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Biosystematics of Old World Triatominae

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Abstract

Morphometric analysis of Old World species of *Linshcosteus* and *Triatoma* showed the two genera to be well separated. However, although the analysis showed clear distinction between the five species of *Linshcosteus*, there was considerable overlap between the eight Old World species of *Triatoma*, including specimens of *T. rubrofasciata* from Old and New World populations. The results are interpreted as supporting the idea of a New World origin for the Old World species of *Triatoma*, with an independent Old World origin for *Linshcosteus*. © 1997 Elsevier Science B.V. All rights reserved

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1. Introduction

The 123 currently recognised species of Triatominae form a distinct subfamily within the Reduviidae, characterised by their obligate haematophagy and various adaptations associated with this habit (Schofield and Dolling, 1993). Several are important vectors of *Trypanosoma cruzi*, causative agent of Chagas disease or American trypanosomiasis (Lent and Wygodzinsky, 1979).

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Most species of Triatominae occur exclusively in the New World, between the great lakes of North America and southern Argentina (roughly between latitudes 42N and 46S). One species however, *Triatoma rubrofasciata*, occurs both in the New World (mainly North East Brazil) and is also recorded from tropical and subtropical port areas in many parts of the Old World. A further seven species of *Triatoma* are known only from Asia, as are the five species recognized within the genus *Linshcosteus* (Ghauri, 1976; Lent and Wygodzinsky, 1979; Ryckman and Archbold, 1981).

The origin of the Old World species of Triatominae has long been a subject of debate, centred around the question of a New World or Old World origin for the subfamily (Schofield, 1988). In this paper we report a morphometric study of the Old World species in an attempt to clarify this question.

2. Materials and methods

2.1. The insects

2.1.1. *Linshcosteus*

L. carnifex (Distant, 1904) is known only from the female (holotype, NHM collection) which was used in this study. The specimen bears a label reading 'E. India' but Distant (1904) indicates the specimen to be from North India.

L. chota (Lent and Wygodzinsky, 1979) is known only from the male (holotype, NHM collection) which was used in this study. This specimen is from South India and was previously labelled as the allotype of *L. carnifex*.

L. confumus (Ghauri, 1976), four specimens of this species (including the holotype) are in the NHM collection and were used in this study. All are from South India (Mysore) where the species (as *L. carnifex*) has been collected from under rocks (Sankaran and Nagaraja, 1975).

L. costalis (Ghauri, 1976), eight specimens from the NHM collection (including the holotype) were used in this study. They appear to be completely sympatric with *L. confumus* and to share the same microhabitat.

L. kali (Lent and Wygodzinsky, 1979), this species is recorded from several localities in South India. One specimen (NHM collection) was available for this study.

2.1.2. *Triatoma*

T. amicitiae (Lent, 1951), is known only from a single female (holotype, NHM collection) which was used in this study. The specimen is believed to have been collected in southern Sri Lanka (Monteith, 1974).

T. bowieri (Larrousse, 1924), has been reported from localities in the Philippines and Vietnam. We have not seen this species, and relied on morphometric data of Lent and Wygodzinsky (1979) for this analysis.

T. cavernicola (Else et al., 1977), is known only from bat caves in Northern Malaysia (Perlis). Four paratypes (NHM collection) were used in this study.

T. leopoldi (Schouteden, 1933) (= *novaeguineae* Miller, 1958), we have not seen this species, and relied on morphometric data of Lent and Wygodzinsky (1979) for this analysis. This species has been collected in Australia (North Queensland) and in Indonesia (West Irian, Sulawesi) (Monteith, 1974).

T. migrans (Breddin, 1903) (= *pallidula* Miller, 1941), has been recorded from localities in India, Indonesia, Malaysia, Phillipines and Thailand. Nineteen specimens (NHM collection) including the holotype of *pallidula*, were used in this study.

T. pugasi (Lent, 1953), this is a rare species recorded only from Java, Indonesia. The holotype (NHM collection) was used in this study.

T. rubrofasciata (De Geer, 1773), is widely distributed from port areas throughout the tropics and subtropics (for distribution records, see Ryckman and Archbold, 1981) although many records are old and may no longer represent the current distribution. *T. rubrofasciata* is also known from inland areas of North East India (Assam) and Brazil. We obtained three groups of this species as follows: group 1, 34 specimens in the NHM collection whose labels indicate the following Old World localities: Arabia, Ceylon, China, Malaya, Maldive islands, Okinawa, Siam, West Africa; group 2, 18 specimens from the Bishop Museum collection, Honolulu, whose labels indicate the following localities: Taiwan, Thailand, Philippine islands, Honolulu, South India; group 3, 15 specimens from the collection held at the Instituto Oswaldo Cruz (FIOCRUZ) Rio de Janeiro, comprising four specimens originally collected in the state of Paraiba, and 11 from the state of Rio de Janeiro, Brazil.

T. sinica (Hsaio, 1965), has been recorded only from China (Nanking). We have not seen this species and relied on morphometric data of Lent and Wygodzinsky (1979) for this analysis.

Table 1
Mean (mm) and standard error (se) of metric variables for species of *Linshcosteus*

Variable	<i>L. confusus</i> n = 4	<i>L. costalis</i> n = 8	<i>L. carnifex</i> n = 1	<i>L. kali</i> n = 1	<i>L. chota</i> n = 1
Body length	19.82 (0.54)	18.55 (0.58)	23.30 (—)	18.70 (—)	16.30 (—)
Protonum width	4.50 (0.07)	4.41 (0.14)	5.10 (—)	4.40 (—)	3.50 (—)
Abdomen width	8.97 (0.25)	8.54 (0.37)	9.70 (—)	8.50 (—)	5.70 (—)
Eye width:head length	0.36 (0.0048)	0.41 (0.0072)	0.47 (—)	0.39 (—)	0.38 (—)
Post-ocular length:protonum width	0.36 (0.016)	0.31 (0.013)	0.31 (—)	0.34 (—)	0.31 (—)
Synthlipis:eye width	2.73 (0.098)	2.11 (0.08)	1.79 (—)	2.33 (—)	2.70 (—)
Second rostral segment: first rostral segment	1.91 (0.036)	2.01 (0.051)	2.22 (—)	1.88 (—)	1.68 (—)
Third rostral seg- ment:first rostral seg- ment	0.56 (0.011)	0.62 (0.012)	0.54 (—)	0.59 (—)	0.44 (—)
Second rostral seg- ment:third rostral seg- ment	3.41 (0.011)	3.25 (0.053)	4.12 (—)	3.20 (—)	3.84 (—)

Table 2
Mean (mm) and standard error (se) of metric variables for Old World species of *Tritotoma*

Variable	<i>T. amicitiae</i>	<i>T. bouvieri</i>	<i>T. cavernicola</i>	<i>T. leopoldi</i>	<i>T. migrans</i>	<i>T. pugasi</i>	<i>T. sinica</i>
	n = 1	n = 1	n = 4	n = 1	n = 19	n = 1	n = 1
Body length	22.10 (—)	18.50 (—)	18.05 (0.86)	21.00 (—)	21.31 (1.65)	14.50 (—)	23.00 (—)
Protonum width	5.70 (—)	4.40 (—)	3.82 (0.10)	5.75 (—)	5.87 (0.46)	3.70 (—)	6.00 (—)
Abdomen width	9.00 (—)	7.50 (—)	6.60 (0.46)	8.50 (—)	8.19 (0.64)	6.30 (—)	9.00 (—)
Eye width:head length	0.53 (—)	0.70 (—)	0.59 (0.04)	0.60 (—)	0.62 (0.04)	0.55 (—)	0.07 (—)
Post-ocular length: protonum width	0.25 (—)	0.10 (—)	0.29 (0.05)	0.06 (—)	0.20 (0.03)	0.32 (—)	0.40 (—)
Synthlipsis: eye width	2.07 (—)	2.20 (—)	2.24 (0.42)	2.10 (—)	1.69 (0.21)	4.00 (—)	1.70 (—)
Second rostral segment:first rostral segment	1.28 (—)	1.60 (—)	1.53 (0.06)	1.50 (—)	1.44 (0.11)	1.33 (—)	1.50 (—)
Third rostral segment:first rostral segment	0.36 (—)	0.50 (—)	0.55 (0.02)	0.40 (—)	0.43 (0.05)	0.40 (—)	0.50 (—)
Second rostral segment:third rostral segment	3.51 (—)	3.20 (—)	2.79 (0.17)	3.75 (—)	3.43 (0.49)	3.33 (—)	3.00 (—)

2.2. Morphometric analysis

We carried out a discriminant analysis using the nine morphometric characters considered by Lent and Wygodzinsky (1979) as most relevant to triatomine classification: (ii) body length, (ii) pronotum width, (iii) abdomen width, (iv) ratio of eye width:head length, (v) ratio of post-ocular length:pronotum width, (vi) ratio of synthlipis:eye width, (vii) ratio of second rostral segment:first rostral segment, (viii) ratio of third rostral segment:first rostral segment and (ix) ratio of second rostral segment:third rostral segment. All measurements were made under the binocular microscope using a micrometer eyepiece (Tables 1–3).

Using these variables, we carried out discriminant analyses and UPGMA cluster analyses (Sneath and Sokal, 1973) using average taxonomic distances calculated from the standardised values for each of the above nine variables. *Linshcosteus* and *Triatoma* species were analysed together (Fig. 1) and separately (Figs. 2 and 3). The discriminant analysis calculates linear functions of the form: $DF = a*V1 + b*V2 + \dots + h*V9$, where $a-h$ are the coefficients and $V1-9$ are the metric variables, giving the maximum variance amongst the species groups. The method derives $n-1$ functions (where n is the number of variables) and, in general, the first two functions contained almost all the variability ($> 95\%$). The position of each of our specimens in the space defined by these discriminant functions is given in Figs. 1 and 2 and 3.

UPGMA cluster analysis to derive the phenograms was based on standardised values of the nine variables for each individual (Fig. 4), or standardised mean values for each species (Figs. 5 and 6), from which was calculated the average taxonomic distance according to the methods of Sneath and Sokal (1973). The *Triatoma* species were analysed twice, with the three groups of *rubrofasciata* specimens considered either separately (Fig. 5) or pooled (Fig. 6).

Table 3
Mean (mm) and standard error (se) of metric variables for the three groups of *Triatoma rubrofasciata*

Variable	NHM	Bishop Museum	FIOCRUZ	All groups
	$n = 34$	$n = 18$	$n = 15$	$n = 67$
Body length	20.03 (0.216)	20.59 (0.391)	17.13 (0.421)	19.75 (0.17)
Pronotum width	4.78 (0.303)	5.13 (0.403)	4.04 (0.417)	4.78 (0.04)
Abdomen width	7.01 (0.702)	7.45 (0.853)	5.48 (0.843)	6.94 (0.09)
Eye width:head length	0.61 (0.033)	0.61 (0.032)	0.60 (0.030)	0.60 (0.00)
Post-ocular length:pronotum width	0.26 (0.027)	0.24 (0.033)	0.26 (0.022)	0.25 (0.00)
Synthlipis:eye width	2.16 (0.396)	2.08 (0.326)	2.26 (0.325)	2.16 (0.04)
Second rostral segment:first rostral segment	1.62 (0.142)	1.55 (0.054)	1.52 (0.089)	1.58 (0.01)
Third rostral segment:first rostral segment	0.56 (0.057)	0.55 (0.034)	0.61 (0.033)	0.57 (0.01)
Second rostral segment:third rostral segment	2.91 (0.217)	2.80 (0.156)	2.49 (0.182)	2.80 (0.02)

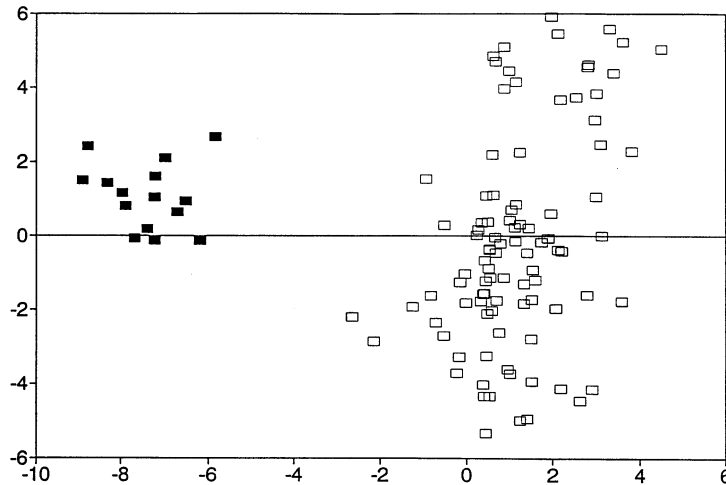


Fig. 1. Plot of *Linshcosteus* (■) and *Triatoma* (□) in the space defined by the first two discriminant functions.

3. Results

3.1. *Linshcosteus*

The discriminant analysis clearly separated *Linshcosteus* from *Triatoma* (Fig. 1) and showed that all five species of *Linshcosteus* could easily be classified without error (Fig. 2). Only one specimen each of *carnifex*, *chota* and *kali* was available, so that no measure of variability was possible for these species. However, their distance apart in the discriminant space leaves us in no doubt as to their taxonomic validity (Fig. 2). The average taxonomic distances defined by UPGMA clustering

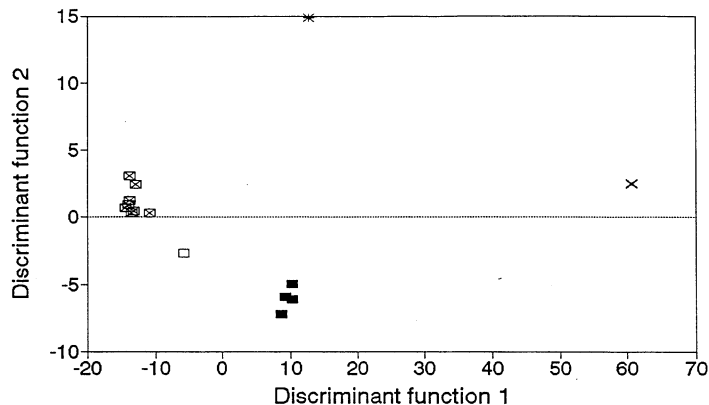


Fig. 2. Plot of *Linshcosteus* species in the space defined by their first two discriminant functions (■, *L. confumus*; ⊠, *L. costalis*; □, *L. kali*; ×, *L. chota*; *, *L. carnifex*).

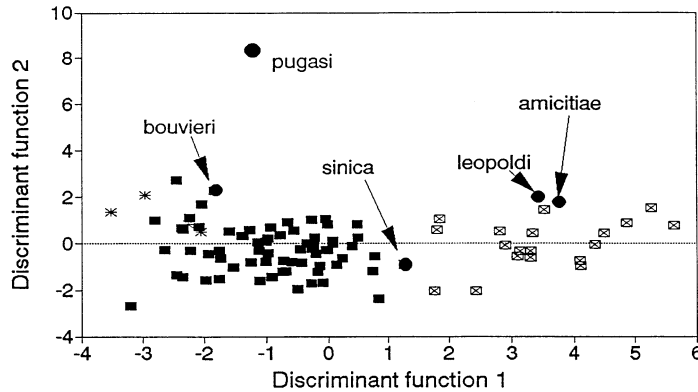


Fig. 3. Plot of *Triatoma* species in the space defined by their first two discriminant functions (■, *T. rubrofasciata* (all groups); ☒, *T. migrans*; *, *T. cavernicola*; other species as marked).

(Fig. 4) suggest *costalis* and *kali* to be the most closely related, with *chota* as the most dissimilar of the five species.

3.2. *Triatoma*

The discriminant analysis pooling the *rubrofasciata* specimens showed some overlap between species (Fig. 3). The analysis classified *amicitiaie*, *bouvieri*, *cavernicola*, *leopoldi*, *pugasi*, and *sinica* without error, but gave 7.5% error with *rubrofasciata* (6.5% misclassified as *cavernicola* and 1% as *sinica*) and 10.5% error with *migrans* (misclassified as *leopoldi*).

When our three groups of *rubrofasciata* were considered separately, the discriminant analysis showed even greater overlap. The analysis classified without error *amicitiaie*, *cavernicola*, *leopoldi*, *pugasi*, and the group 3 *rubrofasciata* (FIOCRUZ collection). However, there was 38.3% classification error for *rubrofasciata* of group 1 (NHM collection) (8.8% misclassified as *cavernicola*, 20.6% misclassified as group 2 *rubrofasciata*, and 8.8% misclassified as group 3 *rubrofasciata*), there was 16.7% classification error for *rubrofasciata* of group 2 (Bishop Museum) (5.5 and 5.5% as group 1 and 3, respectively), and there was 25% classification error for *rubrofasciata* of group 3 (Brazil) (misclassified as group 1). In addition, *migrans* was classified with 10.5% error (as *cavernicola*). Had more specimens been available, it is possible that even more overlap would have been apparent.

Average taxonomic distances defined by UPGMA clustering analysis (Fig. 5) suggest *cavernicola* to be very close to *rubrofasciata*, with *pugasi* as the most dissimilar of the eight species.

4. Discussion

The Reduviidae are currently considered to comprise over 6000 species grouped into 25 subfamilies and, on morphological and developmental characteristics, the position of the Triatominae as a subfamily of the Reduviidae is very clear (Maldonado Capriles, 1990). In general, the predatory reduviids are widespread throughout tropical and many temperate regions of the world, whereas the Triatominae are mainly restricted to the New World, being virtually absent from Africa and uncommon in Asia (Lent and Wygodzinsky, 1979; Ryckman and Archbold, 1981). The Old World species could plausibly have arisen there, or have been carried there in association with their vertebrate hosts. As suggested by Schofield (1988), we believe both processes to have occurred.

Our working hypothesis considers the Triatominae to represent a polyphyletic assemblage of blood-sucking Reduviidae, defined on the basis of their obligate haematophagy and the various apomorphic characters associated with this habit

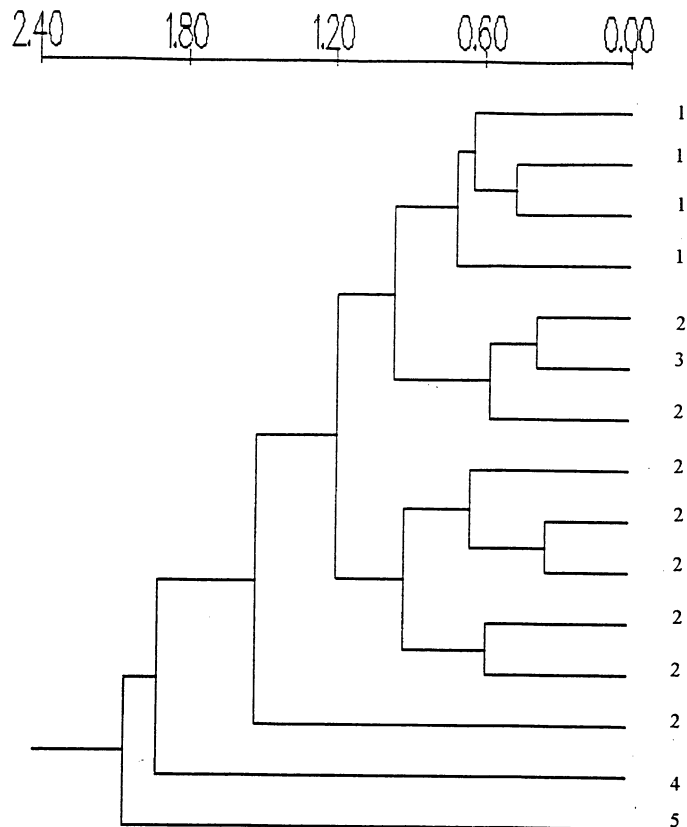


Fig. 4. Average taxonomic distances between individuals of *Linshcosteus* (1, *L. confumus*; 2, *L. costalis*; 3, *L. kali*; 4, *L. carnifex*; 5, *L. chota*).

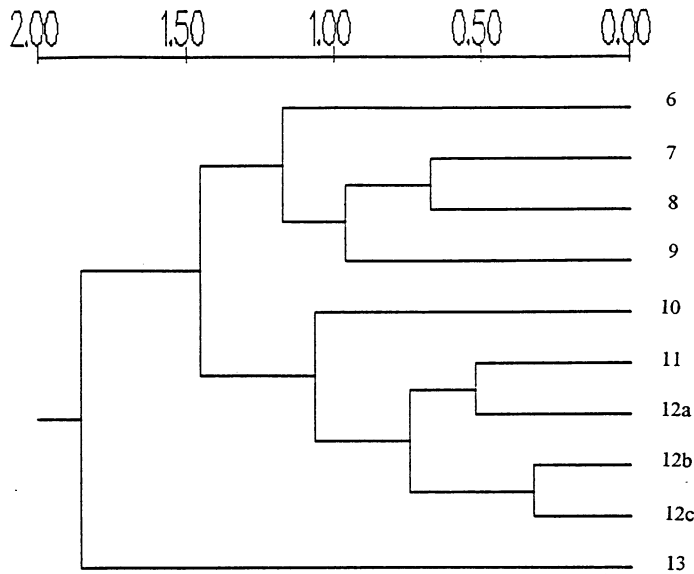


Fig. 5. Average taxonomic distances between Old World species of *Triatoma* (6, *T. amicittiae*; 7, *T. leopoldi*; 8, *T. migrans*; 9, *T. sinica*; 10, *T. bowieri*; 11, *T. cavernicola*; 12, *T. rubrofasciata* (12a, Brazil, FIOCRUZ collection; 12b, Bishop Museum collection; 12c, NHM collection); 13, *T. pugasi*.

(Schofield, 1988; Schofield and Dolling, 1993). We consider the diversity and worldwide distribution of the Reduviidae to indicate a very successful and long-established family of invertebrate predators. In contrast, we assume that adaptation to a blood-sucking habit has been relatively recent, associated with the evolution of nest-building mammals and birds which today represent the hosts of the majority of the Triatominae. The evolution of haematophagy within the Reduviidae is thought to be associated with progressive adaptation of ‘free-living’ predatory forms to occupy different vertebrate nests, exploiting firstly the guilds of invertebrates within those nests and then progressively adapting to exploit the host vertebrates themselves.

This hypothesis implies that the adaptive steps from ‘free-living’ predators to ‘nest-dwelling’ blood-suckers could have occurred several times, not just within different groups of the Reduviidae but also amongst other groups of Hemiptera. Within the Anthocorid line for example, a similar sequence of adaptations could have given rise to the Cimicidae (bedbugs) and to the Polytentidae (batbugs). Both of these are families of obligate blood-suckers, almost ectoparasites, with striking morphological similarities to the Anthocoridae. Most anthocorids are predators on other invertebrates but several of the nest-dwelling species, for example *Lyctocoris campestris*, are known to take vertebrate blood on occasion and are considered to be facultative intermediates between predatory and haematophagous forms (Usinger, 1966). Amongst the Triatominae, similar facultative intermediates are suggested by species such as *T. sordida*, *T. rubrovaria* and *T. rubrofasciata*, which

will feed from soft-bodied invertebrates on occasion (Abalos and Wygodzinsky, 1951; Kalshoven, 1970; Lent and Wygodzinsky, 1979), and by *Eratyrus mucronatus* whose early nymphal stages feed from invertebrates but whose later nymphs and adults are haematophagous (Miles et al., 1981).

It is of interest then, to compare the biogeographical diversity of these three groups of blood-sucking Hemiptera. Within the Triatominae, 123 species are now recognized, of which 110 species occur only in the New World¹ (Schofield and Dolling, 1993). Within the Cimicidae however, 76 of the 91 recognised species occur in Africa (Ryckman et al., 1981; Usinger, 1966). Amongst the Polyctenidae, only a single genus (with 16 species) occurs in the New World, while there are four genera (also with 16 species) in Africa and Asia (Ryckman and Sjogren, 1980) (see Table 4). On the basis of this diversity, even acknowledging distributional distortions due to passive transport by their vertebrate hosts, it seems reasonable to assume mainly Old World origins for at least the majority of the Cimicidae and Polyctenidae, compared to the New World origin of most of the Triatominae (Schofield, 1988).

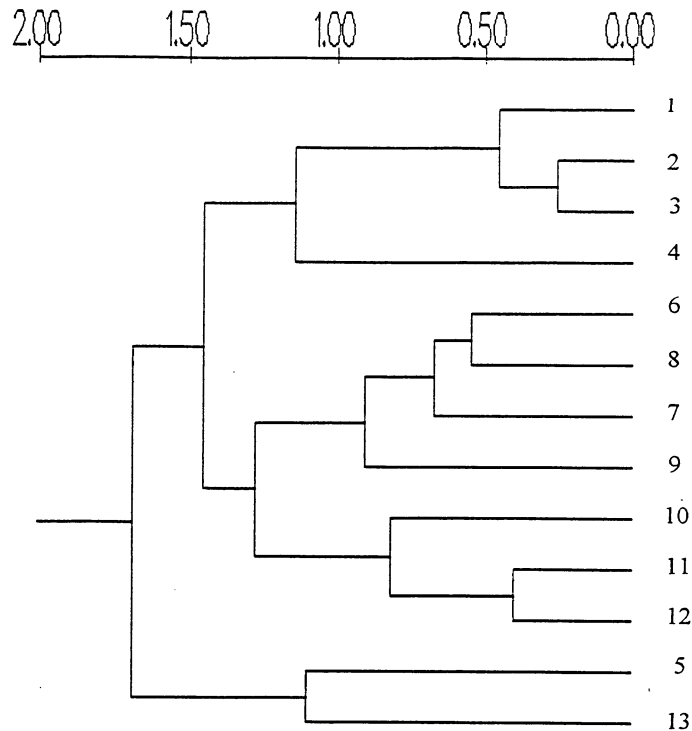


Fig. 6. Average taxonomic distances between Old World species of *Linshcosteus* and *Triatoma* (1, *L. confusus*; 2, *L. costalis*; 3, *L. kali*; 4, *L. carnifex*; 5, *L. chota*; 6, *T. amicittae*; 7, *T. leopoldi*; 8, *T. migrans*; 9, *T. sinica*; 10, *T. bouvieri*; 11, *T. cavernicola*; 12, *T. rubrofasciata* (all groups); 13, *T. pugasi*).

¹ Schofield and Dolling (1993) list 118 species of Triatominae, to which should now be added *Belminus laportei* (Lent et al., 1995), *B. pittieni* (Osuna and Ayala, 1993), *Rhodnius stali* (Lent et al., 1993), *Triatoma melanosoma* (Lent et al., 1994), and *T. gomeznuzei* (Martinez et al., 1994).

Table 4
Biogeographical diversity of blood-sucking Hemiptera

	Africa	Asia	Americas	Total ^a
Cimicidae				
Genera	11	8	14	23
Species	76	11	20	91
Polycetenidae				
Genera	3	4	1	5
Species	7	10	16	32
Triatominae				
Genera	1	2	13	14
Species	1	13	111	123

^a Note that some genera and species occur in more than one continent.

In the New World, species of Triatominae can be found in a very wide variety of habitats offering climatic shelter and regular access to a vertebrate blood source. These include silvatic habitats such as birdnests, armadillo burrows, bat caves, opossum lodges, and rockpiles inhabited by nest-building rodents, as well as peridomestic chicken coops, goat corrals and stables, and the domestic habitats occupied by man and his domestic animals. The most widely distributed and numerous of the 14 genera is *Triatoma* with 71 well-characterised species distributed from northern USA to southern Argentina. From their morphological affinities, these species can be ranked in a series of species groups, with the *rubrofasciata* group comprising the majority of *Triatoma* species, and occupying almost the entire geographic range of the genus (Lent and Wygodzinsky, 1979). Although many authors have assumed an Old World (oriental) origin for *T. rubrofasciata* (e.g. Lent and Wygodzinsky, 1979; Ryckman and Archbold, 1981) we consider this idea untenable, raising unanswerable questions about the subsequent evolution and diversification of the other New World species of the *rubrofasciata* group (Schofield, 1988). Instead, we interpret the morphological affinities of the group, their geographic range and habitat diversity, to indicate a New World origin. Our interpretation is also supported by the wide distribution of *T. rubrofasciata* itself in NE Brazil, even in areas distant from the coast, although, as pointed out by Ryckman and Archbold (1981) *T. rubrofasciata* has also been collected from inland areas in NE India (Assam).

T. rubrofasciata does provide the link between New and Old World *Triatoma*. This species has been recorded from many port areas throughout the Americas, Africa and Asia (Ryckman and Archbold, 1981). It is also widespread in the Northeastern Brazilian States of Maranhão, Paraíba, Pernambuco and Bahia, where it is mainly found in peridomestic habitats associated with sinanthropic rodents, especially *Rattus rattus* (Lent and Wygodzinsky, 1979). This close association with rats is confirmed by the frequent finding of bugs, from New and Old World sites, infected with *Trypanosoma conorhini*, a stercorarian trypanosome

normally transmitted between rats (e.g. Monteith, 1974; Morishita, 1935; Ghosh and Biswas, 1951; Hoare, 1972). The distributional records from port areas, and the association with *R. rattus*, are strongly suggestive of maritime dispersal of *T. rubrofasciata*, for example on sailing ships during the 17–19th century. North East Brazil, especially coastal Pernambuco, was settled by Dutch planters during the 17th century, and the first description of *T. rubrofasciata* was from specimens collected in the then Dutch East Indies during the 18th century (De Geer, 1773).

The other seven Asian species of *Triatoma* are also recorded from regions colonised by the Dutch and/or Portuguese during the 17–19th centuries. They share many morphological similarities with *T. rubrofasciata*, and are grouped by Lent and Wygodzinsky (1979) as the *rubrofasciata* complex (within the *rubrofasciata* group) characterised particularly by their distribution and by the intricate cuticular structure of the adult venter. Lent and Wygodzinsky (1979) conclude that ‘the highly derived integumental structure (of the *rubrofasciata* complex) suggests that this is a monophyletic group’. Our analysis, based on other morphological characters, supports the idea of a very close relationship between members of the *rubrofasciata* complex. It also indicates greater variability between groups of *T. rubrofasciata* than between *T. rubrofasciata* and *T. cavernicola* (Fig. 5), although from its cavernicolous habitat and yellowish colour patterns (characters not considered in our analysis) it is easy to distinguish *cavernicola* from *rubrofasciata*.

T. rubrofasciata is known to be a highly variable species, ranging from bright orange-red-marked specimens in south India (Gillett, 1934) to almost melanic forms in Hawaii (Lent and Wygodzinsky, 1979). It also has an unusually large chromosome complement of $2n = 25$ (22A + X1X2Y) (Manna, 1950, 1951) compared to the 18–20 autosomes of all other triatomine species so far studied (Panzeria et al., 1996), and shows several other characteristics considered to be primitive relative to other species (Schofield, 1988). For example, it will readily feed on soft-bodied invertebrates (Kalshoven, 1970) and its bite can be extremely painful to humans (Ryckman and Bentley, 1979) whereas the bite of the most specialised domesticated species such as *T. infestans* is usually barely perceptible (Lavoipierre et al., 1951; Schofield et al., 1986).

It is unfortunate that so many of the Old World species are known only from single specimens, and many are very old records, so it may be that further specimens will not be found. Nevertheless, we feel that this analysis of available material helps to support the idea of a New World origin for *Triatoma*, compared with an independent Old World origin for *Linshcosteus*. The latter has several features that clearly distinguish it from other Triatominae (Lent and Wygodzinsky, 1979) and the morphometric distinction between the genera is well confirmed by the present analysis. In contrast, we find considerable overlap between Old World species of *Triatoma* and *T. rubrofasciata*, to such an extent that it seems quite plausible that the Old World *Triatoma* could have arisen from isolated populations of *T. rubrofasciata* originating from the New World.

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