SECTION E

EVOLUTIONARY APPROACH
The Division of Reduviidae into two groups on the basis of the presence or absence of tibiarolium, as detailed in the foregoing account, is advocated. An attempt on the origin of tibiarolium in Reduviidae inevitably necessitates the study of the tibiae of all the subfamilies which is beyond the scope of the present discourse.

Among the tibiaroliate subfamilies studied, the Salyavatinae could be considered as the subfamily having the least developed tibiarolium, both in the fore and mid tibiae and with the exception of Nudiscutella frontispina, an apterous species endemic to drought prone ecosystems, all others are inhabitants of Tropical Rainforests and other habitats of dense Scrub Jungles, feeding on litter insects. While the tibiarolium in Petalochirus spp. is distinctly formed, but rudimentary in nature, in Lisarda spp. and in N. frontispina they conspicuously project in front of the tibiae. Petalochirus is endemic to Tropical Rainforests where as Lisarda sp. are not strictly restricted to drought prone areas but predominantly found in Scrub Jungles.

In all species of Ectrichodiinae and in Pirates species of Piratinae, the tibiarolia are restricted to the distal 1/4 of the tibia and this area of the tibia, bearing the tibiarolium, is conspicuously swollen. In Pirates, however, the tibiarolium is much more extended anteriorward than in Ectrichodiinae. In Catamiarus, Ectomocoris and Sirthenea on the
other hand, unlike *Pirates*, the tibiarolium occupies more than 3/4 the length of the tibia and in *Sirthenea* the mid tibia is free of tibiarolium. Thus, it is reasonable to suggest that in the evolution of tibiarolium in the tibiaroliate group of Reduviidae the *Petalochirus* of Salyavatinae represents the lowest grade of development and organization and the assumption is that a more plesiomorphic tibiarolium could be defined as a more apical differentiation of tibia (Pl. VIII: 21 - 32) typically found in the Salyavatinae representatives of the Tropical Rainforests. The Ectrichodiinae that feed on millipedes are also residents of Tropical Rainforests and more humid areas of dense Scrub Jungles and they too have more apical differentiation of fore and mid tibiae. Among Piratinae, the members of the genus *Pirates* are more or less endemic to the Tropical Rainforest habitats, frequenting Scrub Jungles and other drought prone ecosystems during monsoon. They too have more apical differentiation of tibiarolium, in marked contrast with their counter parts such as *Ectomocoris* and *Catamiarus* which are endemic to the drought prone ecosystems. The more they move into the interior of drought prone ecosystems the more extensive their tibiarolia develop, as demonstrated by the *Ectomocoris* species of Piratinae. It is interesting that the tibiarolia of *Pirates affinis* (Pl. X:15&16) a resident of the Tropical Rainforest compares well with the tibiarolia of most species of Ectrichodiinae (Pl. VIII: 11 - 14).

All the species of Acanthaspidinae (with the exception of *M. kovaii* and *N. maculatus*) have relatively well developed tibiarolia. It is also interesting that species such as *Centrocnemis* and *Apeclitia mesopyrrha* which are not endemic to drought prone ecosystems but commonly found in Tropical Rainforests, have more apical differentiation of tibiarolium similar to those of Ectrichodiinae and *Pirates*. The total absence of
tibiarolium in Triatominae, as discussed earlier, is correlated with haematophagy and habitat selection associated with large warm blooded animals.

The foregoing account will clearly indicate that the plesiomorphic condition of the tibiarolium, characterised by more apical development of tibiarolium and the apomorphic condition is characterised by the development of tibiarolium in both directions on the tibiae. The former condition is associated with the endemic species of the Tropical Rainforest and the latter with those of drought prone ecosystems. In that respect, the *Ectomocoris* spp. of the drought prone ecosystems have attained the highest rank in the evolution of tibiaroliate group of Reduviidae, a view maintained earlier by Livingstone and Ambrose (1978 and 1984) and Ambrose (1986 and 1987). Though Parker (1965, 1969 and 1971) and Edwards (1963, 1966 and 1970) have also studied the tibiarolia of a few reduviids, the idea of attributing evolutionary importance of predation and habitat selection to these structures has evaded their attention, perhaps due to lack of such massive materials available with them for comparison.

The tentative scheme suggested here (Fig. 48) is liable to be modified when more and more informations on less understood species are brought to light. However, the Salyavatinae among the tibiaroliate group will remain with us as one having the most plesiomorphic feature of the tibiarolium development among Reduviidae and without any exception all species of this subfamily are known to be entomophagous. From such an ancestral stock, the myriophagous *Ectrichodiinae* might have evolved within the niches of the Tropical Rainforest ecosystem and subsequently the genus *Pirates* also, under similar ecological conditions, towards entomophagy.
FIG. 48. EVOLUTIONARY TREND AMONG THE TIBIAROLIATE REDUVIIDAE OF SOUTHERN INDIA

ACANTHASPIDINAE
Mesacanthaspis & Neoacanthaspis (Entomophagy)

PIRATINAE (Entomophagy)

HARPACTOROID COMPLEX (Entomophagy)

TRIATOMINAE (Haematophagy)

Loss of Tibiarolium

Acanthaspis (Entomophagy)

Pirates (Entomophagy)

Edoela

ECTRICHOIDIINAE (Myriophagy)

Centrocnemis —— Apechntia

Lisarda

Petalochirus (Entomophagy)

SALYAVATINAE (Entomophagy)

HARPACTOROID COMPLEX
Nontibiaroliate Complex (Entomophagy)

(Ectomocoris Catamarius Sirthenea)
From Pirates, such as P. affinis of the Tropical Rainforest ecosystem other genera have evolved towards a life in a drought prone ecosystem, with corresponding exaggerated development of tibiariolium, since prey species is relatively scarce under such dry conditions. The Acanthaspidinae appears to have developed independently towards entomophagy in a drought prone ecosystem from the Salyavatinae stock such as the Lisarda. The Apechtia and Edocla appear to be the connecting link between the Acanthaspidinae and the Lisarda as evidenced by the similarity of their tibiariolia.

One of the unique features of the Salyavatinae is the two segmented condition of the adult fore leg tarsomeres though such segmentation characterises the nymphal instars of all the species of Reduviidae examined. It is this character that prompts one to include the genus Petalocharus along with Lisarda and Nudiscutella under the subfamily Salyavatinae. However, it is premature in this context to emphasise that the two segmented condition of adult tarsomere in Reduviidae is a plesiomorphic feature met with in Salyavatinae.

An assessment of the stylets of all the species further suggests that the Salyavatinae of the tibiariolate group has more plesiomorphic characters than the rest, as indicated by 1. development of extra serrations on the mandibular stylets far behind the tip; 2. the right maxillary stylets with multiplicity of barbs both on the dorsal and ventral edges; 3. presence of barbs on the left maxillary stylets as well. Multiplicity of barbs, as described earlier, is an indication of plesiomorphy (Cobben 1978) and interestingly the Piratinae too have similar characters. Whereas most of the Acanthaspidinae representatives of the drought prone ecosystems have abbreviated barbs (in the form of serrations) system on the dorsal
edge alone of the maxillary stylets, certain other species such as *Apechtia mesopyrrha*, *Pasira perpusilla*, *Reduvius delicatula* and *Neoacanthaspis maculatus*, which are known to be residents of Tropical Rainforests, have barbs on both edges of their right maxillary stylets and the rear row of serrations of their mandibular stylets are more or less similar to those of Salyavatinae.

In all species of Ectrichodiinae, the characteristic spatulate mandibular stylets are similarly specialized blades and their right and left maxillary stylets are both profusely barbed. Interestingly, in Piratinae too the right maxillary stylets are barbed on both edges and the left one has a series of few spines along the dorsal edge as well. The Triatominae, in contrast, has absolutely smooth maxillary stylets and the mandibular stylets having only one row of serrations.

Therefore, the assessment of the mandibular and maxillary stylets, on the basis of the manner of development of barbs, also clearly indicates that the Salyavatinae of the Tropical Rainforests represents the more primitive stock of the tibiaroliate group of Reduviidae and members of other subfamilies such as Ectrichodiinae, Piratinae and those exceptions of Acanthaspidinae, which are residents of Tropical Rainforests, tend to preserve such plesiomorphic features.

Thus it is clear also that the formation of tibiarolium is correlated with the mandibular and maxillary armature. A plesiomorphic tibiarolium is apical differentiation of tibia and a plesiomorphic stylet is with extensive armature. Both conditions are met with in Salyavatinae, Ectrichodiinae, Piratinae and a few exceptional species of Acanthaspidinae. Interestingly, all these examples, without any exception, are inhabitants of Tropical Rainforests.
It is worthwhile also to compare the mandibular lever of the representatives of all the subfamilies of the tibiaroliate group for an assessment of their evolutionary status. In Salyavatinae (Pl. II : 13) Ectrichodiinae and Piratinae (Pl. III : 13 & 18) the lever is triangular in a graded pattern but in Acanthaspidinae (Pl. II : 21) it is more towards quadrangular shape. As discussed earlier, a triangular lever is plesiomorphic and according to Cobben (1978) a more quadrangular lever, that originates ontogenetically from a triangular lever, ensures a more predatory attack. This may suggest that the triangular lever of Salyavatinae may represent the more primitive condition of predatory behaviour than the Acanthaspidinae and both Ectrichodiinae and Piratinae retain more Salyavatinae features than those of Acanthaspidinae.

It is difficult to attribute evolutionary significance to the rostral tip and an attempt in this direction will demand more informations on the cephalic morphology and feeding strategy.

Yet another important evidence in favour of considering the Tropical Rainforest forms as candidates for plesiomorphy, is provided by the male genitalia. As described earlier, if plesiomorphy is indicated by the complexity of the armature of structures, of which the intromittent organ is not an exception, there is no difficulty in suggesting that Salyavatinae represents the lowest step in the ladder of evolution of the tibiaroliate group of Reduviidae of this region.

The complexity of armature of the phallotheca has been found to have reached the maximum in Salyavatinae, especially in Petalochirus (Pl. XX : 10 & 11) by the development of too many spinous coiled pouches on the ventral wall of the phallothecal cup. A more or less similar complex
highly spinous coiled pouches on the ventral wall of the phallothecal cup have been recognised in Piratinae (Pl. XXI : 10 - 24) and Ectrichodiinae (Pl. XX : 1 - 7) also. Interestingly, the Acanthaspidinae and Triatominae have relatively more simplified armature of the Phallotheca and the ventral phallic sclerite is better defined as a median anteroventral plate, without any significant development of such armoured coiled pouches, commonly met with in the other tibiariolate subfamilies of the Tropical Rainforests.

However, it is difficult to generalise the relationship and evolutionary significance of pygophore spine in relation to the development of phallothecal armature, since a few species of Acanthaspidinae such as A. siva, A. quinquespinosa etc. do not have pygophore spine at all, though their phallothecal armature is greatly simplified. In Salyavatinae too the pygophore is absent while the phallothecal armature is highly elaborated. In Piratinae, the pygophore spine as well as the genocoxal spine (sub genital plate) are well developed (Pl. 2,4,6,8,10,12,14,16,18,20, 22,24 & 26) inspite of the fact that their phallothecal armature is as complex as in Salyavatinae.

Thus, on this account too, the Salyavatinae, the Ectrichodiinae and the Piratinae retain the plesiomorphic characters of the intromittent organ, in having an over exaggerated development of complicated armature and the Acanthaspidinae and Triatominae have more apomorphic features.

An overview of the origin and evolution of the ecosystems of Southern India, as outlined in the preface, will clearly suggest that the Tropical Rainforest ecosystem of Southern India, represented by isolated patches in the Western Ghats, still harbour a sizable variety of the reduviid fauna, retaining plesiomorphic features such as those cited above.
Livingstone and Ambrose (1978 and 1984) and Ambrose (1985), after having studied the biology of a number of species of Reduviidae collected from different ecosystems of this region concluded that the endemic species of the Reduviidae of the Tropical Rainforests could be identified by the following features. 1. Polyphagy (feeding on litterforms); 2. lack of tibiarolium in the fore and mid tibiae; 3. lifting of the prey while feeding and running to shelter; 4. congregational feeding; 5. bright colouration with predominance of reddishness; 6. predominantly arboreal and diurnal; 7. lack of nymphal camouflaging behaviour; 8. complex pre-copulatory riding behaviour before connection is achieved; 9. gluing of their eggs to the sustratum and cluster formation of eggs and 10. higher percentage of hatching, mostly during day time. All these characters are attributes of plesiomorphism.

From the present studies the more apical differentiation of the tibiarolium and the complexities of the armature of the stylets and intromittent organs are additional evidences in support of the theory that the endemic species of Reduviidae of the Tropical Rainforests manifest almost all the plesiomorphic features and as they gradually find their abode in drought prone ecosystems, they attain the apomorphic features such as the loss of complex armature of the stylets and phallotheca and increase in the extent of development of the tibiarolium on the fore and mid tibiae. Casual observations on the biology of such tibiaroliate reduviids also suggest that they are: 1. predominantly apterous; 2. if winged they manifest warning colouration with yellow and black spots; 3. increasingly monophagous; 4. mostly crepuscular; 5. majority of the species with well formed tibiarolium both on the fore and mid tibiae; 6. ovipositing solitary eggs haphazardly, without gluing materials and a few of them like the
Pirates and Catamiarus bury their eggs in the soil; 7. cannibalistic tendency highly developed and camouflaging developed in Acanthaspidinae and Salyavatinae; 8. rarely arboreal; 9. hatching percentage very low and hatching and emergence occur invariably at dusk or at night.

Thus it is apparently unequivocal to conclude that Salyavatinae represents the most primitive stock of the tibiaroliate group of Reduviidae and the Acanthaspidinae represents the most highly evolved group. The Piratinae, though it has evolved for a life in a drought prone ecosystem, it retains the more plesiomorphic features and the Ectrichodiinae, having retained its original abode in Tropical Rainforests habitats, has perfected well for myriophagy and congregational feeding. The Triatominae has succeeded in encroaching the habitats of the mammalian hosts and though it has discarded a raptorial tibiarolium, its piercing mechanism is well suited for vascular haematophagy and in that direction it has been highly specialized. However, a perusal of these structures in the nontibiaroliate group of Reduviidae of this region is most expedient before confirming the theory of co-evolution of the structures of these predatory insects and the ecosystems, as suggested in the present discourse.