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Functional morphology of the fossula spongiosa in some reduviids (Insecta—Heteroptera—Reduviidae)

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Abstract. Legs of Reduviidae show modifications and specialised structures adapted for their predatory habits and efficient prey capture. The variable forelegs of these insects apparently reflect the correlation between the structure of the legs and the types of prey. The tibial pads or fossula spongiosa are a common feature in the forelegs or fore- and midlegs of most of subfamilies of Reduviidae. The functional morphology of the tibial pads of the forelegs of three insects, *Haematorrhophus nigroviolaceus* (Reuter), *Pirates affinis* Serville and *Triatoma rubrofasciata* (De Geer) has been studied. The oily substance produced by the cushion-like secretory tissue and the minute tenet hairs on them increase the ability to sustain static tension and enhance the gripping efficiency of the legs. Scanning electron micrographs reveal distinct morphological variations among the tibial pads. In addition to the shape and size of the organs, the number, structure and density of the tenet hairs on them markedly vary. The ability of the foretibial pad to sustain static tension on smooth and rough surfaces has been found to differ among the insects studied and this is remarkable in predatory insects.

Keywords. Reduviidae ; tibial pad ; gripping ; tenet hairs.

1. Introduction

The thoracic appendages of Heteroptera that ordinarily serve as organs of terrestrial locomotion assume diverse functions like saltatory, fossorial, natatory, raptorial, etc. with accompanying structural modifications. In several species of Nabidae, Ploiaridae, Lygaeidae, and Enicocephalidae, the forelegs are specially adapted as raptorial organs extensively used for food capture, while members of Notonectidae and Belostomatidae have their forelegs modified into raptorial arms, their mid- and hindlegs being adapted for natatory functions (Imms 1965; Miller 1971). In exclusively predatory Reduviidae also the forelegs show modifications or specialised structures for efficient prey capture; the forelegs of Emesinae are raptorial (Wygodzinsky 1966) and the forelegs of Apimerinae are coated with resin to capture prey-like fly-paper (Miller 1971). In other subfamilies of Reduviidae the tibiae and femora of both fore- and midlegs are armed with spines or teeth or with numerous thick setae. The variable forelegs apparently reflect a correlation between the structure of legs and the types of prey they capture. In addition to these, the ventral apical surface of the foretibiae and sometimes the midtibiae also show an organ, the tibial pad, which the systematists call the "fossula spongiosa". Dufour (1833) made a thorough study of the tibial pads and characterised them as pre-eminently functional organs, helping the predatory insects to exercise an act of touch or prehension. Spinola (1837), who also studied these organs, termed them as 'ventouse tibiale' and suggested that they help the predators to provide an easy adhesion to the prey's body. With a number of experimental evidences, Gillett and Wigglesworth (1932) and Edwards (1962) clearly established that the fossula spongiosa of reduviids possess numerous tenet hairs and secrete an oily substance, the molecular forces of which increase the static tension sustained by the legs as well as the adhesion of the pads, enhancing the gripping efficiency of the reduviids. The tibial pads of three reduviids, *Haematorrhophus nigroviolaceus* (Reuter) (Ectrichodiinae), *Pirates affinis* Serville (Piratinae), and *Triatoma rubrofasciata* (De Geer) (Triatominae), which have diplopodophagous, insectivorous, and haematophagous habits respectively (Haridass 1978), have been investigated to find out the morphological differences among them, as well as to assess the correlation between the functional efficiency and their prey types.

2. Materials and methods

The reduviids were collected and reared in the laboratory as described elsewhere (Haridass and Ananthakrishnan 1980). The legs of dead insects, preserved in 70% alcohol, were treated with 5% KOH solution for 3–4 days and the remaining chitinous parts were washed with acetic acid, dehydrated, stained with eosin and mounted in DPX. Fore, and midlegs, removed from freshly moulted insects before undergoing hardening by chitinisation, were fixed in aqueous Bouin's solution for 4–5 hr. Serial sections of 8–10 μ thickness were made followed by the standard procedures of dehydration, clearing, and embedding. Sections were stained with haematoxylin and eosin and mounted in canada balsam. Forelegs preserved in 70% alcohol were dried in an oven and mounted on aluminium studs. After gold coating they were examined with a scanning electron microscope (Model JSM-U3 of JOEL company).

The approximate total surface area of the ellipsoidal fossula spongiosa of the foretibiae of *H. nigroviolaceus*, *P. affinis*, and *T. rubrofasciata* was determined, using the formula $4/3\,\pi\ (ab + bc + ca)$, where a, b, and c represent the half length, half width, and half height of these tibial pads. The size and frequency of distribution of hairs per 100 sq.μ were calculated using a micrometer and the approximate total number of such hairs on the whole surface of the tibial pads in these reduviids was determined.

The static tension sustained by the legs of the three reduviids on smooth (glass slide) and rough surfaces (dead millipede for *H. nigroviolaceus*; dead carabid beetle for *P. affinis* ; piece of sheep skin for *T. rubrofasciata*) was measured by using a sensitive spring balance (after Edwards 1962). Photomicrographs were taken with Asahi Pentax MX 1·4 mm camera.

3. Observation and results

In all insects presently examined (figure 1A, B and C) both the fore- and midtibiae show the ellipsoidal or ovoid fossula spongiosa. In all the cases, this tibial pad shows numerous adhesive hairs embedded on a cushion of cuticle, above which is seen a soft, spongy tissue and haemolymph. This is in turn bordered on the inner side by the sclerotised wall of the tibia (figure 2A). The tibial pad region receives a good supply of tracheal and nervous ramifications. These adhesive pads secrete an oily substance, which can be observed when the pads of a live insect are drawn over a clean polished surface like that of a glass slide.

In *H. nigroviolaceus* the tibial pads (figure 1A) are well developed both on the fore- and midtibiae. The pad on the foretibia is 1828 μ long and 1037 μ wide, having an ovoid spherical shape with a height of 225 μ. It offers a total surface area of 3·27 sq. mm. There are approximately 1·69 hairs per 100 sq. μ and the total number of hairs on the tibial pad is about 55,000, each measuring 45–47 μ long (table 1). The S.E. micrographs (Figure 3A, B and C) clearly show the shallow tips of the adhesive hairs. With such well-developed organs on their legs, *H. nigroviolaceus* is able to grip its powerful millipede prey firmly, in spite of the prey's smooth and shiny exoskeleton (figure 2B).

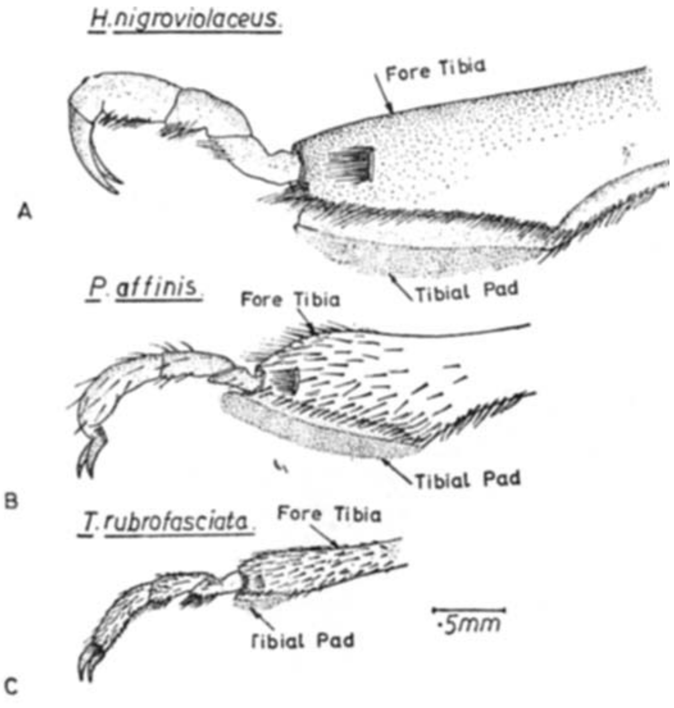

Figure 1. Tibial pads.

Table 1. Adhesive hairs and the static tension sustained on smooth and rough surfaces by the foretibial pads of some reduviids.

Insect	Tibial pads						
	Length (i) $\frac{1}{2}\mathrm{i} = a^*$	Width (ii) $\frac{1}{2}\mathrm{ii} = b^*$	Height (iii) $\frac{1}{2}\mathrm{iii} = c^*$	Density of hairs in 100 sq. μ	Total surface area ($) in sq. mm.	Total number of hairs (approx.)	Length hairs in μ
H. nigroviolaceus	1828 μ	1037 μ	225 μ	1·69	3·266	55,000	45–47 μ
P. affinis	1425 μ	813 μ	300 μ	3·00	2·353	70,500	40–43 μ
T. rubrofasciata	328 μ	266 μ	75 μ	9·20	0·169	15,500	20–22 μ

$\$ =$ Total surface area of an ellipsoid $= 4/3\,\pi\,(ab^* + bc^* + ca^*)$.

Insect	Static tension	
	Smooth surface	Rough surface
H. nigroviolaceus	20·0–21·5 g	9·5–12·0 g
P. affinis	25·0–27·0 g	13·5–16·0 g
T. rubrofasciata	Negligible	1·0–2·0 g

The greatest development of the tibial pad is seen in *P. affinis* (figure 1B). The ellipsoidal organ measures 1425 μ long 813 μ wide and 300 μ high, offering a surface area of nearly 2·35 sq. mm. The total number of adhesive hairs approximates 70,500 and each hair is 40–43 μ long (table 1). The S.E. micrographs (figures 4A, B and C) reveal the tip of the hairs to be lanceolate and concave. In this insect also the tibial pads help to establish a firm grip on the robust and fast moving carabid beetles, which form its natural prey (figure 2C).

The tibial pads of *T. rubrofasciata* (figure 1C) seen on both fore- and midlegs, are more or less round in shape, comparatively smaller in size and poorly developed. They occupy a negligible part of the tibiae and each measuring only 328 μ long, 266 μ wide and 75 μ high. The total surface area offered is hardly 0·169 sq. mm. The adhesive hairs are 20–23 μ long and are closely packed with a density of 9·2 hairs per 100 sq. μ. There are approximately 15,500 hairs on each of the tibial pads, a very small number when compared to other predatory insects (table 1). The S.E. micrographs (figures 5A, B and C) reveal the simple nature of the hairs with only pointed tip and without any adhesive area.

The static tension sustained by the legs of the three reduviids varies considerably (table 1). On smooth surfaces *H. nigroviolaceus* sustains 20·0 to 21·5 g and between 9·5 to 12·0 g on rough surfaces (body of the millipede). *P. affinis* sustains 25·0 to 27·0 g and 13·5 to 16·0 g on smooth and rough surfaces (glass slide and body of carabid beetle respectively. *T. rubrofasciata* is unable to sustain any

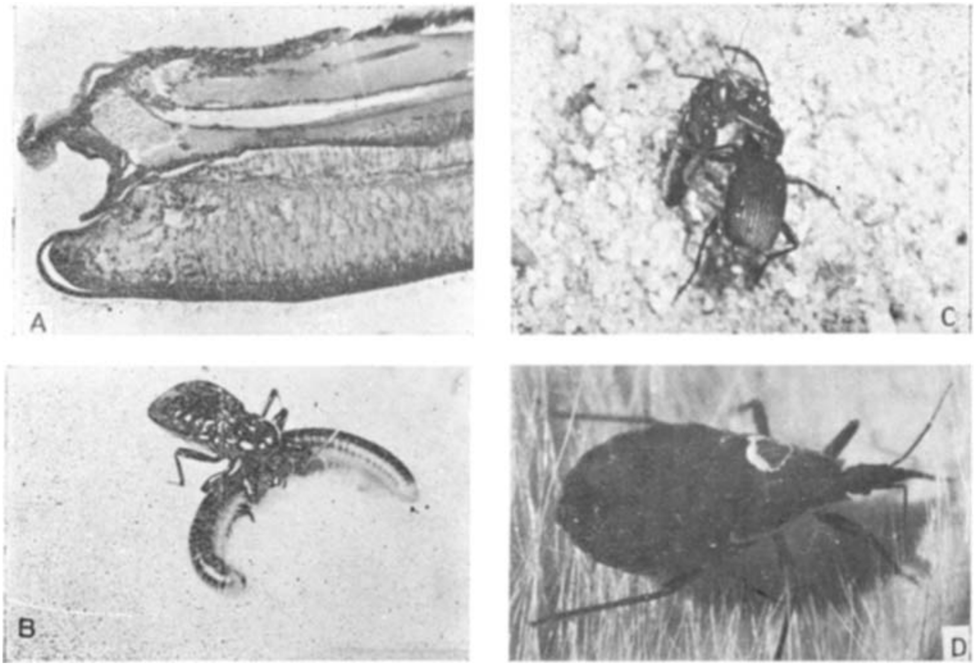

Figure 2. A. L.S. of the apex of the foretibia of *H. nigroviolaceus* showing the tracheation, spongy secretory tissue and the tenet hairs of the tibial pad. B. Adult female of *H. nigroviolaceus* grips the paralysed body of the millipede with fore - and mid-legs and feeds. C. Fifth Neanide of *P. affnis* gripping and paralysing the carabid beetle prey. D. Fifth Neanide of *T. rubrofasciata* engorging on dog's blood.

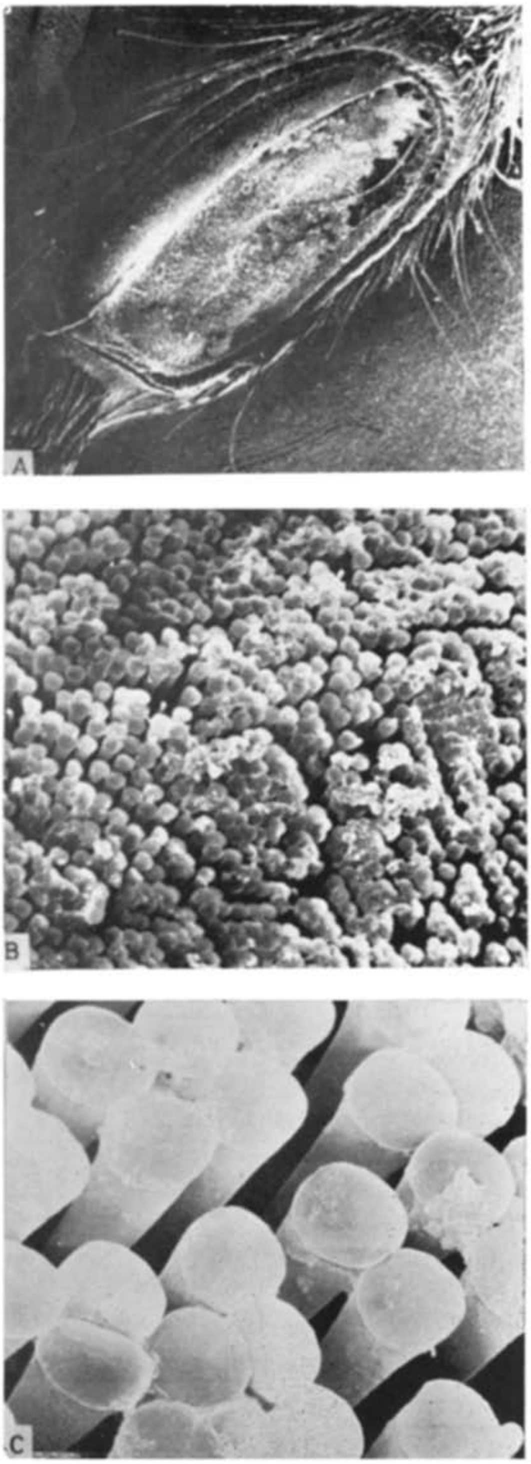

Figure 3. Electron micrographs of fore tibial pad of *H. nigroviolaceus*. A. Ventral view of the fore tibia showing the fossula spongiosa (40). B. Tenet hairs of the tibial pads (× 500). C. The same enlarged (× 3000).

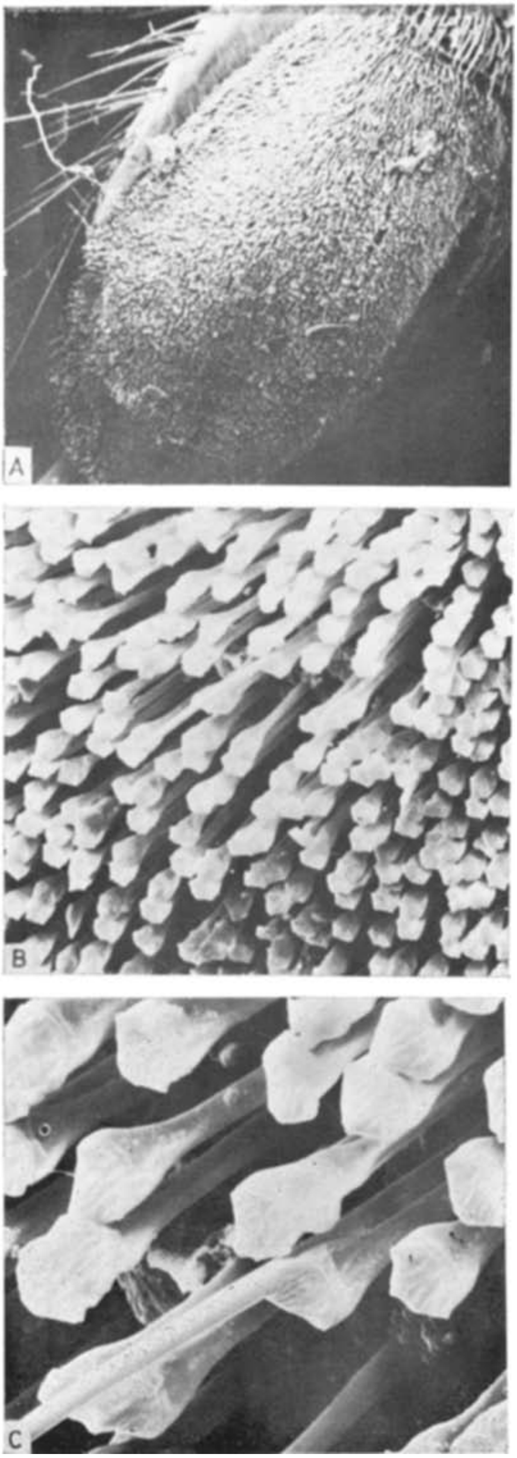

Figure 4. Electron micrographs of fore tibial pad of *P. affinis*. A. Ventral view of the foretibia showing the fossula spongiosa (× 80). B. Tenet hairs of the tibial pad (× 800). C. The same enlarged (× 2400).

Figure 5. Electron micrographs of fore tibial pad of *T. rubrofasciata*. A. Ventral view of the fore tibia showing the fossula spongiosa (× 120). B. The same enlarged (× 250). C. Tenet hairs on the tibial pad (× 800).

weight on smooth surfaces and it is only 1–2 g on rough surfaces (sheep skin). In the first two reduviids, the fossula spongiosa are effectively used against their millipede and carabid beetle prey to ensure a firm grip when the respective prey is attacked. In *T. rubrofasciata* gripping the prey is unnecessary as it feeds on the blood of large vertebrates (Haridass 1978) (figure 2D).

4. Discussion

Fossula spongiosa on the legs of reduviids occupy nearly 1/3 of the front part of tibiae. But in some, like *Ectomocoris* spp. they are very well-developed and project beyond the tip of the tibia (Distant 1904). In majority of the reduviids the tibial pads are present, both on fore- and/or midlegs and rarely they are wanting. The presence or absence of tibial pads has been used as a taxonomic character in Reduviidae (Distant 1904). In addition to this variation, the tenet hairs of these pads also exhibit structural variation as seen in the scanning electron micrographs of the species studied here (figures 3C; 4C; 5C), a character which can be used as a useful tool in the classification of Reduviidae.

Investigations made on the functional efficiency of the fossula spongiosa of reduviids like, *Rhodnius prolixus* Stal (Gillett and Wigglesworth 1932) and *Rhinocoris* sp. and *Platymeris* sp. (Edwards 1962) have clearly shown the occurrence of numerous tenet hairs on the tibial pads and the secretion of an oily substance in the angle between the oblique end of the hairs. The surface molecular forces of this secretion are said to increase the adhesion of the tibial pads (Gillett and Wigglesworth 1932) enabling the legs to sustain and support greater weight (Edwards 1962) and thus enhancing the gripping ability of the predatory reduviids.

In *H. nigroviolaceus* the tibial pads are well-developed and are effectively used in prey capture. The insect has a total body length of 26·2 to 27·0 mm and a body weight of 0·925 to 1·153 g and is able to sustain a static tension of 20·0 to 21·5 g on smooth surfaces and 9·5 to 12·0 g on rough surfaces. Like other members of the subfamily Ectrichodiinae, this reduviid feeds exclusively on millipedes (Haridass 1978). The hard, smooth and cylindrical body of the millipede prey is firmly held with the help of the tibial pads on fore- and midlegs. Similar millipede-prey capture, involving the effective use of the tibial pads of the legs, is also noticed in other Ectrichodiinae like, *Guionius nigripennis* (Fab.) and *Ectrichotes pilicornis* (Fab.) (Haridass 1978). The insectivorous *P. affinis* predates on the robust and fast moving carabid beetles *Omphora pilosa* Klug and *O. atrata* Klug in nature. The hard and smooth exoskeleton of these beetles offers sufficient surface area for the tibial pads of *P. affinis* which is comparatively smaller than *H. nigroviolaceus* and measures 21·9 to 23·7 mm long and weighs about 0·33 to 0·38 g. Despite its smaller size it is able to sustain and support a static tension of 25 to 27 g on smooth surfaces and 13·5 to 16 g on rough surfaces. Other members of the subfamily Piratinae like *Ectomocoris vishnu* Distant and *E. ochropterus* Stal, are also known to be predaceous but prefer field gryllids as their natural prey and like *P. affinis* they also use their tibial pads as effective gripping organs during prey hunting (Haridass 1978).

The tibial pads show their least development in *T. rubrofasciata* and though its total body length and weight are similar (21·2 to 23·3 mm; 0·26 to 0·28 g) to those of *P. affinis*, this reduviid is unable to support and sustain any weight on smooth surfaces and supports merely 1-2 g on rough surfaces. The reduction and simplicity of the tibial pads in this insect agree well with the observation that in these haematophagous forms there is no gripping of the vertebrate hosts involved as seen in other predatory reduviids. A similar situation is also observed in other Triatominae, *Linshcosteus costalis* Ghauri and *L. confumus* Ghauri (Haridass 1978). The presence of fossula spongiosa, both on the fore- and mid-tibiae, of these blood feeding insects could still afford them with enough gripping power to walk on smooth surfaces in their hiding places. The function in enhancing the gripping ability of the legs of the reduviids could be better realised when the sustenance of the static tension of these legs is compared with those of the larger bodied acridid, *Schistocera* sp. (Edwards 1962), whose tarsal pads sustain a static tension of only 5 g on smooth surfaces.

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