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

NASREEN MEMON,1,2 FRANCIS GILBERT,2,3 AND IMTIAZ AHMAD4

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. Carenoplus was always basal, and Jugalpada and Mustha were plesiomorphic in most best-branched trees. Two relatively plesiomorphic clades were identified, the Halys group (Salisocoris, Halys, and Neohalys) and the Paranevisianus group (Erthesina, Apodiplus, and Paranevisianus). Although strong bootstrap support existed for a clade of 12 genera (Tipulparra, Sarju, Isharocoris, Dalpada, Tachengia, Merindinda, Cahara, Ameridalpa, Etapaleopada, Meridalpa, Lodosocoris, and Neolodosocoris), the only consistent clades within it were a Dalpada group (Sarju, Isharocoris, 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 The as-yet unpublished part of the Ph.D. dissertation of Wall (2004) outlines a phylogeny of many of the world genera, but the major part of his study was focused on Australian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 Megarrhampini, 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...
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; Kiritschenko 1963; Hoferlandt 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, 1985a,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, 2006; 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 scutellum 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 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 gland apparatus is on the mesosternum and has a ventral, usually lobe-like structure, the peritreme. To determine 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 pygophore, 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 paratergite 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**

Orthoschizops Spina 1852 (f), Paranevisanus Distant 1908, Phricodus Spina 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 Faizula Ghauri 1988, the monotypic Osucha 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, Den- 
drites, Iskenderia, Nevisanus, Neonevisanus, Orthoschi-
zops, Saontarana, and Surenus contained missing data 
for 21 characters because they cannot be scored for 
male characters. Taxa with a large proportion of miss-
ning 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-Scheidning, 1999) 
(fide Wall 2004). Hamid (1974) and Menon 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 heu-
ristic search (HSEARCH) with the default settings 
(ADDSEQ = SIMPLE, SWAP = TBR, MULTITREE = 
YES, RECONFLICT = 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 re-
lation 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 uninformative but are 
included because they are important diagnostic char-
acters 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 Parane-
visanus) 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 
etire 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, Par-
anevisanus, 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 pron-
notum; (2) a wide yellow stripe in the middle of the 
 anterior part of the pronotum; (3) four raised impunc-
tate ochraceous spots, and a median line on the an-
terior 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, Iskend-
eria, Asyla, Paranevisanus, and Erthesina (2); Apodi-
phus (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), 
extcept in two genera: Apodiphus (1) and Paranevis-
anus (2) where the variable thickness of the stem of the 
T-shaped fascia 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 Tanchengia (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: Ezhacosiris, Tipulparra, and Tanchengia 
(1); and Phricodus (0). Most Carenoplistus have state 
1, but one species (C. brevis) shares state 2 with Ph-
ricodus: 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 
vividly divergent 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,
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

Fig. 1. Habit 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 iraqiensis. (c) Asyla indicatrix. (d) Carenoplis 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.
genera have state 0, but in some genera this trait is greatly modified: Asylia (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 paraclypeal, 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; (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 paraclypeal are more or less separated between their apices, leaving the clypeus free in between; and (2) tips of the projected parts of the paraclypeal adhere together, enclosing the clypeus. Nearly all included halyine genera have state 0, except Phricodus, Carenevolistus, 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, Carenevolistus, Jugalpada, Mustha, and Orthoschizops (0); Agaeus, Iskenderia, Halys, Neolohalys, Salixocoris, Neolodosocoris, Santarana, Erthesina, and Tachengia (1); Sarju to Dalpada in Table 1 (2); Nevisanus, Neonevisanus, Paranevisanus, and Apodiphus (3); and Surenus and Asylia (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 Carenevolistus 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 Carenevolistus, 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 Carenevolistus (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 Dendritus (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); Carenevolistus, Jugalpada, Mustha, Asylia, Apodiphus, Sarju, Izharocoris, Tipulparra, Ameridalpa, Eupaleopoda, Meridalpa, Dendritus, and Dalpada (2); Agaeus, Halys.
Neohalys, Salixocoris, Paraeneicanus, Cahara, Lodosocoris, Neolodosocoris, Meridindia, and Erthesina all have a labium extending to the fifth abdominal sternite, except N. longirostratus and E. abernys, 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 Saontaran 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) spinoise. 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, Ezharcoris, and Ameridapala (2); Sarju (3); Lodosocoris, Neolodosocoris, Dalpada, and Tachenigia (4), although a few Dalpada species have state 3, and one species of Tachenigia 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); Izharocoris 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, Neolodosocoris, and Meridindia, a large group of genera (Jugalpada, Cahara, Izharocoris, Lodosocoris, Neolodosocoris, Ameridalpa, Meridindia, Eupaleopada, Dalpada, and Tachengia (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
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 invariably among all genera (0) apart from *Mustha* (1) and *Merindindia* (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, Izharcoris, 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, Jugulopa, and Neohalys* (1); *Paranevisanus and Apodiphus* (2); *Sarju, Izharcoris, Dalpada, and Tachengia* (3); *Cahara and Ameridalpa* (4); *Salixocoris* (5); *Tipulparra and Merindindia* (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 *Jugalopa, Mustha, Halys, Neohalys, Salixocoris, Izharcoris, 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 *Merindindia and Meridalpa* (2) and *Cahara and Ameridalpa* (6).

**Thecal Process (Males).** (0) absent; (1) membranous, ear-like, lateral; (2) small, sclerotized or semi-sclerotized, ear-like; and (3) small, highly sclerotized. The thecal process is a specialized character found only in four genera: *Izharcoris* (1); *Dalpada and Sarju* (2); and *Jugalopa* (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, Merindindia, 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 Jugalopa* (1); *Carenoplistus, Surenus, Orthoschizops, Apodiphus, Ameridalpa Meridalpa, and Erthesina* (2); and *Aegus 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, Merindindia, and Eupaleopada* (1); *Meridalpa*...
(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

<table>
<thead>
<tr>
<th>Branch</th>
<th>Character</th>
<th>Steps</th>
<th>CI</th>
<th>Change</th>
</tr>
</thead>
<tbody>
<tr>
<td>node → Phricodus</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>node_1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>node_2</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>node_3</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>node_4</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Continued on following page
<table>
<thead>
<tr>
<th>Branch</th>
<th>Character</th>
<th>Steps</th>
<th>CI</th>
<th>Change</th>
</tr>
</thead>
<tbody>
<tr>
<td>node 5 → Salixocoris</td>
<td>11</td>
<td>1</td>
<td>0.667</td>
<td>3 → 2</td>
</tr>
<tr>
<td></td>
<td>45</td>
<td>1</td>
<td>0.938</td>
<td>2 → 5</td>
</tr>
<tr>
<td></td>
<td>47</td>
<td>1</td>
<td>1.000</td>
<td>1 → 4</td>
</tr>
<tr>
<td></td>
<td>48</td>
<td>1</td>
<td>0.859</td>
<td>0 → 5</td>
</tr>
<tr>
<td>node 4 → node 7</td>
<td>5</td>
<td>1</td>
<td>0.500</td>
<td>0 → 2</td>
</tr>
<tr>
<td></td>
<td>45</td>
<td>1</td>
<td>0.938</td>
<td>2 → 4</td>
</tr>
<tr>
<td></td>
<td>49</td>
<td>1</td>
<td>0.333</td>
<td>1 → 0</td>
</tr>
<tr>
<td></td>
<td>50</td>
<td>1</td>
<td>0.500</td>
<td>1 → 0</td>
</tr>
<tr>
<td>node 7 → node 8</td>
<td>2</td>
<td>1</td>
<td>1.000</td>
<td>0 → 1</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>1</td>
<td>1.000</td>
<td>0 → 2</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>1</td>
<td>0.750</td>
<td>0 → 2</td>
</tr>
<tr>
<td>node 8 → node 9</td>
<td>5</td>
<td>1</td>
<td>0.500</td>
<td>2 → 0</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>1</td>
<td>1.000</td>
<td>0 → 1</td>
</tr>
<tr>
<td></td>
<td>9</td>
<td>1</td>
<td>1.000</td>
<td>0 → 2</td>
</tr>
<tr>
<td></td>
<td>10</td>
<td>1</td>
<td>0.667</td>
<td>0 → 2</td>
</tr>
<tr>
<td></td>
<td>11</td>
<td>1</td>
<td>0.667</td>
<td>3 → 1</td>
</tr>
<tr>
<td></td>
<td>15</td>
<td>1</td>
<td>0.690</td>
<td>1 → 3</td>
</tr>
<tr>
<td></td>
<td>43</td>
<td>1</td>
<td>0.200</td>
<td>0 → 1</td>
</tr>
<tr>
<td></td>
<td>45</td>
<td>1</td>
<td>0.938</td>
<td>4 → b</td>
</tr>
<tr>
<td></td>
<td>48</td>
<td>1</td>
<td>0.859</td>
<td>0 → 2</td>
</tr>
<tr>
<td>node 9 → Paranevisanus</td>
<td>6</td>
<td>1</td>
<td>1.000</td>
<td>1 → 2</td>
</tr>
<tr>
<td></td>
<td>18</td>
<td>1</td>
<td>0.500</td>
<td>2 → 1</td>
</tr>
<tr>
<td></td>
<td>36</td>
<td>1</td>
<td>0.250</td>
<td>1 → 0</td>
</tr>
<tr>
<td></td>
<td>39</td>
<td>1</td>
<td>0.333</td>
<td>0 → 1</td>
</tr>
<tr>
<td></td>
<td>51</td>
<td>1</td>
<td>1.000</td>
<td>0 → 4</td>
</tr>
<tr>
<td></td>
<td>56</td>
<td>1</td>
<td>0.400</td>
<td>2 → 1</td>
</tr>
<tr>
<td></td>
<td>57</td>
<td>1</td>
<td>1.000</td>
<td>0 → 1</td>
</tr>
<tr>
<td></td>
<td>60</td>
<td>1</td>
<td>0.390</td>
<td>3 → 5</td>
</tr>
<tr>
<td>node 9 → Apodiphus</td>
<td>4</td>
<td>1</td>
<td>0.750</td>
<td>2 → 3</td>
</tr>
<tr>
<td></td>
<td>21</td>
<td>1</td>
<td>0.286</td>
<td>3 → 2</td>
</tr>
<tr>
<td></td>
<td>37</td>
<td>1</td>
<td>0.500</td>
<td>0 → 2</td>
</tr>
<tr>
<td></td>
<td>42</td>
<td>1</td>
<td>0.152</td>
<td>0 → 1</td>
</tr>
<tr>
<td></td>
<td>45</td>
<td>1</td>
<td>0.938</td>
<td>b → c</td>
</tr>
<tr>
<td></td>
<td>47</td>
<td>1</td>
<td>1.000</td>
<td>1 → 0</td>
</tr>
<tr>
<td>node 5 → Erthesina</td>
<td>3</td>
<td>1</td>
<td>1.000</td>
<td>2 → 4</td>
</tr>
<tr>
<td></td>
<td>33</td>
<td>1</td>
<td>0.500</td>
<td>0 → 1</td>
</tr>
<tr>
<td></td>
<td>34</td>
<td>1</td>
<td>1.000</td>
<td>0 → 1</td>
</tr>
<tr>
<td></td>
<td>35</td>
<td>1</td>
<td>1.000</td>
<td>0 → 2</td>
</tr>
<tr>
<td>node 7 → node 10</td>
<td>9</td>
<td>1</td>
<td>1.000</td>
<td>0 → 1</td>
</tr>
<tr>
<td></td>
<td>12</td>
<td>1</td>
<td>0.500</td>
<td>0 → 1</td>
</tr>
<tr>
<td></td>
<td>15</td>
<td>1</td>
<td>0.690</td>
<td>1 → 2</td>
</tr>
<tr>
<td></td>
<td>25</td>
<td>1</td>
<td>1.000</td>
<td>0 → 1</td>
</tr>
<tr>
<td></td>
<td>36</td>
<td>1</td>
<td>0.250</td>
<td>1 → 0</td>
</tr>
<tr>
<td></td>
<td>39</td>
<td>1</td>
<td>0.333</td>
<td>0 → 2</td>
</tr>
<tr>
<td></td>
<td>45</td>
<td>1</td>
<td>0.938</td>
<td>4 → 6</td>
</tr>
<tr>
<td>node 10 → node 11</td>
<td>21</td>
<td>1</td>
<td>0.286</td>
<td>3 → 2</td>
</tr>
<tr>
<td></td>
<td>45</td>
<td>1</td>
<td>0.500</td>
<td>0 → 4</td>
</tr>
<tr>
<td>node 11 → node 12</td>
<td>8</td>
<td>1</td>
<td>0.500</td>
<td>2 → 1</td>
</tr>
<tr>
<td></td>
<td>39</td>
<td>1</td>
<td>0.333</td>
<td>2 → 1</td>
</tr>
<tr>
<td></td>
<td>43</td>
<td>1</td>
<td>0.200</td>
<td>0 → 2</td>
</tr>
<tr>
<td></td>
<td>47</td>
<td>1</td>
<td>1.000</td>
<td>1 → 3</td>
</tr>
<tr>
<td>node 12 → node 13</td>
<td>26</td>
<td>1</td>
<td>0.500</td>
<td>0 → 2</td>
</tr>
<tr>
<td></td>
<td>45</td>
<td>1</td>
<td>0.938</td>
<td>6 → 7</td>
</tr>
<tr>
<td></td>
<td>48</td>
<td>1</td>
<td>0.859</td>
<td>6 → 5</td>
</tr>
<tr>
<td></td>
<td>52</td>
<td>1</td>
<td>1.000</td>
<td>0 → 2</td>
</tr>
<tr>
<td>node 13 → Sarju</td>
<td>8</td>
<td>1</td>
<td>0.500</td>
<td>1 → 2</td>
</tr>
<tr>
<td></td>
<td>26</td>
<td>1</td>
<td>0.500</td>
<td>2 → 3</td>
</tr>
<tr>
<td></td>
<td>41</td>
<td>1</td>
<td>0.800</td>
<td>0 → 1</td>
</tr>
<tr>
<td></td>
<td>54</td>
<td>1</td>
<td>1.000</td>
<td>0 → 1</td>
</tr>
<tr>
<td>node 13 → node 14</td>
<td>39</td>
<td>1</td>
<td>0.333</td>
<td>1 → 2</td>
</tr>
<tr>
<td></td>
<td>40</td>
<td>1</td>
<td>0.577</td>
<td>0 → 2</td>
</tr>
<tr>
<td></td>
<td>49</td>
<td>1</td>
<td>0.333</td>
<td>0 → 1</td>
</tr>
<tr>
<td>node 14 → Izharocoris</td>
<td>38</td>
<td>1</td>
<td>0.667</td>
<td>0 → 1</td>
</tr>
<tr>
<td></td>
<td>42</td>
<td>1</td>
<td>0.182</td>
<td>0 → 1</td>
</tr>
<tr>
<td></td>
<td>44</td>
<td>1</td>
<td>1.000</td>
<td>0 → 1</td>
</tr>
<tr>
<td></td>
<td>52</td>
<td>1</td>
<td>1.000</td>
<td>2 → 1</td>
</tr>
<tr>
<td>node 14 → node 15</td>
<td>7</td>
<td>1</td>
<td>1.000</td>
<td>0 → 1</td>
</tr>
<tr>
<td></td>
<td>26</td>
<td>1</td>
<td>0.500</td>
<td>2 → 4</td>
</tr>
<tr>
<td></td>
<td>43</td>
<td>1</td>
<td>0.200</td>
<td>2 → 4</td>
</tr>
<tr>
<td></td>
<td>45</td>
<td>1</td>
<td>0.938</td>
<td>6 → 8</td>
</tr>
</tbody>
</table>
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-
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, Eupa-leopada, 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, Ageaeus, and Skenderia are placed together with the Halys and Paranewisanus 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. 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.
4. Antennae cylindrical.
5. 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.
6. Bucculae short; tibiae black with broad pale annulus medially, first segment of tarsi pale, rest black.
7. Clypeus equal or slightly longer than paraclerype, paraclerype 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 node-like or into small horn; scutellum with prominent basal ochraceous spots, apical area comparatively broad.
8. Clypeus distinctly longer than paraclerype, paraclerype 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 subacutate and not angulately produced; scutellum with-
out basal ochraceous spots; apical area narrower

7. Paraclypei single-lobed; scutellum with distinct 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 .... Salticoris 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 Kiritsenko
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. Basal antennal segment reaching apex of head. 28. Basal antennal segment shorter than apex of head.

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

23. Paraclypei longer than clypeus; lateral margin of pygophore without pair of hook-like structures. 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 on outer angle.

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 deep cavity and with a median excavation; posterior margin of first gonocoxae slightly produced on outer angle. Sarju Ghauri

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

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

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. Tipulpara 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.

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 spermatothecal 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 semiscerotized 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 halines, 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 Paranevisanus 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 spermatothecal 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.
Acknowledgments

We thank the museums that have lent material to Imtiaz Ahmad: the Natural History Museum in London, the Smithsonian Museum in Washington, and the Natural History Museum of Karachi. We also thank Abdul Manan for scanning literature.

References Cited


Ahmad, I., and J. E. McPherson. 1998. Additional information on male and female genitalia of Parabrachy-


Fabricius, J. C. 1775. Systema entomologiae, sistense insecurum classes, ordines, genera, species adjectis synony-
Spinola, M. 1837. Essai sur les genres d’insectes appartenants à l’Ordre des Hemiptères, Lin. ou Rhyngotes, Fab., et à la section Heteroptères, Dufour. Gravier, Genova, Italy.


Received 9 July 2010; accepted 17 June 2011.

Appendix

Material Examined

*Agaeus tesselatus* 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 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 Sandeman (Pakistan), on *Prunus americana* (apricot) collected by Q. A. Abbasi, 3-VI-1969 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.

*Apodiphus jaglotensis* Ahmad & Ahmad, 1993: one holotype ♂; Northern areas, Jaglot (Pakistan), on *Salix acomophila* (willow), collected by A. A. Khan, 9-VII-1985, 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-IX-1967, collected by I. Ahmad, deposited at NHMUK.

*Carenoplistus karachiensis* Memon & Ahmad, 2002: holotype 1 ♀; Karachi, Sindh (Pakistan), on unidentified host, 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.


*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 mulerriensis 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, Temicr), 5-VI-1998, collected by N. Memon, deposited at NHMUK.

Izharocoris aceros Afzal & Ahmad, 1981; holotype 1 ♂; Ayubia, NWFP (Pakistan), 14-VIII-1976, collected by M. Moizuddin and I. Ahmad, deposited at NHMUK; paratype 1 ♀, 22-VI-1977 with the same data as holotype deposited at Smithsonian Museum in Washington (USNM).

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


Mustha iznirensis 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-1953, collected by I. Ahmad, deposited at NHMUK.

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


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

Paranaisanusus 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 ramassissium (Boraginaceae), 20-XI-1972, collected by Q. A. Abbasi, deposited at HMUK.

Salixocoris peshawarenisis Ahmad & Abbasi, 1984; 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 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.