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Additional data on variation in the specialized cuticular patches of true bugs in the family Pentatomidae (Heteroptera)

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Heteroptera, Pentatomidae, Pentatominae, Phyllocephalinae, abdomen, morphology, specialized cuticular patches, variation

Abstract. In previous papers, the presence of patches of specialized cuticle on the sternites of true bugs of the family Pentatomidae has been reported. The patches, it is thought, are an aid to thermoregulation by aiding heat loss at high temperatures.

In this paper, additional descriptions given of patch patterns in Pentatominae and for the first time in Phyllocephalinae extend the range of variation previously recorded in Pentatomidae.

More than thirty species of Pentatominae in four tribes (Pentatomini, Antestiini, Halyini, Carpocorini) were examined. Patches were extensively developed in African and Asian Halyini. They were absent, however, in all Australian halyines examined, suggesting the existence of different mechanisms of resistance to heat.

Patches were well developed in all 11 species of Phyllocephalinae examined. The most extensive area development of patch cuticle now known in Pentatomidae was observed in two phyllocephalines from deserts, *Phyllocephala negus* and *Schyzops aegyptiaca*. In Phyllocephalinae, the anatomical distribution of patch cuticle extends to areas of sternite lateral to the spiracles as well as to the laterotergites. Patch area surfaces in some phyllocephalines are fragmented by bristle-bearing discs.

Concerning the pentatomines examined, possible seasonal area variation and variation correlated with geographical isolation was detected in *Nezara viridula*, a tendency to ventral mid-line fusion of patches on sternites III observed in Carpocorini, and a possible east-west gradient detected in Asian *Plautia fimbriata*. A high degree of individual variability was recorded in a sample of *Carpocoris pudicus* from Turkey.

Epidermal glands, abundant in males, are generally but not invariably absent in areas occupied by patch cuticle. The absence of glands as an additional tissue element might be explained if their presence retarded heat loss from the patches.

INTRODUCTION

In recent papers (Staddon, 1992; Staddon & Ahmad, 1994), the presence of patches of specialized cuticle on the abdominal sternites in true bugs of the family Pentatomidae has been reported. From the evidence of distribution then available it was suggested that the patches are involved in thermoregulation as an aid to heat loss. Elsewhere among the insect orders, similar patches (Slifer's patches) have been described only in Orthoptera in the family Acrididae (Slifer, 1951, 1953a, 1953b, 1957).

The fact that the patches in Pentatomidae had escaped examination for so long may in part be explained by the traditionalism of taxonomists and in part by the fact that the

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* Permanent address: Zoology Department, University of Queensland, St Lucia, Brisbane, Queensland 4067, Australia

** Permanent address: Department of Zoology, University of Karachi, Karachi 75270, Pakistan patches are not always easy to detect either in fresh or in museum specimens. They are best revealed in cuticular isolates examined in the dark-field microscope where they appear brightly on a dark field. Features of patch cuticle as seen in *Piezodorus purus* included: smooth external surface, presence of wide-diameter pore canals, and sparcity or absence of epidermal glands (Staddon, 1992). Information on the structure of patch forming cells is unavailable at present.

Slifer (1951), from behavioural observations, concluded that the patches in Acrididae contain receptors sensitive to heat. Their role, she suggested, was to control the characteristic orientation reactions shown by these insects to heat. One derived benefit for males would be protection of the spermatozoa against the damaging effects of high temperatures (Slifer, 1953a). However, Makings (1968, 1987; Makings & Saeed, 1989) provides evidence that the patches provide surfaces for evaporative cooling. Makings (1968) described area specific transpiration from the patches by application of a water detecting film.

In all Pentatomidae previously examined, patches were paired and segmentally disposed on areas of the abdominal sternites median to the spiracles. They showed considerable variation within and between species. Indications that in some species this variation has a geographic basis was obtained. In several species each sex was distinguished by its own pattern. Above all, however fragmentary the evidence, there seemed to be a clear indication that the occurrence of patches was correlated with heat. Moreover, experiments carried out on *Nezara viridula* revealed not only area specific transpiration from the patches as described by Makings (1968) in Acrididae but also patch area augmentation in females reared at 32°C compared with siblings reared at 22°C.

It seemed unlikely to us that the work previously reported was giving a complete picture of the variation to be found in the Pentatomidae. *Dalpada eremica* alone among Halyini was examined and it had the most extended system of patches so far been seen in Pentatomidae (Staddon & Ahmad, 1994). Yet more extended systems, it seemed possible, were to be found in the tropical Pentatomidae, and distributional studies on variation could be rewarding if they supported the proposed link with climate.

In this work, we have examined additional material in the subfamily Pentatominae and for the first time examined representatives of the tropical subfamily Phyllocephalinae. Mostly museum specimens were examined. Genera and species were chosen on grounds of availability and geographical occurrence. It is our hope that the data here supplied will be of value in any future search made for possible correlations between patch occurrence and climatic conditions.

MATERIAL AND METHODS

Table 1 supplies a list of the species studied. The taxonomic works consulted included Kirkaldy (1909), Gross (1976), Linnavuori, (1973, 1982), Roche (1979), Rolston et al. (1980), Rolston & McDonald (1979, 1981), and Tamanini (1959). There is no final agreement on the classification of the Pentatomidae and so the arrangement of the species of Pentatominae in subfamily and tribal groupings must be regarded as provisional. Some authors have suggested that Phyllocephalinae should be reduced in status from a subfamily to a tribe within the subfamily Pentatominae (discussion in Linnavuori, 1982).

TABLE 1. Check list of Pentatomidae examined.

A. Subfamily Pentatominae

1. Tribe Pentatomini
Nezara viridula (L.). Australia: 4♂ and 5♀ from Queensland and New South Wales. Mainland N. and S. America: 36♂ and 44♀ from localities in the eastern United States (South Carolina, Alabama, Louisiana, Florida, Texas, Mexico, Chile, and Uruguay. Hawaiian Is.: 1♂ and 2♀ from Kawai I., West Indies: 4♂ and 6♀ from St. Thomas I., Virgin Is.; 1♀ from Puerto Rico.
Nezara antennata Scott. Japan: 2♂ and 2♀.
Glaucias amyoti (Dallas). Australia: 1♂ and 1♀.
Pausias martini (Puton). Iran (Bakhtaran): 20♂ and 10♀.

2. Tribe Antestiini
Plautia affinis (Dallas). Australia (Queensland, New South Wales): 4♂, 10♀.
Plautia brunnipennis (Montrouzier & Signoret). Australia (New South Wales): 1♂, 2♀. Vanuatu Is.: 5♂, 1♀.
Plautia fimbriata (Fabricius). Pakistan: 2♂ (Taxila), 2♀ (Changamanga, Murree). South India: 3♂. Sri Lanka: 1♂. Vietnam: 1♂. South China: 1♂. Luzon I., Philippine Is.: 2♂, 1♀. Java: 1♂. Malay Peninsula: 2♂. Singapore: 1♀.
Plautia discolor (Walker). Malay Peninsula: 1♂, 1♀.
Plautia viridicollis (Westwood): Singapore: 1♂. Geographical source unknown: 2♀.

3. Tribe Carpocorini
Brachynema cincta (Fabricius). Pakistan: 1♂, 1♀.
Carpocoris pudicus (Poda). Turkey: Turgutlu, 14♂, 18♀; Kahramanmaras, 1♀; Goksun, 1♂.
Codophila varia (Fabricius). Pakistan: 1♂.
Codophila pusio (Kolenati). Pakistan: 1♂, 1♀.
Croantha ornatula (Herrich-Schaefer). Pakistan: 2♀.
Dolycoris baccarum (L.). Turkey: Bosdag, Nr. Izmir, 5♂, 5♀. Iraq: 1♂.
Dolycoris indicus Stål. Pakistan: 1♂, 1♀.
Montiethiella humeralis (Walker). Australia: 1♂.

4. Tribe Halyini
Ethiopean distribution
Atelocera foveata Dallas. South Africa: 1♂, 1♀.
Atelocera notatipennis Stål. South Africa: 1♂, 1♀.
Atelocera serrata (Fabricius). Uganda: 1♂, 1♀.
Atelocera spinulosa (Palisot & Beauvois). Guinea: 1♂, 1♀.
Oriental distribution
Apodiphus integriceps Horvath. Pakistan: 1♂, 1♀.
Halys dentatus (Fabricius). Pakistan: 2♀.
Nevisanus tectus (Walker). Pakistan: 1♂.
Sarju eremica (Hoberlandt). Pakistan: 1♂, 1♀.
Prytanicoris ambivirens Gross. Papua, New Guinea: 1♂, 1♀.
Australian distribution
Alcaeus varicornis (Westwood), 1♂.
Omyta centrolineata (Westwood), 1♂, 1♀.
Poecilometis armatus (Fabricius), 1♂.
Poecilometis apicalis (Westwood), 1♂.
Poecilometis fuscescens (Stål), 1♂.
Poecilometis grandicornis (Erichson), 1♂.
Poecilometis gravis (Fabricius), 1♂.
Poecilometis lineatus (Westwood), 1♂.
Poecilometis punctiventris (Stål), 1♂.

Poecilometis strigatus (Westwood), 1♂.
Theseus modestus (Stål). 1♂.

B. Subfamily Phyllocephalinae

Basicryptus interruptus (Westwood) [= *Dalsira rugicollis* (Westwood)]. Australia, New South Wales: 1♂, 1♀.
Chalcopis glandulosa (Wolff). South Africa: 1♂, 1♀.
Dalsira distincta (Signoret). Cameroons: 1♂, 1♀.
Gonopsis affinis (Uhler). Japan: 1♂, 1♀.
Macrina juvencus (Burmeister). Rhodesia: 1♂, 1♀.
Megarrhamphus hastatus (Fabricius). Luzon I., Philippine Is.: 1♂. Malaya: 1♀.
Metonymia affinis (Amyot & Serville). South Africa: 1♂, 1♀.
Phyllocephala negus (Distant). Arabia: 1♂, 1♀.
Schyzops aegyptiaca (Lefebvre). Sudan: 1♂. Egypt: 1♀.
Tantia vicina (Signoret). Cameroons: 1♂, 1♀.
Tetroda histeroides (Fabricius). India: 1♂, 1♀.

The specimens examined comprised for the most part dried, pinned, museum material. In many cases it was considered impracticable in the interests of a broad survey to examine more than a single male and single female specimen from the same species. The Pentatomidae, one of the numerically most important families in the Heteroptera, comprises more than 2,500 described species (Miller, 1971). In only a few cases was it possible to examine numerically adequate samples of freshly collected material from the field.

Specimens were examined using a binocular dissecting microscope and the appearance of the patches, if at all visible, noted. Next the abdomen was carefully removed and soaked in a solution of hot caustic potash to remove all digestible tissues. Finally, sternites and tergites were mounted on slides for detailed microscopic examination. For temporary mounts, ethanolic glycerol was used (1 part glycerol; 1 part 70% ethanol). For permanent mounts, Euparal was used as the mounting medium. In the case of female specimens, the spermatheca was examined to provide a check on generic identity. The cuticular materials in temporary mounts were subsequently removed, washed in water, carefully dried, and attached to the pin supporting the untreated anterior part of the specimen. Restored specimens were returned to the collection from which they had been taken.

The maps showing the anatomical distribution of the patches were drawn to scale on graph paper with the aid of an eyepiece graticule. The slide bearing the specimen was placed for drawing on the rim of a 5 cm diameter petri dish located on the stage of a binocular dissecting microscope. The beam of light used to illuminate the specimen was aranged at an oblique angle so that the patches would appear bright against a dark field (Staddon, 1992). The drawings depict sternites II to VII on one side commencing with the ventral mid-line. Those of Phyllocephalinae additionally contain the laterotergites and, where required in females, rudimentary sternite VIII.

The area measurements were made by one of two methods: (1) by counting squares using an eye-piece graticule (Pentatominae); (2) by cutting out and weighing patch-containing and patch-free areas of the patch distribution maps (Phyllocephalinae). The light micrographs of Phyllocephalinae patches were recorded on Ilford monochrome Pan F (50 ASA) Plus film.

RESULTS

The Pentatomidae is a very large family with a worldwide distribution. Of the thirteen subfamilies listed by Miller (1971) we have concentrated on two: the subfamilies Pentatominae and Phyllocephalinae. Although several Pentatominae have been studied no previous information exists for Phyllocephalinae. Concerning another subfamily, the Asopinae, we examined but did not find patches in *Zicrona caerulea* (L.) (United Kingdom: 1♂, 1♀; Pakistan: 1♂, 1♀). In this investigation we have concentrated on Old

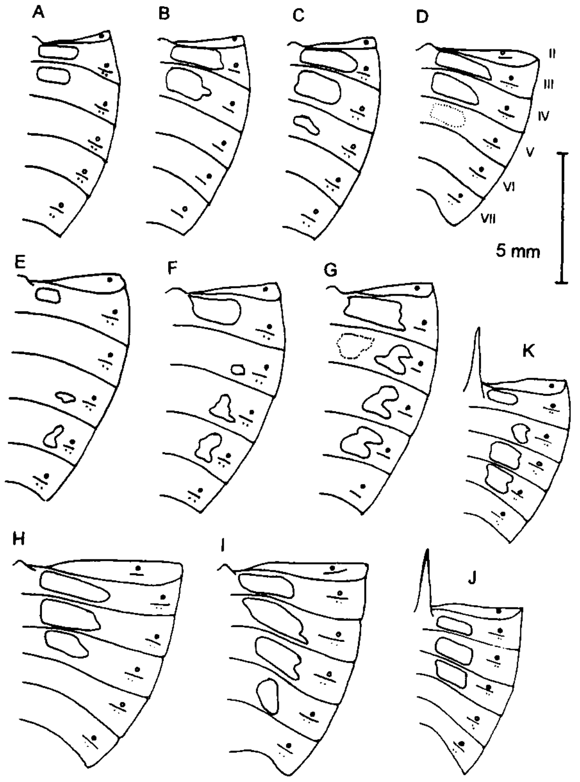

Fig. 1. Pentatomini. Comparison of sternal patch patterns. A–D – *Nezara viridula* males: A – South Carolina, laboratory reared, B, C – St. Thomas I., Virgin Is., D – Turkey, laboratory reared at 33°C; E–G – *N. viridula* females: E – Kawai, Hawaiian Is., F – St. Thomas I., Virgin Is., G – Texas, Brazoo County, USA; H – *Glaucias amyoti* male, Australia; I – *G. amyoti* female, Australia; J – *Pausias martini* male, Iran; K – *P. martini* female, Iran.

World material but observations previously made on Old World *Nezara viridula* (Staddon & Ahmad, 1994) have been extended to include New World material.

Subfamily Pentatominae

1. Tribe Pentatomini

Nezara viridula. This pentatomine has been recorded worldwide from many localities, mainland and island, between latitudes 45° North and 45° South (Todd, 1989). Material from N. and S. America, the West Indies, and the Hawaiian Is. was studied (Table 1). Patch distribution patterns selected to show the range of area variation in males are shown in Fig 1A–D and in females in Fig. 1E–G.

Patch distribution patterns were similar to those previously described in Old World material. With the exception of a single male, from St. Thomas I., Virgin Is., which had three pairs of patches (Fig. 1C), all males examined had two pairs of patches. In females Fig. 1E–G), the patches on sternite III are well developed but those on sternite IV usually greatly reduced (Fig. 1F) or missing (Fig. 1E). Females also have additional patches laterally located on sternites V and VI.

Possible seasonal area differences were detected in a mixed collection of material from Texas. Extended patches were present in seven July females from Texas (Fig. 1G) but in only one female in a group of seven March females. Reduced patches were present in two of three females taken in the period September–December (Fig. 1E). Patches of intermediate extent were present in the remaining specimens (Fig. 1F). In some July females additional faint patches were present near the mid-line on sternite III (Fig. 1G, area enclosed by broken line). Among the males examined, the smallest patches were seen in a laboratory reared male from S. Carolina (Fig. 1A).

The results of a simple temperature experiment previously reported (Staddon & Ahmad, 1994) indicate that patch areas are increased in females, but not in males, in response to

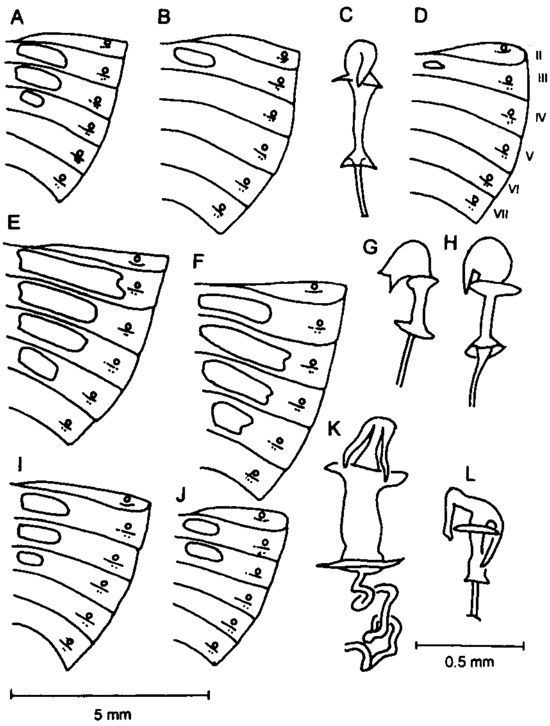

Fig. 2. Antestiini. Spermatheca and sternal patch patterns. A–D – *Plautia affinis*, Australia: A – male, B – female, C – female, spermatheca, D – female; E–J – *Plautia fimbriata*: E – male, Pakistan, F – female, Pakistan, G – female, Singapore, spermatheca, H – female, Pakistan, spermatheca, I – male, Luzon I., Philippine Is., J – male, Java; K – *Plautia viridicollis* female, geographical origin unknown, spermatheca; L – *Plautia discolor* female, Borneo, spermatheca.

heat. However, rexamination of one high temperature (33°C) male utilized in this experiment by dark-field revealed the existence of faint patches on sternite V (Fig. 1D; area enclosed by broken line).

Among the pentatomines examined, female patterns were similar in *N. viridula*, *N. antennata*, and *Pausias martini* (Fig. 1K) but area differences were observed in *Glaucias amyoti* (Fig. 1I). Males of *N. viridula* and *N. antennata* were similar with two pairs of patches and those of *P. martini* (Fig. 1J) and *Glaucias amyoti* (Fig. 1H) similar with three pairs of patches.

2. Tribe Antestiini

Five species presently included in the genus *Plautia* were examined (Table 1) but data obtained on the spermatheca indicated that the genus is in need of revision. The spermatheca in the genus *Plautia* as now defined has a single horn-like tubulus (Linnavuori, 1973, 1982; Roche, 1979). This condition was observed in *P. affinis* (Fig. 2C), *P. brunnipennis*, and *P. fimbriata* (Fig. 2H) but not in either *P. discolor* or *P. viridicollis*. The bulb in *P. discolor* (Fig. 2L) had two tubuli like that of a *Parantestia*. The bulb in *P. viridicollis* (Fig. 2K) was of a type unknown to us. The spermatheca of the Luzon I. and S. China *P. fimbriata* females was similar to that of *P. fimbriata* from Pakistan. A bifurcation in the tubulus was observed in a female from Singapore (Fig. 2G).

Plautia affinis. Patches were present on sternites III, IV, and V in the four males examined (Fig. 2A). In one male, those on sternite V were reduced. Patches were present on sternite III in nine of ten females examined (Fig. 2B, 2D) and absent in one.

Plautia brunnipennis. On the basis of the taxonomic characters available to us and structure of the spermathecal bulb, it seems likely that *P. brunnipennis* and *P. affinis* are conspecific. Two pairs of patches were present in the Australian male *P. brunnipennis* examined and one pair in the female. In the female, a faint, irregular, unsymmetrical

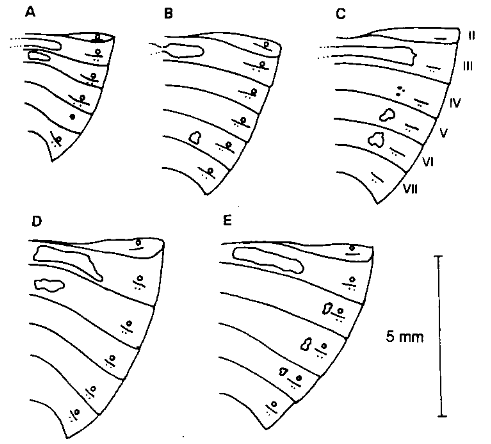

Fig. 3. Carpocorini. Comparison of sternal patch patterns. A – *Brachynema cincta* male, Pakistan; B – *B. cincta* female, Pakistan; C – *Croantha ornatula*, female, Pakistan; D – *Carpocoris pudicus* male, Turkey; E – *C. pudicus* female, S. Turkey.

patchiness was detected in areas of sternite lateral to the spiracles. Patches were missing in *P. brunnipennis* from the Solomon Is. and Vanuatu.

P. fimbriata. Specimens from widely scattered locations in Asia were examined (Table 1). Specimens of both sexes from Pakistan had four pairs of patches (Fig. 2E, 2F). Three pairs of patches were present in the males from South India, Sri Lanka, and Luzon I. (Fig. 2I) and in one of the two males from the Malay Pensinsula. The Java males and the other of the two males from the Malay peninsula (Fig. 2J) had two pairs of patches. As a rule it was difficult to detect patches in the intact specimens but those of a male from Sri Lanka were clearly visible in the untreated specimen. Patches were absent in the females from South China, Luzon I., and Singapore.

P. discolor. Patches were absent.

P. viridicollis. Patches were absent on the sternites of the male from Singapore. One of the two females examined had one pair, the other female four pairs, of patches.

3. Tribe Carpocorini

Several Eurasian species in this group offer material of promise for studies on the distribution of geographic variation and taxonomic variation in the sternal patches.

Brachynema cincta. In the male, patches were present on sternites III and IV (Fig. 3A). In the female, large patches were present on sternite III, a small pair on sternite VI, but none present on intervening sternites IV and V (Fig. 3B). The patches on sternite III extended medianly to join in the ventral mid-line, as previously noted in *Brachynema simony* Horvath (Staddon & Ahmad, 1994).

Croantha ornatula. In the two females examined, the large patches present on sternite III extended over the ventral mid-line (Fig. 3C). Additional small laterally located patches were present on sternites IV, V, and VI. The patches on sternite IV were reduced to a collection of small fragments of patch cuticle.

Carpocoris pudicus. The Turgutlu sample yielded the patch area frequencies given for future reference in Table. 2. In several Turgutlu males and females, patches were absent. Some males had one pair, others two pairs of patches (Fig. 3D). The remaining females had one pair of patches. In one male, the patches on sternite III extended almost to the ventral mid-line. More extended patches have been seen in *C. pudicus* from southern Turkey (Table 2). In one female from Kahramanmaras, additional small laterally located patches were present on sternites IV, V, and VI (Fig. 3E).

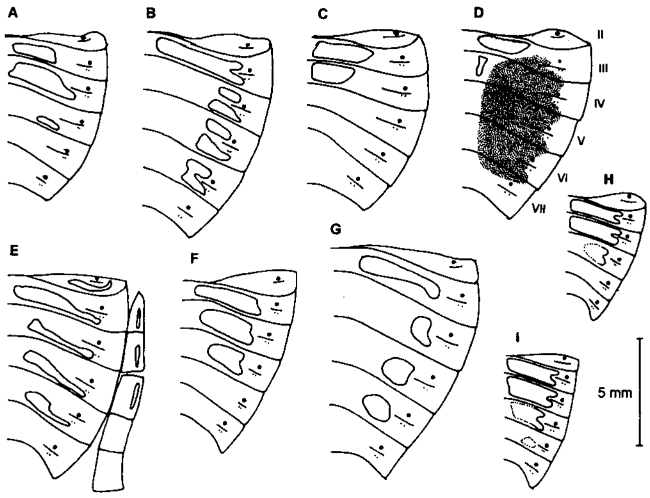

Fig. 4. Halyini. Comparison of sternal patch patterns. A – *Apodiphus integriceps* male, Pakistan; B – *A. integriceps* female, Pakistan; C – *Atelocera serrata* male, Uganda; D – *A. serrata* female, Uganda (wax secreting area stippled); E – *Halys dentatus* female, Pakistan; F – *Prytanocoris ambivirens* male, Papua, New Guinea; G – *P. ambivirens* female, Papua, New Guinea; H – *Sarju eremica* male, Pakistan; I – *S. eremica* female, Pakistan.

TABLE 2. *Carpocoris pudicus*. Frequency distribution of area totals of patches on sternites III and IV in a point sample of eleven males and fifteen females from Turgutlu (near Izmir), W. Turkey (collection: September 1993).

Area (mm^2 x 100)*	Male		Female
	III	IV	III
0–9	4	6	5
10–19	0	0	2
20–29	1	1	1
30–39	1	1	1
40–49	1	2	2
50–59	0	0	3
60–69	4	1	1

* Greater areas have been recorded: III, 110; IV, 34 in a single male from Goksun, S. Turkey; III, 112; IV, 17; V, 15; VI, 5 in a female from Kahramanmaras, S. Turkey.

Codophila varia. Patches were not detected in the single male examined.

Codophila pusio. Patches were missing in both specimens examined.

Dolycoris baccarum. The variability in the Bosdag sample was similar to that observed in *C. pudicus*. Patches were missing in three females and missing in one male. Two females and four males had patches on sternite III. In one male, the patches on sternite III came together in the ventral mid-line. In the male from Iraq, patches extending to the mid-line were present on sternite III and additional patches present on sternite IV.

Dolycoris indicus. Patches were present in the male on sternite III and IV and in the female on sternite III. The patches on male sternite III extended to the ventral mid-line.

Montiethiella humeralis. Gross (1976) provisionally places *M. humeralis* in an Australian *Carpcoris* group. The single male examined had three pairs of sternal patches.

4. Tribe Halyini

Representative material from Ethiopean, Oriental, and Australian sources was examined.

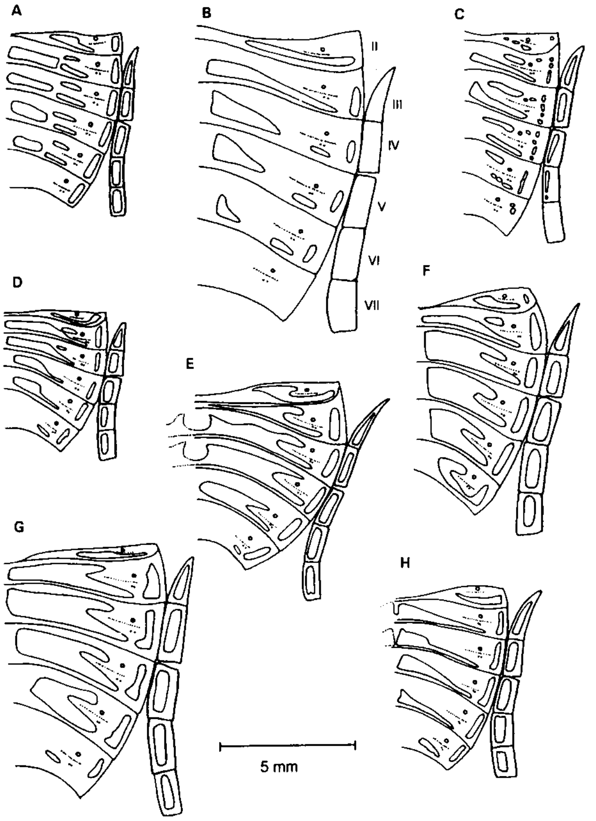

Fig. 5. Phyllocephalinae. Comparison of patch patterns on sternites and laterotergites in males. A – *Basicryptus interruptus*, Australia; B – *Dalsira distincta*, Cameroons; C – *Gonopsis affinis*, Japan; D – *Metonymia affinis*, S. Africa; E – *Phyllocephala negus*, Arabia; F – *Schyzops aegyptiaca*, Sudan; G – *Tantia vicina*, Cameroons; H – *Tetroda histeroides*, India.

Ethiopean Halyini

Atelocera serrata. Patches were present on sternites III and IV in both sexes (Fig. 4C, 4D). In the female, wax glands occupied the area shown by stippling in Fig. 4D. Patch patterns were similar in *A. foveata*, *A. notatipennis*, and *A. spinulosa*.

Oriental Halyini

Apodiphus integriceps. In the male from Pakistan (Fig. 4A), patches were present on sternites III to V, on sternites III to VI in the female (Fig. 4B).

Halys dentatus. In the two females examined, uniquely among pentatomines so far examined, the patch system extended to sternite II and to the laterotergites (Fig. 4E). The patches on sternites III to VI were conspicuously linear and the lateral part located in the posterior half of the sternite. Males of *H. dentatus* were not available for examination.

Sarju eremica. Patches were present on sternites III, IV, and V in the male (Fig. 4H), on sternites III to VI in the female (Fig. 4I). Under dark-field conditions, the patches on sternites III and IV were distinctly brighter than those on sternites V and VI.

Nevisanus tectus. Patches were absent in the single male examined.

Prytanicoris ambivirens. Three pairs of patches were present in the male, three pairs in the female (Fig. 4F).

Australian Halyini

Patches were absent in all Australian halyine material examined although the list in Table 1 includes species from arid regions (Gross, 1976).

Subfamily Phyllocephalinae

Distribution patterns for males of eight of the eleven species examined are shown for comparison in Fig 5 and for conspecific females in Fig. 6. Patterns in conspecific males and females were broadly similar. The patch system, considered in general terms, extended to all visible sternites (II to VII in males; II to VIII in females), to areas of sternite lateral to the spiracles, and to the laterotergites. In males of two species, *Phyllocephala negus* and *Tetroda histeroides*, patch cuticle extended to the ventral mid-line (Fig. 5E, male sternites IV and V in *P. negus*; Fig. 5H, male sternite III in *T. histeroides*).

Area measurements have been summarised for inspection in Table 3. The term At refers to total area of sternites and laterotergites, the term Ap to patch area totals. The term in brackets (Ap%) gives the patch area total (Ap) as a percentage of the total area. Patch area totals in males and females were positively correlated (Spearman's rank corelation coefficient = 0.715) suggesting that valid interspecies comparisons can be made on the basis of data obtained from single specimens.

TABLE 3. Phyllocephalinae. Results of area measurements, one side from the mid-ventral line. At, total area enclosed by sternites and laterotergites (mm^2); Ap, total area of patches (mm^2); Ap(%), relative patch area totals (Ap/At × 100).

Species	Male		Female	
	At	Ap (Ap%)	At	Ap (Ap%)
Basicryptus interruptus	29	6 (20)	56	11 (20)
Dalsira distincta	72	7 (10)	95	13 (14)
Gonopsis affinis	30	3 (11)	39	6 (16)
Metonymia affinis	23	5 (22)	24	5 (19)
Phyllocephala negus	38	14 (36)	47	17 (37)
Schyzops aegyptiaca	41	18 (44)	50	22 (45)
Tantia vicina	59	20 (35)	58	14 (24)
Tetroda histeroides	32	7 (23)	42	13 (30)
Megarramphus hastatus	25	6 (24)	50	11 (21)
Chalcopis glandulosa	63	13 (20)	84	25 (30)
Macrina juvencus	32	7 (22)	30	7 (22)

Interspecies comparisons are best made using relative patch area totals (Ap%). It may be observed from Table 3 that Ap% varied between around 10 and 45%. Ap% was greatest in *Schyzops aegyptiaca* and *Phyllocephala negus*, two desert phyllocephalines, and least in *Dalsira distincta* and *Gonopsis affinis*. Sex area differences were greatest in *Tantia vicina* and *Tetroda histeroides*.

Observations on the microscopic structure of the patches were made on potashed material. In *Basicryptus interruptus* (Fig. 3A, male sternite: Fig. 7b, male laterotergite) patches were clearly delimited. Bristle sockets were small and contiguous with surrounding patch cuticle. In the other phyllocephalines examined, the patches although clearly delimited were much broken up by the presence of bristles with large diameter sockets (Figs 7c–f). In the case of *Macrina juvenca*, it was observed that bristle sockets were surrounded by several rows of ordinary epithelial cells including epidermal glands, forming what might be called bristle discs.

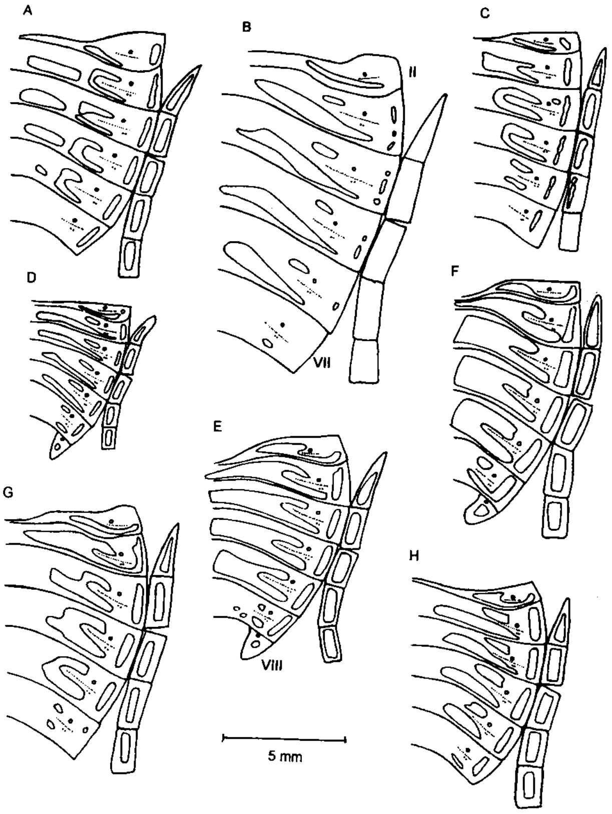

Fig. 6. Phyllocephalinae. Comparison of patch patterns on sternites and laterotergites in females. A – *Basicryptus interruptus*, Australia; B – *Dalsira distincta*, Cameroons; C – *Gonopsis affinis*, Japan; D – *Metonymia affinis*, S. Africa; E – *Phyllocephala negus*, Arabia; F – *Schyzops aegyptiaca*, Egypt; G – *Tantia vicina*, Cameroons; H – *Tetroda histeroides*, India.

Patch cuticle was absent on sternite in the immediate vicinity of the spiracles, trichobothria, and muscle insertions (Fig. 7h). Patch cuticle was absent on the laterotergites alone in *Dalsira distincta* among the phyllocephalines examined (Figs 5B, 6B).

Epidermal glands were abundantly present in the sternites of all male phyllocephalines examined. As a general rule, epidermal glands are missing from the patches. However, epidermal glands were detected in males in the patches of *Basicryptus interruptus* and *Dalsira distincta*. There is no doubt that these epidermal glands in males are a source of male-produced pheromones (Carayon, 1981; Aldrich, 1988).

The need for space for glands may be a factor limiting the further spread of patch cuticle. In male *Chalcopis glandulosa*, patches were reduced and epidermal gland numbers consequently greatest in the posterior sternites. In male *Gonopsis affinis*, epidermal glands were concentrated in paired symmetrically disposed stripes on sternites IV, V, and VI. These glandular stripes (Fig. 7d, pg) alternated with stripes containing patch cuticle. Elsewhere in male *G. affinis*, glandular stripes were present on the posterior margin of sternite II and on the anterior margin of sternite VII. In addition, glandular islands were present mid-ventrally on sternites IV, V, and VI.

DISCUSSION

The paper provides new data concerning the occurrence of cuticular patches in the subfamily Pentatominae and for the first time data on their occurrence in the subfamily Phyllocephalinae. Some considerations arising from the investigation follow.

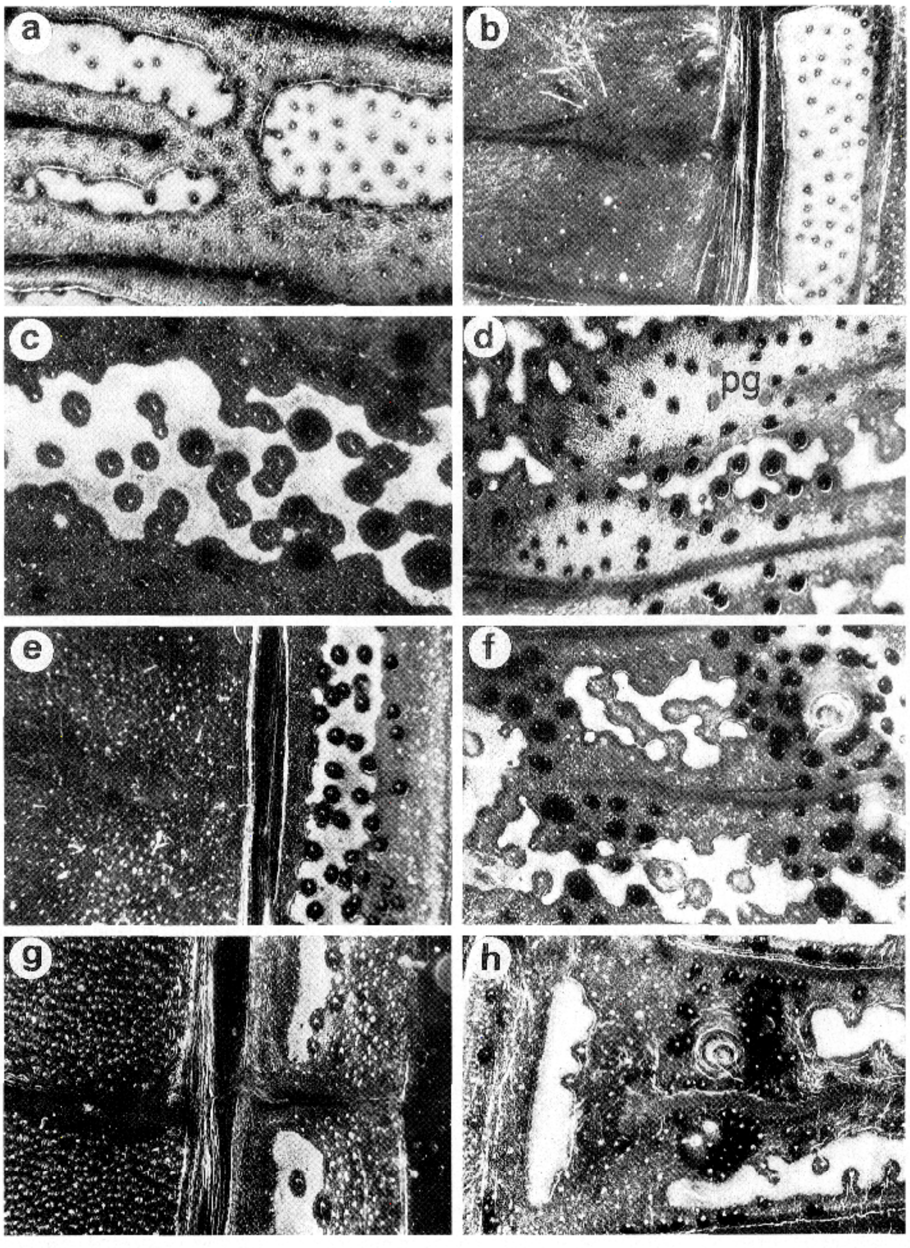

Fig. 7. Phyllocephalinae. Light micrographs (phase contrast) of cuticular isolates showing details of patch patterns. a – *Basicryptus interruptus* male, sternite III; b – *B. interruptus* male, laterotergite corresponding to sternite IV; c – *Dalsira distincta* male, sternite III; d – *Gonopsis affinis* male, sternite IV (pg, glandular stripe); e – *G. affinis* male, laterotergite corresponding to sternite IV; f – *Macrina juvenca* male, sternite III showing absence of patch cuticle in areas occupied by spiracle and muscle insertion; g – *Megarrhamphus hastatus* male, laterotergites corresponding to sternites IV and V; h – *Metonymia affinis*, female sternite V showing absence of patch cuticle in areas occupied by spiracle, muscle insertion and trichobothria.

Patch morphology

The potential of integument to form patch cuticle is not, as previously suspected (Staddon, 1992), restricted to areas of the sternites median to the spiracles. In phyllocephalines, additional patches were present on the sternites in areas lateral to the spiracles as well as on the laterotergites. As well as in the Phyllocephalinae examined, patches were detected on the laterotergites in a pentatomine, *Halys dentatus*.

A tendency to fusion of patches on sternite III in the ventral mid-line seems to be a characteristic of Carpocorini. Mid-line fusion in other sternites was observed in some Phyllocephalinae.

The sexual dimorphism so noticeable in many Pentatominae (e.g. *Nezara viridula*) was much less pronounced in Phyllocephalinae.

Exceptions to the general rule that epidermal glands are sparse or absent in patch cuticle were found in two phyllocephalines, *Basicryptus interruptus* and *Dalsira distincta*.

The patches in many Phyllocephalinae exhibit a fragmented appearance. In *Macrina juvenca*, the patches are broken up by bristle discs comprising a bristle socket surrounded by several rows of ordinary epithelial cells including epidermal glands.

Patches in Pentatomidae so far as now known are probably confined to the abdomen. In a careful examination of *Basicryptus interruptus*, no patches were found on either head or thoracic structures.

We have no new observations to make on the fine structure of the patches. Using *N. viridula*, we attempted to examine patch epicuticle ultrastructure for comparison with that of ordinary cuticle but, in the limited time available for this study, without success.

Geographic and taxonomic variation

The data concerning geographic and taxonomic distribution of variation, although fragmentary, contain pointers of interest for future studies.

Some species showed a high degree of uniformity. In cosmopolitan *Nezara viridula*, for example, patch patterns were uniformly similar in all mainland material examined. However, additional patches were present in male from St. Thomas I., Virgin Is., demonstrating the potential for variation in geographically isolated populations. Aldrich et al. (1987) have detected pheromone strains in geographically isolated populations of *N. viridula*. It is possible that the variation observed in the other pentatomines examined has a climatic basis.

Species showing a high degree of variability include *Carpocoris pudicus*. Instability as observed in the point sample from Turgutlu suggests that variation may extend along a character gradient, presumably a gradient from north to south. The variability observed in Asian *Plautia fimbriata* is similarly indicative of a character gradient, but in this case from east to west.

Functional considerations

The observations here reported in no way appear to contradict the hypothesis that the occurrence of patches is linked to heat. In fact, the most extended system of patches now known in Pentatomidae was found in two desert specialists, *Schyzops aegyptiaca* and *Phyllocephala negus*. It is not a difficulty for a thermoregulatory hypothesis that patches were missing in the Australian Halyini examined. In several studies carried out on Central

Asian Heteroptera, Toms (1981, 1983, 1984, 1989) has revealed something of the variety of thermoregulatory adaptations, physiological and behavioural, to be found in Heteroptera.

Heat loss by evaporative cooling has been described in cicadas (Hadley et al., 1989; Sanborn et al., 1992), sawfly larvae (Seymour, 1974), and shield bugs (Toms, 1983). In such cases it is possible to maintain the body at a lower temperature than the air temperature. In the flying insect heat loss is achieved by radiation and convection through the relatively thin integument forming the abdominal wall (Heinrich, 1975; Kammer, 1981). Heat loss in such cases is possible of course only when the temperature of the body exceeds that of the external environment.

In a previous paper, it was suggested that the patches in Pentatomidae are specialised for evaporative cooling (Staddon, 1992). However, we suggest that the patch system of desert phyllocephalines is simply too extensive to allow loss of water. It is the general view that desert arthropods are too small to lose much heat by evaporation since this would quickly lead to death by dehydration (Crawford, 1981). Makings' film method (Makings, 1968) of detecting transpiration certainly revealed area specific transpiration from the patches in *Nezara viridula* (Staddon & Ahmad, 1994). However, the applied film by disrupting patch epicuticle may itself have been the cause of the area specific transpiration detected.

Another hypothesis to be considered is that the patches facilitate rapid heat loss and so are an aid to thoracic temperature regulation during flight. The absence of glands in patch integument is explained if by the presence of this additional tissue element the flow of heat from the body to the surface is impeded.

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