



PHYLOGENETIC ANALYSIS OF SUBFAMILY HARPACTORINAE (HEMIPTERA: REDUVIIDAE)

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ABSTRACT

Phylogeny of the representatives of three tribes, Harpactorini, Rhapidosomini and Tegini from the subfamily Harpactorinae has been studied and their relationships analysed of the genera and tribes. Analysis of 58 characters for 57 species and two outgroups indicates that the subfamily Harpactorinae is monophyletic by having hexagonal cubital cell on forewing and cylindrical head. Within the subfamily Harpactorinae, the tribe Harpactorini got recovered as paraphyletic group and the tribe Rhapidosomini and Tegini as monophyletic. Besides their generic and tribal relationship, insights on radiation of foliage feeding sticky bugs from the primitive raptorial bugs got also reflected.

Key words: Harpactorinae, tribes, monophyly, hexagonal cubital cell, cylindrical head, Rhapidosomini, Tegini, sticky trapping, raptorial

Reduviidae are the second largest cosmopolitan family in the hemipteran suborder Heteroptera described by Latreille during 1807 and the third most megadiverse family in the order Hemiptera after Cicadellidae and Miridae with 7000 described species in the world that are grouped in 25 subfamilies and 28 tribes. Assassin bugs, as these are often called, are most diverse in tropics of Old and New world and several subfamilies and tribes are confined to specific zoogeographical regions. Among 25 subfamilies, Harpactorinae are the top most megadiverse subfamily consisting of 30% of the assassin bugs fauna with >2800 described species under 320 genera in the world (Weirauch et al., 2014) and 149 species belonging to 41 genera under three tribes (Harpactorini, Rhapidosomini and Tegini) in India (Bhagyashree, 2017). These bugs are characterised by cylindrical head, strikingly elongate scape, hemelytron with quadrate cell and 2-segmented fore tarsi.

Harpactorinae are found to be the morphologically most diversified due to the evolution of their fore legs for the development of key innovative strategies such as “sticky trap predation” to capture the prey. Fore femur in primitive reduviids is raptorial with short, stout and powerful flexor muscles for strong mechanical support for gripping and grabbing the prey whereas in case of recently evolved Harpactorinae, fore femur is slender and long because they use novel and innovative sticky trapping strategy for predation. Bugs acquire resin from plants or secrete endogenously by themselves and then apply to the legs which helps the bugs to grasp, grip

and handle the prey easily. Therefore, sticky bugs may not depend on mechanical support of strong fore femur which potentially resulted in trade off between thick and short raptorial fore femur with long and slender to reach the prey (Zang and Weirauch, 2012).

Apart from these key innovative prey capturing strategies, their wide ecological adaptation in various microclimate and microhabitat, high diversity, venomous saliva and ranges of predation from stenophagy to euryphagy drives fast lineage diversification and also make them potential biocontrol agents, however, their application in biocontrol is limited because of gaps in nomenclature and classification due to poor understanding of their phylogentic relationship. This study attempts to reconstruct the phylogeny for the Indian genera of Harpactorinae which is left unstudied by various overseas researchers .

MATERIALS AND METHODS

The current study comprises of 57 species under 25 genera, representing almost 60 per cent of generic diversity of tribe Harpactorinae along with *Acanthaspis siva* Distant, 1904 (subfamily Reduvinae) and *Ectomocoris quadriguttatus* (Fabricius 1781) (subfamily Peiratinae) as the outgroups were scord. Rich collections of Reduviidae present in the insect repository of the Department of Agricultural Entomology, University of Agricultural Sciences, GKVK, Bengaluru (UASB) were extensively used for the study. Taxon samples depend on the availability of the material. Classification adopted in

the study follows the tribal scheme of Davis (1969) and many of the character used by the Davis were utilized in the present study.

Fifty-eight character states were coded for 57 species and 2 outgroups (*Acanthaspis siva* and *Ectomocoris quadriguttatus*) (Table 1). Parsimony was used as the optimality criterion. All the searches were completed in NONA (Goloboff, 1999) spawned from Winclada (Nixon, 2002). All the cladograms including bootstrap* and Jack knife** values were generated using Winclada. For this analysis, the matrix was developed and scored using 58 characters. Among 58 characters, 15 are

multistate and 43 are binary. These characters were processed using Winclada to run NONA where in the default settings for the ratchet functions were used. A heuristic search was carried out holding a maximum of 1000 trees in memory, with 1000 replications and 10 trees to hold per replication in random addition sequence. The number on the nodes reflects the percentage of bootstrap, and also can act as a support for the clades/lineages in a given phylogenetic tree. **Jack knife value: It is the percentage of times that a clade appears when a specified percentage of characters are randomly removed from the data set.

Table 1. Characters and character states used for phylogenetic analysis

Characters	Character states
Body	
0 Integument	Smooth (0), Tuberculate (1), Spinous (2), Pubescent (3)
1 Structure	Oval (0), Elongated (1)
Head	
2 Head structure	Oval (0), Cylindrical (1)
3 Length of anteocular and post ocular	Anteocular shorter than postocular (0), Anteocular longer than postocular (1), Anteocular and post ocular subequal (3)
4 Structure of postocular	Globose (0), Cylindrical (1)
5 Clypeus projections	Anteriorly projected (0), Not projected (1)
6 Shape of maxillary plate	Not lobed (0), Lobed (1)
7 Distance between eyes and antennae	Short (0), Long (1)
8 Antennal insertion	Lateral (0), Dorsal (1), Apical (2)
9 Armature behind the antennal base	Absent (0), If present Spinous (1), tuberculate (2)
10 Proportion of scape and pedicel	Scape shorter than pedicel (0), Scape longer than pedicel (1)
11 Position of eye	Lateral (0), Dorsal (1), Apical (2)
12 Ocelli	Absent (0), Present (1)
13 Position of ocelli	Lateral (0), Dorsal (1)
14 Proportion of labium II and III	II shorter than III (0), II longer than III (1)
15 Ventral surface of labium II	Straight (0), notched (1)
16 Curvature of labium	Straight (0), Slightly curved (1), Acutely curved (2)
17 Surface of scape	Smooth (0), Spinous (1), Tuberculate (2)
18 Structure of scapo-pedicellar articulation	Straight (0), Bent (1)
19 Antennae	Longer than body (0), shorter than body (1)
Thorax	
20 Anteriolateral process on thorax	Absent (0), if present spinous (1), tuberculate (2)
21 Marginal process on anterior pronotal lobe	Absent (0), Present (1)
22 Discal process on anterior pronotal lobe	Absent (0), if present spinous (1), tuberculate (2)
23 Discal process on posterior pronotal lobe	Absent (0), if present spinous (1), tuberculate (2)
24 Humeral process	Absent (0), if present spinous (1), tuberculate (2)
25 Coxae	Short than trochanter (0), Longer than trochanter (1)
26 Forefemora structure	Swollen (0), Not swollen (1)
27 Fossula spongiosa	Present (0), Absent (1)
28 Forefemur	Short and swollen (0), long and slender (1)
29 Setal comb on fore femora and tibia	Absent (0), Present (1)

Table 1 (Contd...)

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30	Wings	Absent (1), Present (0)
31	Cubital cell on corium	Absent (0), Present (1)
32	Length of hemelytra	Passing apex of abdomen (0), shorter than abdomen (1)
33	Fore legs	Shorter than body (0), longer than body (1)
34	Nodules on forefemur	Absent (1), Present (0)
35	Armature on scutellum	Absent (0), if present tuberculate (1), Spinous (1)
Abdomen		
36	Abdomen shape	Oval (0), Linear (1)
37	Ventral connexival suture	Absent (0), Present (1)
38	Connexival membrane	Absent (0), Present (1)
39	Vestiture on abdominal sternites	Smooth (0), Setose (1)
40	Resins on abdominal terminalia	Absent (0), Present (1)
Male genitalia		
41	Shape of pygophore	Round (0), oblong (1),
42	Median pygophore process	Round (0), lobate (1), spinous (2)
43	Rami	Simple (0), bifid (1)
44	Paramere	Absent (0), Present (1)
45	Shape of paramere	Linear (0), Slightly curved (1), Strongly curved (2)
46	Pedicel	Reduced (0), Short (1), Long (2)
47	Struts	Short (0), Long (1)
48	Endosoma	Lobate (0), Spinous (1)
49	Sclerotized vesical rod	Absent (0), Present (1)
50	Lateral phallosomal sclerites	Absent (0), Present (1)
51	Shape of phallus	Oval (0); Elongated (1)
52	Proportion of lateral arms and transverse bridge of basal plate	Lateral arms subequal in length to transverse bridge (0); lateral arms shorter than transverse bridge (1)
Female genitalia		
53	Subrectal glands	Absent (0), Present (1)
54	Dilations on bursa	Absent (0), Present (1)
55	Paired lateral spermatheca	Absent (0), Present (1)
56	Gonoplac structure	Fused (0), Free (1)
57	Apical folds of bursa	Membranous (0), Sclerotized (1),

RESULTS AND DISCUSSION

The phylogenetic analysis of the subfamily Harpactorinae (Tribes: Harpactorini, Raphidosomini, tegini) based on the morphological data set of 59 (including 2 outgroups) taxa including 58 characters resulted in 24 parsimonious trees. The strict consensus tree had 242 steps, a consistency index (CI) of 36 and a retention index (RI) of 78. Only those branches with bootstrap and jack-knife values above 50 were considered which are indicated above and below the branches or nodes, respectively. The phylogenetic analysis of the subfamily Harpactorinae using *Acanthaspis siva* and *Ectomocoris quadriguttatus* as out groups revealed that the subfamily Harpactorinae is monophyletic by having hexagonal cubital cell on forewing and a cylindrical head with *Coranus* as basal

clade. The position of *Coranus* is well supported as sister group for all the remaining clades of Harpactorinae.

Within subfamily Harpactorinae, the tribe Harpactorini was recovered as paraphyletic group and the tribes Raphidosomini and Tegini as monophyletic group nested within the Harpactorini. Weirauch (2008) also recovered the monophyly of Harpactorinae, which was supported by the presence of quadrate cell in the forewing, absence of the dorsal connexival suture, reduction of the vermiform gland and absence of the metathoracic gland. Raphidosomini are found to be the sister group of Tegini by the absence of subrectal glands and anteriolateral process of prothorax. Monophyly of the *Rhaphidosoma* comes from lateral position of the ocelli, coxa which is longer than trochanter, the absence of wings and the presence of ventral connexival

suture. Paraphyly of Harpactorini is due to sister group relationship of [(*Coranus* spp. + *Bergrothellus* spp.) + *Henricohahnia* spp.] with (*Lopocephala* spp. + *Rhaphidosoma* spp.) (Fig. 1).

Harpactorini that use of sticky plant material or resin from external sources recovered as paraphyletic

at the base of Harpactorinae. Weirauch (2008) reported that these relationships have implications for a scenario on the evolution of sticky trap predation in Reduviidae i.e. the affinity to exogenous sticky substances may have evolved early in Harpactorinae and may have been retained in some Harpactorini. The capability of secreting endogenous sticky secretion

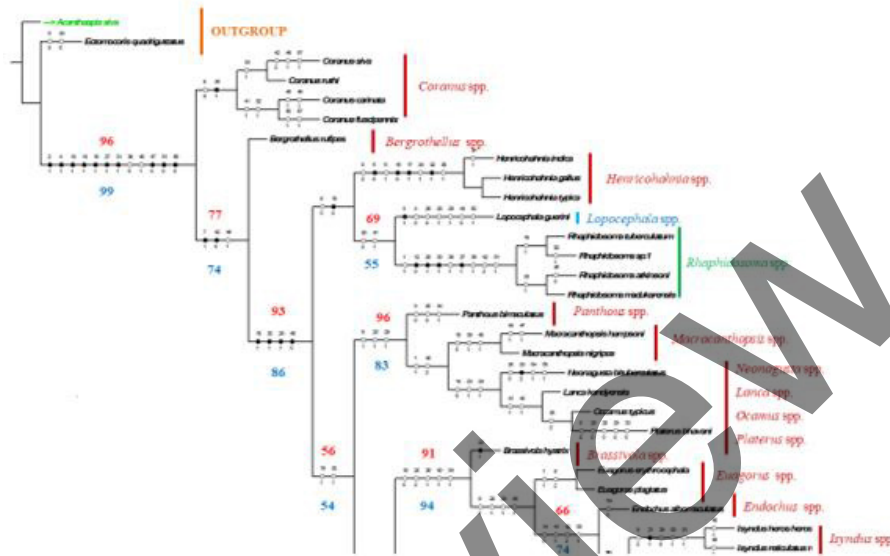


Fig. 1. Strict consensus cladogram of the most parsimonious tree of the subfamily Harpactorinae. Number above and below are Bootstrap and Jack-Knife support values, respectively. (values below 50% are not shown). Consistency Index : 36, Retention Index : 78, Genera indicated by Red, green & blue represents the tribe Harpactorial, Raphidosomini & Tegeini, respectively.

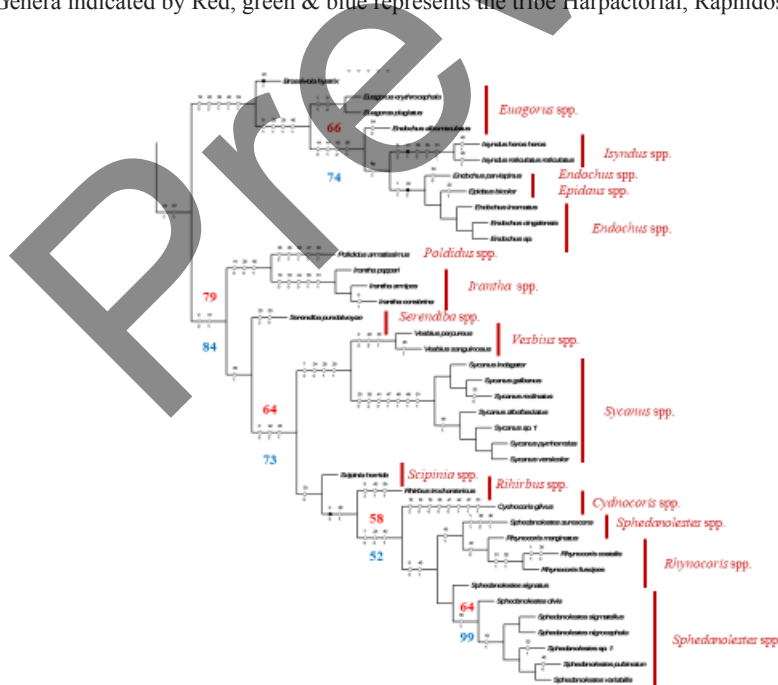


Fig. 1 Continued. Strict consensus cladogram of the most parsimonious tree of the subfamily Harpactorinae. Number above and below are Bootstrap and Jack-Knife support values, respectively. (values below 50% are not shown). Consistency Index : 36, Retention Index : 78, Genera indicated by Red, green & blue represents the tribe Harpactorial, Raphidosomini & Tegeini, respectively.

(Ex: *Sycanus* spp.) has been documented for several species of Harpactorini (Barth, 1953; Wolf and Reid, 2001; Weirauch, 2006) and presumably represents a derived trait within this group. According to Weirauch (2008), substitution of exogenous sticky materials with endogenous secretions would have rendered the assassin bug independent of external plant secretions. Besides to the key innovative sticky trap predation, at the base of the clade, tree exclusively holds the bugs which are soil and cracks and crevices dwelling, clay or bark shaded body colored with well muscled, stout and raptorial fore legs, whereas, at the middle and terminal end of the tree, foliage dwelling, brightly coloured and less muscled non-raptorial bugs were accommodated. This throws a insight on the radiation of foliage dwelling bugs from soil dwelling ancestors in the Harpactorinae.

Within the tribe Harpactorini, even though the results are found to be paraphyletic, most of the genera recovered as monophyletic with good bootstrap and jack-knife values such as *Henricohahnia* spp. (83/97), *Coranus* spp. (66/71), *Irantha* spp. (93/88) and *Sycanus* spp. (58/67) respectively. Genus *Sphedanolestes* Stål, 1866 was found to be polyphyletic by forming the sister group relationship with the genus *Rhynocoris* Kolenati 1857 and the *Endochus* Stål, 1859 were found to be polyphyletic with *Epidaus* Stål, 1859 and *Isyndus* Stål, 1858. Most of the historically proposed supra-generic groups within the Harpactorini are either paraphyletic or polyphyletic in the current phylogeny.

Despite sampling of only Indian taxa, the results of the present phylogeny agree with the morphological and molecular phylogeny constructed by overseas researchers, Weirauch (2008) and Hwang and Weirauch (2012). Still, phylogeny would be greatly improved by

including more number of taxa for all the tribes along with addition of more morphological characters and sequencing data to refine tribal and generic relationship for the development of validated keys for identification.

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