Phylogeny of the South Asian Halyine Stink Bugs (Hemiptera: Pentatomidae: Halyini) Based on Morphological Characters

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ABSTRACT A phylogenetic analysis of 31 Oriental and Palaearctic genera of the tribe Halyini of South and Central Asia is presented here, concentrating upon the 22 genera for which complete data were available. Sixty-one morphological characters were analyzed using parsimony, including characters of the scent-gland apparatus and internal and external male and female genitalia. Using *Phricodus* as an outgroup, a single most-parsimonious tree resulted, following character reweighting according to their fit to the 52 multiple shortest trees initially found. *Carenoplistus* was always basal, and *Jugalpada* and *Mustha* were plesiomorphic in most bootstrapped trees. Two relatively plesiomorphic clades were identified, the *Halys* group (*Salixocoris*, *Halys*, and *Neohalys*) and the *Paranevisanus* group (*Erthesina*, *Apodiphus*, and *Paranevisanus*). Although strong bootstrap support existed for a clade of 12 genera (*Tipulparra*, *Sarju*, *Izharocoris*, *Dalpada*, *Tachengia*, *Meridindia*, *Cahara*, *Ameridalpa*, *Eupaleopada*, *Meridalpa*, *Lodosocoris*, and *Neolodosocoris*), the only consistent clades within it were a *Dalpada* group (*Sarju*, *Izharocoris*, *Tachengia*, and *Dalpada*) and a *Lodosocoris* group (*Lodosocoris* and *Neolodosocoris*). Tentative placements of the other nine genera are made, and a generic key is provided.

KEY WORDS phylogeny, Halyini, Pentatomidae

The Pentatomidae causes many difficulties for systematists, not least of which is that the higher taxonomy is a "morass of poorly defined higher taxa, particularly the tribes" (Wall 2004: 45), making the selection of reasonable outgroups very difficult: "for the masochist, however, the Pentatomidae makes good sport" (Wall 2004: 46). In this paper, we are concerned with the Halyini, a heterogeneous and widespread group in great need of taxonomic revision on a world basis. Its systematic position has been a matter of discussion for a long time, but there has been a consensus over the last half-century that the Halyini is a monophyletic group (Ahmad 1979, Abbasi 1986, Rider 2006). No published phylogeny of the Halyini exists: there are suggested phylogenies of the species of three genera, *Erthesina* (Ahmad et al. 2004), *Sarju* (Memon and Ahmad 2008), and *Mustha* (Memon and Ahmad 2009), but these were not done numerically. The as-yet unpublished part of the Ph.D. dissertation of Wall (2004) outlines a phylogeny of many of the world genera, but the major part of his study was focused on Australian genera and species (see Wall 2007). His tentative world phylogeny included 62 of the 85 genera reported in the Palaearctic catalog of Rider (2006) (but note that Rider lacks many of the genera and species described from South and central Asia), but the taxon sampling of 40 non-Australian taxa was very scanty, usually using only a single species per genus. Hasan and Kitching (1993) grouped the Halyini with the Megarrhamphini, Tetrodini, and Phyllocephalini, but because they did not publish the species on which their cladograms were based, it is difficult to use their work to inform ours. The only molecular study (Grazia et al. 2008) is of the whole of the Pentatomoidea, and does not try to resolve relationships within the Pentatominae.

Interestingly, almost all the Old World genera, from the type genus *Halys* to all present genera (many of which arose from the splitting of obviously different species from *Halys* and *Dalpada* into new genera such as *Sarju*, *Cahara*, and *Jugalpada*), have always been placed in one monophyletic group, whatever its status (Distant 1902; Kirkaldy 1909; Ahmad et al. 1974, Ahmad 1979; Ghauri 1975, 1977, 1980, 1988; Ahhasi 1986; Ahmad and Kamaluddin 1978; Ahmad and Afzal 1984a,b; 1986; Ahmad et al. 1998; Ahmad and Memon 2001; Ahmad et al. 2002, 2004; Memon and Ahmad 2002a,b 2003, 2008, 2009; Memon et al. 2006). The best-known Halyini are the genera from South Asia (i.e., India, Pakistan, Bangladesh, Afghanistan, Russia, China, Iran, Iraq, and Turkey), following the work of Ghauri and then Ahmad; there has been very little work on this tribe from other regions over the past 40–50 yr apart from the New World *Brochymena*/*Parabrochymena* genera (McDonald, 1966; McPherson & Ahmad 2007). Many genera have been described from other parts of the world, such as Africa and Australia, but their inclusion in the Halyini is still under discussion, especially those from Australia (Gross 1975): most have four-segmented antennae

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and females with external genital plates, apparently closer to *Phricodus*, whereas almost all Asian halyine genera have been included in the Halyini since Distant (1902, 1918) and Kirkaldy (1909). Given this emphasis, we concentrate on this fauna here.

In the Oriental and Palaearctic regions of South and Central Asia and some neighboring countries, the fauna of halyine stink bugs comprises 31 genera, with ≈121 described species, encompassing tremendous structural diversity. Since 1900, the status of many taxa has changed, and is still changing, with various work (Fabricius 1803; Spinola 1839; Amyot and Serville 1843; Dallas 1851, 1857; Spinola 1837, 1852; Walker 1867; Distant 1879, 1893, 1902, 1908, 1918; Jakovlev 1882; Atkinson 1888; Lethierry 1891; Kirkaldy 1909; Kiritshenko 1963; Hoberlandt 1959, 1995) adding many new species and genera, and synonymizing and transferring many species. However, their descriptions were based only on external morphology (coloration, length of antennal segment, length of labium of some species, length of body, habitus, and female external genital plate) and did not include anything about the male or internal female genitalia. This led to a high risk of species misidentification; hence, modern workers have spent a lot of time and effort on synonymization and transfer of species and genera (Abbasi and Ahmad 1971, 1976; Chopra 1974; Ghauri 1975a,b, 1977a,b,c, 1980, 1982a, 1988a,b; Afzal and Ahmad 1981; Ahmad and Parveen 1982; Ahmad and Kamaluddin 1978; Abbasi 1986; Ahmad and Ahmad 1993; Memon and Ahmad 1998, 1999, 2001, 2002a,b, 2003, 2008, 2009; Ahmad et al. 2002, 2003, 2004a,b; Memon et al. 2002, 2006; Rider 2006).

Halys is the most cosmopolitan genus, present in most parts of South and Central Asia. *Halys* species feed on a variety of host plants, and they show great structural variation with geography and ecology. Recently, Abdul Manan (unpublished) observed great variation in supposedly diagnostic characters (even in the male and female genitalia, previously considered diagnostic at both generic and species levels) among specimens within single populations, mostly from Sindh (Pakistan) but not across the whole of Pakistan and India, where these characters were very constant: DNA sequencing confirms that these were all a single species (Memon et al. 2006). The significance of this variation is not yet clear.

We define membership of the South Asian Halyini as the possession of a set of characters: the first antennal segment is shorter than the apex of the head; the antenna has five segments; the labium reaches or exceeds the hind coxae; the antero-lateral margins of the pronotum are distinctly denticulate; the scent-gland apparatus is on the mesosternum and has a ventral, usually lobe-like structure, the peritreme; the spermathecal bulb (in females) has a process; and the abdomen is distinctly sulcate with a median carina. As noted by Wall (2004), these characters are homoplasious within the tribe and outside, and it is not possible to define the tribe with a synapomorphy, but Ahmad et al. (1974) used many of the characters that we use here for our phylogeny for the identification of the genera and species. Thus, all current researchers use the same set of characters: some play a vital role in identification, whereas others are less important but still used in diagnosis.

Continuous or discrete external and internal morphological characters play a key role in identification, and can also be used for estimating phylogenetic relationships (Pereyra and Mound 2009). Among Asian halyine genera, many characters have been considered important in determining relationships: number and length of antennal segments, paraclypeal structure, head length-to-width ratio, and head-to-pronotal length ratios. To these we can add characters of the external and internal male and female genitalia: the shape of the dorsal and ventral posterior margin of the male pygophor, the shape of the paramere (which has tremendous diversity among genera, particularly in the blade, the most diagnostic trait in the identification of halyine species and genera), and even the male's inflated aedeagus varies among genera in the number, shape, and size of its dorsal conjunctival appendages, which together with the presence of penial lobes are diagnostic. The technique of inflating the aedeagus, and its use in identifying species was introduced by McDonald (1966), Gross (1975), Ahmad (1986), and Ahmad and McPherson (1990, 1998), used since by almost all researchers at both generic and species levels.

Among female genital characters, the shape of the posterior margin of the first gonocoxae, the posterior margin of the eighth paratergite, and the length of the ninth parartergite are all variable. Previously, internal female genital characters were not considered useful in diagnosis, but as a result of emphasis by Ahmad and colleagues, today we know that these traits are important and also could be useful in estimating phylogenetic relationships among genera, particularly the presence of bulb processes. As shown here, *Carenoplistus*, *Phricodus*, and the monotypic genus *Lodosocoris* all have a bulb without processes, unusual for Halyini because this state is supposed to be diagnostic for the tribe (Ghauri 1975, 1980, 1982; Ahmad and Afzal 1984, 1986; Ahmad and Memon 2001; Memon 2002a,b). The shape, size, and number of bulb processes is considered important both for estimating the phylogeny and species identification.

The goal of the current study is to estimate the phylogenetic relationships among the South Asian genera of the Halyini from morphological characters.

Materials and Methods

All existing South and Central Asian genera within the tribe Halyini were included (see Appendix): *Agaeus* Dallas 1851 (f), *Ameridalpa* Ghauri 1982, *Apodiphus* Spinola 1837, *Asyla* Walker 1867 (f), *Cahara* Ghauri 1887, *Carenoplistus* Jakovlev 1882, *Dalpada* Amyot & Serville 1843, *Dendrites* Kirkaldy 1909 (f), *Erthesina* Spinola 1837, *Eupaleopada* Ghauri 1982, *Halys* Fabricius 1803, *Iskenderia* Kiritshenko 1963 (f), *Izharocoris* Afzal & Ahmad 1981, *Jugalpada* Ghauri 1975, *Lodosocoris* Ahmad & Afzal 1986, *Meridalpa* Ghauri 1982, *Meridindia* Ghauri 1982, *Mustha* Amyot & Serville 1843, *Neohalys* Ahmad & Parveen 1982, *Neolodosocoris* Memon & Ahmad 2002 (m), *Neonevisanus* Distant 1918 (f), *Nevisanus* Distant 1893 (f),

Table 1. Character table for characters scored on taxa, and reconstructed on the cladogram of Fig. 4

Genus	Character						
	1	1111111112	2222222223	3333333334	4444444445	5555555556	6
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1
Phricodus	0000000006	3041010101	1411051001	2000000000	4000001100	0000100000	0
Carenoplistus	0012000200	3041000101	2000001001	0000011000	0000105800	0000020000	1
Jugalpada	1000000203	3042001211	2100021001	2100000025	0120a01111	3310010131	1
Surenus	1000000200	3041401011	0210001001	2100??????	??????????	???002????	1
Mustha	1000000206	3041001211	2410051111	2100012000	3120f11012	0010200131	1
Orthoschizops	1000000205	3041001211	1410051001	2100??????	??????????	???002????	1
Agaeus	1034300200	3000101211	3100001000	1100??????	??????????	???0030141	1
Iskenderia	1022000200	3020101211	?100001001	2100??????	??????????	??????????	1
Halys	1001000203	3020101211	3100001001	2100011000	0110301011	0010000131	1
Neohalys	1001000200	3020101211	3100001001	2100011000	0200201111	0010000111	1
Salixocoris	1001000200	2020101211	3100001001	2100010000	0000504511	0010000131	1
Asyla	1002000221	3020401211	2100110001	2100??????	??????????	???003????	1
Nevisanus	1000100220	1020301011	1100001001	2100??????	??????????	???000????	1
Neonevisanus	1000100222	0020301111	1100001001	2100??????	??????????	???000????	1
Paranevisanus	1122020222	1020301111	3100001001	2100000010	0010b01200	4010011153	1
Apodiphus	1123010222	1020301211	2100001001	2100012000	0110c00200	0010020131	1
Sarju	1000200210	3120201211	2100131001	2100000010	1020703300	0211000131	1
Cahara	1000200210	3130201211	3100121001	2100000023	0020701400	6012100131	1
Izharocoris	1000200110	3120201211	2100121001	2100000122	0121703311	0110000131	1
Lodosocoris	1000200210	3110201211	3100141001	2100000121	0110d02000	7010000000	1
Neolodosocoris	1000200210	3110101211	3100141001	2100000021	0000e01000	80????????	1
Tipulparra	1000200110	3120201211	2100101001	2100000210	2120603600	5010000132	1
Ameridalpa	1000200210	3110201011	2100121001	2100000024	1110701400	6010120111	1
Meridindia	1000200210	3120201011	3100101001	2100100023	0100721600	2010100111	1
Eupaleopada	1000200210	3120201211	2300101001	2100000025	0200901700	1010000111	1
Meridalpa	1000200210	3120201211	2100101001	2100000010	0010601700	2010100121	1
Dendritis	1000202210	3120201210	21001?1001	2100??????	??????????	??????????	1
Dalpada	1000201210	3120201211	2100141001	2110000022	0000803311	0210100132	1
Saontarana	1001000200	3020101211	1100001001	2100??????	??????????	???000????	1
Erthesina	1142200200	3020101211	3100001001	2111210000	0000401000	0010020131	1
Tachengia	1000201114	2030101211	1100141001	2100000026	0000803311	021???????	1
1	0000000200	3041000101	2000001001	2000000000	0000001100	0000000000	1
2	1000000200	3041001211	2100001001	2100000000	0120201111	0010000131	1
3	1000000200	3041001211	2100001001	2100010000	0120201011	0010000131	1
4	1000000200	3020101211	3100001001	2100010000	0000201011	0010000131	1
5	1001000200	3020101211	3100001001	2100010000	0000201011	0010000131	1
6	1001000200	3020101211	3100001001	2100011000	0100201011	0010000131	1
7	1000200200	3020101211	3100001001	2100010000	0000401000	0010000131	1
8	1122200200	3020101211	3100001001	2100010000	0000401000	0010020131	1
9	1122010222	1020301211	3100001001	2100010000	0010b01200	0010020131	1
10	1000200210	3120201211	3100101001	2100000020	0000601000	0010000131	1
11	1000200210	3120201211	2100101001	2100000020	0000601600	0010000131	1
12	1000200110	3120201211	2100101001	2100000010	0020603600	0010000131	1
13	1000200110	3120201211	2100121001	2100000010	0020703300	0210000131	1
14	1000200110	3120201211	2100121001	2100000022	0020703311	0210000131	1
15	1000201110	3120201211	2100141001	2100000022	0000803311	0210100132	1
16	1000200210	3120201211	2100101001	2100000020	0000601600	2010100111	1
17	1000200210	3120201011	3100101001	2100000023	0100701600	2010100111	1
18	1000200210	3110201011	3100121001	2100000023	0110701400	6010100111	1
19	1000200210	3120201211	2100101001	2100000020	0000601700	2010100111	1
20	1000200210	3110201211	3100141001	2100000021	0000d01000	7010000000	1

Orthoschizops Spinola 1852 (f), *Paranevisanus* Distant 1908, *Phricodus* Spinola 1839, *Salixocoris* Ahmad & Abbasi 1974, *Saontarana* Distant 1918 (f), *Sarju* Ghauri 1977, *Surenus* Distant 1901 (f), *Tachengia* China 1925 (m), and *Tipulparra* Ghauri 1980. "f" indicates genera only known from females, and "m" those only known from males. We were unable to examine the three species of *Faizuda* Ghauri 1988, the monotypic *Ouscha* Distant 1921 (both from Vietnam) or the two species of *Sinometis* Zheng & Lin 1987 from China.

We examined the phylogenetic relationships among the genera using adult morphological characters, including the scent-gland apparatus, and external and internal male and female genitalia. The characters were extracted from the literature and by observation of material including the holotype and paratype of species of all taxa. Literature data were essential in some cases: for example, *Asyla*, *Dendrites*, *Iskenderia*, *Nevisanus*, *Neonevisanus*, *Orthoschizops*, *Saontarana*, and *Surenus* are taxa described by many old authors, but not recorded or mentioned since, except in the catalog of Rider (2006). We used both presence/absence coding and true multistate characters, the latter because of the great structural diversity particularly in male and female genital characters. In total, 61 characters were used (see below: Table 1), most of them as far as is known constant among species within each genus.

In the data matrix (Table 1), *Agaeus*, *Asyla*, *Dendrites*, *Iskenderia*, *Nevisanus*, *Neonevisanus*, *Orthoschizops*, *Saontarana*, and *Surenus* contained missing data for 21 characters because they cannot be scored for male characters. Taxa with a large proportion of missing characters decrease the accuracy of phylogenetic inference (Huelsenbeck 1991; Novacek 1992; Wiens 2003). Thus, we conducted separate analyses on the 22 genera with more-or-less complete data, and the full set of 31 genera.

Phricodus was our chosen outgroup because this genus was included in the Halyini by Kirkaldy (1909) but then placed in its own tribe (Cachan 1952), albeit still in association with the Halyini (Göllner-Scheiding, 1999) (fide Wall 2004). Hamid (1974) and Memon and Ahmad (2003), following Kirkaldy (1909), described the genus *Phricodus* in the tribe Halyini.

Trees were found with PAUP, version 4.0 (Swofford 2003) under the parsimony criterion, by using heuristic search (HSEARCH) with the default settings (ADDSEQ = SIMPLE, SWAP = TBR, MULTREES = YES, RECONLIMIT = INFINITY, STEEPEST = NO); all character states were treated as unordered. There were numerous equally parsimonious trees: the characters were then reweighted (REWEIGHT, with default options INDEX = RC, FIT = MAXIMUM, TRUNCATE = NO, MINFORFIT = RANGE) in relation to their fit to these trees, and the search started again. On the final single resulting tree, we used the Bootstrap command to assess confidence in each branch.

Results

Characters

In total, 61 characters were defined and scored (Table 1); 16 were parsimony uniformative but are included because they are important diagnostic characters for particular genera.

Body Size. (0) small (3.7–13 mm); (1) large (16–38 mm). Although *Phricodus* is the smallest of all the genera, its species are also the most variable (3.7–6.5 mm); almost all species of *Carenoplistus* have similar body sizes of ≈13 mm with only minor variation (both 0). All the other genera have large body sizes of 16–38 mm (1). This split is based on a distinct gap in the size spectrum.

Body Surface. (0) smooth, patterned; (1) mottled with raised ochraceous or bright yellow irregular spots. The body color of most genera is normally smooth and not raised, and the pattern is ochraceous, light brown, dark brown, or blackish brown (0). All species have dark punctures arranged in a pattern that is sometimes shared among a group of genera. There are three genera (*Erthesina*, *Apodiphus*, and *Paranevisanus*) that differ in having raised spots (1).

Head. (0) unicolored, with ochraceous, brown or black punctures; (1) three to four impunctate oblique ochraceous spots; (2) a median fine yellow line on the posterior part; (3) three pale stripes, two broad along the entire length of the head, and one thin; (4) a marginal impunctate ochraceous stripe around the entire head, together with a median yellow line. In almost all included halyine genera the head is mostly unicoloured, usually with ochraceous or sometimes brown or black punctures (0). A few genera have a different pattern: *Carenoplistus* (1); *Apodiphus*, *Paranevisanus*, and *Iskenderia* (2); *Agaeus* has what looks like a modified version of state 1 (3); and *Erthesina* (4).

Pronotum. (0) smooth; (1) a wide ochraceous and brown stripe in the middle of anterior part of pronotum; (2) a wide yellow stripe in the middle of the anterior part of the pronotum; (3) four raised impunctate ochraceous spots, and a median line on the anterior part; and (4) 10 very prominent triangular black spots of various sizes. Most halyine genera have a smooth unicoloured pronotum without any pattern (0). A number of genera are different: *Halys*, *Neohalys*, *Salixocoris*, and *Saontarana* (1); *Carenoplistus*, *Iskenderia*, *Asyla*, *Paranevisanus*, and *Erthesina* (2); *Apodiphus* (3); and *Agaeus* (4).

Scutellum Pattern. (0) unicoloured; (1) two yellow, impunctate, almost round, relatively broad spots at the basal angles of the scutellum; (2) two to five yellow impunctate basal V-shaped or triangular spots; and (3) with two large, black, oval and two very small round spots. A large group of genera have a unicoloured scutellum with no pattern (0). Several genera differ from this: *Nevisanus* and *Neonevisanus* (1); a relatively large group of genera has state 2, sometimes variable in number and shape, mostly among the species of *Sarju* and *Dalpada;* and *Agaeus* (3).

Connexivum Color. (0) mostly unicoloured, light or dark brown; (1) smoky or black brown with square or rectangular ochraceous fascia; and (2) with yellow T-shaped fascia. Generally the color of the connexiva is not variable among included halyine species (0), except in two genera: *Apodiphus* (1) and *Paranevisanus* (2) where the variable thickness of the stem of the T-shaped fascai is diagnostic among species.

Tibia Color. (0) Usually ochraceous with light-brown scattered spots; (1) brownish punctate with dark brown; and (2) black with broad pale medial annulus, the first segment of the tarsi is pale, and the rest black. Nearly all genera have ochraceous tibiae (0); *Dalpada* and *Tachengia* (1); and *Dendritis* (2).

Length of Head. (0) distinctly wider than long; (1) equal or subequal to its width; and (2) distinctly longer than wide. The length:width ratio of the head is quite an important character differentiating the Halyini from other tribes. In almost all included halyines, the head is distinctly longer than wide (2) but this differs in a few genera: *Izharocoris*, *Tipulparra*, and *Tachengia* (1); and *Phricodus* (0). Most *Carenoplistus* have state 1, but one species (*C. brevis*) shares state 2 with *Phricodus:* we have scored the genus as state 1.

Shape of Head. (Fig. 1) (0) head broad at the base, gradually tapering anteriorly; (1) head broad at the base, only slightly tapering anteriorly; and (2) head very broad, almost rectangular. This character divides genera into two large groups with states 0 (*Phricodus* to *Salixocoris* in Table 1, plus *Saontarana* and *Erthesina*) and 1 (*Sarju* to *Dalpada* in Table 1,

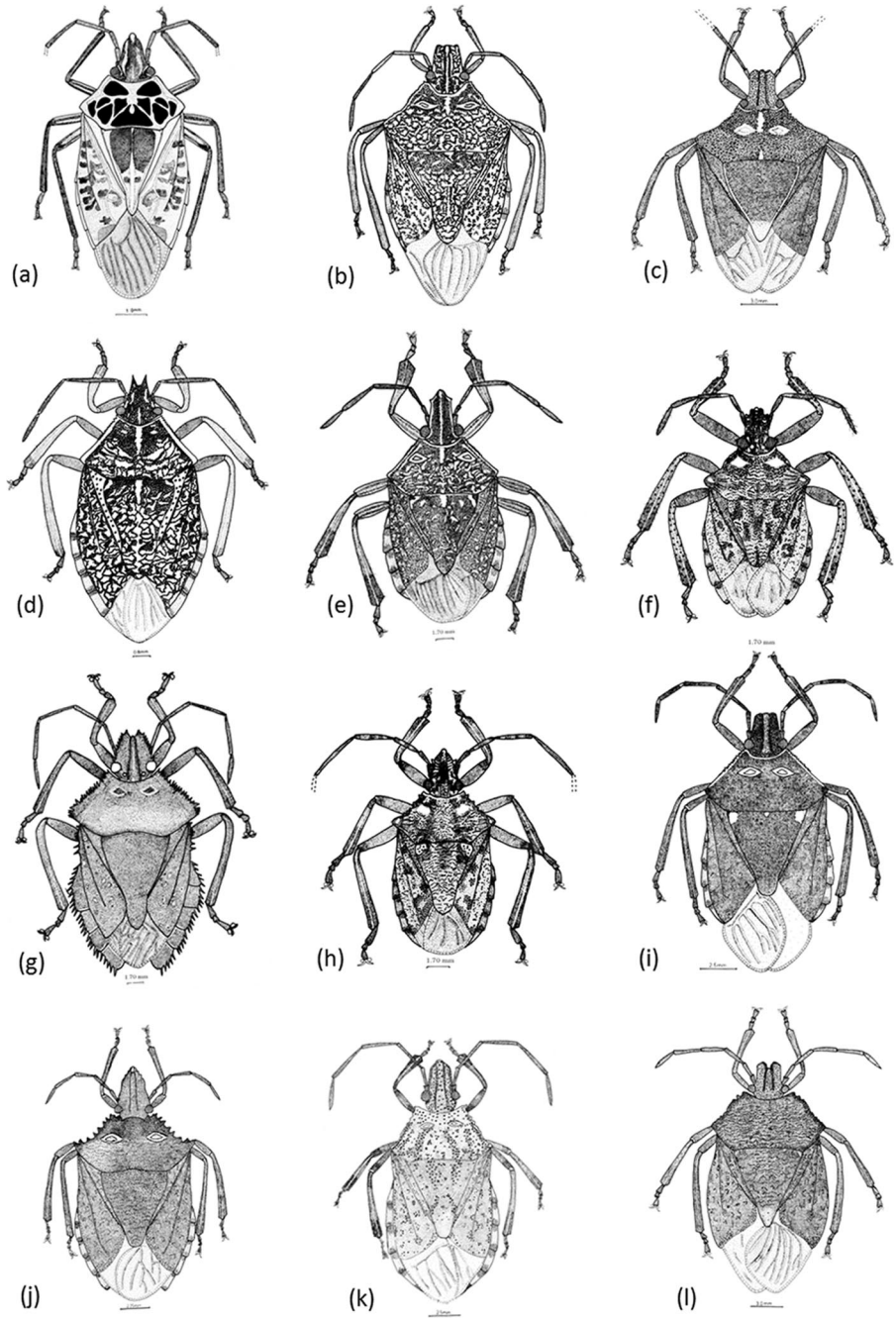

Fig. 1. Habitus drawings of representative species of Halyini, showing the features of the head (lateral margins, and the length, lobes and apex of the paraclypei), and pronotum (lateral margins, humeral angle). (a) *Agaeus tesselatus.* (b) *Apodiphus iraquiensis.* (c) *Asyla indicatrix.* (d) *Carenoplistus karachiensis.* (e) *Erthesina pakistanensis.* (f) *Lodosocoris azhari.* (g) *Mustha ismirensis.* (h) *Neolodosocoris chinensis.* (i) *Nevisanus alternans.* (j) *Orthoschizops assimilis.* (k) *Saontarana burmanica.* (l) *Surenus normalis.*

plus *Tachengia*); there with five genera with state 2 (*Asyla*, *Nevisanus*, *Neonevisanus*, *Paranevisanus*, and *Apodiphus*).

Shape of Lateral Margins of Head. (Fig. 1) (0) moderately and concavely sinuate; (1) reflexed; (2) more or less upwardly recurved; (3) smooth head margin or with small tooth: (4) with two teeth, one small just above eyes and the other large and round, toward the apex of the head; (5) anteriorly dentate; and (6) entirely armed with denticles or spines. The majority of

genera have state 0, but in some genera this trait is greatly modified: *Asyla* (1); *Neonevisanus*, *Paranevisanus*, and *Apodiphus* (2); in *Paranevisanus* it is much more distinctly recurved; *Jugalpada* and most species of *Halys* (3); *Tachengia* (4); *Orthoschizops* (5); and *Phricodus* and *Mustha* (6). Some species of *Sarju* might be construed as having two "teeth" in front of the eyes (state 4), but in these species the first "tooth" is actually the outer lobe of paraclypei, forming a very distinct angle with the inner lobe, whereas only the second tooth is a real tooth, near the eye.

Ratio of Head Length to Pronotum Length. (0) head much shorter than pronotum; (1) head slightly shorter than pronotum; (2) head equal to pronotum; and (3) head longer than pronotum. Almost all included halyine genera have the head longer than pronotum (3), also one of the halyine tribal characters. Some genera differ: *Neonevisanus* (0); *Nevisanus*, *Paranevisanus*, and *Apodiphus* (1); and *Salixocoris* and *Tachengia* (2).

Lobes of Paraclypei. (Fig. 1) (0) unilobed; and (1) bilobed. We consider this character very important for phylogeny. It divides the analyzed halyine genera into two groups: *Phricodus* to *Apodiphus* in Table 1, plus *Saontarana*, *Erthesina*, and *Tachengia* (0); and *Sarju* to *Dalpada* in Table 1 (1), in which the outer lobes usually form a distinct angle with the inner lobes. Some species of *Halys* look as if they should be scored as state 1 with two lobes, because of the presence of a small tooth- or spine-like structure on the lateral margin of the head. However, this is a small tooth rather than a distinct outer lobe which forms an angle with an inner lobe. Some published and unpublished species (see Memon et al. 2002, Manan 2010) have smooth or slightly sinuate lateral margins.

Length of Paraclypei. (Fig. 1) (0) distinctly shorter than clypeus; (1) slightly shorter than clypeus; (2) usually equal or subequal to the clypeus; (3) distinctly longer than the clypeus; and (4) extending well beyond the clypeus. This trait is very variable among and sometimes within genera. Most genera are state 2, with the following exceptions: *Agaeus* (0); *Lodosocoris*, *Neolodosocoris*, and *Ameridalpa* (1); *Cahara* and *Tachengia* (3); and in six genera (*Phricodus* to *Orthoschizops* in Table 1) (4). Characters 13, 15, and 41 have a great deal of variation among genera and species that is difficult to score as separate states; after studying a large number of specimens, we regard the current splitting into states as the best that can be achieved at present. The states represent distinctly different entities (e.g., Fig. 1), but we cannot give quantitative justification.

Width Between Projected Part of Paraclypei. (0) entirely attached to clypeus; (1) the projected parts of the two paraclypei are more or less separated between their apices, leaving the clypeus free in between; and (2) tips of the projected parts of the paraclypei adhere together, enclosing the clypeus. Nearly all included halyine genera have state 0, except *Phricodus*, *Carenoplistus*, *Surenus*, *Mustha*, and *Orthoschizops* (1); and *Jugalpada* (2). A few species of *Mustha* and one of *Cahara* (*C. jugatoria*) also have state 2. This character could be correlated with character 9 because the tips of the paraclypei adhere when they are projected, but not in all taxa, which is why they are listed separately.

Apex of Paraclypei. (Fig. 1) (0) acute; (1) subacute; (2) rounded; (3) broad, straight, or slightly concave; and (4) broadly triangular at the apex. This character divides the genera: *Phricodus*, *Carenoplistus*, *Julgapada*, *Mustha*, and *Orthoschizops* (0); *Agaeus*, *Iskenderia*, *Halys*, *Neohalys*, *Salixocoris*, *Neolodosocoris*, *Saontarana*, *Erthesina*, and *Tachengia* (1); *Sarju* to *Dalpada* in Table 1 (2); *Nevisanus*, *Neonevisanus*, *Paranevisanus*, and *Apodiphus* (3); and *Surenus* and *Asyla* (4).

Shape of Antenniferous Tubercles. (0) usually simple, cylindrical; and (1) developed into long spines. All included halyine genera have state 0, except *Phricodus*, where the tubercles are modified into long spines (1).

Number of Antennal Segments. (0) four; and (1) five. All included halyine genera have five-segmented antennae (1) except *Phricodus* and *Carenoplistus* that have four (0). Most included halyine species have four-segmented antennae in the nymphal stages. The four-segmented state may be plesiomorphic for halyines, but this character varies in a number of pentatomid groups.

Length of First Antennal Segment. (0) extends to a level equal to that of the apex of the head; (1) extends slightly shorter than the level of the apex of the head; and (2) extends distinctly shorter than the level of the apex of the head. Also considered a halyine tribal character, most have state 2, with the following exceptions: *Surenus*, *Nevisanus*, *Ameridalpa*, and *Meridindia* (0); and *Phricodus Carenoplistus*, *Neonevisanus*, and *Paranevisanus* (1).

Length of Second Antennal Segment. (0) remarkably long, almost equal to the combined length of the third and fourth segments; (1) equal, subequal, or a little longer than the third segment. The length of all the antennal segments is a variable trait, particularly at species and to some extent at generic level. Most included genera have state 1, except *Phricodus* and *Carenoplistus* (0); the nymphal instars of all halyine species have state 1.

Length of Bucculae. (0) short, hardly reaching halfway along the head; and (1) long, reaching to the base of the head. All included Halyini have state 1 (with slight variation among species, a little longer or shorter than the first labial segment) except *Dendritis* (0).

Position and Length of Labium. (0) extending just to the mesocoxae; (1) reaching to or slightly beyond the metacoxae; (2) reaching to the third or the base of the fourth abdominal sternite; (3) extending to the fifth–seventh abdominal sternite. With the exception of *Surenus* (0), all included halyines have a long labium, reaching at least to the metacoxae. The character is variable among species within genera, and among genera: *Phricodus*, *Orthoschizops*, *Nevisanus*, *Neonevisanus*, *Saontarana*, and *Tachengia* (1); *Carenoplistus*, *Jugalpada*, *Mustha*, *Asyla*, *Apodiphus*, *Sarju*, *Izharocoris*, *Tipulparra*, *Ameridalpa*, *Eupaleopada*, *Meridalpa*, *Dendritis*, and *Dalpada* (2); *Agaeus*, *Halys*,

Neohalys, *Salixocoris*, *Paranevisanus*, *Cahara*, *Lodosocoris*, *Neolodosocoris*, *Meridindia*, and *Erthesina* all have a labium extending to the fifth abdominal sternite, except *N. longirostratus* and *E. aberrans*, where it reaches the middle or posterior margin of the seventh sternite (all state 3). No specimen of *Iskenderia* was available, and the description did not mention the length of the labium; thus we are not able to score this genus for the character.

Shape of Lateral Margins of Pronotum. (Fig. 1) (0) slightly sinuate throughout; (1) anteriorly dentate and posteriorly sinuate; (2) with two to three denticles on the anterior part, and three on the posterior part; (3) with about six large and six small teeth; and (4) entirely armed with distinct denticles or long spines. A dentate lateral margin to the pronotum is a halyine character differentiating genera of the tribe from most others (apart from some Australian genera); only *Carenoplistus* lacks teeth, with only a sinuate margin (0). Most genera have state 1, except the following: *Surenus* (2); *Eupaleopada* (3); and *Phricodus*, *Mustha*, and *Orthoschizops* (4).

Shape of the Anterior Angle of the Pronotum. (0) smooth, subacute; (1) distinctly produced into a spine. Almost all included halyine species have state 0, except *Phricodus*, *Surenus*, *Mustha*, and *Orthoschizops* (1).

Shape of the Anterior Margin of the Pronotum. (0) smooth, without spines; and (1) with four to eight distinct spines. This trait is constant in all included halyine genera (0) except *Phricodus* (1), and even in this genus, one of its species (*P. hysterix*) lacks the marginal spines.

Humeral Angles. (Fig. 1) (0) not produced; and (1) produced. This trait divides the studied halyine genera into two large groups: *Phricodus* to *Apodiphus* in Table 1 (except *Asyla*) plus *Saontarana* and *Erthesina* (0); and *Sarju* to *Dalpada* in Table 1 (except *Saontarana* and *Erthesina*) plus *Asyla* and *Tachenigia* (1). In the latter group of genera, the humeral angles are produced either laterally, extending beyond the hemelytra (*Asyla*), or vertically upward (still usually extending beyond the basal angles of the scutellum). This character varies among species within some genera.

Shape of Humeral Angles. (Fig. 1) (0) not produced and subacute (1) moderately prominent and rounded; (2) gently raised in a small horn; (3) distinctly raised upward at an angle into a horn of variable length, with an acute apex; (4) as state 3, but a nodule rather than a horn; and (5) spinose. The shape and size of the humeral angles are important characters for identification and phylogeny, usually constant at the generic level in halyines (but not other tribes) but sometimes variable among species within a genus. Most included genera have state 0, with the following exceptions: *Asyla* (1); *Jugalpada*, *Cahara*, *Izharocoris*, and *Ameridalpa* (2); *Sarju* (3); *Lodosocoris*, *Neolodosocoris*, *Dalpada*, and *Tachengia* (4), although a few *Dalpada* species have state 3, and one species of *Tachengia* has state 5; and *Phricodus*, *Mustha*, and *Orthoschizops* (5). We regard this as a single character (Fig. 1) that cannot be split.

Length of Scutellum. (0) reaching half the length of the abdomen; and (1) reaching two thirds of the length of the abdomen. Scutellum length is a halyine tribal character, with virtually all included genera showing state 1, except *Asyla* (0).

Lateral Margins of Corium. (0) sinuate; (1) with three to five small distinct teeth. All included genera have state (0) except *Mustha* (1).

Shape of the Lateral Margins of the Abdomen. (0) sinuate; and (1) armed with distinct denticles or long spines. All included genera show state 0 except *Mustha* (1); the number, size, and shape of the spines are variable in the different species, but always present.

Shape of Evaporatoria. (0) poorly defined, with an indistinct outer margin; and (1) well defined, with a distinct outer margin. All the studied halyines have state 1, with little variation, except *Agaeus* (1). The unique state of *Agaeus* in this and the next character (31) are the reason it has sometimes been placed in its own tribe.

Shape of Peritreme. (0) absent; (1) poorly developed, very thin and slit-like; and (2) very well developed, thick, and sword-, sickle-, or lobe-like. All included halyines show state 2, with variation in the length, size, and shape among species, except in *Carenoplistus* (0) and *Agaeus* (1). Memon and Ahmad (2003) described *Carenoplistus karachiensis*, and Manan (unpublished Ph.D. dissertation) has another new species of *Carenoplistus*, both from Sindh (Pakistan), and both possessing a peritreme.

Sternites. (0) not sulcate; and (1) distinctly sulcate. All included halyines (1) except *Phricodus* and *Carenoplistus* (0) have a sulcate abdomen.

Shape of Anterior Tibiae. (Fig. 1) (0) cylindrical; and (1) more or less dilated. Cylindrical in all included halyines (0) except *Dalpada* and *Erthesina* (1). In *Erthesina* there can be some within-species variation in the degree of dilatation.

Shape of Posterior Tibiae. (0) cylindrical; and (1) distinctly dilated. Cylindrical in all included halyines (0) except *Erthesina* (1) (Fig. 1).

Shape of the Lateral Margins of the Cavity in the Dorso-Posterior Wall of the Pygophore (Males). (0) sinuate; (1) strongly sclerotized, with strongly dentate appendages; and (2) with a leaf-like structure on a highly sclerotized ridge on each side. All included genera have state 0, except *Meridindia* (1) and *Erthesina* (2).

Shape of the Median Part of the Cavity in the Dorso-Posterior Wall of the Pygophore (Males). (0) smoothly concave; and (1) with a distinct median projection. Most included genera have state (0) except *Carenoplistus*, *Mustha*, *Halys*, *Neohalys*, *Salixocoris*, *Apodiphus*, and *Erthesina* (1).

Shape of the Median Projection of the Cavity in the dorso-Posterior Cavity of the Pygophore (Males). (0) absent; (1) small and relatively thin; and (2) broad, thick, and usually bilobed. Of the included halyine genera with a median projection (see character 36), with some intrageneric shape variation, all have state 0 except *Carenoplistus*, *Halys*, *Neohalys* (1) and *Mustha* and *Apodiphus* (2).

Shape of the Lateral Margins of the Cavity in the Ventro-Posterior Wall of the Pygophore (Males). (0) smooth or sinuate; (1) with a hook-like structure on each side; and (2) with sclerotized ridged sensory processes on each side. All included genera have state 0, except: *Lodosocoris* and *Izharocoris* (1); and *Tipulparra* (2).

Shape of the Cavity in the Ventro-Posterior Wall of the Pygophore (Males). (0) usually with deep, rounded or V-shaped cavity; (1) usually with a shallow, cup-shaped cavity without a median excavation; and (2) shallow cavity with a median excavation. About half the included genera have state 0. The genera that differ are *Paranevisanus, Sarju, Tipulparra,* and *Meridalpa* (1); and a large group of genera (*Jugalpada, Cahara, Izharocoris, Lodosocoris, Neolodosocoris, Ameridalpa, Meridindia, Eupaleopada, Dalpada,* and *Tachengia* (2).

Shape of the Median Excavation in the Cavity in the Ventro-Posterior Wall of the Pygophore (Males). (0) absent; (1) broadly V-shaped; (2) distinctly U-shaped; (3) U-shaped with a distinct lobe-like projection on both sides; (4) with a central swollen process; (5) V-shaped with lateral emargination; and (6) deep, U-shaped, with two smaller lateral excavations. Most of the included genera lack this trait (0), but those with it possess the following states:, *Lodosocoris* and *Neolodosocoris* (1); *Izharcoris* and *Dalpada* (2), modified in *Cahara* and *Meridindia* (3); *Ameridalpa* (4); *Jugalpada* and *Eupaleopada* (5); and *Tachengia* (6).

Length of the Lateral Lobes of the Pygophore (Males). (0) usually broad, not produced upward; (1) broad and produced on the inner margin as a beak-like structure (2) slightly raised upward; (3) relatively longer, narrower, and usually with a rounded apex; and (4) much narrower, remarkably prolonged, more than the length of the pygophore. Most included genera are state 0, but there is some variation among species within genera; genera that differ are: *Ameridalpa* and some species of *Sarju* (1); *Tipulparra* (2); *Mustha* (3); and *Phricodus* (4).

Size of Paramere Stem (Males). (Fig. 2) (0) thin and short; (1) relatively thick and long; and (2) narrow and rectangular. *Phricodus, Carenoplistus, Salixocoris, Paranevisanus, Sarju, Cahara, Neolodosocoris, Dalpada, Erthesina,* and *Tachengia* have state 0; all others have state 1, except *Neohalys* and *Eupaleopada* (2).

Shape of Parameral Stem (Males) (Fig. 2). (0) without inner spine; (1) with indistinct spine; (2) with well-developed thumb-like process. This trait divides the included genera into three groups: *Phricodus, Carenoplistus, Neohalys, Salixocoris, Neolodosocoris, Meridindia, Eupaleopada, Dalpada, Erthesina,* and *Tachengia* (0); *Halys, Paranevisanus, Apodiphus, Lodosocoris, Ameridalpa,* and *Meridalpa* (1); and *Jugalpada, Mustha, Sarju, Cahara, Izharocoris,* and *Tipulparra* (2).

Outer Process of Parameral Stem (Males). (0) absent; and (1) present. All included genera lack this character (0) except *Izharocoris* (1).

Shape of Parameral Blade (Males). (Fig. 2) (0) usually small, flat and broad, with a round apex; (1) elongate, with apical portion triangular; (2) as narrow as stem, almost rectangular, with a straight apical margin; (3) broad, usually leaf-like, with an apical and an inner spine; (4) small, highly sclerotized, bilobed; (5) large, with the apical part produced forward into a long narrow projection; (6) blade broad, apex beak-shaped with a large ridged area; (7) broad, with an elongated ridge, and the inner margin produced as a finger-like process of variable size; (8) blade narrow, outer margin convex, the apex beak-like, with no ridged area; and (9) equally broad throughout, with a fairly rounded apex, with no ridged area; (a) broad, short, almost square, with a broad apex, apical margin straight, ridged area present but thumb-like; (b) wide, outer upper margin high like a hump, apex narrowly produced, ridged area crenulated; (c) fairly rectangular, upper margin concave, inner sinuate, apex little produced, triangular; (d) broad, with straight upper

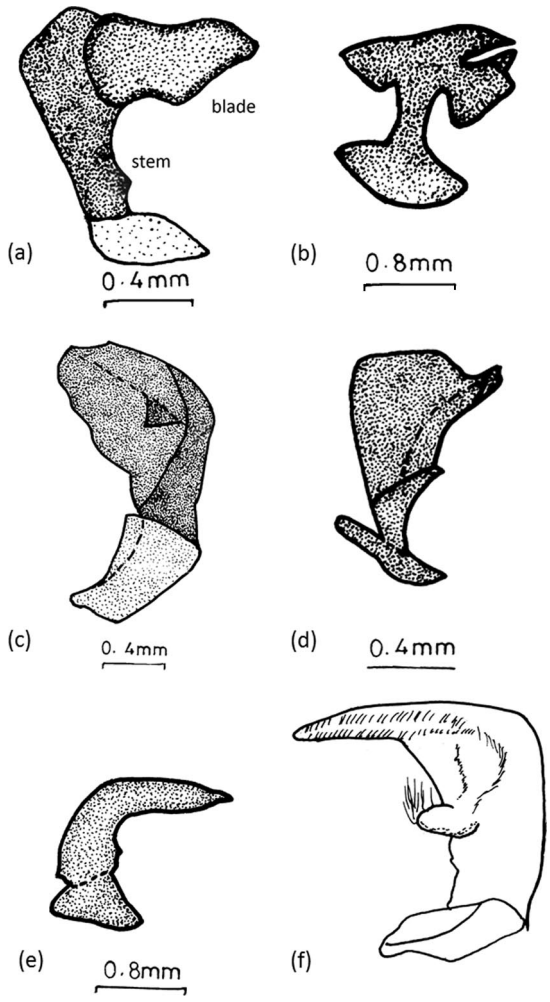

Fig. 2. Parameres of selected genera of Halyini, showing the shape of the stem and the blade (upper and inner margins, and the apex). (a) *Apodiphus iraquiensis.* (b) *Erthesina pakistanensis.* (c) *Halys hyderabadiensis.* (d) *Lodosocoris azhari.* (e) *Mustha izmirensis.* (f) *Sarju enigma.*

and outer margin, apex a little produced upward; (e) relatively narrow, apex broadly triangular, outer margin rounded; (f) blade with an expanded apex, ridge present on apex of blade, with a long thumb-like process. Among all the traits diagnostic of halyine genera, the parameral blade has the greatest diversity of states. It has great modifications in the size and shape of the apex, the outer and inner margin, etc., and is usually different in every genus, and often among species within genera. Allotting so many states is unsatisfactory, but at least some phylogenetic information is present.

Shape of Vesica (Males). (0) tube-like; (1) a simple curved tube; and (2) shaped like a question mark. Although variable in length, the shape of the vesica is invariable among all genera (0) apart from *Mustha* (1) and *Meridindia* (2).

Number of Dorsal Conjunctival Appendages (Males). (0) a single dome-shaped appendage; (1) one pair of appendages; (2) two pairs of almost equal size, overlapping each other; (3) trilobed appendages; (4) three appendages, one of which is dome-shaped; and (5) four pairs. Almost all South Asian genera of Halyini have one pair (1), except the following: *Apodiphus* (0); *Lodosocoris* (2); *Sarju, Izharocoris, Tipulparra, Dalpada,* and *Tachengia* (3); *Salixocoris* (4); and *Carenoplistus* (5).

Size and Shape of Dorsal Conjunctival Appendages (Males). (0) membranous, usually long and broad; (1) membranous, but very thin; (2) membranous, but small; (3) membranous, small and broad;(4) membranous or semisclerotized; (5) one pair sclerotized, and one dome-shaped membranous appendage; (6) broad, long, semisclerotized; (7) spatulate or thin, long, sclerotized; and (8) three pairs semisclerotized, one pair membranous. In most of the included genera these are membranous, but their size and shape is variable: *Mustha, Halys, Lodosocoris, Neolodosocoris,* and *Erthesina* (0); *Phricodus, Jugalpada,* and *Neohalys* (1); *Paranevisanus* and *Apodiphus* (2); *Sarju, Izharocoris, Dalpada,* and *Tachengia* (3); *Cahara* and *Ameridalpa* (4); *Salixocoris* (5); *Tipulparra* and *Meridindia* (6); *Eupaleopada* and *Meridalpa* (7); and *Carenoplistus* (8).

Ventrolateral Conjunctival Appendages (Males). (0) absent; and (1) one pair present. Absent (0) in all included genera except *Jugalpada, Mustha, Halys, Neohalys, Salixocoris, Izharocoris, Dalpada,* and *Tachengia* (1).

Shape and Size of Ventrolateral Conjunctival Appendages (Males). (0) absent; (1) short, membranous, apically lobed; and (2) thin, highly sclerotized. Most included genera with these ventrolateral conjunctival appendages have state 1, except *Mustha* (2).

Pair of Ventral Conjunctival Appendages (Males). (0) absent; (1) sclerotized, longer than the dorsal conjunctival appendages; (2) narrow or broad, sclerotized or semisclerotized; (3) semisclerotized, somewhat kidney-shaped; (4) short, thin, sclerotized; (5) semisclerotized, broad on basal half, apical half tapering gently; (6) moderately large, semisclerotized; (7) highly sclerotized; and (8) thin, small, membranous. About half of included genera have state 0. Of genera with these appendages, all have a single pair, but these vary in shape, size, and texture, mostly semisclerotized or sclerotized, except *Lodosocoris* (7) and *Neolodosocoris* (8). Shared states are only shown in *Meridindia* and *Meridalpa* (2) and *Cahara* and *Ameridalpa* (6).

Thecal Process (Males). (0) absent; (1) membranous, ear-like, lateral; (2) small, sclerotized or semisclerotized, ear-like; and (3) small, highly sclerotized. The thecal process is a specialized character found only in four genera: *Izharocoris* (1); *Dalpada* and *Sarju* (2); and *Jugalpada* (3).

Penial Lobes (Males). (0) absent; and (1) pair of highly sclerotized appendages present. hese vary in length, but are present in all included halyines (1) except *Phricodus* and *Carenoplistus* (0).

Shape of Posterior Margin of First Gonocoxae (Females). (0) usually straight, more or less convex, slightly sinuate or lobed on inner angle; (1) may or may not be produced into an outer angle; and (2) produced at outer angle as a finger-like process. Absent (0) in most included genera, except in some but not all species of *Sarju* (1), where if present it is short and thick; and *Cahara* (2), where in different species the finger-like process can be thin, thick, short, long, or very long—so long that it reaches to the posterior margin of the eighth paratergite. Outside the Halyini, this character can vary greatly within a single genus.

Shape of Posterior Margin of Eighth Paratergite (Females). (0) smooth; (1) with a distinct median spine; and (2) whole margin armed with spines. Almost all included halyine genera have state 0, except the following: *Phricodus, Cahara, Ameridalpa, Meridindia, Meridalpa* and *Dalpada* (1); and *Mustha* (2). Outside the Halyini, this character can vary greatly within a single genus.

Length of Ninth Paratergite (Females). (0) distinctly shorter than eighth paratergite; (1) equal to the eighth paratergite; (2) a little longer than the eighth paratergite; and (3) much longer than the eighth paratergite. A large number of studied halyines have state 0), but others are *Paranevisanus* and *Jugalpada* (1); *Carenoplistus, Surenus, Orthoschizops, Apodiphus, Ameridalpa Meridalpa,* and *Erthesina* (2); and *Agaeus* and *Asyla* (3). Outside the Halyini, this character can vary greatly within a single genus.

Shape of Spermathecal Bulb (Females). (0) oval or round; and (1) mostly irregular shaped. All included genera have state 0 except *Paranevisanus* (1).

Spermathecal Bulb Processes (Females). (0) absent; and (1) present. This is a tribal character for the Halyini, present in all included genera (1) except *Phricodus, Carenoplistus,* and the monotypic genus *Lodosocoris* (0).

Number of Spermathecal Bulb Processes Among Species Within Genera (Females). (0) none; (1) always two; (2) two to three; (3) normally three, occasionally two or four (even within s apecies); (4) four to five; and (5) six to 16. Apart from those with none (see character 58), most included halyines have three bulb processes. The scoring is as follows: *Neohalys, Ameridalpa, Meridindia,* and *Eupaleopada* (1); *Meridalpa*

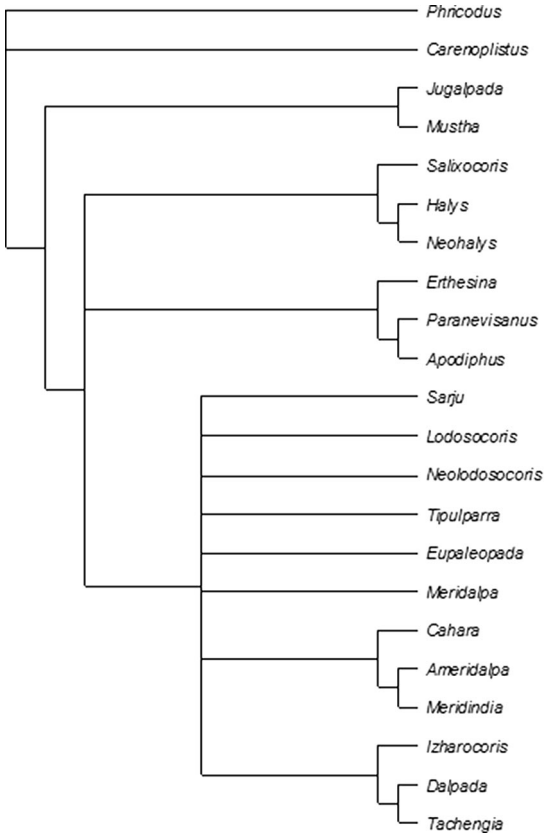

Fig. 3. Strict consensus tree of the 52 equally short trees generated from characters scored for the 22 genera out of the total of 31 with complete data.

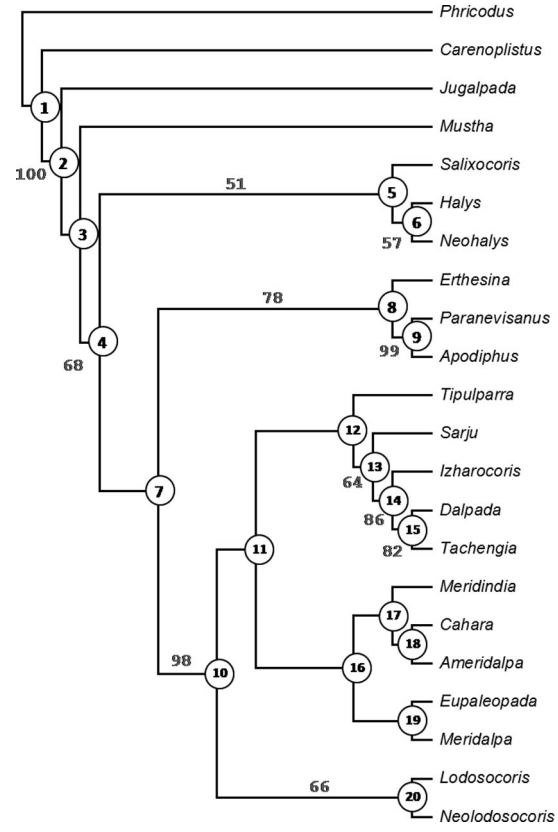

Fig. 4. The single most parsimonious tree generated by reweighting characters in proportion to their fit to the 52 equal-length trees (whose consensus tree is shown in Fig. 1) generated from characters scored for the 22 genera out of the total of 31 with complete data. Figures in circles are node numbers. Figures next to branches refer to the bootstrap support for that branch: only values above 50% are shown. Tree length = 95.74, Consistency index (CI) = 0.8382, Homoplasy index (HI) = 0.1618, CI excluding uninformative characters = 0.8032, HI excluding uninformative characters = 0.1968, retention index (RI) = 0.8050, rescaled consistency index (RC) = 0.6747, f value = 68.17857, f-ratio = 0.0897.

(2); *Jugalpada*, *Mustha*, *Halys*, *Salixocoris*, *Apodiphus*, *Sarju*, *Cahara*, *Izharocoris*, *Tipulparra*, *Dalpada*, and *Erthesina* usually have three, apart from a couple of species that have either two or four; (3); *Agaeus* (4); and *Paranevisanus* (5).

Shape of Spermathecal Bulb Processes (Females). (0) absent; (1) usually finger-like, sometimes bifid; (2) elongated, tubule-shaped; and (3) various different shapes—bifid, bifurcated, long, short, thick, thin, or branched. The shape of bulb processes is variable among genera, and among species within most genera (but not all). A large group of included genera have state 1: *Jugalpada*, *Mustha*, *Agaeus*, *Halys*, *Neohalys*, *Salixocoris*, *Apodiphus*, *Sarju*, *Cahara*, *Izharocoris*, *Amerdalpa*, *Meridindia*, *Eupaleopada*, *Meridalpa*, and *Erthesina.* The following are different: *Tipulparra* and *Dalpada* (2) (*Cahara jugotaria* also has very elongated thin tubule-like processes, but this is the only species of the genus like this: the rest have small finger-like processes); and *Paranevisanus* (3), where there is great variation among species, individuals within species, and even among processes within an individual female!

Length of First Labial Segment. (0) very short, the entire first segment and half of the second segment enclosed by the bucculae; and (1) more or less the length of the bucculae. All included genera have the first labial segment equal or subequal to the bucculae (1) except *Phricodus* (0), which is unusual for halyine species.

Cladograms

There were 52 equally short trees for the 22 taxa for which more or less complete character data were available: the strict consensus tree is shown in Fig. 3. After reweighting, only a single most parsimonious tree resulted (Fig. 4). The bootstrap support for the various branches are shown in Fig. 4, and the character-state changes are listed in Table 2. A few characters had low (<0.5) consistencies on this tree (characters 21, 36, 39, 42, 43, 49, 55, and 56), but the majority were high.

Table 2. Apomorphy lists for the character changes along the tree of Fig. 4

Branch	Character	Steps	CI	Change
node_1 → *Phricodus*	8	1	0.500	2 → 0
	10	1	0.667	0 → 6
	16	1	1.000	0 → 1
	21	1	0.286	2 → 1
	22	1	0.750	0 → 4
	23	1	0.500	0 → 1
	24	1	1.000	0 → 1
	26	1	0.500	0 → 5
	41	1	0.800	0 → 4
	55	1	0.400	0 → 1
	61	1	1.000	1 → 0
node_1 → *Carenoplistus*	3	1	1.000	0 → 1
	4	1	0.750	0 → 2
	31	1	1.000	2 → 0
	36	1	0.250	0 → 1
	37	1	0.500	0 → 1
	45	1	0.938	0 → 1
	47	1	1.000	1 → 5
	48	1	0.889	1 → 8
	56	1	0.400	0 → 2
node_1 → node_2	1	1	1.000	0 → 1
	17	1	1.000	0 → 1
	18	1	0.500	1 → 2
	19	1	1.000	0 → 1
	22	1	0.750	0 → 1
	32	1	1.000	0 → 1
	42	1	0.182	0 → 1
	43	1	0.200	0 → 2
	45	1	0.938	0 → 2
	49	1	0.333	0 → 1
	50	1	0.500	0 → 1
	53	1	1.000	0 → 1
	58	1	0.500	0 → 1
	59	1	0.571	0 → 3
	60	1	0.600	0 → 1
node_2 → *Jugalpada*	10	1	0.667	0 → 3
	14	1	1.000	1 → 2
	26	1	0.500	0 → 2
	39	1	0.333	0 → 2
	40	1	0.857	0 → 5
	45	1	0.938	2 → a
	51	1	1.000	0 → 3
	52	1	1.000	0 → 3
	56	1	0.400	0 → 1
node_2 → node_3	36	1	0.250	0 → 1
	48	1	0.889	1 → 0
node_3 → *Mustha*	10	1	0.667	0 → 6
	22	1	0.750	1 → 4
	23	1	0.500	0 → 1
	26	1	0.500	0 → 5
	28	1	1.000	0 → 1
	29	1	1.000	0 → 1
	37	1	0.500	0 → 2
	41	1	0.800	0 → 3
	45	1	0.938	2 → f
	46	1	1.000	0 → 1
	50	1	0.500	1 → 2
	55	1	0.400	0 → 2
node_3 → node_4	13	1	0.600	4 → 2
	14	1	1.000	1 → 0
	15	1	0.600	0 → 1
	21	1	0.286	2 → 3
	42	1	0.182	1 → 0
	43	1	0.200	2 → 0
node_4 → node_5	4	1	0.750	0 → 1
node_5 → node_6	37	1	0.500	0 → 1
	42	1	0.182	0 → 1
node_6 → *Halys*	10	1	0.667	0 → 3
	43	1	0.200	0 → 1
	45	1	0.938	2 → 3
node_6 → *Neohalys*	42	1	0.182	1 → 2
	48	1	0.889	0 → 1
	59	1	0.571	3 → 1

Continued on following page

Table 2. Continued

Branch	Character	Steps	CI	Change
node_5 → *Salixocoris*	11	1	0.667	3 → 2
	45	1	0.938	2 → 5
	47	1	1.000	1 → 4
	48	1	0.889	0 → 5
node_4 → node_7	5	1	0.500	0 → 2
	45	1	0.938	2 → 4
	49	1	0.333	1 → 0
	50	1	0.500	1 → 0
node_7 → node_8	2	1	1.000	0 → 1
	3	1	1.000	0 → 2
	4	1	0.750	0 → 2
	56	1	0.400	0 → 2
node_8 → node_9	5	1	0.500	2 → 0
	6	1	1.000	0 → 1
	9	1	1.000	0 → 2
	10	1	0.667	0 → 2
	11	1	0.667	3 → 1
	15	1	0.600	1 → 3
	43	1	0.200	0 → 1
	45	1	0.938	4 → b
	48	1	0.889	0 → 2
node_9 → *Paranevisanus*	6	1	1.000	1 → 2
	18	1	0.500	2 → 1
	36	1	0.250	1 → 0
	39	1	0.333	0 → 1
	51	1	1.000	0 → 4
	56	1	0.400	2 → 1
	57	1	1.000	0 → 1
	59	1	0.571	3 → 5
	60	1	0.600	1 → 3
node_9 → *Apodiphus*	4	1	0.750	2 → 3
	21	1	0.286	3 → 2
	37	1	0.500	0 → 2
	42	1	0.182	0 → 1
	45	1	0.938	b → c
	47	1	1.000	1 → 0
node_8 → *Erthesina*	3	1	1.000	2 → 4
	33	1	0.500	0 → 1
	34	1	1.000	0 → 1
	35	1	1.000	0 → 2
node_7 → node_10	9	1	1.000	0 → 1
	12	1	0.500	0 → 1
	15	1	0.600	1 → 2
	25	1	1.000	0 → 1
	36	1	0.250	1 → 0
	39	1	0.333	0 → 2
	45	1	0.938	4 → 6
node_10 → node_11	21	1	0.286	3 → 2
	48	1	0.889	0 → 6
node_11 → node_12	8	1	0.500	2 → 1
	39	1	0.333	2 → 1
	43	1	0.200	0 → 2
	47	1	1.000	1 → 3
node_12 → node_13	26	1	0.500	0 → 2
	45	1	0.938	6 → 7
	48	1	0.889	6 → 3
	52	1	1.000	0 → 2
node_13 → *Sarju*	8	1	0.500	1 → 2
	26	1	0.500	2 → 3
	41	1	0.800	0 → 1
	54	1	1.000	0 → 1
node_13 → node_14	39	1	0.333	1 → 2
	40	1	0.857	0 → 2
	49	1	0.333	0 → 1
	50	1	0.500	0 → 1
node_14 → *Izharocoris*	38	1	0.667	0 → 1
	42	1	0.182	0 → 1
	44	1	1.000	0 → 1
	52	1	1.000	2 → 1
node_14 → node_15	7	1	1.000	0 → 1
	26	1	0.500	2 → 4
	43	1	0.200	2 → 0
	45	1	0.938	7 → 8

Continued on following page

Table 2. Continued

Branch	Character	Steps	CI	Change
	55	1	0.400	0 → 1
	60	1	0.600	1 → 2
node_15 → *Dalpada*	8	1	0.500	1 → 2
	33	1	0.500	0 → 1
node_15 → *Tachengia*	10	1	0.667	0 → 4
	11	1	0.667	3 → 2
	12	1	0.500	1 → 0
	13	1	0.600	2 → 3
	15	1	0.600	2 → 1
	21	1	0.286	2 → 1
	40	1	0.857	2 → 6
node_12 → *Tipulparra*	38	1	0.667	0 → 2
	41	1	0.800	0 → 2
	42	1	0.182	0 → 1
	51	1	1.000	0 → 5
	60	1	0.600	1 → 2
node_11 → node_16	51	1	1.000	0 → 2
	55	1	0.400	0 → 1
	59	1	0.571	3 → 1
node_16 → node_17	18	1	0.500	2 → 0
	21	1	0.286	2 → 3
	40	1	0.857	0 → 3
	42	1	0.182	0 → 1
	45	1	0.938	6 → 7
node_17 → node_18	13	1	0.600	2 → 1
	26	1	0.500	0 → 2
	43	1	0.200	0 → 1
	48	1	0.889	6 → 4
	51	1	1.000	2 → 6
node_18 → *Cahara*	13	1	0.600	1 → 3
	18	1	0.500	0 → 2
	42	1	0.182	1 → 0
	43	1	0.200	1 → 2
	54	1	1.000	0 → 2
	59	1	0.571	1 → 3
node_18 → *Ameridalpa*	21	1	0.286	3 → 2
	40	1	0.857	3 → 4
	41	1	0.800	0 → 1
	56	1	0.400	0 → 2
node_17 → *Meridindia*	35	1	1.000	0 → 1
	46	1	1.000	0 → 2
node_16 → node_19	48	1	0.889	6 → 7
node_19 → *Eupaleopada*	22	1	0.750	1 → 3
	40	1	0.857	0 → 5
	42	1	0.182	0 → 2
	45	1	0.938	6 → 9
	51	1	1.000	2 → 1
	55	1	0.400	1 → 0
node_19 → *Meridalpa*	39	1	0.333	2 → 1
	43	1	0.200	0 → 1
	59	1	0.571	1 → 2
node_10 → node_20	13	1	0.600	2 → 1
	26	1	0.500	0 → 4
	40	1	0.857	0 → 1
	45	1	0.938	6 → d
	51	1	1.000	0 → 7
	58	1	0.500	1 → 0
	59	1	0.571	3 → 0
	60	1	0.600	1 → 0
node_20 → *Lodosocoris*	38	1	0.667	0 → 1
	42	1	0.182	0 → 1
	43	1	0.200	0 → 1
	47	1	1.000	1 → 2
node_20 → *Neolodosocoris*	15	1	0.600	2 → 1
	45	1	0.938	d → e
	51	1	1.000	7 → 8

All trees placed *Carenoplistus* with the outgroup *Phricodus.* We regard this as an important result—the outgroup relationship of *Carenoplistus* and *Phricodus* to the rest of the genera. Other recognizable groups of genera were the *Halys* group (*Salixocoris*, *Halys*, and *Neohalys*), the *Paranevisanus* group (*Erthesina*, *Apodiphus*, and *Paranevisanus*), the *Dalpada* group (*Sarju*, *Izharocoris*, *Dalpada*, and *Tachengia*), and the *Lodoso-*

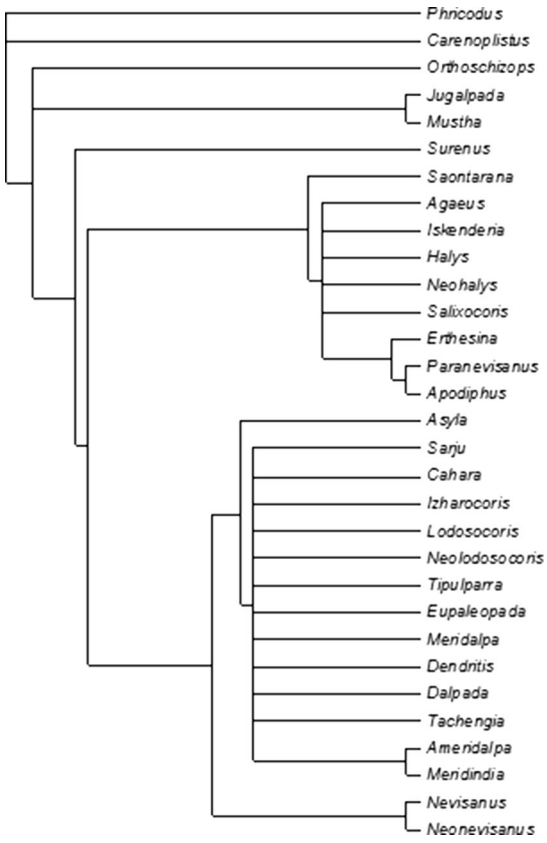

Fig. 5. Strict consensus tree of the 5,825 equally parsimonious trees produced from the full data set of 31 genera scored for all 61 characters.

coris group (*Lodosocoris* and *Neolodosocoris*). Nearly all possibilities joined together the *Dalpada* group, the *Lodosocoris* group, and a set of variously placed genera (*Tipulparra*, *Meridindia*, *Cahara*, *Ameridalpa*, *Eupaleopada*, and *Meridalpa*).

The placement of the remaining nine genera is more uncertain because of the missing character states for sex-specific characters. More than 5,800 equally parsimonious trees resulted from analyzing all 31 genera: the strict consensus tree (Fig. 5) allows us to place these genera at least approximately on the tree. Thus *Orthoschizops* is plesiomorphic, placed close to *Jugalpada* and *Mustha.* In all trees, *Surenus* is placed as branching off between nodes 3 and 4 of Fig. 4. *Saontarana*, *Agaeus*, and *Iskenderia* are placed together with the *Halys* and *Paranevisanus* groups. *Nevisanus* and *Neonevisanus* are sister-genera and together with *Asyla* are placed basal to the large group of genera emerging from node 10 of Fig. 4. *Dendritis* is placed within the group of genera based on node 11.

Key to South Asian Genera of Tribe Halyini Stål

The key includes all genera recorded in South Asia, with the possible exception of *Sinometis.* They all possess the following character states: the first antennal segment is shorter than the apex of the head; the antenna has five segments; the labium reaches or exceeds the hind coxae; the antero-lateral margins of the pronotum are distinctly denticulate; the scent-gland apparatus is on the mesosternum, and has a ventral, usually lobe-like structure, the peritreme; the spermathecal bulb (in females) has a process; and the abdomen is distinctly sulcate with a median carina.

1. Antennae four-segmented; second antennal segment remarkably long, almost equal to third and fourth together; paraclypei much produced with acute apices; spermathecal bulb without processes 2
   Antennae five-segmented; second antennal segment a little longer or shorter than third; paraclypei not as above; spermathecal bulb with processes 3
2. Lateral margins of head in front of eyes armed with long spines; antenniferous tubercles developed into long spines; entire lateral margins of pronotum armed with spines; humeral angles spinose; posterior margins of eighth paratergites with tooth in middle; lateral lobes of pygophore narrow and remarkably prolonged . . . . . *Phricodus* Spinola
   Lateral margins of head without spines; antenniferous tubercles simple; lateral margins of pronotum serrated; humeral angles subacute; posterior margins of eighth paratergites without tooth; lateral lobes of pygophore broad and not produced . . . . . *Carenoplistus* Jakovlev
3. Anterior tibiae dilated 4
   Anterior tibiae cylindrical 7
4. Posterior tibiae dilated; dorsolateral margin of pygophore with leaf-like structure on sclerotized ridge; parameral blade lobed, outer lobe gradually narrowing with acute apex, inner lobe trilobed . . . . . *Erthesina* Spinola
   Posterior tibiae cylindrical; dorsolateral margin of pygophore and parameral blade not as above 5
5. Bucculae short; tibiae black with broad pale annulus medially, first segment of tarsi pale, rest black . . . . . *Dendrites* Kirkaldy
   Bucculae long, reaching to base of head; legs ochraceous with brown spots 6
6. Clypeus equal or slightly longer than paraclypei, paraclypei bilobed, outer lobe forming distinct angle with inner lobes; second antennal segment longer than third, and third longer than fourth; humeral angles angulately produced, either nodule-like or into small horn; scutellum with prominent basal ochraceous spots, apical area comparatively broad. . . . . *Dalpada* Amyot & Serville
   Clypeus distinctly longer than paraclypei, paraclypei single lobed and broadly rounded at apex; third and fourth joints of antennal segment a little longer and subequal in length, second and fifth joints a little shorter and also subequal in length; humeral angles subacute and not angulately produced; scutellum with-

out basal ochraceous spots; apical area narrower . . . . . *Saontarana* Distant

7. Paraclypei single-lobed; scutellum with indistinct basal angular spots 8
Paraclypei distinctly bilobed, outer lobe forming distinct angle with inner lobe; scutellum with distinct basal angular spots 21
8. Paraclypei equal or little shorter than clypeus; labium long 9
Paraclypei much extending beyond clypeus; labium short 18
9. Paraclypei gradually tapering upward with subacute apex; body with smooth color pattern 10
Paraclypei a little tapering upward with broadly rounded apex; body mottled with raised irregular ochraceous spots 14
10. Head distinctly shorter than pronotum; ventrolateral margin of pygophore with a hook-like structure; paramere apically narrowly produced much . . . . *Salixocoris* Ahmad & Afzal
Head longer than pronotum; ventrolateral margin of pygophore sinuate; paramere not as above 11
11. Body shining, testaceous, with dark matt punctures; pronotum black, with five large and five small triangular brown spots; scutellum with two large oval-shaped and two small round brownish-black spots; spermathecal bulb with four to five finger-like processes including one prolongation of bulb . . . . . *Agaeus* Dallas
Body pale ochraceous; with brown punctures; pronotum and scutellum with light and dark stripes; spermathecal bulb with two to three processes 12
12. Fairly wide light stripe along middle of head and anterior part of pronotum; antennal segments slightly swollen at apex; fourth antennal segment longer than second, third, and fifth . . . . . *Iskenderia* Kiritshenko
Middle of head and anterior part of pronotum without wide light stripe; antennal segments uniformly cylindrical; fourth antennal segment equal to second and third 13
13. Paraclypei either with tooth or not; ventroposterior margin of pygophore with median projection; parameral blade broad with inner and apical spine; dorsal membranous conjunctival appendages long and broad; penial lobes broad and spatulate . . . . . *Halys* Fabricius
Paraclypei always without tooth; parameral blade narrow, rectangular, as long and wide as stem; without inner apical spine; dorsal membranous conjunctival appendages narrower; penial lobes narrow and bent outward. . . . . *Neohalys* Ahmad & Parveen
14. Lateral margins of head slightly sinuate; humeral angles of pronotum moderately prominent with subacute apices; scutellum gradually narrowed posteriorly with subacute apices, reaching to half length of abdomen . . . . . *Asyla* Walker
Lateral margins of head slightly sinuate; humeral angles not as prominent as above; scutellum delicately narrowed, with U-shaped apical lobe, reaching two thirds the length of abdomen 15
15. Lateral margins of head moderately and concavely sinuate; labium reaches to slightly further than posterior coxae 16
Lateral margins of head more or less upwardly recurved; labium extending to middle of abdomen 17
16. Head about as long as pronotum; basal antennal segment reaching to apex of head . . . . . *Nevisanus* Distant
Head much shorter than pronotum; basal antennal segment reaching about to apex of head . . . . . *Neonevisanus* Distant
17. Body broader; head equal to pronotum; paraclypei equal to clypeus and distinctly upwardly recurved; second antennal segment distinctly longer than third; paramere with stem short, without thumb process, blade broad, apex produced laterally with ridged or crenulated area facing base; spermathecal bulb with more than three unequal, finger-like, tubules or bifid processes . . . . . *Paranevisanus* Distant
Body comparatively narrower; head distinctly shorter than pronotum; paraclypei slightly longer than clypeus; second antennal segment distinctly shorter than third; parameral stem long, with well-developed thumb process, blade narrower, apex slightly produced with sinuated inner margin; spermathecal bulb with three to five simple finger-like processes . . . . . *Apodiphus* Spinola
18. Paraclypei entirely enclosing clypeus; anteroventral angles produced into sclerotized spine; humeral angles of pronotum slightly produced and horn-like . . . . . *Jugalpada* Ghauri
Paraclypei more or less cleft between their apices; anteroventral angle without sclerotized spine; humeral angles subacute 19
19. Basal antennal segment reaching apex of head; lateral margins of pronotum dentate, humeral angles subprominent and subacute; labium extending only to intermediate coxae . . . . . *Surenus* Distant
Basal antennal segments shorter than apex of head; lateral margins of pronotum armed with spines, humeral angles distinctly spinose; labium extending beyond hind coxa 20
20. Lateral margins of head and abdomen armed with long or short spines; corium on anterior part with a few small teeth; labium reaching to middle of abdominal sternite . . . . . Mustha Amyot & Serville

Lateral margins of head anteriorly dentate; lateral margins of abdomen without spines; corium without teeth; labium extending to or beyond hind coxae . . . . . *Orthoschizops* Spinola

21. Humeral angles distinctly angulately produced; vesica straight, tube-like 22
Humeral angles not produced as above; vesica curved, or like a question mark 27

22. Paraclypei distinctly longer than clypeus; humeral angles more or less acutely produced; stem of paramere with well-developed thumb process 23
Paraclypei distinctly shorter than clypeus; humeral angles prominently nodulose; thumb process of stem reduced 25

23. Humeral angles distinctly long, horn-like; ventroposterior margin of pygophore with shallow cavity and without median excavation; posterior margin of first gonocoxae slightly produced on outer angle . . . . . *Sarju* Ghauri
Humeral angles comparatively short, like a horn; ventroposterior margin of male pygophore with deep cavity and with a median excavation; posterior margin of first gonocoxae much produced, finger-like on outer angle 24

24. Outer lobe of paraclypei prominent, forming a distinct angle with inner lobe; apex of scutellum impunctate and pale yellow; ventroposterior margin of pygophore with pair of median lobes; paramere without outer processes, blade apically produced, finger-like . . . *Cahara* Ghauri
Outer lobe of paraclypei less prominent; apex of scutellum neither impunctate nor pale yellow; ventroposterior margin of pygophore without pair of median lobes; paramere with outer process, blade apex slightly produced. . . . . *Izharocoris* Afzal & Ahmad

25. Apex of paraclypei round; ventrolateral margin of pygophore with a pair of hook-like structures . . . . . *Lodosocoris* Ahmad & Afzal
Apex of paraclypei subacute; ventrolateral margin of pygophore slightly sinuate 26

26. Paraclypei shorter than clypeus; lateral margin of paraclypei bilobed, outer lobe forming a distinct angle with inner lobe; ventroposterior margin of pygophore with wide V-shaped excavation . . . . . *Neolodosocoris* Memon & Ahmad
Paraclypei longer than clypeus; lateral margin of paraclypei with two teeth, one just in front of eyes and other round toward apex of head; ventroposterior margin of pygophore with three U-shaped excavations, one deep median and two relatively smaller lateral . . . . . *Tachengia* China

27. Body reddish or yellow, punctate, unevenly tinged with dark brown or black, congregated in small patches; male pygophore with lateroventral angle produced into well developed processes; paramere curved, blade mostly with a more-or-less thumb-like process, apex produced posteriorly as a beak . . . . . *Tipulparra* Ghauri
Body coloration not as above; lateroventral angles of pygophore without processes; paramere not curved, blade always without thumb process and apex not produced posteriorly 28

28. Basal antennal segment reaching apex of head 29
Basal antennal segment shorter than apex of head 30

29. Humeral angles gently raised; basal spots of scutellum as broad as long; scent gland peritreme always distinctly shorter; apex of paramere not so produced . . . . . *Ameridalpa* Ghauri
Humeral angles not raised; basal spots of scutellum narrower; scent gland peritreme long, reaching nearly to outer margin of evaporatoria; apex of paramere distinctly produced, beak-like . . . . . *Meridindia* Ghauri

30. Paraclypei distinctly shorter than clypeus; marginal tooth in front of eyes absent; lateral margins of pronotum with more or less six large and six small teeth; apex of paramere without ridge; eighth paratergite without median tooth on posterior margin. . . . . *Eupaleopada* Ghauri
Paraclypei equal or shorter than clypeus; marginal tooth in front of eyes present; lateral margins of pronotum not dentate as above; apex of paramere with prominent ridge; eighth paratergite with median tooth on posterior margin . . . . . *Meridalpa* Ghauri

Discussion

The morphological evidence gathered and analyzed in this study indicates that all genera including *Phricodus* have the basic halyine tribal characters and therefore come under the tribe Halyini. Several nodes of the final tree of Fig. 4 are clearly supported by many apomorphies, creating some robust clades (although in some cases support values may be inflated by the occurrence of correlated characters, e.g., 9 and 14). It is true that some genera lack some of the halyine characters, but we consider this a consequence of their plesiomorphic condition. As Wall (2004) discussed, there are no clear-cut synapomorphies by which one can define the tribe. The unusual morphology of the genus *Phricodus* in particular has often been the topic of discussion by researchers about its position and placement within the Halyini, or in its own tribe the Phricodini (Cachan 1952, Göllner-Scheiding 1999). This is the reason we used it as our outgroup, despite considering it as a halyine.

In our analysis, *Carenoplistus* is clearly the most plesiomorphic ingroup genus: the separation between *Phricodus* + *Carenoplistus* and all other genera (the branch between nodes 1 and 2 of Fig. 4) is supported by 15 character-state changes (Table 2), including five

synapomorphies and 100% bootstrap support. The synapomorphies separating these two plesiomorphic genera from the rest are body size (character 1), number of antennal segments (character 17), the length of the second antennal segment (character 19), sulcate sternites (character 32), and presence of penial lobes (character 53). Other states of *Phricodus* + *Carenoplistus* have homoplasies elsewhere in the tree: for example, the short first antennal segment (character 18) is also present in *Paranevisanus;* the lack of spermathecal bulb processes (character 58) is shared with *Lodosocoris.* Thus all the considered genera except *Phricodus* and *Carenoplistus* form a clear monophyletic group.

The next most plesiomorphic genera are *Jugalpada* and *Mustha.* In all the 52 initial trees before reweighting, these formed a pair of sister genera in a monophyletic clade (but with no unique defining synapomorphies), but with weighted characters the branching was ambiguous. *Jugalpada* has some autapomorphies, especially male genital characters such as the shape of the parameral blade (character 45), its semisclerotized kidney-shaped ventral conjunctival appendages (character 51) and highly sclerotized thecal processes (character 52). *Mustha* also has many unusual character states: its thin and highly sclerotized ventrolateral conjunctival appendages (character 50); long paraclypei (character 13); denticulate lateral margins of head (character 10), pronotum (character 22), corium (character 28), and abdomen (character 29); and well-developed inner processes of the parameral stem (character 43). Some of these character states are present in other genera, but *Mustha* itself has an almost complete package. Thus, the position of *Mustha* is a surprise, because its character states are normally thought of as apomorphies, and thus before this analysis we would have expected it to come out as a derived genus.

Two monophyletic groups of genera with moderately good bootstrap support are the *Halys* and the *Paranevisanus* groups. *Halys*, *Neohalys*, and *Salixocoris* are very similar in many characters, such as the color of the pronotum (character 4) and scutellum (character 5), and the male pygophore (characters 36 and 37). However, the shape of the male parameral blade (character 45) is completely different in each of these genera. *Salixocoris* has the apical part of the blade narrowly but greatly produced, and its two species also have evolved teeth on the upper and lower margin of this projected part (an autapomorphy not scored in this study). The projection of the apical part of the parameral blade is not an unusual character in halyines, but in most genera it is small and spine-like, or sometimes finger-like. *Salixocoris* is the only genus in which it is so produced: species of *Sarju* also have a similar-looking projection, but that is created by the elongation of the ridged area that is absent in *Salixocoris;* furthermore, most *Sarju* species have small finger-like projections, and in only a few is it very long.

The *Paranevisanus* clade (*Apodiphus*, *Paranevisanus*, and *Erthesina*) is defined mostly on color characters: the body mottled with raised spots (character 2), head spots (character 3) present in *Apodiphus* and *Paranevisanus*, and modified further in *Erthesina* with its bright yellow stripe around the entire margin of head. These genera also share a lengthened ninth paratergite (character 56), equal to the eighth paratergite in *Paranevisanus* and longer in the other two genera. *Erthesina* seems more derived, with two specialized tibial apomorphies (characters 33 and 34) and the unique leaf-like structure on a sclerotized ridge of the lateral margin of the dorso-posterior cavity of the pygophore (character 35). The monophyly of *Paravenisanus* and *Apodiphus* is supported by several synapomorphies: the rectangular head (character 9), and the recurved margin (character 10) and broad apex of the paraclypei (character 15).

The strongest bootstrap support is for the clade based on node 10, based on characters 9, 12, 15, 25, 36, 39, and 45: characters 9 (head shape), 25 (produced humeral angles), and 45 (parameral shape) have the highest consistency, with bilobed paraclypei (12) with rounded apices (15) also high. Apart from the monophyly of *Lodosocoris* + *Neolodosocoris*, and the *Dalpada* clade (*Sarju* + *Izharocoris* + *Dalpada* + *Tachengia*), there is little clear resolution among the genera of this clade by our character set.

Lodosocoris and *Neolodosocoris* have many similarities in body color, length, the shape of the humeral angles and many characters of the male genitalia. It is thus not surprising that they have reasonable bootstrap support (66%), but if this hypothesis is correct, then each of these genera has one reversed character. *Neolodosocoris* is the only genus in the clade based on node 10 that has paraclypei distinctly tapering upward with a subacute apex (state one of character 15), which it shares with the more plesiomorphic *Halys* group. Likewise, *Lodosocoris* is the only genus apart from the outgroup *Phricodus* and the very plesiomorphic *Carenoplistus* that lacks spermathecal bulb processes.

The monophyly of *Dalpada* + *Tachengia* has reasonably high bootstrap support (82%). The author of the genus *Tachengia* China (1925) called it a close ally of the New World genus *Brochymena* Amyot & Serville, but he did not document the resemblance between the two genera. Ahmad (2004) discussed their resemblance in both having bidentate paraclypei, but he considered *Tachengia* to be close to the Indo-Malaysian genus *Dalpada* on the basis of character states of the lateral margin of the pronotum, the humeral angles, the shape of scent gland peritreme, and the deep ventral excavation of the male pygophore.

The shape of the parameral blade (character 45) has tremendous diversity among the genera that was very difficult to capture in scoring; in our data matrix this was the only character with a multitude of states. Despite this, there are interesting mappings of this character among the more derived genera, and it clearly does contain useful phylogenetic information.

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Appendix

Material Examined

Agaeus tessellatus Dallas: 2♀; Nigeria(Africa), 22-IX-1998, collected by Dr. S.N.H. Naqvi, deposited at Natural History Museum of Karachi (NHMUK).

Apodiphus iraqiensis sp. n. (Memon & Ahmad); 1 holotype ♂; Kalat (Iraq), 4-X-1972, collected by I. Ahmad, deposited in Ahmad's collection; Paratype, 15 ♂ and 9 ♀ with same data as holotype.

Apodiphus metallicus Ahmad & Memon: one holotype ♀; Quetta, Baluchistan (Pakistan), collected by I. Ahmad, 10-IX-2000 on *Malus pumila* Mill. (apple), deposited at NHMUK.

Apodiphus integriceps Horvath, 1888: 65 ♂, 80 ♀; Baluchistan, Quetta, Munzaky, Sariah, Fort Sandman, Pishin and NWFP Abbotabad (Pakistan), on *Malus pumila* Mill. (apple), *Prunus americana* L. (apricot); collected by. I. Ahmad, M. Moizuddin, Q. A. Abbasi, M. Aslam, A. A. Khan, 16-VII-1966, 18–20-VIII-1967, 3-VI-1969, 22-VII-1971, 9, 10-V-1974, 23–25, 28, 30-VII-1983, 5-VII-1985; deposited at NHMUK, Natural History Museum in London (BMNH), and in Ahmad's coll.

Apodiphus bilobatus Ahmad & Ahmad, 1993: holotype 1 ♂; Baluchistan, Fort Sandeman (Pakistan), on *Prunus americana* Linn. (apricot) collected by Q. A. Abbasi, 3-VI-1969, deposited at NHMUK; paratype 39 ♂ and 62 ♀; Baluchistan, Fort Sandman (Pakistan), on *Prunus americana* (apricot) collected by Q. A. Abbasi, 3-VI-1969 deposited at NHMUK, and in Ahmad's collection.

Apodiphus gilgitensis Ahmad & Ahmad, 1993: holotype 1 ♂; Northern areas, Gilgit (Pakistan), on *Salix acomophila* (willow) collected by A. A Khan, 6-IX-1996 deposit at NHMUK; paratype 18 ♂ and 30 ♀; Northern Areas, Gilgit (Pakistan), on *Salix acomophila* (willow), *Populus* sp., *Malus pumila* Mill., leg. A. A. Khan, 2-VI-1994, 22-VII-1994, 2-VI-1975, 13-VII-1975, 11-VIII-1975, and 11-IX-1996, deposited at NHMUK and in Ahmad's collection.

Apodiphus wahensis Ahmad & Ahmad, 1993: one holotype ♂; Punjab; Wah Cantt (Pakistan), on *Juglans regia* L. (walnut); collected by I. Ahmad, 13-VIII-1976, deposited at NHMUK; paratype 4 ♂ and 10 ♀; Punjab; Wah Cantt (Pakistan), on *Juglans regia* L. (walnut); collected by I. Ahmad, 13-VIII-1976, deposited at NHMUK.

Apodiphus jaglotensis Ahmad & Ahmad, 1993: one holotype ♂; Northern areas, Jaglot (Pakistan), on *Salix acomophila* (willow), collected by A. A. Khan, 9-VIII-1975, deposited at NHMUK; Paratype, 2 ♂ and 9 ♀; Jaglot and Peshawar (Pakistan), on *Salix acomophila* (willow), collected by A. A. Khan, N. A. Rana, I. Ahmad, 9-VIII-1975, 28-VI-1977; deposited at NHMUK.

Carenoplistus acutus Signoret, 1880: 1 ♂ and 1 ♀; Balochistan, Quetta (Pakistan), 8-VI-1967, collected by I. Ahmad, deposited at NHMUK.

Carenoplistus karachiensis Memon & Ahmad, 2002: holotype 1 ♀; Karachi, Sindh (Pakistan), on unidentified grass, 1-VIII-1983, collected by I. Ahmad, deposited at NHMUK.

Dalpada oculata (Fabricius, 1775): 2 ♂ and 3 ♀; Srimangal, Sylhet, Kaptai and Rangamati (Bangladesh), on teak and wild grass, collected by I. A. Khan, F. Ahmad, and I. Ahmad, 6-V-1964 and 26–27-VII-1969, deposited at NHMUK.

Dalpada robusta Ahmad & Afzal, 1984: holotype 1 ♀; Bangladesh, on unidentified host plant, collected I. Ahmad, 6-V-1964, lodged at NHMUK.

Erthesina pakistanensis Ahmad & Memon, 2004: holotype 1 ♂; Islamabad (Potohar), Wah Garden (Pakistan), 1-VII-1997, Rana, deposited at NHMUK; paratype 57 ♂ and 144 ♀; Punjab: Wah Garden, Wah Cantt; NWFP, Peshawar, Azad Kashmir: Muzafarabad (Pakistan), collected by Rana, Moiz, I. Ahmad and S. Ali, 13-VIII-1976, 1-VII-1977, and 19-X-1978 deposited at NHMUK.

Halys fabricii Memon & Ahmad, 2002: 1 ♂ and 3 ♀ of *H. dentatus* F. with four white labels, "USNM", "S. Malabar Walayar Forest 1,000 feet (S. India), VII-1952, P. S. Nathan," "J. C. Lutz collection 1961" and "Karika Territory, Kurumbagaram (India), VII-1957"; and 1 ♂ and 2 ♀ of *H. serrigera* Westwood, with two white labels, one hand written, "BASEL" and the other printed, "S. India, 29–10-52".

Halys hyderabadiensis sp. n. (Memon & Ahmad): holotype 1 ♂; Sindh, Hyderabad (Pakistan), on *Tamarindus indica* (Tamarind, Temeric), 10-VI-1999, collected by N. Memon, deposited at NHMUK; paratype, 1 ♂ and 2 ♀ with the same data as holotype, deposited at NHMUK.

Halys mulberriensis sp. n (Parveen & Ahmad); 1 holotype ♂; Punjab, Lahore (Pakistan), on *Morus alba* L., 14-V-1974, collected by M. A. Aslam, deposited at NHMUK; paratype, 1 ♂ and 1 ♀ with the same data as holotype.

Halys naokotiensis sp. n. (Parveen & Ahmad): holotype 1 ♂; Sindh, Naukot (Pakistan); on *Ziziphus jujuba* Mill., 15-IV-1971; collected by A. Khan, deposited at NHMUK; paratype 1 ♀ of the same data as holotype; other material 3 ♂ and 2 ♀; Sindh, Hyderabad (Pakistan) on *Tamarindus indica* (Tamarind, Temeric), 5-VI-1998, collected by N. Memon, deposited at NHMUK.

Izharocoris aceras Afzal & Ahmad, 1981: holotype 1 ♂; Ayubia, NWFP (Pakistan), 14-VIII-1976, collected by M. Moizuddin, deposited at NHMUK; paratype 2 ♀; Punjab, Murree (Pakistan), 22–23-VI-1977 collected by M. Moizuddin and I. Ahmad, deposited at NHMUK.

Izharocoris cretohumeralis Afzal & Ahmad, 1981; holotype 1 ♂; Punjab, Murree (Pakistan), 23-VI-1977, collected by I. Ahmad, deposited at NHMUK; paratype, one ♀, 22-VI-1977, with same data as holotype deposited at Smithsonian Museum in Washington (USNM).

Izharocoris excatus Afzal & Ahmad, 1981: one holotype ♂; Murree, Punjab (Pakistan), 28-IX-1972, collected by Mumtaz, deposited at NHMUK.

Lodosocoris azhari Ahmad & Afzal, 1986: holotype 1 ♀; NWFP, Abbotabad (Pakistan), 13-VIII-1976, leg. A. A. Khan, deposited at NHMUK; paratype 3 ♂ and 4 ♀, NWFP, Abbotabad, Potohar; Islamabad, and Taxila (Pakistan), 13-VIII-1976, 1-VII-1981, and 1-VII-1985, collected by. A. A. Khan and deposited at NHMUK.

Mustha izmirensis Memon & Ahmad, 2009: holotype 1 ♂; Barnova (Turkey), 29-VI-1978 deposited at NHMUK; paratype,1 ♀, Barnova (Turkey), 12-VII-1978 with same data as holotype, deposited at NHMUK.

Mustha spinosus Ahmad & Kamaluddin, 1984: holotype 1 ♂; Balochistan, Quetta-Ziarat road, near Ahmadoon (Pakistan), on *Malus pumila* Mill., 30-VII-1983, collected by. I. Ahmad, deposited at NHMUK.

Neohalys acuticornis Ahmad & Parveen, 1982: holoytpe 1 ♂; NWFP, Mingora (Pakistan), on *M. pumila* Mill., 13-VI-1974, collected by A. A. Khan, deposited at NHMUK; paratype,1 ♀; with the same data as holotype, deposited at NHMUK.

Neohalys longirostratus Ahmad & Parveen, 1982: holotype 1 ♂; NWFP, Peshawar (Pakistan), on *Pinus* sp., 13-X-1978, collected by I. Ahmad, deposited at NHMUK; paratype 17 ♂, 9 ♀; NWFP Peshawar, Swat, Saidu Shard, Mingora, Azad Kashmir Nochera; Punjab: Islamabad, Wah garden, Rawalpindi (Pakistan), on *Salix* sp., 8-VII-1975, 4-I-1976, 1-VII-1977, 26-VI-1977, 13-VII-1978, 13-X-1978, and 29-VIII-1981, collected by I. Ahmad, A. A. Khan, and M. Moizuddin, deposited at NHMUK and in Ahmad's collection.

Neohalys minirostratus Ahmad & Parveen, 1982: holotype 1 ♂; NWFP, Swat, Saidu Sharif (Pakistan), on *Salix* sp., 8-VII-1975, collected by A. A. Khan, deposited at NHMUK; 23 ♂ and 9 ♀; NWFP Swat, Saidu Sharif, Mingora, Peshawar, Abbotabad; Punjab Wah garden, Islamabad, Sindh: Miani Forest, Azad Kashmir Nochera (Pakistan), on *Salix* sp., *Malus pumila* Mill. (apple), 11 and 20-VIII-1975, 26-VI-1977, 1-VII-1977, 13-X-1978, leg. A. A. Khan, I. Ahmad, M. Moizuddin, and M. Rahim, deposited at NHMUK and in Ahmad's collection.

Neolodosocoris chinensis Memon & Ahmad, 2002: one holotype ♂; China: 12-V-1937, collection of USNM.

Paranevisanus melania Distant 1908: 1 ♂ and 1 ♀; UP (India), 22–1946, collected by J. K Uniyal, collection of USNM.

Phricodus pakistanensis Hamid, 1974: holotype 1 ♂; lodged at USNM; 1 ♂ and 1 ♀; Sindh, Karachi (Pakistan), on *Heliotropium ramosissimum* (Boraginaceae), 20-XI-1972, collected by Q. A. Abbasi, deposited at HMUK.

Salixocoris peshawarensis Ahmad & Abbasi, 1974: holotype 1 ♂; Peshawar (Pakistan), on *Salix* sp., 11-VI-70, collected by H. Rehman, deposited at NHMUK; paratype 1 ♀; Peshawar (Pakistan), on *Salix* sp., 11-VI-1970, 1♀ with the same data.

Salixocoris sindellus Ahmad & Kamaluddin, 1978: holotype 1 ♂, Sindh, Hyderabad (Pakistan),on *Albizia lebbeck* (L.), 15-XII-1976, collected by M. Rahim, deposited at NHMUK; paratype 1 ♂ and 1 ♀;: Sindh, Makli (Thatta) on Light trap (Pakistan), 22-VI-1978, collected by M. Rahim, deposited at NHMUK.

Sarju farida Ghauri, 1977a: 2 ♂ and 4 ♀; NWFP, Mingora, Haripur, Punjab, Changamanga (Pakistan), 28-VII-1977, 9-IX-1983, collected by M. Moizuddin, N. A. Rana and A. A. Khan, deposited at NHMUK.

Sarju eremica (Hoberlandt 1959): 34 ♂ and 28 ♀; Punjab, Taxilla, Islamabad, Wah garden, NWFP, Peshawar, Tarnab, Abbotabad (Pakistan), on 4-V-1971, 9-VI-1972, 9-VIII-1972, 30-VI-1974, 21-VI-1976, 13-VIII-1976, 20 to 30-VI-1972, 22 and 23-X-1977, on *Pyrus* sp. and on grasses, collected by Ahmad, deposited at NHMUK and in Ahmad's collection.

Sarju enigma Ghauri, 1977b: 6 ♂ and 5 ♀; northern areas, Manora, Gilgit, Kargah (Pakistan), 22-VII-1974, 18 and 22-VII-1974, 22-VIII-1975, on *Populus* sp., *Salix* sp., collected by A. A. Khan, deposited at NHMUK.

Sarju angulata Ahmad & Afzal, 1984: holotype 1 ♂; on *Salix* sp., 7-VII-1975, collected by A. A. Khan, lodged at NHMUK; paratype 1 ♂; Manora (Pakistan), on *Populus* sp., 22-VII-1974, collected by A. A. Khan, deposited at NHMUK.