figures. The detailed description of Pachybrachiis fracticollis (Schilling), was a notable exception. Collett's (1927) description of Chilacis typhae (Perris) is similarly inaccurate. Heterogaster urticae nymphs were characterised in studies
on the insect fauna of *Urtica dioica* Linnaeus by Southwood and Scudder (1956). Southwood's (1956a) key to nymphal instars and Leston & Scudder's (1956) artificial key to the nymphs of British Heteroptera retain value but are superseded by Dolling (1991). Southwood & Leston (1959) included brief descriptions of some lygaeid nymphs, occasionally accompanied by whole animal drawings; but, as yet, there is no key to British fifth instar lygaeid bugs.

British species that feature in continental literature, in addition to Puchkov (1958a, 1969), include four *Cymus* species. These received considerable attention, particularly *C. glandicicolor* Hahn, for which Butler (1923) described the "final instar". This is the fourth instar as stated by Slater (1952a). Jordan (1935) described and figured instars 1-4, but his implication that there was no fifth instar was incorrect (Ledvinka, 1970).

Servadei (1951) characterised all stages of *Heterogaster urticae*, while Holste (1922) and Aitkins (1936) described the life history and instars of *Gastrodes abietum* Bergroth. Ollivier (1979) studied the bionomics and ecology of *Kleidocerys truncatus ericae* (Horváth), figuring and describing all instars, while Cobben (1953) described all instars of *Pterotmetus staphyliniformis*. Late instar nymphs of *Megalonotus chiragra* (Fabricius) = *sabulicola* Thomson, a species introduced into North America, were described by Slater & Sweet (1958).

3.4 Other Studies on Adult Lygaeidae

Investigations on the 200 Hawaiian archipelago Orsillinae, half of the total world orsiline species, revealed rapid insular radiation and form a classic evolutionary study (White, 1878; Kirkaldy, 1902, 1907a, 1910; Usinger, 1942; Usinger & Ashlock, 1959; Ashlock, 1963, 1966; Beardsley, 1966).
Table 1. Summary of Descriptive Studies on World Lygaeidae

<table>
<thead>
<tr>
<th>Subfamily</th>
<th>World Fauna</th>
<th>Total Number of Species</th>
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<tr>
<td>Rhyparochrominae</td>
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<td>Phasmosomini</td>
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<td>8</td>
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<tr>
<td>Myodochini</td>
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<td>14</td>
</tr>
<tr>
<td><strong>Totals</strong></td>
<td></td>
<td>277</td>
</tr>
</tbody>
</table>
Recent adult single character studies include work on the phallus (Ashlock, 1957; Çağatay, 1989; Deckert, 1990; O'Donnell, 1991), male-produced scents (Harrington, 1991), stridulatory structures (Ashlock & Lattin, 1963), the metathoracic wing (Slater & Hurlburt, 1957), wing polymorphism (Sweet, 1963; Slater, 1977), pulvillus (Goel & Schaefer, 1970), trichobothria (Schaefer, 1966, 1975) and rostrum (Cobben, 1978). Cytotaxonomy has been studied by Ueshima & Ashlock (1980) and egg structure investigated (Puchkova 1956; Southwood 1956b; Cobben 1968).

The world Orsillinae (Ashlock, 1967), Ischnorrhynchinae (Scudder, 1962a), Cyminae (Hamid, 1975), Blissinae (Slater, 1979), Bledionotinae (Scudder, 1963a), Pachygronthinae (Slater, 1955), Heterogastrinae (Scudder, 1962b) and Rhyparochrominae tribes Lilliputocorini (Slater & Woodward, 1982) and Myodochini (Harrington, 1980) have all been systematically revised at generic or species level and the higher Rhyparochrominae taxa have received considerable attention (Scudder, 1957a, 1962c, 1967, 1969, 1970a, 1970b, 1977, 1981a, 1981b, 1984). Other important regional revisions e.g. on Australian and Western Hemisphere Lygaeinae (Slater (A.), 1985, 1992) and studies on tropical faunas are referred to in the annotated checklist (Section 5).

These studies, together with research on immature stages, have advanced our knowledge and understanding of world Lygaeidae. They have redefined the family concept, moving from the European perspective of Stål (1872, 1874) and other nineteenth century workers, to a new, mature and relatively stable definition of the higher taxa based on multi-character analysis of all stages across the world fauna.

3.5 British and Palaearctic Faunal Studies

Stichel's (1957-59) illustrated keys, individual species descriptions and accompanying country distributions are still the standard reference for the European Heteropteran fauna. European former USSR Lygaeidae are keyed in Kerzhner & Yachevskii (1967). The British lygaeid fauna is relatively well-studied, with a number of books providing
keys to adults together with distributional and biological accounts (Douglas & Scott, 1865; Saunders, 1892; Butler, 1923; Southwood & Leston, 1959). Recently, the biology and taxonomy of British Hemiptera was reviewed within a world context by Dolling (1991).

3.6 British Regional Distributional Studies

There is some information on the county distribution of the British Lygaeidae (Bedwell, 1945; Massee, 1955) and records for Kent (Massee, 1954, 1962) and the London area (Groves, 1965) are the most detailed regional lists. Other notable county faunas and distribution record sources are listed in Appendix 11. Halbert (1935) records the distribution of Irish Lygaeidae.

3.7 Biology of the Lygaeidae

Little is known about lygaeid ecology or developmental stages, except for the economically important or experimental species (Miller, 1971). The most notable exception is a detailed study on 39 New England rhyparochromines by Sweet (1963, 1964).

There are outline biological accounts of varying quality for all British species (Douglas & Scott, 1865; Saunders, 1892; Butler, 1923; Southwood & Leston, 1959). Thomas (1955) provided additional notes on eleven species and Eyles (1964) discussed the feeding habits of five Rhyparochrominae, describing experiments showing the effects of different foods on development. Thirty-four uncommon species had their habitat, ecology and conservation status reviewed by Kirby (1992).

Detailed bionomic studies on the British and West Palaearctic fauna are limited. The most extensive is on Lygaeus equestris (Linnaeus) (Solbreck & Kugelberg, 1972; Kugelberg, 1973a, 1973b, 1973c, 1974, 1977a, 1977b), with a related study on Spilostethus pandurus (Kugelberg, 1976). Puchkov (1956) studied basic trophic groups of phytophagous Hemiptera and changes in feeding habits during the process of development and two cone dwelling British Gastrodes Westwood were the subject of detailed biological studies.
(Nageli, 1933; Aitkins 1936). *Nysius groenlandicus* (Zetterstedt), *Nithecus jacobaeae* (Schilling), and *Ischnodemus sableti* (Fallén) were extensively investigated by Böcher (1972, 1975a, 1975b, 1976, 1978), Coulianos (1961), Scudder, (1957b) and Tischler (1960) respectively. The life history and food plant preferences of British *Kleidocerys resedae* (Panzer) and *K. truncatulus* were recorded by Woodroffe (1960a) and Wheeler (1976) and the biology of the former species on European White birch, *Betula pendula* Roth, and ericaceous species in North America was investigated.


Slater (1975, 1976b) studied the biology and zoogeography of South-West Australian Lygaeidae and there are life history and host plant data for 24 species of Lygaeidae from South-East Queensland (Malipatil, 1979). Recent American work records the phenology of the pterygopolytrophic myodochine *Ligyrocoris barberi* Sweet (Sweet, 1986), the biology and foodplants of *Lygaeus turcicus* Fabricius (Slater, 1983a) and also covers the introduced British *Chilacis typhae* and the seasonal history of the arboreal North American orsilline *Belonochilus numenius* (Wheeler, 1984; Wheeler & Fetter, 1987).

Other, limited biological studies on the subfamilies include: Lygaeinae (Simanton & Andre, 1936; Dhamdhere & Rawat, 1967; Baranowski & Slater, 1975; Thangavelu, 1978; Slater, 1983a); Orsillinae (Kirkaldy, 1907a; Beardsley, 1966, 1977, 1979), Blissinae (Hidaka, 1959; Baranowski, 1979), Cyminae (Slater, 1952a; Hamid, 1975), Artheneinae (Chopra & Rustagi, 1980), Heterogastrinae (Slater, 1971a) and Rhyparochrominae (Baranowski & Bennett, 1979; Baranowski & Slater, 1979; Slater, 1982).
3.8 Experimentally Important Species of Lygaeidae

An extensive 'experimental' literature exists on Oncopeltus fasciatus (Dallas) (e.g. Ralph, 1976; for pre-1964 references see Slater, 1964a). Similarly, Nearctic Neacoryphus bicrucis (Say) and Palaearctic Horvathiolus gibbicollis (Costa) are widely used for controlled bionomic and morphological studies (Solbreck, 1979, 1986; Solbreck & Pehrson, 1979; McLain, 1984). Predatory geocorines are also kept as laboratory experimental animals (Dunbar & Bacon, 1972; Cohen & Debolt, 1983; Cohen, 1984, 1985; Naranjo & Stimac, 1985; Rogers & Sullivan, 1986).

3.9 Economically Important Species of Lygaeidae

Economically important agricultural and horticultural pests are found in the Lygaeinae, Orsillinae, Blissinae, Oxycareninae and Rhyparochrominae.

Members of the Blissinae such as the North American Chinch bug, Blissus leucopterus, include pests of cultivated crops. Among the Orsillinae, Nysius thymi (Wolff) is injurious to farm crops in the former USSR (Puchkov & Puchkova, 1956). Several Nysius Dallas are pests of cultivated crops (Hoffmann, 1932) and the Rutherglen bug, N. vinitor Bergroth, is a major Australian pest of sunflowers (Kehat & Wyndham, 1972, 1973, 1974). Oxycarenus are economically important pests of cotton and okra (Kirkpatrick, 1923; Odhiambo, 1957; Hammad et al., 1972; Ewete, 1984). Spilostethus pandurus causes sporadic damage to crops in India (Ahmad, 1946; Chopra, 1971; Thangavelu, 1981).

In the Rhyparochrominae, Dieuches albostriatus (Fabricius) and D. armatipes (Walker) attack groundnuts in tropical Africa (Eyles, 1973), as does Elasmolomus sordidus (Fabricius) (Hoffmann, 1932; Corby, 1947). Movements by large numbers of this insect were audible in one infestation, where accumulations up to half an inch thick of exuviae were found. Other related species such as Myodocha serripes Olivier attack strawberries (Bryson, 1939).
Lygaeidae are not normally considered household pests but aggregations of *Eremocoris borealis* (Dallas) and *E. ferus* (Say) were reported infesting, respectively, a mountain home in Pennsylvania and a household in Connecticut, USA (Wheeler, 1989). *Kleidocerys resedae* congregates on sidewalks and enters houses in America, where infestations of *Neacoryphus lateralis* (Dallas) and *Ischnodemus falcicus* Say are also reported (Wheeler, 1975, 1982).

Geocorinae may have value as biological control agents for agricultural pests. *Geocoris* Fallén adults and nymphs, predate on economically important thrips in India (Veer, 1984). Other Lygaeidae that feed on fallen weed seed may beneficially prevent germination.

The observation that *Leptodemus minutus* (Jakovlev) sucks human blood (Bergevin, 1923) was dismissed as random exploration for moisture (Slater, 1972a). This probably also applies to *Macropternella inermis* (Fieber), and to *Nysius* swarms in Sudan and Kuwait, where specimens inflicted painful bites and swellings on exposed parts of the human body (Priesner & Alfieri, 1953; Lewis, 1958; Al-Houty, 1990).

### 3.10 Parasites and Fungi

There is much scope for research on the natural enemies of Hemiptera in Britain (Dolling, 1991). Tachinid flies are the major endoparasites of Lygaeidae (Sweet, 1963; Attia, 1973; Malipatil, 1979; Loudon & Attia, 1981; Sweet, 1986). *Cinochira atra* Zetterstedt is an occasional parasite of *Scolopostethus thomsoni* Reuter, *S. decoratus* (Hahn), *Drymus sylvaticus* (Fabricius) and *D. brunneus* (Sahlberg) and *Alophora pusilla* Meigen is recorded from *Stygncoris fuligineus* (Geoffroy), *Stygncoris sabulosus* (Schilling) and *Chilacis typhae* (Van Emden, 1954; Eyles, 1962). *Scolopostethus thomsoni* and *Eremocoris plebejus* (Fallén) are parasitised by tachinids in Germany (Michalk, 1935, 1938).

Japanese Blissinae host the Stresipteran *Blissoxenos esaklii* Miyamato & Kifune and eggs of a further species are
parasitised by a trichogramatid wasp (Yashiro, 1979). A chalcid is recorded from *Eremocoris plebejus* (Michalk, 1940) and a scelionid from the eggs of *Gastrodes grossipes* (Nageli, 1933). *Scolopostethus affinis* (Schilling) is parasitised by the larvae of an *Allothrombium* mite (Michalk, 1938) and *Thrombidium* mites are recorded on *Myodocha serripes* and *Scolopostethus diffidens* Horváth (Sweet, 1963).

The sole fungal record is a tentative association between British *Stygnocoris fuligineus* and a *Paecilomyces* fungus (Eyles, 1962).

### 3.11 Predators of Lygaeidae

There are no recorded specific predators of Lygaeidae (Malipatil, 1979). Two prostemmatine bug genera are recorded predating Hemiptera, and Lygaeidae in particular (Péricart, 1987). Two dead *Scolopostethus affinis* were found bound in a spider's web (Eyles, 1962). Thomas (1955) thought nabids, anthocorids and *Lithobius* centipedes were important British predators. The reduviid *Coranus subapterus* (De Geer) feeds on an unknown rhyparochromine (Morley, 1905) and an asilid fly, *Dioctria atricapilla*, preys on the ground-dwelling *Peritrechus geniculatus* (Hahn) (Dolling, 1991).

*Nysius ericae* (Schilling), the False Chinch bug, was recorded in the stomachs of 46 species of birds in Utah (Knowlton & Wood, 1943). Sweet (1963) listed birds, lizards and insects predating rhyparochromines, concluding that it is unlikely, as Thomas (1955) thought, that rhyparochromines have unusually low mortality rates.

### 3.12 Feeding Strategies of Lygaeidae

Most Lygaeidae are seed feeders (Puchkov & Puchkova, 1956; Puchkov, 1956; Sweet, 1960, 1964; Eyles 1964) and, although normally oligophagous, many species show distinct preference for the seeds of certain species (Malipatil, 1979). Seed bugs is still a good vernacular name for the family, even though seed feeding is not universal as Sweet (1960) implied (Sweet, 1963). Lygaeids can feed on a
variety of plants to sustain maintenance metabolism, but require specific seeds for reproduction (Eyles, 1964). Corpora allata hormone production in Oncopeltus fasciatus is controlled by seed feeding, with seed starvation causing egg production to cease (Johansson, 1958).

Nysius ericae, the False Chinch bug, can be reared on hulled sunflower seeds and close crowding in rearing containers is beneficial (Burgess & Weegar, 1986). Biney (1984) studied aggregation of Dieuches femoralis Dohrn and observed that solitary specimens developed more frequently into females than males. Janzen (1971) suggested that the pattern of seed predation is highly coevolved at the chemical, spatial and temporal level.

Most Rhyparochrominae feed on fallen seeds. The British Gastrodes species, found in conifer cones, and two Indonesian Botocudo Kirkaldy species from vertical rock faces, are exceptions (Slater & Polhemus, 1987), so are host specific, West Palaearctic Artheneini associated with Tamarix, Salix and Typha. Slater (1971a) noted that the most striking feature of South African Heterogastrinae was the almost uniquely arboreal association of the entire fauna with Ficus spp. British Heterogaster urchiae are frequently swept from the developing seed heads of Urtica dioica, as are Platylax salviae (Schilling) on Salvia. Other species, particularly Lygaeinae, such as Caenocoris neri (Germar) on Oleander, are host specific on shrubs and trees and the related milkweed bugs sequester cardiac glycosides from their specific host plants (Scudder & Duffey, 1972; Scudder & Meredith, 1982). Cymophyes Fieber (Pachygronthinae) and Cyminae comprise a unique trophic guild of Lygaeidae by feeding on sedge seed (Baranowski & Slater, 1982), while Botocudo cavernicola Slater and Cligenes subcavicola Scudder feed on seeds in bat guano (Slater, 1983b).

Not all phytophagous Lygaeidae are seed feeding and laminaphile Blissinae, for example, breed on the monocotyledon plants where they feed on sap (Slater, 1967, 1976c, 1979). Lipostemmata Berg species from Trinidad are highly stenophagous and are associated with a single species of aquatic fern (Baranowski & Bennett, 1979).
Paromius gracilis (Rambur) is exceptional among rhyparochromines in that leaves, stems and developing seed heads (not ripe seeds) support both growth and oviposition (Malipatil, 1979). Similarly, the Indian lygaeine, Aethalotus horni Breddin, is not an obligatory seed feeder, and survives and reproduces on its host plant all year round (Mukhopadhyay et al., 1991). Thomas (1955) investigated the feeding habits of some British rhyparochromines and found that they fed on buds, moss, dead and dying insects. Finally, in contrast, the Australian Oxycarenus arctatus Walker completes post-embryonic development in cow dung during drought conditions (Woodward, 1984).

Geocorines are the only large group of entomophagous lygaeids. The drymine Mizaldus nidulus is, with the addition of the haematophagous Cleradini, unique among Rhyparochrominae in being zoophagous (Miyamoto, 1955; Slater & Carayon, 1963) and beetle larvae did support growth to fifth instar in British Drymus sylvaticus (Fabricius), which may be partially omnivorous (Eyles, 1964). The myodochine Xenydrium formiciforme Bergroth is a predator on eggs and larvae of a ponerine ant (Sweet, 1963).

Habitat information and host associations, recorded during fieldwork, are found in Appendices 2 and 3 and should be used in conjunction with the records for species in Appendix 5.

3.13 Dispersal

Leston (1957) defined the spread potential of a taxon, an expression of its relative ability to disperse and colonise. Lygaeidae have the second highest spread potential after Miridae in the Heteroptera.

Most successful colonisers are good flyers. Lygaeidae have been recorded 250km out to sea (Johnson, 1969) and at high altitudes (Glick, 1939; Freeman, 1945). Southwood (1960) showed that species trapped most frequently in light and suction traps throughout the world were those that bred on annual plants, or plants in semi-arid and seral
communities. Miridae and Lygaeidae were particularly common. Furthermore, these two families are common in remote locations, such as islands in the Pacific, which suggests that they spread prolifically (Leston, 1957). Scudder (1968) recorded sixteen species over world oceans.

Migratory flights are well documented. Neacoryphus bicrucis Say and Oncopeltus fasciatus undergo long-range migration in North America and are regularly collected at high altitudes (Solbreck, 1979). In Sweden Lygaeus equestris, a British vagrant, has four separate periods of flight: post teneral trivial flights, autumn migration, spring migration and trivial migration (Solbreck & Kugelberg, 1972).

Flights of the Hawaiian orsilline, Nysius coenosulus Stål, have interrupted observations of the sun at an observatory: a person standing in the swarm could not see or breathe (Beardsley, 1966). In temperate regions blissines and rhyparochromines exhibit diurnal flight: in Southern England this is mostly post-hibernation, during warm days in early May, and to a lesser extent pre-hibernation in the autumn. Heterogaster urticae, in particular, undertakes numerous short flights (Southwood, 1960).

Wing reduction, or brachyptery, is well known in the Lygaeidae (Sweet, 1963). Slater (1977) found a correlation between brachyptery and permanency of habitat, especially for xerosere habitats. He suggested that the proportion of species showing wing polymorphism may be indicative of the stability of an area, both in evolutionary and ecological time. The occurrence of flightless individuals and the resulting isolation has produced rapid speciation in some genera, such as in the Palaearctic Plinthisus Stephens (Slater, 1964b).
4. Materials and Methods

4.1 Availability of Material for Study

At the start of this study there was little available nymphal material of British or West Palaearctic Lygaeidae. The British Museum had only 12 species in the Southwood spirit collection and more comprehensive freeze dried Woodroffe specimens were not ideal for detailed examination. Other persons, listed in Appendix 4, kindly made material available. A large amount of new material was collected in the field: 274 separate collecting visits were made to sites throughout Britain (Map 1, Appendix 2) and a further 369 collecting visits were made to sites in France, Italy, Spain, Yugoslavia and Turkey (Map 2, Appendix 3).

Nymphs of elusive and undescribed British Taphropeltus limbatus (Fieber) and Peritrechus distinguendus (Flor) remain unrepresented in this study; the latter is a rare, unestablished vagrant. A further two native British species, Acompus pallipes (Herrich-Schaeffer) and Lasiosomus enervis (Herrich-Schaeffer), and the vagrants Lygaeus equestris, L. simulans Deckert, Metopoplax ditomoides Fieber, Peritrechus angusticollis (Sahlberg) and Xanthochilus quadratus (Fabricius) were represented by European or Channel Island specimens.

Adult Nysius present difficult taxonomic problems, which go beyond this study. It is almost certain that nymphs of all the six British and Channel Island species were collected, but only two have been described because of the uncertainty of adult identification and association. The collection of some 1,048 adults and associated Nysius nymphs could form the nucleus for a future study.

A total of 2,228 specimens representing 165 West Palaearctic lygaeid species were collected as fifth or earlier instar nymphs. Representatives of all 13 subfamilies, 16 out of the 17 tribes and 80 of the 111 recorded West Palaearctic genera, were studied (see checklist, descriptive accounts and collection catalogue). Eleven of the remaining 31 unseen genera are monobasic, and eight of these, together with a further six species, are on
the extremes of their range in the West Palaearctic and do not occur in Western Europe. The Oxycareninae was the most poorly represented subfamily with specimens of nine of the 15 genera unavailable. Nymphs of Phasmosomus araxis Kiritshenko, the only member of the monobasic Phasmosomini, were the most notable omission.

The majority of fifth instar nymphs were collected in association with adults, which aided identification. Some critical species and problem specimens were reared through to adult on sunflower seeds (Sweet 1960, 1963; Coulianos & Kugelberg, 1973).

Adult and immature ground-dwelling Lygaeidae were searched for by hand, or by sieving litter, an operation admirably summarised as "very much like a busy hen, scratching and searching for her juicy morsels among the dead leaves" (Barber, 1928). Arboreal species were knocked onto a beating tray and herbage was swept with a sweep net, for plant-dwelling species. Adults and nymphs were collected and placed into 70% alcohol. Each collection site was given a unique running number which was subdivided to associate adults with nymphs and with specific habitat or other biological information.

A full collection catalogue is presented in Appendix 5. This can be cross-referenced using the collecting site code to Appendices 2 and 3, which provide additional site and other biological information. West Palaearctic genera not recorded in this study are listed in Appendix 6.

4.2 Descriptions of Fifth Instar Lygaeid Nymphs

4.2.1 Written Descriptions

Generic descriptions are provided for 80 of the 111 West Palaearctic and all of the British and Channel Island genera. The species illustrations are supported by full written fifth instar descriptions for all but two of the 90 British and Channel Island species. Descriptions are, where possible, ideally based on fifth instar specimens from across the range of a species. Very occasionally they are based on earlier instars. The number of specimens examined
per species is listed after the descriptive account and the codes refer to material cited in the catalogue (Appendix 5). Additional loan material is listed in full, after the species or generic accounts; it is not entered in the Liverpool Museum collection catalogue.

Diagnostic keys to British species and West Palaearctic subfamilies, tribes and 80 genera are provided. Occasionally it was possible to key species using literature sources, even if reference material was unavailable.

4.2.2 Measurements

Character ratios and lengths are particularly important for the separation of critical species. For the British species 37 character measurements were made (Fig. 1), up to a maximum of ten specimens per species. The range and mean are presented for each species (Appendix 7) for all recorded British and Channel Island species, except where confusion existed with regard to adult identification. Continental specimens were used when British material was unavailable. The number of specimens measured and their catalogue code numbers in Appendix 5 are listed after the species description.

4.2.3 Habitus Drawings

Examination of British lygaeid nymphs revealed a variety of shapes, colours and markings, contrasting with the dull browns and blacks of the respective adults. With experience, many nymphs can be identified to generic and species level by the shape and colour of the whole animal. The production of detailed habitus drawings was, therefore, given high priority. Representative species from all the British and Channel Island genera were drawn (Figs 2-52), together with additional striking or distinct species, such as Heterogaster artemisiae Schilling.

4.2.4 Figures

Certain morphological features provide consistently good identification characters and are illustrated for all
available West Palaearctic genera. Characters illustrated are:-

1) Lateral view of sterna; showing trichobothrial pattern, sutures and spiracle position (Figs 53-121).

2) Dorsal abdominal gland apertures and evaporative areas (Figs 122-212).

3) Prothoracic femur; showing distinct arrangement of spines in profile on antero-ventral edge (spineless species excluded) (Figs 213-287).

4) Additional figures to illustrate characters used in the keys and descriptive accounts (288-336).

4.3 Distributional Information

Distributional information was acquired by original fieldwork, by abstraction from the literature, from biological records centres (Appendix 8) and from individual entomologists (Appendix 9). Literature references are listed separately from those cited in this text (Appendix 11).

Over 8,000 specimens were examined from 15 major institutional collections (Appendix 10). The 70 collectors who provided more than ten site records each are listed in Appendix 9. Identifications were checked, dates, collector and distributional information were extracted and National Grid References interpreted. Information was stored on the National Biological Records Centre GEN 13 cards and transferred to a D Base 3 file (Example of file structure Appendix 12). 'Plot 3' software, developed by the Joint Nature Conservation Council (Ball, 1992a) for its Recorder package was used to generate national distribution maps, using a ten kilometre square scale for each species (Maps 3-93).

Literature records and records provided by 20 data banks and individuals (Appendix 8), which were not supported by Museum voucher specimens, were not checked. Unlikely records, records for taxa which have subsequently been
split and historic records for taxa now known to include more British species are retained on the database, but were not usually included on maps.

4.4 The Lygaeid Research Collection at Liverpool Museum

A total of 10,061 specimens was collected, comprising 5,203 adults and 4,858 nymphs. These specimens, combined with donations and the original Museum British collection gives a total of 13,122 specimens (Table 2).

Table 2. Summary of Liverpool Museum (National Museums and Galleries on Merseyside) West Palaearctic Lygaeidae Collection

<table>
<thead>
<tr>
<th>Number of Specimens</th>
<th>Adult</th>
<th>Instars</th>
<th>Totals</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>5</td>
<td>4</td>
<td>3-1</td>
</tr>
<tr>
<td>British</td>
<td>2,695</td>
<td>1,775</td>
<td>650</td>
</tr>
<tr>
<td>West Palaearctic</td>
<td>4,966</td>
<td>1,541</td>
<td>838</td>
</tr>
<tr>
<td>Total</td>
<td>7,661</td>
<td>3,316</td>
<td>1,488</td>
</tr>
</tbody>
</table>

Adult specimens were micro-pinned and staged on polyporous strips, to allow examination of under-side characters. Nymphs were stored at eight degrees centigrade in 70% alcohol.

All adults and nymphs were labelled with collector’s name, collection date, location and a six or eight figure grid reference for British specimens. A running number is cross-referenced with a field notebook which contains detailed biological and site information (Appendices 2 and 3). Exuviae from reared adults are associated with adults and a cross-referencing labelling system is used for nymphs and associated field-caught adults.
All 3,000 world lygaeid species described before 1964 are catalogued by Slater (1964a). Subsequently the North American fauna was re-catalogued by Ashlock & Slater (1988).

The checklist below reflects current taxonomic and nomenclatural thinking. Essentially it updates Stichel (1957-1959), incorporating information from adult and immature Lygaeidae, and presenting the current systematic position of all taxa. The sequence of subfamilies follows Slater (1964a); genera and species are presented alphabetically and grammatical corrections to names in Slater are noted (Steyskal, 1973). For British species this list updates nomenclature in Southwood & Leston (1959, 1964). Synonyms and subspecies are not included. All nomenclatural changes post-Southwood & Leston (1959) for British species and post-Slater (1964a) for the remaining West Palaearctic fauna are annotated.

The West Palaearctic is defined, for the purposes of this study, as comprising Europe, Turkey, Cyprus and republics in the European former USSR west of the Urals (Map 2). All European islands are included, but Macaronesia is excluded. The fauna includes 424 species in 111 genera distributed across 13 subfamilies (Table 3). Only four world subfamilies, Slaterellinae, Psamminae, Cryptorhamphinae and Henicocorinae are absent.

The British and Channel Island fauna, comprising 90 species in 42 genera (Table 3), is highlighted in the checklist by the following symbols:

- GB - 76 British breeding, or probable breeding species.
- CI - 6 Channel Island species, not recorded even as vagrants from the British Isles (Le Quesne, 1953, 1984).
- * - 8 British vagrants (including two Channel Island species).

Channel Island species represent possible future additions to the British list.
Three Palaearctic subfamilies, the Geocorinae, Bledionotinae and Pachygronthinae are absent from Britain, whilst the Lygaeinae are only represented by vagrants and Channel Island species. This is discussed further in chapter 11.

Štys & Kerzhner (1975) ordered the higher classification of Heteroptera taxa, but noted a general disagreement among heteropterists. They agreed with Cobben (1968) that there was a bewildering array of higher classifications. Most recent world classifications place Lygaeidae with Berytidae, non-Palaearctic Colobathristidae and Malcidae in the Lygaeoidea, a superfamily within the infraorder Pentatomomorpha (Dolling 1991; Ashlock & Slater, 1988).

Major changes in subfamily status have taken place since the publication of Slater's catalogue. The 20 subfamilies were reduced to 17 (Table 1) as follows:

Monobasic Idiostolus Berg and Trisecus Bergroth, which were removed from the Heterogastrinae and placed in the new subfamily Idiostolinae (Scudder, 1962d), are now together with a new genus Monteithocoris (Woodward, 1968) a superfamily of Pentatomomorpha (Štys, 1964). Malcinae and Chauliopinae are subfamilies of Malcidae (Štys, 1967). Monobasic Thaumastellinae is a Pentatomoidea family (Štys, 1964). Two subfamilies have been reduced to tribes: Nothochrominae in Artheneinae (Malipatil, 1977b) and Phasmosominae in Rhyparochrominae (Sweet, 1967). Stål's (1859) Cryptorhamphinae is now revived, for two Australian genera (Hamid, 1971b). Psamminae is raised from a geocorine tribe to full subfamily status (Slater & Sweet, 1965) and the Henicocorinae is erected to contain a single species, the 'peculiar' Henicocoris monteithi Woodward (Woodward, 1968).
Table 3. The Tribal, Generic and Species Representation of the West Palaearctic and British Lygaeid Fauna Across Subfamilies

<table>
<thead>
<tr>
<th>Subfamilies</th>
<th>West Palaearctic</th>
<th>British = GB; Vagrant = *; and Additional Channel Island = CI</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Tribes</td>
<td>Genera</td>
</tr>
<tr>
<td></td>
<td>GB */CI</td>
<td>GB * CI</td>
</tr>
<tr>
<td>Lygaeinae</td>
<td>1</td>
<td>11</td>
</tr>
<tr>
<td>Orsillinae</td>
<td>2</td>
<td>5</td>
</tr>
<tr>
<td>Ischnorhynchinae</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td>Cymini</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Blissinae</td>
<td>-</td>
<td>3</td>
</tr>
<tr>
<td>Henestarinae</td>
<td>-</td>
<td>2</td>
</tr>
<tr>
<td>Geocorinae</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>Bledionotinae</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Oxycareninae</td>
<td>-</td>
<td>16</td>
</tr>
<tr>
<td>Artheneinae</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>Pachygronthinae</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Heterogastrinae</td>
<td>-</td>
<td>2</td>
</tr>
<tr>
<td>Rhyparochrominae</td>
<td>10</td>
<td>61</td>
</tr>
<tr>
<td><strong>Totals</strong></td>
<td>17</td>
<td>111</td>
</tr>
</tbody>
</table>
5.1 Checklist of West Palaearctic Lygaeidae

Subfam. 1. LYGAEINAE Schilling, 1829

Historically, this comprised four tribes: Lygaeini, Orsillini, non-Palaearctic Metragini and Robinscorini. It is now retained in the sense of the suprageneric tribe only, which is credited to Schilling not Stål (Hamid & Meher, 1973). Recent work (see Orsillinae and Ischnorhynchinae) conclusively shows that Lygaeini are unrelated to these other taxa and their subcostal vein is unique within the Lygaeidae (Slater & Hurlbutt, 1957).

Classification still extensively follows Stål (1874). Extensive reliance on adult colour patterning has produced an identification system that obscures phylogenetic relationships (Slater, 1964b; Ashlock, 1975). The resulting confusion has been widely commented on (e.g. Simanton & André, 1936; Slater & Sperry, 1973). A generic level Palaearctic revision is urgently required to complement recent generic revisionary work on the Western Hemisphere and Australian faunas (Slater (A.), 1985, 1992).

Gen. 1. APTEROLA Mulsant & Rey, 1866

Subgen. 1. APTEROLA s. str.
1. gridelli Mancini, 1942
2. kunckeli Mulsant and Rey, 1866
3. lownii (Saunders, 1876)
4. rubicunda Stål, 1872

Subgen. 2. PARAPTEROLA Pelaez, 1942
5. iberica Horváth, 1899
6. ramburi Pelaez, 1932

Gen. 2. AROCATUS Spinola, 1837
1. longiceps Stål, 1872
2. melanoccephalus (Fabricius, 1798)
3. melanostoma Scott, 1874
4. oshanini Kiritschenko, 1913
5. roeselii (Schilling, 1829)

Gen. 3. CAENOCORIS Fieber, 1860
1. nerii (Germar, 1847)

Gen. 4. GRAPTOSTETHUS Stål, 1868
1. servus (Fabricius, 1787)

Gen. 5. HORVATHIOLUS Josifov, 1965
1. fulvescens (Puton, 1874)
2. gibbicollis (Costa, 1882)
3. guttatus (Rambur, 1839)
4. *kiritshenkoi* Josifov, 1965
6. *superbus* (Pollich, 1779) CI
7. *syriacus* (Reuter, 1885)

Separated from *Melanocoryphus* Stål by Josifov (1965).

Gen. 6. *LYGAEOSOMA* Spinola, 1837

1. *anatolicum* Seidenstücker, 1960
2. *angulare* Reuter, 1885
3. *sardea* Spinola, 1837 CI

Two distinct *Lygaeosoma* groups and one new species are recognised (Seidenstücker, 1960). Nomenclature in Slater (1964a) is corrected = *L. sardeum* for *L. sardae* (Steyskal, 1973), but Spinola’s original spelling should be adopted. This species is frequently referred to as *L. reticulatum* (Herrich-Schaeffer, 1838), but was synonymised by Baerensprung (1860).

Gen. 7. *LYGAEUS* Fabricius, 1794

1. *creticus* Lucas, 1854
2. *equestris* (Linnaeus, 1758) GB*
3. *hanseni* Jakovlev, 1883
4. *murinus* (Kiritshenko, 1913)
5. *simulans* Deckert, 1985 GB*

Winkler & Kerzhner (1977), keyed, figured and mapped Palaearctic *Lygaeus*. They recognised Eastern Palaearctic *L. vicarius* as being new to science and raised *L. murinus* to full specific status. *Lygaeus equestris* was shown to be two distinct sympatric species (Deckert, 1985).

Gen. 8. *MELANOCORYPHUS* Stål, 1872

1. *albomaculatus* (Goeze, 1778)
2. *tristrami* (Douglas & Scott, 1868)

This genus was divided into *Melanocoryphus* [nov. sens.] and *Horvathiolus* [gen. nov.] (Josifov, 1965).

Gen. 9. *PARANYSZUS* Horváth, 1895

1. *fraterculus* Horváth, 1895

Gen. 10. *SPILOSTSTHUS* Stål, 1868

1. *furcula* (Herrich-Schaeffer, 1850)
2. *pandurus* (Scopoli, 1763)
3. *rubriceps* (Horváth, 1899)
4. *saxatilis* (Scopoli, 1763)

Full generic status is given to this traditional *Lygaeus* subgenus (Slater, 1964a).
Gen. 11. TROPIDOTHORAX Bergroth, 1868

1. leucopterus (Goeze, 1778)
2. sternalis (Dallas, 1852)

*T. sternalis* is recorded new to Italy and the West Palaearctic (Melber, 1988).

Subfam. 2. ORSILLINAE Stål, 1872

Small, not very attractive and taxonomically difficult (Ashlock, 1967). Scudder's (1958) unsubstantiated separation of Orsillini from Lygaeinae is confirmed by Usinger and Ashlock (1959) and supported by wing venation, male genitalia and cytological studies (Slater & Hurlbutt, 1957; Ashlock, 1957; Southwood, 1956b). Ashlock (1967) reviewed the systematic history, providing detailed classification and character analysis for the world genera and also divided the subfamily into four tribes.

Tribe 1. ORSILLINI Stål, 1872

Gen. 1. CAMPTOCORIS Puton, 1886

1. longicornis (Puton, 1874)

Gen. 2. ORSILLUS Dallas, 1852

1. depressus Dallas, 1852
2. maculatus (Fieber, 1861)
3. reyi Puton, 1871

Gen. 3. ORTHOLOMUS Stål, 1872

1. carinatus (Lindberg, 1932)
2. jordani Hoberlandt, 1953
3. punctipennis (Herrich-Schaeffer, 1838)

Tribe 2. NYSIINI Uhler, 1852

The least well defined of the tribes, without a single uniting character. Membership is dependent on character combinations (Ashlock, 1967).

Gen. 1. NITHECUS Horváth, 1890

1. jacobaeae (Schilling, 1829)

Gen. 2. NYSIUS Dallas, 1852

1. cymoides (Spinola, 1837)
2. ericae (Schilling, 1829)
3. eximius Stål, 1858
4. graminicola (Kolenati, 1845)
5. groenlandicus (Zetterstedt, 1840)
6. helveticus (Herrich-Schaeffer, 1850)
7. senecionis (Schilling, 1829)
Wagner’s (1958) four Palaearctic subgenera: - Anorthuna Strand, Macroparius Stål, Tropinysius Wagner and the nominate subgenus Nysius Dallas are not followed. They are "unwise" and characters do not indicate world phyletic lines (Ashlock, 1967). Reliance on differing buccula shapes is mistaken: they represent steps within a continuum; and erect hairs, although a valuable specific character, are not enough to separate Palaearctic Anorthuna from world Nysius with adpressed pubescence.

There are three recent first British records: - N. ericae (Woodroffe, 1959a), N. graminicola (Allen, 1984) and I have recently confirmed N. senecionis (Hodge, in press).

Subfam. 3. ISCHNORHYNCHINAE Stål, 1872

Scudder’s (1958) unsubstantiated separation of the Kleidocerini (= Ischnorhynchini) from the Lygaeinae is followed, in part, by later workers (Stichel, 1957-1959; Usinger & Ashlock 1959; Slater, 1964a), who consider it a distinct subfamily and not an Orsillinae tribe - a move that was unfortunately not followed by Southwood & Leston (1959). The 58 world-wide species were revised by Scudder (1962a).

Gen. 1. KLEIDOCERYS Stephens, 1829

1. resedae (Panzer, 1797) GB

2. truncatulus truncatulus (Walker, 1872)
   truncatulus ericae (Horváth, 1909) GB

Barber (1953) in a revision of United States genera, observed great similarity and confusion among the various species, a statement equally applicable to the two British and West Palaearctic species. Darker phena of K. resedae on Alnus glutinosa may refer to K. privignus (Horváth, 1894).

Subfam. 4. CYMINAE Baerensprung, 1860

Hamid (1975) in a world systematic revision, credited the subfamily to Baerensprung, not Stål (1862). He noted that studies tended to group strikingly different taxa within Cyminae on apparent similarity of general shape and puncturation. Single adult structural characters indicated considerable heterogeneity within this polythyletic group.

Researchers have attempted to show the phylogenetic relationship between the 68 cymine species and other groups in the Pentatomomorpha. This, Hamid concluded, was premature, because most of the shared characters with the Berytidae, Malcinae, Chauliopinae and Piesmatidae are either plesiomorphic (found in many other groups of
Lygaeidae), or are present in members of the groups under discussion, both in the primitive and the derived states. Southwood & Leston’s (1959) unsubstantiated placement of the Cyminae as a Berytinidae tribe is rejected (Sweet & Slater, 1961; Slater, 1963, 1964b; Štys, 1967; Ledvinka, 1970; Hamid, 1975), but is still followed by Kirby (1992).

Tribe 1. CYMINI Baerensprung, 1860

Gen. 1. CYMODEMA Spinola, 1837
1. tabida Spinola, 1837

Gen. 2. CYMUS Hahn, 1831
1. aurescens Distant, 1883 GB
2. claviculus (Fallén, 1807) GB
3. glandicolor Hahn, 1831 GB
4. marginatus Puton, 1895
5. melanocephalus Fieber, 1861 GB
6. minutus Lindberg, 1939
7. simplex Horváth, 1882

C. obliquus Horváth 1888 is synonymised with C. aurescens (Hamid, 1975).

Subfam. 5. BLISSINAE Stål, 1862

Slater (1979) reviewed world blissine systematics and his checklist divided the subfamily into 46 genera and 369 species.

Gen. 1. DIMORPHOPTERUS Stål, 1872
1. blissoides (Baerensprung, 1859)
2. brachypterus (Rambur, 1839)
3. doriae (Ferrari, 1874)
4. spinolae (Signoret, 1857)

D. obsoletus (Jakovlev, 1881) is synonymised with D. blissoides (Josifov & Kerzhner, 1978). See Geoblissus discussion.

Gen. 2. GEOBLISSUS Hidaka, 1959
1. hirtulus (Burmeister, 1835)
2. putoni (Jakovlev, 1875)

Slater & China (1961) recognised that Palaearctic and Nearctic Blissus species were not congeneric and placed B. hirtulus and B. putoni in Geoblissus and B. doriae in Dimorphopterus. Stichel’s (1957–1959) inclusion of B. albipennis Dallas, 1852 is confusing, particularly since it is now synonymised with B. leucopterus, the Chinch bug, which fortunately, is not recorded from the Palaearctic.
Gen. 3. ISCHNODEMUS Fieber, 1837

1. caspius Jakovlev, 1871
2. genei (Spinola, 1837)
3. quadratus Fieber, 1837 GB
4. sabuleti (Fallén, 1826) GB
5. suturalis Horváth, 1883

I. quadratus, which was treated as a subspecies of I. sabuleti (Southwood & Leston, 1959), was subsequently given full specific status (Southwood & Leston, 1964; Slater, 1979).

Subfam. 6. HENESTARINAE Douglas & Scott, 1865

Gen. 1. ENGISTUS Fieber, 1864

1. boops (Dufour, 1857)
2. commendatorius Puton, 1878
3. exsanguis Stål, 1872
4. salinus (Jakovlev, 1874)

Gen. 2. HENESTARTS Spinola, 1837

1. cremeus Kiritshenko, 1924
2. halophilus (Burmeister, 1835) GB
3. irroratus Horváth, 1892
4. kareli Hoberlandt, 1956
5. laticeps (Curtis, 1836) GB
6. wagneri Lindberg, 1960


Subfam. 7. GEOCORINAE Baerensprung, 1860

Taxonomically confused and in need of a world revision. Thirteen genera, 199 species and 61 infra-specific forms were catalogued by Slater (1964a).

Tribe GEOCORINI Montandon, 1913

Gen. 1. GEOCORIS Fallen, 1814

1. arenarius (Jakovlev, 1861)
2. ater (Fabricius, 1787)
3. chloroticus Puton, 1888
4. desertorum (Jakovlev, 1871)
5. dispar (Wage, 1839)
6. erythrophthalmus Reuter, 1880
7. grylloides (Linnaeus, 1761)
8. lapponicus Zetterstedt, 1838
9. lineolus (Rambur, 1839)
10. maurus Jakovlev, 1883
11. megacephalus (Rossi, 1790)
12. oschanini (Jakovlev, 1871)
13. pallidipennis (Costa, 1843)
14. pubescens (Jakovlev, 1871)
15. scutellaris Puton, 1886
16. siculus (Fieber, 1844)

The large omnibus genus Geocoris contains over 100 species, many of which exhibit quite considerable infraspecific colour variation. Péricart & Ribes (1992) established several new synonymies and Ribes (1979) recorded G. scutellaris, for the first time in the West Palaearctic, from Italy and Spain. Geocoris siculus, reduced to a subgenus of G. megacephalus, is worthy of full generic status (see 7.7).

Gen. 2. PIOCORIS Stål, 1872

1. erythrocephala (Lepeletier & Serville, 1825)
2. luridus (Fieber, 1844)
3. scutellatus Montandon, 1908

Linnavauri (1972) regarded Piocoris as a subgenus of Geocoris, the only certain distinguishing feature being the ratio between the length of rostral joints. However, it is usually regarded as a good genus (Stichel, 1957-1959; Kerzhner & Yachevskii, 1967; Puchkov, 1969) and Slater (1964b) considers it worthy of generic status. The nomenclature in Slater (1964a) was corrected for P. erythrocephalus (Steyskal, 1973).

Gen. 3. STENOPHTHALMICUS Costa, 1875

1. fajoumensis Costa, 1875

Subfam. 8. BLEDIONOTINAE Reuter, 1878

Scudder (1963a), refuted assumptions that Bledionotus (China & Miller, 1959) and the Pamphantinae (Slater & Hurlbutt, 1957) are aberrant members of the Rhyparochrominae. He claimed that they were sufficiently alike to warrant amalgamation as two tribes in a single family, the Bledionotinae. A second Bledionotus species was discovered during this study, prior to which the Bledionotini consisted of two monobasic genera. The 21 non-Palaearctic Pamphantini species were reviewed by Slater (1981).

Tribe 1. BLEDIONOTINI Scudder, 1963

Gen. 1. BLEDIONOTUS Reuter, 1878

1 new species
2. systellonotoides Reuter, 1878

Subfam. 9. OXYCARENINAE Stål, 1862

This isolated group of primitive Lygaeidae comprises 118 species in 20 genera and is primarily Palaearctic in distribution. Slater (1964b, 1972a) studied the South
African fauna and keyed all the genera. Stichel (1957-1959) remains the standard guide to the West Palaearctic fauna.

Gen. 1. **ANOMALOPTERA** Amyot & Serville, 1843
   1. helianthemi Amyot & Serville, 1843

Gen. 2. **AUCHENODES** Horváth, 1891
   1. capito Horváth, 1891
   2. conspersus (Jakovlev, 1885)
   3. joakimoffi Seidenstücker & Josifov, 1961

Gen. 3. **BIANCHIELLA** Reuter, 1907
   1. sarmatica Kiritshenko, 1926

Gen. 4. **BRACHYPLAX** Fieber, 1860
   1. tenuis (Mulsant & Rey, 1852)

Gen. 5. **BYCANISTELLUS** Reuter, 1890
   1. costalis (Lathierry, 1875)

Gen. 6. **CAMPTOTELUS** Fieber, 1860
   1. lineolatus (Schilling, 1829)
   2. parallelus Horváth, 1894

C. lineolatus comprises two subspecies. C. aeonii is not characteristic of this genus and has been transferred to *Neocamptotelus* gen. nov. (Hoberlandt, 1987).

Gen. 7. **JAKOWLEFFIA** Puton, 1875
   1. setulosa Jakovlev, 1874

Gen. 8. **LEPTODEMUS** Reuter, 1900
   1. bicolor Lindberg, 1924
   2. minutus (Jakovlev, 1876)

Gen. 9. **MACROPLAX** Fieber, 1860
   1. fasciata fasciata (Herrich-Schaeffer, 1835) CI
   2. preyssleri (Fieber, 1837) GB
   3. vicina Puton, 1889

Gen. 10. **MACROPTERNELLA** Slater, 1957
   1. bicolor (Scott), 1872
   2. convexa (Fieber, 1837)
   3. inermis (Fieber, 1852)
   4. marginalis (Fieber, 1861)

Wagner (1956) examined the Macropternella conica complex.
and keyed Western Palaearctic species. Subsequently *M. conica* Rey, 1888 was reduced to a subspecies of *M. bicolor* and *M. foveicollis* Costa, 1881 was synonymised with *M. convexa* (Péricart, 1992b).

Gen. 11. *METOPOPLAX* Fieber, 1860

1. *ditomoides* Fieber, 1860
2. *fuscinervis* Stål, 1872
3. *origani* (Kolenati, 1845)

Gen. 12. *MICROPLAX* Fieber, 1860

Subgen. 1. *MICROPLAX* s. str.

1. *plagiata* (Fieber, 1837)

Subgen. 2. *PSEUDOMICROPLAX* subgen. n.

2. *albofasciata* (Costa, 1847)
3. *interrupta* (Fieber, 1837)
4. *limbata* (Fieber, 1864)

The nomenclature in Slater (1964a) was corrected for *M. albofasciatus* (Steyskal, 1973).


1. *aeonii* Lindberg, 1953


Subgen. 1. *OXYCARENUS* s. str.

1. *hyalinipennis* (Costa, 1847)
2. *lacteus* Kiritshenko, 1913
3. *lavaterae* (Fabricius, 1787)
5. *modestus* (Fallén, 1829)

Subgen. 2. *EUOXYCARENUS* Samy, 1969

6. *pallens* (Herrich-Schaeffer, 1850)

Ethiopian region *Oxycarenus* were revised and divided into three subgenera (Samy, 1969).

Gen. 15. *PHILOMYRMEX* Sahlberg, 1848

1. *insignis* Sahlberg, 1848

Gen. 16. *TROPIDOPHLEBIA* Kerzhner, 1967

1. *costalis* (Herrich-Schaeffer, 1850)

Removed from *Camptotelus* (Kerzhner, 1967).
Subfam. 10. ARTHENEINAE Stål, 1872

The 17 species in five genera divide into three monobasic tribes (Slater et al., 1962; Malipatil, 1977b; Chopra & Rustagi, 1980; Slater & Brailovsky, 1986b) and the primarily Palaearctic Artheneini.

Tribe 1. ARTHENEINI Slater, Woodward & Sweet, 1962

Gen. 1. ARTHENEIS Spinola, 1837
1. aegyptiaca Lindberg, 1939
2. alutacea Fieber, 1861
3. balcanica (Kormilev, 1938)
4. foveolata Spinola, 1837
5. hyrcanica (Kolenati, 1845)
6. intricata Puchkov, 1969

Gen. 2. CHILACIS Fieber, 1864
1. typhae (Perris, 1857)

Gen. 3. HOLCOCRANÜM Fieber, 1860
1. diminutum Horváth, 1898
2. saturejae (Kolenati, 1845)

Subfam. 11. PACHYGRONTHINAE Stål, 1865

This small subfamily with approximately 80 species in two tribes was revised by Slater (1955, 1966).

Tribe 1. TERACRIINI Stål, 1872

Gen. 1. CYMOPHYES Fieber, 1870
1. golodnajana Seidenstücker, 1953
2. ochroleuca Fieber, 1870

Seidenstücker (1953) keyed and described four Mediterranean species, including two new and two West Palaearctic species.

Subfam. 12. HETEROGASTRINAE Stål, 1872

A moderately-sized subfamily, primarily tropical, but recorded from all world regions. Slater (1964a) catalogued 80 species in 20 genera. Scudder (1962b) keyed world genera.

Gen. 1. HETEROGASTER Schilling, 1829
1. affinis Herrich-Schaeffer, 1835
2. albida Kiritshenko, 1911
3. artemisiae Schilling, 1829
4. catharīae (Geoffroy, 1785)
5. distincta Jakovlev, 1881
6. longirostris Wagner, 1949

38
7. urticae (Fabricius 1775) GB

Gen. 2. PLATYPLAX Fieber, 1860

1. inermis (Rambur, 1839)
2. salviae (Schilling, 1829)

Subfam. 13. RHYPAROCROMINAE Amyot & Serville, 1843

Tribes follow Ashlock (1964) and Sweet (1967); their sequence follows the cladogram in Slater & Woodward (1982). Megalonotinae is synonymised with Rhyparochrominae (Slater & China, 1961).

Tribe 1. PLINTHISINI Slater & Sweet, 1961

Plinthisus was separated from Scudder's (1957a) polyphyletic Cleradini (= Stygnocorini) by Slater & Sweet (1961), an action subsequently endorsed by Sweet (1967) and the 75 species now comprise a monotypic tribe. The most important characters are the absence of a Y-suture, presence of a complete suture between sterna 4-5, the structure of the phallus and the relative position of two trichobothria on sternum 7.

Gen. 1. PLINTHISUS Stephens, 1829

1. andalusicus Wagner, 1963
2. angulatus Horváth, 1876
3. bicolor Rey, 1888
4. brevicollis Ferrari, 1874
5. brevipennis (Latreille, 1807) GB
6. convexus (Fieber, 1864)
7. coracinus Horváth, 1876
8. elongatus Horváth, 1886
9. fasciatus Horváth, 1881
10. flavipes Fieber, 1861
11. humilis Horváth, 1886
12. hungaricus Horváth, 1875
13. laevigatus Puton, 1884
14. longicollis Fieber, 1861
15. lusitanicus Horváth, 1886
16. maderi Lindberg, 1924
17. major Horváth, 1876
18. marginatus Ferrari, 1874
19. megacephalus Horváth, 1876
20. mehadiensis Horváth, 1882
21. minutissimus Fieber, 1864
22. otini Vidal, 1951
23. parvulus Kerzhner, 1962
24. perpusillus Wagner, 1963
25. pilosellus Horváth, 1876
26. pseudoconvexus Wagner, 1963
27. pusillus (Scholtz, 1847)
28. putoni Horváth, 1876
29. pygmaeus Horváth, 1882
30. soongoricus Kerzhner, 1962
Wagner (1963) keyed and described the 38 Palaearctic species, dividing them into five subgenera; an arrangement not followed in this checklist and which Slater (1971b), on examining the South African fauna, found to bring together disparate and phylogenetically unrelated species assemblages.

**Tribe 2. ANTILLOCORINI Ashlock, 1964**

The 60 "monotonous" antillocorine species were separated from the Lethaeini (Ashlock, 1964) (see Lethaeini). Slater (1980) assessed the systematic relationship of Western Hemisphere Antillocorini and modified the tribal definition of Slater et al. (1977) and earlier workers. His tentative generic cladogram showed that the Antillocorini does not have a single synapomorphic character to unite the various taxa and so may well be paraphyletic.

**Gen. 1. HOMOSCELIS Horváth, 1884**

1. ruficollis Horváth, 1884

**Gen. 2. TROPISTETHUS Fieber, 1860**

1. albidipennis Horváth, 1888
2. fasciatus Ferrari, 1874
3. holosericeus (Scholtz, 1846) GB
4. majusculus Horváth, 1882
5. nitidicollis Puton, 1887
6. pallipes Reuter, 1902

**Tribe 3. LETHAEINI Stål, 1872**

This moderate-sized tribe, with just over 100 species (Slater, 1964a), has an extensive world distribution, but is poorly represented in the West Palaearctic.

Scudder's (1957a) Lethaeini, represents a return to the concept of Stål (1872) and is characterised by the presence of ventral abdominal spiracles and the linear arrangement of trichobothria on sternum 5. Slater & Sweet (1961) recognised the presence of several natural units within the taxon. But it was left to Ashlock (1964), to make further divisions, with the creation of two new tribes, the Antillocorini and Targaremini, using characters of the bucculae, parameres, trichobothria, abdominal spiracles and nymphal Y-suture. The Lethaeini sensu Ashlock (1964) was endorsed by Sweet (1967) and considered a monophyletic assemblage (Slater & Woodward, 1982), on the basis of the unique sperm reservoir (Slater & O'Donnell, 1978), lack of a Y-chromosome, linear trichobothria on sternum 5 and iridescent patches on the dorsal surface of the head.

Ashlock (1964) rejected Wagner's (1961a) concept of the Camptocerini for the two West Palaearctic Lethaeini genera, which are not unusual once a wider variety of genera is studied.
Gen. 1. CAMPTOCERA Jakovlev, 1877

1. angustula Puton, 1887
2. glaberrima (Walker, 1872)

Gen. 2. LETHAEUS Dallas, 1852

1. cribratissimus (Stål, 1858)
2. lethierryi (Puton, 1869)
3. nitidua (Douglas & Scott, 1868)
4. picipes (Herrick-Schaeffer, 1850)

Tribe 4. STYGNOCORINI Gulde, 1936

Whether Stygnocorini comprise a natural assemblage of species, has been a contentious issue since the tribe was established by Gulde (1936), to include Stygnocoris and two other, then primarily Palaearctic genera, Acompus and Lasiosomus. In its most expansive form, as defined by Scudder (1957a), it embraced 30 genera. Analysis of nymphal material by Sweet (1967) provided decisive evidence for the tribal classification of the Rhyparochrominae, resulting in placement of most of these genera in the Plinthisini, Cleradini (sensu Stål, 1872-74) and the newly erected Ozophorini. The Stygnocorini now total some 50 species. The world genera are keyed by Slater & Sweet (1970b) and do not possess a single exclusive synapomorphy that separates them from other rhyparochromine tribes. They are almost certainly still a paraphyletic assemblage of species, held together by sympleisomorphic characters (Slater & Woodward, 1982; Slater, 1982).

Gen. 1. ACOMPUS Fieber, 1860

1. australis Horváth, 1929
2. garganicus Horváth, 1929
3. laticeps Ribaut, 1929
4. orientalis Horváth, 1929
5. pallipes (Herrich-Schaeffer, 1833) GB
6. rufipes (Wolff, 1804) GB

Gen. 2. XYALOCHILUS Fieber, 1860

1. dolosus Horváth, 1897
2. ovatulus (Costa, 1855)

Gen. 3. LASIOSOMUS Fieber, 1860-1

1. enervis (Herrich-Schaeffer, 1835) GB

This genus was incorrectly placed in the Drymini in Southwood & Leston (1964). O’Rourke’s (1974) analysis of South African Lasiosomus indicated the presence of two distinct, although related genera and resulted in the transfer of 15 species to Sweetocoris O’Rourke, 1974.
Gen. 4. *STYGNOCORIS* Douglas & Scott, 1865

1. *breviceps* Wagner, 1953
2. *faustus* Horváth, 1888
3. *fuligineus* (Geoffroy, 1785) GB
4. *pygmaeus* (Sahlberg, 1848) GB
5. *rusticus* (Fallén, 1807)
6. *sabulosus* (Schilling, 1829) GB
7. *similis* Wagner, 1953
8. *truncatus* (Horváth, 1893)

The commonly referred to species *S. pedestris* (Fallén, 1807) (= *sabulosus*) is preoccupied (Slater, 1964a).

Gen. 5. *STYGNOCORISELLA* Hoberlandt, 1956

1. *mayeti* (Puton, 1879)

Tribe 5. *PHASMOSOMINI* Kiritshenko, 1938
Now reduced to tribal status (Sweet, 1967).

Gen. 1. *PHASMOSOMUS* Kiritshenko, 1938

1. *araxis* Kiritshenko, 1938

Tribe 6. *DRYMINI* Stål, 1872

This large, cosmopolitan tribe with over 150 species in 30 genera (Slater, 1964a) is well represented by 10 genera with 50 species in the West Palaearctic, containing 30% of the British lygaeid fauna.

Stål (1872, 1874), first recognised the Drymaria, then combined it with the Lethaearia. Scudder (1957a) resurrected the Drymini to tribal status because nymphs have three pairs of dorsal gland apertures and the paired trichobothria on sternum 5 are anterior to the spiracle.

Holarctic Drymini receive considerable attention (e.g. Barber, 1928; Walley, 1929; Usinger, 1938a; Ashlock & O'Brien, 1964; Ashlock, 1979), with Wagner (1949, 1951, 1954a) undertaking generic and single species reviews. Le Quesne (1956) separated and keyed British *Drymus* sensu stricto from *Lamproplax* and divided *Drymus* into two distinct groups by erecting the subgenus *Sylvadrymus* and raising *D. ryei* to full specific status.

Gen. 1. *DRYMUS* Fieber, 1860

Subgen. 1. *DRYMUS* s. str.

1. *latus* Douglas & Scott, 1871 GB
2. *major* Wagner, 1953
3. *parvulus* Jakovlev, 1881
4. *pilicornis* (Mulsant & Rey, 1852) GB
5. *pilipes* Fieber, 1861 GB
6. *scambus* Stål, 1872
Subgen. 2. SYLVADRYMUS Le Quesne, 1956

7. brunneus (Sahlberg, 1848) GB
8. pumilio Puton, 1877 GB
9. ryei Douglas & Scott, 1865 GB
10. sylvaticus (Fabricius, 1775) GB

Gen. 2. EREMOCORIS Fieber, 1860

1. abietis (Linnaeus, 1758) GB
2. fenestratus (Herrich-Schaeffer, 1839) GB
3. fraternus Horváth, 1883
4. oblitus Horváth, 1829
5. obscuratus Montandon, 1895
6. plebejus (Fallén, 1807) GB
7. podagricus (Fabricius, 1775) GB

Eremocoris remanei Roubal, 1956 is a synonym of E. fenestratus (Hoberlandt, 1977).

Gen. 3. GASTRODES Westwood, 1840

1. abietum Bergroth, 1914 GB
2. grossipes (De Geer, 1773) GB

Gen. 4. ISCHNOCORIS Fieber, 1860

1. angustulus (Boheman, 1852) GB
2. hemipterus (Schilling, 1829)
3. punctulatus Fieber, 1861

Gen. 5. LAMPROPLAX Douglas & Scott, 1868

1. picea (Flor, 1860) GB

The nomenclature in Slater (1964a) was corrected for L. piceum (Steysskal, 1973).

Gen. 6. NOTOCHILUS Fieber, 1864

1. damryi Puton, 1871
2. ferrugineus (Mulsant & Rey, 1852)

Gen. 7. RIBAUTICORIS Stichel, 1958

1. humilis Ribaut, 1929

Gen. 8. SCOLOPOSTHUS Fieber, 1860

1. affinis (Schilling, 1829) GB
2. brevis Saunders, 1876
3. cognatus Fieber, 1861
4. decoratus (Hahn, 1833) GB
5. grandis Horváth, 1880 GB
6. lethierryi Jakovlev, 1877
7. patruelis Horváth, 1892
8. pictus (Schilling, 1829) GB
Kirby (1985a) keyed all British species.

Gen. 9. TAPHROPELTUS Stål, 1872
1. andrei Puton, 1877
2. championi Reuter, 1905
3. contractus (Herrich-Schaeffer, 1835) GB
4. hamulatus (Thomson, 1870) GB
5. intermedius (Puton, 1881)
6. limbatus (Fieber, 1870) GB
7. nervosus (Fieber, 1861)

Doubt remains over the true status of T. hamulatus. Some authors regard it as a form of T. contractus (Stichel, 1957-1959; Puchkov, 1969). Southwood & Leston (1959) are undecided; they key it as a distinct species, but comment that the British specimens are probably small examples of T. contractus. It is widely regarded as a good species (Kiritschenko, 1951; Woodrffe, 1959b; Kerzhner, 1967; Kirby, 1985b). Kirby (1985b) keys the British species.

Gen. 10. THAUMASTOPUS Fieber, 1870
1. cinnamomeus Horváth, 1884
2. gandolphei Puton, 1871
3. longicollis (Fieber, 1861)
4. marginicollis (Lucas, 1849)
5. noviburgensis d' Antessanty, 1888

Tribe 7. GONIANOTINI Stål, 1872

This moderate-sized tribe of approximately 100 species in 16 genera (Slater, 1964a), is predominantly Palaearctic in distribution. Puchkov (1958a) considered the taxon homogeneous and restored tribal status, rejecting the conclusions of Scudder (1957a), who relegated Stål’s (1872) concept of the Gonianotini to a subtribe of the Rhyparochromini with other Rhyparochrominae genera. Slater & Ashlock (1966) observed that generic concepts in Western Hemisphere gonianotines are complex and need careful analysis. Most work by European authors has concentrated on the two largest critical genera, Trapezonotus and Emblethis. Examinations of the male genital capsule and parameres have distinguished new species (Seidenstücker, 1951, 1954; Wagner, 1954b).

Gen. 1. ALAMPES Horváth, 1884
1. longiusculus Horváth, 1884
Gen. 2. AOPLOSCELIS Fieber, 1860

1. bivirgatus (Costa, 1855)
2. koeppeni Kiritshenko, 1910

Gen. 3. APHANUS Laporte, 1833

1. rolandri (Linnaeus, 1758) GB

Gen. 4. BLETEOGONUS Reuter, 1885

1. beckeri (Frey-Gessner, 1863)
2. currax (Horváth, 1895)

Gen. 5. DIOMPHALUS Fieber, 1864

1. hispidulus Fieber, 1864

Gen. 6. EMBLETHIS Fieber, 1860

1. amplus Seidenstücker, 1987
2. angustus Montandon, 1890
3. brachynotus Horváth, 1897
4. ciliatus Horváth, 1875
5. denticollis Horváth, 1878 CI
6. dilaticollis (Jakovlev, 1874)
7. duplicatus Seidenstücker, 1963
8. gracilicornis Puton, 1883
9. griseus (Wolff, 1802) GB
10. karamanus Seidenstücker, 1963
11. kareli Hoberlandt, 1956
12. latus Seidenstücker, 1966
13. major Montandon, 1890
14. minutus Kiritshenko, 1911
15. nox Kiritshenko, 1912
16. osmanus Seidenstücker, 1963
17. parvus Montandon, 1890
18. sabulosus Seidenstücker, 1963
19. setifer, Seidenstücker, 1966
20. verbasci (Fabricius, 1803)

All species standing in British and Channel Island collections as Emblethis verbasci are E. griseus, and E. denticollis was recorded for the first time, during this study, from the Channel Islands. Emblethis amplus, E. latus, E. nox and E. setifer are recorded for the first time for the West Palaearctic, from Turkey and records for E. tenellus Jakovlev, 1883 from Russia are mistaken (Seidenstücker, 1987).

Gen. 7. GONIANOTUS Fieber, 1860

1. galactodermus Fieber, 1861
2. marginepunctatus (Wolff, 1804)
3. parilis Kiritshenko, 1951
Gen. 8. HYALOCORIS Jakovlev, 1874
1. pilicornis Jakovlev, 1874

Gen. 9. ISCHNOPEZA Fieber, 1860
1. hirticornis (Herrich-Schaeffer, 1850)
2. pallipes Puton, 1892
3. taborskyi Hoberlandt, 1956

Gen. 10. MACRODEMA Fieber, 1860
1. microptera (Curtis, 1836) GB

The nomenclature in Slater (1964a) is corrected for M. micropterum (Steyskal, 1973).

Gen. 11. NEUROCLADUS Fieber, 1860
1. brachiidens (Dufour, 1851)

Gen. 12. PIONOSOMUS Fieber, 1860
1. depressus Horváth, 1895
2. fuscipes Horváth, 1895
3. heterotrichus Horváth, 1884
4. opacellus Horváth, 1895
5. persimilis Horváth, 1895
6. trichopterus (Thomson, 1870)
7. varius (Wolff, 1804) GB

Gen. 13. PTEROTMETUS Amyot & Serville, 1843
1. dimidiat us Fieber, 1861
2. parnassius Horváth, 1882
3. staphyliniformis (Schilling, 1829) GB

Woodroffe (1962) added Pterotmetus staphyliniformis to the British list, which is misspelt in Southwood & Leston (1964) (= Pterometus).

Gen. 14. TRAPEZONOTUS Fieber, 1860

Subgen. 1. TRAPEZONOTUS s. str.
1. arenarius (Linnaeus, 1758) GB
2. breviceps Jakovlev, 1881
3. desertus Seidenstücker, 1951 GB
4. dispar Stål, 1872 GB
5. montanus Wagner, 1957
6. seductor Horváth, 1883
7. ullrichi (Fieber, 1837) GB

Subgen. 2. GONOPHERUS Stål, 1872
8. anorus (Flor, 1860)

Woodroffe's (1960b) re-examination of British Trapezonotus
revealed that species standing in British collections as T. arenarius included T. desertus and that T. dispar was a good British species.

Tribe 8. MEGALONOTINI Slater, 1957

This moderate-sized tribe with 70 species in 18 genera (Slater, 1964a), is predominantly Palaearctic in distribution. Slater & Sweet's (1961) redefinition (See Rhyparochromini) was substantiated by Sweet (1967) primarily on the basis of nymphal taxonomy. Generic boundaries are well established except for the Lasiocoris complex, where Scudder (1962c) resurrected Hadrocnemis, Leptomelus and Pezocoris primarily on adult setal characters.

Gen. 1. HADROCNEMIS Jakovlev, 1881

1. diversipes (Kiritshenko, 1922)

Gen. 2. ICUS Fieber, 1860

1. angularis Fieber, 1861

Puchkov (1969) placed this genus in the Gonianotini, but it is traditionally considered a megalonotine.

Gen. 3. LAMPRODEMA Fieber, 1860

1. maura Fabricius, 1803
2. weyseri Puton, 1877

Gen. 4. LASIOCORIS Fieber, 1860

1. albamaculatus (Jakovlev, 1883)
2. anomalus (Kolenati, 1845)
3. antennatus Montandon, 1889
4. crassicornis (Lucas, 1849)
5. pachycerus Kiritshenko, 1922

Gen. 5. LEPTOMELUS Jakovlev, 1881

1. dorsatus Jakovlev, 1881

Gen. 6. MEGALONOTUS Fieber, 1860

Subgen. 1. MEGALONOTUS s. str.

1. antennatus (Schilling, 1829) GB
2. brevicornis (Puton, 1883) GB
3. chiragra (Fabricius, 1794) GB
4. colon Puton, 1874
5. emarginatus (Rey, 1888) GB
6. hirsutus Fieber, 1861
7. lederi (Horváth, 1880)
8. longipilus (Puton, 1884)
9. maximus (Puton & Noualhier, 1895)
10. nitidicollis Puton, 1874
Taxonomic confusion surrounds the *Megalonotus chiragra* complex. Southwood (1963), studying British specimens, found, on a priori grounds, that *M. sabulicola* could not be considered a subspecies of *M. chiragra*: it was either a colour and size form of *chiragra*, or a distinct species. He acknowledged that there was no strong evidence why *sabulicola* should be regarded as a true species; proportions of structures measured in both species are similar and simple ratios fail to disclose distinctions. This conclusion supported Kiritshenko's (1951) earlier action.

Roubal (1965), in a paper overlooked by British heteropterists, studied the nomenclatural history, taxonomy and zoogeography of the *chiragra* complex. He erected the subgenus *Ktenofer* to contain *M. dilatatus*, *M. mixtus* and possibly *M. opaconatum* and raised *M. emarginatus*, which was previously known as a subspecies of *chiragra*, to full specific status, noting in passing its presence for the first time in Britain. Aukema & Nau (1992) recognised *M. emarginatus* 'new to Britain' (despite Roubal), from specimens put to one side during this study, at the Natural History Museum.
Gen. 11. SPHRAGISTICUS Stål, 1872

1. nebulosus (Fallén, 1807)

Tribe 9. RHYPAROCROMINI Amyot & Serville, 1843

This second largest rhyparochromine tribe, with some 229 species (Slater, 1964a), is the subject of much taxonomic and nomenclatural confusion. Stål (1872) made the Rhyparocromaria (= Megalonotini) and Beosaria (= Rhyparocromini) two of his original six rhyparochromine divisions. Scudder (1957a) combined most members of these two divisions in the Rhyparocromina, a subtribe of the Rhyparocromini. Slater & Sweet (1961) recognised both Megalonotini and Beosini as distinct tribes, Beosini being a synonym of Rhyparocromini (Slater & China, 1961). Generic limits of taxa, particularly within the type genus Rhyparochromus, are uncertain and require detailed study.

Gen. 1. AELLOPUS Wolff, 1811

1. atratus (Goeze, 1778)
2. syriacus (Reuter, 1885)

Gen. 2. BEOSUS Amyot and Serville, 1843

1. maritimus (Scopoli, 1763) GB
2. quadruplicatus (Muller, 1766)

Gen. 3. DIEUCHES Dohrn, 1860

1. armatipes (Walker, 1872)
2. syriacus Dohrn, 1860

The 70 species were monographed by Eyles (1973), who noted that practically all the records attributed to D. armipes (Fabricius, 1794) in Slater (1964a), including all Palaearctic records, apply to D. armatipes.

Gen. 4. GRAPTOPELTUS Stål, 1872

1. consors (Horváth, 1878)
2. lynceus (Fabricius, 1775) GB
3. validus Horváth, 1875

See Rhyparochromus.

Gen. 5. PASATUS Stål, 1872

1. lundi (Gmelin, 1790) GB

Nymphal characters substantiate the raising from synonymy of Stål's (1872) monobasic genus to contain Peritrechus lundi (see 7.13.9).
Gen. 6. PERITRECHUS Fieber, 1860

1. ambiguus Horváth, 1888  
2. angusticollis (Sahlberg, 1848) GB*  
3. convivus (Stål, 1858)  
4. distinguendus (Flor, 1860) GB*  
5. flavicornis Jakovlev, 1876  
6. geniculatus (Hahn, 1832) GB  
7. gracilicornis Puton, 1877  
8. insignis Jakovlev, 1892  
9. meridionalis Puton, 1877  
10. nubilus (Fallén, 1807) GB  
11. oculatus Jakovlev, 1885  
12. oshanini (Kiritschenko, 1911)  
13. pusillus Horváth, 1884  
14. rhomboidalis Puton, 1877

Gen. 7. RAGLIODES Reuter, 1885

1. delveatus (Rambur, 1839)

Gen. 8. RAGLIUS Stål, 1872

1. alboacuminatus Goeze, 1778 GB  
2. confusus (Reuter, 1886)  
3. pineti (Herrich-Schaeffer, 1835)  
4. tristis Fieber, 1861  
5. vulgaris (Schilling, 1829)  
6. zarudnyi (Jakovlev, 1905)

See Rhyparochromus.

Gen. 9. RHYPAROCHROMUS Hahn, 1826

Subgen. 1. RHYPAROCHROMUS s. str.

1. ibericus Baerensprung, 1858  
2. phoeniceus (Rossi, 1794)  
3. pini (Linnaeus, 1758) GB  
4. taleus Lucas, 1846

Rhyparochromus s. str. with 29 species and a further 31 species in nine subgenera is a problematic "dumping ground" for medium-size 'beosines' (Slater, 1964a, 1964b). Le Quesne (1957) examined genitalia of the four British species and raised Raglius and Graptopeltus to full generic status, with Xanthochilus as a subgenus of Graptopeltus. This was ignored by Wagner (1961b, 1962) who, in a major study of Palaearctic Rhyparochromus, recognised four Rhyparochromus s. str. species with a further 24 species in six subgenera.

Subgen. 2. AELLOPIDEUS Seidenstücker, 1963

5. nigritus Seidenstücker, 1963
Subgen. 3. **CALLISTONOTUS** Horváth, 1906
   6. *nigroruber* Stål, 1858

Subgen. 4. **LIOLOBUS** Reuter, 1885
   7. *walkeri* (Saunders, 1876)

Subgen. 5. **MICROTOMIDEUS** Reuter, 1885
   8. *carbonarius* Rambur, 1839
   9. *leucodermus* Fieber, 1861
   10. *seidenstuckeri* Seidenstücker, 1963

Subgen. 6. **PANAORUS** Kiritshenko, 1951
   11. *adspersus* (Mulsant & Rey, 1852)

Gen. 10. **TRICHAPHANUS** Kiritshenko, 1926
   1. *fuentei* (Puton, 1894)

Gen. 11. **XANTHOCHILUS** Stål, 1872
   1. *douglasi* (Fieber, 1864)
   2. *minusculus* (Reuter, 1885)
   3. *omissus* (Horváth, 1911)
   4. *quadratus* (Fabricius, 1798)
   5. *reuteri* (Horváth, 1885)
   6. *saturnius* (Rossi, 1790)
   7. *turanicus* Wagner, 1961


**Tribe 10. **MYODOCHINI** Boitard, 1827**

With 56 genera and 260 species, this is the largest of the rhyparochromine tribes. The normally small, dull, cryptically coloured species are extremely diverse in the tropics and subtropics. Slater & Sweet (1961) returned the Myodochini to the status of Stål (1872), overturning Scudder's (1957a) concept of the taxon as a subtribe within an expanded Rhyparochromini. Sweet (1967) recognised that certain aberrant Australian and Neotropical Myodochini with inner laterotergites constituted a distinct tribe, the Udeoconini, which on the basis of the shared spiracle pattern of 2-4 dorsal must be the sister group of the Myodochini and is possibly ancestral.

Harrington (1980), keyed, diagnosed, summarily described and analysed cladistically world genera. She and Malipatil (1978c), who keyed and described all Australian species, reviewed the literature and systematic history of the tribe.
Gen. 1. LIGYROCORIS Stål, 1872
   1. sylvestris (Linnaeus, 1758)

Gen. 2. PACHYBRACHIUS Hahn, 1826
   1. capitatus (Horváth, 1882)
   2. fasciatus (Fieber, 1861)
   3. fracticollis (Schilling, 1829) GB
   4. luridus Hahn, 1826 GB

Pachybrachius is highly polyphyletic (Malipatil, 1978c; Harrington, 1980). The genus, which has included up to 100 species, was reduced to ten Palaearctic species.

Gen. 3. PAROMIUS Fieber, 1860
   1. gracilis (Rambur, 1839)
   2. leptopoides (Baerensprung, 1859)

Gen. 4. REMAUDIEREANA Hoberlandt, 1954
   1. annulipes (Baerensprung, 1859)

Harrington (1980) resurrected Remaudiereana, which had previously been synonymised with Pachybrachius (Malipatil, 1978c).
6. Analysis of Lygaeid Fifth Instar Nymphal Characters

This account outlines and evaluates diagnostic and systematic characters, which distinguish immature Lygaeidae from other Heteroptera, from one another, from different instars and from adults. Form and colour are related to function and protective adaptation. Characters of non-Palaearctic taxa are included for completeness.

Lygaeid nymphs vary greatly between species in size, colour and shape. There are normally five instars (Weber, 1930; Southwood & Leston, 1959), except for the Chinch bug, *Blissus leucopterus*, which has an extra instar (Yuasa, 1918; Luginbill, 1922). Fortunately, a number of stable characters reliably separate whole groups of genera and, unlike Pentatomidae or Miridae, these remain practically unchanged during ontogenesis, some but not all being shared with the adult (Puchkov, 1958a).

Nymphs are admirable material for study; trichobothria, abdominal segments and spiracular arrangements are clearly visible, but often very difficult to see in adults and sometimes require dissection or clearing (Sweet & Slater, 1961). They also possess other taxonomically significant structural characters, that are absent in adults, such as the dorsal abdominal gland apertures and rhyparochromine Y-suture. Their study has been neglected because of the untenable belief that nymphal and adult stages in hemimetabolous orders may be identified through the use of adult structural characters (Slater, 1951).

6.1 Size and Shape

Palaearctic species range in total body length (TBL) from *Stygnocorisella mayeti* under 1.5mm to *Spilostethus pandurus* nymphs which reach up to 10mm, with most species between 2.5mm and 7mm in TBL. Fifth instar British nymphs are on average 79% of the full adult lengths given in Stichel (1957-1959).

Few structural changes occur during development, the most obvious are allometric changes involving a relative
decrease in head size and increase in appendage length (Sweet, 1963).

Shape is normally constant within subfamilies and related to trophic position. However, four adaptive adult morphological modifications are recognised in world Blissinae (Slater, 1976c). Elongate, slender, dorso-ventrally flattened British *Ischnodemus* (Fig. 9) are heavily sclerotized on the abdomen and live between closely adpressed leaf surfaces. The sclerotized 'skid plates' are thought to facilitate body movement enabling them to move backwards almost as rapidly as forwards. Short, stout, thick bodied species, e.g. *Geoblissus*, are found near the base of plants; they often burrow into sand using their fossorial forelegs and sclerotized skid plates are absent or much reduced.

Ground-dwelling nymphs, particularly those occurring in the litter layer, are generally suboval, more than twice as long as broad and moderately dorso-ventrally flattened, with the dorsum being flatter than the more convex venter. Elongate, parallel sided Blissinae, Pachygronthinae, Cymodema (Cyminae), and *Paromius* (Rhyparochrominae) are adapted to feed on grasses and sedges. Other moderately elongate Rhyparochrominae, e.g. *Pterotmetus*, *Raglius* and presumably *Phasmosomus*, are long-legged and fast running, whilst *Platyplax* (Heterogastrinae) and in particular *Piocoris* (Geocorinae) are broadly circular. *Gastrodes* (Rhyparochrominae) and *Orsillus* (Orsillinae) are dorso-ventrally compressed.

Sweet (1967) considered a compact body with short appendages and a declivent head to be a plesiomorphic complex of characters for the Rhyparochrominae, an elongate body form, with long appendages and a porrect head, being apomorphic.

The nymphs of grass and sedge feeding species in the Cyminae, Pachygronthinae and some Rhyparochrominae show a strong 'mimetic' resemblance to the seeds upon which they feed (Van Duzee, 1888; Butler, 1923; Slater, 1952b; Malipatil, 1977a). Palaearctic *Bledionotus* nymphs, recorded for the first time in this study, are myrmecophilous, as are
the South African *Aegyptocoris cotoni* Slater & Sweet (Myodochini) and *Barberocoris myrmecoides* Slater & Sweet (Oxycareninae), which move with the jerky movements of ants (Slater & Sweet, 1970a). Resemblance to ants is discussed in detail by Sweet (1963).

### 6.2 Colour and Texture

A few Henestarinae, Stygnocorini, Artheneini, Megalonotini and Orsillini are, in part, punctate, but this character is only useful at the specific level and cannot be used to define higher taxa.

Dull, predominantly brown and black, cryptically coloured adult Lygaeidae often contrast with their attractive, brightly coloured, intricately and distinctively patterned nymphs. Brightly coloured adult Lygaeinae have similarly coloured nymphs. Diagnostic adult markings are unreliable when identifying nymphs of the same species, a fact confirmed by Eyles (1963a), in relation to antennal markings in three *Scolopostethus* species.

Colour and markings are probably a direct consequence of shared selection pressures relating to behaviour, habitat and host plant preference and can be used as a crude guide to subfamily placement. Colour markings are constant for genera, subtle variations define species and the majority of West Palaearctic genera are identifiable by colour and markings alone.

Colour intensity, brilliance and demarcation are enhanced by immersion of specimens in alcohol. Punctures, pruinescence, shine and mattness are obscured whilst red colour, in particular, fades. Specimens need to be taken out of alcohol to view certain characters, but for convenience are described when in alcohol in this and other studies.

Puchkov (1958a) divided lygaeid nymphs into two colour groups, with either a predominantly pale body or a sharply differentiated dark head and thorax with a lighter abdomen. Three categories, relating to behaviour, are recognised by Sweet (1963): 1) procryptic or concealing colouration,
2) ant mimicry, 3) aposematic or warning colouration. Both authors document major trends in colour change during ontogenesis. These are confirmed by Eyles (1963a), who recorded normal adults from abnormal nymphal colour variants in field and laboratory reared *Scolopostethus affinis* and *Stygnocoris fuligineus*.

Three functional, adaptive, broad colour trends occur in the West Palaearctic fauna:

(1) Cryptic: Head, pronotum, scutellum and mesothoracic wing-pads are predominantly brown-black (Megalonotini part, Gonianotini part); or pale, straw-coloured, unpattered species (Cyminae and Pachygronthinae); or with a predominantly light-brown to dark-brown head, pronotum, mesothoracic wing-pads and scutellum, with a pale, pinky-red abdomen (Stygnocorini, Drymini).

(ii) Disruptive: Pale with a darker, spotted, irrorate, mottled or variegated abdomen (Gonianotini - Diomphalus, Emblethis, Gonianotus and Ischnopeza); or pale species with red, transverse or longitudinal stripes on the abdomen (Artheneinae and some Oxycareninae); or species with pale spots (Orsillinae, Henestarinae, Ischnorhynchinae, Cyminae and some Oxycareninae).

(iii) Aposematic: Predominantly bright, red and black species (mainly Lygaeinae and some Heterogastrinae). Sweet (1963) would include rhyparochromine tribes such as Drymini and Stygnocorini here. Blissinae could also be included. It has been experimentally demonstrated that red *Lygaeus equestris* nymphs have a 6.4 times higher rate of survival from bird attack than a mutant, cryptic grey form of this species (Sillén-Tullberg, 1985).

6.3 Pubescence

Setae are simple (Figs 319-328), occasionally capitate (Fig. 318) (*Lygaeosoma, Ortholomus, Ischnorhynchinae, Oxycareninae*), or thickened, adpressed and almost scale-like in *Cymophyes*. Adult and possibly nymphal Slaterellinae, Psamminae, *Heinsiuss Distant* (Blissinae) and *Sisamnes Distant* have waxy, scale-like hairs, as do taxa
recently transferred from the Lygaeidae - Malcinae and Chauliopinae (Slater, & Sweet, 1965). Setal length and density are variable, ranging from the almost glabrous Cymus (Fig. 8) to the hirsute Lasiosomus enervis (Fig. 18). Pubescence is erect to adpressed, normally longer on the antennae and often stout, almost bristle-like on rhyparochromine tibiae. Spiny prominences on the head or body, typical of Rhopalidae and recently transferred Malcinae and dense silvery pubescence, so characteristic of Gerridae, Veliidae and Hydrometridae, are absent.

Pruinosity, most noticeable in Blissinae, is caused by hundreds of minute microtrichia. 'Bald' elevated surfaces in blissines, which are probably adaptations to enable the insects to slide more easily between closely adpressed leaf sheaths, are useful specific diagnostic characters (Slater, 1979).

Pilosity varies between instars of the same species (Puchkov, 1958a). Pubescence is dense throughout all Stygnocoris fuliginous instars, becomes progressively sparse in late instar Scolopostethus, whilst almost glabrous fifth instar Drymus sylvaticus contrast with hirsute first instars (Eyles, 1963a). Cobben (1978) found chaetotaxy too heterogeneous to allow useful phylogenetic speculation for first instar Heteroptera nymphs.

6.4 Trichobothria

Trichobothria, specialised sensory, mechanoreceptive hairs, occur on sterna 3-7 and three cephalic pairs are found in most Rhyparochrominae (see below). They probably have a 'cat's whiskers' function, at least in ground-dwelling taxa (Sweet, 1963; Schaefer, 1975). McGavin (1979) reviewed the literature on these structures, which evolved from normal setae, and studied their structure and arrangement in British mirid nymphs.

They comprise a slender, normally long, longitudinally fluted shaft or trich, tapering slightly into a basal bothrium, which is either tuberculate, recessed or flush with the trichome, a surrounding region of cuticular sculpturing. They are often difficult to distinguish from
setae on nymphs, particularly in the Rhyparochrominae, Blissinae and Oxycareninae and remain constant in length from instar 1 to adult. They also show a progressive ontogenic increase in numbers and display infraspecific variation within clusters (Schaefer, 1975).

The trichobothrial hairs are long on arenicolous Thaumastellidae and ground-dwelling cydnids and short on plant living pentatomids and cydnids (Schaefer, 1975). A similar divergence can be observed in the West Palaearctic Lygaeidae: - between predominantly plant living taxa in the Lygaeinae, Orsillinae, Ischnorhynchinae, Blissinae, Artheneinae, Heterogastrinae and predominantly ground-dwelling taxa in the Rhyparochrominae. The plant mode may be more primitive in the Lygaeidae than life on the ground, which may be a recent acquisition (Schaefer, 1975).

6.5 Head

This is eucephalous, normally triangular, moderately declivent and, in Palaearctic species, not constricted anterior to the eyes. It is large relative to the body in Oxycareninae (Figs 11, 12), globose in Bledionotinae (Figs 335, 336), vertically compressed in Engistus, strongly transverse in Geocorinae (Fig. 290), particularly Piocoris, but less so in Stygnocorini (Figs 19, 20). It is more porrect in some drymine genera e.g. Eremocoris (Fig. 25) and in Oxycareninae.

Bliss & Beard (1954), in a study of Oncopeltus fasciatus, demonstrated a small but significant increase in head size within instars, whilst Mailloux & Streu (1981) found less instar size overlap in Blissus leucopterus hirtus head measurements than for other structures measured, but found it easier to determine first and second instars of this species, by comparing head width to thorax width.

A subocular ecdysial suture, starting in front of the eyes, converges mesally beneath the pronotum and normally forms an epicranial stem (head must be fully exserted to view). The stem is absent in the Oxycareninae and the Ischnorhynchinae and is much longer than the epicranial arms in Myodocha Latreille (Slater & Sweet, 1961).
The apically blunt tylus, which is bulbous in some Oxycareninae and Cyminae, extends clearly beyond the juga, normally reaching between the mid-point to the apex of the first antennal segment, but clearly extends further in some Oxycareninae and Cymophyes and less far in Beosus.

Compound eyes, on the side of the head, touch or are, in some Lygaeinae, Blissinae, Pachygronthinae, Oxycareninae and Drymini, at most, distanced by no more than their diameter from the anterior pronotal margin. The eyes bear long setae in Plinthisini (Fig. 291), are reniform and protrude laterad in Henestarinae (Figs 288, 289) and Geocorinae (Fig. 290). Cobben (1968, 1978) studied the eye of the first instar Heteroptera nymph. Ocelli are absent in all nymphs and adults of some flightless species.

Three pairs of cephalic trichobothria are present in the Rhyparochrominae, but are difficult to see in hirsute species such as Lamproplax, Taphropeltus and Pachybrachiuis and are secondarily lost in others e.g. Hyalochilus, Gonianotus, Lamproplax, Lasiocoris and Piezoscelis.

Long, four segmented terete antennae, clearly visible in dorsal view, are inserted at the antenniferous tubercle, on or below an imaginary line between the eye centre and tylus apex. Individual segments may be differentially thickened or lengthened and antennal oligomery is recorded. Normally the fourth or sometimes second segment is longest, but with the exception of Camptocoris segment four is never extremely long or curved. Segment one, with the exception of Henestaris laticeps, is shorter and always equal to, or shorter than, the first labial segment. The antenniferous tubercles are normally short, truncate and only just visible in dorsal view. This is the plesiomorphic condition: they are elongate in species with strongly porrect heads.

The four segmented, straight rostrum normally reaches between the pro- and metathoracic coxae but extends considerably further in arboreal seed feeding species (Arocatus, Orsillus, Caenocoris, Gastrodes) and in Camptocoris. The relative length of the rostrum is useful
in separating closely related genera and species (e.g. Geocorinae, Drymini, Gonianotini and Cymus), although Beardsley (1977) experienced considerable difficulties with this character for adult Hawaiian Nysius, which he found somewhat variable, even within populations.

A pair of ventral flanges, the bucculae, occur either side of the first rostral segment; their size and shape can be an important taxonomic character, although this does often appear to be a concomitant of head shape (Sweet, 1967).

6.6 Thorax

A well defined medial ecdysial suture runs from the anterior of the pronotum to the apex of the 'presumptive scutellum'.

The pronotum is normally trapezoidal and wider than long (Fig. 1). It is occasionally more nearly quadrate, (e.g. in Raglius, Fig. 37), semi-circular (some Geocorini) or globose (Bledionotinae, Figs 335, 336), with weak meso-longitudinal and transverse posterior impressions. Laminate and carinate lateral margins are widely present and considered plesiomorphic (Harrington, 1980), or apomorphic (Slater, 1980); they are almost absent in Oxycareninae totally absent in some Rhyparochrominae and most foliaceous in Emblethis. Myodochini (Dieuches and Beosus) have anterior collars (probably also Phasmosomini). Most Lygaeinae (Figs 2-4) and Ischnorhynchinae (Fig. 7.) have distinct impressed black anterior calli; these are pale and strongly pronounced in Diomphalus (Fig. 307) and not impressed in Orsillinae.

Distinct pronotal lobes, associated with wing development in adults, are absent, or faintly evident in some Drymini and Rhyparochromini. Brachypterous adults have a smaller thorax and larger abdomen than macropters (Solbreck, 1986). Other adult specific characters, such as concave lateral pronotal margins, are not always apparent in nymphs of the same species.

An indistinct, triangular 'presumptive scutellar area' is present, but not clearly differentiated as in adults. The
apex is bluntly rounded but never forms a lobe, projecting freely over the abdomen as in some Heteroptera families.

Fully developed wings, characteristic of adults, are absent; instead two undifferentiated mesonotal and metanotal pairs of fleshy wing-pads, lacking venation and positioned close together, are present from instar 3 and normally reach tergum 3 in instar 5. Adult alary polymorphism is reflected in wing-pad length; nymphs with brachypterous adults (e.g. Pterotmetus and Ischnodemus) have wing-pads reaching tergum 2. Some confusion may occur with extreme micropters such as those Apterola nymphs examined, or with the Asian Karachiocoris seidenstuckeri ßtys, which also have extreme reduction in instar 5 wing-pads (Hamid & Meher, 1973). Southwood's (1956a) key to instars works for all species except where micropterous or brachypterous adults occur.

Dolling (1991) and Southwood (1956a) adapted the earlier work of Slater (1951) to key Heteroptera instars. Dolling noted that the separation of first and second instars using the relative lengths of the meso- and metanotum is not as easy as his couplet implies. This is an understatement: field samples of the first two instars can only reliably separated using size differences if all three early instars are present. Wing-pads, except in some atypical Australian Coreoidea (Kumar, 1966), are first visible at least on the mesothorax in third instar nymphs; they are longer than the length of the mesonotum in fourth instars, but the tips of the mesothoracic wing-pads do not extend beyond the tips of the metathoracic wing-pads as they do in fifth instars.

Terminology relating to adult wing development follows Slater (1975, 1977), who reviewed the incidence and evolutionary significance of wing polymorphism in Lygaeidae and concluded that it is restricted to geophiles and laminaphiles. It is correlated with groups from stable habitats and occurs in the highest proportions and, with the greatest degree of modification, in the oldest, stable areas of the world, in the taxa that presumably have occupied such areas the longest.
Six separate abdominal characters were considered by Scudder (1963b) to be of special use in the higher classification of the Lygaeoid-Coreoid complex. Spiracle arrangement, trichobothrial position and number, while extremely valuable in the classification of the subfamily, are not quite so constant in the Rhyparochrominae as one might first be led to believe (Slater & Sweet, 1961).

Nine abdominal segments with an anal tube or proctiger are present. These are particularly hardened and heavily sclerotized in some Gonianotini and Megalonotini. Tergum one is covered by the wing-pads in fifth instars and the posterior two segments are particularly reduced in size. The lateral margins are smooth, but scalloped in Cyminae (Fig. 8) and Cymophyes. Elongate blissines have heavily sclerotized, black skid plates, which probably facilitate their movement between closely adpressed leaf surfaces (Slater, 1976c). The letter coding system devised to aid identification for these plates is followed (Slater & Wilcox, 1973a).

Genitalia are absent, but modifications to the boundaries of sterna 8 and 9 and large darkened mesal areas on sterna 7 and 8 in Rhyparochrominae females enable fifth instar nymphs to be accurately sexed (Johansson, 1958; Eyles, 1960, 1963a, 1963b; May, 1965). This is not true for all subfamilies and Usinger (1942) found Orsillinae nymphs sexually indistinguishable, although size tended to correlate with sex.
Table 4. Distribution of Spiracle Position in Fifth Instar Lygaeidae


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<th>Subfamily</th>
<th>Abdominal segment</th>
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63
6.7.1 Abdominal Spiracles

Segments 2-8 have a pair of spiracles (Figs 53-121). The 8th pair is sometimes absent and ventral or lateral, if present. Their relative positioning (Table 4) is of great importance in delimiting subfamilies and Rhyparochrominae tribes, but was considered of little further value until Hamid (1975) recognised the variable position of spiracle 7 in Cyminae, which usefully differentiates and relates genera. Spiracle 7 is ventral for Cymodema (Fig. 66) and dorsal for Cymus (Fig. 67), spiracles 2-6 are dorsal (Hamid, 1975), but often specimens examined had spiracles close to the lateral edge of the abdomen and their position might be misinterpreted.

Spiracles are sometimes very difficult to see, particularly in pale species. They should not be confused with similar black spots, characteristic of some taxa (e.g. Lygaeinae, and Heterogastrinae), which appear almost to be 'pseudospiracles' in Henestarinae. Great care should be taken in determining precise spiracle positions, as they are often so close to the lateral abdominal margin as to be seen in both aspects. Spiracles that are either clearly dorsal or ventral in adults are often lateral in nymphs. There is no correlation between spiracle position and dorsal abdominal gland aperture positions, or in the presence or absence of a rhyparochromine Y-suture. Ventral spiracles are the plesiomorphic condition in the Heteroptera (Slater et al., 1962; Slater, 1980; Slater & Woodward, 1982).

6.7.2 Abdominal Sutures

Suture structure and direction are fundamentally important in defining higher lygaeid taxa. Unless otherwise stated all sutures are simple and straight. Their characters are summarised in Table 5 and illustrated in Figures 53-121.

Five Palaearctic Rhyparochrominae tribes have a distinctive, wide, "troughed suture" (e.g. Fig. 1), sometimes almost appearing to be double and normally highlighted by a pale margin between terga 3-4 (Puchkov,
1958a). It was given the name Y-suture (Slater & Sweet, 1961), because it branches near the lateral abdominal margin. One branch reaches the margin as normal, the other is directed anteriad, parallel to the lateral abdominal margin and, although obscured by the wing-pads in fifth instars, clearly reaches the suture between terga 1-2 in earlier instars. It is absent in instar 1 and hard to see in instar 2 (Puchkov, 1958a; Eyles, 1963a; Sweet, 1963). The Y-suture is an apomorphic character for these five tribes and its secondary loss is recognised in the ancestor of the Gonianotini and Megalonotini (Slater, 1982; Slater & Woodward, 1982). Its branch is also surprisingly absent from Aellopus.

In Taphropeltus sutures between sterna 2-3 and 3-4 are deeply grooved, lined and contiguous with the Y-suture (Fig. 93). These unlined sutures are often deep and more clearly defined in many Rhyparochrominae. They are, with the exception of Raglius, not margined with white.

Rhyparochrominae nymphs in the Lethaeini, Antillocorini and Lilliputocorini share an important synapomorphy in the double or troughed sutures between terga 3-4 and 4-5 (Fig. 316). This modified cuticle resembles that found between the sutures in the Y-suture (Slater et al., 1977; Slater & Woodward, 1982). It enhances the flow of scent gland secretion to the lateral abdominal margins where it collects and volatilises over minute tubercles or a roughened surface (Slater et al., 1977). Lethaeus nymphs have a shallow, broad, meso-lateral longitudinal trough (Fig. 316), which may also fulfil a transportation or evaporative function.

Nymphs, unlike adults, in some lygaeid subfamilies, Coreoidea and Pentatomoeidea, do not have a clearly defined connexivum. Slater et al. (1962) present general observations on the lygaeid connexivum. Ischnorhynchinae, Orsillinae and Bledionotinae nymphs have a dorsal longitudinal lateral impression and Cleradini have a unique unimpressed lateral suture, running the whole length of the abdomen (Sweet, 1967).
### Table 5. Distribution of Abdominal Suture Characteristics of Fifth Instar Lygaeidae Subfamilies

<table>
<thead>
<tr>
<th>Subfamily</th>
<th>2-3</th>
<th>3-4</th>
<th>4-5</th>
<th>5-6</th>
<th>Genus or Species</th>
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<td>Orsillus Ortholomus</td>
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<td>Ischnorhynchinae</td>
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<td>Cyminaes</td>
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<td>Rhyparochrominae</td>
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<td>Phasmosomini</td>
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<td>Gonianotini</td>
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<td>Megalonotini</td>
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<tr>
<td>Rhyparochromini</td>
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<tr>
<td>Myodochini</td>
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</tr>
</tbody>
</table>

*S* Sterna

- simple, straight or only gently curving

*v* curving strongly anteriad from middle of abdomen

*t* troughed

Y Y-suture

*X* directed anteriad, embracing trichobothrium and not

or * = only faintly reaching abdominal margin

---

66
Rhyparochrominae, with a few notable exceptions, are separated from all other subfamilies by the suture between sternum 4-5, which is directed anteriad, embracing the anterior trichobothrium on sternum 5, then curving posteriad, not, or only faintly, reaching the lateral abdominal margin (Figs 81, 82, 84-88, 90-95, 97-121). Striking differences occur between genera in the forward curvature of this suture (Slater & Sweet, 1961). It is straight and does reach the lateral margin in the following West Palaearctic taxa studied: Plinthisini, Acompus, Gastrodes, and Diomphalus (Figs. 80, 83, 89, 96) and has also been noted to be straight and complete among Antillocorini and Stygnocorini taxa, Phasmosomus (Phasmosomini), Prosomeus Scott (Ozophorini), Nocellochromus (Rhyparochromini), Astemmoplitus Spinola (Udeocorini) and is complete but strongly curved in most Cleradini (Sweet, 1967; Slater & Sweet, 1970b; Slater, 1980). Slater & Sweet's (1970b) inclusion of the stygnocorine, Hyalochilus, is surprising, as West Palaearctic specimens of H. ovatulus do have an incomplete suture.

The incomplete suture between terga 4-5 also occurs in some Largidae and Pyrrhocoridae. Its use as a synapomorph character requires caution (Slater, 1980), as it is anapomorph and developed several times after the adaptive fusion of sternum 4 and 5, which provided increased anterior abdominal rigidity in ground-living bugs.

The sutures between terga 4-5 and 5-6 curve strongly anteriad in the middle in the Geocorinae (Fig. 314) and this character usefully defines a limited number of other genera (Table 5). It is of no value in defining Lygaeoidea into superfamilies, even though sutures between terga 5-6 in the Pyrrhocoridae, and 3-4 and 4-5 in the Largidae curve strongly in the mid-line (Scudder; 1963b). Sutures 4-5 and 5-6 are never reflexed mesally into tergum 5, placing the scent gland apertures close together as in Rhopalidae.
6.7.3 Dorsal Abdominal Gland Apertures

Sac-like dorsal abdominal glands are located mesally between the terga in immature Heteroptera. They open to the outside by paired or single ostioles or scent gland apertures and their secretions are probably toxic to arthropods and repellent to predators. Remold (1962) demonstrated that Heteroptera scent gland secretion repels and also acts as a temporary paralytic poison to ants and carabid beetles and Sweet (1963) noted that all species in all instars of New England rhyparochromines studied had a burning acrid taste. The glands may not all be equal-sized and in pyrrhocorids the first two abdominal glands produce odours which encourage aggregation, whilst the last pair are for defence and alarm (Schmuck, 1987).

The position and number of dorsal gland apertures, between the terga, were the first nymphal characters to receive attention (Gulde, 1902; Usinger, 1938b; Dupuis, 1947; Leston, 1954; Puchkov, 1958a, 1969; Kumar, 1966). McGavin (1979) studied the glands of 130 British Miridae and made histological sections for some species. Cobben (1978) has summarised this literature and tabulated the distribution of these glands in the Heteroptera. Their arrangement (Table 6, Figs 122-212) is of great assistance in defining subfamilies and Rhyparochrominae tribes, whilst the relative distance apart of the gland apertures in each pair together with the size of evaporative areas, are major taxonomic characters in defining genera. Gland apertures are linked or almost touching in Oxycareninae and Cymophyes and more widely separated in remaining taxa.

The possession of four, perhaps five, dorsal abdominal glands was an attribute of the proto-heteropterons. The last gland, between terga 6-7, underwent rapid loss and remnants remain in two Dipsocoromorpha families and in some cimicoid stem groups (Cobben, 1978). The trend within the Heteroptera is towards a reduction in the number of dorsal abdominal glands. Six categories of gland aperture are recognised in Miridae, with single or paired apertures between terga 3-4 (Akingbohungbe, 1974).
Table 6. Distribution of Dorsal Gland Aperture Positions in Fifth Instar Lygaeidae Across the Subfamilies. The Table Follows the Reduction Sequence

+ Paired dorsal gland apertures present  
- Dorsal gland apertures absent  
* Single gland aperture present  
∨ Vestigial gland aperture present

<table>
<thead>
<tr>
<th>Subfamily</th>
<th>Taxa</th>
<th>Terga</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
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<td>3-4</td>
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<tr>
<td></td>
<td></td>
<td>+</td>
</tr>
<tr>
<td>1 Ischnorhynchinae</td>
<td>All</td>
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</tr>
<tr>
<td>Artheneinae</td>
<td>Part</td>
<td>+</td>
</tr>
<tr>
<td>Rhyparochrominae</td>
<td></td>
<td>+</td>
</tr>
<tr>
<td>Plinthisini</td>
<td></td>
<td>+</td>
</tr>
<tr>
<td>Antillocorini</td>
<td></td>
<td>+</td>
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<tr>
<td>Lethaeini</td>
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<td>+</td>
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<tr>
<td>Stygnocorini</td>
<td></td>
<td>+</td>
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<tr>
<td>Phasmosomini</td>
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<tr>
<td>Drymini</td>
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<td>+</td>
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<tr>
<td>Megalonotini</td>
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<td>+</td>
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<tr>
<td>Rhyparochromini</td>
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<tr>
<td>2 Artheneinae</td>
<td>Chilacis</td>
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<tr>
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<td>+</td>
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<td></td>
<td></td>
<td>+</td>
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<tr>
<td>3 Rhyparochrominae</td>
<td>Part</td>
<td>*</td>
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<tr>
<td>Lethaeini</td>
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<td>+</td>
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<tr>
<td></td>
<td></td>
<td>+</td>
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<tr>
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</tr>
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<td>5 Cyminae</td>
<td>C. claviculus</td>
<td>+</td>
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<tr>
<td>6 Lygaeinae</td>
<td>Most</td>
<td>-</td>
</tr>
<tr>
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<td>-</td>
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<tr>
<td>Blissinae</td>
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<tr>
<td>Henestarinae</td>
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<tr>
<td>Geocorinae</td>
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<tr>
<td>Bledionotinae</td>
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<tr>
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<td>Rhyparochrominae</td>
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<td>Gonianotini</td>
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<td>Megalonotini</td>
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<td></td>
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<td>+</td>
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<tr>
<td>7 Rhyparochrominae</td>
<td>Icus, M. antennatus</td>
<td>-</td>
</tr>
<tr>
<td>Megalonotini</td>
<td></td>
<td>-</td>
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<tr>
<td>Rhyparochrominae</td>
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<td>-</td>
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<tr>
<td>Gonianotini</td>
<td></td>
<td>-</td>
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<tr>
<td>8 Cyminae</td>
<td>Cymodema</td>
<td>-</td>
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<tr>
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<td>-</td>
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<tr>
<td>Megalonotini</td>
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</tr>
<tr>
<td>9 Lygaeinae</td>
<td>Apterola</td>
<td>-</td>
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</table>
The situation in Lygaeidae is more complex, with nine basic combinations of paired or vestigial dorsal gland apertures, normally with the evaporative areas, occurring in a variety of combinations between terga 3-4, 4-5 and 5-6. These are presented in order of reduction in Table 6. The distance apart of gland apertures and the presence or absence of evaporative areas further increases the number of combinations.

Table 6 summarises gland aperture arrangement and indicates inter-generic, tribal and subfamily variation. Arrangements are generally consistent within subfamilies (not Lygaeinae, Artheneinae, Cymina, Ischnorhynchinae or Rhyparochrominae). Openings are sometimes vestigial or single and surprisingly absent in Apterola, although McGavin (1979) recorded similar absences in Miridae for two Dichrooscytus Fieber species.

Three pairs of gland apertures is the plesiomorphic condition, but care should be taken in determining synapomorphies, as reduction and loss has occurred independently a number of times during lygaeid evolution. Loss of the anterior glands, between terga 3-4, usually occurs first. A countertrend occurs in the lethaeine, Lethaeus and in Cymina, which has three pairs in Ontiscini and some Ninini whilst the posterior and sometimes intermediary pairs are absent in Cymini. Gland loss is due to selection pressures and concomitant development of other more advantageous protective adaptations.

Ontogenic reduction occurs in Cymina. Ledvinka (1970) found a difference in number and position of the dorsal abdominal gland apertures in Cymus, between the first and remaining instars. The number of glands also varies between species (Figs 136-138). Ledvinka also noted the presence of a third abdominal gland in the first three instars of C. claviculus and C. melanocephalus and an aperture between terga 5-6 for this gland in first instars only. These structures are absent in C. aurescens and C. glandicolor.

Three pairs of gland apertures are always present in rhyparochromine tribes with a Y-suture. The anterior pair has a larger evaporative area than the intermediate and
posterior areas. The anterior gland in species with a Y-suture is white and apparently of a tubular nature, in contrast to the bright orange walls of the posterior two glands and the adult metathoracic glands. In groups without a Y-suture, the anterior gland, when present, resembles the posterior two (Sweet, 1963). The Y-suture may be associated with the transportation of liquid from the anterior gland (Slater & Sweet, 1961). Gland apertures are reduced (some Megalonotini) or absent (Gonianotini and remaining Megalonotini) in tribes which lack a Y-suture (Table 5).

Gland secretions are spread and volatilised on evaporative areas. These are largest in aposematically coloured species, and in genera found on plants and also for most Rhyparochrominae. They are reduced to a narrow sclerotized margin in many pale species (Orsillinae, Figs 131-134; Cymina, Figs 136-138; Henestarinae, Fig. 143; Pachygronthinae, Fig. 157) or absent (Oxycareninae, Fig. 147-153).

Dorsal abdominal glands are not functional in adults although their aperture scars are visible. Leston (1954) reports their persistence, in adults, for a very few cases, but gives no examples. Paired adult metathoracic scent glands with metapleural peritremes are absent in nymphs.

Dolling (1991) questions the function of the adult metathoracic evaporative area and suggests that it is an unwettable region, protecting the bug from the corrosive effect of its own secretion. This is also possible but unlikely for the nymphal abdominal glands. Two East African Coreidae were found to secrete a less complex mixture of more unsaturated compounds with less cuticle soluble chemicals than adults Prestwich (1976). Scudder & Duffey (1972), who discuss the sequestration of cardiac glycosides by adult Lygaeinae, cite work on the butterfly Danaus plexippus (Linnaeus) which shows that liquids do not have to be secreted onto the outside of an insect to be effective.
The Trichophora, a natural unit within the Heteroptera, comprising the superfamilies Pentatomoidea, Idiostoloidea, Piesmatoidea, Lygaeoidea, Pyrrhocoroidea and Coreoidea, is defined by the presence of abdominal trichobothria and bipartite pulvilli (Tullgren, 1918; Schaefer, 1966, 1975). Schaefer (1975) described and diagrammed trichobothria positions for many taxa and discussed their phylogenetic significance within the Trichophora, whilst Scudder (1957a) studied their adult distribution in the Rhyparochrominae.

The spatial arrangement of trichobothria on sterna 3-7 and their position relative to the spiracles is important in defining the Lygaeidae as a family, the Oxycareninae as a subfamily and also defines tribes within the Rhyparochrominae, particularly, Plinthisini, Drymini and the Lethaeini/Antillocorini/Targaremini complex. It is of little value for lower taxa as cluster position varies too little at species level, their internal arrangement varies too much and bilateral asymmetry sometimes occurs (Schaefer, 1975).

Trichobothria are absent from sterna 2 and 8 and are usually present in bilaterally symmetrical pairs on terga 3-7 in the formula 3:3:3:3:2. One representative species for each available West Palaearctic genus is figured in lateral view (Figs 53-121). This information significantly adds to Schaefer (1975).

The paired trios of trichobothria on sterna 3 and 4 are close to the middle. Clusters are variable on sternum 4 and arranged in a linear, vertical or diagonal sequence on sternum 3 (Figs 53-121) for all subfamilies, excepting the Rhyparochrominae and for the lygaeine Lygaeosoma which are triangularly clustered (Fig. 57). Only two trichobothria are present on both sterna in Ischnodemus and Dimorphopterus (Figs 68, 69).

Trichobothria on sterna 4-7 are lateral, normally with a single prespiracular and with a postspiracular pair on sterna 5 and 6; sternum 7 has only a postspiracular pair.
The trichobothrial seta nearest to the abdominal margin in the postspiracular pair is normally the longest.

Trichobothria are absent from sternum 5 in Oxycareninae, Bledionotinae and Cymophyes although Schaefer (1975) records them in other Pachygronthinae. They are in a highly derived linear sequence in Lethaeini, some Antillocorini and non-Palaearctic Targaremini (Figs 81, 82). The posterior pair have migrated anteriad to the spiracle in all Drymini (Figs 87-93) except Gastrodes in which they are directly under it (Fig. 89). Post- and prespiracular trichobothria are closer together in Ischnorhynchinae (Fig. 65), Cyminae (Fig. 67), Artheneinae (Fig. 74, 75), Henestarinae (Fig. 70), Heterogastrinae (Figs 77-79) and Plinthisini (Fig. 80).

The trichobothria on sternum 6 are almost linear in Lygaeinae (Figs 53-60) and uniquely, all three are post-spiracular in Oxycareninae (Schaefer, 1975), although almost invisible. The vertical pair on sternum 7 in Plinthisini are notably more widely separated than in other taxa (Fig. 80).

Schaefer (1975) noted two evolutionary trends: with the acquisition of the adult trichobothrial complement increasingly earlier in instars or failure to attain the normal adult condition (Blissinae, Cyminae). The more primitive the taxon, the later in its ontogeny it attains the adult trichobothria complement.

6.8 Legs

Ground-dwelling, fast running species not associated with particular host plants, such as many Rhyparochromini, are elongate and long-legged. Arboreal species, many Blissinae (Dimorphopterus, Ischnodemus), Artheneinae and more sedentary ground-dwelling species, associated with particular and readily apparent host plants, such as Henestarinae and Oxycareninae, are short-legged. Prothoracic and mesothoracic legs are normally cursorial, similar in length and noticeably shorter than the metathoracic pair.
The prothoracic femur is usually incrassate and may be mutic, unispinose or armed with one or two rows of spines on the antero- and postero-ventral edges. All spinose British and West Palaearctic genera are figured in profile (Figs 213-287). Spine arrangements assist generic delineation and species identification, despite some intra-specific variation. Their phylogenetic use is limited and Slater (1979) in a study of world Blissinae, observed both different and similar femoral spine conditions in different phyletic lines, even in the same genera. He suggested that mutic prothoracic femora are ancestral in Lygaeidae, with the early development of a single femoral spine.

Nymphal spine patterns do not necessarily correspond to the full adult complement or dimensions. The appearance of spines in different instars varies between species (Eyles, 1963a). Mutic Geocorinae and some Gonianotini have a row of fine setae on the antero-lateral edge of the prothoracic femur instead. Comparable spines occur on the other femora in Raglius and Aellopus. Mesothoracic and metathoracic femora do not have trichobothria as in the Miridae and some other families.

Lygaeidae are primarily seed feeding. The strongly raptorial appearance of the prothoracic femora wrongly suggests that they are predatory, a mistake most recently made by Miller (1971). Spines are used for seed manipulation and the use of the prothoracic femora to move seeds to protected sites was first recorded in Elasmolomus sordidus (Maxwell-Lefroy, 1909). They are also used by some rhyparochromines for the defence of seeds (Sweet, 1963). Spines aid free movement among litter, seeds and foliage (Malipatil, 1979). Slater (1976c) suggested they are used as tibial holding braces when laminaphilous blissines move through narrow spaces and they possibly have a seed cracking function in the myodochine Dieuches (Eyles, 1973).

Geocorinae, the only predatory Lygaeids, have mutic, weakly incrassate prothoracic femora. Spongy fossae, thin adhesive areas of cuticle present on the apical ventral parts of the prothoracic tibiae in many predacious Heteroptera (Reduviidae, Nabidae, Anthocoridae) and used for prey retention, are not present.
The labium is pulled through prothoracic tibial cleaning brushes during grooming, in second to fifth instar lygaeids as well as adults (Sweet, 1963).

Nymphs have two tarsal segments, one less than all adults, excepting Psamminae. The first metathoracic tarsal segment is longer or equal to the second in Rhyparochrominae and shorter or equal to the second segment in other subfamilies, excepting Lygaeosoma (Lygaeinae) and Heterogaster urticae (Heterogastrinae). This ratio also applies to the pro- and mesothoracic segments for all subfamilies excepting Rhyparochrominae, where it is variable in Drymini, Gonianotini, Megalonotini and Rhyparochromini. Paired tarsal claws are inserted apically and adult pretarsal characters were studied by Goel & Schaefer (1970).
7. Systematic and Taxonomic Discussion

It is important to study and analyse British Lygaeidae within a Palaearctic and world context. Slater (1964a) warns of the unfortunate tendency to produce species lists from restricted areas without carefully reviewing the past literature, so that the significance of the local study can be evaluated in ecological, evolutionary and zoogeographic terms. For instance, McGavin (1979), in a study restricted to immature stages of British Miridae, found valuable information indicating relationships, which was not supported by adult characters. However, he found it difficult to examine phylogenetic implications when dealing with the restricted fauna of a small geographic region. Similarly, Wagner's (1951, 1954b, 1956, 1958, 1961a, 1961b, 1963, 1967) work on adult Palaearctic Lygaeidae, while retaining value for identification purposes, is of little systematic value, as it often reflects phyletic trends within the Palaearctic fauna, which cannot be substantiated for the world fauna.

The Blissinae are the most intensively studied of all the subfamilies; even so, Slater (1979) concluded that, although nymphs appear to have features important to an understanding of phylogeny, it was difficult to use these characters in phylogenetic work, as nymphs of many species (including all species in several genera) remain unknown.

This study involved analysis and evaluation of all morphological and other characters as indicators of evolutionary directions and relationships among the Lygaeidae. Examination of Western Palaearctic material puts British studies into the wider geographical context necessary to investigate relationships suggested by the study of nymphal morphology, whilst reference to the world literature on immature and adult Lygaeidae prevents a blinkered regional systematic analysis.

Changes at generic and species level for primarily Palaearctic taxa are recommended in this section, but caution is exercised with the higher taxa, where only provisional phylogenetic relationships are suggested. It would be unwise to produce a cladogram analysing
relationships within the restricted Palaearctic fauna and premature to attempt analysis for the world fauna. Such a project requires full integration of immature and adult characters and awaits the discovery of nymphs of considerable numbers of New World and tropical species.

Mature lygaeid subfamily limits are confirmed by this study. There is, however, still confusion over the true composition of tribes and genera, particularly in the Rhyparochrominae. Subfamilies are discussed below in systematic sequence. For each subfamily, relationships within West Palaearctic tribes and genera are considered first, followed by a discussion of British species.

7.1 Lygaeinae

Distinct lygaeine nymphal generic colour patterns are clearly recognisable and are important in the separation of Horvathiolius from Melanocoryphus. However, care must be taken to ensure that adult taxonomic mistakes are not replicated by the creation of a parallel colour identification scheme for nymphs. Colour markings are only used to substantiate morphological differences. Potential confusion in separating species by markings alone is highlighted in Lygaeus equestris, where nymphs exhibit infraspecific variation.

Adult and immature Lygaeinae are described, from Stål (1872) to Slater (A.) 1985 as having all spiracles dorsal. However, spiracle 8 is lateral in Caenocoris, Melanocoryphus and Tropidothorax nymphs (Table 4).

Schaefer (1975) incorrectly stated that plant-living Lygaeinae are atypical, with short trichobothrial hairs that do not extend beyond the body. West Palaearctic Lygaeosoma, Melanocoryphus and Horvathiolius adults and nymphs, which were always collected on the ground, have trichobothrial hairs extending beyond the body and have large evaporative areas. Lygaeus and Spilostethus adults and nymphs, which were frequently swept from herbage, although they do also occur on the ground, have short trichobothrial hairs.
Many of Stål’s (1874) subgenera of *Lygaeus* have been raised to full generic status. Elevation of *Spilostethus* is substantiated by nymphal morphology. *Melanocoryphus* is a valid genus, but nymphal analysis alone does not warrant the further division proposed by Josifov (1965). *Arocatus*, *Caenocoris*, and *Tropidothorax* warrant generic status, the position of *Cosmopleurus* is less convincing and *Lygaeosoma* problematic. Unfortunately, nymphs were not available to test whether *Parapterola* is a good subgenus of *Apterola*, or Hoferlandt’s (1967) assertion, that adult *Paranysius* show considerable relationship to *Arocatus*.

Stål’s (1874) separation of *Melanocoryphus* from *Lygaeus*, using adult colour markings is confirmed by structural nymphal analysis. *Lygaeus* nymphs (Figs 58, 127) share trichobothrial and abdominal suture characters, but are almost glabrous, with larger evaporative areas and have the gland apertures in each pair closer together than *Melanocoryphus* (Fig. 128).

Further division of *Melanocoryphus* (Josifov, 1965) into *Melanocoryphus* [nov. sens.] and *Horvathiolus* Josifov, using the shape of the male genital capsule opening and adult colour markings, is not supported by nymphal structural characters, confirming Slater & Sperry’s (1973) examination of South African adult material which did not completely substantiate the grouping either. The consistent colour markings which divide the taxa are not worthy of generic status. *Horvathiolus* has white posterior pronotal corners and terga 2-7 transversely marked (Fig. 2), whilst *Melanocoryphus* lacks white pronotal corners and has longitudinal tergal stripes.

Full generic status for *Spilostethus* is convincing. Nymphal characters represent an intergrade between *Lygaeus* and *Melanocoryphus*. Meso-lateral longitudinal rows of black spots on terga 2-7 in *Spilostethus* and *Melanocoryphus* are absent in *Lygaeus* (Fig. 4). However, unlike *Melanocoryphus*, the gland apertures are similarly spaced to *Lygaeus*. The maximum width of the evaporative area in *Spilostethus* is larger than in *Melanocoryphus* relative to the eye width, but is significantly smaller than for *Lygaeus*.
Adults of *Cosmopleurus* are structurally similar to *Spilostethus*, suggesting similarity, but the relative position of the dorsal gland apertures, which are close together in each pair in *Spilostethus* (Fig. 129) and apart in *Cosmopleurus* (Fig. 124), confirm the generic separation.

Slater & Sperry's (1973) suspicion that *Arocatus* is so closely related to *Caenocoris* that they do not represent separate genera is unfounded. Both are arboreal and share common characters, notably a strongly curving suture between terga 5-6. However, *Arocatus* nymphs have equal, or almost equal sized evaporative areas mainly anterior to the suture, with the gland apertures distinctly separated by more than their width (Fig. 122). *Caenocoris* (Fig. 123) in contrast, has distinctive evaporative areas, with the posterior area twice as wide as the anterior area and only the posterior apertures are separated by more than their width. Colour markings are quite different and also *Caenocoris* is the only Palaearctic genus with a spine on the antero-ventral margin of the prothoracic femur and with the fourth antennal segment distinctly longer than the second.

Ground-dwelling *Apterola kunckeli* nymphs, discovered here for the first time, pose an evolutionary puzzle, unique for Lygaeidae. They lack dorsal abdominal gland apertures and evaporative areas. Even nymphs of the Asian *Karachiocoris seidenstuckeri*, one of the two other micropterous lygaeine genera, have small dorsal abdominal gland apertures between terga 4-5 and 5-6 (Hamid & Meher 1973). Slater & Sperry (1973) consider the ancestral condition for the subfamily to be the macropterous state, living for at least part of the life cycle on herbaceous plants. Life on the ground is a recent acquisition (Schaefer, 1975). Absence of gland apertures in *Apterola* is probably, like wing loss, a secondary adaptation, associated with ground living lygaeines in stable habitats. More *Apterola* and *Parapterola* nymphs are required, to test if this is generally applicable.

Small, cryptically coloured, *Lygaeosoma* adults and nymphs are atypical lygaeines with an extended bulbous tylus. They possibly link with *Orsillinae*, being the only lygaeines
with capitate setae, a character shared with some, Orsillinae, Oxycareninae and Ischnorhynchinae. The trichobothrial pattern on sternum 3 is unique within the Lygaeinae examined (Figs 53-60).

Further examination of world Lygaeinae, particularly Apterola and Lygaeosoma adults and nymphs, may substantiate the erection of two new tribes to contain these aberrant taxa.

7.1.1 The Lygaeus equestris Complex

Adult L. equestris and L. simulans are consistently marked, and possess subtle, unambiguous structural characters. Nymphs, by contrast, are confusingly marked and both species show variation, with Sillén-Tullberg (1985) recording a mutant grey form of L. equestris which lacks the red pigment. Typically L. equestris has red terga 2-7, with white along the sutures (Fig. 4), whilst L. simulans has three red longitudinal stripes on terga 2-7 (Fig. 311), less black on the head and pronotum. Morphometric analysis (Appendix 7) illustrates their closeness, with L. simulans slightly the larger. Both species also have the same colour form intermediate between the species, with broad mesolateral white bars along the sutures, not quite forming longitudinal stripes (Fig. 310). A mixed L. simulans sample, comprising four intermediate fifth instars, two striped fourth instars and one striped third instar was collected. Further collecting will probably reveal that both species exhibit several phenotypic forms.

Colour variation in Lygaeus is probably a direct result of external stimuli on individual specimens or a genetic response. Climate, geography, population density, host plant association or a combination of factors may be important. Initially, infraspecific variation must be determined, by controlled experimental investigation and extensive field collection throughout the species' range. Examination of closely related L. creticus and L. murinus nymphs may similarly prove instructive.

Slater & Knop (1969) constructed a hybrid index to analyse geographical variation for six colour characters in North
American *L. kalmii* Stål and *L. reclivatus* Say. Adults could not be separated by differences in the male paramere and were variable in colour. The authors considered that climatic factors, especially humidity, influenced the colour markings.

A total of 46 second to fifth instar *Lygaeus equestris* and *L. simulans* nymphs were collected (Appendix 5), but these were insufficient to enable any positive conclusions to be drawn. Puchkov (1958a) keys *L. equestris* (= *L. simulans*) nymphs for the Ukraine as striped and all striped nymphs recorded are from Spain and Turkey. No mention is made of variation or stripes in Swedish *L. equestris*, despite extensive bionomic and behavioural investigations. Nymphs collected in France and Greece were also unicolorous. Further investigation may reveal unicolorous nymphs to be predominantly mid and North European (one was collected in Turkey), with striped nymphs occurring predominantly in the Mediterranean and Irano-Turanian regions, but with a large area of intergradation.

Kugelberg (1973a), noted that lighter coloured adults resulted from increased nymphal density, but made no comment on nymphal colouration.

Host plant selection may also effect colour. Solbreck & Kugelberg (1972) record *L. equestris* adults feeding on 26 plant species in 21 families, and nymphs were recorded feeding from 13 plant species in 11 families. Puchkova (1954), by contrast, reared *L. equestris* (= *simulans*) to the adult stage on various diets and found that the kind of seeds was of little importance. However, field observations show that *L. equestris* is associated with *Cynanchium vincetoxicum* (Linnaeus) in greater parts of Europe (Kugelberg, 1973b).

### 7.2 Orsillinae

Examination of nymphs supports the generic divisions within this subfamily. There is, however, confusion surrounding adult *Nysius* species and their nymphs show no obvious additional colour or morphological characters that might be used to assist with the problem.
7.3 Ischnorhynchinae

Ischnorhynchinae cause systematic confusion and the subfamily status owes much to nymphal taxonomy (Slater, 1952a, 1963; Sweet & Slater, 1961; Puchkov, 1958a).

*Kleidocerys* nymphs have three pairs of dorsal abdominal gland apertures (Fig. 135), leading Slater (1952a) to suggest a link with the Rhyparochrominae. He wisely avoided taxonomic rearrangement until further nymphs in other genera were studied. Nymphs of one more species, the South American *Polychisme poecilus* (Spinola) have subsequently been described and found to lack anterior gland apertures, allying them with the Orsillinae. They possess, however, the characteristic lateral abdominal impression of the Ischnorhynchinae (Slater, 1963). Additional material, particularly for tropical genera, is required, to determine which of the abdominal gland character traits is typical. Only then can relationships between genera and with the Orsillinae be resolved.

Variation in dorsal abdominal gland aperture numbers and positions occurs in other subfamilies (Table 6), most notably the Rhyparochrominae, where there are normally three pairs, but where the absence of an anterior pair occurs, this partly defines the Gonianotini. By analogy, *Kleidocerys*, which is already recognised to be an "aberrant" genus (Scudder, 1962a), and *Polychisme* may belong to separate Ischnorhynchinae tribes.

7.3.1 Western Palaearctic *Kleidocerys* and the *Kleidocerys resedae* Complex

Arboreal *K. resedae* is Holarctic, whilst *K. truncatulus ericae* occurs throughout most of the West Palaearctic (Table 10) and appears restricted to *Erica Linnaeus* and *Calluna Salisbury* (Ollivier, 1979; Wheeler, 1976). Both species have synchronised life histories and surprisingly *K. truncatulus ericae* can be reared on birch, one of *K. resedae’s* main hosts (Woodroffe, 1960a).

Individual adults and nymphs of *K. resedae* are difficult
to separate from *K. truncatulus ericae* but are generally larger across a series of specimens. Size distribution for nymphs (Appendix 7) and adults, contrary to Stichel (1957-1959), overlap. There are slight paramere differences between the two species and pronotal calli in *truncatulus ericae* are less pronounced than in *resedae* adults, but not for nymphs.

Biological information provides the most convincing evidence for separating these two British *Kleidocerys* species. *K. truncatulus ericae* stridulates at exactly half the pulse rate of *K. resedae* (Haskell, 1958).

It was also hoped that this study would determine whether:

1) Dark adults of *K. resedae* found on *Alnus glutinosa* (Linnaeus) are *K. privignus*. This has variously been considered a smaller and darker melanistic form of *resedae* (Kiritshenko, 1951), or a good species (Stichel, 1957-1959). It was synonymised with *resedae* by Scudder (1962a).

2) The species on *Rhododendron ponticum* Linnaeus is Nearctic *K. resedae fuscomaculatus* Barber or *K. resedae geminatus* Say, constituting part of the shrub's increasing alien fauna (Judd & Rotherham, 1991, attached).

Unfortunately, type specimens of *K. privignus* were on loan and requests for Nearctic types were unforthcoming. There were no differences between parameres of males from *Betula, Rhododendron* and darker *Alnus* specimens. *Alnus* nymphs were slightly smaller (Appendix 7).

*K. resedae flavicornis* (Duda) is Palaearctic, but not recorded from Britain. Stichel (1957-1959), lists *flavicornis* as a colour form of *resedae*.

7.4 Cyminae

Cyminae are possibly worthy of family status. They have been erroneously linked with other Pentatomomorpha.

Hamid (1975) found a "very great" degree of difference from Berytidae, refuting Southwood & Leston's (1959) unsubstantiated placement of Cymini in this family. He noted similarities with Lygaeidae which suggest they should
be retained within this family but did not consider if the Cyminae warrant family status.

Slater (1952a) warned that it was inadvisable to characterise Cymini on the basis of nymphal characters, until representatives of more of the exotic genera were known. The presence of dorsal abdominal gland apertures between terga 3-4 and or 4-5 was mistakenly considered unique amongst the Lygaeidae and indicative of the isolated position of the Cyminae (Sweet & Slater, 1961). However, there is a much reduced third pair between terga 5-6 in Ontiscini and some Ninini (Hamid, 1975) and they are present in first instar Cymus claviculus and C. melanocephalus (Ledvinka, 1970).

The number of nymphal scent gland apertures in the Kleidocerini and Cymini was, therefore, used incorrectly to separate Ischnorrhynchinae from the Cyminae (Slater, 1952a). However, nymphal characters do still substantiate this division. The posterior scent gland apertures are reduced ahead of the anterior ones, a condition shared with Piesmatidae and Berytidae, although the median orifice in the latter is unlike that in the Cyminae.

Variation in dorsal abdominal gland apertures and spiracle positions means that, unlike for most other subfamilies, they can be used to define tribes, genera and species. For example, Cymodema spiracles are not all dorsal as stated by Hamid (1975) and Slater (1963, 1976a). Instar 5 C. claviculus have the posterior pair of gland apertures reduced (Fig. 137) and which are apparently non-functional; only the anterior pair have small evaporative areas.

Štys (1959) suggested that a large number of the dorsal abdominal gland apertures was a primitive character and Ledvinka (1970) concluded that the claviculus/melanocephalus group was primitive and the obliquus/glandicolor group derived. He ignored the vestigial gland apertures between terga 4-5 in C. claviculus, which implies that this species is the most derived of all.

Relative lengths of second and third antennal segments,
rostrum length relative to coxae, and the position and structure of gland apertures are the only useful characters separating nymphs of the four Cymus species studied. Ledvinka (1970) found no differences valid for all instars which could be used for a definitive key to species. Distinctions between sympatric C. aurescens and C. glandicolor are particularly subtle and unreliable. Identification requires the use of multiple character sets and host food plant associations.

British Cymus nymphs mistakenly key with Tingidae and Piesmatidae in Dolling (1991), because of shared scent gland characters.

7.5 Blissinae

Nymphal character analysis aids understanding of the phylogeny of this subfamily (Slater & Wilcox, 1973a; Slater, 1979). Representatives of 20 blissine genera remain undescribed and Slater & Wilcox (1973a) were unable to characterise genera in their key to South African species.

The spiracle position of 2-6 dorsal and 7-8 ventral is restricted within Lygaeidae to Blissinae and considered a characteristic of the subfamily (Slater, 1979). Southwood & Leston's (1959) statement that spiracles up to 7 are dorsal is ambiguous and Puchkov (1958a) is wrong when he states that only spiracle 7 is ventral. Care must be taken with this character as in Dimorphopterus doriae nymphs spiracles 2-6 are dorso-lateral (for one specimen latero-ventral).

Dimorphopterus presents a complex problem (Slater & Wilcox, 1973a). Nymphs of only two species were available and none of the closely allied Geoblissus were found. However, it is unlikely that D. doriae and the type species D. spinolae are truly congeneric (see descriptions). The evaporative areas are clearly separated by more than the width of the posterior area in D. spinolae (Fig. 140) and are much closer together in D. doriae, where they are not separated by the length of the posterior area (Fig. 139). D. spinolae evaporative areas are equal, but the anterior area is smaller in D. doriae.
The two British *Ischnodemus* are closely related. The abdominal markings are identical as is the pubescence length and density. The species can only be separated using body measurements; *I. quadratus* is shorter and narrower than *I. sabuleti* (Appendix 7).

### 7.6 Henestarinae

This subfamily is uncontroversial. Nymphal morphology substantiates *Henestaris* and *Engistus* as good genera.

### 7.7 Geocorinae

The structurally uniform Nearctic species are very difficult to separate (Readio & Sweet, 1982). The variable adult colour characteristics have led to the formal description of a bewildering number of varieties (Slater, 1964b) by authors who, in the words of Torre-Bueno (1946), "without an acquaintance with the forms in the vast numbers in which they are found in the field, revelled in the least nuances of colour, in a group which is as variegated in this respect as the offspring of ranging tom cats".

Readio & Sweet (1982) studied 12 species, observing diverse colour patterns, which differed from the adults and provided information for species separation. West Palaearctic nymphs also vary infraspecifically. *Geocoris ater* range from forms with bright red to white abdomens. *Geocoris melanocephalus* normally have a white spotted, red abdomen with the head and thorax yellow and black, or they can be pale yellow with a white abdomen and little black. *Piocoris erythrocephala*, in contrast, has a pale abdomen with red transverse bands, very pale specimens without red also occurring. Intermediate colour morphs were collected for all three species and large samples contained several forms. Pale specimens have not faded in alcohol and are not teneral. Variation cannot be attributed to differing host plant preferences and appears not to be density dependent. Geocorines are predators and, although sometimes common, do not aggregate. Similarly, there were no obvious geographical, seasonal or habitat correlations with morphs, but polymorphism must be of advantage to the species.
Geocoris, with over 100 species, is, contrary to the view of Linnavuori (1972), distinct from Piocoris. Nymphs of two Piocoris species studied were rounded and convex in profile with the rostrum reaching, or extending beyond the hind coxae and with R2 longer than R3. Furthermore, the gland apertures were more slit-like and the evaporative areas not bilobed (Figs 144, 145).

Geocoris siculus is given specific status in the checklist but is often treated as a subspecies of G. melanocephalus. Nymphs were unavailable, but two Maltese adults (see Appendix 5), identified using Stichel (1957-1959), have shorter, stubby, erect pubescence on the head and pronotum than the erect setae of G. melanocephalus, which are as long as the base of the second antennal segment.

7.8 Bledionotinae

The systematic position of the Bledionotini, which comprises the monobasic genera Bledionotus and Bethylimorphus Lindberg, has been controversial. China & Miller (1959) considered Bledionotus an aberrant Rhyparochrominae. Scudder's (1963a) placement of the tribe, together with the Pamphantini, in a distinct subfamily, the Bledionotinae, is supported by examination of Bledionotus nymphs, which were collected for the first time.

Two third instar nymphs and five adults were collected in Southern Turkey (Appendix 5). These adults are larger and darker than two specimens from Afghanistan, determined by Hoberlandt, of B. systellonotoides in the Natural History Museum. It is probable that either the Afghanistan or more likely, the Turkish specimens represent a new species. The Turkish adults are described after the nymphal description. The adults are separated as follows:-
Larger; total body length from base of abdomen to tylus apex = 2.7 - 3.0mm. Appendages longer and thicker; A4 0.64mm long and as wide or wider than eye width. Darker; head, pronotum, scutellum, and pubescence brown-black. Bledionotus probable new species (from Turkey).

Smaller; total body length from base of abdomen to tylus apex = 2.2 - 2.6mm. Appendages shorter and thinner; A4 0.45mm long and width less than eye width. Lighter; head, pronotum, scutellum and pubescence yellow-brown. Bledionotus systellonotoides (from Bashgultal, 1500m, Kamu, Nuristan, Afghanistan; coll. J. Klapperich, 20 and 26.04.1953.).

The third instar nymphs are ant-mimics, with a strongly globose head and pronotum, a petiole-like constriction between the meso- and metathorax and a distinct, scale-like, upwardly projecting protuberance on the first abdominal segment, with a smaller protuberance on the 'scutellum' (Figs 335-336). This ant-like appearance and the yellow and red chequered abdomen is not shared with any known rhyparochromine species, although many imitate ants in their movement. The nymphs do not have a rhyparochromine Y- or trough suture between terga 4-5 (Table 5) and the presence of two pairs of dorsal abdominal gland apertures is otherwise limited in the Rhyparochrominae to the Gonianotini and a few Megalonotini, which also lack a Y-suture. However, Bledionotus is not an aberrant member of these tribes. Nymphs lack an evaporative area and, like the Oxycareninae (Figs 147-153) have the inconspicuous gland apertures almost touching (Fig. 146) and not widely separated as in the Gonianotini and Megalonotini (Figs 178-188, 191, 194, 198).

7.9 Oxycareninae

Slater & Hurlbutt (1957) recognised the unique oxycarenine wing structure and concluded that the subfamily represented a side branch in lygaeid development, probably originating from artheneine and orsilline stock. Swollen hairs, trichobothrial position and genitalia structure all indicate the isolated position of Oxycareninae (Slater & Sweet, 1970a).
The glabrous Oxycarenus laticeps, O. pallens, Macropternella conica and M. inermis all lack the "peculiar swollen hairs" that Slater & Sweet (1970a) observed on all species in eight genera. Macropternella have a few simple setae. All other Oxycarenus and other genera have capitate setae. Ischnorhynchinae and Orsillinae also have capitate setae, which are not, as Slater and Sweet suggested, unique to the Oxycareninae. Capitate setae appear primitive in the Oxycareninae and their presence strengthens the argument that Oxycareninae are derived from orsilline stock.

Nymphal taxonomy will contribute to the revision of world oxycarenine genera. Examination of Brachyplax, Metopoplax and Macroplax nymphs confirms they are good genera. Nymphal characters also substantiate Samy’s (1969) findings on Oxycarenus but suggest changes are required in the status of Microplax.

Microplax, comprises five species, with the West Palaearctic M. plagiata the type. The genus is polyphyletic and collectively M. albofasciata and M. limbata are distinct from M. plagiata. M. plagiata nymphs are, in contrast with the other two species, oval and pale, lacking a black shining head, thorax and wing-pads. The pronotum is trapezoidal, and the head is significantly less porrect. Adults have the interface between the corium and the membrane almost parallel to the base of the pronotum, forming an obtuse angle with the claval suture. This angle is more acute in the other two species, and the corium-membrane junction is not parallel with the pronotal base.

A new subgenus, Pseudomicroplax, containing albofasciata and limbata, is proposed. Nymphs of the remaining two species should provisionally be placed in the new subgenus on the shared adult wing structure. Confirmation of their position will warrant full generic status for Pseudomicroplax.

Only six of the forty Oxycarenus species occur in the West Palaearctic. Nymphs of five of these divide into three groups, the first two corresponding to Samy’s (1969) subgenera (checklist ref. 9.14) with the third intermediate:-
1) *O. hyalinipennis* and *O. lavaterae* - Body with short capitate pubescence. Head, pronotum, mesothoracic wing-pads and scutellum black and brown, contrasting with a unicolorous red abdomen.

2) *O. luteolus* and *O. pallens* - Body glabrous and predominantly white, with very limited red markings on the abdomen.

3) *O. modestus* - Body with very short, capitate pubescence. Abdomen either unicolorous red or predominantly white.

It is premature to draw even tentative conclusions from these divisions. Slater (1972a) suggested that cross-breeding populations is desirable, before relationships can be established.

Samy (1969) used adult colour to identify species. In his revision of African species, *O. hyalinipennis* and *O. lavaterae* were retained in Oxycarenus s. str. and *O. pallens* placed with one other species in Euoxycarenus subgen. n. *Oxycarenus luteolus* and *O. modestus* do not occur in Africa and none of the three species in Samy's third subgenus, *Pseudoxycarenus*, is Palaearctic.

However, adult *O. luteolus* is close to Euoxycarenus, confirming the close colour and structural similarities in the nymphs. *O. modestus* adults were unavailable, but the sinuate pronotal margins and head dimensions illustrated in Puchkov (1969) indicate that they belong in Oxycarenus s. str.. Slater (1972a) considered it desirable to wait before raising Samy's subgenera to generic status, but the nymphal characters confirm Samy's observations.

*O. modestus* nymphs are intermediate between the two subgenera. The occurrence of two colour forms poses questions: it may be that the species is sexually dimorphic; the two red specimens of nymph were male and the white specimen female.
Recent tribal changes in the Artheneinae are supported by nymphal studies. The British species, *Chilacis typhae*, was one of the first lygaeid nymphs described (Péneau, 1909) and has subsequently been redescribed four times (Appendix 1). Southwood & Leston's (1959) comments on Artheneinae require revision. Dilompini, Nothochromini and Polychismini have all spiracles ventral and only the Artheneini have spiracle 2 dorsal and 3-7 ventral. Only *Chilacis typhae* has a single reduced anterior gland aperture, all other described species have paired apertures. Collett (1927) and Jordan (1935) incorrectly figured fifth instar *Chilacis typhae* as fourth instar and the implication that there was no fifth instar is incorrect. Puchkov (1958a) repeated Jordan's mistaken description of it as lacking red stripes on the abdomen. They are present, but sometimes indistinct, and he later figured a fourth instar with red stripes (Puchkov, 1969).

Puchkov (1958a) keyed *Artheneis foveolata* nymphs as having the distance between the scent gland apertures in each pair the same, but later figured fourth instar *Artheneis balcanica* with the distance between the gland apertures in each pair declining posteriad as in *Artheneis aegyptiaca/hyrcanica* and *Holcocranum* (Puchkov, 1969). The separation of the gland apertures is variable in *Artheneis* and is unreliable for separating *Artheneis* and *Holcocranum* nymphs. The vestigial *Chilacis* anterior gland apertures conform to the normal lygaeid reduction trend (Table 6).

7.11 Pachygronthinae

Puchkov (1958a) considered the almost fused scent gland apertures to indicate a possible relationship with the Pyrrhocoridae and felt that the Pachygronthinae might warrant full family status. However, fused scent gland apertures are correlated with the narrowing and elongation of body in species living on grass sheaths.
7.12 Heterogastrinae

Puchkov (1958a) noted that this was a homogenous family, although nymphs of tropical species are yet to be described. Size of the anterior 'pseudo-evaporative' area between terga 3-4, relative to the other two functional areas, and shape of the lateral pronotal margins are consistently good generic characters which separate Platyplax from Heterogaster.

Leston (1954) figured the dorsal gland apertures between terga 4-5 and 5-6, for Heterogaster urticae, but curiously did not discuss the non-functional evaporative area between terga 3-4. Its presence suggests that gland loss is relatively recent, particularly in Heterogaster, with reduction occurring earlier for Platyplax, where it is smaller than the other functional areas. This is confirmed by Sweet & Slater (1961), who key the American Heterogaster behrensii (Uhler) with a single circular scent gland aperture between terga 3-4.

Lateral abdominal banding in H. urticae differs from that in H. artemisiae, H. affinis and H. cathariae and is closer to Platyplax salviae. Heterogaster urticae and P. salviae are structurally different, but H. urticae may be closer to P. salviae than other Heterogaster species. Both these species ascend host plants, whilst the others are more ground-dwelling.

7.13 Rhyparochrominae

7.13.1 Plinthisini

An understanding of Plinthisus is fundamental to the systematic analysis of the Rhyparochrominae. Plinthisini is the most isolated and primitive rhyparochromine tribe and Plinthisus nymphs represent the most generalised generic condition (Slater & Sweet, 1961; Sweet, 1967; Slater, 1971b; Schaefer, 1975; Slater & Woodward, 1982).

It is frustrating that little material was collected during fieldwork, particularly considering that over half of all Plinthisus species are Palaearctic, with the majority
occurring in the West Palaearctic. A nymphal character, the Y-suture, separates Plinthisini from the Stygnocorini, where it was mistakenly placed by Scudder (1957a). Nymphal taxonomy is the key to *Plinthisus* generic limits and Plinthisini status. Long fine setae on the eye and prothoracic tibia, trichobothrial hair length and direction of the suture between terga 5-6 may prove useful diagnostic characters. Most potential lies with the separation of the dorsal abdominal gland apertures in each pair and their concomitant evaporative area widths.

Three groupings are apparent in the five species (Appendix 1.) and these form a basis for division of the Plinthisini. They are:

1) Species with distance between the gland apertures in each pair and evaporative area width increasing posteriad: - includes *Plinthisus brevipennis* (Fig. 160) and *P. americanus* Van Duzee (Sweet, 1967; Slater et al., 1977).

2) Species with intermediate pair of gland apertures closest together, posterior pair furthest apart with very narrow evaporative areas: - *Plinthisus* sp. (indet.).

3) Species with anterior gland aperture pairs furthest apart with widest evaporative area. Other pairs and evaporative areas equal: - *Plinthisus pusillus*.

Plinthisini are worthy of full subfamily status, as suggested by Puchkov (1958a). Sweet (1967) maintained that head trichobothria and rhyparochromine habitus were sufficient to retain the tribe in the Rhyparochrominae. However, the presence of a fused suture between sterna 4-5, which is lacking in *Plinthisus*, is the only synapomorphy holding Rhyparochrominae together as a monophyletic group. *Plinthisus* possesses a number of autapomorphies (Slater & Woodward, 1982) and the trichobothrial pattern on sternum 7 is unique within the Lygaeidae.
7.13.2 Antillocorini

The lack of associated nymphs and an inability to check for a Y-suture in adults prevented definite distribution of species between Antillocorini and Stygnocorini (Slater et al., 1977). For example Bathydema nymphs lack a Y-suture and were transferred to the Antillocorini by Slater et al. (1977), confirming suspicions of earlier workers (Sweet, 1967; Slater & Sweet, 1970b).

Antillocorines are small, cryptically coloured, normally ground-dwelling insects. Ashlock's (1964) tribal concept was subsequently redefined by Slater et al. (1977) and Slater (1980). Typically, nymphs have bordered sutures between terga 3-4 and 4-5, an important synapomorphy with the Lethaeini and Lilliputocorini (see Lethaeini). Three pairs of scent gland apertures were claimed to be present, but the anterior gland apertures in Antillocoris Kirkaldy are obsolete, and examination for abdominal scars on adults suggests that species in four other genera may also lack the anterior pair. Similarly, the trichobothria on sternum 5 were thought to be in a linear row, anterior to the spiracle, except in Antillocoris. However, examination of Neotropical taxa has shown that this is a highly derived condition typical of only two genera.

The examination of a single Palaearctic antillocorine, the British T. holosericeus, poses questions and suggests that the Antillocorini are paraphyletic (Slater, 1980; Slater & Woodward, 1982). Tropistethus nymphs have the trichobothria on sternum 5 arranged in the derived linear condition (Fig. 81). The dorsal gland apertures are open between terga 3-4, although closer than in the other two pairs (Fig. 161). The bordered sutures between terga 3-4 and 4-5 are little differentiated from the other sutures, and are not as distinct as in species illustrated by Slater et al. (1977). The associated tubercular or roughened lateral abdominal surface was, if present, inconspicuous.

The presence of anterior scent glands, an ancestral condition, suggests that Tropistethus is a primitive, relict antillocorine taxon, but with a highly derived linear trichobothria pattern on sternum 5. Examination of
other Palaearctic nymphs, particularly Homoscelis ruficollis, is urgently required.

7.13.3 Lethaeini

Ashlock (1964) found that scarcity of specimens prevented a thorough study of nymphal characters. However, he used the three paired dorsal abdominal gland apertures, with the posterior much narrower than the anterior pair, and the absence of a Y-suture to define the taxa. Lethaeini have synapomorphies in the reduced posterior scent gland apertures and adult genitalia characters (Slater, 1980) and share with Antillocorini and Lilliputocorini nymphs an important synapomorphy in the double or troughed suture between terga 3-4 and 4-5.

Lethaeus cribratissimus nymphs are the first from the Palaearctic to be described. They have closed posterior scent glands (Fig. 162), a reduction that is unique among Rhyparochrominae, where taxa typically lose the anterior scent gland apertures first (Table 6). Lethaeini nymphs, however, still share a synapomorphy in their characteristic widely spaced anterior and intermediate gland apertures and narrow evaporative areas.

The bordered sutures between terga 3-4 and 4-5 (Fig. 316) are obscure and it is unclear if they facilitate scent movement from the glands to the granular outer edge of the abdomen or whether scent is directed along shallow mesolateral longitudinal abdominal grooves.

Rhyparochrominae with the Y-suture normally have the anterior paired gland apertures more widely spaced apart, with a larger evaporative area. By analogy, it might be expected that widely separated posterior and intermediate gland apertures in Lethaeus correspond with the troughed sutures in Lethaeini. The posterior gland apertures appear closer together because the anterior and intermediate apertures are wider.
7.13.4 Stygnocorini

Stygnocorini are important in understanding the phylogeny and evolution of Rhyparochrominae (Slater & Sweet, 1970b). They represent the most primitive of the Y-suture rhyparochromine tribes and are probably ancestral to the Rhyparochromini, Ozophorini, Drymini, Udeocorini and Myodochini (Slater & Sweet, 1970b).

Most nymphs examined have a uniform colour pattern, a brownish body and unicolorous red or mottled red abdomen. The normally more widely spaced anterior gland apertures have larger evaporative areas than the other pairs. New Zealand Margareta dominica B. White and West Palaearctic Hyalochilus ovatulus exceptionally have all the gland apertures equally separated with equal sized evaporative areas (Fig. 164). Hyalochilus ovatulus nymphs also have a yellow body with black, irregular, disruptive, zig-zag markings, similar to those found on Peritrechus geniculatus, and a brown abdomen with round white spots.

The suture between sterna 4-5 was almost straight, reaching the margin of the abdomen in all Acompus and Hyalochilus nymphs examined. This is characteristic of some, but not all, species in seven stygnocorine genera, including Lasiosomus (Slater & Sweet, 1970b; O'Rourke, 1974, 1975). Specimens of L. enervis studied had a normal rhyparochromine suture, which curves strongly anteriad, embraces the trichobothrium and does not reach the abdominal margin (Fig. 85).

No unique, nymphal stygnocorine characters were identified that might separate them from other rhyparochromine taxa. Stygnocorini are almost certainly a paraphyletic assemblage, held together by sympleisomorphic characters (Slater, 1982; Slater & Woodward, 1982). Nymphs, however, do share a similar habitus and the lack of synapomorphies probably results from the taxon's stem position among rhyparochromine tribes with a Y-suture.
7.13.5 Phasmosomini

Nymphs of *Phasmosomus*, the sole genus, are undescribed.

7.13.6 Drymini

Drymini, except for *Gastrodes* and possibly *Ischnocoris*, comprise an holophyletic group of taxa containing a number of problematic species complexes.

*Gastrodes*, is either an aberrant, highly adapted drymine genus or a monogeneric Rhyparochrominae tribe. The straight suture between sterna 4-5 that reaches the margin of the abdomen, the position of the posterior trichobothria on sternum 5 relative to the spiracle (Fig. 89), the strongly dorso-ventrally flattened body and the short trichobothrial hairs are all incongruent drymine characters. The last two are of little phylogenetic value and represent structural adaptation in a genus highly specialised to live inside pine cones. The first two do not reflect a single selection pressure and pose a considerable evolutionary problem.

*Gastrodes* are probably aberrant drymines. Slater (1980) thought the fused sterna provided ground-dwelling Rhyparochrominae with extra rigidity. This feature is not required in arboreal flattened *Gastrodes*. The trichobothrial positioning on sternum 5 is a function of the straight suture; the pair have moved and, although not in the typical drymine position, are under the spiracle. All spiracles are dorsal, the scent gland aperture arrangement is typically drymine and the facies resembles a flattened *Eremocoris* or *Drymus*.

Comparison of *G. abietum* and *G. grossipes* nymphs provided no evidence to suggest that they should be placed in different genera as suggested by Stål (1872).

*Ischnocoris* nymphs lack a typically drymine facies and Sweet (1967) suggested the genus may be a deviant member of the Stygnocorini, citing chromosome work by Pfaler-Collander (1941) and the the lack of 'drymine' pores near spiracles 3 and 4 (a difficult character). However, the posterior trichobothria on sternum 5 in *I. angustulus*
nymphs are clearly anterior to the spiracle (Fig. 90), not slightly so, as Sweet stated. Scent gland aperture positions and evaporative area proportions are also typically drymine.

Le Quesne's (1956) subgeneric division of Drymus, using parandria shape, adult tibial pilosity and pronotal puncturation is supported by nymphal characters. Ratios of the evaporative area length anterior as opposed to posterior of the suture between terga 3-4 are significantly greater than 2:1 for Sylvadrymus [s.g.] (Figs 170-171) and less than 2:1 in Drymus [s. str.] (Figs 167-169). There are no obvious morphological or morphometric differences (Appendix 7), between Drymus [Sylvadrymus] sylvaticus and D. ryei nymphs.

Nymphal characters support Le Quesne's (1956) removal of Lamproplax picea from Drymus, which was based on the male genital capsule, anterior femoral spines and shining impunctate anterior pronotal lobes. Spiracle 4 is anterior to the single trichobothrium on sternum 5 in Drymus (Fig. 87) and posterior in Lamproplax (Fig. 91). The lateral position of spiracle 4 relative to the dorsal spiracles in Lamproplax suggests close relationship with Drymus.

Taphropeltus hamulatus nymphs are smaller than those of T. contractus but, except for a slight but not significant difference in the ratio of the anterior to posterior pronotal margins, are morphologically identical. Nymphs of T. limbatus are unknown.

Scolopostethus contains 12 closely related West Palaearctic species, six of which occur in Britain. Eyles (1963a) found no clear differences between S. affinis, S. decoratus and S. thomsoni nymphs, but confirmed by statistical analysis their different shapes. Scolopostethus affinis, however, has shorter, more adpressed pubescence than the other two species, with the first two antennal segments over 50% yellow. No similar morphological differences were found between S. decoratus and S. thomsoni, but both have distinct host associations and subtle adult morphological distinctions. More measurements of S. grandis nymphs are required to confirm differences from S. affinis.
7.13.7 Gonianotini

Slater & Woodward (1982) placed this tribe in the same clade as the Megalonotini. Nymphs in both taxa have secondarily lost the Y-suture and are heavily sclerotized. The tribe, however, is not as homogenous as adult analyses indicate and crudely divides into two groups which possibly deserve tribal status (Hyalocoris and Neurocladus are unplaced due to lack of material).

<table>
<thead>
<tr>
<th>Group 1</th>
<th>Group 2</th>
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<tbody>
<tr>
<td>Aoploscelis</td>
<td>Emblethis</td>
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<tr>
<td>Aphanus</td>
<td>Gonianotus</td>
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<tr>
<td>Macrodema</td>
<td>Ischnopeza</td>
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<tr>
<td>Pionosomus</td>
<td>Diomphalus</td>
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<td>Pterotmeteus</td>
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<tr>
<td>Trapezonotus</td>
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<tr>
<td>Bleteogonus?</td>
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The six genera in group one and probably Bleteogonus, are typically black and brown and heavily sclerotized, with narrow but distinct black evaporative areas and posteriad directed sutures between terga 4-5 and 5-6. Group two taxa, including the type genus, are pale, mottled or spotted without or with at most a narrow collar bordering the dorsal abdominal scent gland apertures.

It is premature to resurrect Gulde's (1936) Pterotmetini, for genera in group one. Nymphs of more species, particularly from Nearctic genera, must be examined. The two groups must be regarded as distinct phyletic lines within the Gonianotini, on the basis of their shared strong antennal and tibial spines, and the opening of the spiracles and dorsal glands.

The genera in group two are aberrant. Puchkov (1969) considered *D. hispidulus* should be placed in a monogeneric tribe, close to Gonianotini. It has an almost straight suture between sterna 4-5, a raised rim around the gland apertures and black puncturation. *Ischnopeza hirticornis* differs strikingly from other Gonianotini and is unique.
within the Lygaeidae, with one functional, closely separated posterior pair of dorsal abdominal gland apertures and another vestigial pair between terga 4-5 (Fig. 183).

Secondary loss of the Y-suture and two pairs of dorsal abdominal gland apertures suggest that the Gonianotini is a highly derived tribe within the Rhyparochrominae. The condition in I. hirticornis suggests that the tribe has evolved towards loss of glands, particularly amongst group two taxa.

Ischnopeza nymphs are long-legged and fast running and may depend upon the combination of disruptive colour pattern and speed to avoid predation. Nymphs of the other five Ischnopeza species are unknown.

Nymphs substantiate species separation in two large complex genera Emblethis and Trapezonotus. Emblethis nymphs are intricately marked and coloured. Examination of E. verbasci adults from Jersey and mainland Britain revealed them to be E. griseus. True verbasci does not occur in Britain or the Channel Isles.

West Palaearctic Gonianotus require close examination; the nymphs indicate a close relationship with Emblethis and the presence of new species is likely.

Colour markings, size ranges and paramere shape used to separate T. arenarius, T. desertus and T. dispar adults are unconvincing and show clinal gradation. However, T. arenarius nymphs are brighter and shinier than the other species and T. desertus is distinctly smaller than T. dispar (Appendix 7).

7.13.8 Megalonotini

Both Gonianotini and Megalonotini contain aberrant genera and have distinct infra-tribal groupings. The two tribes can be reliably separated by the position of spiracle 3. Sweet's (1967) use of the presence or absence of scent gland apertures between terga 3-4 is unreliable.
Hadrocnemis, Leptomelus, Metastenothorax, Pezocoris and Sphragisticus nymphs were unavailable. Lamprodema, Megalonotus and to a lesser extent Lasiocoris nymphs have strongly sclerotized dark abdomens. Icus and Proderus abdomens are yellow and red.

Dorsal abdominal gland apertures vary within the Megalonotini (Table 6), particularly in Megalonotus. Lamprodema, Lasiocoris, Megalonotus chiragra, M. emarginatus, M. praetextatus, M. puncticollis, M. sabulicola, Pezocoris, Piezoscelis and Sphragisticus nymphs all have three pairs. The anterior pairs and evaporative areas are absent in Icus, Megalonotus antennatus and M. dilatatus. Megalonotus dilatatus also has the intermediate gland apertures absent, with only a minute evaporative area. These apertures are vestigial in Proderus. Variation in the size of evaporative areas, and the presence/separation of gland apertures are important in the separation of higher taxa within the Lygaeidae. Only within the Megalonotini and Cyminae is variation present within lower taxonomic units.

The isolated position of M. dilatatus nymphs, which have only a single pair of gland apertures, supports Roubal's (1965) use of the subgenus Ktenofer.

Puchkov (1969) transferred Icus from the Megalonotini to the Gonianotini, a move not followed here. The nymphs have the dorsal scent gland apertures widely separated between T4-5 and 5-6, similar to the 'group one' gonianotines'. However, they are not heavily sclerotized and show relationships to the megalonotine Proderus and the two taxa may be synonymous. The armature of the prothoracic femora in Icus is typically megalonotine and although spiracle 3 is lateral in nymphs of the two taxa, it is clearly dorsal in adults.

Scudder's (1962c) resurrection of monobasic Pezocoris from Lasiocoris, is supported by nymphal characters. The fifth instar P. ipimacula, figured in Puchkov (1969), has anterior scent gland apertures which are twice as wide apart as the posterior scent gland apertures, with correspondingly larger evaporative areas. Lasiocoris
anomalus nymphs have all evaporative areas equally spaced (Fig. 190).

7.13.8.1 Megalonotus chiragra complex

Support for raising *M. emarginatus* and *M. sabulicola* to specific status is provided by the density, length and composition of pubescence in the *chiragra* complex. True *chiragra* nymphs have, on the dorsal surface of the abdomen, moderately long adpressed and less dense, long, stout, suberect setae (Fig. 326). *Megalonus emarginatus* is almost glabrous, with only very short adpressed setae (Fig. 327) whilst the denser, dorsal abdominal pubescence in *M. sabulicola* (Fig. 328) is more even-lengthed than in *M. chiragra*.

*Megalonus emarginatus* nymphs are always larger than *M. sabulicola*. *Megalonus chiragra* body length overlaps with both these species (Appendix 7). The evaporative areas are slightly narrower in *M. emarginatus* than in the other species and the relative shapes of the evaporative areas are diagnostic (Table 6).

Entirely black nymphs of *Megalonus* were collected from Porthcothan, Cornwall (Appendix 5). Repeat visits to collect adults were unrewarded. The specimens have typical scent gland apertures and the short adpressed pubescence of *M. emarginatus*. The single reared adult has the distinct basal pronotal lobes typical of *emarginatus*. These specimens are probably what Roubal (1965) named *Megalonus emarginatus* v. *atricornis*. Further adults and nymphs may indicate that this is a good species.

Pronotal characters vary with wing development and can be unreliable. Some *M. chiragra* adults have baso-lateral pronotal lobes and an excavate posterior pronotal margin similar to, but not as pronounced as, *M. emarginatus*. This variation causes confusion as in Aukema & Nau (1992). Adult *M. chiragra* and *M. emarginatus* are best separated by elytral pubescence.
7.13.9 Rhyparochromini

West Palaearctic Rhyparochromini divide into four groups of increasing complexity. *Beosus*, *Dieuches* and *Peritrechus* are uncontroversial, with the exception of *Peritrechus lundi*. However, *Aellopus* and *Rhyparochromus* are problematic and nymphal analysis indicates incongruences within the adult classification.

*Beosus* and *Dieuches*, characterised by long second antennal segments, comprise a distinct division within the Rhyparochromini. *Beosus maritimus* is one of the largest and most characteristic British species. The collar, or anterior transverse pronotal constriction, in *Beosus* separates it from *Dieuches*.

Nymphs of six West Palaearctic *Peritrechus* species, except *P. lundi*, are characterised by suboval, pear-shaped facies and diagonally red-streaked abdomens (Figs 35, 36). *Peritrechus geniculatus* and *P. gracilicornis* form a distinct group and are similar, apart from the relative width of the first antennal segment and the different head markings. Their anterior dorsal gland apertures are more widely spaced than the intermediate and posterior pairs, with larger oval evaporative areas (Fig. 204). Separation of the gland aperture pairs and evaporative area sizes are constant in *P. nubilus* (Fig. 205) and spaced as for *P. geniculatus* and *P. gracilicornis* in *P. angusticollis*, which has narrow evaporative areas.

*Peritrechus lundi* nymphs (Fig. 34) are smaller than but superficially similar to *Rhyparochromus pini* (Fig. 38), but differ from other *Peritrechus* nymphs. The anterior dorsal gland apertures are more widely spaced, with a larger evaporative area than the other pairs. The more elongate, parallel sided body has adpressed pubescence with additional long, erect setae. The abdomen is uniformly red, with faint white markings each side of the intermediate and posterior evaporative areas. These characters are shared with *Rhyparochromus*, a genus to which it appears more distantly related. The tylus almost reaches, or reaches the apex of the first antennal segment, the rostrum is stout, spiracle 3 is almost lateral and nymphs lack the stout,
semi-erect tibial setae characteristic of *Rhyparochromus*. *Peritrechus lundi* does not, therefore, belong in *Peritrechus* and should not be transferred to *Rhyparochromus*. Stål (1872) erected the monobasic genus *Pasatus* to contain *P. lundi*; this genus should be resurrected from synonymy.

*Peritrechus distinguendus* has similar adult pronotal characteristics to *P. lundi*, to which it is otherwise more distantly related. The adult membrane lacks the white apical macula characteristic of certain *Rhyparochromus* and *P. lundi*.

The systematic position of *Aellopus* is perplexing. Adults lack a typical Rhyparochromini facies and are broadly oval and predominantly black. Spiracles 2 and 3 are dorsal and three fully formed pairs of scent gland apertures are present. The suture between terga 2-3 is typically troughed with a white margin, but uniquely reaches the lateral abdominal margin without branching to form the characteristic Y-suture (Fig. 317). All other tribes with a single, deep suture between terga 2-3 (Stygnoecorini, Drymini, Udeocorini, Ozophorini, Myodochini and Targaremini) have this Y-branch. The distance apart of the anterior scent gland apertures and evaporative area size, relative to the other pairs, varies in *A. atratus*. One specimen had the anterior gland apertures closer together than the posterior pairs, a typically Megalonotini characteristic.

*Aellopus* is either an aberrant rhyparochromine genus, occupying a position analogous to *Gastrodes* in the Drymini, or is deserving of full tribal status. Partial suture reduction between terga 2-3 potentially provides an important taxonomic link between the Rhyparochromini and Megalonotini.

*Graptopeltus, Xanthochilus (Neoxanthochilus)* and *Raglius* are treated by Wagner (1961b) as subgenera of *Rhyparochromus*. However, their dorsal abdominal gland apertures and other nymphal characters, particularly the consistent colour markings, warrant generic status.
Graptopeltus, as Le Quesne's (1957) adult study indicated, is distinct from Rhyparochromus. Nymphs lack long erect body setae, and the broad pronotal carinae project beyond the anterior pronotal margin (Fig. 295). Furthermore, they have equally spaced gland apertures, with large equal sized evaporative areas (Fig. 202), and shining patches present on the head, pronotal disc and base of scutellum (Fig. 33).

Xanthochilus nymphs always have longitudinal yellow and black disruptive markings on the mesothoracic wing-pads. The genus is not, as suggested by Le Quesne (1957), a subgenus of Graptopeltus. Nymphs of some species lack erect long setae on the dorsal surface of the body, pronotal carinae project only slightly forward, distinctive shining patches are absent and the anterior evaporative area is over twice as wide as the others (Fig. 208).

Raglius is a natural unit within the Rhyparochromini. The instantly recognisable nymphs have a continuous broad white band along abdominal suture 2-3, long erect body setae, equally spaced and sized dorsal abdominal gland apertures and evaporative areas (Fig. 206).

Further analysis will probably confirm the full generic status of other Rhyparochromus subgenera, once specimens are available.

7.13.10 Myodochini

Slater & Sweet (1961) note that Puchkov (1958a) misinterpreted the position of the Myodochini, misidentifying the nymph named Ligyrocoris sylvestris.

Colour and markings of congeneric lygaeid species are usually strikingly uniform. Harrington's (1980) separation of Remaudiereana from Pachybrachius is supported by examination of P. annulipes nymphs as the former lacks the distinctly spotted abdomen. Interestingly, the two British Pachybrachius species, the type P. luridus and P. fracticollis, are differently marked, suggesting that examination of other Palaearctic species will confirm that Pachybrachius is still paraphyletic.
1 EITHER suture between sterna 4 and 5 curving anteriad, embracing trichobothrium, then curving posteriad at lateral abdominal margin, and not, or at most only faintly reaching margin (Figs 81,82,84-88,90-95,97-121) OR, if this suture is straight (Plinthisus, Acompus, Gastrodes, Diomphalus) (Figs 80,83,89,96), then either a Y-suture between terga 3 and 4 (Fig. 1) and/or head trichobothria (sometimes with short trichobothrial hairs) present (Rhyparochrominae) ..................... 2

- Suture between sterna 4 and 5 straight, not curving posteriad at lateral margin or embracing trichobothrium (Figs 53-79) AND, lacking both a Y-suture and cephalic trichobothria. ................................. 45

2 Trichobothria on sternum 7 one above the other and widely separated (Fig. 80). Very long trichobothria-like seta arising from eye (Fig. 291) and apex of prothoracic tibia (Fig. 330) Plinthisini*). .................... Plinthisus Stephens

*Undiscovered Phasmosomus (Phasmosomini) nymphs may key out here if they lack a Y-suture. They will be elongate and linear with a TBL of c6mm. Trichobothria on sternum 7 will not be widely separated. Sweet (1967) noted that the posterior and intermediate gland apertures are narrowly separated with S4-5 straight and reaching the abdominal margin.

- Trichobothria on sternum 7 not widely separated. Long trichobothria-like eye and tibial setae absent. ........ 3

3 Spiracles ventral; occasionally spiracle 3 or 4, but not both, lateral. ................................. 4

- At least one of spiracles 2-4 dorsal. .................... 17

4 Y-suture absent. Trichobothria on sternum 5 in a linear series (Figs 81,82). .......................... 5

- Y-suture present but sometimes weak. Trichobothria on sternum 5 not in a linear series, posterior pair one above the other (Figs 83-121). ................................. 6

106
5 Gland apertures widely separated between terga 3-4 and 4-5, posterior pair between terga 5-6 vestigial. Evaporative areas absent posteriad of suture (Fig. 162). Terga with a shallow, broad, meso-longitudinal trough (Fig. 316). Spiracle on S5 anteriad of posterior trichobothrium (Fig. 82) (Lethaeini). Lethaeus Dallas

- 3 pairs of gland apertures present, becoming more widely separated posteriad and with evaporative areas present both sides of suture (Fig. 161). Terga without a longitudinal trough. Spiracle on sternum 5 just above posterior trichobothrium (Fig. 81) (Antillocorini). ...

Tropistethus Fieber

6 Paired trichobothria on sternum 5 posteriad of spiracle or directly under it (Figs 83-86). Body not strongly dorso-ventrally flattened (Stygnocorini). .............. 7

- All trichobothria on sternum 5 clearly anterior to spiracle (Figs 87-93) or, if directly under it, body strongly dorso-ventrally flattened (Gastrodes) (Drymini) ............................................. 11

7 TBL < 1.5mm. ............... Stygnocorisella Hoberlandt

(Stygnocorisella nymphs were not available for study. Stichel (1957-1959) gave the adult measurement of S. mayeti as 1.42mm - 1.48mm. Any fifth instar stygnocorine nymphs significantly under 2mm in length will be this species. Stygnocoris pygmaeus with 2.3mm - 2.5mm long adults is the next smallest species.)

- TBL > 2.0mm. ...................................................... 8

8 Evaporative areas almost equal sized (Fig. 164). Abdomen brown with numerous pale spots. ................................................. Hyalochilus Fieber

- Anterior evaporative area distinctly larger than intermediate and posterior areas (Fig. 163). Abdomen without pale spots. ................................. 9

9 Lateral pronotal margins distinctly concave (Fig. 298). Evaporative areas transversely oblong (Fig. 163). Prothoracic femur with a single minute antero-ventral spine (Fig. 226). ............... Acompus Fieber

- Lateral pronotal margins almost straight or convex (Figs 299,300). Evaporative areas not oblong (Figs 165,166). Prothoracic femur mutic, or with a row of tuberculate setae. ................................. 10
10 Anterior trichobothrium on sternum 5 almost equidistant between spiracles 4 and 5; not closely embraced by sternal suture 4-5 as it turns posteriad (Fig. 85). Body pubescence at least as long as eye width. ............. Lasiosomus Fieber

- Anterior trichobothrium on sternum 5 closer to spiracle 4 and embraced immediately by suture between sterna 4-5 as it turns posteriad (Fig. 86). Body pubescence distinctly shorter than eye width. ... Stygnocoris Douglas & Scott

11 Suture between abdominal sterna 4-5 straight and reaching abdominal margin (Fig. 89). Spiracle 5 directly above posterior trichobothria on sternum 5 (Fig. 89). Body strongly dorso-ventrally flattened. ...

.............. Gastrodes Westwood

- Suture between abdominal sterna 4-5 curving strongly anteriad, looping around anterior trichobothrium, then directed posteriad and not reaching abdominal margin (Figs 87, 88, 90-93). Spiracle 5 posteriad of posterior trichobothria on sternum 5. Body not strongly dorso-ventrally flattened. ......................... 12

12 Maximum length of anterior evaporative area < eye width (Fig. 174). Prothoracic femur mutic. Ischnocoris Fieber

- Maximum length of anterior evaporative area \( \geq \) to eye width (Figs 167-173, 175-177). Prothoracic femur with at least 1 small antero-ventral spine (Figs 228-242). .......................... 13

13 Maximum length of anterior evaporative area > 2.4 x eye width (Fig. 177). .......................... Taphropeltus Stål

- Maximum length of anterior evaporative area < 2.4 x eye width (Figs 167-173, 175, 176). .......................... 14

14 Rostrum reaching beyond metathoracic coxae at least to suture between sterna 2-3. Tylus not reaching mid-point of first antennal segment. (Fig. 25). Eremocoris Fieber

- Rostrum reaching between meso- and metathoracic coxae, or if just reaching metathoracic coxae never extending to sternal suture 2-3. Tylus reaching to or beyond mid-point of first antennal segment. .......................... 15
15 Spiracle on sternum 4 not closer to abdominal margin than other spiracles (Fig. 92). Abdomen mottled (Fig. 28). ........................................ Scolopostethus Fieber*

* Thaumastopus Fieber will probably key out here. Puchkov (1969) figured the nymph of T. marginicollis which had a very prorect head 1.4 x as long as the pronotal length. All Scolopostethus, except S. pictus, have the head shorter in length than the pronotal length. The maximum ratio of head length to pronotal length in S. pictus and other drymine species is x 1.2.

- Spiracle on sternum 4 slightly closer to abdominal margin than other spiracles or actually lateral (Figs 87,91). Abdomen, excluding evaporative, areas unicolorous (Figs 21-24,27). ................................................. 16

16 Spiracle 4 posterior to anterior trichobothrium on sternum 5 (Fig. 91). Prothoracic femur Figs 241,242. .................................................... Lamproplax Douglas & Scott

- Spiracle 4 anterior to anterior trichobothrium on sternum 5 (Fig. 87). Prothoracic femur (Figs 228-234). ......................................................... Drymus Fieber

17 Suture between terga 3-4 simple, not branching at lateral abdominal margin, nor deep with white borders. 18

- Y-suture present between terga 3-4 (Fig. 1), or if indistinct, or absent, then suture between terga 3-4 always deeper than other dorsal abdominal sutures and with a white margin. .................................................. 33

18 Spiracle 3 ventral (Figs 94-103) (Gonianotini). ...... 19

- Spiracle 3 dorsal (Figs 104-108) (Megalonotini). ...... 28

19 Evaporative areas absent or very reduced (Figs 180-183. Body pale, abdomen spotted or mottled with red and brown highlights. ................................. 20

- Narrow evaporative areas present (Figs 178,179,184-187). Body black with a heavily sclerotized castaneous abdomen. .............................................. 23

20 Anterior abdominal gland apertures between terga 4-5 considerably smaller and closer together than those between terga 5-6 (Fig. 183). Body elongate. ................................. Ischnopeza Fieber

- Anterior abdominal gland apertures between terga 4-5 only just smaller and closer together than those between terga 5-6 (Figs 180-182). ......................... 21
21 Pronotum with strongly pronounced calli, divided by a broad, strong, meso-longitudinal impression (Fig. 307). Tylus long, stout, apically blunt and extending to first antennal segment apex. Spiracle 4 lateral. ..................................................... 

*Diomphalus Fieber*

- Pronotum without strong calli or a longitudinal impression. Tylus not stout or apically blunt and not quite reaching to first antennal segment apex. Spiracle 4 dorsal. ................................................................. 22

22 Lateral explanate pronotal margins unicolorous, pale and projecting beyond antero-lateral pronotal margin (Fig.293). Antennae predominantly pale. ................................................................. 

*Emblethis Fieber*

- Lateral explanate pronotal margins mottled and not projecting beyond antero-lateral pronotal margin (Fig. 294). Antennae brown-black. .......... *Gonianotus Fieber*

23 Rostrum reaching between meso- and metathoracic coxae. Prothoracic femur mutic. ............... *Macrodema Fieber*

- Rostrum not reaching beyond mesothoracic coxae. Prothoracic femur spinose or with long setae on antero-ventral edge (Figs 250,251,257-261). ...................................................... 24

24 Prothoracic tibia with a single long seta near apex (Fig. 331). ........................................ *Aoploscelis Fieber*

- Prothoracic tibia either with a series of long, or short, adpressed setae. ............................................ 25

25 Tylus only reaching mid-point of first antennal segment. Prothoracic femur with 2 very small spines on antero-ventral edge (Fig. 251). ........ *Aphanus Laporte*

- Tylus reaching beyond or almost up to apex of first antennal segment. Prothoracic femur with either 1 small spine (Fig. 257), 4 to 5 spines (Figs 258-261), or long setae on antero-ventral edge. .................................................. 26

26 Body elongate and parallel sided (Fig. 49). Prothoracic femur with 1 very small spine on antero-ventral edge (Fig. 257). ............... *Pterotmetus Amyot & Serville*

- Body suboval. Antero-ventral edge of prothoracic femur multi-spinose (Figs 258-261), or with long setae. ... 27

27 Lateral explanate pronotal margins with stout, erect setae (Fig. 308). Prothoracic femur and tibia with long erect setae. ...................... *Pionosomus Fieber*

- Setae absent from pronotal margins, short and adpressed on prothoracic femur, with 4 to 5 long tuberculate setae on prothoracic femur (Figs 258-261). .................... 

*Trapezonotus Fieber*
28 Anterior evaporative area between terga 3-4 larger than posterior area between terga 5-6. Third antennal segment with very dense, dark, adpressed and longer semi-erect setae. .................. Lasiocoris Fieber

*Sphragisticus Stål should key out here according to the illustration in Puchkov (1969). S. nebulosus will have a TBL of < 4.5mm and lack the antennal characteristics of Lasiocoris.

- Anterior evaporative area between terga 3-4 absent, equal in size, or smaller than posterior evaporative area between terga 5-6 (Figs 188-189, 191-198. Third antennal segment not as above. ................... 29

29 Equal sized evaporative areas present between terga 3-4, 4-5, and 5-6 (Fig. 189). Distinctly oval, small species. ......................... Lamprodema Fieber

- Anterior evaporative area between terga 3-4 absent or, if present, distinctly smaller than area between terga 5-6. Body at most suboval. .................... 30

30 Second antennal segment length > head width across eyes. Body yellow and red. ..................... 31

- Second antennal segment length < head width across eyes. Body without yellow, black and brown or red. .... 32

31 Gland apertures vestigial between terga 5-6 (Fig. 198). Pronotum as long as its posterior width. Abdomen red, with 2 longitudinal yellow-white stripes. Larger, TBL > 4.5mm. ...................... Proderus Fieber

- Widely spaced gland apertures between terga 5-6 (Fig. 188). Pronotum distinctly shorter than its posterior width. Abdomen yellow with distinctive red markings above the evaporative areas and as a lateral longitudinal stripe along the abdominal margin. Smaller, TBL < 4mm. ..................... Icus Fieber

32 Sutures between terga 4-5 and terga 5-6 curving strongly anteriad. .................. Piezoscelis Fieber

- Sutures between terga 4-5 and terga 5-6 almost straight. ....................... Megalonotus Fieber

33 Spiracle 2 dorsal (3-4 dorsal, 5-8 ventral) (Myodochini). .......................... 34

- Spiracle 2 ventral (3-4 dorsal, 5-8 ventral) (Rhyparochromini). .......................... 37
34 Body very elongate, TBL > 3 x maximum body width. Rostrum not reaching mesothoracic coxae. .......................... Paromius Fieber

- Body less elongate, TBL < 3 x maximum body width. Rostrum reaching to or beyond mesothoracic coxae. ...... 35

35 Abdomen without distinct pale spots. Pachybrachius Hahn

- Abdomen with very distinct pale spots. .............. 36

36 Dorsal abdominal gland apertures all almost equally spaced in their pairs, with equal sized evaporative areas (Fig. 212). Body with dense, long, erect and semi-erect pubescence, distinctly longer than A1 width. ................................ Remaudiereana Hoberlandt

- Anterior dorsal gland apertures more widely spaced, with a larger evaporative area than intermediate and posterior pairs (Fig. 209). Pubescence adpressed, sparse and distinctly shorter than A1 width. ...................... Ligyrocoris Stål

37 Suture between terga 3-4 deep but not branching laterally anteriad (Fig. 317). Evaporative areas slightly increasing in width posteriad and very short between terga 4-5 and 5-6 (Fig. 199). Body broadly oval. ...................... Aellopus Wolff

- Y-suture present between terga 3-4 (Fig. 1); if indistinct then evaporative areas not both increasing in width posteriad and very short (Figs 200-208). Body suboval, or elongate and parallel sided. .......... 38

38 Width of anterior evaporative area between terga 3-4 > 2x width of posterior evaporative area between terga 5-6 (Fig. 208). .............................. Xanthochilus Stål

- Anterior evaporative area width < 2x posterior evaporative area width. ........................................... 39

39 Y-suture with a broad white margin, white continuing on venter to form a broad abdominal band. ... Raglius Stål

- Y-suture with inner red and or brown margin as well as outer white margin. White not continuing on venter of abdomen. .......................................... 40

40 Anterior evaporative area and posterior evaporative area equal in width (Fig. 202). Pronotal carinae projecting forward beyond anterior margin and partly embracing eye (Fig. 295). ............. Graptopeltus Stål

- Anterior evaporative area always at least slightly wider than posterior evaporative area (Figs 200,201,203-207). Pronotal carinae never projecting beyond anterior pronotal margin. ...................... 41
41 Distance between anterior margin of anterior evaporative area and posterior margin of posterior evaporative area < head width across eyes. ............... 42
- Distance between anterior margin of anterior evaporative area and posterior margin of posterior evaporative area > head width across eyes. ............... 43

42 Tylus reaching or almost reaching first antennal segment apex. Width of anterior evaporative area > 1.6x posterior evaporative area width (Fig. 203). Prothoracic femur unispinose on antero-ventral edge (Fig. 276). .............................................. Pasatus Stål
- Tylus at most extending two-thirds along length of first antennal segment. Width of anterior evaporative area < 1.5x posterior evaporative area width (Figs 204, 205). Prothoracic femur multispinose (Figs 277-279). .............................. Peritrechus Fieber

43 Second antennal segment length < head width across eyes. ............................................. Rhyparochromus Hahn
- Second antennal segment length > head width across eyes. ............................................. 44

44 Anterior pronotal collar present, similar in colour and structure to carinae. ........ Beosus Amyot & Serville
- Pronotal collar absent. .......................... Dieuches Dohrn

45 All spiracles ventral. ............................... 46
- At least spiracle 2 dorsal. ............................... 48

46 Evaporative areas reduced to an apical, sclerotized margin around indistinct, narrow, almost contiguous gland apertures on terga 4-5 and 5-6 (Fig. 157). Elongate, narrow, pale, yellow-white nymphs with 5 faint, brown, longitudinal stripes (Pachygronthinae). .............................................. Cymophyes Fieber
- Large, black, subspherical evaporative areas surrounding dorsal gland apertures on terga 4-5 and 5-6 (Figs 158, 159). Gland apertures absent from terga 3-4, but large evaporative area present. Brightly coloured and suboval (Heterogastrinae). .............................. 47

47 Lateral pronotal margins strongly convex. Anterior evaporative area between terga 3-4 smaller than intermediate and posterior areas (Fig. 159). Sub-circular in shape. .......................... Platyplax Fieber
- Lateral pronotal margins weakly concave. Anterior evaporative area at most only slightly smaller than intermediate and posterior areas (Fig. 158). Suboval. ............................................. Heterogaster Schilling
48 3 pairs of gland apertures present, anterior sometimes reduced to a single gland aperture (Figs 135,154-156). 49
- 2 to 0 pairs of gland apertures present (Figs 122-134,136-153). .......................................................... 52

49 Black pronotal calli present (Fig. 7). Spiracles all dorsal. Body with short, scale-like, capitate setae and short, suberect setae (Ischnorhynchinae). .................................................. Kleidocerys Stephens
- Pronotal calli absent. Spiracle 2 dorsal, remainder ventral (often difficult to see). Body almost glabrous (Artheneinae). ........................................ 50

50 Only a single, small dorsal abdominal gland aperture between terga 3-4) (Fig. 155). Pronotum and scutellum partly punctate. ......................... Chilacis Fieber
- Anterior scent gland apertures paired (Figs 153,154). Pronotum and scutellum impunctate. .................. 51

51 Rostrum reaching between or beyond mesothoracic coxae. Maximum width of A4 2x maximum width of A3. Smaller, TBL < 2.5mm. .................. Artheneis Spinola
- Rostrum reaching prothoracic coxae. Maximum width of A4 1.5x maximum width of A3. Larger, TBL > 2.5mm. .......... Holcocranum Fieber

52 Distinct, long, dark pronotal calli present (Figs 2-4) (Lygaeinae). .......................................................... 53
- Pronotal calli absent. ........................................ 62

53 Gland apertures and evaporative areas absent. Mesothoracic wing-pad not reaching beyond suture between terga 2-3. .......................... Apterola Mulsant & Rey
- Gland apertures and evaporative areas present between terga 4-5 and 5-6. Mesothoracic wing-pads reaching to at least tergum 2 and normally to tergum 3. ........... 54

54 Prothoracic femur with distinct antero-ventral spine (Fig. 213). Width of posterior evaporative area 2 x anterior area width (Fig. 123). Terga 2-7 unicolorous red (excluding evaporative areas). ... Caenocoris Fieber
- Prothoracic femur mutic. Evaporative areas subequal in size. Terga 2-7 red with other markings. ............... 55
55 Gland apertures closer to each other in each pair than to lateral evaporative area margin and sometimes touching (Figs 127,129,130). Evaporative areas separated by less than the length of the anterior area between terga 4-5. ............................................. 56

- Gland apertures closer to lateral evaporative area margin than each other and sometimes touching margin (Figs 122,124-126,128). Evaporative areas separated by more than the length of the anterior area. ............. 58

56 Body covered with stout, erect, black setae. ............. .................................. *Tropidothorax* Bergroth

- Body almost glabrous, with a few small scattered setae. 57

57 Maximum width of posterior evaporative area at least 2 x eye width. Mesothoracic wing-pads with light central area always reaching, or restricted to, the lateral margin (Figs 332,333). Terga 3-6 without meso-lateral black streaks. ...................... *Lygaeus* Fabricius

- Maximum width of posterior evaporative area 1.5 x eye width. Mesothoracic wing-pads black with lighter, usually red, central area enclosed and never reaching lateral margin (Fig. 334). Terga 3-6 usually with meso-lateral black streaks (absent in *S. pandurus militaris*). .................. *Spilostethus* Stål

58 Pubescence capitate. Terga yellow, with red latticed pattern normally forming 7 red longitudinal stripes (Fig. 3). .......................... *Lygaeosoma* Spinola

- Pubescence, if present, simple. Terga not latticed and red longitudinal stripes, if present, not more than 3. 59

59 TBL > 7.5mm. ......................... *Cosmopleurus* Stål

- TBL < 7.5mm. ................................. 60

60 Suture between terga 5-6 in the middle curving moderately to strongly anteriad (Fig. 309). Rostrum reaching beyond metathoracic coxae. Abdomen with a series of interrupted longitudinal and transverse red stripes. Pronotal carinae white throughout whole length. .................. *Arocatus* Spinola

- Suture between terga 5-6 almost straight (Fig. 2). Rostrum reaching between meso- and metathoracic coxae. Abdomen and pronotal carinae not marked as above. ..... 61

61 Posterior pronotal corners white. Terga 2-7 without continuous longitudinal stripes and often with transverse red stripes. (Fig 2). .......................... *Horvathiolus* Josifov

- Posterior pronotal corners not white. Terga 2-7 with longitudinal stripes and without transverse red stripes. .................. *Melanocoryphus* Stål

115
62 Spiracles 7 and 8 ventral or lateral, remainder dorsal. Distinct evaporative areas present (Figs 139-141). Abdominal segments 7-9 heavily sclerotized and black (Figs 9,313). (Blissinae). ............................. 63

- Spiracles not as above and spiracle 8 often absent. Evaporative areas absent, indistinct, or narrowly surrounding each individual gland aperture (Figs 131-134,142-153). Abdominal segments 7-9 not heavily sclerotized and black. ............................. 64

63 Black sclerotization (excluding evaporative areas) on terga 2-6 distinct, with some spots almost equal in width to eye width (Fig. 141). Antennae longer than combined width of head and pronotum, length reaching to at least mid-point of scutellum. ... Ischnodemus Fieber

- Black sclerotization (excluding evaporative areas) on terga 2-6 indistinct, spots less than half as wide as eye width (Figs 312,313). Antennae at most only just longer than combined length of head and pronotum. ..... ............................. Dimorphopterus Stål*

*Geoblissus Hidaka will also key out here.

64 Eyes large, reniform and pronounced (Figs 288-290). Head distinctly transverse. ............................. 65

- Eyes and head not as above. ............................. 68

65 Spiracle 2 ventral and 5 dorsal. Sutures between terga 4-5 and 5-6 not curving strongly anteriad (Henestarinae). ............................. 66

- Spiracle 2 dorsal and 5 ventral. Sutures between terga 4-5 and 5-6 curving strongly anteriad in the middle (Fig. 314) (Geocorinae). ............................. 67

66 Body with interrupted raised dorso-longitudinal mesal ridge. ............................. Engistus Fieber

- Body without longitudinal mesal ridge. ............................. Henestaris Spinola

67 Rostrum reaching between or beyond metathoracic coxae. Second rostral segment longer than third segment. Evaporative area at most only slightly constricted between gland apertures (Fig. 145). Body rounded. ..... ............................. Piocoris Stål*

- Rostrum at most just reaching metathoracic coxae. Second rostral segment shorter than third segment. Evaporative areas constricted between apertures (Fig. 144). Broadly oval to more elongate. ............................. Geocoris Fallén*

*Stenophysalamicus Costa will key out to one of these.
68 Gland apertures between terga 4-5 well spaced and not touching (Figs 131-134, 136-138). Spiracle 6 dorsal. ... 69

- Gland apertures between terga 4-5 touching, or not separated by more than their width (Figs 146-153). Spiracle 6 ventral. ........................................ 74

69 Gland apertures absent between terga 5-6. Abdominal margins scalloped (Fig. 8) (Cyminae). ................. 70

- Gland apertures present between terga 5-6. Abdominal margins smooth (Figs 5, 6, 42) (Orsillinae). ............ 71

70 Spiracle 7 lateral. Paired dorsal gland apertures between terga 4-5 only (Fig. 136). Third antennal segment approximately 1.5 x length of second segment. ........................................... Cymodema Spinola

- Spiracle 7 ventral. Paired dorsal gland apertures present between terga 3-4 and 4-5, posterior pair sometimes closed and lacking an evaporative area (Figs 137, 138). Third antennal segment shorter, or only just longer than length of second segment. ...... Cymus Hahn

71 Rostrum reaching to, or distinctly beyond sternum 3. ... 72

- Rostrum not reaching beyond metathoracic coxae. .......... 73

72 A4 longer than A2. Head, pronotum, scutellum and mesothoracic wing-pads coarsely punctate with irregular, faint black stripes. ........ Camptocoris Puton

- A4 shorter than A2. Head pronotum, scutellum and mesothoracic wing-pads impunctate and red with white spots. ................................ Orsillus Dallas

73 Pubescence capitate (Fig. 318). ....... Ortholomus Stål

- Pubescence simple. .................................. Nysius Dallas

74 Body constricted at meso- and metathorax (Figs 335, 336). Scutellum with long, erect protuberance. Abdomen with red and yellow chequer pattern. ... (Bledionotinae). ........................................ Bledionotus Reuter

- Body not constricted at meso- and metathorax. Scutellum without an erect protuberance. Body not patterned with red and yellow chequers. (Oxycareninae). ............... 75

75 Prothoracic femur mutic. ........................................ 76

- Prothoracic femur spinose (Figs 216-219) (Spine very small in Metopoplax). .................................... 80
76 Posterior evaporative area larger than anterior area, both pairs with some adjacent sclerotization. Abdomen with 5 longitudinal red stripes. ... *Camptotelus Fieber*

*Based on Puchkov (1958a, 1969).

- Evaporative areas not as above. Abdomen without 5 longitudinal red stripes. ........................................ 77

77 Terga pale with transverse rows of red spots. ........

......................................................... *Leptodemus Reuter*

- Terga without red spots. ............................... 78

78 Terga with transverse red bands. .... *Brachyplax Fieber*

- Terga without transverse red bands. ........................ 79

79 Body oval, almost glabrous, with a few simple scattered setae. Rostrum reaching to mesothoracic coxae. ........

......................................................... *Macropternella Slater*

- Probably not as above - *Philomyrmex Sahlberg, Tropidophlebia Kerzhner, Bianchiella Reuter, Jakowleffia Puton.*

80 Terga red with large ochreous spots in transverse rows (Fig. 11). Prothoracic femur with 3 spines (Fig. 216).

......................................................... *Macroplax Fieber*

- Terga predominantly unicolorous, or with longitudinal red stripes, but without spots. ............................. 81

81 Tergum 3 with a broad, sometimes faint, transverse white band. Prothoracic femur unispinose (Fig. 218).

......................................................... *Microplax Fieber*

- Terga striped or unicolorous and without a transverse band on tergum 3. Prothoracic femur with 2 or 4 spines (Figs 217, 219). .............................................. 82

82 Abdomen with 4 longitudinal red stripes (Fig. 12). ...

......................................................... *Metopoplax Fieber*

- Abdomen pale with 2 latero-longitudinal red stripes or predominantly unicolorous red. .... *Oxycarenus Fieber*
9. Key to Species of Fifth Instar Nymphs of British Lygaeidae

(For abbreviations see page 133)

1 EITHER suture between sterna 4 and 5 curving anteriad, embracing trichobothrium, then curving posteriad at lateral abdominal margin and not, or at most only faintly, reaching margin (e.g. Fig. 92). OR, if this suture is straight (Plinthisus, Gastrodes), then either a Y-suture between terga 3 and 4 (Fig. 1) and/or head trichobothria (sometimes with short trichobothrial hairs) present. ................................. 2

- Suture between sterna 4 and 5 straight (Figs 53-79). Both Y-suture and head trichobothria always absent. .... 61

2 Trichobothria on sternum 7 one above the other and widely separated (Fig. 80). Long setae arising from eye (Fig. 291) and apex of prothoracic tibia (Fig. 330). TBL 1.9mm - 2.3mm. Fig. 16. .......................... Plinthisus brevipennis (Latreille)

- Trichobothria on sternum 7 close together (Figs 81-121). Long seta absent from eye and prothoracic tibia. ........ 3

3 Spiracles all ventral, occasionally spiracle 3 or 4, but not both, lateral. ................................. 4

- At least one of spiracles 2-4 dorsal. ............. 34

4 Y-suture absent between terga 3-4. Trichobothria on sternum 5 in a linear series (Fig. 81). TBL 1.9mm - 2.3mm. Fig. 17. ........................ Tropistethus holosericeus (Scholtz)

- Y-suture present (Fig. 1), but sometimes weak. Trichobothria on sternum 5 with posterior pair one above the other (Figs 83-119). ........................ 5

5 Paired trichobothria on sternum 5 posteriad of spiracle, or directly under it (Figs 83-86). ............ 6

- All trichobothria on sternum 5 clearly anterior of spiracle (Figs 87,88,90-119), except for strongly flattened Gastrodes (Fig. 89). ........................ 11

6 Lateral pronotal sides concave (Fig. 298). Evaporative areas oblong (Fig. 163). Prothoracic femur with a minute spine on antero-ventral edge (Fig. 226). ......... 7

- Lateral pronotal sides almost straight, or convex (Figs 299,300). Evaporative areas more quadrate (Figs 165,166). Prothoracic femur mutic, or with a row of fine setae on antero-ventral edge. ............. 8

119
7 Body shining and almost glabrous, with very short, adpressed scattered pubescence. Third antennal segment yellow, with base and apex brown, or completely brown. Pronotal carinae black. TBL 2.6mm - 3.6mm. Fig. 44.  

- Body matt with dense, short, adpressed pubescence. Third antennal segment yellow. Pronotal carinae predominantly yellow. TBL 2.6mm - 3.2mm.  

\textit{Acompus rufipes} (Wolff)

\textit{Acompus pallipes} (Herrich-Schaeffer)

8 Anterior trichobothrium on sternum 5 almost equidistant between spiracles 4 and 5 and not embraced by suture 4-5 as it turns posteriad (Fig. 85). Body pubescence at least as long as eye width. TBL 3.2mm. Fig. 18.  

\textit{Lasiosomus enervis} Herrich-Schaeffer

- Anterior trichobothrium on sternum 5 closer to spiracle 4 (Fig. 86) and embraced by suture 4-5 as it turns posteriad. Body pubescence distinctly shorter than eye width.  

9 Head and pronotal pubescence decumbent (Fig. 319), shorter than median width of second antennal segment. Abdomen red, apart from evaporative areas; Y-suture narrowly margined off-white, with short, transverse, off-white streaks, adjacent to intermediate and posterior evaporative areas (Fig. 19). TBL 2.1mm - 3.1mm.  

\textit{Stygnocoris fuligineus} (Geoffroy)

- Head and pronotal pubescence semi-erect (Fig. 320), as long as median width of second antennal segment. Abdomen not marked as above.  

10 Abdomen red with yellow-white transverse bands along sutures, almost reaching lateral abdominal margin (Fig. 20). TBL 2.1mm - 2.6mm.  

\textit{Stygnocoris sabulosus} (Schilling)

- Abdomen unicolorous red (apart from dark evaporative areas). TBL 2.5mm - 3.4mm.  

\textit{Stygnocoris rusticus} (Fallén)

11 Suture between sterna 4-5 straight and reaching lateral abdominal margin (Fig. 89). Spiracle 5 directly above posterior trichobothria on sternum 5 (Fig. 89). Body strongly dorso-ventrally flattened.  

- Suture between sterna 4-5 curving strongly anteriad, looping around anterior trichobothrium and not reaching lateral abdominal margin. Spiracle 5 posteriad of posterior trichobothria on sternum 5 (Figs 87, 88, 90-93). Body not strongly dorso-ventrally flattened.  

120
12 Prothoracic femur with at least 5 and normally 10 - 15 small spines proximal to large spine on antero-ventral edge (Fig. 240). First antennal segment surpassing apex of tylus by one third of its length. Body brown, pronotum with a narrow meso-basal white mark (Fig. 26). TBL 4.2mm - 5.7mm. Gastrodes grossipes (De Geer)

- Prothoracic femur normally without small spines proximal to large spine on antero-ventral edge and never more than 5 present (Fig. 239). First antennal segment almost reaching tylus apex. Body yellow with basal third of pronotum white. TBL 5.4mm - 6.8mm. ........... Gastrodes abietum Bergroth

13 Maximum length of anterior evaporative area < 1 x eye width (Fig. 174). Prothoracic femur mutic. TBL 1.9mm - 2.5mm. Fig. 45. ....... Ischnocoris angustulus (Boheman)

- Maximum length of anterior evaporative area > or equal to 1 x eye width. Prothoracic femur with at least 1 small spine. ........................................... 14

14 Maximum length of anterior evaporative area > 2.4 x eye width (Fig. 177). ........................................... 15

- Maximum length of anterior evaporative area < 2.4 x eye width (Figs 167-172,175,176). ........................................... 16

15*TBL 2.56mm - 3.06mm. Posterior width of pronotum < 1.8 x anterior width. Fig. 29. ............... Taphropeltus contractus (Herrich-Schaeffer)

- TBL 2.30mm - 2.48mm. Posterior width of pronotum > 1.85 x anterior width. .... Taphropeltus hamulatus (Thomson)

* Taphropeltus limbatus Fieber will key out here.

16 Rostrum reaching beyond metathoracic coxae at least to suture between sterna 2-3. Tylus not reaching mid-point of first antennal segment. ....................... 17

- Rostrum reaching between meso- and metathoracic coxae or, if just reaching metathoracic coxae, then not extending beyond to suture between sterna 2-3. Tylus reaching mid-point of first antennal segment or further. ....................... 20

17 Abdomen with long, erect to suberect pubescence. Pronotum not quadrate, lateral margins converging towards head (Fig. 304). Antero-lateral tergal margins with broad discontinuous white markings. ....................... 18

- Abdomen with short, adpressed pubescence. Pronotum almost quadrate, lateral margins almost parallel (Fig. 303). Antero-lateral tergal margins with a continuous narrow longitudinal white stripe. ....................... 19

121
18 Head, pronotum, scutellum and mesothoracic wing-pads uniformly covered with long, erect, fairly dense pubescence. Pronotal carinae uniformly yellow. TBL 4.9mm - 6.0mm. Fig. 25. .......................... Eremocoris podagricus (Fabricius)

- Head, pronotum, scutellum and mesothoracic wing-pads almost glabrous with a few scattered long setae. Pronotal carinae brown in posterior half. TBL c4.7mm. .......................... Eremocoris plebejus (Fallén)

19 Metathoracic tibia with adpressed setae, shorter than tibial width. TBL 4.3mm - 5.2mm. .......................... Eremocoris abietis (Linnaeus)

- Metathoracic tibia with erect setae as long as or longer than tibial width. TBL 5.0mm - 5.6mm. .......................... Eremocoris fenestratus (Herrich-Schaeffer)

20 Spiracle 4 not closer to lateral abdominal margin than other spiracles (Fig. 92). Abdomen mottled (Fig. 28). 21

- Spiracle 4 slightly closer to lateral abdominal margin than other spiracles, or actually lateral (Fig. 92). Abdomen with exception of evaporative areas unicolorous. .......................... 27

21 First and second antennal segments over half yellow. 22

- First and second antennal segments brown-black and under half yellow. .......................... 24

22 Pronotal carinae uniformly yellow. TBL > 3.9mm. (3.9mm - 4.2mm). .......................... Scolopostethus pictus (Schilling)

- Apical third to half of pronotal carinae brown-black. TBL < 3.7mm. .......................... 23

23 Pubescence short, mainly adpressed on head, pronotum, mesothoracic wing-pads and scutellum. Rostrum not reaching metathoracic coxae. TBL 2.6mm - 3.4mm. .......................... Scolopostethus affinis (Schilling)

- Pubescence medium-short and semi-erect on head, pronotum, mesothoracic wing-pads and scutellum. Rostrum reaching metathoracic coxae. TBL c3.3mm. .......................... Scolopostethus puberulus Horváth

24 Head and pronotum with short, adpressed pubescence and a few short semi-erect setae (Fig. 321). .......................... 25

- Head and pronotum with medium-short, semi-erect pubescence (Fig. 325). .......................... 26
25 Apical third of first antennal segment and basal third of second antennal segment yellow. Dense pubescence on terga; most setae separated by less than their length from other setae (Fig. 322). Tergum 3 with 50 or more setae (view dry with top lighting). Under mixed herbs, coarse vegetation, *Urtica dioica* or strawberries. TBL 2.6mm - 3.4mm. ...... *Scolopostethus affinis* (Schilling)

- Only extreme apex of first antennal segment and base of second antennal segment yellow. Less dense pubescence on terga, setae separated by more than their length from other setae (Fig. 323). Tergum 3 with fewer than 50 setae. In coarse litter under trees, bushes or shrubs. TBL 3.1mm - 3.7mm. ...

........................................ *Scolopostethus grandis* Horváth

26 Maximum width of anterior evaporative area > 0.37mm. Associated with *Urtica dioica*. TBL 2.7mm - 3.3mm. ..... *Scolopostethus thomsoni* Reuter

- Maximum width of anterior evaporative area < 0.37mm. Associated with heathers. TBL 2.7mm - 3.1mm. Fig.28. ....

........................................ *Scolopostethus decoratus* (Hahn)

27 Spiracle 4 posterior to anterior trichobothrium on sternum 5 (Fig. 91). Prothoracic femur as Figs 241,242). TBL 2.9mm - 4.1mm. Fig. 27. .............. Lamproplax picea (Flor)

- Spiracle 4 anterior to anterior trichobothrium on sternum 5 (Fig. 87). Prothoracic femur as Figs 228-234. 28

28 Slender, erect or suberect setae on tibiae, as long as or longer than maximum tibial width. Anterior length of anterior evaporative area > 2 x length of posterior area. ........................................ 29

- Slender, adpressed setae on tibiae, distinctly shorter than maximum tibial width. Anterior length of anterior evaporative area < 2 x length of posterior area. ...... 31

29 TBL < 3.6mm. 2.7mm - 3.6mm. ....................... *Drymus plicicornis* (Mulsant & Rey)

- TBL > 3.6mm. ........................................ 30

30 Prothoracic femur with 1 small antero-ventral spine (Fig. 228). Anterior evaporative area oval (Fig. 167). TBL ≤4.1mm. ............ *Drymus iatus* Douglas & Scott

- Prothoracic femur with 1 small antero-ventral spine and a row of minute spines (Fig. 230). Anterior evaporative area not oval (Fig. 169). TBL 4.5mm - 4.8mm. Fig. 21. ..

........................................ *Drymus pilipes* Fieber
31 Second antennal segment shorter than fourth antennal segment. TBL < 2.9mm. (2.1mm - 2.9mm). Fig. 23. ........... Drymus pumilio Puton

- Second antennal segment longer than or equal to fourth segment. TBL > 2.9mm. ......................................... 32

32 Pronotum with concave lateral margins and with brown pigmentation anterior of transverse impression. Prothoracic femur with 1 small antero-ventral spine (Fig. 231). TBL 3.2mm - 4.3mm. Fig. 22. ....................... Drymus brunneus (Sahlberg)

- Pronotum at most weakly concave and lacking distinct brown marking. Prothoracic femur with 1 small antero-ventral spine and 4 minute spines (Figs 233, 234). .... 33

33 Vertex > 5 x eye width. TBL 3.2mm - 4.0mm. ............... Drymus ryei Douglas & Scott

- Vertex < or equal to 5 x eye width. TBL 2.9mm - 4.00mm. Fig. 24. .................. Drymus sylvaticus (Fabricius)

34 Suture between terga 3-4 simple, not deep, nor branching at lateral abdominal margin. .................. 35

- Y-suture present; if indistinct, then suture T3-4 always deeper than other abdominal sutures. ........... 50

35 Spiracle 3 ventral (Figs 30,46-50,96-104). ............... 36

- Spiracle 3 dorsal (Figs 106-119). ......................... 45

36 Evaporative areas absent (Fig. 181). Body pale, abdomen spotted or mottled with red and brown. ............ 37

- Narrow evaporative areas present (Figs 179,185-187). Body black with castaneous abdomen. ................. 38

37 First metathoracic tarsal segment > or equal to 1.5 x second tarsal segment length. All antero-ventral spines on prothoracic femur equal sized (Fig. 254). Anterior of head predominantly pale (Fig. 30). TBL 3.8mm - 5.00mm. ...................... Emblethis griseus (Wolff)

- First metathoracic tarsal segment < 1.4 x length of second tarsal segment. Apical antero-ventral spine on prothoracic femur larger than other spines (Fig. 253). Head black with 5, irregular, pale, antero-longitudinal stripes (Fig. 292). TBL 3.9mm - 4.9mm. ..................... Emblethis denticollis Horváth

124
38 Rostrum reaching between meso- and metathoracic coxae. Prothoracic femur mutic. TBL 2.4mm - 3.1mm. Fig. 47. ........................................... Macrodema microptera (Curtis)

- Rostrum not reaching beyond mesothoracic coxae. Prothoracic femur spinose or with long setae on antero-ventral edge. ........................................... 39

39 Tylus reaching mid-point of first antennal segment. Prothoracic femur with 2 very small antero-ventral spines (Fig. 251). TBL 4.1mm - 5.4mm. Fig. 46. ......................... Aphanus rolandri (Linnaeus)

- Tylus reaching just before, or beyond, apex of first antennal segment. Prothoracic femur with either long setae, or 1 or 4-5 spines on antero-ventral edge (Figs 257-261). ........................................... 40

40 Body elongate and parallel sided (Fig. 49). Prothoracic femur with 1 very small antero-ventral spine (Fig. 257). TBL 3.4mm - 3.8mm. ......................... Pterotmetus staphyliniformis (Schilling)

- Body suboval (Figs 48,50). Prothoracic femur multipinose, or with long setae (Figs 258-261). ....... 41

41 Stout, erect setae on lateral explanate pronotal margins (Fig. 308). Prothoracic femur and tibia with long, erect setae. TBL 2.2mm - 2.6mm. Fig. 48. ......................... Pionosomus varius (Wolff)

- Setae absent from lateral pronotal margins, short and adpressed on prothoracic tibia. Prothoracic femur with 4-5 tuberculate setae (Figs 258-261). ......................... 42

42 All first tarsal segments and second and third antennal segments yellow. Prothoracic femur with 1 small antero-ventral spine and 3 tuberculate setae (Fig. 261). TBL 4.1mm - 5.1mm. .......... Trapezonotus ullrichi (Fieber)

- All appendages brown-black. Prothoracic femur with 1 small antero-ventral spine and 4-5 tuberculate setae (Figs 258-260). .............................. 43

43 Body strongly shining. TBL 2.3mm - 3.7mm. Fig. 50. ....... Trapezonotus arenarius (Linnaeus)

- Body matt or at most only slightly shining. .......... 44

44 Smaller; TBL 2.9mm - 3.5mm. Vertex < or equal to 0.65mm. .......... Trapezonotus desertus Seidenstücker

- Larger; TBL 3.6mm - 4.3mm. Vertex > or equal to 0.65mm. ........................................... Trapezonotus dispar Stål

125
45 One or 2 pairs of dorsal abdominal gland apertures and associated evaporative areas between terga 4-5 and 5-6. Glands and evaporative area absent between T3-4 (Figs 191,196). ............................................. 46

Three pairs of gland apertures with evaporative areas between terga 3-4, 4-5 and 5-6 (Figs 192-195). ............. 47

46 Distinct evaporative area between terga 4-5 (Fig. 191). Appendages predominantly yellow. TBL 2.8mm - 4.1mm. Fig. 31. ........ Megalonotus antennatus (Schilling)

Evaporative area between terga 4-5 reduced to a small, black spot (Fig. 196). Appendages predominantly brown-black. TBL 4.1mm - 5.6mm. ......................... Megalonotus dilatatus (Herrich-Schaeffer)

47 Intermediate evaporative area wider than anterior area (Fig. 194). Posterior pronotal margin coarsely punctate. TBL 3.3mm - 4.1mm. Fig. 52. ..................... Megalonotus praetextatus (Herrich-Schaeffer)

Anterior evaporative area wider than intermediate area (Figs 192,193,195). Posterior pronotal margin not coarsely punctate. ................................. 48

48 Abdomen with very short, adpressed, uniform pubescence. TBL 4.4mm - 5.0mm. ...... Megalonotus emarginatus (Rey)*

*Abdomen and appendages predominantly brown-black = M. emarginatus atricornis.

- Abdomen with medium length adpressed and long semi-erect pubescence. ................................. 49

49 Maximum width of posterior evaporative area > 1.8 x maximum width of intermediate area. Pubescence on dorsum of abdomen dense; semi-erect, long setae not more than 2 x length of short adpressed setae (Fig. 328). TBL 3.3mm - 4.3mm. Megalonotus sabulicola Thomson

- Maximum width of posterior evaporative area < 1.8 x maximum width of intermediate area. Pubescence on dorsum of abdomen less dense; suberect long setae 2.5 x length of shorter adpressed setae (Fig. 326). TBL 3.7 - 4.9mm. Fig. 51. ...... Megalonotus chiragra (Fabricius)

50 Spiracle 2 dorsal. ..................................................... 51

- Spiracle 2 ventral. ..................................................... 52

126
51 Prothoracic femur with 1 medium and 1 or 2 small, antero-ventral spines (Fig. 284). Medium-length adpressed pubescence on terga. Head, pronotum, scutellum and mesothoracic wing-pads brown-black and yellow (Fig. 40). TBL 3.6mm - 4.6mm. .......................... *Pachybrachius fracticollis* (Schilling)

- Prothoracic femur with a medium, medium-small and 4 small antero-ventral spines (Fig. 285). Very long, erect and semi-erect pubescence on terga. Head, pronotum, scutellum and mesothoracic wing-pads predominantly yellow-brown. TBL 3.6mm - 4.0mm. Fig. 41. ........................... *Pachybrachius luridus* Hahn

52 Width of anterior evaporative area > 2 x posterior evaporative area width (Fig. 208). TBL 3.4mm - 4.8mm. Fig. 39. ........... *Xanthochilus quadratus* (Fabricius)

- Width of anterior evaporative area < 2 x width of posterior evaporative area. .......................... 53

53 Y-suture with a broad white margin. White colouration continuing on venter, forming a broad abdominal band along suture 3-4. TBL 3.6mm - 4.5mm. Fig. 37. ................. .......................... *Raglius alboacuminatus* Goeze

- Y-suture with an inner red or brown margin and a broad outer white margin. White colouration not continuing along sterna 3-4. .............................. 54

54 Width of anterior and posterior evaporative areas equal, or posterior area slightly wider (Fig. 202). Pronotal carinae projecting beyond anterior pronotal margin and partly embracing eye (Fig. 295). TBL 4.7mm - 6.5mm. Fig. 33. ....... *Graptopeltus lynceus* (Fabricius)

- Anterior evaporative area always slightly wider than posterior area (Figs 200, 203-205, 207). Pronotal carinae not projecting beyond anterior pronotal margin. ....... 55

55 Distance between anterior margin of anterior evaporative area and posterior margin of posterior evaporative area < head width across eyes. .......... 56

- Distance between anterior margin of anterior evaporative area and posterior margin of posterior evaporative area > head width across eyes. .......... 60

56 Tylus reaching or almost reaching apex of first antennal segment. Width of anterior evaporative area > 1.5 x width of posterior area. Prothoracic femur unispinose on antero-ventral edge (Fig. 276). TBL 3.0mm - 3.8mm. Fig. 34. ................. .......................... *Pasatus lundi* (Gmelin)

- Tylus at most extending two-thirds along length of first antennal segment. Width of anterior evaporative area < 1.5 x width of posterior area. Prothoracic femur multi-spinose (Figs 277-279). .......................... 57
57 Head, pronotum and scutellum yellow with 8 longitudinal black stripes (Fig. 35). .................................................. 58

- Head and pronotum predominantly brown and/or black with yellow patches but without longitudinal black stripes. 59

58 Meso-longitudinal black stripe on head narrower than eye width (Fig. 296). First antennal segment slightly wider than third antennal segment. TBL 3.8mm - 4.9mm. Fig. 35. ................. *Peritrechus geniculatus* (Hahn)

- Meso-longitudinal black stripe on head broader than head width (Fig. 297). First antennal segment slightly narrower than third antennal segment. TBL 3.6mm - 4.8mm. ............ *Peritrechus gracilicornis* Puton

59 Anterior evaporative area only slightly wider than intermediate and posterior areas. All evaporative areas broadly oval and length of anterior area > 2 x gland aperture width (Fig. 205). TBL 3.6mm - 4.7mm. Fig. 36. ............................ *Peritrechus nubilus* (Fallén)

- Anterior evaporative area wider than intermediate and posterior areas. All evaporative areas broadly oval and length of anterior area < 2 x gland aperture width. TBL 3.7mm - 4.0mm. ... *Peritrechus angusticollis* (Sahlberg)

60 Length of second antennal segment < head width across eyes. TBL 5.7mm - 6.6mm. Fig. 38. ........................................... *Rhyparochromus pinii* (Linnaeus)

- Length of second antennal segment > head width across eyes. TBL 4.3mm - 6.0mm. Fig. 32. .......................... *Beosus maritimus* (Scopoli)

61 Gland apertures between terga 3-4 and 4-5 (sometimes vestigial between terga 4-5) (Figs 137,138). Spiracles 2-6 dorsal and 7 ventral. Antennifers long and visible in dorsal view (Fig. 8). Lateral abdominal margins scalloped, broadest at tergum 3 and strongly tapering posteriad (Fig. 8). ............................. 62

- Gland apertures between terga 4-5 and 5-6, absent from 3-4. Spiracles not as above. Antennifers short and not visible in dorsal view. Abdominal margins not scalloped and strongly tapering posteriad. .......................... 65

62 Rostrum not extending beyond meso-thoracic coxae. Second antennal segment slightly shorter than third. ........ 63

- Rostrum reaching metathoracic coxae. Second antennal segment equal to or slightly longer than third. ....... 64
63 Gland apertures between terga 4-5 closed (compare with anterior pair between terga 3-4) and not surrounded by an evaporative area (Fig. 137). Pale nymphs, normally with a distinct latero-ventral continuous longitudinal red stripe. TBL 2.3mm - 3.2mm. ........................................ Cymus claviculus (Fallén)

- Gland apertures between terga 4-5 open (the same as anterior pair) and surrounded by individual evaporative areas (Fig. 138). Dark nymphs without a distinct latero-ventral continuous longitudinal red stripe (Fig. 8). TBL 2.0mm - 3.3mm. .... Cymus melanocephalus Fieber

64 Rostrum reaching just beyond metathoracic coxae. Tylus reaching beyond apex of first antennal segment. Larger species TBL 2.7 - 4.1mm. ........ Cymus glandicolor Hahn

- Rostrum reaching to, but not beyond, metathoracic coxae. Tylus only just reaching apex of first antennal segment. Smaller species TBL 2.4mm - 3.1mm. ................. Cymus aurescens Distant

65 Distinct black pronotal calli present (Figs 2-4,7). Spiracles all dorsal or spiracle 8 only ventral. ...... 66

- Pronotal calli absent. Spiracles not all dorsal and if 2-7 dorsal then spiracle 8 lateral not ventral. ........ 71

66 3 pairs of dorsal abdominal gland apertures present between terga 3-4, 4-5 and 5-6 (Fig. 135). Spiracle 8 dorsal. ............................................................ 67

- Only 2 pairs of dorsal abdominal gland apertures present between terga 4-5 and 5-6 (Figs 125-127). Spiracle 8 ventral (Figs 56-58). ...................... 68

67 TBL 3.0mm - 4.0mm. Fig. 7. Kleidocerys resedae (Panzer)

- TBL 2.6mm - 3.3mm. ... Kleidocerys truncatulus (Walker)

68 Evaporative areas large, width > 2.4 x eye width (Fig. 127). TBL 6.2mm - 8.0mm. Fig. 4. ...................... 69

- Evaporative areas smaller, width less than 1.5x eye width (Figs 125,126). TBL < 4.5mm. ....................... 70
69 Mesothoracic wing-pads uniformly dark-brown to black with a pale outer lateral margin (Fig. 333). Abdomen usually with 3 red and 4 white longitudinal red stripes (Fig. 310). Or, if stripes interrupted (Fig. 311), then width of anterior evaporating area > 0.79mm and ratio with eye width < 1.5. ........ Lygaeus simulans Deckert

- Mesothoracic wing-pads brown-black with a distinct pale central area reaching the outer lateral margin (Fig. 332). Abdomen usually red, with white narrowly along sutures (Fig. 4). Or, if white areas are broader (as Fig. 311), then width of anterior evaporative area < than 0.77mm and ratio with eye width > 1.5. ........ Lygaeus equestris (Linnaeus)

70 Terga with meso-longitudinal rows of black spots. Posterior pronotal corners white (Fig. 2). Simple, short, scattered, adpressed pubescence. TBL 3.6mm - 4.4mm. .......... Horvathiolus superbus (Pollich)

- Terga without meso-longitudinal rows of black spots. Pronotal corners not white. Moderately long, dense, erect and semi-erect capitate pubescence. TBL 2.8mm - 3.6mm. Fig. 3. ............ Lygaeosoma sardea Spinola

71 Single, weak anterior gland aperture between terga 3-4 and paired apertures between terga 4-5 and 5-6 (Fig. 155). Pronotum, scutellum and mesothoracic wing-pads partly punctate. TBL 2.7mm - 3.9mm. Fig. 13. .............. Chilacis typhae (Perris)

- Paired dorsal gland apertures between terga 4-5 and 5-6 but glands completely absent between terga 3-4. Pronotum, scutellum and mesothoracic wing-pads impunctate. ........................................ 72

72 Distinct, black, evaporative areas surrounding gland apertures between terga 4-5 and 5-6 (Figs 141,158). .... 73

- Gland apertures absent or present with narrow, pale, individual evaporative areas (Figs 132-134,143,149, 151). .......................................................... 76

73 Large, black sclerotized plate between terga 3-4 (Fig. 158). Body suboval. Lateral pronotal margins slightly concave. All spiracles ventral. .......................... 74

- Plate absent between terga 3-4. Body elongate and parallel sided. Lateral pronotal margins not concave. Spiracles 2-6 dorsal. ........................................ 75
74 Pronotum with a broad, uninterrupted, white transverse stripe along posterior margin. Pubescence short, pronotal setae shorter than width of second antennal segment. TBL 3.3mm - 4.0mm. Fig. 14. .......................... *Heterogaster artemisiae* Schilling

- Pronotum without a white transverse stripe. Pubescence long, pronotal setae longer than width of second antennal segment. TBL 4.8mm - 6.2mm. Fig. 15. .......................... *Heterogaster urticae* (Fabricius)

75 Larger: TBL > 4.1mm (4.1mm - 4.9mm); head width > 0.8mm; posterior pronotal width > 1.0mm; body width across apex of scutellum > 1.1mm. TBL 3.0mm - 4.1mm .......................... *Ischnodemus quadratus* Fieber

- Smaller: TBL < 4.1mm; head width < 0.7mm; posterior pronotal width < 0.8mm; body width across apex of scutellum < 1.1mm. TBL 3.6mm - 4.8mm. .......................... *Ischnodemus sabuleti* (Fallén)

76 Eyes large, reniform and distinctly pronounced (Figs 288,289). Spiracles 2-5 dorsal, remainder ventral. .... 77

- Eyes normal. Spiracles not as above. ....................... 78

77 Pronounced process directly above eye (Fig. 289). Distance between gland apertures in each pair < width of first antennal segment. Venter of bucculae dark. Pale spots visible on antennae. TBL 3.6mm - 4.8mm. Fig. 10. .......................... *Henestaris laticeps* (Curtis)

- Process absent above eye (Fig. 288). Distance between gland apertures in each pair > first antennal segment width. Venter of bucculae pale. Antennae black without pale spots. TBL 3.7mm - 4.5mm. .......................... *Henestaris halophilus* (Burmeister)

78 Gland apertures widely separated in each pair (Figs 132,134). Spiracles either dorsal, with spiracle 8 lateral, or all lateral. ................................. 79

- Gland apertures contiguous or almost contiguous in each pair. Spiracle 2 dorsal, remainder ventral but often indistinct. ................................. 81

79 Rostrum reaching to, or beyond, sternum 3. A4 shorter than A2. Larger, TBL 5.5mm - 6.3mm. .......................... *Orsillus depressus* Dallas

- Rostrum not reaching beyond metathoracic coxae. A4 longer than A2. Smaller, TBL < 4.5mm. .......................... 80
80 Pubescence capitate. TBL 2.9mm - 4.1mm. Fig. 5. ........
............... Ortholomus punctipennis (Herrich-Schaeffer)

- Pubescence simple. Fig. 6. .............. Nysius Dallas*

*N. cymoides (Spinola), N. ericae (Schilling), N. graminicola (Kolenati), N. helveticus (Herrich-Schaeffer), N. senecionis (Schilling) and N. thymi (Wolff) cannot, as yet, be reliably separated on nymphal characters.

81 Terga red with transverse rows of large ochreous spots. Prothoracic femur with 3 antero-ventral spines (Fig. 149). .................................................. 82

- Terga either predominantly unicolorous, or with longitudinal red stripes, but without spots. Prothoracic femur with 1 or 4 spines (Figs 151,152). ... 83

82 Head dark-brown, contrasting in colour with paler pronotum and scutellum. Body broadly oval and squat (Fig. 11). Second antennal segment shorter than fourth. Vertex > 4.1 x eye width. Pronotum > 2 x as wide as long. TBL 2.3mm - 3.0mm. Macroplax preyssleri (Fieber)

- Head red-brown or yellow-brown, predominantly the same colour as pronotum and scutellum. Body more elongate. Second antennal segment equal to or longer than fourth. Vertex < than 4 x eye width. Pronotum < 2 x as wide as long. TBL 2.7mm - 2.9mm. ......................... Macroplax fasciata (Herrich-Schaeffer)

83 Tergum 3 with a broad, sometimes faint transverse white band. Prothoracic femur unispinose (Fig. 43). TBL 2.7-3.0mm. ......................... Microplax albofasciata (Costa)

- Terga with 4 longitudinal red stripes. Prothoracic femur with 2 spines. TBL 2.7mm - 3.0mm. Fig. 12. ...... .............................. Metopoplax ditomoides Fieber

132
10. Descriptive Accounts of the Nymphs of West Palaearctic Lygaeidae

Descriptions are provided for fifth instar West Palaearctic genera and British species. The sequence and numbering system is the same as in the checklist (Cl.)

The following abbreviations are used:

- A = antennal segment
- R = rostral segment
- T = tergum
- Ts = tarsi
- MWP = mesothoracic wing-pads
- S = sternum
- TBL = total body length

Abdominal sutures are listed relative to adjacent sterna or terga e.g. T2-3 or S4-5. Suture directions are described as curving anteriad or posteriad from their mid-point.

An indication of total body length (TBL) is provided within the following size ranges:

- Small < 3mm
- Medium 3mm - 6mm
- Large > 6mm

Full data for specimens examined are provided in the Liverpool Museum collection catalogue of Palaearctic Lygaeidae (Appendix 5). Data for non-Liverpool Museum specimens are provided in full.

Detailed measurements of all British species are given in Appendix 7.
LYGAEINAE SCHILLING, 1829

Apterola Mulsant & Rey, 1866 (Cl. 1.1; Fig. 53)

Medium length, oval, matt, yellow, brown, white and red nymphs, with seven red, dorso-longitudinal abdominal stripes. Irregular long, pale, erect to suberect pubescence, arising from small black-ringed pits, with short, black, adpressed setae also on dorsum of abdomen. Eyes small, touching anterior pronotal margin. Tylus almost reaching apex of A1. Pronotum trapeziform, maximum width 2 x length, with long, black impressed calli. Scutellum 2-3 x as wide as long. MWP very short, not extending beyond suture T1-2. Gland apertures and evaporative areas absent. All abdominal sutures straight, T2-6 with a meso-lateral longitudinal row of black impressed spots on and mid-way between the sutures. Spiracles 2-7 dorsal, 8 ventral. Trichobothrial hairs moderately long and just visible in dorsal view (Fig. 53). Prothoracic femur mutic and not incrassate. Rostrum extending beyond metathoracic coxae.

Material examined: A. kunckeli x 10.

Arocatus Spinola, 1837 (Cl. 1.2; Figs 54, 122, 309)

Medium length, broadly oval, shining, brown, black, cream and red nymphs with very short, sparse body pubescence and semi-erect, medium length setae on appendages and venter of abdomen. Eyes distanced from anterior pronotal margin. Tylus extending to, or just beyond, apex of first antennal segment. Pronotum trapeziform, 2.5 x as wide as long, with black calli, a shallow, broad meso-longitudinal impression and white, downwardly reflexed sinuate carinae. Scutellum broad. Abdomen with distinct lateral, longitudinal impression. Narrow slit-like gland apertures between T4-5 and T5-6, separated in each pair by 2 x their width and with weak subcircular evaporative areas, predominantly anterior to the suture (Fig. 122). Suture between S5-6 curving in the middle moderately anteriad (Fig. 309), but very distinctly curving anteriad in A. melanocephalus (Puchkov, 1969). Spiracles 2-7 dorsal, 8 lateral. Trichobothria (Fig. 54), not clear if trichobothrial hairs present on T3. Rostrum reaching beyond metathoracic coxae.

134
Prothoracic femur mutic and not incrassate.

Material examined: A. longiceps x 4.

Caenocoris Fieber, 1860 (Cl. 1.3; Figs 55, 123, 213)

Large, elongate, red and brown-black nymphs, with long, slender appendages and dense, moderately long, fine, erect and suberect, pale pubescence. Eyes small, distanced from anterior pronotal margin and somewhat produced. Tylus reaching apex of A1. Pronotum trapeziform, with black calli; lateral margins concave in posterior quarter, upwardly reflexed posteriad of deep transverse impression and with an indistinct meso-longitudinal impression. MWP reaching centre of T3. Abdominal segments 2-7 red. Gland apertures between T4-5 not separated by more than their width, those between T5-6 separated by distinctly more than their width. Evaporative areas elongate; posterior area often almost bilobed and twice the size of anterior area (Fig. 123). Suture T5-6 in the middle curving strongly anteriad. Trichobothria as Fig. 55. Spiracles 2-7 dorsal, 8 lateral. A4 distinctly longer than A2. Prothoracic femur with distinct spine (Fig. 213). Rostrum reaching well beyond metathoracic coxae.

Material examined: C. nerii x 25.

Cosmopleurus Stål, 1872 (Fig. 124)

Large, elongate, suboval, nymphs with short, sparse, decumbent pubescence and long, slender appendages. Terga with three red and four yellow-white, longitudinal stripes. Eyes small and touching anterior pronotal margin. Tylus reaching half-way along A1. Pronotum trapeziform, with dark, indistinct calli, meso-longitudinal and postero-lateral impressions. MWP reaching to or just beyond T2-3. Small gland apertures between T4-5 and T5-6; apertures closer to evaporative area margin than each other. Evaporative areas black, shining, circular, equal sized and relatively small, with maximum width equal to eye width (Fig. 124). All sutures straight. Trichobothrial hairs short. Spiracles 2-7 dorsal and 8 ventral. Prothoracic femur mutic, not incrassate. Rostrum reaching metathoracic coxae.

*Graptostethus* Stål, 1868 (Cl. 1.4)

No material available for study.

*Horvathiolus* Josifov, 1965 (Cl. 1.5; Figs 2, 56, 125)

Medium length, oval nymphs, with variable length pubescence and white posterior pronotal corners. Eyes touching anterior pronotal margin, tylus not quite reaching apex of A1 and antennae fairly stout. Pronotum trapeziform, with black calli, slightly concave lateral margins, and a broad meso-longitudinal and postero-lateral impression. Scutellum with weak meso-longitudinal carina. MWP reaching T3-4 (probably less in brachypters). All abdominal sutures straight. Gland apertures between T4-5 and T5-6 small, separated by more than their width and closer to evaporative area margin than each other. Evaporative areas equal sized, brown-black, circular and slightly wider than eye width (Fig. 125). T2-7 with a row, (sometimes faint), of meso-longitudinal, brown spots. Trichobothria as Fig. 56. Spiracles 2-7 dorsal, 8 ventral. Prothoracic femur mutic. Rostrum reaching between meso- and metathoracic coxae.

Material examined: *H. superbus* x 4. *H. syriacus* x 5.

*Horvathiolus superbus* (Pollich, 1779) (Cl. 1.5.6; Figs 2, 56, 125)

Colour: Eyes black with red margins. Head, pronotum, scutellum, pleura and MWP brown. Head margined with black, vertex with two, darker brown, rectangular marks. Pronotum darker along anterior and middle of posterior margins. Terga either with unicolorous red central area and broad white lateral margins, or yellow-white with limited red suffusion, or yellow-white with red wedge-shaped, lateral stripes along sutures and red above evaporative areas.
Evaporative areas, T8 and T9 dark brown. Sterna yellow-white, with variable meso-lateral, red suffusion. S2-7 with up to ten, staggered, brown, meso-lateral dashes on and mid-way between sutures. Legs and rostrum brown. Antennal articulations, femoral and tibial apices white. Coxae and trochanters brown and white.

Structure: Body shining, with very fine, short, scattered, semi-erect pubescence. Appendages with short, dark, decumbent setae.

x 4 specimens measured: coll. T. Warne, 1988, Jersey.

**Lygaeosoma Spinola, 1837 (Cl. 1.6; Figs 3, 57, 126)**

Medium-small, squat, broadly oval nymphs, with moderately long, erect and semi-erect, capitate pubescence. Terga with red latticed pattern, forming seven, sometimes faint, longitudinal stripes. Eyes touching anterior pronotal margin. Slightly bulbous tylus protruding beyond juga, but not reaching apex of A1. Antennae stout. Pronotum trapeziform, calli brown and lateral margins slightly concave, with meso-longitudinal and postero-lateral impressions. Scutellum with weak meso-longitudinal carina and slightly rounded posterior process. MWP reaching T2-3. Abdominal sutures 4-5 and 5-6 in the middle curving slightly anteriad. Gland apertures between T4-5 and T5-6 small, separated by more than their width and touching evaporative area margin. Evaporative areas equal sized, subcircular with width slightly less than, or equal to, eye width (Fig. 126). Trichobothria as Fig. 57. Spiracles 2-7 dorsal, 8 ventral. Prothoracic femur mutic. Rostrum reaching between meso- and metathoracic coxae.

Material examined: *L. sardea* x 17.

**Lygaeosoma sardea Spinola, 1837 (Cl. 1.6.3; Figs 3, 57, 126)**

Colour: Eyes red. Head, pronotum, pleura, scutellum, MWP, legs, antennae and evaporative areas brown, often with red suffusion. Juga and sometimes MWP margined brown-black. Terga 2-7 creamy white with faint to bold red longitudinal
stripes and deeper red areas above evaporative areas; S7-9, T8-T9 with dark-brown. Rostrum often dark-brown with R4 brown-black.

Structure: As generic description.

x 10 specimens measured: - F87.8A x 1; F87.11 x 1; F87.12B, D x 3; F87.26A x 2; F87.27A x 3.

Lygaeus Fabricius, 1794 (Cl. 1.7; Figs 4, 58, 127, 310, 311, 332, 333)

Large, oval, red and black, shining, almost glabrous nymphs, with long slender appendages. Eyes small and touching anterior pronotal margin. Tylus reaching to mid-point of A1. Pronotum trapeziform, with distinct black calli; lateral margins slightly concave, with postero-lateral and weak meso-longitudinal impressions. All abdominal sutures straight. Gland apertures between T4-5 and T5-6 small, closely spaced and separated by less than their width. Evaporative areas oval, black, shining, equal sized and very large (Fig. 127). Terga 2-7 without meso-longitudinal row of brown spots; weak lateral impressions, unicolorous with terga present in meso-longitudinal row, along and mid-way between sutures. Spiracles 2-7 dorsal (sometimes can be viewed ventrally), 8 ventral. Trichobothrial hairs short (Fig. 58). Prothoracic femur mutic. Rostrum reaching to metathoracic coxae.


Lygaeus equestris (Linnaeus, 1758) (Cl. 1.7.2; Figs 4, 58, 127, 311, 332)

Colour: Morphs with varying degrees of white on a red abdomen: (i) T2-7 red with white restricted to sutures (Fig. 4); (ii) T2-7 red, with broad, meso-lateral and narrow, lateral white areas (Fig. 311). Black markings on head, pronotum and scutellum also variable, other markings more constant. Tylus black with two elongate black marks on vertex. Pronotum red, narrowly to broadly margined with white; calli black, linked by faint black patches to
pronotal base, which often obscure white margin. These markings often confluent with anterior black marks on scutellum; remainder of scutellum red, with white margins. MWP black; normally with lighter mesal area of varying size, but if present always linked to external lateral margin and occasionally dividing wing-pad into two dark areas (Fig. 332). T8, S7 and S8 black mesally, segment 9 black. Legs brown and black; femoral bases and apices, dorsal longitudinal stripes on pro- and mesothoracic tibiae off-white. Coxae mainly red and white, trochanters brown and white. Rostrum and antennae brown-black, A1-3 rarely red-brown.


x 8 specimens measured: x 4 coll. M. Hull, 05-07.06.1989, Skala Kallonis, Lesbos, Greece; x 1 F90.5G/I; x 2 T89.?; x 1 T90.4A.

*Lygaeus simulans* Deckert, 1985 (Cl. 1.7.5; Figs 310, 311, 333)

Colour: Similar to *L. equestris*. But MWP unicolorous dark-brown to black with only a narrow, pale, outer lateral margin (Fig. 333). Abdomen usually with three red and four white, longitudinal stripes (Fig. 310), but stripes sometimes interrupted (Fig. 311).

Structure: Morpheologically identical to *L. equestris*, but slightly larger, with larger evaporative areas.

x 5 specimens examined: x 1 T89.5; x 4 T90.73B, C.

*Melanocoryphus* Stål, 1872 (Cl. 1.8; Figs 59, 128)

Medium length, oval nymphs with red and yellow-white, longitudinally striped abdomens. Pubescence very short, fine and scattered or short, suberect and pale. Eyes touching anterior pronotal margin. Tylus not quite reaching apex of A1. Pronotum trapeziform with shallow, longitudinal, mesal and lateral posterior impressions and
black, elongate calli. MWP just reaching T2 in brachypters or T3 in macropters. All abdominal sutures straight. Gland apertures between T4-5 and T5-6 separated by more than their width and closer to evaporative area margin than each other. Evaporative areas oval, equal sized, shining, black-brown, and smaller than eye width (Fig. 128). T2-7 with 0-2 meso-lateral longitudinal rows of black spots. Spiracles 2-7 dorsal, 8 lateral. Trichobothria as Fig. 59. Prothoracic femur mutic. Rostrum reaching between meso- and metathoracic coxae.

Material examined: M. alboacuminatus x 1. M. tristrami x 5.

Paranysius Horváth, 1895 (Cl. 1.9)

No material available for study.

Spilostethus Stål, 1868 (Cl. 1.10; Figs 60, 129, 334)

Large to very large, oval, red, black and yellow-white nymphs with slender appendages. Body almost glabrous with very short, sparse pubescence. Eyes small and touching pronotal margin. Tylus not quite reaching apex of Al. Pronotum trapeziform, with slightly concave lateral margins, a lateral posterior and weak meso-longitudinal impression and black calli. Black MWP reaching T3-4; lighter, normally red, mesal areas completely bordered with black and never open to MWP margin (Fig. 334). Sutures T4-5 and T5-6 almost straight. T2-7 with a black longitudinal row of meso-lateral streaks or large black spots. Gland apertures between T4-5 and T5-6 close together in each pair, separated by less than their width and distant from evaporative area margin. Evaporative areas circular to oval, moderately large, maximum width 1 to 1.5 x eye width (Fig. 129). Spiracles 2-7 lateral, 8 ventral. Trichobothria in linear sequence or almost so, on S3 with lateral pair closer together (Fig. 60). Prothoracic femur mutic. Rostrum reaching between meso- and metathoracic coxae.

Material examined: S. pandurus x 7. S. saxatilis x 30.
Tropidothorax Bergroth, 1868 (Cl. 1.11; Fig. 130)

Large, red and black nymphs with slender appendages, completely covered with moderately long, stout erect and suberect pubescence. Eyes small, not touching anterior pronotal margin. Tylus reaching mid-point of A1. Pronotum 2 x as wide as long with distinct calli, a straight anterior margin, slightly concave lateral margins, broad postero-lateral and fainter meso-longitudinal impressions. MWP reaching T3. All abdominal sutures straight. Gland apertures slit-like, not separated by more than their width and closer to each other than evaporative area margin. Anterior evaporative area wider than posterior area, anterior margin straight and 2-3 x as long as eye width (Fig. 130). Trichobothria in linear sequence on S3. Spiracles 2-7 dorsal, 8 lateral. Prothoracic femur mutic. Rostrum reaching mesothoracic coxae.

Material examined: T. leucopterus x 1 coll. J. Péricart no. 348.

ORSILLINAE STÅL, 1872

ORSILLINI STÅL, 1872

Camptocoris Puton, 1886 (Cl. 2.1.1; Figs 61, 131)

Medium-small, broadly oval, faintly shining, yellow nymphs with long, slender appendages, irregular, often faint, dark-brown, longitudinal stripes on the head, pronotum, scutellum and MWP and red mottling on the abdomen. Body almost glabrous with very short, sparse, adpressed pubescence. Short, semi-erect, sparse pubescence on appendages. Head, pronotum, scutellum and MWP coarsely punctate. Head porrect and declivent. Eyes touching anterior pronotal margin and tylus extending to apex of A1, or considerably beyond (Slater & Ashlock, 1980) (A4 will be very long in males). Pronotum trapeziform, 2.5 x as wide as long with pale but distinctly impressed calli, a meso-longitudinal keel, pale, narrow, upwardly reflexed carinate lateral margins and a mesally concave posterior margin. Scutellum apically broad with a meso-longitudinal keel concurrent with the pronotum. MWP reaching suture T3-
4, to centre of T4. Abdominal sutures simple, T4-5 in the middle curving anteriad and latero-longitudinal impression present. Gland apertures with evaporative area reduced to a narrow sclerotized margin between terga 4-5 and 5-6, posterior apertures more widely spaced (Fig. 131). Trichobothria lacking hairs (Fig. 61). Spiracles 2-8 lateral. Prothoracic femur mutic and rostrum very long, extending to, or well beyond, S4.

Material examined: Camptocoris sp. x 6 (some badly damaged and antennae absent) coll. J. A. and S. Slater, T. Schuh, and M. Sweet. 18.01.1968, killed 05.04.1968, 12 miles N-W Kimberley, Cape Province, South Africa.

**Orsillus Dallas, 1852** (Cl. 2.1.2; Figs 42, 62, 132, 214)

Medium-large, broadly oval, dorso-ventrally flattened, matt, red and yellow spotted nymphs with slender appendages and a very long rostrum. Body almost glabrous with very short, scattered, stub-like, simple pubescence and short adpressed setae on appendages. Eyes small, slightly distanced from anterior pronotal margin. Head strongly porrect and non-declivent with tylus extending beyond apex of A1. Pronotum trapeziform, 2 x as wide as long with narrowly carinate, downwardly reflexed, convex lateral margins. Scutellum apically broad. MWP reaching suture T3-4. All abdominal sutures simple and straight except for T5-6 which curves strongly anteriad in the middle; lateral longitudinal impression present. Gland apertures between terga 4-5 and 5-6 with the evaporative areas reduced to a sclerotized rim. Anterior pair distinctly smaller and closer together than posterior pair (Fig. 132). Trichobothria lacking hairs. Spiracles 2-7 dorsal, 8 lateral (Fig. 62). Prothoracic femur multi-spinose (Fig. 214). Rostrum reaching to, or distinctly beyond, S3.

Material examined: O. depressus x 35. O. maculatus x 3.

**Orsillus depressus Dallas, 1852** (Cl. 2.1.2.1; Figs 42, 62, 132, 214)

Colour: Body covered with yellow circular spots, highlighted by brown on the head, pronotum, scutellum and
MWP, with some red suffusion on the abdomen. Pale unspotted or faintly spotted areas on centre of head, along abdominal sutures and in meso-ventral areas of body. Appendages yellow. A4, R4 and Ts2 brown-black.

Structure: As generic description. Rostrum reaching suture S3-4. Prothoracic femur with five antero-ventral spines (Fig. 214).

x 8 specimens measured: GB90.3.

Ortholomus Stål, 1872 (Cl. 2.1.3; Figs 5, 63, 133, 318)

Medium-small, oval, matt, yellow spotted nymphs, highlighted by brown and red mottling with black on appendages. Body and appendages with medium-short, semi-erect, pale, capitate pubescence (Fig. 318) with additional simple setae on legs and sterna. Eyes large and touching anterior pronotal margin. Tylus just extending to apex of first antennal segment. Pronotum trapezoidal with pale carinate margins and very weak pale calli. Scutellum broad and trapezoidal. Abdomen with lateral longitudinal impression. MWP reaching suture between T3-4 to T4-5. All sutures simple and T5-6 curving moderately to strongly anteriad. Tear-shaped gland apertures between T4-5 and T5-6; posterior pair slightly more widely separated and both pairs with the evaporative area reduced to a narrow margin (Fig. 133). Spiracles 2-7 just dorsal, 8 ventral. Trichobothrial hairs short (Fig. 63). Prothoracic femur mutic. Rostrum reaching meso- or metathoracic coxae.

Material examined: O. punctipennis x 15. Ortholomus sp. x 7.

Ortholomus punctipennis (Herrick-Schaeffer, 1838) (Cl. 2.1.3.1; Figs 5, 63, 133, 318)

Colour: Eyes red-black. Body with yellow-white spots, highlighted by brown on head, pronotum, MWP and red on abdomen. Highlighting sometimes faint in some areas, leaving larger pale areas or merged spots. Carinate pronotal margins, coxae, apart from extreme margins and trochanters white. Antennae black with faint, pale spots
and pink articulations. Dappled markings on femora, base and apex of tibiae and tarsi dark-brown. A median pale ring on all tibiae. Rostrum brown-black with some pale areas on R1 and R2.

Structure: As generic description. Rostrum reaching metathoracic coxae.

x 4 specimens measured: x 2 Y89.26C; x 2 Y89.58.

**NYSIINI UHLER, 1852**

*Nithecus* Horváth, 1890 (Cl. 2.2.1)

No specimens available for study.

*Nysius* Dallas, 1852 (Cl. 2.2.2; Figs 6, 64, 134)

Medium-small, broadly oval, matt, yellow nymphs with red mottled abdomens and an irregularly brown-black, striped head, pronotum, scutellum and MWP. Dorsum of body almost glabrous with very short, scattered, stub-like simple pubescence and slightly longer setae on venter and appendages. Eyes large and touching anterior pronotal margin. Tylus extending to apex of A1. Pronotum trapeziform, at least 2.5 x as wide as long, normally with dark, but sometimes weak calli and carinate lateral margins. Scutellum apex broadly flattened. MWP reaching T3. All abdominal sutures simple, S4-5 and S5-6 curving anteriad in the middle and latero-longitudinal impression present. Gland apertures without evaporative areas between terga 4-5 and 5-6, posterior pair larger and more widely spaced (Fig. 134). Spiracles 2-7 dorso-lateral and 8 ventero-lateral. Trichobothria lacking hairs (Fig. 64). Rostrum reaching from meso- to metathoracic coxae. Prothoracic femur mutic.

Material examined: Require confirmation (see catalogue).
**Nysius ericae** (Schilling, 1829) (Cl. 2.2.2.2; Figs 6, 64, 134)

Colour: Eyes red. Head, pronotum, scutellum and MWP yellow with brown-black, irregular, sometimes mesally faint, longitudinal stripes. Abdomen yellow, mottled with red and with large, red maculae above gland apertures. Antennae, femora, Ts2 and rostrum yellow-black. Tibiae and Ts1 yellow.

Structure: Rostrum reaching at least between, or beyond, metathoracic coxae.

**Nysius helveticus** (Herrich-Schaeffer, 1850) (Cl. 2.2.2.6)

As *N. ericae* but larger (Appendix 7). Black stripes on body narrower.

**Nysius thymi** (Wolff, 1804) (Cl. 2.2.2.9)

Colour and structure: As *N. ericae*. Rostrum reaching to or between mesothoracic coxae but not between metathoracic coxae.

**ISCHNORHYNCHINAE STÅL, 1872**

**Kleidocerys** Stephens, 1829 (CL. 3.1; Figs 7, 65, 135)

Medium-small, red-brown, oval nymphs. Body with scattered, short, pale, adpressed, scale-like, capitate pubescence and equally short, pale, fine, suberect setae. Longer, fine, suberect setae on appendages. Tylus long and slender, extending well beyond juga and reaching apex of A1. Antennae relatively slender, A1 and A4 broader than A2-3. Eyes touching anterior pronotal corner. Pronotum trapeziform, posterior width at least 2 x length; with distinct black calli, carinate lateral margins and a weak meso-longitudinal impression. MWP reaching T3. Abdomen widest at T3, with distinct lateral longitudinal impression, all sutures simple and straight. Widely separated gland apertures with brown-black, short, broad evaporative areas between T3-4, T4-5 and T5-6; anterior pair more widely separated than subequal intermediate and
posterior pairs (Fig. 135). Spiracles dorso-lateral. Trichobothrial hairs short and not visible in lateral view. Trichobothria close together on on S5 and S6, and linear on S3 and S4 (Fig. 65). Prothoracic femur incrassate and mutic. Rostrum reaching to or beyond metathoracic coxae.


*Kleidocerys truncatulus ericae* (Horváth, 1909) (Cl. 3.1.2)

Colour: Eyes red. Body with yellow, circular, sometimes indistinct spots. Head, pronotum, scutellum and MWP brown, with red suffusion and brown-black external margins. Pronotal carinae yellow-white. Pleura brown-black, margins red. Terga red, evaporative areas brown-black; T8 with brown mesal area, T9 black. Sterna red; spots indistinct or merging mesally and S6-8 brown mesally. Antennae brown-black; A2 and A3 sometimes with broad yellow median rings, base of A4 sometimes yellow. Femora red-brown, tibiae yellow-brown, TS1 brown, TS2 and rostrum brown-black.

Structure: Rostrum reaching S4.

x 10 specimens measured: x 1 GB86.10A; x 1 GB87.36A; x 2 J89.19D; x 2 coll. P. Kirby, 30.06.1982, Chobham Common, Surrey and x 1 30.08.1982; x 3 coll.?, --.08.1947 New Forest.

*Kleidocerys resedae* (Panzer, 1797) (Cl. 3.1.1; Figs 7, 65, 135)

As *K. truncatulus ericae*, but larger (Appendix 7). Nymphs on Alnus are slightly smaller and darker than those collected on Betula and A2 often almost completely dark-brown.

x 18 specimens measured: Betula - x 6 GB84.27B; x 2 GB87.36B; x 2 coll. T. Eccles, 1986, Stockton Wood, Merseyside. Alnus - x 8 GB90.1.
CYMINAE BAERENSPRUNG, 1860

CYMINI BAERENSPRUNG, 1860

Cymodema Spinola, 1837 (Cl. 4.1; Figs 66, 136)

Medium-small, narrowly elongate, almost glabrous, yellow, light-brown and red nymphs, with pale circular spots. Body broadest at abdominal segment 3, strongly tapering anteriad and posteriad with abdomen indented inwards at each suture. Head slightly wider than long; bulbous tylus extending well beyond juga and reaching two-thirds along A1. A1 broader and shorter than other segments and A3 at least 1.5 x length of A2. Eyes touching or almost touching anterior pronotal margin. Pronotum trapeziform, with distinct mesolateral depression and downwardly reflexed, emarginate, carinate, narrowly hyaline, jagged lateral margins. MWP reaching T4. Small, well spaced gland apertures with individual evaporative areas, between T4-5 only (Fig. 136). All sutures simple, straight and reaching abdominal margin. Spiracles 2, 3 and 7 lateral, 4 dorso-lateral and 5-6 clearly dorsal. Trichobothria as Fig. 136. Prothoracic femur mutic and not incrassate. Rostrum reaching between meso- and metathoracic coxae.


Cymus Hahn, 1831 (Cl. 4.2; Figs 8, 67, 137, 138)

Medium-small, distinctive, oval nymphs, with relatively short, stout appendages and a pale, spotted, almost glabrous body. Head just wider than long; tylus long, bulbous, extending well beyond juga, to or just beyond apex of A1. Antennifers long and visible in dorsal view, A1 broader and shorter than A2 and A3. Eyes small, positioned close to anterior angle of pronotum. Pronotum trapeziform, impressions absent; lateral edge narrowly carinate, uneven and reflexed downwards. MWP reaching T3-4. Abdominal sides scalloped, broadest at T3 and strongly tapering posteriad. Gland apertures between T3-4 and T4-5; anterior pair more widely separated (Fig. 138), posterior pair sometimes
closed, vestigial and lacking an evaporative area (Fig. 138). Evaporative areas small, distinctively shaped and individually surrounding each gland aperture (Figs. 137, 138). All sutures simple, reaching abdominal margin and either straight or almost straight. Trichobothria as Fig. 67. Spiracles 2-6 dorsal, 7 ventral, 8 absent*; spiracles 2-3 sometimes lateral. Prothoracic femur mutic and not incrassate.

*Dorsal in some tropical species e.g. C. novaezelandiae Woodward (Malipatil, 1978b).

Material examined: C. aurescens x 11. C. claviculus x 39. C. glandicolor x 49. C. melanocephalus x 84. Cymus sp. x 2.

Cymus aurescens Distant, 1883 (Cl. 4.2.1)

Very similar to C. glandicolor. Usually smaller and less elongate (Appendix 7), with the following other differences:

Colour: Limited red suffusion usually present on lateral margins of abdomen and pronotum.

Structure: Tylus only just reaching beyond apex of A1. Rostrum reaching to, but not beyond, metathoracic coxae.

x 7 specimens measured: GB86.64A.

Cymus claviculus (Fallén, 1807) (Cl. 4.2.2; Fig. 137)

Colour: Eyes red. Body pale, yellow-white, with brown and red markings. Head and pronotum with lateral, broad, longitudinal, light-brown stripe. MWP light-brown at base and apices. Paler mesal areas of head and pronotum often lacking spots. Basal corners of scutellum with black spots. Abdominal yellow spots variable and often indistinct. Terga often with red suffusion, either limited to area between gland apertures or more widespread and forming meso-lateral longitudinal stripes. Anterior evaporative areas black. Venter normally with continuous, sometimes faint, meso-lateral, longitudinal pair of red stripes along whole
length. Antennae brown-black. Femora brown, pale at bases and apices. Tibiae and tarsi yellow-white, T2 brown. Rostrum brown, apex of R4 black.

Structure: Dorsum glabrous. Venter with sparse semi-erect, pale pubescence. Legs and antennae with short, decumbent setae. Paired gland apertures on T4-5 closed, apparently vestigial and lacking evaporative areas (Fig. 137). Tylus reaching apex of A1. A2 shorter than A3. Rostrum not extending beyond mesothoracic coxae.

x 10 specimens measured: x 4 GB86.29A; x 2 GB86.35B; x 4 GB87.15B.

_Cymus glandicolor_ Hahn, 1831 (Cl. 4.2.3; Fig. 67)

Colour: Eyes red. Body brown, with yellow spots and a pale, sometimes faint, meso-longitudinal stripe; spots absent in mesal and ventral areas of head and mesal area of sterna and obscured or less numerous on MWP. Lateral sides of head, pronotum and inner margin of MWP with broadly dark-brown, longitudinal stripe; MWP apices dark-brown. Scutellum, centre of head and pronotum lighter brown. Pleura brown or dark-brown. Pronotal carinae white, and hyaline. Scutellum with black spots in basal corners. Tylus and juga margined with black. Abdomen lighter brown with red suffusion between gland apertures and on meso-anterior areas of sterna. Antennae, femora, except for bases and apices, apical third to half of tibiae, and tarsi, all brown-black; remainder yellow, with first tarsal segments sometimes brown. Rostrum yellow-brown, darker apically.

Structure: Body almost glabrous, with very short, scattered, stub-like pubescence and short, semi-erect, scattered pubescence on venter. Antennae and legs with short, sparse, semi-erect setae, longer and more dense on apical third of A4. Legs with short, sparse, semi-erect setae; slightly longer at tibial apices and on tarsi. Tylus extending to or slightly beyond apex of A1. A2 longer or equal to A3. Rostrum reaching to or beyond metathoracic coxae.
Cymus melanocephalus Fieber, 1861 (Cl. 4.2.5; Fig. 8)

Very similar to C. glandicolor.

Colour: Generally darker (British species only). Terga with meso-lateral, longitudinal red stripes, linking between gland apertures to form an H shaped marking (Fig. 8).


x 10 specimens measured: x 1 GB85.50; x 4 GB85.28; x 3 GB86.21; x 2 GB86.68.

BLISSINAE Stål, 1862

Dimorphopterus Stål, 1872 (doriae) (Cl. 5.1.3; Figs 68, 139, 215, 312, 329)

Small, squat, stout, red and brown-black nymphs with short appendages. Dorsum with long, fine pubescence. Eyes small and distanced from anterior pronotal margin by less than their own width. MWP often only reaching T1. Abdominal segments 7-9 black and heavily sclerotized, other black sclerotization limited (Fig. 313). All sutures simple, T5-6 sometimes curving anteriad. Gland apertures with distinct, almost equal sized, black evaporative areas between T4-5 and T5-6; apertures widely separated in each pair, touching evaporative area margin and greater part of evaporative area between terga 4-5 anterior of suture (Fig. 139). Evaporative areas separated by length of the posterior area. Spiracles 2-6 dorso-lateral, 7-8 ventral. Trichobothrial hairs long, slender and visible in dorsal view on sterna 5-7, but only bothria visible on sterna 3 and 4 (Fig. 68). Antennae short, only just equal to combined length of head and pronotum. Prothoracic coxal cavities open. Prothoracic femur with one meso-ventral spine (Fig. 215). Distally flattened, broadened prothoracic tibia (Fig. 329). All tibiae with an apical circle of short, stout, black spines. Rostrum reaching to and beyond
metathoracic coxae.

Material examined: D. doriae x 3.

*Dimorphopterus spinolae* (Signoret, 1857) Instar 4.
(Cl. 5.1.4; Fig. 140, 313)

As for *D. doriae* with the following differences:-

Medium-small, elongate, parallel sided, shining nymphs with scattered, short pubescence. Paired gland apertures less widely separated; anterior pair with significantly smaller evaporative area and posterior pair with equal areas above and below suture (Fig. 140). Evaporative areas separated by significantly more than their widths. Spiracles 2-6 dorsal, 7 and 8 lateral. Prothoracic femur mutic and mildly incrassate. Prothoracic tibia simple, with apical circle of short, stout black spines. Rostrum reaching mesothoracic coxae.

x 7 specimens examined: (Instar 4) coll. J. Péricart, (361), adults associated.

*Geoblissus* Hidaka, 1959 (Cl. 5.2)

No specimens available for study.

*Ischnodemus* Fieber, 1837 (Cl. 5.3; Figs 9, 69, 141)

Medium length, elongate, narrow, dorso-ventrally flattened, red, black and cream nymphs, with short, slender appendages. Eyes small, distanced from anterior pronotal margin by less than their width. Tylus narrow, not quite extending to apex of A1. Pronotum with weak meso-longitudinal and postero-lateral impressions. Mesosternum with furrow. Abdominal segments with black sclerotized spots, 7-9 heavily sclerotized (Fig. 69). Venter with distinct lateral, longitudinal impression. All sutures simple and straight. Widely separated gland apertures with distinct black evaporative areas between T4-5 and T5-6, apertures touching evaporative area margin (Fig. 141). Spiracles 2-6 dorsal and 7-8 ventral. Trichobothria not clearly visible and reduced in number (Fig. 69).
Prothoracic coxal cavity closed. Antennae longer than combined length of head and pronotum. Prothoracic femur mutic.

Material examined: *I. quadratus* x 16. *I. sabuleti* x 51.

**Ischnodemus quadratus** Fieber, 1837 (Cl. 5.3.3)

As *I. sabuleti*, but smaller and narrower (Appendix 7). TBL < 4.1mm; head width < 0.7mm; posterior pronotal width < 0.8mm; body width across apex of scutellum < 1.1mm.

x 10 specimens measured: x 1 GB91.5; x 9 F90.8.

**Ischnodemus sabuleti** (Fallén, 1826) (Cl. 5.3.4; Figs 9, 69, 141)

Colour: Eyes red. Head, pronotum, scutellum, MWP and antennae predominantly black. Cream markings on venter of head and along ecdysial suture, on posterior pronotal corners, MWP apices (sometimes extending along external lateral margin) and on antennal articulations. Abdomen distinctively patterned claret, red and cream with variable black markings (Fig. 9). TM* 8 and 9 black, TM7 with either a single black mesal area (Fig. 9) or area divided longitudinally and/or laterally. TPC4 and TPC5 either separate spots or fused together to form a linear streak (one specimen had both, on left and right sides). Antennae black. Rostrum with black suffusion, most marked on R4. Legs predominantly black; Ts1, apices of Ts2, femoral and tibial bases pale.

Structure: Body covered with moderately short, semi-decumbent pubescence; mesal areas of head and pronotum with a few noticeably longer erect and suberect setae, antennal setae also slightly longer. MWP reaching T2, or occasionally just onto T3. Prothoracic femur mutic. Rostrum reaching between pro- to mesothoracic coxae.

TBL > 4.1mm; head width > 0.8mm; posterior pronotal width > 1.0mm; body width across scutellum > 1.1mm.

* Letter coding for sclerotized areas follows Slater &
Wilcox (1973a).

x 10 specimens measured: GB86.63A.

HENESTARINAE DOUGLAS & SCOTT, 1865

Engistus Fieber, 1864 (Cl. 6.1; Fig. 142)

Medium-small, almost spherical, pale, yellow nymphs with red spots and adpressed, short pubescence. Body with interrupted, raised meso-longitudinal ridge along full length. Appendages moderately short and stout. Head declivent, distinctly wider than long, with large, reniform, protuberant eyes embracing anterior pronotal margin and separated from centre of head by longitudinal impression. Bulbous, broad tylus extending two-thirds along length of A1. A1 broader than A2 and A3. Pronotum at least 2 x as wide as long, anterior margin convex and posterior margin emarginate; less obvious meso-lateral and latero-longitudinal ridges present, the former with two distinct anterior protuberances and all ridges divided by a broad, antero-transverse impression. Gland apertures between T4-5 and T5-6, both equally widely spaced and lacking an evaporative area, except for a small posterior dark area (Fig. 142). Sutures all simple, directed anteriad and all reaching abdominal margin. Trichobothria indistinct and not figured. Spiracles 2-4 lateral, 5 dorsal and 6-7 ventral. Prothoracic femur mutic and incrassate. Rostrum reaching metathoracic coxae.


Henestaris Spinola, 1837 (Cl. 6.2; Figs 10, 70, 143, 288, 289)

Medium length, punctate, red and black spotted, squat nymphs, with stout appendages. Antennal segment 1 wider than A2-4 and extending beyond tylus apex. Eyes large, reniform and distinctly protruding (Figs 288, 289). Pronotum wider than long, with meso-anterior, transverse
impression. Abdomen reflexed laterally upwards, stepping inwardly posteriad at each suture. MWP reaching T3-4. Sutures all simple. Gland apertures between T4-5 and T5-6; apertures individually margined with incomplete black lunular evaporative areas (Fig. 143). Spiracles 2, 6-7 ventral, 3-5 dorsal and 8 absent. Trichobothrial hairs difficult to see on S3 and S4 (Fig. 70). Prothoracic femur mutic and moderately incrassate.


Henestaris laticeps (Curtis, 1836) (Cl. 6.2.5; Figs 10, 289)

Colour: Eyes red. Body ochreous, with irregularly scattered, dense, small, brown-black and red spots; brown spots slightly larger, sometimes merging on appendages, red spots on abdomen and sometimes head and legs. Head, pronotum and scutellum with pale longitudinal mid-line. Body with yellow-brown margin to sutures. Red suffusion sometimes present on head, scutellum and abdomen, most pronounced above and below anterior gland apertures. Black markings between antennifer and rostral base, on venter of juga and either side of pronotal mid-line, close to anterior margin. Appendages with dark suffusion, blackest on femora, Ts2, A2-4 and R3-4. Coxae and trochanters white with limited dark markings.

Structure: Body with short, stout, pale, adpressed pubescence, arising from spots; setae longer on appendages and venter. Head with pronounced, curved process between eye and antennifer (Fig. 289). Rostrum reaching mesothoracic coxae.

x 10 specimens measured: x 1 GB85.22C; x 7 GB85.38A; x 2 GB86.51A.

Henestaris halophilus (Burmeister, 1835) (Cl. 6.2.2; Figs 70, 143, 288)

Colour: Similar to H. laticeps, but brown-black spots more distinct. Antennae black, except for pale articulations
and spots not even visible on A1. Black spots almost absent adjacent to eyes. Juga pale ventrally. Red suffusion more distinct on abdomen, and meso-lateral, longitudinal stripe present on T3-5.

Structure: As H. laticeps, but without a pronounced process over eyes (Fig. 288). Rostrum reaching mesothoracic coxae.

x 10 specimens measured: GB85.41.

GEOCORINAE BAERENSPRUNG, 1860

GEOCORINI MONTANDON, 1913

Geocoris Fallén, 1814 (Cl. 7.1; Figs 71, 144, 290, 314)

Medium-small, broadly oval, to more elongate, shining nymphs. Head transverse. Eyes large, reniform, embracing lateral margin of pronotum and always projecting out as far as posterior pronotal corner (Fig. 290). Tylus short, not quite extending to apex of A1, with distinct, longitudinal impression which continues to base of head. A1 not broader than A4. Pronotum semi-circular or rectangular. Scutellum broadly rounded at apex. MWP reaching T3. Small, tear-shaped gland apertures with evaporative areas between T4-5 and T5-6; evaporative areas constricted between apertures and posterior apertures slightly more widely spaced than anterior pair, with a wider evaporative area (Fig. 144). Sutures between T4-5 and T5-6 in the middle curving strongly anteriad, remainder straight and all simple (Fig. 314). Trichobothria as Fig. 71. Spiracles 2-4 dorsal, 5-7 ventral. Prothoracic femur mutic, venter with a row of long fine setae. Rostrum at most just reaching metathoracic coxae, R2 shorter than R3.

Piocoris Stål, 1872 (Cl. 7.2; Figs 72, 145)

Small, broadly circular, convex, shining, glabrous nymphs, with very slender antennae. Eyes large, reniform, embracing lateral margin of pronotum, but not projecting further than posterior pronotal corner. Head extremely transverse. Tylus short, not extending to apex of A1, and with a weak longitudinal impression which continues to base of head. A1 broader than A2-4. Pronotum semi-circular. Scutellum broadly rounded at apex. MWP reaching T3. Small, slit-like gland apertures, with evaporative areas at most only slightly constricted between apertures, on T4-5 and T5-6; posterior pair slightly more widely spaced than anterior pair and with a wider evaporative area (Fig. 145). Sutures between T4-5, T5-6 and sometimes T6-7, in the middle curving strongly anteriad, remainder almost straight and all simple. Trichobothrial hairs short (Fig. 72). Spiracles 2-4 dorsal, 5-7 ventral. Prothoracic femur mutic, venter with a row of long fine setae. Rostrum reaching between or beyond metathoracic coxae. R2 longer than R3.

Material examined: P. erythrocephala x 4. P. scutellatus x 1.

Stenophthalmicus Costa, 1875 (Cl. 7.3)

No specimens available for study.

Bledionotinae Reuter, 1878

Bledionotini Scudder, 1963

Bledionotus Reuter 1878 (Instar 3) (Cl. 8.1.1; Figs 146, 335, 336)

Small, distinctive, yellow and red, shining, myrmecophile nymphs, with scattered, long, erect pubescence and long, slender appendages. Body elongate, constricted at meso- and metathorax, with abdomen narrow and almost parallel sided, or distinctly widening up to segment 6. Head strongly globose, porrect and declivent. Tylus broadening slightly apically and almost extending to apex of A1. A4 distinctly broader and longer than other antennal
segments. Eyes small and distanced from anterior pronotal margin by as much as their diameter. Pronotum globose, length noticeably shorter than head length, narrow, with strongly concave, faintly carinate lateral margins. Scutellum with a small protuberance and first abdominal segment with a very prominent erect protuberance (Fig. 336). Narrow, slit-like gland apertures, without evaporative areas, between T4-5 and T5-6 (Fig. 146). All sutures simple, straight apart from T4-5 and T5-6 which in the middle curve anteriad. Lateral longitudinal impressions present throughout abdomen length. Trichobothria and spiracles not clearly visible (adults have spiracles 2-4 dorsal and 5-7 ventral; trichobothria of typical Lygaeoid pattern, those on S5 sometimes absent (Scudder, 1963a). Prothoracic femur mutic and not incrassate. Prothoracic coxae almost contiguous, meso- and metathoracic pairs widely separated. Rostrum stout and reaching metathoracic coxae.

Colour: Head, pronotum and apex of MWP yellow; MWP base and scutellum more yellow-white. Abdomen chequered with four adjoining yellow blocks (anterior square more yellow-white) and four red squares radiating from the corners, mesal area around dorsal gland apertures orange yellow. Appendages yellow; tibiae, base of A2, A3 all of A4 and R4 red-brown.

Material examined: Bledionotus sp. x 2 (instar 3).

**Bledionotus new species** Adult (Cl. 8.1.1)

Structure: Small, TBL 2.7 - 3.0mm, elongate, brown-black, yellow and silver species with long slender appendages. Pubescence long, outstanding and erect on body and hemielytra, shorter and semi-erect on appendages.

Head, pronotum and scutellum coarsely punctate. Head broad, with slightly bulging eyes. Antennae long and slender; A4 noticeably broader than A1-3 and at least as wide as eye width. Pronotum globose, ecarinate; longer than broad and strongly constricted in posterior third. Hemielytra elongate and just extending to end of abdomen. Commisure margin longer than scutellum. Clavus with three rows of
punctures, the middle row incomplete and the external row most compact. Corium with a row of punctures along margin with clavus, an incomplete row along fore-margin and along median vein. Membrane long. Abdomen as Scudder (1963a). Legs slender, femora mildly incrassate and prothoracic femur mutic. Rostrum reaching between meta- and mesothoracic coxae.

Colour: Brown-black; A1-3, first Ts1 and Ts2 yellow. Hemilelytra brown with a distinctive silvery-white apical and basal mark on the corium.


This species is similar to B. systellonotooides but is brown-black and larger with longer, stouter appendages.

**OXYCARENINAE STÅL, 1862**

*Anomaloptera* Amyot & Serville, 1843 (Cl. 9.1)

No specimens available for study.

*Auchenodes* Horváth, 1891 (Cl. 9.2)

No specimens available for study.

*Bianchiella* Reuter, 1907 (Cl. 9.3)

No specimens available for study.

*Brachyplax* Fieber, 1860 Instar 4 (Cl. 9.4)

Small, elongate nymphs, broadest at T5, with very sparse, fine, medium length, faintly capitate pubescence and red transverse banded terga. Eyes small and distanced from head by less than their width. Tylus reaching apex of A1. Pronotum trapezoidal, concave in lateral view with antero-lateral and postero-lateral impressions. Linked, small gland apertures without evaporative areas between T4-5 and T5-6. Suture T5-6 curving moderately anterior, remainder
straight and all simple. Trichobothria indistinct and not figured. Spiracles indistinct; presumably spiracle 2 dorsal and spiracles 3-8 ventral. Prothoracic femur mutic. Rostrum reaching mesothoracic coxae.

Material examined: *B. tenuis* (instar 4) x 1.

*Bycanistellus* Reuter, 1890 (Cl. 9.5)

No specimens available for study.

*Camptotelus* Fieber, 1860 (Cl. 9.6)

No specimens available for study.

*Jakowleffia* Puton, 1875 (Cl. 9.7)

No specimens available for study.

*Leptodemus* Reuter, 1900 (Fig. 148) (Cl. 9.8)

Very small, suboval, yellow and red nymphs with red, transverse spots on terga, and a few scattered, short, semi-erect setae on body. Head porrect, 2 x as long as wide. Tylus extending beyond apex of A1. Eyes just distanced from anterior pronotal margin. Pronotum trapezoidal, with very distinct, posterior, transverse impression. MWP reaching T4. Very small linked gland apertures, without evaporative areas, between T4-5 and T5-6 (Fig. 148). T5-6 curving strongly anteriad, all other sutures straight and simple. Trichobothria absent or indistinct. Spiracles indistinct. Prothoracic femur mutic. Rostrum reaching mesothoracic coxae.

Material examined: (Non-Palaearctic) *L. iroratus* Slater, x 1 (Laboratory culture) J.A. Slater, 20.01.1968, South Africa.

*Macroplax* Fieber, 1860 (Cl. 9.9; Figs 11, 149, 216)

Small, brownish nymphs, with large ochreous spots on a red abdomen. Body and legs with semi-erect to erect, short, stout, capitate pubescence and longer, semi-erect setae on
appendages. A1 wider than A2-4 and extending beyond tylus apex by up to a third of its length. Eyes small and distanced by a half their width from anterior pronotal margin. Head large in relation to pronotum. Pronotum trapeziform, wider than long, with narrow, hyaline, carinate lateral margins. Scutellum with broadly rounded apex. MWP reaching T3-4, lateral margins strongly reflexed downwards and embracing body. Small, linked gland apertures, with brown sclerotized margins, but without evaporative areas between T4-5 and T5-6 (Fig. 149). Sutures between T4-5 and T5-6 curving anteriad. Spiracle 2 ventral, 3-8 lateral. Trichobothria indistinct and not figured. Prothoracic femur incrassate, with three anteroventral spines decreasing in size apically (Fig. 216). Rostrum reaching to at least metathoracic coxae.


**Macroplax fasciata** (Herrich-Schaeffer, 1835) (Cl. 9.9.1)

Colour: As M. preyssleri, but paler, with red, brown and yellow-brown in place of dark-brown markings.

Structure: More elongate than M. preyssleri. A2 longer or equal to A4. Vertex less than 4 x eye width. Pronotum less than 2 x as wide as long.

x 2 specimens measured: x 1 coll. M. Hull, 13.07.1990, La Aliseda De Tormes, Spain; x 1 coll. M. Hull, 04.08.1990, Bronchales, Spain.

**Macroplax preyssleri** (Fieber, 1837) (Cl. 9.9.2; Figs 11, 149, 216)

Colour: Eyes red. Dorsum of head dark-brown, with yellow-brown spots; black lateral margins between tylus and antennifer; venter pink with two brown longitudinal streaks radiating from tylus. Ecdysial suture pink. Scutellum and MWP apices darker brown. Abdomen red, with large ochreous spots running in transverse bands on terga, red along sutures and normally large, deep red circular patches above gland apertures; spots on venter indistinct, normally obscured by lateral ochreous bands or a red
suffusion; abdominal segments 9 and 10 dark-brown. Antennae dark-brown, articulations white and apex of A4 paler. Coxae and tibiae white. Femora dark-brown with narrowly pale apices. Tarsi brown, Ts1 often paler, particularly metathoracic pair. Rostrum brown, apex darker.

Note: one specimen, probably a teneral, was much paler than in the above description.

Structure: Squat, oval nymphs (Fig. 11). A2 shorter than A4. Vertex at least 4.1 x eye width. Pronotum at least 2 x as wide as long. Rostrum reaching metathoracic coxae.

x 7 specimens measured: GB85.39B.

**Macropternella Slater, 1957** (Cl. 9.10; Fig. 150)

Small, oval nymphs, with scattered simple pubescence on body and appendages. Eyes small and only slightly distanced from anterior pronotal margin. Tylus long, blunt and extending beyond apex of A1. Pronotum trapeziform, with indistinct, narrowly carinate, hyaline lateral margins; shallow anterior and posterior lateral impressions. MWP with lateral margins reflexed downwards and embracing body. Small, linked, gland apertures without evaporative areas, between T4-5 and T5-6 (Fig. 150). Suture T5-6 curving anteriad, remainder straight and all simple. Trichobothria indistinct and not figured. Spiracles indistinct (presumably spiracle 2 dorsal and spiracles 3-8 ventral). Prothoracic femur incrassate and mutic. Rostrum reaching mesothoracic coxae.


**Metopoplax Fieber, 1860** (Cl. 9.11; Figs 12, 151, 217)

Small, narrow to suboval, cylindrical, red, yellow and dark-brown nymphs with slender appendages. Head, pronotum, scutellum and prothoracic femur with scattered, slender, semi-erect, capitate pubescence and appendages with slender, semi-erect, simple setae. Eyes small and distanced from anterior pronotal margin by slightly less than their
width. Head elongate, large in proportion to pronotum. Tylus prominent and extending beyond first antennal segment apex. Pronotum trapeziform, lateral margins reflexed downwards and narrowly carinate. Scutellum large, with broadly rounded apex. MWP reaching T2-4. Terga with four longitudinal red stripes and red transverse bands along the sutures. Small, linked gland apertures, without evaporative areas between T4-5 and T5-6 (Fig. 151). Suture T5-6 curving anteriad, remainder all straight and simple. Spiracle 2 dorsal, 3-8 ventral, but not clearly visible. Trichobothria indistinct and not figured. Prothoracic femur with one large and one small antero-ventral apical spine (Fig. 217). Rostrum reaching between meso- and metathoracic coxae.


Metopoplax ditomoides (Costa, 1843) (Cl. 9.11.1; Figs 12, 151, 217)

Colour: Eyes red. Head dark-brown or red-brown, with black lateral margins between tylus and antennifer, yellow ecdysial suture and red venter. Pronotum, scutellum and MWP yellow-white, light-brown, with some red suffusion and two quadrate, long, red-brown marks on pronotal discs. Terga yellow with four longitudinal red stripes (middle pair sometimes faint), red lateral stripes along sutures and normally two, large, red oval marks above gland apertures. Sterna yellow with red, lateral stripes. Abdominal segments 9 and 10 brown to black. Antennae red-brown, A2 broadly yellow in mesal area. Coxae, trochanters, tibiae and Tsl yellow-white, sometimes with red suffusion on tibiae. Femora red-brown, yellow at bases and apices; Ts2 grey-red. Rostrum brown, apical segments darker.

Structure: Rostrum reaching metathoracic coxae.

x 3 measured: x 2 J89.12A; x 1 J89.18.

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Microplax (Microplax) Fieber, 1860 (Cl. 9.12.1; Figs 43, 152, 218)

Small, elongate, brown, yellow and red nymphs, with a broad lateral white band on abdominal segment 3. Head, pronotum, scutellum and MWP shining black. Body and appendages with moderately long, slender, capitate pubescence. Eyes small, distanced from anterior pronotal margin by up to one eye width. Tylus not particularly prominent, rounded apex extending beyond or to the apex of A1. Pronotum subquadrate, lateral margins slightly convex and not carinate. Scutellum with rounded apex. MWP reaching T2, lateral margins reflexed downwards and embracing body. Small, usually linked, gland apertures, with narrow evaporative areas between T4-5 and T5-6; anterior pair slightly smaller than posterior pair and sometimes slightly separated (Fig. 152). All sutures simple, T4-5 dipping slightly at the sides and T5-6 in the middle most distinctly anteriad, remainder straight. Spiracle 2 dorsal, 3-8 ventral. Trichobothria indistinct and not figured. Prothoracic femur incrassate with one medium sized antero-ventral spine and sometimes a second minute apical spine present (Fig. 218). Rostrum reaching mesothoracic coxae.


Microplax (Pseudomicroplax) plagiata (Fieber, 1837) (Cl. 9.12.1.1; Figs 43, 152, 218)

Colour: Eyes red. Head, pronotum, scutellum, MWP, abdominal segments 9 and 10 shining dark-brown. Abdomen red or sometimes paler pink with a continuous white lateral band on T3 and large, deeper red maculae above the evaporative areas; posterior macula considerably larger than the anterior. Appendages yellow-white, A1, A4, femora, except for bases and apices, R1 and most of R4 brown.

Structure: Small, with moderately slender appendages and scattered, erect, fine, long, capitate pubescence on body and some appendages; appendages also with simple setae. Eyes small, distanced from anterior pronotal margin by almost their width. Tylus rounded and only just extending
beyond apex of A1. Pronotum subquadrate, with very weak posterior transverse impression and downwardly reflexed lateral margins. Small, slightly separated, gland apertures, with a weak, narrow evaporative area between T4-5 and T5-6 (Fig. 152). Sutures between T4-5 moderately and T5-6 strongly curving anteriad, remainder straight and all simple. Spiracles very indistinct; 2 dorsal, 3-8 ventral. Trichobothria indistinct and not figured. Prothoracic femur with one very small antero-ventral spine (Fig. 218). Rostrum reaching mesothoracic coxae.

Neocamptotelus Hoberlandt, 1987 (Cl. 9.13)

No specimens available for study.

Oxycarenus Fieber, 1837 (Cl. 9.14; Figs 73, 153, 219)

Either small, pale bodied and glabrous or medium-small, with head, pronotum, MWP and scutellum black to brown, abdomen red and short, capitate pubescence. Eyes small, not distanced from anterior pronotal margin by more than their width. Tylus not normally extending beyond apex of A1 (except O. modestus?). Pronotum trapezoidal, with disc faintly impressed. Scutellum with slightly rounded apex. MWP reaching T2-4 and laterally reflexed downwards. Small gland apertures with narrow evaporative areas between T4-5 and T5-6, not separated by more than an aperture's width apart (Fig. 153). Sutures simple, T4-5 slightly, and T5-6 moderately curving anteriad, remainder straight. Trichobothria as Fig. 73. Spiracle 2 dorsal, 3-8 ventral. Prothoracic femur incrassate with 2-4 antero-ventral apical spines (Fig. 219). Rostrum reaching to at least metathoracic coxae.


Philomyrmex Sahlberg, 1848 (Cl. 9.15)

No specimens available for study.
Tropidophlebia Kerzhner, 1964 (Cl. 9.16)

No specimens available for study.

ARTHENEINAE STÅL, 1872

ARTHENEINI SLATER, WOODWARD & SWEET, 1962

Artheneis Spinola, 1837 (Cl. 10.1; Figs 154, 315)

Small, oval, almost glabrous, predominantly pale nymphs, with fairly slender, short appendages. Head moderately porrect and declivent; juga long, almost reaching apex of tylus, which extends to apex of A1. A1, and particularly A4, noticeably broader than A2 and A3. Maximum width of A4 2x maximum width of A3. Eyes touching anterior pronotal margin. Pronotum trapeziform, with carinate, convex, lateral margins, a straight posterior margin, slightly concave anterior margin, meso-longitudinal and transverse posterior impressions. MWP reaching T3-4. Narrow, slit-like, widely separated, gland apertures, with inconspicuous evaporative areas, between sutures T3-4, T4-5 and T5-6; distance apart of apertures decreasing slightly posteriad (Fig. 154). Sutures all straight and reaching abdominal margins, with a distinct lateral longitudinal furrow extending between sutures T2-3 and T4-5 (Fig. 315). Trichobothria indistinct and not figured. Spiracles indistinct; spiracle 2 dorsal, remainder ventral. Rostrum reaching between or beyond mesothoracic coxae. Prothoracic femur mutic and not incrassate.

Material examined: A. aegyptiaca/hyrcanica x 1.

Chilacis Fieber, 1864 (Cl. 10.2; Figs 13, 74, 155)

Medium-small, oval nymphs, with short appendages and an almost glabrous body. Pronotum, scutellum and MWP partly punctate. Head elongate, tapering toward a broad, long, apically blunt tylus. Juga long, narrow, not reaching apex of tylus. Antennal tubercles pronounced. Maximum width of A4 1.25x maximum width of A3. Eyes close to anterior pronotal margin. Pronotum trapeziform and narrowly carinate. Paired gland apertures between T4-5 and T5-6,
with a single aperture only between T3-4. Narrow evaporative areas surrounding intermediate and posterior apertures, anterior area very small and weak (Fig. 155). Sutures simple, indistinct and reaching abdominal margin. Spiracle 2 dorsal, 3-7 ventral and 8 absent. Trichobothrial hairs short and indistinct on T3 and T4 (Fig. 74). Rostrum reaching mesothoracic coxae. Prothoracic femur mutic and incrassate.

Material examined: C. typhae x 69.

Chilacis typhae (Perris, 1857) (Cl. 10.2.1; Figs 13, 74, 155)

Colour: Eyes red. Head, pronotum, scutellum and MWP light to dark-brown, punctures darker; interocular areas with limited red markings (masked in darker specimens); carinae, meso-lateral stripe on head, pronotal disc, mesal and basal areas of MWP all yellow. Abdomen yellow, with red maculae between evaporative areas, red along tergal sutures and in meso-lateral, longitudinal streaks on terga and sterna. Pleura yellow with brown margins. A1-3 and R1-3 and legs, coxae and trochanters yellow; A4 reddish brown, R4 brown-black, femora with brown median suffusion, Ts2 apically darker brown.

Note: Scottish material examined is much darker; appendages and pleura are dark-brown and abdominal red markings are more distinct.

Structure: Body with very short, sparse, semi-erect, adpressed, pale pubescence and terga almost glabrous. Longer, more dense setae on appendages. Mesothoracic tibia with longitudinal rows of short, dark spines; spines less pronounced on metathoracic tibia and absent from prothoracic tibia. Punctures present on scutellum and pronotum, except for disc, but becoming more scattered on MWP. Rostrum reaching between meso- and metathoracic coxae.

x 10 specimens measured: X.4 GB84.12A; x 2 GB85.69B; x 4 coll. I.C. Christie, 11.1987, Paisley Moss, Strathclyde.
**Holocranum Fieber, 1860** (Cl. 10.3; Figs 75, 156)

Medium-small, oval, pale nymphs with short appendages and an almost glabrous body. Head elongate, tapering into a long, apically blunt tylus; juga long and narrow, not reaching apex of tylus. Maximum width of A4 1.5x maximum width of A3. Pronotum trapeziform and narrowly carinate. Gland apertures, with narrow evaporative areas, between T3-4, T4-5 and T5-6; anterior evaporative area distinctly wider than subequal intermediate and posterior areas (Fig. 156). Sutures simple and all reaching abdominal margin. Spiracle 2 dorsal, 3-7 ventral and 8 absent. Trichobothrial hairs longer than for *Chilacis*. Trio of trichobothria on T3 clearly visible (Fig. 75). Prothoracic femur mutic. Rostrum reaching prothoracic coxae.

Material examined: *H. saturejae* x 34.

**PACHYGRONTHINAE STÅL, 1865**

**TERACRIINI STÅL, 1872**

**Cymophyes Fieber, 1870** (Cl. 11.1; Figs 76, 157, 220)

Medium-small, elongate, narrow, pale, yellow-white nymphs, with five faint, longitudinal brown stripes and short, stout appendages. Body with adpressed, pale, short, thickened, almost scale-like pubescence. Head porrect, non-declivent, antennifers and juga distinctive, tylus very pronounced and distinctly extending beyond apex of A1. A1 and A3 shorter than A2 and A4. Eyes touching anterior pronotal margin. Pronotum trapeziform, with five longitudinal impressions extending posteriad to scutellum and MWP. MWP long and narrow, reaching suture T3-4. Abdominal sides strongly scalloped and tapering inward posteriad. Indistinct, small, oval, almost contiguous gland apertures with narrow evaporative areas reduced to an apical sclerotized margin, between T4-5 and T5-6 (Fig. 157). All sutures simple and reaching abdominal margins; straight except for A7-8 and A8-9 which laterally curve anteriad. Trichobothrial hairs short and not visible in dorsal view. Trichobothria indistinct on S5 (Fig. 76). Spiracles all ventral. Prothoracic femur incrassate and
multi-spinose (Fig. 220). Rostrum reaching prothoracic coxae.

Material examined: C. ochroleuca x 2.

HETEROASTRINAE STÅL, 1872

Heterogaster Schilling, 1829 (Cl. 12.1; Figs 14, 15, 77, 78, 158, 221, 222).

Medium length, oval, brightly coloured nymphs, with relatively short, slender appendages. Head rounded, strongly convex in profile and tylus short, not extending to apex of A1. Pronotum trapeziform, lateral margins carinate, slightly concave, with sometimes weak, transverse impression. MWP reaching T3. Gland apertures small, slit-like on T4-5, T5-6 and absent from T3-4 (Fig. 158). Large subcircular evaporative areas on T3-4, T4-5 and T5-6; relative sizes variable, either (i) all equal, (ii) 4-5 and 5-6 equal or > 3-4 (iii) increasing in size posteriad. T4-7 and sometimes T3 with meso-lateral clusters or rows of black spots. All sutures simple and reaching abdominal margin, ventral sutures often laterally curving anteriad. Trichobothrial hairs very short (Figs 77, 78). Spiracles 2-8 ventral. Prothoracic femur not incrassate, with at most three antero-ventral, small, inconspicuous spines (Figs 221, 222). Rostrum reaching between pro- and metathoracic coxae.


Heterogaster artemisiae Schilling, 1829 (Cl. 12.1.3; Figs 14, 78, 158, 221)

Colour: Head, pronotum, scutellum and MWP predominantly black; posterior margin of pronotum broadly white; MWP with broad, subapical, transverse, yellow band. Pleura mainly black. Abdominal segments 1-2 cream, 3 cream and red, 8-9 black; T4-6 with broad meso-longitudinal cream stripe, apical third to half of T3 cream; S3-5 with broad cream mesal area, narrowing posteriad; T7 with anterior mesal black mark, S6 and S7 with large, quadrate, black, mesal
marks. A1-3 yellow; base of A1 and apex of A3 broadly brown, base of A2 and A3 narrowly brown; A4 brown. Femora dark-brown, apices yellow. Tibiae brown, lighter basally and apically. Ts2 apex and base of Ts1 brown, remainder of Ts1 yellow. Coxae pink with brown, trochanters and rostrum brown.

Structure: Body and appendages with short, semi-erect fairly sparse pubesence. Deep transverse pronotal impression. Prothoracic femur with two very small antero-ventral spines (Fig. 221).

x 6 specimens measured: x 1 GB85.61B; x 1 GB87.28; x 4 coll. G.E. Woodroffe, 08.1956, Swanage, Dorset.

Heterogaster urticae (Fabricius, 1775) (Cl. 12.1.7; Figs 15, 222)

Colour: Head, pronotum, scutellum and MWP brown-black (MWP browner), with variable, pale, yellow-white markings, normally as Fig. 15. Pleura mainly black. Abdomen yellow-white with red suffusion; red markings most pronounced between evaporative areas, along sutures, as lateral and diagonal streaks on terga, and on lateral -sternal margins; abdominal segments 8 and 9 predominantly black, T7 with meso-apical black mark, S6 and S7 with large quadrate mesal black blocks. A1 brown-black, apical third yellow-white; A2-4 yellow-brown with white articulations. Femora brown-black with broad, basal and narrow, apical yellow-white bands. Tibiae yellow-white with three brown bands. Tarsi pale, darker at bases and apices. Coxae and trochanters yellow-white. Rostrum brown-black, R2 and R3 with paler markings.

Structure: Dorsum and legs with long, dense, erect and suberecububesence, setae shorter on venter and antennae. Rostrum reaching between pro- and mesothoracic coxae. Prothoracic femur armed with one to three, but normally two, antero-ventral spines (Fig. 222).

x 10 specimens measured: x 1 coll. T. Eccles, 09.1985, Clarke Gardens, Liverpool; x 7 coll. G.E. Woodroffe (GEW), 03.09.1953, Greatfield and x 2 coll. GEW, 17.10.1956, P.I.L.
**Platyplax Fieber, 1860** (Cl. 12.2; Figs 79, 159)

Medium length nymphs, with very short pubescence, slender appendages and a broadly oval, almost spherical abdomen, with lateral red and white, sometimes faint, striped bands. Tylus short, not reaching apex of A1. Head rounded between tylus and eyes. Eyes touching anterior pronotal margin. Pronotum trapeziform, noticeably wider than long, with carinate, strongly convex lateral margins and a very weak transverse impression. Head, pronotum, scutellum and MWP punctate. MWP reaching T3. Gland apertures separated by less than 2 x their width, between T4-5 and T5-6. Evaporative areas on T3-4, T4-5 and T5-6; posterior and intermediate areas oval and equal sized, distinctly larger than anterior area which is mainly anteriad of suture (Fig. 159). Evaporative areas normally only dark at perimeter. T3-6 with meso-lateral rows of black spots. S2-7 and T8 with meso-lateral clusters of black spots. All sutures simple. Trichobothrial hairs very short. Trichobothria as Fig. 79. Spiracles 2-8 ventral. Prothoracic femur mutic and not incrassate. Rostrum reaching between meso- and metathoracic coxae.

Material examined: P. salviae x 21.

**RHYPAROCROMINAE AMYOT & SERVILLE, 1843**

**PLINTHISINI SLATER & SWEET, 1961**

*Plinthisus Stephens, 1829* (Cl. 13.1.1; Figs 16, 80, 160, 223, 291, 330)

Small, shining bugs with small eyes. Head convex, sunk into anterior of pronotum and with distinct trichobothria. Tylus not quite reaching apex of A1. Pronotum carinate and not bilobed. Slit-like gland apertures, with narrow evaporative areas, between T3-4, T4-5 and T5-6. All sutures simple and reaching margin of abdomen; T4-5, moderately, and T5-6 strongly curving anteriad. Spiracles all ventral, but often indistinct. Trichobothria on S7 widely separated with one below the other, posterior pair on S6 similarly positioned, but closer together and
posterior pair on S5 very close (relative positioning and length of trichobothrial hairs on S3 and S4 difficult to assess and not figured) (Fig. 80). Prothoracic femur strongly incrassate and spinose (Fig. 223). Prothoracic tibia spatulate at apex (Fig. 330).

Material examined: *P. brevipennis* x 8. *Plinthisus* sp. x 8.

*Plinthisus brevipennis* (Latreille, 1807) (Cl. 13.1.1.5; Figs 16, 80, 160, 223, 291, 330)

Colour: Eyes red. Head, pronotum, scutellum and MWP dark-brown, shining and semi-translucent; antennifers dirty-white and ecdysial suture pale. Terga pink or sometimes red, with white meso-ventral spots and white along sutures. Sterna pink, yellow-pink, or red, with white along sutures. Last four abdominal sutures with dark-brown markings. Appendages yellow-brown, A4 and occasionally legs yellow-black; coxae, trochanters and femoral apices pale.

Structure: Eyes touching anterior pronotal margin, but not extending to antero-lateral pronotal angles. Pronotum almost quadrate, antero-lateral angles produced forwards, anterior margin strongly concave, with a weak, meso-anterior chevron-shaped impression and postero-lateral margins sometimes very slightly concave. MWP just reaching T3 or extending to the centre of T4. Separation of paired gland apertures and width of evaporative areas increasing posteriad (Fig. 160). Long trichobothrial hairs on head and abdomen; abdominal trichobothrial hairs clearly visible in dorsal view. Very long, slender trichobothria-like setae arising from eyes (Fig. 291) and from basal edge of prothoracic tibia (Fig 330), which also has an inner row of small spined teeth. Body with scattered, very short pubescence and appearing almost glabrous; longer, semi-erect setae on antennae and short, semi-erect spines on tibiae. Prothoracic femur with two small antero-ventral spines (Fig. 223). Rostrum reaching between meso- and metathoracic coxae.

x 4 specimens measured: x 1 GB85.65B; x 2 GB86.48; x 1 GB87.33.
ANTILLOCORINI ASHLOCK, 1964

Homoscelis Horváth, 1884 (13.2.1)

No specimens available for study.

Tropistethus Fieber, 1860 (Cl. 13.2.2; Figs 17, 81, 161, 224)

Small, brown and red bodied nymphs, widest towards apex of MWP, with long legs, stout antennae and rostrum. Eyes small, almost touching anterior pronotal margin and with short setae. Tylus slender, apex reaching just beyond midpoint of A1. Cephalic trichobothrial hairs long. Pronotum almost rectangular, carinate and without a transverse impression. MWP reaching T3-4. Gland apertures with narrow evaporative areas between T3-4, T4-5 and T5-6; anterior pair distinctly closer together than intermediate and more widely separated posterior pair (Fig. 161). Y-suture absent, T3-4 and T4-5 possibly, but not definitely grooved. T5-6 in the middle curving distinctly anteriad. S4-5 curving sharply anteriad, embracing the trichobothrium and directed posteriad, not reaching abdominal margin.

Trichobothrial hairs long and visible in dorsal view. Trichobothria arranged in a linear row on S5 (relative positions and trichobothrial hair length difficult to determine on S3 and S5) (Fig. 81). Spiracles ventral and spiracle on S5 just positioned between posterior trichobothria. Prothoracic femur incrassate and multi-spinose on antero-ventral edge (Fig. 224).

Material examined: T. holosericeus x 9. Tropistethus sp. x 3.

Tropistethus holosericeus (Scholtz 1846) (Cl. 13.2.2.3; Figs 17, 81, 161, 224)

Colour: Eyes red. Head, pronotum, scutellum and MWP shining, almost translucent brown, with paler patches adjacent to eyes and on tylus. Pleura brown and white. Abdomen pink to red, often deeper red between evaporative areas, pale along tergal sutures and sometimes a distinct round, white spot or spots present in meso-lateral area of

Structure: Body, legs and antennae with medium length, semi-erect, pale pubescence. Tibiae with short slender spines. Prothoracic femur with 5-7 small spines on antero-ventral edge, a ventral groove and a distal spine. Head, pronotum, scutellum and MWP with shallow punctures. Rostrum reaching beyond mesothoracic coxae and normally to metathoracic coxae.

x 7 specimens measured: x 2 GB86.47; x 5 GB87.18A.

LETHAEINI STÅL, 1872

Camptocera Jakovlev, 1877 (Cl. 13.3.1)

No specimens available for study.

Lethaeus Dallas, 1852 (Cl. 13.3.2; Figs 82, 162, 225, 316)

Large, brown, oval nymphs with slender legs and very slender antennae. Eyes small, almost touching anterior pronotal margin. Apex of tylus only reaching half-way along A1. Cephalic trichobothrial hairs shorter than eye width. Pronotum trapezoidal, transverse impression absent and with distinct upwardly reflexed carinate lateral margins. MWP reaching to T3. Gland apertures with elongate evaporative areas between T3-4 and T4-5; apertures in each pair widely separated but distance between two pairs very short and evaporative area absent posteriad of suture (Fig. 162). Posterior scent gland apertures vestigial, with a very small, elongate evaporative area between T5-6 (apertures present and open in instar 4 nymphs). Y-suture absent, all sutures deep and well pronounced; T3-4 curving anteriad at lateral margin (Fig. 316), T3 consequently very narrow, S4-5 curving posteriad and not reaching abdominal margin (Fig. 316). Terga with a shallow, broad, meso-lateral, longitudinal trough (Fig. 316). Trichobothrial hairs moderately long. Trio of trichobothria on S5 in a linear row, the spiracle positioned immediately posteriad to the anterior pair which are widely distanced from the posterior
trichobothrium (Fig. 82). All spiracles ventral.
Prothoracic femur mildly incrassate and multi-spinose (Fig. 225). Rostrum reaching metathoracic coxae.

Material examined: L. cribratissimus x 6.

**STYGNOCORINI GULDE, 1936**

*Acompus Fieber, 1860 (Cl. 13.4.1; Figs 44, 83, 163, 226, 298)*

Medium-small, oval, red and black nymphs with slender appendages. Head declivent, noticeably wider than long, with very short trichobothrial hairs. Eyes projecting laterally beyond and slightly distanced from antero-lateral pronotal margin. Tylus short, rounded and not reaching apex of A1. A1 broader than A2-3. Pronotum with distinctly upwardly reflexed, carinate, sinuate, lateral margins (Fig. 298). MWP carinate and reaching suture T2-3 (micropters) or T3-4 (macropters). Slit-like gland apertures with large, black, shining evaporative areas between T3-4, T4-5 and T5-6; anterior apertures more widely separated and evaporative area larger, than equal sized intermediate and posterior pairs. Y-suture present, distinctly troughed sutures between S2-3 and S3-4, S4-5 clearly embracing trichobothrium on S5 and only faintly reaching abdominal margin. Trichobothria as Fig. 83, anterior trichobothrium on S5 close to suture. Spiracles all ventral. Prothoracic femur with one minute spine and setae on antero-ventral edge (Fig. 226). Rostrum reaching between pro- and meso- to metathoracic coxae.

Material examined: A. australis x 5. A. pallipes x 2*. A. rufipes x 11.

*Acompus rufipes* (Wolff, 1804) (Cl. 13.4.1.6; Figs 44, 83, 163, 226, 298)

Colour: Eyes red. Head, pronotum, pleura, scutellum and MWP black and shining, a with red ecdysial suture and yellow MWP carinae. Abdomen orange-red, occasionally red-brown; darker between evaporative areas, lighter orange-yellow along sutures; abdominal segments 9 and 10 black, T8
and S6-8 with meso-basal black markings. Legs dark-brown; Tsl, femora and tibial apices ochreous; coxae and trochanters ochreous with brown. Antennae variable; occasionally dark-brown, with pale articulations, but normally A1 and A4 dark-brown, A2 yellow with narrow apical and basal brown bands and A3 yellow, with apices narrowly brown or sometimes all dark-brown.

Structure: Body with very short, adpressed, sparse, pale pubescence and slightly longer, semi-erect setae on appendages. Evaporative areas elongate (Fig. 163). Prothoracic femur with fine setae and single antero-ventral spine occasionally absent (Fig. 226). Rostrum reaching between pro- and mesothoracic coxae.

x 10 specimens measured: GB86.63A.

_Acompus pallipes_ (Herrich-Schaeffer, 1833) (Cl. 13.4.1.5)


x 2 specimens measured: Y89.56.

_Hyalochilus_ Fieber, 1860 (Cl. 13.4.2; Figs 84, 164, 227)

Small, oval, distinctively marked nymphs, with a pale-spotted, brown abdomen and short, adpressed pubescence. Head declivent, trichobothria absent and tylus short, not extending to apex of A1. Eyes almost touching antero-lateral pronotal margin. Pronotum trapeziform, with two weak transverse impressions and upwardly reflexed lateral
carinate margins. MWP almost reaching T3-4. Equally spaced gland apertures and equal sized, elongate, transversely oblong evaporative areas between T3-4, T4-5 and T5-6 (Fig. 163). Y-suture present, S2-3 and S3-4 deeply grooved, all sternal sutures reaching abdominal margin, with S4-5 also embracing trichobothrium (Fig. 84). Trichobothrial hairs long and visible in dorsal view. Trichobothria arrangement on S4 indistinct. All spiracles ventral. Prothoracic femur with one small antero-ventral spine (Fig. 227). Rostrum reaching between meso- and metathoracic coxae.

Material examined: H. ovatulus x 23.

Lasiosomus Fieber, 1860-61 (Cl. 13.4.3; Figs 18, 85, 165, 299)

Medium length, oval, shining, pale nymphs, with long, erect, fine pubescence. Head declivent and trichobothrial hairs indistinct amongst other setae. Tylus slender, extending beyond juga and not reaching apex of A1. Eyes almost touching antero-lateral pronotal margin. Pronotum with upwardly reflexed carinate, weakly sinuate, lateral margins and a broad, shallow, postero-transverse impression (Fig. 299). MWP reaching to T3. Gland apertures present between T3-4, T4-5 and T5-6, with large, almost quadrate evaporative areas; intermediate and posterior areas equal sized and slightly smaller then anterior area (Fig. 165). Y-suture present but weak; S2-3 and S3-4 deep and troughed, S4-5 curving posteriadi and not reaching lateral pronotal margin. Trichobothrial hairs long and visible in dorsal view. Anterior trichobothrium on S5 positioned almost mid-way between spiracles (Fig. 85). All spiracles ventral. Prothoracic femur mutic. Rostrum reaching to mesothoracic coxae.

Material examined: L. enervis x 1.

Lasiosomus enervis (Herrich-Schaeffer, 1835) (Cl. 13.4.3.1; Figs 18, 85, 165)

Colour: Eyes red. Head, pronotal and MWP carinae yellow. Pronotum, scutellum and MWP brown. Abdomen off-white with pink markings, particularly between evaporative areas and
meso-laterally on terga; T7 with small, S7 and S8 with large, brown mesal marks, segments 8 and 9 mainly brown. Evaporative areas shining and dark-brown. Appendages yellow; A4 brown, base and apex of A3 and apex of A2 narrowly brown; R4 apically dark-brown.

Structure: As generic description.

x 1 specimen measured: SP89.5.

Stygnocoris Douglas & Scott, 1865 (Cl. 13.4.4; Figs 19, 20, 86, 166, 300, 319, 320)

Medium-small, oval, red and brown-black nymphs. Head declivent and tylus short, not reaching to apex of A1. Medium length cephalic trichobothrial hairs difficult to see in hirsute species. Eyes almost touching antero-lateral edge of pronotum. Pronotum with carinate, almost straight lateral margins and no lateral impression (Fig. 300). MWP reaching T3. Head, pronotum, scutellum and MWP punctate. Small, slit-like gland apertures, with large evaporative areas, between T3-4, T4-5 and T5-6. Anterior gland apertures more widely spaced and with distinctly larger evaporative area than intermediate and posterior pairs, which are almost equal in proportion (Fig. 166). Y-suture present; S2-3 and S3-4 deeply grooved, S4-5 curving posteriad and not reaching abdominal margin (Fig. 86). Trichobothrial hairs long, visible in dorsal view (Fig. 86). Spiracles all ventral. Prothoracic femur slightly incrassate, mutic, but with ventral row of tuberculate setae. Rostrum reaching between meso- and up to metathoracic coxae.

Material examined: S. fuligineus x 61. S. rusticus x 6. S. sabulosus x 104. Stygnocoris sp. x 18.

Stygnocoris fuligineus (Geoffroy, 1785) (Cl. 13.4.4.3; Figs 19, 319)

Colour: Eyes red. Head, pronotum, scutellum, MWP and pleura brown to brown-black; posterior pronotal corners, pronotal and MWP carinae yellow-brown. Ecdysial suture yellow. Abdomen predominantly red with sterna becoming paler.
mesally; off-white along Y-suture, sutures T4-5, T5-6 and adjacent to evaporative areas, the latter occasionally faintly extending laterally to abdominal margin. Evaporative areas, abdominal segments 9 and 10, mesal markings on S7 and S8 all brown-black. Legs and rostrum brown; femoral apices, bases and apices of tibiae and all Ts1, yellow-white. Antennae brown-black, apex of A4 paler and articulations yellow-white.

Structure: Body and appendages with medium-short, pale, adpressed, dense pubescence (Fig. 319). Cephalic trichobothrial hairs short and difficult to see. Paired posterior trichobothria on S6 in line and parallel to suture 6-7. Rostrum just reaching C3.

x 10 specimens measured: x 1 GB85.22B; x 2 GB85.49; x 4 GB87.14; x 2 GB87.18A,B; x 1 GB87.27.

*Stygnocoris rusticus* (Fallén, 1807) (Cl. 13.4.4.5; Figs 86, 166)

Colour: Eyes red. Head, pronotum, scutellum, MWP and pleura shining black; ecdysial suture, pronotal and MWP carinae yellow. Abdomen red-pink or occasionally yellow-red, with red markings along sutures; sterna becoming yellowish postero-mesally; evaporative areas, abdominal segments 9 and 10 and mesal markings on S6-8 shining black. Legs yellow, with faint yellow-brown markings on femora and Ts2 apices. A1 and A4 brown-black in basal half, becoming paler apically; A2-3 yellow. R1 and R4 black; R2 and R3 yellow-brown.

Structure: Head, pronotum and scutellum with medium length, pale, semi-erect to erect pubescence; setae becoming more adpressed on remainder of body and appendages. Posterior trichobothrial pair on S5 not one above the other and parallel to S5-6 (Fig. 86); top trichobothrium slightly more anterior than bottom trichobothrium (Fig. 86). Rostrum reaching to metathoracic coxae.

x 5 specimens measured: x 1 GB85.46A; x 2 GB86.20B; x 1 GB86.29B; x 1 GB87.19.
Stygnocoris sabulosus (Schilling, 1929) (Cl. 13.4.4.6; Figs 20, 320)

Colour: Eyes red. Head pronotum, scutellum, MWP and pleura brown to dark-brown; ecdysial suture, extreme basal corner of pronotum, pronotal and MWP carinae yellow. T1-3 red, sometimes with yellow-brown and yellow-white along Y-suture. T4-8 with yellow-white along sutures and in midsternal transverse bands, or spots; yellow-white banding normally contrasting boldly with red of abdomen, sometimes faint but always distinct. Evaporative areas, abdominal segments 9 and 10 and mesal markings on S6-8 dark-brown. Legs yellow-brown to brown; femora and tibiae with broad basal and apical white bands, tarsi normally white with apex of all Ts2 brown and occasionally all segments brown. Coxae and trochanters mainly white. Antennae dark-brown, A4 paler apically and articulations white. Rostrum brown with apices of R1-3 broadly white.

Structure: Head, pronotum and scutellum with moderately long, dense, pale, suberect pubescence (Fig. 320); setae becoming more adpressed on rest of body and appendages. Cephalic trichobothrial hairs long and clearly visible. Trichobothria on S5 as for S. rusticus. Rostrum reaching between mesothoracic coxae and sometimes to metathoracic coxae.

x 10 specimens measured: x 5 GB85.36; x 5 GB86.36B.

Stygnocorisella Hoberlandt, 1956 (Cl. 13.4.5)

No specimens available for study.

PHASMSOMINI KIRITSHENKO, 1938

Phasmosomus Kiritschenko, 1938 (Cl. 13.5.1)

No specimens available for study.
Drymus Fieber, 1860 (Cl. 13.6.1; Figs 21-24, 87, 167-171, 228-234, 301, 302)

Small to medium sized, yellow to brown nymphs with pinky-grey abdomens. Head moderately declivent with tylus extending to, or beyond, mid-point of A1, but never to apex; eyes small, close to anterior pronotal margin, trichobothrial hairs long and clearly visible. Pronotum trapeziform to quadrate, with somewhat swollen anterior lobe, weak posterior transverse impression and carinate upwardly reflexed, sinuate, lateral margins. MWP reaching between T2 and T3 base. Small gland apertures, with large evaporative areas, between T3-4, T4-5 and T5-6 (Figs 167-171); anterior gland apertures more widely separated and their surrounding evaporative area more elongate, than for subequal intermediate and posterior pairs. Y-suture present and faintly highlighted with pale border; T4-5 and T5-6 directed anteriad, S2-3 and S3-4 deeper than other ventral sutures; S4-5 curving anteriad around trichobothrium and not reaching abdominal margin (Fig. 87). Trichobothrial hairs long and visible in dorsal view. Posterior pair of trichobothria on S5 anterior to spiracle, one above the other and close to anterior trichobothrium, which is just posteriadi from spiracle 4 (Fig. 87). Spiracles all ventral; spiracles 3 and 4 sometimes lateral, or closer to abdominal margin than others. Prothoracic femur incrassate with at least one small spine (Figs 228-234). Tibiae with additional long, erect setae in Drymus sensuo stricto, but only short setae in Sylvadrymus sg. Rostrum reaching between meso- to metathoracic coxae.

**Drymus s.s.**

**Drymus latus, Douglas & Scott, 1871** (Cl. 13.6.1.1; Figs 167, 228)

Colour: Eyes black with red margin. Head, pronotum, scutellum, MWP and pleura shining yellow; scutellum yellow-brown mesally and MWP dark-brown. Abdomen grey with segments 9 and 10, mesal patches on S6-9 and trichobothrial fields dark-brown. Legs and rostrum yellow; coxae and trochanters white, apices of trochanters and apical half of A4 black. A1 and A2 yellow-brown, with darker apices; A3 and A4 dark-brown and all articulations white.

Structure: Body, except for pleura, with long, fine, erect and semi-erect pubescence. Tibiae with short stout setae and fine setae, as long as tibial width. Head moderately porrect, tylus reaching two-thirds along A1. A2 longer than other antennal segments. Lateral margins of pronotum slightly concave in line with weak pronotal impression. MWP just reaching T3. Prothoracic femur incrassate, with one small antero-ventral spine (Fig. 228). Rostrum reaching metathoracic coxae.

x 1 specimen measured: GB88.20.

**Drymus pilicornis (Mulsant & Rey, 1852)** (Cl. 13.6.1.4; Figs 168, 229)

Colour: Eyes red with dark centre. Head, pronotum, scutellum, MWP and pleura shining and predominantly yellow; 'V' shaped anterior pronotal marking, mesal area of scutellum, MWP apices and pleural margins all brown. Abdomen pink or sometimes red, paler along sutures and towards margins; evaporative areas, segments 6,9 and 10, mesal marks on S6-8 and trichobothrial fields dark-brown to black. Legs yellow-brown; femora with white apices and prothoracic femur more yellow. Coxae white, trochanters yellow with black apices. A1, basal two-thirds of A2 and apex of A4 yellow-brown; apical third of A2 brown, A3 and basal third of A4 brown-black and all antennal articulations white. Rostrum yellow-brown, with brown-black markings mainly on R1 and apex of R4.
Structure: Pubescence as *D. latus*. Tylus reaching two-thirds along A1. Lateral pronotal margins slightly concave, posterior to weak transverse impression. MWP just reaching T3. Spiracle 4 closer to lateral abdominal margin than other spiracles. Prothoracic femur incrassate with one small and 2-4 very small antero-ventral spines (Fig. 229). Rostrum reaching between meso- and metathoracic coxae.

x 4 specimens measured: GB87.20.

**Drymus pilipes** Fieber, 1861 (Cl. 13.6.1.5; Figs 21, 169, 230)

Colour: Eyes black, with narrow outer red ring. Head, pronotum, scutellum and MWP shining. Head, pronotum, pleura and outer margin of scutellum yellow, or deep yellow to orange; pronotal disc normally in part light-brown, posterior margin brown, to dark-brown and pleura black edged. MWP and remainder of scutellum dark-brown, MWP becoming black at apices and sometimes lighter mesally. Abdomen pink-red laterally and along sutures; evaporative areas, segments 6, 9, 10, and mesal marks on S6-8 black. Legs and rostrum yellow; tibiae with faint brown suffusion, sometimes quite brown, R1 and R4 tinged with black. Coxae white, trochanters ochreous with black apices. Antennae dark-brown with white articulations, basal half of A1 and apex of A4 yellow-brown.

Structure: Pubescence as *D. latus*, but pronotal disc somewhat glabrous and pleura with scattered, short, adpressed setae. Head porrect and tylus reaching mid-point of A1. A2 longer than other antennal segments. Spiracle 4 closer to abdominal margin than other spiracles. Prothoracic femur incrassate, with one medium-small and 4-6 small, antero-ventral spines (Fig. 230). Rostrum reaching between meso- and metathoracic coxae, or up to metathoracic coxae.

x 5 specimens measured: GB87.20.
Sylvadrymus Le Quesne, 1956 (Cl. 13.6.2.1)

Drymus brunneus (Sahlberg, 1848) (Cl. 13.6.1.7; Figs 22, 170, 231, 301)

Colour: Eyes red. Head, pronotum, scutellum, pleura, MWP apices mainly brown, markings sometimes contiguous on MWP and scutellum. Trichobothrial fields, ecdysial suture, posterior quarter of pronotum, carinae and remainder of MWP all yellow. Pleura margined with black. Abdomen pinky-grey to pale red, sometimes yellow and becoming paler at margins; red markings along sutures and between evaporative areas, sometimes faint or absent; evaporative areas, abdominal segments 9 and 10, mesal patches on S6-8 and trichobothrial fields brown. Appendages yellow; femora and Ts2 faintly brown, basal half of A1, A3, A4, R1 and apex of R4 brown; apices of A2 sometimes dark, and A4 sometimes yellow to yellow brown; antennal articulations and femoral apices white.

Structure: Body and legs with short, adpressed, pale pubescence and a few short, semi-erect, scattered setae on pronotum, scutellum and MWP. Antennal setae longer, semi-erect, becoming erect on A4. Tibiae with short, adpressed and semi-erect, stout setae, all shorter than tibial width. Tylus reaching just beyond mid-point of A1. Pronotum with lateral margins strongly concave (Fig. 301), body widest at T2-3 and strongly bulging posterior to pronotum. Spiracle 4 lateral. A2 longer than other segments. Prothoracic femur with one short antero-ventral spine (Fig. 231). Rostrum reaching to mesothoracic coxae or between meso- and metathoracic coxae.

x 10 specimens measured: x 3 GB85.36; x 2 GB85.53; x 1 GB86.13; x 1 GB86.56; x 3 GB86.65.

Drymus pumilio Puton, 1877 (Cl. 13.6.1.8; Figs 23, 232)

Colour: Eyes red. Head, pronotum, scutellum, MWP and pleura yellow-brown; slightly darker between eyes and tylus, on apex and base of pronotum, mesal and apical areas of MWP. Abdomen yellow-grey, with red suffusion; evaporative area margins, segments 9 and 10, mesal patches on S6-8 and
trichobothrial fields brown. Legs, trochanters and rostrum yellow; coxal and femoral apices white, R1 and R4 with brown suffusion. Antennae brown-black, with white articulations.

Structure: Pubescence as D. brunneus. Tylus almost reaching apex of A1. A2 shorter than A4. Pronotal sides faintly concave. MWP reaching T3. Spiracle 3 lateral. Prothoracic femur incrassate with one small antero-ventral spine (Fig. 232). Rostrum reaching between meso- and metathoracic coxae.

x 4 specimens measured: GB87.26.

**Drymus ryei** Douglas & Scott, 1865 (Cl. 13.6.1.9; Fig. 233)

As D. sylvaticus. Vertex > 5 x eye width.

x 3 specimens measured: x1 GB85.30; x1 GB86.73; x1 GB87.18B.

**Drymus sylvaticus** (Fabricius, 1775) (Cl. 13.6.1.10; Figs 24, 87, 171, 234, 302)

Colour: Eyes red. Pronotum, scutellum, MWP and pleura yellow-brown. Trichobothrial fields and ec dysial suture yellow-white, carinae and normally centre of disc yellow. Head, MWP apices and pleural margins brown-black. Abdomen yellow-grey, pale along sutures and sometimes with faint red suffusion, particularly between evaporative areas. Evaporative areas, segments 9-10, centre of S6-8 and trichobothrial fields dark-brown. Legs yellow, with faint brown suffusion. Ts2 yellow-brown and femoral apices white. Antennae very variable; sometimes all brown-black apart from articulations, but normally with basal half of A2 and apical two-thirds of A4 yellow brown, with white articulations.

Structure: Body with very short, stub-like, adpressed, semi-erect pubescence. Setae longer, semi-erect and adpressed on legs. Tibiae with stouter setae, all noticeably shorter than tibial width. Antennal setae suberect and erect, longest on A4. Tylus reaching just
beyond mid-point of A1. Lateral pronotal margins at most only slightly concave (Fig. 302). MWP reaching T3-4. Spiracle 4 not lateral, but closer to abdominal margin than other spiracles (Fig. 87). Prothoracic femur incrassate, with one small and four very small antero-ventral spines (Fig. 234). Rostrum reaching mesothoracic coxae.

x 10 specimens measured: x 2 GB85.23A; x 3 GB86.42; x 1 GB86.47B; x 2 GB86.69; x 2 GB87.31.

Eremocoris Fieber, 1860 (Cl. 13.6.2; Figs 25, 88, 172, 235-238, 303, 304)

Medium sized, yellow, brown, cream and red nymphs, with long, slender appendages and often long pubescence. Eyes small and not touching anterior pronotal margin. Head strongly porrect, with long, truncate antennifers, long trichobothrial hairs and a slender tylus, extending well beyond juga, but not even reaching mid-point of long A1. Pronotum trapeziform to quadrate, with distinct, upwardly reflexed carinate margins, a weak latero-posterior impression and sometimes slightly globose anterior lobes. MWP reaching T3. Slit-like gland apertures, with short, wide evaporative areas, between T3-4, T4-5 and T5-6; anterior gland apertures more widely separated than other pairs and with a larger evaporative area (Fig. 172). Y-suture distinct and with broad, white margins; sutures T4-5 and T5-6 directed strongly anteriad and T4-5 positioned close to T3-4 at abdominal margin. S2-3 and S3-4 deeper than other ventral sutures, S4-5 curving strongly anteriad, looping around trichobothrium and then directed posteriad, not reaching abdominal margin. Trichobothrial hairs long and visible in dorsal view. Posterior pair of trichobothria on S5 anterior to spiracle 5, positioned one above the other and close to anterior trichobothrial field which is just posteriad from S4 (Fig. 88). All spiracles ventral. Prothoracic femur incrassate, multi-spinose, with one or two large spines and many small spines on antero-ventral edge (Figs 235-238). Prothoracic tibia with a row of short, tuberculate setae. Rostrum reaching beyond metathoracic coxae.

Material examined: E. abietis x 4. E. fenestratus x 2. E.
Eremocoris abietis (Linnaeus, 1758) (Cl. 13.6.2.1; Fig. 235)

Colour: Eyes red. Head, pronotal discs, MWP apices and pleural margins dark-brown; juga, apex of tyulus, remainder of pronotum, scutellum and pleura yellow to yellow-brown; black between eye and ecdysial suture. Abdomen predominantly red, faintly white along sutures, with a latero-longitudinal white stripe and the remainder as E. podagricus. Legs brown, apart from yellow femoral apices and Tsl. Antennae brown-black; A1, basal third of A2 brown and articulations white.

Structure: Body and appendages with short, adpressed pubescence. Head, pronotum and MWP with a few long, erect, fine setae. Fine spines on coxae, tibiae and A1. Pronotum almost quadrate, with straight lateral margins. Prothoracic femur with one large, 3-4 apical and 3-6 basal spines on antero-ventral edge and a row of small spines on postero-ventral edge (Fig. 235). Prothoracic tibia with a row of stout, short spines. Rostrum reaching S4.


Eremocoris fenestratus (Herrich-Schaeffer, 1839) (Cl. 13.6.2.2; Fig. 236, 303)

Colour: Eyes white. Head, pronotum, scutellum, MWP and pleura brown; occipital region, pronotal disc and pleural margins brown-black; carinae yellow-brown and apex of head, except for tyulus base, yellow. Abdomen predominantly pink-brown; narrowly white at margin and faintly white along sutures, the remainder as E. podagricus. Legs brown; femoral apices and tibial bases paler with all Tsl yellow. A3, A4, apical half of A2, extreme base and apex of A1 brown-black, remainder yellow. Rostrum yellow, apex of R4 black.

Structure: Body and appendages with short, adpressed pubescence and long, fine, scattered, erect setae on head,
pronotum, scutellum and metathoracic tibia. Antennal apices with a few semi-erect, short setae. A1, pro- and mesothoracic tibiae with short, fine spines. Pronotum almost quadrate, lateral margins straight in posterior half (Fig. 303). Prothoracic femur incrassate, with one large, five apical, three basal antero-ventral spines and a row of small spines on postero-ventral edge (Fig. 236). Rostrum reaching S3.


**Eremocoris plebejus (Fallén, 1807)** (Cl. 13.6.2.6; Fig. 237)

Colour: Head, pronotum, scutellum, MWP and propleura brown; darker-brown anterior to eyes, on pronotal disc and MWP apices; tylus, anterior two thirds of pronotal carinae, lateral areas of MWP, meso- and metapleura yellow. Abdominal markings similar to *E. podagricus*, but brighter red. Prothoracic femur, excepting apices, apical halves of meso- and metathoracic femora all brown, remainder white. Tibiae brown; pro- and mesothoracic tibiae broadly white at bases and narrowly so at apices, metathoracic tibia narrowly pale at base and apex. Ts1 and base of Ts2 white, remainder brown. Coxae and trochanters white, with trochanter apices black.

Structure: Body with long, pale, semi-erect pubescence; shorter and adpressed on MWP, becoming sparse or absent on head, pronotal disc, scutellum, MWP and pleura. Legs with adpressed to semi-erect setae, longer erect setae on prothoracic femur, meso- and metathoracic tibiae. Antennal setae short and adpressed. Pronotal disc faintly punctate and lateral margin slightly concave in mid-length. Prothoracic femur incrassate, with one large, seven small, antero-ventral spines and three very small, postero-ventral spines (Fig. 237). Prothoracic tibia with a row of short, stout spines. Rostrum just reaching beyond metathoracic coxae to S3.

Eremocoris podagricus (Fabricius, 1775) (Cl. 13.6.2.7; Figs 25, 88, 172, 238, 304)

Colour: Eyes red. Head, pronotum, scutellum, MWP and pleura light matt-brown; becoming more yellow on carinae, lateral margins of head and MWP, anterior pronotal margin, band along pronotal impression and sometimes scutellum base; antennifers edged with black. Abdomen dull-brown or pruinose red-brown; cream along sutures, around evaporative areas and along antero-lateral margins of terga; evaporative areas, segments 9,10, mesal marks on S7, S8 and trichobothrial fields dark-brown. Femora yellow; tibiae yellow-brown; tarsi yellow, with pro- and mesothoracic Ts2 brown, sometimes metathoracic Ts2 or apices of all Ts2 black. Coxae creamy-white. Trochanters yellow, apices of meso- and metathoracic trochanters black. R1 light brown, R2-3 yellow and R4 apically black. A1, basal half of A2 and apical half of A4 yellow, remainder brown-black with articulations pale.

Structure: Body with long and shorter, erect, fine pubescence. Setae on legs moderately long, semi-erect and adpressed. Antennal setae short and adpressed, except for a few longer, semi-erect setae at apices. Lateral pronotal margin slightly concave in the posterior half (Fig. 304). Prothoracic femur incrassate, with one large, 5-11 smaller antero-ventral spines, and 3-6 very small postero-ventral spines (Fig. 238). Prothoracic tibia with four conspicuous basal spines and a series of minute spines. Rostrum reaching S3-4.

x 10 specimens measured: x 1 GB86.38D; x 4 GB86.41A; x 2 GB86.65; x 2 GB86.67B; x 1 GB87.24.

Gastrodes Westwood, 1840 (Cl. 13.6.3; Figs 26, 89, 173, 239, 240, 305, 306)

Medium-large, broadly oval, strongly dorso-ventrally compressed, brown nymphs, with slender appendages. Body and appendages with short, adpressed pubescence. Eyes small and distanced from antero-pronotal margin by less than their width. Head strongly porrect, tylus slender, not reaching apex of A1, antennifers pronounced and trichobothrial hairs
short. Pronotum trapezoidal with distinctly carinate lateral margins, concave in posterior third. MWP reaching T3. Slit-like gland apertures, with oval evaporative areas, between T3-5, T4-5 and T5-6; anterior gland apertures more widely separated and with a larger evaporative area than intermediate and posterior pairs (Fig. 173). Distinct Y-suture with a very broad white margin; sutures T4-5 and T5-6 directed anteriad, all sternal sutures simple, straight and reaching abdominal margin. Trichobothrial hairs short, not visible in dorsal view. Trio of trichobothria on S3 difficult to see and anterior bothria on S5 just anterior to spiracle 5 (Fig. 89). All spiracles ventral. Prothoracic femur incrassate, multi-spinose, with one large spine (Figs 239, 240). Rostrum reaching to or beyond metathoracic coxae.

Material examined: G. abietum x 20. G. grossipes x 11.

**Gastrodes abietum** Bergroth, 1914 (Cl. 13.6.3.1; Fig 239, 305)

Colour: As *G. grossipes*, but paler, more yellowish, with the posterior third of the pronotum white and the apices of A1 and A2 sometimes darker.

Structure: As *G. grossipes* but larger. Body also with a few slightly longer, scattered, erect setae. Tylus almost reaching apex of A1. Lateral pronotal margins distinctly concave in posterior third (Fig. 305). Prothoracic femur with one large antero-ventral spine and 3-5 smaller apical spines, basal spines normally absent but if present never more than ten (Fig. 239). Rostrum reaching to, or beyond, metathoracic coxae.

x 10 specimens measured: GB88.17.

**Gastrodes grossipes** (De Geer, 1773) (Cl. 13.6.3.2; Figs 26, 89, 173, 240, 306)

Colour: Eyes red. Head, pronotum, scutellum, MWP and pleura brown; tylus, carinae and ecdysial suture yellow. Base of head sometimes with yellow streaks and narrow, posterior-mesal white pronotal streak sometimes present. Abdomen
pale-brown to pale reddish-brown; T1 and streaks adjacent to evaporative areas white; red maculae sometimes between intermediate and posterior evaporative areas and red streaks directed posteriad from evaporative areas to suture; evaporative areas, abdominal segments 9, 10 and mesal mark on S8 dark-brown. Legs light-brown, sometimes darker-brown; femoral apices pale and Ts2 dark-brown. A1 and A2 yellow, A3 and A4 dark-brown. Rostrum light-brown, apex of R4 dark-brown.

Structure: Body and appendages with very short, pale, adpressed pubescence and slightly longer, pale, semi-erect setae on tylus apex, coxae, trochanters, tarsi and antennal apices. Lateral pronotal margins slightly concave in posterior third (Fig. 306). A1 surpassing apex of tylus by one third of length. Prothoracic femur with one large antero-ventral spine, 3-5 small apical spines and 5-15 small basal spines (Fig. 240). Rostrum reaching to or just beyond metathoracic coxae.

x 9 specimens measured: x 6 GB85.63; x 1 GB86.72; x 2 GB89.3.

*Ischnocoris* Fieber, 1860 (Cl. 13.6.4; Figs 45, 90, 174)

Small, distinctively shaped, large eyed, shining, almost glabrous, red and black bodied nymphs with a white abdominal margin. Head declivent, tylus almost reaching apex of A1, trichobothrial hairs long, and eyes touching anterior pronotal margin. Antennae slender with A1 broader than A2 and A3. Pronotum subquadrate, parallel sided for most of length, indistinctly carinate, with very weak postero-lateral impressions and unconnected meso-anterior impressions. Strongly convex MWP reaching T2-3, with sides projecting distinctly beyond lateral pronotal margins. Gland apertures between T3-4, T4-5 and T5-6; anterior apertures more widely separated and with a wider evaporative area than subequal intermediate and posterior pairs (Fig. 174). Y-suture present; T4-5 and T5-6 directed anteriad; S2-3 and S3-4 deeper than other ventral sutures, S4-5 not reaching abdominal margin, curving anteriad then posteriad (Fig. 90). Trichobothrial hairs long and visible in dorsal view. Trichobothria close together on S5,
posterior pair one above the other and anterior trichobothrium just posteriad of spiracle (Fig. 90). S8 with long meso-lateral bristle-like spine. All spiracles ventral. Prothoracic femur mutic and strongly incrassate.


Ischnocoris angustulus (Boheman, 1852) (Cl. 13.6.4.1; Figs 45, 90, 174)

Colour: Eyes red. Head, pronotum, scutellum, MWP and pleura shining brown-black, with yellow-red ecdysial suture. Abdomen red; off-white along margin and along sutures; sterna sometimes paler mesally; evaporative areas, T9-10, S7 mesally and S8-10 brown to brown-black. Femora and tibiae yellow-brown to brown; femoral apices, bases and apical halves of tibiae paler. Tarsi yellow-brown to yellow-white. Coxae and trochanters white, with brown. A1 brown-black, apex yellow; A2-4 yellow to yellow-brown, with slightly darker bands on bases and apices of A2-3 and base of A4, all antennal articulations white. Rostrum yellow-brown to brown.


x 10 specimens measured: x 3 GB85.25; x 6 GB86.36B; x 1 GB86.46C.

Lamproplax Douglas & Scott, 1868 (Cl. 13.6.5; Figs 27, 91, 175, 241, 242)

Medium sized, pale, shining nymphs, with slender appendages. Eyes small and touching anterior pronotal margin. Head declivent and semi-porrect. Tylus extending well beyond juga, but only reaching mid-point of A1. Cephalic trichobothrial hairs indistinct amongst other setae. Pronotum carinate and almost rectangular; anterior angles broadly rounded and lateral margins parallel in
posterior half; broad latero-posterior impression present and anterior lobes slightly swollen. MWP reaching T3. Gland apertures between T3-4, T4-5 and T5-6; anterior gland apertures more widely separated and with larger evaporative areas than intermediate and posterior pairs (Fig. 175). Y-suture indistinct and normally without coloured margins. Sutures T3-4, T4-5 and T5-6 directed anteriad, S4-5 not reaching abdominal margin, curving anteriad around trichobothrium and then posteriad; S5-6 also curving anteriad around trichobothrium, but reaching abdominal margin. Trichobothrial hairs long. Trichobothria close together on S5, anteriad of spiracle 5 and either side of spiracle 4, with posterior pair one above other (Fig. 91). Spiracles all ventral, 4 closer to abdominal margin. Prothoracic femur incrassate with fine spines (Figs 241, 242).

Material examined: L. picea x 10.

Lamproplax picea (Flor, 1860) (Cl. 13.6.5.1; Figs 27, 91, 175, 241, 242)

Colour: Eyes red. Head, pronotum, MWP, scutellum and appendages yellow to yellow-brown. Lateral margins of head, posterior margin of pronotum, MWP apices and evaporative areas light-brown, with apex of rostrum and trochanters darker. Abdomen yellow-pink; terga often pinker and sterna more yellow-brown.

Structure: Pale, medium length, scattered, erect and semi-erect, fine pubescence on head, pronotum and appendages; setae shorter and more adpressed on MWP and abdomen. Tibiae, coxae and A1 with brown spines. Prothoracic femur with two or occasionally only one antero-ventral spine (Fig. 241, 242) (one specimen examined had two spines on one femur and only one on the other). Rostrum reaching between meso- and metathoracic coxae.

x 8 specimens measured: x 2 GB85.53; x 3 GB86.35C; x 2 coll. NCC, 16.07.1987, Rhos Rhydd; x 1 coll. NCC, 17.08.1987, Cors Caron.
Notochilus Fieber, 1864 (Cl. 13.6.6)

No specimens available for study.

Ribauticoris Stichel, 1958 (Cl. 13.6.7)

No specimens available for study.

Scolopostethus (Fieber, 1860) (Cl. 13.6.8; Figs 28, 92, 76, 243-248, 322-325)

Medium-small, intricately patterned, brown, yellow and red nymphs. Eyes close to anterior pronotal margin. Head moderately declivent, trichobothria distinct and tylus reaching to mid-point of A1. Pronotum trapezoidal, with distinctly carinate, faintly concave, lateral margins and a weak posterior transverse impression. MWP reaching T3. Gland apertures and wide, transversely oblong evaporative areas between T3-4, T4-5 and T5-6; anterior gland apertures more widely separated and with a larger evaporative area than equal sized intermediate and posterior pairs (Fig. 176). Y-suture with a broad white margin. Sutures T4-5 and T5-6 directed strongly anteriad; S2-3 and S3-4 strongly grooved; S4-5 curving anteriad around trichobothrium then directed posteriad and not reaching abdominal margin. Trichobothrial hairs long and visible in dorsal view. Trichobothria positioned close together on S5 with pair one above the other and singleton just posteriad of spiracle 4 (Fig. 92). Spiracles ventral. Prothoracic femur incrassate with one medium sized spine in a row of small spines, on antero-ventral edge (Figs 243-248). Rostrum reaching between meso- and metathoracic coxae.

Scolopostethus affinis (Schilling, 1829) (Cl. 13.6.8.1; Figs 92, 176, 243, 321, 322)

Colour: Head, pronotum, scutellum, MWP and pleura brown to brown-black, with yellow markings as follows; - along ecdysial suture, on posterior half of pronotal carinae, as three separate yellow areas on posterior pronotal margin and as one small mesal area on anterior margin, on corners of scutellum and as four irregular areas on MWP. Abdomen reddish-brown, with white markings on anterior margins of each segment; white also on T1, along tergal sutures, on margins of evaporative areas on T4-5 and T5-6 and in mesolateral areas of T5-7; faint red lining sometimes present along Y-suture and red suffusion sometimes present in mesal areas of terga. Evaporative areas, abdominal segments 9 and 10 and mesal patch on S8 (if present) dark-brown. Legs variable; femora brown with white bases and apices; tibiae all white or brown for most of mesal area; tarsi all white or Ts2 sometimes brownish. Coxae and trochanters white with a black spot on trochanter apices. Antennae dark-brown, apical third of A1 and basal third of A2 white; A2 sometimes almost completely white or yellow. Rostrum brown, base and apex of R3 yellow-white.

Structure: Body and appendages with short, pale, adpressed pubescence, also a few semi-erect to erect setae on head, pronotum and MWP (Figs 321, 322). MWP reaching white margin of Y-suture. Prothoracic femur with one medium sized spine in a row of 4-8 apical small spines and sometimes also some very small basal spines (Fig. 243). Rostrum reaching between meso- and metathoracic coxae.

x 10 specimens measured: x 4 GB85.49; x 3 coll. B. Wallace, 16.08.1985, Thingwall, Merseyside; x 3 GB86.31B.

Scolopostethus decoratus (Hahn, 1833) (Cl. 13.6.8.4; Figs 28, 244)

Colour: As S. affinis, but often richer and darker. Yellow markings on base of pronotum usually but not always linked, forming a continuous transverse band along impression and enveloping the two isolated meso-lateral brown marks. Only anterior third of pronotal carinae brown.

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Apical yellow area on MWP small or often absent. All of tarsi and tibiae, except for bases and apices brown. Only apex of A1 and base of A2 white.

Structure: As *S. affinis*. Prothoracic femur with one medium sized spine, 4-7 small apical spines, and sometimes a row of basal spines on antero-ventral edge (Fig. 244).

x 10 specimens measured: x 1 GB84.21A; x 1 GB85.22E; x 2 GB85.55; x 1 GB85.58A; x 5 GB85.62B.

*Scolopostethus grandis* Horváth, 1880 (Cl. 13.6.8.5; Fig. 245, 323)

Colour: As *S. affinis*. Posterior, transverse, yellow pronotal band occasionally present.

Structure: Larger than *S. affinis* with smaller pronotum. MWP only just reaching T3. Pubescence shorter and less dense than for *S. affinis* (Fig. 323). Prothoracic femur with one medium sized spine, normally four small apical spines and a row of very small basal spines on antero-ventral edge (Fig. 245).

x 10 specimens measured: x 3 GB86.49; x 7 GB86.67B.

*Scolopostethus pictus* (Schilling, 1829) (Cl. 13.6.8.8; Fig. 246)

Colour: Markings similar to *S. affinis*, but paler and more faint. Distinct yellow meso-anterior spot present on pronotal margin, posterior markings irregular and carinae uniformly yellow. Apex and base of MWP brown, mesal area uniformly yellow, not divided into four separate areas. A1, A2 and apical half of A4 yellow. Tibiae and Ts1 all yellow. R3 uniformly yellow.

Structure: Larger, with longer more slender appendages than other *Scolopostethus*. Pubescence as *S. affinis*. MWP just reaching T3. Prothoracic femur with one medium sized spine and 6-8 apical, smaller spines on antero-ventral edge (Fig. 246). Rostrum reaching metathoracic coxae.
Scolopostethus puberulus Horváth, 1887 (Cl. 13.6.8.11; Fig. 247, 324)

Colour: As *S. affinis*. MWP with only three irregular yellow mesal areas, apices brown and at most only a faint small apical spot present. Prothoracic femur brown with white apices, meso- and metathoracic femora yellow with a broad apical brown band. Prothoracic tibia yellow-brown, meso- and metathoracic tibiae yellow, with a broad basal band. Ts1 yellow and Ts2 brown. Antennae brown-black, apex of A1 and A2 completely yellow. Rostrum brown; R2 apex, R3 and base of R4 yellow.

Structure: Head, pronotum, MWP and scutellum with medium length, semi-erect, pale pubescence (Fig. 324); setae shorter, more compressed on abdomen and appendages. Prothoracic femur with one medium sized spine on antero-ventral edge, six small apical spines and some minute basal spines (probably variable) (Fig. 247). Rostrum reaching between metathoracic coxae.

x 1 specimen measured: GB87.26.

Scolopostethus thomsoni Reuter, 1874 (Cl. 13.6.8.12; Fig. 248, 325)

Colour: As *S. affinis*. MWP with 4-6 irregular yellow mesal areas. Only apical quarter of A1 and basal quarter of A2 yellow-white.

Structure: Medium-short, compressed, semi-erect pubescence (Fig. 325). Prothoracic femur with one medium sized spine, 4-5, small apical spines and a series of six, basal, small spines (Fig. 248). MWP reaching T2-3 or white margin of Y-suture. Rostrum only reaching mesothoracic coxae.

x 6 specimens measured: GB85.68.
Small, colourful, shining nymphs, with stout antennae. Head porrect, moderately declivent with long trichobothrial hairs (difficult to see amongst setae); tylus at most reaching middle of A1. Eyes small and distanced from anterior pronotal margin by almost one eye width. Pronotum trapeziform, with upwardly reflexed, narrowly carinate lateral margins. MWP reaching T3. Gland apertures with large evaporative areas between T3-4, T4-5 and T5-6; anterior apertures more widely separated, with a larger evaporative area than subequal intermediate and posterior pairs (Fig. 177). Sutures T4-5 and T5-6 directed anteriad, S2-3 and S3-4 strongly grooved, apparently lined and contiguous with Y-suture; S4-5 curving anteriad around trichobothrium, not reaching abdominal margin and directed posteriad. Trichobothrial hairs long and visible in dorsal view. Trichobothria positioned close together on S5 with the posterior pair one above the other and the anterior trichobothrium posteriad of spiracle 4 (Fig. 93). Bristle-like spine present on S8. Spiracles all ventral. Prothoracic femur incrassate and multi-spinose (Fig. 249).

Material examined: T. contractus x 24. T. hamulatus x 3.

_Taphropeltus contractus_ (Herrich-Schaeffer, 1835)  
(Cl. 13.6.9.3; Figs 29, 93, 177, 249)

Colour: Eyes red. Head, pronotum, pleura and middle of MWP yellow; scutellum, pleural margin, remainder of MWP, sometimes pronotal disc and occipital region brown. Ecdysial suture white. T3-7 red mesally; T2, T8 and lateral margins white. Sterna yellow-white with red markings adjacent to lateral trichobothria. Evaporative areas, T9, T10, mesal areas of S7 and S8 brown. Legs yellow; tarsi and prothoracic tibia sometimes yellow-brown; coxae, trochanters and femoral apices yellow-white. A1 and A2 yellow; with A1 base, base and apex of A2 brown (A2 colour variable but marking constant). A3 and basal two-thirds of A4 brown; apex of A4 and all articulations white. Rostrum yellow-brown.

Structure: Dorsal surface of body with very long, pale,
erect, fairly sparse pubescence; ventral body surface and prothoracic femur with medium length, semi-erect setae and shorter adpressed setae on antennae and remainder of legs. Lateral pronotal sides slightly concave. Prothoracic femur with one medium sized spine and 7-11 (normally 11), small spines on antero-ventral edge (Fig. 249). Rostrum reaching to meso- or metathoracic coxae.

x 10 specimens measured: x 3 GB86.26A; x 2 GB86.47; x 1 GB86.48; x 2 GB86.51A; x 2 GB87.18A.

**Taphropeltus hamulatus** (Thomson, 1870) (Cl. 13.6.9.4)

Colour and structure as *T. contractus*, but smaller. TBL = 2.30mm - 2.48mm and posterior width of pronotum > 1.85 x anterior width.

x 3 specimens measured: x 1 GB86.52B; x 2 GB87.29.

**Thaumastopus Fieber, 1870** (Cl 13.6.10)

No specimens available for study.

**GONIANOTINI STÅL, 1872**

**Alampes Horváth, 1884** (Cl. 13.7.1)

No specimens available for study.

**Aoploscelis Fieber, 1860** (Cl. 13.7.2; Figs 94, 178, 250, 331)

Small, dark-brown, shining nymphs, with a matt abdomen. Body with short, sparse pubescence; long, erect and semi-erect setae on head, posterior and mesal area of sterna, and one long erect seta on apex of prothoracic tibia. Stout, short, semi-erect spines on all tibiae. Head moderately short, declivent, with long, conspicuous trichobothrial hairs. Tylus reaching apex of A1. Eyes slightly distanced from anterior pronotal margin. Pronotum trapeziform, with narrow, rib-like, carinate lateral margins, almost straight anterior and posterior margins and a weak posterior transverse impression. MWP reaching T3 or
T4. Slit-like gland apertures present between T4-5 and T5-6, posterior pair slightly more widely spaced and both pairs with narrow, inconspicuous evaporative areas (Fig 178). Y-suture absent. Sutures between T4-5 and T5-6 very strongly curving anteriad. S4-5 curving slightly anteriad, embracing trichobothrium and weakly reaching abdominal margin (Fig. 94). Trichobothrial hairs long and visible dorsally. Trichobothria on S5 widely spaced with spiracle closer to posterior pair (Fig. 94). Spiracle 4 dorsal, remainder ventral. Prothoracic femur incrassate and mutic, with a row of fine seta-like spines on antero-ventral edge (Fig. 250). Prothoracic tibia with one long basal spine (Fig. 331). Rostrum not reaching beyond prothoracic coxae.

Material examined: A. bivirgatus x 4.

**Aphanus Laporte, 1833** (Cl. 13.7.3; Figs 46, 95, 179, 251)

Medium length, black and brown heavily sclerotized, almost glabrous nymphs, with slender appendages. Eyes touching antero-lateral pronotal margin. Tylus slender, snub ended and only reaching mid-point of A1. Head short, declivent, with long trichobothrial hairs. Pronotum with a weak posterior transverse impression, lateral margins convex to straight, downwardly reflexed and narrowly carinate. MWP reaching T3. Equal sized and spaced, slit-like, gland apertures, with equal sized narrow evaporative areas between T4-5 and T5-6 (Fig. 179). Y-suture absent. Sutures T4-5 and T5-6 curving strongly anteriad, S2-3 and S3-4 deep, S4-5 curving anteriad near trichobothrium, embracing trichobothrium and not reaching abdominal margin. Trichobothrial hairs visible in dorsal view. Anterior and posterior pair of trichobothria on S5 widely spaced with spiracle equidistant between them (Fig. 95). Spiracle 4 dorsal, others ventral. Terga often, but not always, with a latero-longitudinal impression. Prothoracic femur slightly incrassate with a small and very small antero-ventral spine (Fig. 251). Tibiae and A1 with short, semi-erect spines. Rostrum reaching between pro- and mesothoracic coxae, or just to mesothoracic coxae.

Material examined: A. rolandri x 12.
Aphanus rolandri (Linnaeus, 1758) (Cl. 13.7.3.1; Figs 46, 95, 179, 251)

Colour: Eyes red. Head, pronotum, scutellum and MWP uniformly matt-black, with a pink ecdysial suture. Abdomen castaneous to brown-black; trichobothrial fields pink (often visible dorsally), evaporative areas, markings on S7, abdominal segments 8 and 9 black. Appendages normally brown to black with paler articulations, but sometimes yellow-brown. Coxae white, with brown markings. Rostrum brown.

Structure: Body with very short, sparse pubescence and dense, short adpressed setae on appendages.

x 8 specimens measured: x 3 GB87.18B; x 5 J89.16C.

Bleteogonus Reuter, 1885 (Cl. 13.7.4)

No specimens available for study.

Diomphalus Fieber, 1864 (Cl. 13.7.5; Figs 96, 180, 252, 307)

Medium-small, suboval, pale, yellow-white nymphs with a faintly spotted red abdomen. Body with very short, sparse, pale, adpressed pubescence; short, erect, stout, scattered, black setae on head and longer, stout, black, semi-erect setae on appendages. Head strongly porrect and slightly declivent. Tylus long, stout, apically blunt and extending to apex of A1. A3 very short, strongly contrasting with long A4. Eyes large, slightly distanced from and protruding beyond anterior pronotal corner. Pronotum subtrapezoidal, with narrowly carinate, sinuate lateral margins and strongly pronounced calli, divided by a broad, strong meso-longitudinal impression (Fig. 307). MWP widely separated, with very convex outer margins. Small gland apertures with narrow evaporative areas between T4-5 and T5-6. Posterior pair fractionally more widely separated and with a straighter linking channel (Fig. 180). Y-suture absent, T4-5 and T5-6 curving anteriad, remainder straight and all reaching abdominal margin. Trichobothrial hairs short and just visible in dorsal view. Trichobothria on S5.
close together, either side of spiracle (Fig. 96). Spiracles 2 and 3 just ventral, 4 clearly lateral and 5-8 clearly ventral. Prothoracic femur incrassate with rows of short, stout, black setae on antero-ventral and antero-lateral edges (Fig. 252). Rostrum reaching metathoracic coxae.

Material examined: *D. hispidulus* x 2.

**Emblethis Fieber, 1860** *(Cl. 13.7.6; Figs 30, 97, 181, 253, 254, 292, 293)*

Medium length, suboval, almost glabrous, brown and yellow nymphs, with a mottled, red abdomen and stout, short setae on the head and appendages. Head moderately declivent, trichobothria absent, tylus not quite reaching apex of Al, and eyes touching, or sometimes embraced by, antero-lateral pronotal margins (Figs 292, 293). Pronotum trapezoidal to subquadrate, with broadly carinate often strongly sinuate lateral margins, a weak transverse posterior impression and deeper meso-longitudinal impression along stem of ecdysial suture. MWP reaching T3. Gland apertures, with narrow, rim-like evaporative areas, between T4-5 and T5-6; posterior apertures larger and more widely spaced apart (Fig. 181). Y-suture absent. Suture T3-4 slightly and T5-6 more strongly curving anteriad. S2-3 and S3-4 more deeply impressed and S4-5 curving anteriad, embracing trichobothrium and not reaching abdominal margin. Trichobothrial hairs visible in dorsal view. Trichobothria widely spaced on S5, with the pair closer to spiracle 5 (Fig. 97). Spiracle 4 dorsal, remainder ventral with spiracle 3 often positioned closer to lateral abdominal margin. Prothoracic femur incrassate, with a row of short, fine spines on ventral edge (Figs 253, 254). Al broader and shorter than A2-4. Rostrum reaching pro- to mesothoracic coxae.

Emblethis denticollis Horváth, 1878 (Cl. 13.7.6.5; Figs 253, 292)

Colour: Head, pronotum, scutellum and MWP strongly patterned yellow and dark-brown, becoming black on anterior of pronotum and head. Head with five distinct, dorsal, interrupted yellow stripes (Fig. 292). Carinate sides of pronotum and MWP yellow-white. Red suffusion sometimes present near eyes, along posterior margins of pronotum and scutellum. Abdomen with numerous small, yellow-white spots, highlighted with brown and red mottling; spots sometimes merging and becoming indistinct. Distinct red meso-lateral spots on T3-7 and all sutures normally lined with red. Mesal areas on S6-7 and abdominal segments 8-9 brown, to brown-black. Appendages yellow; legs, particularly femora, dappled brown; A4, very occasionally apex of A3, Ts1 apices and Ts2 brown to brown-black.

Note: A Turkish instar 4 nymph is much darker, with an overall brown suffusion (Appendix 5, ref. T90.73C).

Structure: Body and appendages with very short, adpressed pale pubescence. Prothoracic femur with seven short, fine, dark, antero-ventral spines, with the apical spine more robust. Dark, semi-erect spines on anterior of head, coxae and tibiae, becoming shorter on tarsi, longer and finer on antennae. Rostrum just reaching mesothoracic coxae. Prothoracic femur as Fig. 253).

x 10 specimens measured: x 9 J89.21A,C; x 1 J89.12C.

Emblethis griseus (Wolff, 1802) (Cl. 13.7.6.9; Figs 30, 97, 181, 254, 293)

Colour: Eyes red-brown. Head and pronotum yellow, with interocular area and pronotal lobes brown-black. Scutellum mainly brown, with darker basal corners. MWP yellow with broad, brown, irregular shaped, mesal markings, extending throughout length. Brown markings extremely variable; sometimes variegated on pronotum, almost absent on scutellum, except for basal corners, and very restricted on MWP. Pleura primarily dark-brown. Abdomen with yellow spots, highlighted by brown and some red; spots sometimes
faint on margins. Evaporative rim of gland apertures, mesal areas on S6-7 and abdominal segments 8-9 brown to black. Red suffusion sometimes evident over body; red most frequently present along sutures, anterior to scent gland apertures and as dark red-brown meso-lateral spots on T4-7. Appendages yellow; tibial and Ts2 apices faintly brown, Ts2 and A4 brown and R4 predominantly brown-black.

Structure: Body distinctly oval, with very short, adpressed, pale pubescence. Stout, semi-erect setae on head, coxae, tibiae and tarsi, becoming longer and finer on antennae. Prothoracic femur with an antero-ventral row of seven, small, equal sized, fine, dark spines and a weak postero-ventral row (Fig. 254). Rostrum reaching between pro- and mesothoracic coxae.

x 10 specimens measured: x 7 GB85.22A; x 3 GB86.48A.

**Gonianotus Fieber, 1860** (Cl. 13.7.7; Figs 98, 182, 255, 294)

Medium-small, oval, mottled nymphs with pale spots. Almost glabrous, with stout spines on appendages, head and centre of sterna. Head short and declivent, tylus not quite reaching apex of A1 and trichobothria absent. Eyes large, touching lateral corners of anterior pronotal margin. Pronotum trapezoidal, transverse impression absent, lateral margins sinuate and broadly carinate, anterior margin straight and almost parallel with posterior margin (Fig. 294). MWP reaching T3-4. Gland apertures with narrow, rim-like evaporative areas between T4-5 and T5-6; posterior pair slightly more widely separated (Fig. 182). Y-suture absent; sutures T4-5 and T5-6 almost straight, only slightly curving anteriad; S4-5 curving anteriad, embracing trichobothrium and not reaching abdominal margin. Trichobothrial hairs short and not always visible in dorsal view. Trichobothria widely spaced on S5, with spiracle just closer to posterior pair (Fig. 98). Spiracle 4 dorsal, remainder ventral. Prothoracic femur moderately incrassate, with a row of evenly spaced, short, fine, spines (Fig. 255). Rostrum reaching between pro- and mesothoracic coxae to mesothoracic coxae.
Material examined: Gonianotus sp. x 9.

**Hyalocoris Jakovlev, 1874 (Cl.13.7.8)**

No specimens available for study.

**Ischnopeza Fieber, 1860 (Cl. 13.7.9; Figs 99, 183, 256)**

Medium length, with long appendages and a red and brown mottled body, with pale, white spots. Body pubescence short and sparse with very long, erect and suberect setae present on antennae and a few on head. Stouter, short, semi-erect spines on tibiae and A1. Head elongate, parallel sided, with semi-protuberant eyes, only slightly distanced from antero-pronotal margin. Tylus long, thin, parallel sided, slightly bulging at apex and reaching two-thirds along length of A1. Juga long, thin and strongly concave along outer lateral margin. Pronotum trapeziform, shorter than head, with upwardly reflexed, broadly carinate lateral margins, a straight posterior margin, transverse anterior and posterior impressions. MWP narrow, widely spaced and reaching T3. Very small gland apertures, with only slight evidence of an evaporative area, between T5-6; apertures separated by only twice their width. Vestigial aperture remains, without an evaporative area, between T4-5, normally, but not always, just visible (Fig. 183). Y-suture absent; sutures T4-5 and T5-6 curving only slightly anteriad; S4-5 curving strongly anteriad, embracing trichobothrium and not reaching abdominal margin. Trichobothrial hairs visible in dorsal view. Trichobothria widely separated on S5, with the spiracle closer to the posterior pair (Fig. 99). Spiracle 4 dorsal, remainder ventral but 2, and particularly 3, close to lateral margin. Prothoracic femur moderately incrassate, with a row of small spines along antero-ventral edge (Fig. 256). Rostrum reaching between meso- and metathoracic coxae.

Material examined: *I. hirticornis* x 2. *I. pallipes* x 2.
Macrodema Fieber, 1860 (Cl. 13.7.10; Figs 47, 100, 184,)

Small, black and castaneous, shining, suboval nymphs, with short, moderately stout legs. Body with sparse adpressed pubescence and longer, semi-erect antennal setae. Short, stout spines on A1 and tibiae; longer, stout setae on head and centre of sterna. Head declivent, with distinct trichobothria; tylus extending to, or slightly beyond, apex of A1 and eyes slightly distanced from anterior pronotal margin. Pronotum trapeziform, narrowly carinate with weak anterior and posterior transverse impressions. MWP short, only reaching T2 (probably T3 for macropters). Slit-like, subequally spaced gland apertures with narrow evaporative areas between T4-5 and T5-6 (Fig. 184). Y-suture absent. Sutures T4-5 and T5-6 curving strongly anteriad; S2-3 and S3-4 deep, S4-5 curving anteriad near trichobothrium, embracing trichobothrium and not reaching abdominal margin. Trichobothrial hairs visible in dorsal view. Trichobothria widely separate on S5, with spiracle slightly closer to posterior pair (Fig. 100). Spiracle 4 dorsal, remainder ventral. Prothoracic femur mutic and strongly incrassate. Rostrum reaching between meso- and metathoracic coxae.

Material examined: M. microptera x 60.

Macrodema microptera (Curtis, 1836) (Cl. 13.7.10.1; Figs 47, 100, 184)

Colour: Eyes red. Head, pronotum, scutellum, MWP and pleura black. Abdomen castaneous; evaporative areas, mesal area on S7 and abdominal segments 9 and 10 black. Appendages brown; tarsi yellow-brown, antennal articulations and femoral apices pale; bases and apices of A2 and A3 sometimes with slightly darker annuli

Structure: As generic description.

x 10 specimens measured: x 3 GB84.17B; x 4 GB85.23; x 1 GB86.18D; x 2 GB86.48C.

205
Neurocladus Fieber, 1860 (Cl. 13.7.11)

No specimens available for study.

Pionosomus Fieber, 1860 (Cl. 13.7.12; Figs 48, 101, 185, 308)

Small, broadly oval, heavily sclerotized, brown and black, shining nymphs. Stout, long, erect setae on head, lateral pronotal margin (Fig. 308), centre of sternum and femora; finer on antennae, shorter and stouter on tibiae. Eyes touching antero-lateral pronotal margin. Tylus reaching apex of A1. Head short, declivent, with long trichobothrial hairs. Pronotum trapeziform, with weak posterior transverse impression and narrowly emarginate lateral margins. MWP reaching T3-4. Narrow, slit-like, widely spaced gland apertures, with narrow, subequal evaporative areas, between T4-5 and T5-6 (Fig. 185). Y-suture absent; suture T4-5 curving slightly and T5-6 strongly anteriad; S2-3 and S3-4 deep; S4-5 curving anteriad, slightly embracing trichobothrium and not reaching abdominal margin. Trichobothrial hairs visible in dorsal view. Anterior and posterior trichobothria on S5 widely separated with the spiracle closer to the posterior pair (Fig. 101). Spiracle 4 dorsal, the remainder ventral. Terga normally, but not always, with a longitudinal lateral impression. Prothoracic femur incrassate and motic, but with long setae. Rostrum reaching between pro- and mesothoracic coxae.


Pionosomus varius (Wolff, 1804) (Cl. 13.7.12.7; Figs 48, 101, 185, 308)

Colour: Eyes red. Head, pronotum, scutellum and MWP shining, brown-black, with a pink ecdysial suture. Abdomen castaneous to dark-brown; evaporative areas, markings on S7, abdominal segments 8 and 9 brown-black. Appendages yellow-brown to brown; femoral apices, antennal articulations and most of coxae pale.
Structure: Body almost glabrous, with very short, sparse pubescence. Rostrum reaching mesothoracic coxae.

x 9 specimens measured: x 7 GB85.37B; x 2 GB86.46B.

**Pterotmetus Amyot & Serville, 1843** (Cl. 13.7.13; Figs 49, 102, 186, 257)

Medium length, elongate, narrow, parallel sided, heavily sclerotized, black and dark-brown to castaneous, matt nymphs. Body almost glabrous and tibiae with short, stout spines. Head declivent, moderately porrect, with tylius almost reaching apex of A1 and eyes only slightly distanced from anterior pronotal margin. Pronotum narrowly and inconspicuously carinate, with weak anterior and posterior transverse impressions. MWP short, reaching T2, or at most suture between T2-3. Equal sized and spaced gland apertures, with evaporative areas, between T4-5 and T5-6 (Fig. 186). Y-suture absent; sutures T4-5 and T5-6 curving very strongly anteriad; sutures S2-3 and S3-4 deep and S4-5 curving anteriad near trichobothrium, slightly embracing trichobothrium and not reaching abdominal margin. Trichobothrial hairs visible in dorsal view. Trichobothria widely spaced on S5, with spiracle just closer to posterior pair (Fig. 102). Spiracle 4 dorsal, remainder ventral, but often difficult to see. Prothoracic femur moderately incrassate and unispinose (Fig. 257). Rostrum reaching mesothoracic coxae.

Material examined: *P. staphyliniformis* x 3.

**Pterotmetus staphyliniformis** (Schilling, 1829) (Cl. 13.7.13.3; Figs 49, 102, 186, 257)

Colour: Eyes red. Head, pronotum and scutellum black. Abdomen castaneous to brown-black; evaporative areas, mesal marks on S6-7 and abdominal segments 8-9 black. Coxae and trochanters white, with brown markings. Appendages brown-black; tarsi sometimes brown, antennal articulations and femoral apices pink-white.

Structure: Body with very short, sparse, adpressed pubescence. Short, dense adpressed setae on antennae,
becoming longer and semi-erect at apices. Prothoracic femur with one very small antero-ventral spine (Fig. 257).

x 2 specimens measured: GB86.48.

**Trapezonotus Fieber, 1860** (Cl. 13.7.14; Figs 50, 103, 187, 258-261)

Medium to small, black and castaneous, suboval, almost glabrous nymphs, with stout tibial, tarsal and antennal setae. Pronotum, scutellum and MWP rugose and abdomen finely punctate. Head declivent, with either stout trichobothrial hairs or long fine setae; eyes touching antero-lateral pronotal margins and tylus not quite, or just reaching A1 apex. Pronotum trapeziform, narrowly emarginate, with weak transverse posterior and meso-longitudinal impressions. MWP reaching T3-4. Paired, equally widely spaced scent gland apertures with narrow, equal sized evaporative areas between T4-5 and T5-6. Y-suture absent; sutures T4-5 mildly, and T5-6 strongly curving anteriad. Sutures S2-3 and S3-4 strongly impressed; S4-5 curving anteriad, embracing trichobothrium, not reaching abdominal margin, although a weak line is present. Trichobothrial hairs visible in dorsal view. Trichobothria widely spaced on S5, with the pair closer to the spiracle (Fig. 103). Spiracle 4 dorsal or lateral, remainder ventral and often difficult to see. Prothoracic femur incrassate, with 4-5 medium-small, tuberculate, setose spines and a row of long, fine setae on postero-ventral edge (Figs 258-261). Rostrum reaching mesothoracic coxae.


**Trapezonotus arenarius** (Linnaeus, 1758) (Cl. 13.7.14; Figs 50, 103, 187, 258)

Structure: Body with very short, adpressed pubescence; slightly longer on venter and sparse on head, pronotum, scutellum and MWP. Appendages with medium length, adpressed and stout setae. Lateral pronotal margins slightly sinuate. Tylus reaching A1 apex. Prothoracic femur with one medium sized spine, 2-4 tuberculate setae and a number of very small spines on antero-ventral edge (Fig. 258).

x 10 specimens measured: x 1 GB84.10; x 3 GB85.38B; x 2 GB85.51; x 4 GB85.65B.

*Trapezonotus desertus* Seidenstücker, 1951 (Cl. 13.7.14.3; Fig. 259)

Colour and structure as *T. arenarius*, but body matt, or at most faintly shining.

x 10 specimens measured: x 3 GB85.14C; x 7 GB85.32A.

*Trapezonotus dispar* Stål, 1872 (Cl. 13.7.14.4; Fig. 260)

Colour and structure as *T. arenarius*. Body larger and matt, or only slightly shining. Lateral pronotal margins not sinuate. Spiracle 4 sometimes almost lateral.

x 10 specimens measured: x 8 GB86.33A,C; x 2 GB86.66A.

*Trapezonotus ullrichi* (Fieber, 1837) (Cl. 13.7.14.7; Fig. 261)

As *T. arenarius* with following exceptions:-

Colour: Ts1, sometimes Ts2, A2, A3, with exception of extreme bases and apices, yellow.

Structure: Pronotum, MWP and scutellum almost glabrous. Tylus not quite reaching apex of A1. Pronotal sides not sinuate. Prothoracic femur with only three tuberculate setae and a spine on antero-ventral edge (Fig. 261).

x 10 specimens measured: J89.21.
MEGALONOTINI SLATER, 1957

Hadrocnemis Jakovlev, 1881 (Cl. 13.8.1)

No specimens available for study.

Icus Fieber, 1860 (Cl. 13.8.2; Figs 104, 188, 262)

Medium-small, yellow-brown and red, shining, distinctive nymphs with an elongate, oval, parallel sided body. Head slightly porrect, declivent and with distinct trichobothria. Tylus broad and almost extending to apex of A1. Eyes small and touching antero-lateral pronotal margin. Pronotum subquadrate, without transverse impression, its lateral margins not carinate, but distinctly sinuate behind middle. MWP reaching T3. Gland apertures and evaporative area absent from T3-4. Pair between T4-5 and T5-6 widely spaced, with narrow, inconspicuous evaporative areas; posterior pair slightly more widely spaced (Fig. 188). Y-suture absent; T3-4, T4-5 and T5-6 curving strongly anteriad. S2-3, S3-4 deep; S4-5 curving strongly anteriad, embracing trichobothrium and not reaching lateral margin of abdomen (sutures indistinct in alcohol and best viewed dry). Trichobothrial hairs long and visible in dorsal view. Pair of trichobothria on S5 equidistant between spiracle and S5-6 (Fig. 104). Spiracles 2, 5-8 ventral, 3 latero-dorsal, 4 dorsal?. Prothoracic femur strongly incrassate, antero-ventral edge with a slender, medium length spine, in a row of small spines (Fig. 262). Rostrum reaching between pro- and mesothoracic coxae.

Material examined: I. angularis x 1.

Lamprodema Fieber, 1860 (Cl. 13.8.3; Figs 105, 189, 263)

Medium-small, black and castaneous, heavily sclerotized oval, hirsute nymphs, with short, stout legs and slender antennae. Head, pronotum, scutellum and MWP all shining. Abdomen matt, strongly rugose, with long, stout setae. Head declivent, tylus almost extending to apex of A1, trichobothria seemingly absent and eyes touching antero-lateral pronotal margin. Pronotum trapezoidal, with
carinate lateral margins and a weak posterior transverse impression. MWP reaching T3 or T4. Small, equal sized and spaced gland apertures, with equal sized, elliptical evaporative areas between T3-4, T4-5 and T5-6 (Fig. 189). Y-suture absent; S2-3 and S3-4 deep, S4-5 curving anteriad, embracing trichobothrium and not reaching abdominal margin (Fig. 105). Trichobothrial hairs long and visible in dorsal view. Pair of trichobothria on S5 equidistant between spiracle and S5-6. Spiracles 3-4 dorsal and 2, 5-8 ventral. Prothoracic femur incrassate, with one medium-small spine on antero-ventral edge (Fig. 263). Mesothoracic tibiae with short, stout, semi-erect, dark spines. Rostrum reaching mesothoracic coxae.

Material examined: L. maura x 51.

*Lasiororis* Fieber, 1860 (Cl. 13.8.4; Fig. 190)

Medium to large, suboval, very distinctive, red-brown and yellow nymphs, with long appendages and very long, erect to semi-erect pubescence. Setae particularly dense on A2 and A3. Head strongly prorect and mildly declivent. Eyes small, close together, but not touching anterior pronotal margin. Tylus projecting distinctly beyond juga, only just extending beyond mid-point of A1. Cephalic trichobothria absent. Pronotum trapezoidal with carinate lateral margins. MWP either just reaching T3 or extending to T4. Very small, slit-like gland apertures and narrow evaporative areas between T3-4, T4-5 and T5-6; anterior pair slightly more widely spaced with slightly larger evaporative areas. All evaporative areas almost absent, anteriad of suture (Fig. 190). Y-suture absent; T4-5 curving anteriad; S2-3 and S3-4 more trough-like than other sutures, S4-5 curving anteriad, embracing trichobothrium and not reaching abdominal margin. Trichobothrial hairs visible in dorsal view. Posterior pair of trichobothria on S5 positioned mid-way between spiracle and suture S5-6. Spiracles 3 and 4 dorsal, 2, 5-8 ventral. Prothoracic femur mutic and slightly incrassate. Rostrum reaching between pro- and mesothoracic coxae.

Material examined: L. anomalus x 3.
Leptomelus, Jakovlev, 1881 (Cl. 13.8.5)

No specimens available for study.

Megalonotus Fieber, 1860 (Cl. 13.8.6; Figs 31, 51, 52, 106, 191-196, 264-269, 326-328)

Medium length, suboval, black and castaneous bodied nymphs, often with yellow on the appendages. Head, pronotum, scutellum and MWP shining, often punctate or rugose. Head declivent; eyes small, slightly projecting and close to anterior pronotal margin. Tylus narrow, projecting distinctly beyond juga, but not quite extending to apex of A1. Cephalic trichobothria present, trichobothrial hairs short and not always clearly visible in hirsute species. Pronotum trapezoidal to quadrate, with narrowly carinate, sinuate lateral margin, often projecting anteriad towards the eyes. MWP reaching T3 or just onto T4. Narrow, small, often closely separated gland apertures, with oval, black, shining evaporative areas present but variable (Figs 191-196). Gland apertures and evaporative areas on T3-4, often absent, sometimes also strongly reduced between T4-5; posterior apertures on T5-6 always the most widely spaced, with the largest evaporative area. Y-suture absent; sutures between T4-5 and T5-6 projecting slightly anteriad, S2-3 and S3-4 deep, S4-5 curving anteriad, embracing trichobothrium and not or at most only faintly reaching lateral abdominal margin. Trichobothrial hairs visible in dorsal view. Posterior pair of trichobothria on S5 mid-way between spiracle and S5-6 (Fig. 106). Spiracles 2, 5-8 ventral and 3-4 dorsal. Prothoracic femur strongly incrassate, multi-spinose (Figs 264-269).


Megalonotus antennatus (Schilling, 1829) (Cl. 13.8.6.1; Figs 31, 191, 264)

Colour: Head, pronotum, scutellum and MWP black. Apical margin of scutellum, between MWP, yellow-brown. S7 and S8,
T8 in part and all of abdominal segments 9-10 black. Legs, apical halves of A1, A2, apical halves of R2, R3 and basal half of R4 yellow, remainder black, with Ts2 sometimes brown.

Structure: Body and appendages with medium length, suberect pubescence. Head, pronotum and MWP strongly shining, rugose, although pronotal discs more polished. Scutellum rugose, matt and only faintly shining towards apex. Pronotum quadrate, lateral margins strongly sinuate, clearly projecting anteriad towards eyes. Body bulging outwards at MWP, which often only just reach T3. Dorsal abdominal gland apertures and evaporative area absent between T3-4. Gland apertures between T4-5 very close together, possibly non-functional, with an almost circular small evaporative area. Posterior apertures more widely spaced, with a distinctly larger oval evaporative area (Fig. 191). Prothoracic femur with one large and three, clearly visible, small antero-ventral spines (Fig. 264). Rostrum reaching between meso- and metathoracic coxae.

x 7 specimens measured: x 5 coll. B.C. Eversham, 05.1987, Monks Wood, Cambridgeshire; x 2 GB89.9.

_Megalonotus chiragra_ (Fabricius, 1794) (Cl. 13.8.6.3; Figs 51, 192, 265, 326)

Colour: Head, pronotum, scutellum and MWP black. Black markings on abdomen as for _M. dilatatus_. Appendages dirty-yellow; basal half of A1, extreme apices of A2, A3-4 (not always apex of A4), apex of R4 all brown-black; rostrum, femoral apices and tibiae often fuscous.

Structure: Body and appendages with dense, medium length, adpressed pubescence and long, erect more scattered setae, longer than eye width (Fig. 326). Head, pronotum, MWP and scutellum slightly shining. Pronotum quadrate, transverse impression weak, lateral margins slightly sinuate and projecting anteriad towards eyes. MWP reaching T2-3. Paired gland apertures with oval evaporative areas between T3-4, T4-5 and T5-6. Posterior apertures most widely spaced and with larger evaporative area. Intermediate apertures most closely spaced, with smallest evaporative area (Fig. 192).
Prothoracic femur with 3-4 small spines distal to large spine, on antero-ventral edge, and two small spines on postero-ventral edge (Fig. 265). Rostrum reaching mesothoracic coxae.

x 10 specimens measured: x 4 GB85.65A; x 5 GB86.48; x 1 GB86.44.

**Megalonotus emarginatus** (Rey, 1888) (Cl. 13.8.6.5; Fig. 193, 266, 327)

Colour: As *M. chiragra*, but A1 all brown-black, femora and tibiae predominantly brown. Form *atricornis* darker, abdomen brown-black and appendages dark.

Structure: Pubescence short, sparse and adpressed on body (Fig. 327), longer and suberect on appendages, erect on prothoracic tibia. Abdomen smooth, evaporative areas oval and more elongate than *M. chiragra* (Fig. 193). Prothoracic femur with 3-4 small apical spines, one large spine and 2-4 basal small spines on antero-ventral edge (Fig. 266). Abdomen strongly rugose in form *atricornis*, the prothoracic femur with only 2-3 apical small spines, one large spine and 1-2 basal small spines on antero-ventral edge.

x 7 specimens measured: x 1 GB87.16; x 1 GB87.21; x 1 GB90.2; x 4 F90.5. x 6 specimens *M. emarginatus atricornis* measured: GB86.49.

**Megalonotus praetextatus** (Herrich-Schaeffer, 1835) (Cl. 13.8.6.11; Figs 52, 106, 194, 267)

Colour: Body brilliantly shining. Head, pronotum, scutellum and MWP black. Abdomen red with black apical markings as *M. dilatatus*. Appendages yellow; basal half of A1, extreme bases and apices of A3, A4 faintly, femora, excepting bases and apices, R1 and most of R4, all dark-brown. Coxae and trochanters white.

Structure: Head, pronotum, MWP and scutellum strongly but sparsely punctate, with short, semi-erect setae arising from punctures. Pubescence medium-short, adpressed on abdomen, becoming longer and with semi-erect setae on
appendages. Head strongly declivent. Pronotum subquadrate, lateral margins sinuate and slightly projecting anteriad towards eyes. MWP reaching T2-3 or onto T3. Gland apertures becoming more widely separated and with a larger evaporative area posteriad. Apertures between T3-4 vestigial, and very close together on T4-5 (Fig. 194). Prothoracic femur with 4 anterior small spines, one large spine and 3-4 very small anterior spines (Fig. 267). Rostrum just reaching mesothoracic coxae.

x 10 specimens measured: x 8 GB86.46B; x 1 coll. C. Felton, 26.06.1989, Dawlish Warren, Devon; x 1 GB89.12.

_Megalonotus sabulicola_ Thomson, 1870 (Cl. 13.8.6.13; Fig. 195, 268, 328)

Colour: As _M. chiragra_.

Structure: Body more matt, pubescence on dorsum of body more uniform in length and more dense, than for _M. chiragra_ (Fig. 328). Evaporative areas on T5-6 > 1.8 x maximum width of evaporative area on T4-5 (Fig. 195). Prothoracic femur with 3-4 small apical spines, one large spine and two small basal spines on antero-ventral edge (Fig. 268). Postero-ventral edge with two small spines.

x 10 specimens measured: x 3 GB87.27A; x 7 GB88.9.

_Megalonotus dilatatus_ (Herrich-Schaeffer, 1840) (Cl. 13.8.6.17; Figs 196, 269)

Colour: Head, pronotum, MWP and scutellum black. Abdomen almost red, with S6-8, T8 in part and segments 9 and 10 black. Appendages brown-black; antennal articulations, apical half of A1, sometimes basal two-thirds of A2, coxae, trochanters, bases and apices of prothoracic femur, other femoral apices, often tarsi, R2-3 and base of R4 all off-white to yellow.

Structure: Body broadly oval, with dense, short, adpressed pubescence; setae longer and suberect on appendages. Head, pronotum, MWP and scutellum rugose. Pronotum trapezoidal, lateral margins sinuate and projecting weakly towards eyes.
Distinct, widely spaced gland apertures with an oval evaporative area between T5-6 only. Apertures and evaporative areas absent from T3-4, vestigial between T4-5, with only a small, black spot remaining of the evaporative area (Fig. 196). Prothoracic femur with four apical, small spines, one large spine and two basal spines, on antero-ventral edge (Fig. 269). Rostrum reaching mesothoracic coxae.

x 10 specimens measured: x 1 GB87.18B; x 8 GB89.22.

*Metastenothorax* Reuter, 1884 (Cl. 13.8.7)

No specimens available for study.

*Pezocoris* Jakovlev, 1875 (Cl. 13.8.8)

No specimens available for study.

*Piezoscelis* Fieber, 1870 (Cl. 13.8.9; Figs 107, 197, 270)

Small, elongate, brown-black, brown, yellow and pink-red, shining nymphs with scattered coarse setae bearing punctures on the head, pronotum scutellum and MWP. Scattered fine, adpressed pubescence with a few longer, fine, semi-erect setae. Eyes small, distanced from anterior pronotal corners by half their diameter. Head declivent and porrect, tylus extending to apex of A1. Pronotum almost quadrate, narrowly carinate with a weak transverse impression close to posterior margin. MWP reaching suture between terga 3-4. Gland apertures between T3-4, 4-5, 5-6, anterior and intermediate pairs with narrow equal sized evaporative areas separated in pairs by less than a gland aperture's width and significantly smaller than posterior evaporative area and apertures (Fig. 197). Y-suture absent; sutures between T4-5 and 5-6 projecting strongly anteriad (Fig. 107), S2-3 and 3-4 deep, S4-5 curving anteriad, embracing trichobothrium and not reaching lateral abdominal margin. Trichobothrial hairs clearly visible in dorsal view. Posterior pair of trichobothria on S5 mid-way between spiracle and suture 5-6 (Fig. 107). Spiracles 2, 5-8 ventral, 3-4 dorsal. Prothoracic femur strongly incrassate and multi-spinose (Fig. 270). Rostrum reaching
metathoracic coxae.

Material examined: *P. staphylinus* x 1.

*Proderus Fieber, 1860* (Cl. 13.8.10; Figs 108, 198, 271)

Medium length, narrow, parallel sided, elongate nymphs, with long appendages and a glabrous, shining, red and yellow body. Head porrect, slightly declivent, without trichobothria and with the tylus almost extending to the apex of A1. Eyes small and touching anterior pronotal corners. Pronotum as long as its maximum posterior width, with narrowly carinate, sinuate lateral margins. MWP extending to T3. Slit-like, widely spaced gland apertures with only faint remnants of an evaporative area between T5-6 (Fig. 198). Y-suture absent; T4–5 and T5–6 gently curving anteriad, S4–5 directed strongly anteriad, embracing trichobothrium and not reaching abdominal margin. Trichobothrial hairs clearly visible in dorsal view. Posterior pair of trichobothria on S5 positioned mid-way between spiracle and S5–6 (Fig. 108). Spiracles difficult to see, spiracles 3 and 4 lateral, 2, 5–8 ventral. Prothoracic femur strongly incrassate, antero-ventral edge multi-spinose (Fig. 271). Rostrum reaching mesothoracic coxae.

Material examined: *P. bellevoyei/crassicornis* x 1.

*Sphragisticus Stål, 1872* (13.8.11)

No specimens available for study.

**RHYPAROCHROMINI AMYOT & SERVILLE, 1843**

*Aellopus Wolff, 1811* (Cl. 13.9.1; Fig. 109, 199, 272, 317)

Large, broadly oval, almost glabrous, matt-black, red, brown and white nymphs, with slender appendages. Head declivent, short and small relative to pronotum. Eyes small and touching anterior pronotal margin. Tylus extending two-thirds along A1. Cephalic trichobothrial hairs very short, but clearly visible. Pronotum large, with only a weak transverse impression, lateral margins distinctly convex,
broadly carinate, with antero-lateral margin embracing eyes. Scutellum broad. MWP reaching T3. Widely spaced gland apertures, with narrow evaporative areas, between T3-4, T4-5 and T5-6; spacing between gland apertures increasing posteriad and anterior pair with longer evaporative area (Fig. 199). Y-suture absent, but T3-4 troughed and margined with white (Fig. 317); T4-5 and T5-6 directed anteriad; S2-3, S3-4 deep and S4-5 curving anteriad, embracing trichobothrium and only faintly reaching abdominal margin. Trichobothrial hairs clearly visible in dorsal view. Posterior pair of trichobothria on S5 slightly closer to spiracle than S5-6 (Fig. 109). Spiracles 2, 5-8 ventral and 3-4 dorsal. Prothoracic femur incrassate, with one large spine and six small spines on antero-ventral edge (Fig. 272). Meso- and metathoracic femora also with a row of small spines. Rostrum reaching between pro- and mesothoracic coxae.

Material examined: A. atratus x 6.

**Beosus Amyot & Serville, 1843** (Cl. 13.9.2; Figs 32, 110, 200, 273)

Medium length, elongate, narrow bodied, almost glabrous, black, yellow, red and white nymphs, with very long, slender legs. Eyes prominent and slightly distanced from anterior pronotal margin. Head moderately to strongly declivent, trichobothrial hairs long and clearly visible, tylus not reaching mid-point of A1. Pronotum either trapezoidal or subquadrate, with a distinct collar and upturned, carinate lateral margins, weakly to strongly defined posterior transverse impression and globose disc if impression strongly defined. MWP reaching T3. Widely spaced gland apertures between T3-4, T4-5 and T5-6; anterior apertures larger, further apart and with larger evaporative area than subequal intermediate and posterior apertures (Fig. 200). Y-suture boldly or faintly margined with red; T4-5 and T5-6 curving strongly anteriad, S2-3 and S3-4 deep, S4-5 curving anteriad, embracing trichobothrium and not reaching abdominal margin (Fig. 32). Trichobothrial hairs very long and clearly visible in dorsal view. Pair of trichobothria on S5 positioned slightly closer to spiracle than S5-6. Spiracles 2, 5-8 ventral and 3-4 dorsal.
Prothoracic femur elongate, moderately incrassate, with one medium sized spine on antero-ventral edge (Fig. 273). Rostrum reaching mesothoracic coxae.

Material examined: *B. maritimus* x 49. *B. quadripunctatus* x 20.

*Beosus maritimus* (Scopoli, 1763) (Cl. 13.9.2.1; Figs 32, 110, 200, 273)

Colour: Eyes red. Head, disc of pronotum, extending to latero-posterior corners, pleura and all but extreme apex of scutellum black; pronotal collar, all but extreme base of carinae, MWP, apart from three meso-longitudinal, brown-black streaks, all yellow. Abdomen yellow, with red markings incompletely along Y-suture, along other sutures, as meso-lateral streaks, latero-posterior marks on T4-7 and most noticeably as spherical marks between evaporative areas. T2-3, most of sterna, except for lateral margins, centre of S6 and S7 red-brown. Marks on S6-8, all T8, abdominal segments 9-10 all black. Appendages brown-black; femoral bases and apices, all of tibiae except for apices, basal half of Tsl and sometimes A1-2, basal two-thirds of A3, basal third of A4, R2 and R3 yellow to yellow-brown.

Structure: Very short, fairly sparse, adpressed pubescence on body, becoming slightly more dense and longer on appendages, and semi-erect on rostrum. Short, erect, stout setae on coxae, A1 and tibiae. Prothoracic femur with two ventral rows of slender erect setae in addition to spine (Fig 273).

x 10 specimens measured: x 5 GB85.45B; x 2 GB86.47A; x 1 GB86.47; x 2 GB87.27A.

*Dieuches Dohrn*, 1860. (Cl. 13.9.3; Figs 111, 201, 274)

Large, elongate, suboval, brown, black, yellow, red and white nymphs with long, slender appendages. Gland apertures between T3-4 more widely spaced and with larger evaporative area than subequal intermediate and posterior pairs (Fig. 201). Y-suture distinct, continuous with lined S2-3 and S3-4; T4-5 and T5-6 curving strongly anteriad; S4-5 curving
anteriad embracing trichobothrium and at most faintly reaching abdominal margin (Fig. 111). Spiracles 2, 5-8 ventral, 3 dorso-lateral and 4 dorsal. Prothoracic femur mildly incrassate with at least one medium length spine (Fig 274).


Graptopeltus Stål, 1872 (Cl. 13.9.4; Figs 33, 112, 202, 275, 295)

Medium to large, suboval, black, yellow, brown, red and white, matt nymphs with long, slender appendages and shining patches on head, pronotal discs and basal corners of scutellum. Head declivent with distinct trichobothria. Eyes small, almost touching anterior pronotal corners. Tylus slender and extending two-thirds along length of A1. Pronotum trapezoidal, with wide, upwardly reflexed, convex, carinate, pale margins, extending anteriad slightly towards eyes (Fig. 295); shallow anterior and posterior transverse impressions and meso-longitudinal impression. MWP reaching T3. Gland apertures almost equally spaced between T3-4, T4-5 and T5-6, with equally wide evaporative areas; anterior evaporative area noticeably longer (Fig. 202). Deep suture with white margin present between T3-4, but distinct lateral branch, characteristic of Y-suture sometimes weak; T4-5 and T5-6 directed anteriad; S2-3 and S3-4 deep; S4-5 directed anteriad, embracing trichobothrium and not reaching abdominal margin. Trichobothrial hairs long and clearly visible in dorsal view. Pair of trichobothria on S5 equidistant between spiracle and suture 5-6 (Fig. 112). Spiracles 2, 4-8 ventral, 3 and 4 dorsal. Prothoracic femur incrassate, with one seta bearing medium spine in a row of smaller spines on antero-ventral edge (Fig. 275). Meso- and metathoracic femora with a row of small spines on antero-ventral edges. Meso and metathoracic tibiae with strong, black, erect spines. Rostrum reaching mesothoracic coxae.

*Graptopeltus lynceus* (Fabricius, 1775) (Cl. 13.9.4.2; Figs 33, 112, 202, 275)

Colour: Eyes red. Head, pronotum scutellum, MWP and pleura black; carinae, small antero-median and large triangular postero-median marks on pronotum, mesal area of scutellum and MWP margins yellow. Abdomen red-grey with an outer yellow and inner red longitudinal lateral stripe, red maculae between evaporative areas and crimson meso-lateral marks on S6-8, T8 and abdominal segments 9-10. Appendages black; femoral apices, bases of tibiae (sometimes more extensive), apical half of A1 and all of A2 yellow. Coxae and trochanters white with brown.

Structure: Body and appendages with short, adpressed pubescence and a few scattered, long erect setae on head and pronotum. Prothoracic femur with one medium length spine and usually two very small basal spines on antero-ventral edge (Fig. 275).

x 10 specimens measured: x 3 GB85.16; x 2 GB85.20; x 2 GB86.48N; x 3 GB87.47B.

*Pasatus Stål, 1872* gen. resur. (Cl. 13.9.5; Figs 34, 113, 203, 276)

Medium length, suboval to elongate, black, red, yellow and white nymphs with a stout rostrum. Pubescence short and adpressed, with scattered, long, erect and suberect setae on body. Tibiae, coxae and A1, with short, suberect, fairly stout setae. Head declivent, eyes almost touching anterior pronotal margin, trichobothria clearly visible and tylus extending, or almost extending, to apex of A1. Pronotum trapezoidal, with weak posterior transverse impression and upwardly reflexed, carinate lateral margins. MWP reaching Y-suture. Widely spaced gland apertures, with large, oval evaporative areas between T3-4, T4-5 and T5-6; anterior pair distinctly more widely spaced and with larger evaporative area than sub-equal intermediate and posterior
pairs (Fig. 203). Y-suture distinctly lined with red and white. Sutures T4-5 and T5-6 curving anteriad, S2-3 and S3-4 deep, S4-5 curving anteriad, embracing trichobothrium, but clearly reaching abdominal margin. Trichobothrial hairs visible in dorsal view. Posterior pair of trichobothria on S5 slightly closer to S6 than spiracle 5 (Fig. 113). Spiracle 3 dorsal, but almost lateral, 4 dorsal and 2, 5-8 ventral. Prothoracic femur with one small tuberculate spine on antero-ventral edge (Fig. 276).

Material examined: P. lundi x 26.

**Pasatus lundi** (Gmelin, 1793) (Cl. 13.9.5.1; Figs 34, 113, 203, 276)

Colour: Eyes red. Head, pronotum, scutellum, MWP and pleura matt-black; pronotal and MWP carinae yellow, sometimes extending to adjacent areas on MWP. Abdomen red, often with black suffusions; lateral margins greyish, faint white flame markings adjacent to evaporative areas and T5-6, and a faint meso-longitudinal black stripe sometimes present on terga. Appendages black; femoral apices, A2, often base of A3 and antennal articulations yellow. Coxae and trochanters white, with some black on trochanters.

Structure: as generic description.

x 10 specimens measured: x 2 GB86.23; x 3 GB86.48D; x 5 GB87.11C.

**Peritrechus Fieber, 1860** (Cl. 13.9.6; Figs 35, 36, 114, 204, 205, 277-279)

Medium length, oval, black, brown, red and yellow nymphs, with distinctly patterned abdomens. Eyes touching or almost touching anterior pronotal margin. Head declivent, trichobothrial hairs long, tylus reaching mid-way to two-thirds along A1. Pronotum trapezoidal, with anterior and posterior transverse impressions, lateral margins sinuate with pale, carinate, upwardly reflexed margins. MWP reaching T3, or just onto T4. Widely spaced gland apertures, with almost equal sized evaporative areas between T3-4, T4-5 and T5-6; anterior pair slightly more
widely spaced with slightly larger evaporative area than intermediate and posterior pairs (Figs 204, 205). Red and white margined Y-suture; T4-5 and T5-6 directed anteriad, S2-3, S3-4 deep and S4-5 curving anteriad, embracing trichobothrium and at most only weakly reaching abdominal margin. Trichobothrial hairs long and clearly visible in dorsal view. Posterior pair of trichobothria on S5 equidistant between spiracle and S5-6 (Fig. 114). Spiracles 2, 5-8 dorsal and 3-4 ventral. Prothoracic femur mildly incrassate and multi-spinose (Figs 277-279).


Peritrechus angusticollis (Sahlberg, 1848) (Cl. 13.9.6.2; Fig. 277)

Colour: Eyes red-black. Head, pronotum, scutellum, MWP and pleura brown-black, darkest on head and anterior of pronotum; ecdysial suture, clypeus (weakly), lateral anterior pronotal margins, part of disc, meso-lateral markings on scutellum and particularly meso-lateral areas of MWP yellow-brown; pronotal and MWP carinae yellow-grey. Abdomen similar to P. geniculatus but more red with yellow restricted. Evaporative areas weak, particularly anteriad of sutures. Appendages dark brown; A1, sometimes A2 and R4 darkest, with paler tarsi. Coxae white, trochanters mainly brown.

Structure: Head and pronotum with short, semi-erect pubescence, becoming adpressed on abdomen and almost absent from MWP. Adpressed setae on appendages, with medium-long, semi-erect setae on antennae. Tylus reaching just beyond mid-point of A1. Anterior gland apertures more widely spaced, and with larger evaporative area, than subequal intermediate and posterior pairs. Prothoracic femur with a small and very small spine in a row of tubercles on antero-ventral edge (Fig. 277). Rostrum reaching mesothoracic coxae.

x 2 specimens measured: Y89.53.
Peritrechus geniculatus (Hahn, 1832) (Cl. 13.9.6.6; Figs 35, 114, 204, 278, 296)

Colour: Eyes black-red. Head, pronotum, scutellum and MWP yellow, with black longitudinal stripes. Single meso-longitudinal stripe on head, narrower than eye width (Fig. 296) and dividing on pronotum and scutellum. Meso-longitudinal stripes on pronotum, arising just beneath eye and running continuously along inner MWP margin. Narrow continuous stripe along inner side of pronotal and MWP carinae and an additional meso-longitudinal stripe on MWP. Pleura with broad longitudinal, black stripe. Abdomen pale yellow to grey, with intricate red, to pale red-brown lateral and diagonal markings on terga (Fig. 35). Mesal markings on S6-8 and abdominal segments 9-10 black. Appendages yellow; A3-4, femoral apices, metathoracic tibia, Ts2 and R4 usually 'off black'; but extreme apices of A1, A2 apices broadly, bases of femora, pro- and mesothoracic tibiae and R1 sometimes also blackish. Coxae white, trochanters white to yellow.

Structure: Body and legs with medium-short, semi-erect pubescence, longer and more dense on antennae. Width of A1 the same as A3. Tylus extending just beyond mid-point of A1. Anterior gland apertures slightly more widely separated and with larger evaporative areas than subequal, intermediate and posterior pairs (Fig. 204). Prothoracic femur normally with one medium apical and a smaller median spine, on antero-ventral edge (Fig. 278). Sometimes only larger spine visible, or two spines present, with two more very small spines. Rostrum reaching mesothoracic coxae.

x 10 specimens measured: x 1 GB85.35A; x 2 GB86.18; x 1 GB86.46; x 2 GB86.48C; x 3 GB87.16; x 1 GB87.31.

Peritrechus gracilicornis Puton, 1877 (Cl. 13.9.6.7; Fig. 297)

Colour: Markings as P. geniculatus, but meso-longitudinal black cephalic stripe filling most of head and noticeably wider than eye width (Fig. 297). Stripes on pronotum often merging near anterior margin.
Structure: Size and pubescence very similar to *P. geniculatus*, but maximum width of A3 slightly less than maximum width of A1.

x 10 specimens measured: x 1 J89.12D; x 3 J89.20; x 6 SP89.18.

*Peritrechus nubilus* (Fallén, 1807) (Cl. 13.9.6.10; Figs 36, 205, 279)

Colour: Eyes red. Head, pronotum, scutellum, MWP and pleura black-brown. Ecdysial suture, MWP and pronotal carinae, except inner margin, all yellow. Normally, two faint to distinct yellow spots on scutellum and two longitudinal lateral yellow stripes on MWP. Further yellow marks sometimes present on basal corners of pronotum and as longitudinal stripes on MWP. Markings on abdomen as for *P. geniculatus*, but very reddish (Fig. 36). Appendages black-brown; antennal articulations, femoral apices pale and Tsl often yellow-brown.

Structure: Body with short, adpressed pubescence, slightly longer on legs, distinctly longer and semi-erect on antennae. Tylus extending to about two-thirds length of A1. Gland apertures all equally spaced in their pairs, with equal sized evaporative areas (Fig. 205). Prothoracic femur with one medium sized spine and up to seven small spines on antero-ventral edge (Fig. 279). Rostrum reaching between meso- and metathoracic coxae.

x 10 specimens measured: GB86.25.

*Ragliodes* Reuter, 1885 (Cl. 13.9.7)

No specimens available for study.

*Raglius* Stål, 1872 (Cl. 13.9.8; Figs 37, 115, 206, 280)

Medium length, narrowly elongate, almost parallel sided, black, yellow, red, grey and white, shining and/or matt nymphs with long appendages. Pubescence short and adpressed, body with long, slender, scattered, erect setae, which make trichobothrial hairs difficult to discern and
tibiae with stout black setae. Head declivent with eyes close to anterior pronotal margin, tyli extending two-thirds along A1. Pronotum quadrate, with carinate lateral margins and disc slightly to distinctly convex between anterior and postero-lateral impressions. MWP reaching T2-3 or onto T3. Equally widely spaced gland apertures, with equal sized oval evaporative areas, mainly anterior to suture, between T3-4, T4-5 and T5-6; or anterior pair slightly more widely spaced with a slightly larger evaporative area (Fig. 206). Y-suture with broad white margin continuing ventrally and forming a distinct white abdominal band. Sutures T4-5 and T5-6 curving strongly anteriad; S2-3, S3-4 deep, S4-5 curving anteriad, embracing trichobothrium and at most only faintly reaching abdominal margin. Trichobothrial hairs clearly visible in dorsal view. Posterior pair of trichobothria on S5 equidistant between spiracle and S6 (Fig. 115). Spiracles 3-4 dorsal, 2, 5-8 ventral. Prothoracic femur incrassate and multispinose on antero-ventral edge. Prothoracic femur with at least one small spine on apical postero-ventral edge (Fig. 280). Rostrum reaching mesothoracic coxae.


Raglius alboacuminatus Goeze, 1778 (Cl. 13.9.8.1; Figs 37, 115, 206, 280)

Colour: Eyes red. Head, pronotum and pleura black; ecdysial suture, pronotal carinae, posterior pronotal corners or whole posterior margin yellow, and apex of tyli sometimes infuscate. Scutellum and MWP yellow, irregularly margined with brown, particularly on MWP apices. Abdomen red with a red-grey pruinescence on T1-4 and centre of sterna; white flame markings from evaporative area margins along T4-5 and T5-6; evaporative areas, large mesal marks on S6-8, small mesal mark on T8 and abdominal segments 9-10 black. Legs sometimes almost entirely brown to black; normally with basal halves of femora and all of tarsi yellow-brown, metathoracic tibia darkest, femoral apices and most of coxae and trochanters white. Basal half of A1 dark-brown, remainder white; A2 yellow, often with faint basal and apical brown bands; A3 and A4 black. Rostrum brown.
Structure: Head, pronotal disc, scutellum, meso-lateral band on scutellum and appendages shining, remainder matt. Prothoracic femur with one medium sized antero-ventral spine, four very small apical spines, one small and two very small, more basal spines (Fig. 280). One apical, small, curved spine on postero-ventral edge of metathoracic femur and a row of short, stout setae on antero-ventral edge.

x 8 specimens measured: x 3 coll. P. Kirby, 08.1984, Hornchurch, Essex; x 5 F87.26C.

**Rhyparochromus Hahn, 1826** (Cl. 13.9.9; Figs 38, 116, 207, 281)

Medium-large, broadly elongate, black, yellow, red, grey and white, matt nymphs with long, slender appendages. Body with short, adpressed pubescence and normally only a few long, slender, erect setae on dorsum. Head declivent, tylus reaching mid-point of A1, trichobothria distinct, slightly protuberant and eyes close to anterior pronotal margin. Pronotum trapezoidal, disc sometimes slightly globose, transverse anterior impression weak, distinct carinate lateral margins weakly reflexed upwards and projecting anteriad towards eyes. MWP reaching T3. Gland apertures, with oval dark evaporative areas, between T3-4, T4-5 and T5-6; anterior pair more widely spaced and with a larger evaporative area, intermediate and posterior pairs closer together and with subequal, small evaporative areas (Fig. 207). Distinct, red and white margined Y-suture; T4-5 and T5-6 curving strongly anteriad; S2-3, S3-4 deep, S4-5 curving anteriad, embracing trichobothrium and not reaching abdominal margin. Trichobothrial hairs visible in dorsal view. Posterior pair of trichobothria on S5 equidistant between spiracle and S6 (Fig. 116). Spiracles 3-4 dorsal and 2, 5-8 ventral. Prothoracic femur mildly incrassate and unispinose (Fig. 281). Metathoracic femur with a ventral row of erect setae. Coxae and tibiae with stout erect black setae. Rostrum reaching mesothoracic coxae.

Rhyparochromus pini Linnaeus, 1758 (Cl. 13.9.9.3; Figs 38, 116, 207, 281)

Colour: Eyes red. Head, pronotum, scutellum, MWP and pleura black; pronotal and MWP carinae varying from broadly black mesally to predominantly yellow, with faint black markings. Abdomen intricately patterned maroon on grey; yellow-white flames lateral to evaporative areas, red between evaporative areas, along sutures and lateral margins; T8 with small and S6-8 with large mesal black markings, abdominal segments 9-10 black. Markings in some exceptionally brightly coloured specimens forming longitudinal red, grey and white stripes on terga. Appendages black; basal halves of femora and prothoracic tibia, extreme apices of meso- and metathoracic tibiae, A1 apart from base, A2 excepting apex all yellow; rostrum more brown-black and antennal articulations yellow. Coxae white and red, trochanters mainly yellow.

Structure: As generic description.

x 10 specimens measured: x 5 GB85.37C; x 1 GB85.61A; x 3 coll. I.D. Wallace, 15.09.1985, Symonds Yat, Worcestershire; x 1 GB86.48C.

Trichaphanus Kiritschenko, 1926 (Cl. 13.9.10)

No specimens available for study.

Xanthochilus Stål, 1874 (Cl. 13.9.11; Figs 39, 117, 208, 282)

Medium length, elongate, suboval, black, yellow, grey, red and white nymphs with long, slender appendages. Pubescence short and adpressed with some medium length erect and semi-erect setae on body. Head declivent, eyes almost touching anterior pronotal margin. Trichobothria distinct and tylus reaching mid-point of A1. Pronotum with carinate, convex, lateral margins projecting slightly forward toward eyes and a weak transverse posterior impression. MWP reaching T3, with distinct longitudinal yellow and black stripes. Gland apertures between T3-4, T4-5 and T5-6; anterior apertures
widely separated with a large oval evaporative area; intermediate and posterior pairs much closer together, with more quadrate subequal evaporative areas (Fig. 208). Y-suture margined with red and white; T4-5 and T5-6 curving anteriad; S2-3, S3-4 deep, S4-5 curving anteriad, embracing trichobothrium and not reaching abdominal margin. Trichobothrial hairs visible in dorsal view. Posterior pair of trichobothria on S5 equidistant between spiracle and S6 (Fig. 117). Spiracles 3-4 dorsal and 2, 5-8 ventral. Prothoracic femur with an apical small tuberculate seta in a row of short, stout setae on antero-ventral edge (Fig. 282). Meso- and metathoracic femora with antero-ventral rows of short, stout setae. Tibiae with stout, semi-erect and adpressed black setae. Rostrum reaching to meso- or metathoracic coxae.

Material examined: X. quadratus x 41. X. reuteri (instar 4) x 2. X. saturnius x 1. Xanthochilus sp. x 21.

Xanthochilus quadratus (Fabricius, 1798) (Cl. 13.9.11.4; Figs 39, 117, 208, 282)

Colour: Eyes red. Head, pronotum, scutellum and pleura black; pronotal and MWP carinae yellow, tinged with black and posterior margin of pronotum yellow with two meso-lateral black marks. Abdomen grey with S2 and S3 red; red markings along sutures, as lateral longitudinal stripe, between evaporative areas and as an interrupted broad meso-lateral stripe on T5-7; white flame-like markings either side of evaporative areas on T4-5 and T5-6; evaporative areas, large mesal marks on S6-8, small mesal mark on T8 and abdominal segments 9-10 black. Legs and rostrum black; femoral apices and basal two-thirds of pro- and mesothoracic tibiae yellow. Antennae yellow; apical half of A1, faint basal annulations on A4 and apical annulations on A2-3 black.

Structure: Erect, medium length setae restricted to head and venter of abdomen. Body matt. Rostrum reaching mesothoracic coxae.

x 10 specimens measured: x 9 J89.12; x 1 J89.18.
**Ligyrocoris** Stål, 1872 (Cl. 13.10.1; Figs 118, 209, 283)

Medium length, oval, fairly elongate, matt, black, brown and yellow nymphs with a pale spotted abdomen and long slender appendages. Adpressed short sparse pubescence on body, more scale-like on head, pronotum, and pleura, more compact and slightly longer on appendages; some species also with scattered long erect setae (*L. diffusus* (Uhler)). Head strongly declivent and with trichobothria. Eyes small, separated from anterior pronotal margin by half their diameter. Tylus reaching from two-thirds along A1 length to apex. Pronotum subquadrate to trapeziform (*L. diffusus*), with anterior collar, posterior transverse impression and upwardly reflexed, concave, carinate lateral margins. MWP reaching T3. Widely spaced gland apertures with transversely oblong evaporative areas between T3-4, T4-5 and T5-6; intermediate and posterior apertures and areas equal sized and significantly smaller than anterior (Fig. 209). Y-suture present, branch extending anteriad beyond suture T2-3; T4-5 and T5-6 curving sharply anteriad; S2-3 and S3-4 deeply impressed; S4-5 embracing trichobothrium, curving sharply posteriad and not reaching lateral abdominal margin. Trichobothrial hairs short and not visible in dorsal view (Fig. 118). Spiracles 2-4 dorsal, 5-8 ventral. Prothoracic femur mildly incrassate and multi-spinose (Fig. 283). Tibiae with fine dark spines. Rostrum reaching meso- or metathoracic (*L. diffusus*) coxae.


**Pachybrachius** Hahn, 1826 (Cl. 13.10.2; Figs 40, 41, 119, 210, 284, 285)

Medium length, moderately to strongly hirsute nymphs, with slender appendages. Head porrect and only slightly declivent, eyes distanced from anterior pronotal margin by
half their width and tylus only reaching to mid-point of A1. Pronotum trapeziform, with anterior collar, narrowly carinate, sometimes sinuate lateral margins and strongly developed meso-longitudinal and posterior transverse impressions. MWP reaching T3. Small, widely spaced gland apertures, with large evaporative areas between T3-4, T4-5 and T5-6; anterior apertures more widely spaced and with larger evaporative areas than intermediate and posterior apertures and evaporative areas, which are almost equal in size (Fig. 210). Distinct Y-suture present; sutures T4-5 and T5-6 curving moderately anteriad, S2-3 and S3-4 deeply troughed, S4-5 curving strongly anteriad, embracing trichobothrium, but faintly reaching abdominal margin. Trichobothrial hairs long and visible in dorsal view. Trichobothria widely separated on S5, with spiracle closer to posterior pair (Fig. 119). Spiracles 2-4 dorsal, 5-8 ventral. Prothoracic femur slightly incrassate and multi-spinose (Fig. 284, 285). Rostrum reaching meso- or metathoracic coxae.


**Pachybrachius fracticollis** (Schilling, 1829)
(Cl. 13.10.2.3; Figs 40, 119, 210, 284)

Colour: Eyes red, with black centres. Head, pronotum, scutellum, MWP and pleura predominantly brown-black. Tylus yellow-brown. Anterior pronotal margin with two inconspicuous yellow marks, either side of yellow ecdysial suture and two larger yellow posterior pronotal marks, normally concurrent with equal sized yellow areas on scutellum. Pronotal carinae yellow, with dark margination. MWP with yellow interrupted longitudinal streaks. Abdomen predominantly red-brown, centre of sterna becoming yellowish and terga with an elaborate pattern of white streaks and marks. Red suffusion variable, from light to deep crimson, but deepest red between evaporative areas. Evaporative areas, mesal marks on S7, S8 and abdominal segment 9 brown-black. Antennae variable; from completely black to yellow, with only apical half of A3 and basal half of A4 with brown suffusion. Coxae, trochanters and antennal articulations white. Legs testaceous; apical half of femora, basal half of tibiae and Tsl yellow, sometimes
with darker suffusion. Rostral segments 1-3 and basal third of R4 yellow, remainder of R4 brown-black.

Structure: Body and appendages with medium length, semi-erect, pale pubescence. Pronotum at most with faintly sinuate lateral margins. Prothoracic femur with one medium sized and one or sometimes two smaller spines, on antero-ventral edge (Fig. 284). Rostrum reaching mesothoracic coxae.

x 10 specimens measured: x 1 GB85.33; x 2 GB85.66A; x 2 coll. NCC, 03.08.1987, Dowrog Common, Dyfed; x 1 coll. NCC, 20.08.1987, Rhos Rhydd, Dyfed; x 4 coll. NCC, 12.08.1987, St. David's Dyfed.

Pachybrachius luridus Hahn, 1826 (Cl. 13.10.2.4; Figs 41, 285)

Colour: Eyes red. Head, pronotum, scutellum, MWP and pleura yellow-brown, with darker, brown-black margination; venter of head, ecdysial suture and carinate pronotal margins yellow. Abdomen yellow-brown with yellow markings, particularly along sutures, trichobothrial furrows, on lateral and meso-lateral areas of terga. Evaporative areas, apart from pale mesal areas, mesal areas of S7-8, parts of abdominal segments 8 and 9 brown-black. Basal two-thirds of A1 yellow, apical third and A2-4 yellow-brown, with darker apical suffusion. Antennal articulations, coxae and trochanters white. Legs and rostrum yellow; apical half of Ts2 sometimes testaceous and R4 with black suffusion on apical half.

Structure: Body and appendages with long, fine, fairly dense, erect and suberect pubescence. Lateral pronotal margins distinctly sinuate. Prothoracic femur armed with two medium sized and four smaller black spines on antero-ventral edge (Fig. 285) and one medium sized spine on postero-ventral edge. Rostrum reaching metathoracic coxae.

x 3 specimens measured: GB86.59C.
Paromius Fieber, 1860 (Cl. 13.10.3; Figs 120, 211, 286)

Medium-large, suboval, very elongate; often narrow, parallel sided, brown-black, yellow-white and red nymphs, with long, erect, or short, sparse pubescence and long, slender appendages. Pronotum, scutellum and MWP sometimes punctate. Head strongly porrect and non declivent; eyes distanced from anterior pronotal margin by at least half their width and tylus reaching mid-point of A1. Cephalic trichobothrial hairs short or difficult to see amongst long setae. Pronotum elongate trapezoidal, with distinct anterior collar, narrow carinate sinuate lateral margins and distinct posterior transverse and meso-longitudinal impressions. MWP reaching T3. Gland apertures with narrow or large evaporative areas between T3-4, T4-5 and T5-6; anterior pair more widely spaced and with larger evaporative areas than subequal intermediate and posterior pairs (Fig. 211). Distinct Y-suture present; sutures T4-5 and T5-6 curving strongly anteriad; sternal sutures impressed, S4-5 curving strongly anteriad, embracing trichobothrium and not or only faintly reaching abdominal margin. Trichobothrial hairs long and visible in dorsal view, or short and not visible dorsally. Trichobothria widely spaced on S5, with the spiracle closer to the posterior pair (Fig. 120). Spiracles 2-4 dorsal, 5-8 ventral. Prothoracic femur mildly incrassate, antero-ventral edge multi-spinose (Fig. 286). Rostrum reaching just beyond prothoracic coxae.


Remaudiereana Hoberlandt, 1954 (Cl. 13.10.4; Figs 121, 212, 287)

Medium length, suboval, elongate, brown nymphs, with a distinctly white spotted abdomen and very long, erect pubescence. Eyes only slightly distanced from anterior pronotal margin. Head porrect and only slightly declivent. Tylus reaching about two-thirds along A1. Pronotum subquadrate, with an anterior collar, narrowly sinuate carinate lateral margins and a posterior transverse impression. Widely spaced gland apertures, with elongate, broad evaporative areas between T3-4, T4-5 and T5-6;
anterior gland apertures very slightly more widely spaced and with a slightly larger evaporative area than intermediate and posterior pairs (Fig. 212). Distinct Y-suture present; T4-5 and T5-6 curving anteriad; S2-3, S3-4 deeply impressed and S4-5 curving sharply anteriad, embracing trichobothrium, but weakly reaching abdominal margin (Fig. 121). Trichobothrial hairs very long and easily visible in dorsal view. Trichobothria widely spaced on S5 with the spiracle closer to the posterior pair. Spiracles 2-4 dorsal, 5-8 ventral. Prothoracic femur mildly incrassate with a medium-small and small antero-ventral spine (Fig. 287). Rostrum reaching to mesothoracic coxae.

Material examined: *R. annulipes* x 20.
The biogeography of the majority of the invertebrates in the British Isles is poorly known (Vincent, 1990). The national Biological Records Centre, established in 1964, has co-ordinated invertebrate recording schemes and produced many provisional distributional atlases. However, there are no maps for the Heteroptera and insect recording coverage, except for Macrolepidoptera and Odonata, compares unfavourably with that for flora and breeding birds (Perring & Walters, 1962; Sharrock, 1976).

Little attempt has been made to analyse the biogeographical implications of most distribution maps. Notable exceptions are found in Hawksworth (1974) and Dennis (1992). Yet there is a good case for the study of biogeography centred on distribution studies. One compelling argument is the need for spatial bench-marks, without which it is impossible to evaluate the impacts of natural and man-made environmental changes on fauna and flora (Vincent, 1990).

Distribution is non-random (Myers & Giller, 1988) and dynamic and is affected by major abiotic processes such as tectonic movements of plates, eustatic changes in sea level and changes in climate, together with more localised fires, hurricanes, floods and volcanic eruptions. Biotic processes are both evolutionary and ecological, involving factors such as speciation, extinction, adaptation, predation and competition. The impact of man’s agricultural, industrial, mining and forestry activities, together with the land requirements of a rapidly expanding world population, are increasingly modifying habitats, normally, but not always, detrimentally, and fragmenting their associated insect populations.

This section attempts to interpret British lygaeid distributions in geographical space and time. British species distributions are related to their ecology and to the Palaearctic and world lygaeid fauna.

A number of phytogeographical and zoogeographical regions
or elements have been identified for the British Isles (e.g. Forbes, 1846; Watson, 1847-49; Matthews, 1937; Jardine, 1972; Jermy & Crabbe, 1978). West-European categories used follow Fitter (1978) and Palaearctic subregions follow Zohary (1966). British status categories for Lygaeidae follow Kirby (1992) for Red Data Book and Nationally Notable species and are taken from the 'Recorder' software package (Ball, 1992a) for local and common species. Status definitions follow Shirt (1987). The range of a species is the total geographical area throughout which it occurs, its distribution refers to the geographical location of populations within this range (Beirne, 1952).

11.1 Caution on Interpretation of Data

The distribution maps (maps 6 - 93) indicate the presence in a 10km square, of a species at a particular time. The closed symbols relate to records of species within the last 20 years and the open symbols to earlier records. Many relate to late nineteenth- and early twentieth-century captures at locations where the habitat may have changed. Some are for casual, non-breeding species, others relate to mobile species, associated with transitory, early successional habitats.

Map 3 shows all records collated for 10km squares. Care must be taken when interpreting such data. The absence of a symbol does not mean that a species is not breeding within a 10km square. Recording, for most invertebrate schemes, is biased to low-lying areas of Southern England and maps often reflect accessibility, classic insect collecting sites and the distribution and intensity of active Heteroptera recording.

Cumulative data acquisition obscures extinctions and declines in the range of species. Changes in species abundance cannot be detected from 'dot maps'. A decline in the range of a species does not necessarily imply a decline in its national abundance or a requirement for proactive conservation. Conversely, a species may be under threat, even if it has not declined in its overall range. The 10km square mapping scale is crude and species
recording cannot be related to habitat. Symbols are centred within the 10km square: this is not a problem when looking at coarse distributions, but would be for smaller scale county recording schemes. Grid squares are unnatural units, as nature abhors straight lines (Stamp, 1962) and they mask physical and biological information, which relates to the presence of the species at a location e.g. elevation. They are, however, analogous to quadrats used in ecological surveys, and should permit future, fixed-interval, repetition of surveys.

Climate is the most important influence on plant and animal distribution (Vincent, 1990), particularly summer heat, winter cold and precipitation. It is conventional to relate climatic zonation to distribution. Tout (1976) figured mean July and January isotherms for Britain whilst the length of the growing season was mapped by Fairbairn (1968). Care again must be taken, in relating distributions to environmental variables. The boundaries of these variables, e.g. isotherms, are statistical averages, and do not, in this case, reflect the micro-climates which strongly influence local animal and plant distributions. It is the extreme environmental variables and not averages that are often of most relevance to lygaeid distribution.

During historic time, changes in plant and animal distribution have been affected, to some extent by man, and as far as climate changes are concerned, we must be cautious. Climatic variables are highly interdependent and synoptic climatic variables may not relate in any simple way to conditions experienced by an organism (Carter & Prince, 1985). For this reason, the length of the growing season gives a natural correlation of numerous climatic factors.

Correlations are too often invested with causative significance, which is theoretically unsound and may be coincidental. Geographical elements are normally grouped subjectively by eye, but Jardine (1972) recognised a tendency for the eye to find groupings where they do not exist leading to pre-conceived conceptions and biased interpretation.

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British taxonomists have been insular in the past (Smith, 1974). Discussion of change, according to Hammond (1974), will have a much sounder basis when the taxonomy of the British species is more fully understood and when more extensive and reliable data concerning habitat and distribution are available. He felt that our knowledge of the present day British Coleoptera fauna was inadequate for any discussion of past change.

The study of insect biogeography is still a young discipline (Gressitt, 1959). Although these reservations must not be forgotten, there is still great value in interpreting British lygaeid distributions, and relating them to Palaearctic and world distribution patterns.

11.2 Palaearctic Lygaeid Subfamilies, Tribes and Genera and British Species in Relation to the World Lygaeid Fauna

Ten of the 17 lygaeid subfamilies occur in all six of the world's major biogeographical regions (Slater, 1964a) (Table 7). Of these ten, the Oxycareninae, although widely distributed, have most species restricted to the Palaearctic. Thirteen subfamilies are represented in the Palaearctic, although none is endemic, unlike three of the remaining subfamilies, Cryptorhamphinae, Henicocorinae and Slaterellinae, which are restricted to Australia. Psamminae are Ethiopian and Oriental and do not occur in the Palaearctic. Bledionotinae are Holarctic and Neotropical, with a depauperate Palaearctic fauna, whilst the Palaearctic Artheneinae are absent from the Nearctic (apart from adventives) and the primarily Palaearctic Henestarinae do not occur in the Australian or Nearctic regions.

Vicariance biogeography places great emphasis on new barriers, subdividing a previously continuous range of distribution, rather than on species dispersing across a pre-existing barrier as in the older 'dispersal approach'. However, we are not yet ready to distinguish vicariant from dispersal patterns in the Rhyparochrominae (Slater (1986), or for the other subfamilies. Certain rhyparochromine tribes, in particular, are not defined on the basis of synapomorphies (Slater & Woodward, 1982) and
might be unsuitable for biogeographic analysis.

Two rhyparochromine tribes, the Gonianotini and Me galonotini, together with the Artheneini are primarily Palaearctic. Gonianotini conform perfectly to the idea of a Holarctic group that arose in the Palaearctic and crossed through Beringia into North America (Slater, 1986). Others, such as the Plinthisini, which previously were thought to be primarily Palaearctic, are more widely spread, although there is a large concentration of Mediterranean Plinthisus species. Furthermore, the African representation of the Stygnocorini was recently increased by 22 species and five new genera (Slater & Sweet, 1970b; O’Rourke, 1974, 1975; Slater, 1982) and this tribe is now thought to show strong secondary radiation in the Palaearctic (Slater, 1986).

Many Geocorinae are Eremian in distribution and the family is surprisingly absent from Britain, given the presence of three Geocoris species in Northern France and Holland. Pachygronthinae are predominantly tropical and subtropical in distribution, with a relict halophytic, grass-feeding fauna, of four closely related Cymophyes species that occur eastwards from the East Mediterranean.

Table 7. Distribution of Lygaeid Subfamilies by Major World Biogeographical Regions

<table>
<thead>
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<th>Palaeartic</th>
<th>Ethio plan</th>
<th>Oriental</th>
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<th>Neotropical</th>
<th>Nearctic</th>
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| 13 | 13 | 13 | 14 | 12 | 11 |
The Pleistocene ice ages stripped North America and Northern Eurasia of virtually all tropical and subtropical animals and plants. This happened so recently that the faunas and floras have, as yet, had little time to develop new characteristic groups (Cox & Moore, 1985). The Palaearctic fauna is isolated from the richer tropical faunas in the south by the Himalayas and by the North African and Southern Asian deserts. Very few species have been able to cross these barriers by 'jump dispersal'.

Table 8, based primarily on Slater (1964a), shows the distribution of West Palaearctic genera across other major world biogeographical regions; those occurring in Britain are marked with an asterisk (*). The West Palaearctic fauna is characterised by its hardiness and relative poverty, compared to tropical faunas. A significant 47% of these genera are endemic to the West Palaearctic and 13 of these genera occur in the British Isles. There are no endemic British Lygaeidae and the three major centres of endemism in the West Palaearctic - the Iberian peninsula (ten species), Turkey (nine species) and the Caucasus (six species) are all mountainous regions occurring below 45 degrees latitude (Table 9).

Movements of species into Britain must be seen in the context of changes in continental Europe. It is likely that some species previously confined to true steppe conditions entered Britain following an advance across much of Europe. The east-west orientation of the Alps and Pyrenees permitted no escape south from cryogenic conditions, and although the maritime fringe of Western Europe must have provided a particularly favourable migration route for southern species during the period following the retreat of the glaciers, there still remains a significant Iberian endemic lygaeid fauna. Some of this may have come in from North Africa where it took refuge and where it no longer occurs.

None of the 90 British or Channel Island species is cosmopolitan and 79% are restricted to the Palaearctic. Thirteen percent of species extend into the Oriental region and only five species also occur in the Ethiopian region (Table 10).
Some common West European taxa have asymmetric ranges which just extend into North America. This commonality of Europe and North America is supported by a wealth of evidence, especially from stratigraphic geology (Cracoft, 1974). Twenty-two West Palaearctic genera are also Nearctic (Table 8) and only five of these, *Melanocoryphus, Geocoris, Camptocera, Ligyrocoris* and *Paromius*, are absent from Britain.

There is a significant (11%) North American element in the British lygaeid fauna (Table 10). Four of these ten species are orsillines; *Ortholomus punctipennis* is circum-Boreal and occurs throughout all the Euro-Siberian and Mediterranean subregions and into the Irano-Anatolian subregion, whilst *Nysius ericae, N. helveticus* and *N. thymi* both extend into the Oriental region as does the taxonomically problematic ischnorhynchine, *K. resedae* and the gonianotine *Trapezonotus arenarius*. The two myodochines, *Pachybrachius fracticollis* and *P. luridus*, are essentially Euro-Siberian, as is *Scolopostethus thomsoni*, which also occurs in the Mediterranean.

Care must be taken not to confuse these distributions with those resulting from recent artificial introductions to the United States. More than half of the British Coleoptera species regarded as ‘culture favoured’ now occur as introductions to North America (Hammond, 1974). This accidental introduction, establishment and dispersal of insects is a dynamic problem of contemporary biogeography (Elton, 1958). The five Palaearctic lygaeid adventives to the United States, *Plinthisus brevipennis, Megalonotus sabulicola, Stygnocoris rusticus, S. sabulosus* and *Chilacis typhae* (Wheeler, 1983; Wheeler & Fetter, 1987; Wheeler, 1989; Asquith & Lattin, 1993), are all, apart from *Megalonotus sabulicola*, common British species. They occur in coastal habitats and were probably introduced to North America in ships' ballast.
### Table 8. Natural Distribution of West Palaearctic Lygaeid Genera by Major World Biogeographical Regions (Excluding Adventives)

* Denotes British genera; ** British vagrants; *** Channel Island genera not found in Britain.

<table>
<thead>
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<th>Lygaeinae</th>
<th>Palaeo-</th>
<th>Ethi-</th>
<th>Oriental</th>
<th>Austr-</th>
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Table 9. Lygaeidae Endemic to Particular West Palaearctic 'Countries' or Regions

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| Henestarinae                   |                          |                          |
| Engistus commendatorius        | Spain                    |                          |
| Henestaris kareli              | Turkey                   |                          |

| Geocorinae                     |                          |                          |
| Geocoris chloroticus           | Portugal                 |                          |
| G. erythrophthalmus            | Turkey                   |                          |

| Oxycareninae                   |                          |                          |
| Auchenodes capito              | Russia/Caucasus          |                          |
| Bianchiella sarmatica          | Russia                   |                          |
| Neocamptotelus aeonii          | Caucasus                 |                          |
| Oxycarenus longiceps           | Sicily                   |                          |

| Rhyparochrominae               |                          |                          |
| Plinthisini                    |                          |                          |
| Plinthisus laevigatus          | Spain                    |                          |
| P. bicolor                     | France                   |                          |
| P. lusitanicus                 | Portugal                 |                          |
| P. megacephalus                | Spain                    |                          |
| P. soongoricus                 | Caucasus                 |                          |
| P. subcarinatus                | Turkey                   |                          |

| Drymini                        |                          |                          |
| Drymus major                   | Turkey/Cyprus            |                          |
| Eremocoris oblitus             | S. Russia/Caucasus       |                          |
| Taphropeltus championi         | Spain                    |                          |

| Gonianotini                    |                          |                          |
| Emblethis karamanus            | Turkey                   |                          |
| E. kareli                      | Turkey                   |                          |
| E. osmanus                     | Turkey                   |                          |
| E. sabulosus                   | Turkey                   |                          |
| Gonianotus parilus             | Russia                   |                          |
| Pionosomus depressus           | Italy                    |                          |
| Pterotmetus parnassius         | Greece                   |                          |
| Trapezonotus breviceps         | Russia/Caucasus          |                          |
| T. montanus                    | Spain                    |                          |

| Megalonotini                   |                          |                          |
| Metastenothorax punctatipennis | Greece                   |                          |

| Rhyparochromini                |                          |                          |
| Peritrechus insignis           | Russia/Caucasus          |                          |
| Rhyparochromus ibericus        | Spain                    |                          |
| R. seidenstuckeri             | Turkey                   |                          |

Totals by Country, Island or Region

|                  |                          |                          |
| Iberian          | 10                       | Russia 2                 |
| Turkey           | 9                        | Greece 2                 |
| Caucasus         | 6                        | France 1                 |
| Italy            | 2                        |                          |

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Table 10. West Palaearctic and World Distribution of British and Channel Island Lygaeid Species

W West; N North; S South; E East; At Atlantic; Bo Boreal; Me Medio-Europae; Po Pontic; Mp Mesopotamian; IA Irano-Anatolian; MA Medio-Asiatic; Ma Macaronesian; Nt Neotropical; Na Nearctic; Et Ethiopian; Or Oriental; * adventives.

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<td>+ - - -</td>
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<td></td>
</tr>
<tr>
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<td>- - - -</td>
<td>+ - - -</td>
<td>- - - -</td>
<td></td>
</tr>
<tr>
<td>P. gracilicornis</td>
<td>+ - + +</td>
<td>+ + + +</td>
<td>+ + + +</td>
<td>- - - -</td>
<td>- - - -</td>
<td></td>
</tr>
<tr>
<td>P. nubilus</td>
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<td>+ + + +</td>
<td>- - - -</td>
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<td>R. alboacuminatus</td>
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<tr>
<td>P. fracticollis</td>
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<td>- - - -</td>
<td>- - - -</td>
<td>- - - -</td>
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<tr>
<td>P. luridus</td>
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<td>- - - -</td>
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</tr>
</tbody>
</table>

**TOTALS** 90 66 89 75 42 57 51 71 77 63 57 24 5 15 1 10 5 12
11.3 Relationship of the British Lygaeid Fauna to the Palaearctic Fauna

Southwood (1957) could not categorise all the British Heteroptera as representatives of his five Holarctic biogeographical areas. He made little reference to the Lygaeidae which, as shown (Table 10), are not problematic, and have remarkably uniform generalised West Palaearctic distributions.

Fitter (1978) found that the Atlantic species of vascular plants were a very large and important group within the flora of the British Isles. This is not paralleled in the Lygaeidae and only Drymus pumilio and perhaps Taphropeltus limbatus have a truly Atlantic distribution. The majority of the British and Channel Island species are widely distributed, with 58 species, 64%, occurring across the Euro-Siberian region, occurring in the Boreal, mid-European and Pontic subregions and most extending into some, but not necessarily all, of the Mediterranean subregions.

Chilacis typhae and Peritrechus distinguendus have a Euro-Siberian distribution, but are northern and absent from the Mediterranean. The specialised niche of Chilacis typhae, which lives inside Typha heads, is occupied by Holcocranum saturejae, another artheneine, in Mediterranean regions.

Frost and exposure, on skeletal soils, in high uplands, restrict the distribution of diapausing lygaeids. None of the Scottish species is purely Boreal in distribution and 24 cold-intolerant species are absent from this region. Many absentees are found where there is a strongly developed soil horizon of mull litter or chalk rendzina to mor litter. Two species, Scolopostethus grandis and S. puberulus, are essentially mid-European and continental. The remainder have their distributional foci further south, but none is predominantly Mediterranean and Henestaris laticeps, described by Southwood (1957) as strikingly Mediterranean, also occurs in Central Europe.

The westerly British distributions of Pterotmetus staphyliniformis (Map 66) and Trapezonotus ullrichi (Map 70) are paralleled by Lusitanian plants such as Erica
vagans, the Cornish Heath. However, both are widely distributed throughout the Palaearctic and there is no Lusitanian faunal element amongst British or Irish Lygaeidae.

The British lygaeid fauna is depauperate with only 18% of the West Palaearctic species present as breeding populations. This conforms to the conventional island biogeography equilibrium model of colonisation and extinction (MacArthur & Wilson 1963), which states that the fauna of an island is related directly to its size and proximity to continental mainland and that islands support fewer species than similar areas on the mainland.

11.4 Comparison with the Turkish Fauna

Seven weeks fieldwork, during this study, was undertaken in Turkey, and a brief comparison between the British and Turkish lygaeid faunas is instructive. The countries have 42 species in common, but their faunas differ markedly due to their respective latitudes, relative positioning, and physical geographies.

Unlike Britain, there is no amateur and little professional entomological tradition in Turkey. Most distributional information, including 712 unique species records, resulting from this study, originates from foreign expeditions, the most notable being that of the Czechoslovakian National Museum in Prague (Hoberlandt, 1955). The Turkish lygaeid fauna is poorly understood and distributional knowledge is minimal. This places earlier criticism of British distributional knowledge into a somewhat different perspective.

Turkey was not covered by Pleistocene ice sheets. It is the meeting ground of three biogeographical subregions: Euro-Siberian, Mediterranean and Irano-Turanian and is a biological melting-pot. Unlike island Britain, this has produced a large, old and diverse lygaeid fauna.

Hoberlandt (1955) surveyed the biogeographical elements of the Turkish Heteroptera. A comparison with the British Lygaeidae is summarised in Table 11.
Table 11. Comparison of Biogeographical Elements in the Turkish and British Lygaeid Faunas

<table>
<thead>
<tr>
<th>Biogeographical Element</th>
<th>Turkish spp.*</th>
<th>British spp.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intertropical</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Ethiopian</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Endemic</td>
<td>8</td>
<td>0</td>
</tr>
<tr>
<td>Caspian</td>
<td>3</td>
<td>0</td>
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<tr>
<td>Holomediterranean</td>
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<td>0</td>
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<tr>
<td>Pontomediterranean</td>
<td>32</td>
<td>0</td>
</tr>
<tr>
<td>Iranian</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Irano-Turanian</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Eremian</td>
<td>9</td>
<td>0</td>
</tr>
<tr>
<td>Euro-Siberian</td>
<td>20</td>
<td>74</td>
</tr>
<tr>
<td>Holarctic</td>
<td>4</td>
<td>10</td>
</tr>
<tr>
<td><strong>Totals</strong></td>
<td><strong>161</strong></td>
<td><strong>84</strong></td>
</tr>
</tbody>
</table>

* Based on Hoberlandt (1955)

There is a marked horizontal and vertical difference in vegetational zone composition. Altitudinal zonation of plants and animals in Turkey does not reflect global latitudinal zonations, complicating the use of simple distribution maps, which require altitudinal overlays for interpretation.

The British lygaeid fauna is clearly impoverished. It is young and has only been isolated from Europe for a short period. The flora and fauna are essentially re-immigrant (Vincent, 1990) and according to Walters (1978) contain no clear case of palaendemic species, which might be a relict from a pre-glacial flora. The percentage of endemics is usually a good guide to the length of time an area has been isolated. Approximately 20% of the Turkish plants are endemic and about a third are, at present, known from only one locality - generally in the mountains; they are almost absent from European Turkey (Davis, 1965). Nine lygaeid species (6% of the Turkish lygaeid fauna) are endemic.

11.5 Notable Turkish Records

A provisional total of 135 lygaeid species have been recorded for Turkey in this study, either as adults, or nymphs (Hoberlandt (1955) recorded 161 species). These include two species, a bledionotine and cymine, that are
probably new to science. Adult Gonianotus specimens and a single Eremocoris are also problematic and may include new species.

The following 17 species are first records for Turkey. Species names followed by a ? are provisional identifications: - Arocatus longiceps, Nysius eximius?, Engistus salinus, Geocoris pubescens, Piocoris scutellatus, Leptodemus bicolor, Oxycarenus luteolus?, Artheneis aegyptiaca, Lasiosomus enervis, Ischnocoris punctulatus, Scolopostethus thomsoni, Taphropeltus nervosus, Diomphalus hispidulus, Megalonotus puncticollis, Piezoscelis staphylinus, Peritrechus lundi and Xanthochilus minisculus.

A record from the Develi district of Kayseri, for Megalonotus tricolor, a North Anatolian mountain range endemic, known previously only from its type locality at Tokat, is notable.

Full data are provided in Appendix 5.

11.6 Distributional Abundance of British Lygaeidae

Species are listed in Table 12 in increasing order of rarity. The British Lygaeidae are primarily southern in distribution and all species, except probably Eremocoris abietis, occur south of an imaginary Thames - Severn line. Only 37% occur north of an imaginary Mersey - Humber line. Half of the total fauna is common or local in status (Table 12). Eighteen percent of British Lygaeidae are Red Data Book (RDB) species and are Endangered (RDB 1), Vulnerable (RDB 2) or Rare (RDB 3); a further 24% are Nationally Notable (Table 12).

The majority of the 15 British Red Data Book species are widely distributed, often common, species within a wider Palaearctic context (Table 10). The rare, Atlantic, Drymus pumilio (Map 42), which has been down-graded to Nationally Notable status, is our most significant Palaearctic species and deserves re-grading to RDB 3. Taphropeltus limbatus (Map 61) and Drymus latus (Map 38) also appear to be rare Palaearctic species.
<table>
<thead>
<tr>
<th>Species</th>
<th>Total 10km Records</th>
<th>Status</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 Stygnocoris sabulosus</td>
<td>315</td>
<td>Common</td>
</tr>
<tr>
<td>2 Drymus sylvaticus</td>
<td>279</td>
<td>Common</td>
</tr>
<tr>
<td>3 Scolopostethus thomsoni</td>
<td>249</td>
<td>Common</td>
</tr>
<tr>
<td>4 Scolopostethus decoratus</td>
<td>226</td>
<td>Common</td>
</tr>
<tr>
<td>5 Drymus brunneus</td>
<td>203</td>
<td>Common</td>
</tr>
<tr>
<td>6 Scolopostethus affinis</td>
<td>202</td>
<td>Common</td>
</tr>
<tr>
<td>7 Stygnocoris fuliginous</td>
<td>189</td>
<td>Common</td>
</tr>
<tr>
<td>8 Heterogaster urticae</td>
<td>164</td>
<td>Common</td>
</tr>
<tr>
<td>9 Kleidocerys resedae</td>
<td>163</td>
<td>Local</td>
</tr>
<tr>
<td>10 Gastrodes grossipes</td>
<td>158</td>
<td>Common</td>
</tr>
<tr>
<td>11=Cymus glandicolor</td>
<td>150</td>
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</tr>
<tr>
<td>11=Peritrechus geniculatus</td>
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<td>Local</td>
</tr>
<tr>
<td>13 Stygnocoris rusticus</td>
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</tr>
<tr>
<td>14 Taphropeltus contractus</td>
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<td>Local</td>
</tr>
<tr>
<td>15 Ischnodemos sableti</td>
<td>114</td>
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<tr>
<td>16 Kleidocerys truncatulus</td>
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<td>Local</td>
</tr>
<tr>
<td>17 Plinthus brevivipennis</td>
<td>105</td>
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<tr>
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<td>103</td>
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<td>19=Macrodema microptera</td>
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<td>Local</td>
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<tr>
<td>19=Pasatus lundi</td>
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</tr>
<tr>
<td>21 Drymus ryei</td>
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<td>22=Cymus claviculus</td>
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<td>Common</td>
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<td>24 Chilacis typhae</td>
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<td>25 Nysius thymi**</td>
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<tr>
<td>26 Rhyparochromus pini</td>
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<td>27 Megalonotus dilatatus</td>
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<tr>
<td>28 Nysius ericae**</td>
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</tr>
<tr>
<td>29 Trapezonotus arenarius*</td>
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</tr>
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</tr>
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<tr>
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<tr>
<td>43 Gastrodes abietum</td>
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<td>46 Eremocoris podagrificus*</td>
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</tr>
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</tr>
<tr>
<td>49 Trapezonotus desertus**</td>
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</tr>
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<td>Status</td>
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<td>52=Megalonotus sabulicola</td>
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</tr>
<tr>
<td>55 Nysius helveticus</td>
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<tr>
<td>56 Eremocoris plebejus</td>
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</tr>
<tr>
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</tr>
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</tr>
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</tr>
<tr>
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</tr>
<tr>
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</tr>
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<tr>
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</tr>
<tr>
<td>(Nysius graminicola)</td>
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<td>RDB3</td>
</tr>
<tr>
<td>(Nysius senecionis)</td>
<td>1</td>
<td>Vagrant</td>
</tr>
<tr>
<td>(Peritrechus angusticollis)</td>
<td>1</td>
<td>Vagrant</td>
</tr>
</tbody>
</table>

Past taxonomic confusion means that some records for specimens marked with a * might be wrong and species marked with ** are under-recorded. Species in parentheses are vagrants.

Status categories are taken from Ball (1992a) and Kirby (1992).
11.7 Range and Distribution of Lygaeidae within the British Isles

The British lygaeid species divide into the following distributional categories:

11.7.1. Cold Tolerant Species

Species that occur throughout the British Isles, can survive mean January temperatures of three degrees Centigrade, and occur in areas with less than a 200 growing day year. Their range extends beyond the predominantly English leached brown soils and related gleys into acid brown soils and semi-podzols. They subdivide as follows:

11.7.1.1 Ubiquitous, widely distributed species

These include species with a wide environmental tolerance range as adults and nymphs. The eurytopic *Stygnocoris sabulosus* (Map 37), Britain’s commonest lygaeid (Table 12), has a broad range of habitat preferences. *Nysius ericae* (Map 10) and *Nysius thymi* (Map 14) are commoner than their distribution maps suggest. Past taxonomic confusion means that many records cannot be correctly attributed to either species. Both are classic ‘r-selected species’ with highly efficient dispersal mechanisms. They are associated with Compositae on disturbed and early successional sites. *Scolopostethus thomsoni* (Map 58) and *S. decoratus* (Map 54) inhabit the litter of their abundant and widely distributed host plants, *Urtica dioica* and *Calluna vulgaris/ Erica spp.*. Arboreal *Gastrodes grossipes* (Map 50) is found in pine cones and has spread with increased afforestation of marginal land. *Drymus brunneus* (Map 41) occurs in dry and wet deciduous leaf litter and is found on peat bogs.

11.7.1.2 Widely distributed local species

These species are restricted to a locally occurring habitat, such as *Lamproplax picea* (Map 52) in or adjacent to peat bogs, or, on a restricted host plant, such as *Gastrodes abietum* (Map 49), which is associated with plantations of Norway Spruce.
11.7.1.3 Common southern species which are increasingly rare in the north

These include Kleidocerys resedae (Map 15), K. truncatulus (Map 16), Pasatus lundi (Map 79), Stygnocoris fuligineus (Map 35), Macrodema microptera (Map 64), Drymus ryei (Map 43), D. sylvaticus (Map 44) and Scolopostethus affinis (Map 53).

11.7.2. Widely Distributed Lowland Species

Stygnocoris rusticus (Map 36), Chilacis typhae (Map 27) and Cymus glandicolor (Map 19) all have a range that extends beyond the classic Severn - Humber distributional limit of so many British invertebrates. However, they are absent from colder and wetter upland areas in Wales and Scotland. It will be interesting to know if C. typhae (Map 27) is truly absent from much of the South-West, where its foodplant Typha latifolia is uncommon. Pachybrachius fracticollis (Map 88) has a marked west-east distributional break, occurring in the heads of Eriophorum angustifolium in western bogs and on Carex spp. in eastern fens. There is also a small southern cluster of records for the New Forest. Megalonotus chiragra (Map 72) and Peritrechus geniculatus (Map 82) occur in a wide variety of habitats (Table 15). Acompus rufipes (Map 33) and Scolopostethus grandis (Map 55) probably also belong in this category.

11.7.3. Species with a Range Reaching to, but Predominantly South of, an Imaginary Severn - Humber Line

One hundred and forty British plants reach their northern limits along this line (Salisbury, 1932, Matthews, 1937, 1955, Carter & Prince, 1985). This range balances higher summer rainfall in the west and higher temperatures in the south. It reflects the climatic contrast between the cool, wet, upland regions in the north and west of Britain and the warm, dry, lowland regions in the south and east. The wide annual temperature range correlates with a high K value in Conrad's continentality index (see Vincent, 1990). Further subdivision can be recognised:-
11.7.3.1 Species that become coastal at the limits of their westerly range, as they extend into South-West England and into South Wales. They are absent from western, upland areas of higher precipitation:-

This coastal extension of range corresponds with a growing season of 260 days. A number of these coastal species are at their northern and, in some cases, western limits in Great Britain. Many are coastal only at the limits to their British range and are common inland on the continent. These include Cymus melanocephalus (Map 20), Ischnocoris angustulus (Map 51), Megalonotus antennatus (Map 71), M. sabulicola (Map 75), M. praetextatus (Map 74), Rhyparochromus pini (Map 86), Graptopeltus lynceus (Map 78) and Peritrechus nubilus (Map 84).

Heterogaster urticae (Map 29), Plinthisus brevipennis (Map 30) and Taphropeltus contractus (Map 59) also have outlying populations along the English North-West coast and Scolopostethus pictus (Map 56), which probably also belongs in this category, has a relict Scottish population on the Solway coast (Crossley, 1975), a well known refugium for warmth loving southern species (Crowson, 1967).

11.7.3.2 Central and South-Easterly species

Typical species with this range include Drymus latus (Map 38); D. pilicornis (Map 39), Eremocoris podagricus (Map 48), Trapezonotus dispar (Map 69) and Cymus melanocephalus (Map 20). Ischnodemus sabuleti (Map 22) falls into this category, but has undergone a range expansion, which is discussed later. T. dispar (Map 69) occurs in moss and leaf litter, in open, sunny areas of coppiced woodland and along rides. There is a strong correlation between its distribution and areas of recent coppicing as mapped by Peterken (1981). Coppicing increases light on the woodland floor and thereby affects temperature and humidity (Rackham, 1967).

11.7.4 Eastern Species

Ortholomus punctipennis (Map 9) occurs on, or close to, the coast at four widely separated easterly locations, but its
centre of distribution is the Suffolk Brecklands, where a number of discrete populations have been recorded. This species may be a recent coloniser of Britain. There are two historic westerly records for *Raglius alboacuminatus* (Map 85), but this species seems to be strongly associated with the widely distributed plant, *Ballota nigra* only in South-East and Eastern England.

11.7.5 Extreme Southern Species

These stenotopic species are sun and warmth loving. *Nysius helveticus* (Map 12) is restricted to sheltered, warm, south facing slopes on Dorset, New Forest and Surrey heaths. *Pachybrachius luridus* (Map 89) has a similar distribution, but is found in *Sphagnum*. A Welsh record requires confirmation. *Heterogaster artemisiae* (Map 28), *Tropistethus holosericeus* (Map 31), *Drymus pilipes* (Map 40) and *Taphropeltus hamulatus* (Map 60) occur primarily on chalk escarpments and along the coast.

Other species are strictly coastal. They are often on the extremes of their range in North-West Europe and occur inland in Central and Southern Europe. *Henestaris halophilus* (Map 23) and *Beosus maritimus* (Map 77) are the most widely distributed. The latter is common along the western coastline, very localised along the south-coast and there are isolated colonies in the south-east. The disjunct east-west distribution of *Emblethis griseus* (Map 63) and *Pionosomus varius* (Map 65) is interesting, as this is unusual in plants (Carter & Prince, 1985).

Other extreme southern species are *Acompus pallipes* (Map 32), *Drymus pumilio* (Map 42) and *Taphropeltus limbatus* (Map 61). *Megalonotus emarginatus* (Map 73) is a recent addition to the British list and may prove more widespread. However, a search for misidentified specimens standing as *Megalonotus chiragra* (Map 72) in collections has not revealed many new records. *Taphropeltus limbatus* (Map 61) and *Aphanus rolandri* (Map 62) appear to be contracting in their ranges toward the south-coast, but there is a puzzling, recent record, of the latter for Warwickshire.
11.7.6 South-Eastern Species

*Henestaris halophilus* (Map 23) is only now known from salt marshes along the Thames estuary. An old West Country record is probably in error for *H. laticeps*.

*Cymus aurescens* (Map 17) occurs on its localised host plant, *Scirpus sylvaticus*, in Kent, Surrey and Berkshire, together with the more polyphagous and widely distributed *C. glandicolor*. However, it is recorded from *Carex* and *Juncus* on the continent (Stichel, 1957-1959). A life-cycle study of three sympatric *Cymus* species in Connecticut showed that adults feed on more than one food plant but nymphs are host plant specific. Where the host plant is shared by two species, their life cycles were temporally separated ensuring that they are not in direct competition (Hamid, 1971a). Thus, *C. aurescens* may well be outcompeted by *C. glandicolor* (Map 19) throughout most of the British Isles. A study is required, to investigate inter-specific relationships between these species. Populations of both occur on *S. sylvaticus*, at the Imperial College Field Station, Silwood Park, Berkshire!

11.7.7 South-Western Species

*Pterotmetus staphyliniformis* (Map 66) occurs along a restricted stretch of the Cornish, Land's End coastline and *Macroplax preyssleri* (Map 25) is associated with *Helianthemum* spp. either side of the Bristol Channel. Both were added to the British list in the last 32 years (Table 16). *Trapezonotus ullrichi* (Map 70) is locally distributed along the coast from Devon to Pembroke. These species occur in the most maritime parts of the country, with the lowest K values on Conrad's continentality index. They appear to prefer a mild, temperate climate, with a small annual temperature range and are limited by winter extremes of cold. Their distribution correlates with the area having the longest growing season, of over 300 days. *Pterotmetus staphyliniformis* is restricted to the only part of Britain with a 365 day growing season.

It is unlikely, because of the distance from the continent, that these species are recently established from adventive
stock. They appear relicts from a much wider distribution and, if they are sensitive to low winter temperatures, must have arrived before the British Isles was separated from the continent. They would have been driven south during the Pleistocene, and Southwood (1957) considered that species with this range in Britain have subsequently became modified, so that they were unable to spread northwards again during warmer conditions.

11.7.8 Recently Established Introductions

Orsillus depressus (Map 8), a recent addition to the Netherlands and Belgium (Aukema, 1988), has extended its range into North-West Europe. It was first recorded in Britain, in 1987, from Surrey on Lawson’s Cypress, Chamaecyparis lawsoniana (Hawkins 1989). The ornamental use of host plants, which include Junipers, Thuja orientalis, Cupressus and Pinus spp. (Stichel, 1957-1959) has resulted in the artificial introduction of this lygaeid with nursery stock. The ready availability of its food source, and wide environmental tolerance, mean that it will almost certainly, like the Juniper shield bug, Cythostethus tristriatus Fabricius, expand its range considerably.

11.7.9 Vagrants

Lygaeus equestris (Map 6) was recorded five times between 1837 and 1907 (Butler, 1923). There are also three Natural History Museum specimens in the Massee collection from Goodwood, Sussex, collected in July 1925. These are labelled 'British' and were bought by a Mr. Fielden from Mr. A. Ford, the Bournemouth entomological dealer. The Natural History Museum specimen, collected by Sidebotham in June, 1864 from Devizes, Wiltshire and cited in Butler (1923) is L. simulans (Map 7).

Migratory flight in Swedish L. equestris has been observed (Solbreck, 1971). This species is not restricted to Cynanchium vincetoxicum as implied in Dolling (1991), and no single plant species provides suitable food for an entire breeding season (Solbreck & Kugelberg, 1972; Kugelberg, 1977): in Sweden its distribution does not overlap C. vincetoxicum (Kugelberg, 1977b). Nevertheless,
the absence from Britain of this main foodplant makes establishment unlikely.

An old record, from the Great Orme, Llandudno, Gwynedd, for Xanthochilus quadratus (Map 87), is puzzling, but not implausible, as this site is a classic refugium for southern insects and plants. This species is common along the French coast and has been recorded from Slapton, Devon, where it may be established.

There are periodic records for three Peritrechus species along the coastline of South and East England. These almost certainly result from migrant stock, but P. gracilicornis (Map 83) and P. distinguendus (Map 81) seem more likely to be, or to become, established than P. angusticollis (Map 80).

A single vagrant of M. ditomoides (Map 26) was recorded from a former rubbish tip in Hounslow, Greater London. This site is now a golf course, but a recent search of this area for the insect was unsuccessful. However, M. ditomoides was, surprisingly, recorded again in 1992, from Oxfordshire. Its continental distribution, together with an abundant supply of its food plant Matricaria, suggest that it may become established.

M. ditomoides, P. gracilicornis and X. quadratus are all common on the Channel Islands.

11.7.10 Aliens

Spilostethus pandurus was recorded by McKinlay (1976) as an accidental introduction to Scotland. There are records from cargoes of groundnuts reaching British ports from Gambia infested with the rhyparochromine Elasmolomus sordidus (Fabricius) (Southwood & Leston, 1959).

11.7.11 Channel Island Species Absent from Great Britain

The Channel Island species Horvathiolus superbus, Lygaeosoma sardea, M. albofasciata, M. fasciatus and E. denticollis are potential additions to the British list.
11.8 Relationship Between Past and Present British Lygaeid Distributions

Early fossil lygaeids are listed in Slater (1964a). The first recognisable Lygaeoidea occurred in the Triassic and two Cretaceous lygaeoids were found in China (Southwood & Leston, 1959), although most known fossils are not earlier than the Oligocene (Slater, 1986). Lygaeids, unlike molluscs and beetles which leave identifiable traces in quaternary deposits, cannot easily be used as indicators of post-glacial environmental changes.

A hypothetical picture of the development of Britain's lygaeid fauna, since the last ice age, 10,000 years ago, can be compiled. This, as Dennis (1992) noted, for the British butterflies, is a speculative, but rewarding process. The immigration, re-immigration and possible occurrence of refugia can be identified using our current knowledge of lygaeid biology and by analogy to the extensive studies on the British vascular plants (e.g. Matthews, 1955; Godwin, 1956; Good, 1974), Coleoptera (Coope, 1959, 1970, 1977, 1979) and Mollusca (Kerney, 1968). Recent studies on Coleoptera, summarised by Hammond (1974), show that post-glacial changes in the British coleopterous fauna were likely to correspond fairly well with the general picture outlined for vascular plants by Godwin (1956).

Good (1974) stated that there was no direct evidence by which the proportion of the pre-glacial flora, which was able to persist unharmed in this country during the Ice Age, could be determined. It is not surprising that there is much difference of opinion. The analysis in Beirne (1952) on the origin and history of the British fauna is now dated but Dennis (1992) provided a good summary of late glacial and Holocene environments.

Greenland, with its arctic flora and fauna comprising cold adapted species is, probably, the one part of the world where conditions parallel those which must have existed in Britain during the Pleistocene (Good, 1974). Coope (1959) listed 53 species, mainly cold-adapted Coleoptera, recorded from the mid-Weichselian interstadial, which are
now extinct in Britain. The primarily Holarctic, arctic-alpine lygaeid, *Nysius groenlandicus*, is the only true Arctic representative of the Heteroptera, and may have been present in Britain during this period, only to be 'pushed-out' during the warmer Pleistocene interstadials or during the Holocene.

Coope (1977) considered that the extinction of all British Coleoptera occurred during the Devensian maximum (c18,000 years B.P). The unleached, frost-shattered soils and dwarf vegetation of Godwin's (1975) protocratic zone would have presented similarly unfavourable conditions for lygaeids. The final retreat of the ice allowed the spread northwards of lygaeid species already present south of a Thames-Severn line, or species entering or re-entering Southern Britain.

*Gastrodes grossipes* (Map 50) and *Kleidocerys resedae* (Map 15) probably arrived with the spread of pine and birch. Their ranges extend throughout the British Isles. The eventual restriction, in the main, of pine forest to Northern Britain, explains the relict populations of pine-litter dwelling, *Eremocoris abietis* (Map 45) and *E. plebejus* (Map 47), which occur primarily in the Eastern Scottish Highlands, under Caledonian pines, junipers or other introduced conifers. Many heathland species (Table 15) would also have been present and there are relict populations of *Ischnocoris angustulus* in Scotland and North Wales.

The Boreal period of increasing temperature probably favoured thermophilous lygaeids. The spread of blanket lowland woodland would have benefited deciduous litter species such as *Drymus brunneus* and *Megalonotus antennatus*. But for many species this could have been as destructive as blanket ice. Kerney (1966) found the snail fauna at the time of the Atlantic climatic optimum was less diverse, with woodland species being favoured as a result of the extensive forest cover. Species such as the two *Pachybrachius* species and *Lamproplax picea* would have benefited from the development of ombrogenous raised bog. Their current scattered populations reflect the subsequent fragmentation of this habitat.
Open habitat Lygaeidae probably became extinct during the Boreal period, over much, or all, of their British range, being restricted to coastal areas, mires, rock scarps and highland regions. The survival of warmth-demanding species, isolated since the post-glacial climatic optimum, is illustrated by several species of beetle still found in parts of Eastern Scotland (Crowson, 1967). Similarly, Scolopostethus pictus (Map 56), Heterogaster artemisiae (Map 28), Megalonotus dilatatus (Map 76), and Ischnocoris angustulus (Map 51) all have markedly southern distributions, but with relict, primarily west-coast northern populations.

Severance of the land connection with continental Europe in c5500 B.C., produced a powerful barrier to those continental species listed by Aukema (1987) which occur along the Channel coast. These show considerable migrational time-lag and must thus have poor dispersal.

Kerney (1966) found no evidence to suggest the extinction of any indigenous land mollusc since the climatic optimum, when temperatures were 2-3 degrees higher than now, and when the molluscan fauna was complete. Outlying records for many southern species, such as Scolopostethus pictus and Megalonotus dilatatus, indicate that they probably occurred further north during this period, subsequently contracting their range.

Amongst invertebrates, lygaeids dominate the fallen seed-feeding niche in Britain. This association with ruderal plants suggests that they are opportunistic and can survive wide climatic variation. They must also have good dispersal as they are frequently associated with ruderals that have a short life and high seed production. These life strategies would all have been favoured by the onset of prehistoric agriculture in the sub-Boreal period, which would have coincided with a rapid expansion in both lygaeid numbers and distribution of species.

Sub-Boreal fragmentation of blanket woodland for Neolithic agriculture created a habitat mosaic. Increased habitat diversity across Europe and the temporary landnam, resulting from shifting land-use patterns, encouraged the
spread of a 'culture steppe fauna' (Hammond, 1974). Culture steppe lygaeids would include some megalonotines, the drymine Drymus sylvaticus and rhyparochromines such as Peritrechus spp., all of which have an extensive central Palaearctic distribution. The rapidity with which these culture-favoured species can invade and colonise areas of newly cleared woodland was demonstrated for North American Coleoptera by Lindroth (1957, 1963). Forest floor Coleoptera, dependent on leaves, seeds and flowers, are apparently able to persist more successfully in small pockets of forest or are able to recolonise such areas (Hammond, 1974).

Orsillines, which are frequently found in disturbed habitats, and species such as Aphanus rolandri, would benefit greatly from the encouragement of ruderal plants in open, broken soil habitats, whilst Heterogaster urticae and Scolopostethus thomsoni, which are associated with the nitrophilous Urtica dioica, would have become widespread. Many other species, associated with early successional habitats and many forest-edge rhyparochromines would have dispersed rapidly.

There were also a few areas of permanent Neolithic deforestation, such as the Suffolk Breck, the coastal plain of South-West Cumberland, fixed dune pasture at Gwithian Cornwall, Strath Tay in Central Perthshire and various parts of the Thames Valley around Oxford and Dorchester (Evans, 1975). These would have encouraged the colonisation and establishment of xerothermic species and some of these locations correspond with lygaeid diversity 'hot-spots' (Table 14).

The sub-Atlantic period was characterised by increased human impact on the landscape and a deterioration in climate towards moister, Atlantic conditions (Godwin, 1956). Grassland species (Table 15) probably expanded their ranges which were significantly paralleled with the increase in sheep grazing during Iron Age and Romano-Britain times.

Relict populations of species restricted to a few locations in the British Isles, are likely to have been isolated from
continental populations for at least 10,000 years and represent important biological capital in the context of conservation (Hammond, 1974). There is a need for a new conservation category in British invertebrate status appraisal - a Red Data Book (RDB) relict class, to protect the relict populations of these species. This would differ from the current Regionally Notable category. Thus, species in Table 13 have either evolutionary, climactic or habitat relict populations. These isolated populations, or demes, may, over evolutionary time, diverge genetically from their congeners and, by allopatric speciation, become new species. Cook (1961) maintained that conditions experienced by peripheral populations could be the most favourable to rapid evolutionary change.

Table 13 Species with Outlying Relict Populations or Markedly Disjunct Distributions in Britain

<table>
<thead>
<tr>
<th>Species</th>
<th>Map</th>
</tr>
</thead>
<tbody>
<tr>
<td>Heterogaster artemisiae</td>
<td>28</td>
</tr>
<tr>
<td>Eremocoris abietis</td>
<td>45</td>
</tr>
<tr>
<td>Eremocoris plebejus</td>
<td>47</td>
</tr>
<tr>
<td>Ischnocoris angustulus</td>
<td>51</td>
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<tr>
<td>Scolopostethus pictus</td>
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<tr>
<td>Taphropeltus contractus</td>
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<td>Taphropeltus hamulatus</td>
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</tr>
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<td>Emblethis griseus</td>
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</tr>
<tr>
<td>Pionosomus varius</td>
<td>65</td>
</tr>
<tr>
<td>Megalonotus dilatatus*</td>
<td>76</td>
</tr>
</tbody>
</table>

* Relict population possibly now extinct

Many animal species have been observed in which populations living near the edge of their range differ from those at the centre. Sometimes different peripheral populations resemble each other more closely than they do the central ones. This must be due either to more rapid change in central than in peripheral localities, or vice versa (Cook, 1961).
Table 14. Selected Lygaeid Diversity 'Hot-Spots' in the British Isles

<table>
<thead>
<tr>
<th>Posi 10km Square</th>
<th>County</th>
<th>Location</th>
<th>Total Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>TR35 Kent</td>
<td>Sandwich - Deal</td>
<td>41</td>
</tr>
<tr>
<td>2</td>
<td>TQ15 Surrey</td>
<td>Box Hill</td>
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<tr>
<td>3</td>
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<td>Ewhurst - Shere</td>
<td>37</td>
</tr>
<tr>
<td>4</td>
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<td>Studland</td>
<td>36</td>
</tr>
<tr>
<td>5</td>
<td>TQ96 Surrey</td>
<td>Horsell</td>
<td>35</td>
</tr>
<tr>
<td>6=</td>
<td>SU49 Oxfordshire</td>
<td>Tubney</td>
<td>34</td>
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<tr>
<td>6=</td>
<td>SU96 Surrey</td>
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<tr>
<td>6=</td>
<td>TL77 Suffolk</td>
<td>Tuddenham</td>
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<td>6=</td>
<td>TQ25 Surrey</td>
<td>Reigate</td>
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<td>Flitwick</td>
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<td>20=</td>
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<td>SS58 West Glamorgan</td>
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<td>Whixall Moss</td>
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<td>Braunton Burrows</td>
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<td>Freshwater West</td>
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<td>165</td>
<td>NH81 Highland</td>
<td>Aviemore</td>
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</tbody>
</table>
11.9 Distributional Gradients in Lygaeids

Populations of a species are distributed along environmental gradients. There are four main types of geographical/ecological gradients - latitudinal, elevational (both functions of temperature), aridity and salinity (Myers & Giller, 1988). The first is of considerable relevance for lygaeid distribution within the British Isles.

Biotic diversity is a product of evolution, and depends on the time over which a biota has developed uninterruptedly (Fischer, 1959). Biotas in regions covered by Pleistocene ice sheets are examples of immature relics of mature temperate tertiary faunas and floras. Biotas in the warm, humid tropics are likely to evolve and diversify more rapidly than those in the higher latitudes.

The total number of species recorded for each 100km square in the British Isles indicate species richness but provides no indication of the conservation value of the species. A 100km square with ten species, all of RDB and Notable status would arguably be of greater conservation value than one containing 40 common and local species. For this reason a species quality index score based on Foster, (1987) and Ball (1992b) was calculated. Status categories (See Table 12) were assigned a score which increased with rarity to give a total rarity score (Common = 1; Local = 2; Notable B = 4; Notable A and probable RDB = 8; RDB = 16. This was divided by the number of species to give a species quality index map. Some coastal areas comprised significantly less land mass than inland 100km squares and were ignored.

The diversity of biotas is often greatest in climates of relatively high and constant temperatures, such as in most of the tropics, and decreases progressively into the fluctuating and the cold climates associated with the higher latitudes (Fischer, 1959). Within the British Isles there is a clear decline in the number of lygaeid species with latitude. This is the general trend for the Heteroptera and most, but not all, insect orders or families. A less marked, but still significant, east-west
The area of greatest species richness for Lygaeidae is the extreme South-East of England. Being closest to continental Europe and, with the addition of coastal habitats it is probably the area of greatest habitat diversity. It is also the most heavily pressurised area of Britain for development and recreation.

This is confirmed by examination of lygaeid diversity 'hot-spots' (Table 14 and Map 4). The greatest concentration is in South-East England at classic entomological sites. The Deal - Sandwich square is the most important area, with 41 species representing nearly half of the British total. This is followed by chalk downland at Box Hill and the Surrey heaths. Studland, Dorset, like Deal, a classic site for marginal species, is fourth, and combines heathland, sand dunes and coastal chalk cliffs. The top five diversity 'hot-spots' are temperature 'hot-spots' which fall within the small area of the British Isles that has mean July temperatures above 17 degrees Centigrade.

Other important sites are the Suffolk Brecklands around Tuddenham, with 34 species, and Whitesand Bay in Cornwall, with 29 species. Wicken Fen, Cambridgeshire, is the prime non-xerothermic wetland site with 23 species. The species 'quality' indices demonstrate clearly the conservation status of the lygaeid fauna in the South of Britain. There are, however, areas of equally high conservation importance in the coastal extremes of South-West Wales and England.

Recording effort biases the results further north. The Whixall Moss complex on the Clwyd/Shropshire border, Delamere Forest, Cheshire and the Lancashire dunes around
Formby with 16 species are regional 'hot-spots'. The Aviemore area, with nine species, scores highest for Scotland.

11.10 Distribution of Lygaeidae by Habitat Within the British Isles

Edaphic soil conditions have a strong secondary influence on lygaeid distribution, particularly in the way that they restrict the range of host plants. Some lygaeids that only occur on chalk may well be stenophagous on calcicole plants. Burnham (1970) has drawn attention to the close correlation between broad climatic divisions within the British Isles and the regional distribution of major groups of soils.

British Lygaeidae have a broad ecological distribution, because they dominate the fallen seed ecological niche. Lygaeid species positively associated with major habitat types are listed in Table 15. New England rhyparochromines are found in a similarly varied series of habitats (Sweet, 1964). Habitat fragmentation, particularly of heathland and wetlands, produces fragmented lygaeid species distributions; e.g. for Pachybrachius fracticollis (Map 88), a mossland and fenland species or for Macrodema microptera (Map 64), a heathland species.

Lygaeid diversity is lowest in stressed habitats such as salt marshes where the RDB2 Henestaris halophilus (Map 23) occurs in a restricted area of North Kent. It is highest in xerothermic southern habitats, such as coastal cliff (42 species) and sand dunes (27 species), heathland (32 species) and chalk escarpment (38 species). Calcareous grasslands are the richest British habitat for Hemiptera (Kirby, 1992). South-facing chalk scarps are particularly important for RDB and Notable thermophilous lygaeids. The two commonest scarp slope angles are 26° and 33°, which span the optimum angle for maximum incident energy at the summer solstice at 50° north which is 27° (Clarke, 1965). Xerothermic species also require low precipitation, and the most arid part of the British Isles, the dry sandy Suffolk Breck, with less than 600mm, supports an important fauna of 22 species.
Table 15. Distribution by Habitat of British Lygaeidae

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O. depressus    
O. punctipennis
N. ericae      
N. graminicola
N. helveticus  
N. thymi      
K. resedae  
K. truncatulus
C. aurescens
C. claviculus
C. glandicola
C. melanocephalus
I. quadratus
I. sabuleti
H. halophilus
H. laticeps
M. preysersleri
C. typhae    
H. artemisiae
H. urticae
P. brevipennis
T. holosericeus
A. pallipes
A. rufipes
L. enervis    
S. fuligineus
S. rusticus
S. sabulosus
D. latus
D. pilicornis
D. pilipes
D. brunnneus
D. pumilio
D. ryei
D. sylvaticus
E. abietis
E. fenestratus
E. plebejus
E. podagricus
G. abietum
G. grossipes
I. angustulus
L. picea
S. affinis
S. decoratus
Table 15 cont. Distribution by Habitat of British Lygaeidae

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TOTAL SPECIES 3 27 14 42 19 28 38 19 5 30 32 22 21 9 13
Wasteland sites support 21, mainly common lygaeid species, but the notable *Raglius alboacuminatus* and *Drymus latus* have both been recorded on derelict land in the London area (Kirby, 1992).

**11.11 Recent Changes in British Lygaeid Distribution**

Southwood (1957) stressed that caution must be exercised regarding changes in British Heteroptera distribution, but recognised trends for certain species. Similarly, only 20 of the 193 species of Coleoptera and five of the 25 aculeate Hymenoptera 'added' to the British list since the 1940's are genuinely new (Hammond, 1974; Felton, 1974). Of the 19 lygaeid species added to the British list this century (Table 16), only seven are genuine additions. Eight result from taxonomic 'splitting' and from the elevation of forms and subspecies to specific status. A further four represent species that were overlooked or mis-placed in collections.

The relict, western populations of *Pterotmetus staphyliniformis* (Map 66) and *Macroplax preyssleri* (Map 25) are unlikely to have originated from recent migrations and appear to have been previously overlooked. It is conceivable that *Pterotmetus staphyliniformis* may have been introduced to its restricted habitat - the traditional small flower-growing fields at Gwenver, Cornwall, with imported bulbs.

The remaining additions are all orsillines, renowned for their 'dispersability' (Usinger, 1942). *Nysius* are frequently swept in large numbers from the heads of Compositae. Eggs have been observed, attached to 'parachute' fruits and seeds, awaiting wind-borne dispersal (Carillo, 1967; Böcher, 1978). Air-borne dissemination of eggs may explain the recent isolated records of *Nysius senecionis* (Map 13) and *N. graminicola* (Map 11) on the south coast of England. It is unknown if either species is established and searches have produced no additional records. Both species appear capable of flying across the English Channel and will probably, eventually become established.
<table>
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<td>Recently established?</td>
</tr>
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<tr>
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Ortholomus punctipennis (Map 9) is probably a recent addition at limited sites in Eastern and Southern England. It has recently been discovered at four coastal locations in the Netherlands (Aukema & Woudstra, 1985). It may have been mistaken for the superficially similar Nysius but is most unlikely to have been overlooked at Deal from where a single specimen was found in 1986. This site has, over the last 150 years, been as intensively collected as anywhere in Britain. The Suffolk Breck has also historically been well studied and this species is unlikely to have been overlooked until 1937 at Tuddenham Heath. Another record is from Studland, Dorset, which, with Deal, is a classic location for marginal species in Britain.

Global warming could produce a major northward expansion of lygaeid ranges. A one degree Centigrade increase in British summer climate could produce a fauna resembling that of the Loire, in France. The most likely new additions to Britain are those species occurring along or close to the Channel coast (Aukema, 1987). Other more long-range additions might include the myodochines Paromius leptopoides and Remaudiereana annulipes. These are two of the few lygaeids which disperse readily across "limited-distance" water gaps (Slater, 1986). Another myodochine, the Holarctic Ligyrocoris sylvestris is also a potential coloniser. The introduction and potential spread of Orsillus depressus was discussed earlier. The other two West Palaearctic Orsillus species are more Mediterranean and are unlikely future introductions.

The changing distribution over time of I. sabuleti (Map 22, 90-93) is a classic example of range expansion. This species was confined to two south-east locations in the last century (Map 90) but is now found as far north as Cheshire and Yorkshire and is the 15th most common lygaeid species in Britain, occurring in 114 10km squares (Table 12, Maps 90 - 93). Peritrechus nubilus is similarly extending its range in Southern and Eastern Britain and Gastrodes grossipes has significantly extended its distribution, but not range, within conifer plantations.

Species hardly ever occupy their full ranges as defined by limiting environmental factors. Local extinctions are most
likely to occur in species at the limits of their ranges. It is often difficult to assess true change but, with a few notable exceptions, most of the native terrestrial biota of the British Isles has suffered range contraction and fragmentation - due primarily to habitat loss (Vincent, 1990). Kirby (1992) summarised the potential threats to all of Britain's RDB and Notable Heteroptera. British lygaeid species most vulnerable are those restricted to threatened habitats in Southern England, particularly heathland, chalk downland and coastal habitats (Table 15), together with those culture-favoured species associated with traditional agricultural practices.
Distribution Maps

Map 1. Distribution of British field collecting sites by 10km squares: - Further site information is provided in Appendix 2.

Map 2. Palaearctic collecting sites: - Further site information is provided in Appendix 3.

Map 3. Total lygaeid distributional records within 10km squares: - Incorporating data from the Liverpool Museum collection (Appendix 5) and sources listed in Appendices 8 - 11.

Map 4. British lygaeid diversity 'hot-spots' (see 11.9).

Map 5. Diversity gradients (see 11.9).

Maps 6 - 89. Individual species distributions.

° = pre-1970 records

• = post-1974 records

? = dubious records

Maps 90 - 93. Ischnodemus sabuleti range extension.
Map - 1 Distribution of British field collecting sites by 10km squares
Map - 3 Total lygaeid records within 10km squares
Map 4 British lygacid diversity hotspots. The size of the symbol represents the number of species recorded within a 10km square.
Map 5 - Diversity gradients. The top figure in each square is the rarity score and the bottom figure is the species quality index (see 11.9). The letters are the national grid 100km square coordinates.
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Map 7 - *Lygaeus simulans*

Map 8 - *Orsillus depressus*

Map 9 - *Ortholomus punctipennis*
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Map 11 - *Nysius graminicola*

Map 12 - *Nysius helveticus*

Map 13 - *Nysius senecionis*
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Map 16 - Kleidocerys truncatulus

Map 17 - Cymus aurescens
Map 26 - Metopoplax ditomoides
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Map 71 - Megalonotus antennatus

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Map 78 - Graptopeltus lynceus
Map 79 - Pasatus lundi
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Map - 90 *Ischnodemus sabuleti*  
Pre 1900

Map 91 - *Ischnodemus sabuleti*  
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Map 92 - *Ischnodemus sabuleti*  
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Map 93 - *Ischnodemus sabuleti*  
Total Records

Total Records: 303
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## Legend

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<tr>
<th>Abbreviation</th>
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