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Morphological Adaptations of Forelegs Associated with Prey Capture in Assassin Bugs (Reduviidae: Heteroptera)

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ABSTRACT

Assassin bugs are one of the most diverse lineage of predatory bugs and have evolved with diversified forelegs for capturing the prey. Preliminary attempts were made to document the morphological diversity of forelegs and to construct the phylogenetic relationship to reveal the patterns of leg evolution across major leg types, based on the morphology of forelegs and prey preference across 46 genera representing 13 subfamilies present in south India. Phylogenetic analysis revealed that, tibiaroliate legs are plesiomorphic, present in common ancestors of Reduviidae. Alternative prey capturing structures were evolved with multiple independent loss of fossula spongiosa for efficient prey capturing.

ASSASSIN bugs are one of the largest and morphologically diverse group of Heteroptera, with 7000 described species worldwide and 448 species in India. They are predatory bugs, whose prey consumption ranges from euryphagy to stenophagy. Evolution of diversified and novel prey capturing strategies in relation to their modified forelegs is one of the key features for their success (in the 178 million years of diversification), in addition to venomous saliva. Their modified forelegs apparently reflect the correlation between the leg structure with respect to prey type and strategies involved in prey capture.

Based on forelegs, assassin bugs are classified into two groups, *i.e.,* tibiaroliate and non-tibiaroliate, based on the presence or absence of '*fossula spongiosa*'. A term referred to the adhesive and cushion-like hairs embedded on the ventroapical surface of the fore tibia and sometimes on midtibia, that helps in grasping the prey during predation. Tibiaroliate legs are shown to be part of ancestral raptorial legs of assassin bugs, which were lost multiple times during the course of evolution. Subsequent to loss of fossula spongiosa, non-tibiaroliate lineages evolved alternative method for capturing different type of prey (Zang *et al.,* 2016). In south India, six subfamilies are known to have tibiaroliate legs and seven are non tibiaroliate having some degree of specialization with respect to their prey during the development of wide repository of novel prey capturing strategies. In this study, morphological differences associated with the forelegs, their functional dynamics with respect to prey type and their phylogenetic relationships are discussed for south Indian species of the family.

Tibiaroliate group of reduviids : Examples : Reduviinae, Peiratinae, Ectrichodinae, Salyavatinae, Centrocneminae and Triatominae.

Members of this group are generalist predators feeding on wide range of prey, except Ectrichodinae (feeding on millipedes), Salyavatinae (feeding on termites) and Triatominae (feeding on vertebrate blood). This generalism is related to the ancestral condition of the tibiaroliate Reduviidae. Prey specialization has evolved independently in Ectrichodinae, Salyavatinae and Triatominae (Hwang and Weirauch, 2012).

Tibiaroliate legs are plesiomorphic and less specialized compared to non tibiaroliate legs, which are almost similar, with slight modification in the length, width, density of hairs and shape of fossula spongiosa. Species of Reduviinae (Fig. 1B), Peiratinae (Fig. 1E) and Salyavatinae (Fig. 1C) are quite active, provided with short and stout powerful forelegs with elliptical fossula spongiosa at the apex of tibia. They prey on medium sized prey like termites, caterpillars, bees, bugs and ants. After finding the prey, they quickly approach and grab it with their forelegs and kill by injecting toxic saliva.

In the case of Ectrichodinae (Fig. 1A), fore and mid femur are short and powerful with oval shaped fossula spongiosa at the apex of tibia to firmly grip the smooth and shining exoskeleton of millipedes. In blood feeding Triatominae (Fig. 1D), fossula spongiosa is restricted to the apex of fore tibia. It is not involved in prey capturing, but helps in smooth climbing on the vertebrate body.

Non-tibiaroliate group of reduviids: Example: Harpactorinae, Holoptilinae, Stenopodainae, Tribelocephalinae, Emesinae, Saicinae and Phymatinae.

Non tibiaroliate vary in morphology and prey capturing strategies. Non tibiaroliate bugs have long and slender forelegs with poor mechanical support, because of this constraint they have evolved various novel strategies to capture prey, which can be grouped into five major types, which includes 1. Sticky trap or fly trap (Weirauch, 2006), 2. Chelated / subchelated (Schuh and Slater, 1995), 3. Raptorial legs (Wignall and Taylor, 2011), 4. Feather legged bugs (Jacobson, 1911) and 5. Legs with spines.

Morphological modifications

Sticky trap or fly trap: Examples: Harpactorinaes. These are generalist predators, feeding on wide variety of insects, they are armed with small bristles and setae on fore, mid and hind legs, which are denser especially on forelegs (Fig. 1G). Females collect resin with forelegs, and transfer to the apex of meso tibia and then to meta tibia, finally transfer to gonocoxae and gonapophysis of genitalic sclerites. Eggs get coated with resin when passing from genital opening to avoid predation by other insects, after hatching nymphs coat the same resin to their fore legs to trap the prey, hence their behaviour is called as sticky trap. Once the bug moults they collect back the resin which is present in their cast skin.

Chelated / subchelated: Example: Phymatinae. These are Ambush bugs and generalist predators. They have enlarged and thicker forefemur and fused tarsus, tend to be more stockier than other reduviids often mimic the flowers (Fig. 1J). Bugs sit motionless on flowers and wait for their prey, once prey lands on flowers, bugs pounce quickly and grab their prey with chelated fore legs.

Raptorial legs: Example: Emesinae and Saicinae. Emesinae are also called as thread legged bugs, look similar to Hydrometridae, Culicidae and Berytidae. Their front legs similar to those of mantids. These bugs are specialized to feed on spiders and psocids and quite small, slender and light enough to walk on spider webs with the help of forelegs by exhibiting aggressive mimicry without entangling. Compared to mid and hind legs their fore legs are stouter and ventrally spinous, coxa are more than three times longer than broad, femora stout and invariably bear two series of ventral spines or denticles and fore tibia are shorter than femora (Fig. 1I). Bugs invade the web and pluck the silk, plucking behaviour of the bugs mimics the vibrations generated by the spiders prey struggling in the web, their by spiders are misled about the presence of bugs.

Feather legged bugs: Examples: Holoptilinae. Feather legged bugs are more unusual in prey choice and prey capturing strategies. They are specialized to feed on ants and posses specialized trichomes on the abdominal venter for secreting honey dew (Fig. 1H). The position of predator when an ant appears itself is unique, when ant appears it raises its body displays abdomen with ant attracting sugar which has paralysing effect. Ants get attracted, feed on honey dew and become motion less. Once the ant gets paralysed, bugs enjoy their meal.

Legs with spines: Example: Stenopodainae. These bugs are generalist predators, having stockier forelegs which gives strong mechanical support for hunting the prey. Structure of forelegs and prey capturing behaviour is similar to that of tibiaroliate group of reduviids but they lack fossula spongiosa rather their forelegs are armed with spines and denticles to grip the prey (Fig. 1F).

Phylogenetic analysis using leg morphology: Preliminary attempts were made to construct the phylogenetic tree to reveal the patterns of leg evolution across major leg types based on the morphology of forelegs and prey preference using binary character across 46 genera representing 13 subfamilies and by fixing Nabidae as out group taxa. Parsimony was used as optimal criterion, all the searches were completed in NONA spawned from WINCLADA for bootstrap

TABLE I

Leg pattern observed in different south Indian genera of Reduviidae

Leg type	Subfamily	Genera
	Centrocnemidinae	*Centrocnemis* sp. and *Paracentrocnemis* sp.
	Ectrichodinae	*Eriximachus* sp., *Haematorrhophus* sp., *Scadra* sp. and *Vilius* sp.
A. Thibiaroliate leg	Peiratinae	*Androclus* sp., *Catamiarus* sp., *Ectomocoris* sp., *Pirates* sp. and *Sirthenea* sp.,
	Reduvinae sp.	*Acanthaspis* sp., *Edocla* sp., *Reduvius* sp. and *Pa*
	Salyavatinae	*Lisarda* sp. and *Petalocheirus* sp.
	Triatominae	*Linshcosteus* sp. and *Triatoma* sp.
B. Non-tibiaroliate leg		
Sticky trap type	Harpactorinae	*Brassoivola* sp., *Coranus* sp., *Endochus* sp., *Epidaus* sp., *Euagorus* sp., *Isyndus* sp., *Neonagusta* sp., *Rhynocoris* sp., *Sphedanolestes* sp., *Sycanus* sp. and *Vesbius* sp.
Chelated/subchelated	Phymatinae	*Carcinocoris* sp., *Amblythyreus* sp. and *Cnizocoris* sp.
Raptorial type	Emesinae	*Stenolemus* sp., *Bagauda* sp., *Schidium* sp. and *Empicoris* sp.
	Saicinae	*Gallobelgicus* sp. and *Polytoxus* sp.
Feathery leg	Holoptilinae	*Holoptilus* sp. and *Ptilocerus* sp.
Legs with spines	Stenopodinae	*Aulacogenia*sp., *Canthesaneus* sp., *Oncocephalus* sp., *Pygolampis* sp., *Staccia* sp. and *Thodelmus* sp.

TABLE II

Characters and character states

Charcaters	Character states	
	0	1
Fore tibial fossula spongiosa	absent	present
Chelated or subchelated fore legs	absent	present
Combs on forelegs	absent	present
Spines or any armatures on forelegs	absent	present
Resin on abdomen	absent	present
Raptorial legs	absent	present
Feathers on legs	absent	present
Prey preference	generalists	specialists
Shape of fore femur	short and stout	long and rounded
Curvatures on forelegs	absent	present
Subrectal glands in female genitalia	absent	present

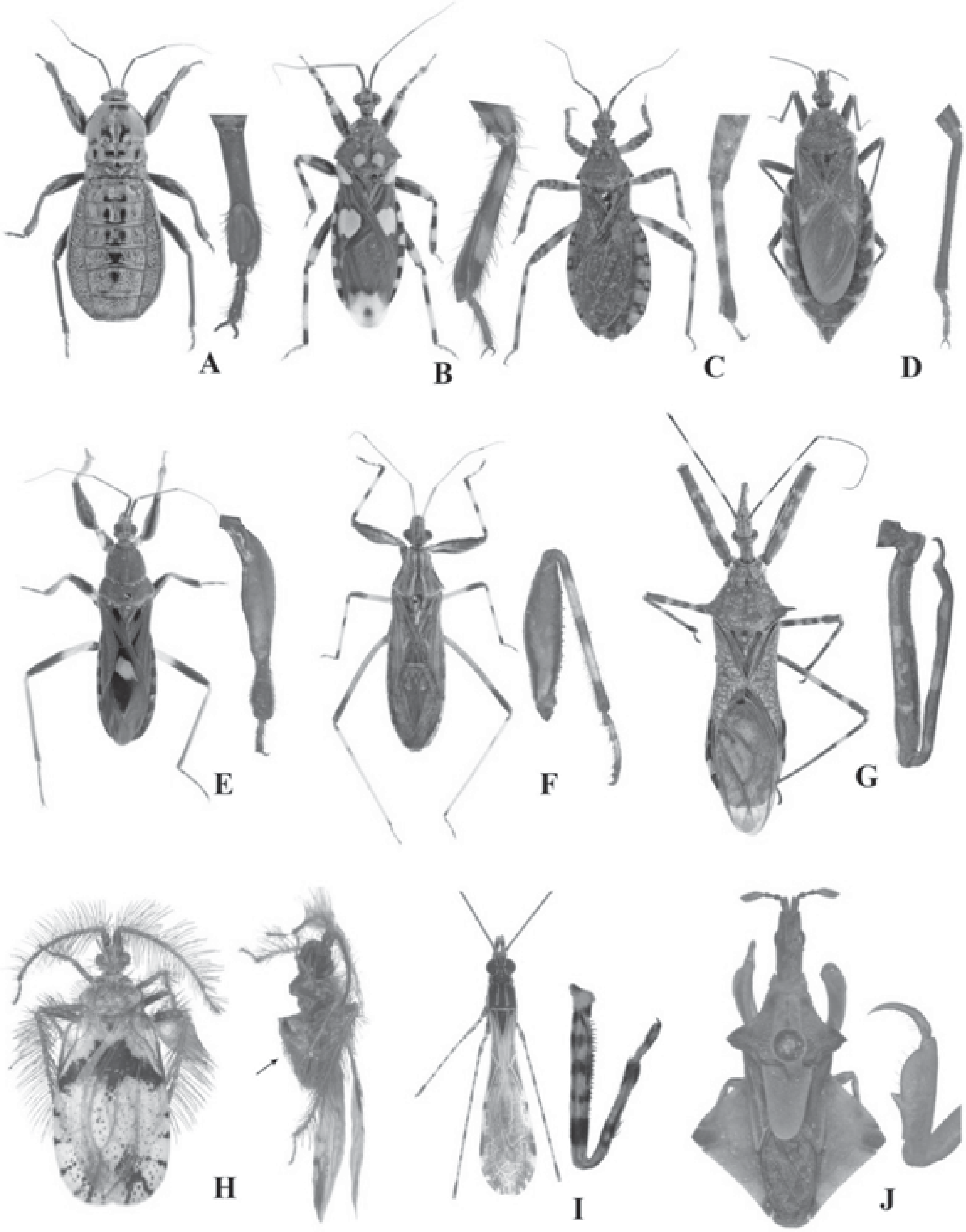

Fig. 1 : Strict consensus tree for tribe Dacini with mapped synapomorphies and bootstrap values

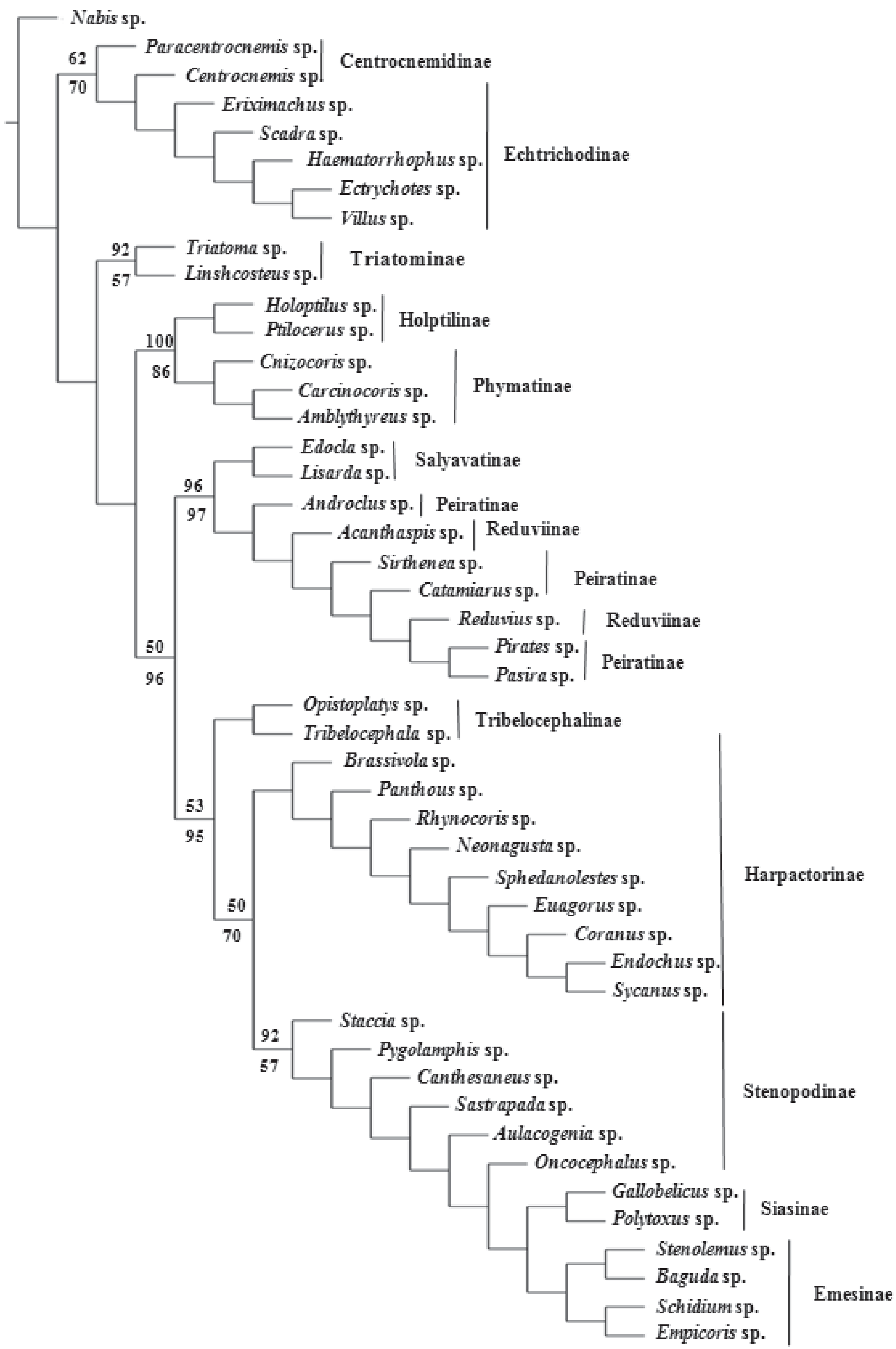

Fig. 2 : Strict consensus clodogram of mostparunonious tree showing patterns of leg evolution in Assassin bugs. Number aboveand respectively, (values below 0 % not shown).Consistency Index ; 69 ; Retention Index ; 94

and Jack knife value. All the cladograms were generated using WINCLADA using the default settings.

Phylogenetic reconstruction of the leg pattern in assassin bugs revealed that, tibiaroliate legs are found to be the plesiomorphic, present in common ancestors of Reduviidae (Fig. 2). Fossula spongiosa was lost multiple times independently in different lineage, such as feathery legs in Holoptilinae, chelated in Phymatinae, sticky trap in Harpactorinae, legs with armature in Stenopodainae to enhance prey capture.

Zhang *et al.* (2016) also reconstructed the phylogeny with the same patterns of evolution. They reported that salivary toxicity may be another factor influencing the evolution of fossula spongiosa. Saliva with higher toxicity may paralyse and kill prey faster and could remove constrains on raptorial legs. Studies have shown that bugs without fossula spongiosa immobilise the prey faster than those with fossula spongiosa (Ambrose, 1999). Therefore, conclude that these alternative raptorial traits likely to have evolved independently from the loss of fossula spongiosa to enhance their prey capture. So understanding morphological adaptation to prey capture in assassin bugs will benefit from further research to show complex inter-relationships involved in prey specialization, predatory behaviour and toxicity of venomous saliva.

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