

SYSTEMATICS OF *TRIATOMA SORDIDA*, *T. GUASAYANA* AND *T. PATAGONICA* (HEMIPTERA, REDUVIIDAE)

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Because of the relative epidemiological significance of Triatoma sordida, T. guasayana and T. patagonica, and the need to resolve doubts about their taxonomic validity, we report here a detailed taxonomic comparison of the three species using multivariate analysis of morphometric measures combined with comparisons of their genitalia and antennal structures.

From the 17 metric variables studied, the length of the second segment of the rostrum and the anteocular length provided a discrimination function able to separate without error T. sordida from T. guasayana and T. patagonica. The multivariate discriminant functions classified T. guasayana and T. patagonica with an error of 2.44%. Comparison of the male genitalia of T. guasayana and T. sordida showed that there are minor differences in the articulatory apparatus, the median process of the pygophore, the phallosome support and the vesica, with bigger differences in the endosomal process and the phallosome. However, the already described male genitalia of T. patagonica is very similar to that of T. sordida. Analysis of antennal structure by scanning electron microscope showed that sensilla distribution around the pedicel is slightly different in the three species and sensilla density is highest in T. sordida and lowest in T. patagonica.

The study showed that the three species form a closely related group. The results confirm the earlier classification of sordida and guasayana as separate species, but they raise some doubts about the taxonomic status of T. patagonica.

Key words: Triatominae – systematics – *sordida* group

Triatoma sordida, *T. guasayana* and *T. patagonica* are morphologically similar species, widely distributed over the cerrado-chaco regions of open savanna-like vegetation of South America (Forattini et al., 1982, 1983; Silveira et al., 1984) (Fig. 1). They occupy a similar variety of sylvatic environments and are frequently reported from peridomestic and domestic habitats where they can act as vectors of *Trypanosoma cruzi* – causative agent of Chagas disease. *T. sordida* is common in chicken houses in Brazil and has been frequently found invading houses from which the primary vector of Chagas disease, *T. infestans*, has been eliminated (Dias, 1987, 1988). *T. guasayana* is common in peridomestic situa-

tions, such as chicken houses, pigeon coops and goat corrals, and *T. patagonica* has also been found in chicken houses and rabbit coops (Jörg, 1955; Lent & Wygodzinsky, 1979). Unpublished work at the Instituto Oswaldo Cruz shows that *sordida* and *guasayana* will interbreed in the laboratory, producing viable offspring, although we are unaware of any similar studies involving *T. patagonica*.

Available distribution records suggest considerable overlap between *T. sordida*, *T. guasayana* and *T. patagonica* throughout Argentina, and overlap between *T. sordida* and *T. guasayana* throughout Argentina, Bolivia, and Paraguay (Abalos & Wygodzinsky, 1951; Gonzalez & Agucro, 1967; Canese, 1978; Forattini et al., 1971, 1983; Silveira et al., 1984) which, combined with their morphological similarities, has cast doubts on the taxonomic status of these three species. A fourth species, *T. garciabesi*, was described from

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Received 3 November 1992.

Accepted 2 March 1993.

specimens from central Argentina (Carcavallo et al., 1967) but was subsequently synonymised with *T. sordida* by Lent & Wygodzinsky (1979), who considered that none of the chromatic and morphological characters used by Carcavallo et al. (1967) and Carcavallo & Martinez (1968) was sufficient to distinguish *garciabesi* from *sordida*.

Because of the relative epidemiological significance of *T. sordida*, *T. guasayana* and *T. patagonica* and the need to resolve doubts about their taxonomic validity, we report here a detailed taxonomic comparison of the three species using multivariate analysis of morphometric measures combined with comparisons of their genitalia and antennal structures.

MATERIALS AND METHODS

The specimens of *T. sordida* used in this study came from the collection of the British Museum (Natural History) (NHM) (16 individuals, 3 from Argentina, 1 from Bolivia, 7 from Brazil [2 from laboratory rearing] and 5 from Paraguay) and from the Reference Centre of Vectors and Hosts of the Servicio Nacional de Chagas (Argentina) (30 individuals, laboratory bred from bugs captured in sylvatic ecotopes near San Martín [Salta, Argentina]). The specimens of *T. guasayana* came from the collection of the NHM (9 individuals, all from Argentina) and from the Reference Centre of Vectors and Hosts of the Servicio Nacional de Chagas (Argentina) (32 individuals, laboratory bred from bugs captured in peridomestic habitats of Río Hondo [Santiago del Estero, Argentina]). The holotypes of these two species were also included in this study. The specimens of *T. patagonica* (6 individuals, including one syntype) came from the collection of the NHM, 3 laboratory reared in Brazil, syntype (Valle del Lago Blanco, Argentina) and 2 individuals collected in southern Argentina. The distribution of these localities is shown in Fig. 1.

The set of 17 variables (length measures) considered by Lent & Wygodzinsky (1979) as important in triatomine taxonomy were selected (Table). All measures were made with an image processing computing device (Videoplan) and a stereo microscope with a drawing tube. A multivariate discriminant analysis was carried out with the 17 variables which were standardized by subtracting the sample mean and dividing by the standard deviation.



Fig. 1: geographical distribution of *Triatoma patagonica* (dotted line), *T. guasayana* (broken line) and *T. sordida* (continuous line), derived from published collection records. Collection sites of material used in this study shown by filled triangles (*T. patagonica*), filled squares (*T. guasayana*) and open squares (*T. sordida*).

In the analysis of the genitalia, seven structures were studied: the paramere, the median process of the pygophore, the endosomal process, the articulatory apparatus, the phallosome, the phallosome support and the vesica. These structures were compared with the description of the genitalia reported by Abalos & Wygodzinsky (1951), and Lent & Jurberg (1978, 1980).

Analysis of antennal sensilla was carried out looking at the antennal pedicel (2nd segment) of three adult females of *T. sordida* and *T. guasayana* and two of *T. patagonica* under scanning electronic microscope (HITACHI S 2500). The pedicels were cleaned with ultrasound and sputter-coated with gold-palladium. The tip, middle and base of the pedicel were considered separately. For each zone, one picture of one quarter of the circumference of the antenna was taken, so that the upper, lower, inner and outer regions were considered separately. Sensilla density is presented as the average of the number counted in an area of $10^4 \mu\text{m}^2$.

TABLE

Summary statistics of the 17 variables measured in *T. sordida*, *T. guasayana*, and *T. patagonica*. The figures represent mean (range) in mm. Sample sizes: 44, 41 and 6 respectively

Variable	<i>T. sordida</i>	<i>T. guasayana</i>	<i>T. patagonica</i>
Body length	17.83 (16.14-20.44)	17.53 (15.22-20.31)	18.57 (17.1-19.2)
Pronotum width	4.09 (3.54-4.95)	3.91 (3.40-4.37)	4.22 (3.8-4.4)
Pronotum length	5.94 (5.08-7.02)	5.85 (4.65-8.00)	6.65 (6.0-7.1)
Abdomen width	6.53 (5.11-7.91)	6.79 (5.11-8.92)	6.97 (5.7-7.7)
Abdomen length	9.78 (8.45-11.98)	9.43 (7.83-11.45)	9.75 (8.5-10.8)
Wide across the eyes	3.93 (3.57-4.41)	3.88 (3.30-4.38)	3.83 (3.7-4.0)
Anteocular length	4.18 (3.61-4.81)	4.53 (3.87-5.06)	4.86 (4.5-5.1)
Post ocular length	1.34 (0.87-1.75)	1.47 (1.12-1.77)	1.30 (1.0-1.5)
1st antennal segment	1.49 (1.26-1.73)	1.43 (1.15-1.82)	1.18 (0.8-1.5)
2nd antennal segment	5.54 (4.80-6.24)	5.83 (4.83-6.39)	5.70 (5.2-6.1)
Head length	7.00 (6.30-7.72)	7.25 (6.39-8.26)	7.82 (7.2-8.4)
Eye width	3.17 (2.38-4.12)	2.98 (2.37-3.51)	2.53 (2.2-3.0)
Synthlipsis	4.06 (3.43-4.76)	4.28 (3.26-5.24)	4.28 (3.7-5.0)
1st rostral segment	4.46 (3.64-5.68)	5.09 (4.45-5.86)	5.95 (5.3-6.7)
2nd rostral segment	11.39 (9.68-13.76)	9.65 (8.29-10.89)	10.31 (10.0-11.0)
3rd rostral segment	5.65 (4.79-7.16)	5.71 (4.59-6.88)	5.98 (5.8-6.1)
Femur width	3.27 (2.71-4.29)	2.88 (2.14-3.35)	3.12 (2.8-3.3)

RESULTS

In the material of *T. sordida* and *T. guasayana* examined, the posterior lobe of the pronotum showed high variability in colour and pattern. According to the dichotomous key of Lent & Wygodzinsky (1979), *T. guasayana* should have a uniformly dark posterior lobe of the pronotum as shown by the holotype specimen. However, only 61% of our material (25/41) showed this feature. The rest had other patterns, with whitish or yellowish spots, and 15% (6/41) showed 2 white spots in this region. *T. sordida*, in turn, should show 2 white spots in the posterior lobe of the pronotum (Lent & Wygodzinsky, 1979) as easily seen in the holotype specimen, but only 25% (11/44) of our material showed this. Although none of the *T. sordida* showed a uniformly coloured

pronotum, 11% showed extremely weak whitish spots, giving the appearance of the uniformly dark pronotum of *T. guasayana*. According to the same key, *T. guasayana* should show dark coxae, and *T. sordida* yellow ones; among the specimens studied the trend was coincident with this, but some individuals showed the colour pattern corresponding to the other species. The colouration pattern of all the *T. patagonica* specimens fitted the descriptions of Abalos & Wigodzinsky (1951) and Lent & Wygodzinsky (1979), i.e. uniformly dark legs, dark bodies and characteristic dark spots in the conxivium.

The basic statistics of the 17 metric variables show that the species share the same range for almost all the features (Table). A discriminant analysis between *T. sordida* and

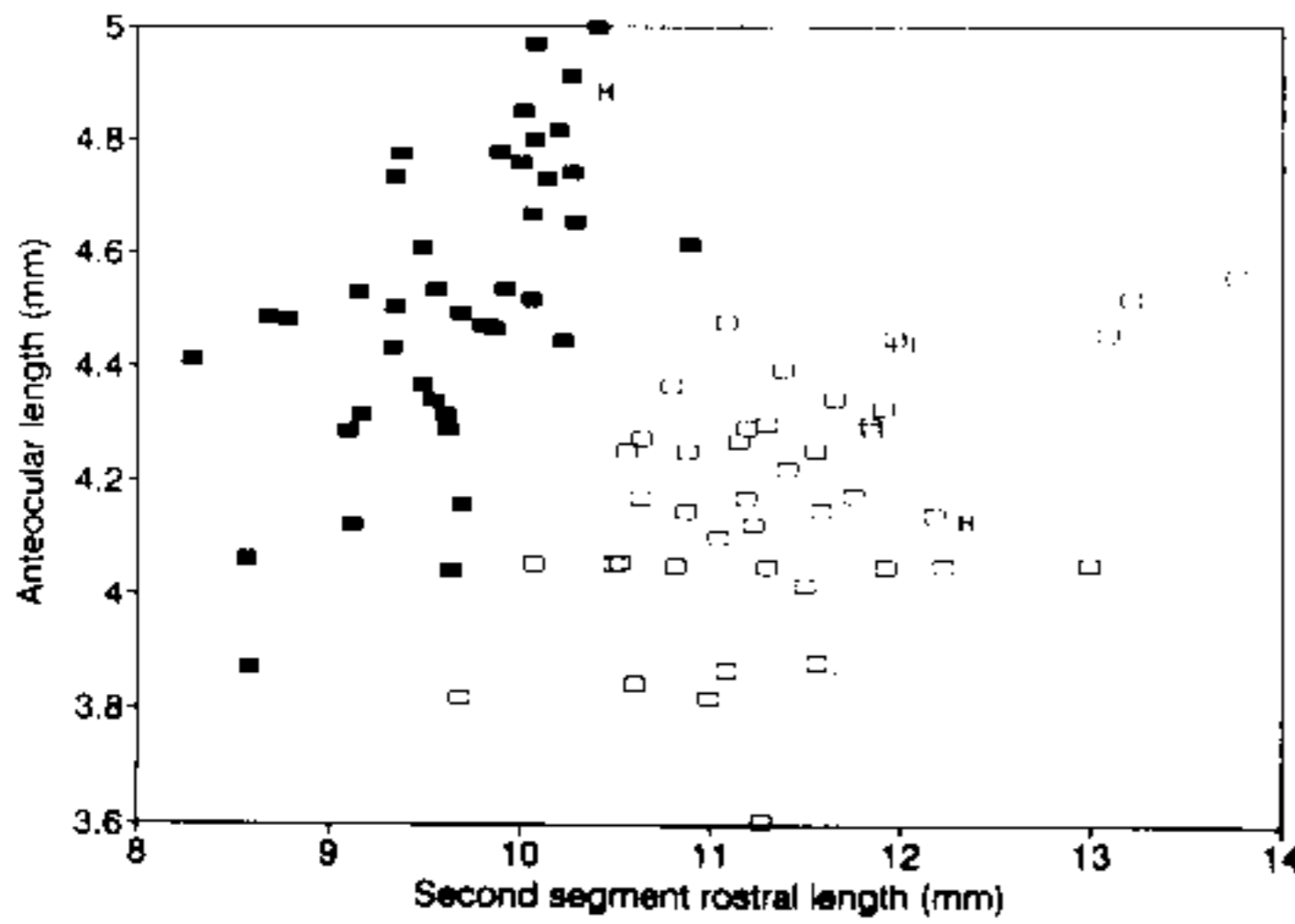


Fig. 2: relationship between the anteocular length and the 2nd rostral segment length *Triatoma guasayana* (■) and *T. sordida* (□). "H" shows positions of the holotype specimens.

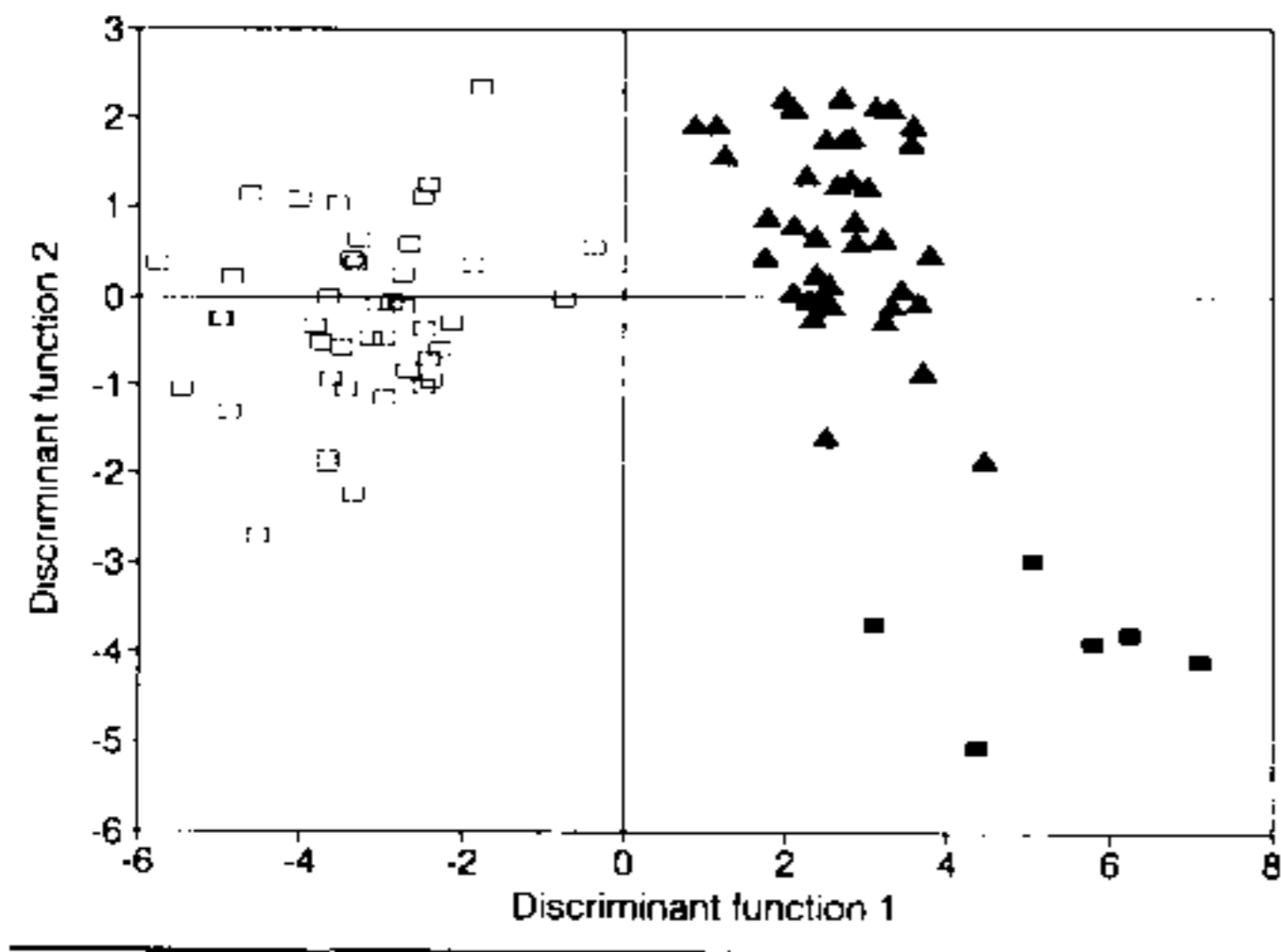


Fig. 3: discriminant analysis of *Triatoma sordida* (□), *T. guasayana* (▲) and *T. patagonica* (■) using 14 morphometric variables.

T. guasayana showed a canonical correlation of 0.927 and a function that classified the specimens without error. Consideration of the standardized discriminant function coefficients showed that the second rostral segment and the anteocular length were the most important distinguishing features. A discriminant analysis with just these two variables showed a canonical correlation of 0.899, and gave another function that classified the specimens without error. This discriminant function (df) had the form $df = -0.813 + 3.901 * \text{anteocular length} - 1.528 * \text{2nd rostral segment length}$. If the function value is greater than 0, the specimen should be classified as *T. guasayana*; if the function value is less than 0, the specimen is *T. sordida* (Fig. 2).

The discriminant analysis for the three species was carried out with 14 of the 17 variables (1st and 2nd antennal segment and femur width were not used because some specimens did not have those parts). The analysis gave two discriminant functions, the first giving a canonical correlation of 0.955, and the second 0.765. The state space defined by these two functions could discriminate between *sordida* and the other two species, but could not completely separate *guasayana* from *patagonica* giving a classification error of 2.44% (Fig. 3). Reducing the number of variables in the analysis led to increasing errors in the species classification.

The comparison of male genitalia showed minor differences between *T. sordida* and *T. guasayana* in six of the seven structures studied. The parameres were similar, but in *T. sordida* the median process of the pygophore was more rounded, the articulatory apparatus was longer, the endosomal process was thinner with teeth only on its apex (as opposed to being more generally distributed in *T. guasayana*) and the vesica shorter. More conspicuous differences were found in the phallosome and phallosome support. In *T. sordida*, the phallosome was longer with a depressed apex and the phallosome support was longer and thinner. In *T. guasayana* the process of the endosome was wider and with teeth over its whole area, the phallosome was shorter and wider with 1+1 apical projections, and the phallosome support was shorter and wider. However, comparison of the genitalia of *T. patagonica* described by Abalos & Wygodzinsky (1951) showed greater similarity to *T. sordida* genitalia, especially regarding the distribution of teeth over the endosomal process.

Regarding the antennal study, the same types of sensilla were observed in the three species. Sensilla density was higher in *T. sordida* (mean = 7.34, s.d. = 1.26) than in the other two species (*guasayana*: mean = 5.51, s.d. = 0.28; *patagonica*: mean = 5.47, s.d. = 0.13) ($P = 0.046$; $F = 6.10$, Anova) (Fig. 4). No difference in trichobothria number was found. This character, which had been suggested as a possible character of importance by Lent & Wygodzinsky, 1979) was found to vary among individuals (between 6-7 trichobothria per antenna), and occasionally between right and left antenna of the same individual.

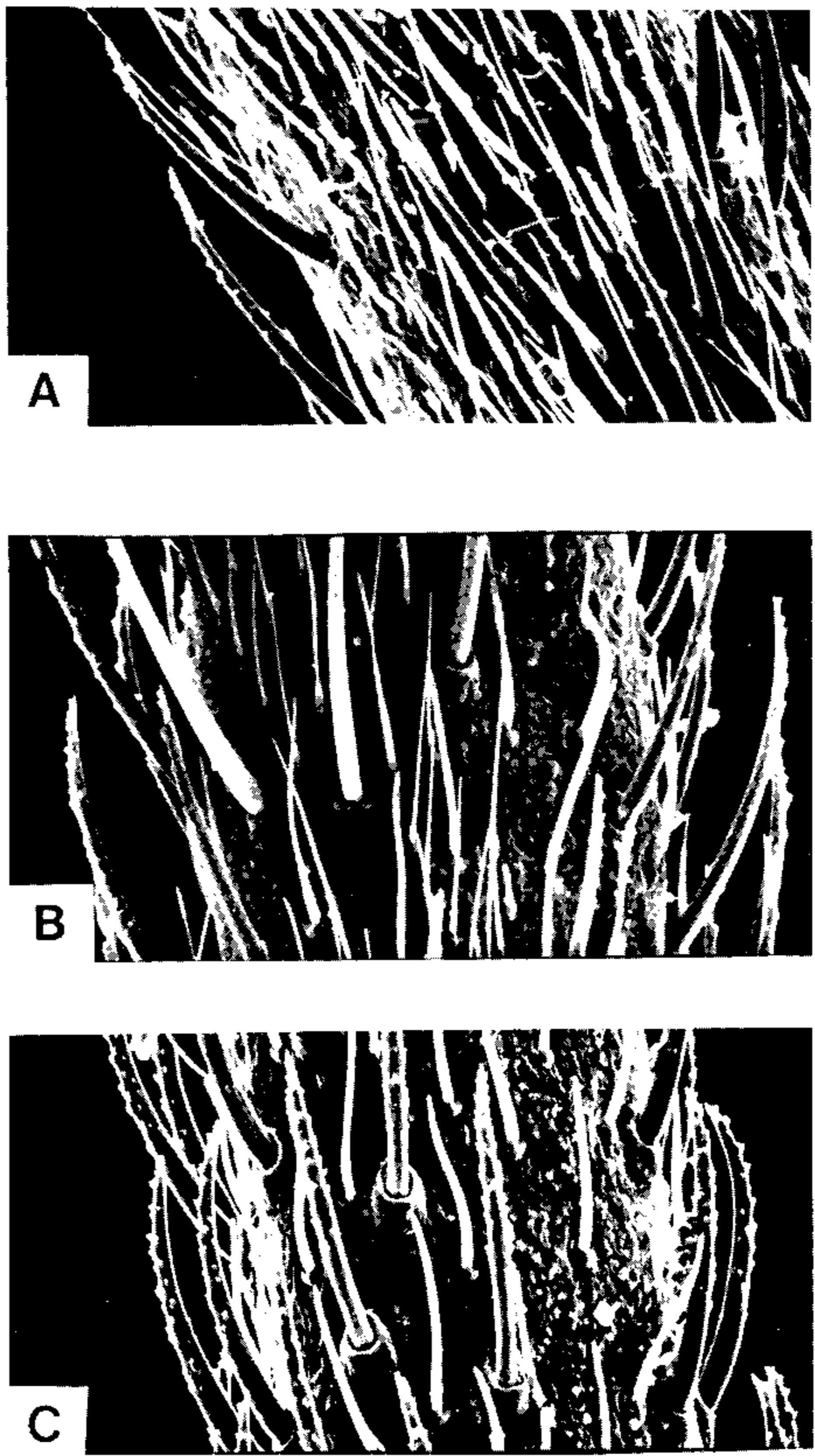


Fig. 4: lower face of the middle pedicel on *Triatoma sordida* (a), *T. guasayana* (b) and *T. patagonica* (c) as seen by SEM (all x300).

DISCUSSION

As pointed out by Abalos & Wygodzinsky (1951), *T. sordida* and *T. guasayana* have been frequently confused with each other. This is not surprising given their morphological similarity and overlapping distribution. Pattern and colour differences appear too variable for reliable discrimination between these species. Instead, the relative length of the second rostral segment may be used (more than twice as long as the first in *sordida*, less than twice as

long in *guasayana*) (Lent & Wygodzinsky, 1979). In contrast, there are no reports on confusion of *T. patagonica* with *T. sordida* or *T. guasayana*, probably because of the difference in the chromatic pattern.

In Brazil, where *T. guasayana* has not been recorded, the distribution of *T. sordida* is given in detail by Silveira et al. (1984). However, neither the southern limits of *sordida* nor the limits to the distribution of *guasayana* are known with certainty, and many early distri-

bution records are questionable. So too are widely-quoted records of finding the two species together in the same habitat. Such claims may result from finding individuals with minor colour or pattern differences alone. Similar uncertainties exist concerning the geographic distribution of *T. patagonica*, especially for the northern limit because of probable confusion with *T. guasayana* specimens as its chromatic pattern changes to lighter coloured individuals towards the tropical semiarid areas (Lent & Wygodzinsky, 1979).

In central and southern Brazil, *T. sordida* has been collected from a variety of sylvatic habitats, particularly bird nests, tree holes and under loose bark. It is common in peridomestic situations – especially in chicken houses. Such habitats are suggestive of a primary association with avian hosts, and studies by Rocha e Silva et al. (1977) concluded that *sordida* has a marked preference for avian blood. Although it frequently invades houses where it feeds readily on mammalian as well as bird hosts (C. Wisnivesky-Colli, unpublished), *sordida* seems to be quickly displaced by more domesticated species such as *T. infestans* (Schofield, 1980) – possibly due to its much slower development time (Juarez & Castro Silva, 1982). However, in parallel with concerted control efforts against *T. infestans* populations, *sordida* has now become more frequently recorded from domestic and peridomestic habitats in Brazil (Dias, 1987, 1988; Filho & Silveira, 1979; Silveira et al., 1984).

T. guasayana has also been collected from a wide variety of sylvatic habitats – under loose bark, under rocks with rodents and toads, under fallen trees with lizards, and in some bird nests. In central and northern Argentina it seems common amongst brushwood and rockpiles frequented by wild guinea-pigs. *T. guasayana* is also common in peridomestic situations – particularly goat corrals, chicken houses, and pigeon coops – and, like *sordida*, will also colonise houses.

Although no doubts have been reported about the taxonomic status of *T. patagonica*, there is agreement that it is very similar to *T. sordida* and *T. guasayana* (Abalos & Wygodzinsky, 1951; Lent & Wygodzinsky, 1979), except for the chromatic patterns that give the basis for the existing taxonomic keys. However, as several authors pointed out, colouration pattern is highly variable in *T. patagonica*,

showing darker specimens in the southeastern individuals and lighter coloured specimens further north. So at present, the taxonomic status of *T. patagonica* seems to be weak, as the only characters that separate it from *T. guasayana* is the greater number of teeth on the endosome process (which has been examined in very few specimens). The three species have all similar habitats and hosts, all have been found naturally infected with *Trypanosoma cruzi* (causative agent of Chagas disease), and all of them are considered competent vectors (Lent & Wygodzinsky, 1979).

The three species clearly form a very closely related group, and with a trend to lighter coloured individuals towards the north and darker ones towards the south. In spite of their morphological and biological similarities, our results confirm the earlier classification of *sordida* and *guasayana* as separate species, but they raise some doubts about the taxonomic status of *T. patagonica*, indicating that more data are needed to clarify the relationship. The three species occupy a very wide geographic range, from northern Brazil (5° S), to south Argentina (42° S). If they have a recent common ancestor (Schofield, 1988), how did they become so widely distributed?

One possibility is that they dispersed passively with their hosts (as is very well known for *T. infestans* among household belongings, and for *Rhodnius prolixus* whose eggs are sometimes attached to the feathers of migratory birds). Eggs and small nymphs of *T. sordida* have been encountered in the plumage of house sparrows in Brazil (Forattini et al., 1971) but, among the variety of wild hosts associated with *sordida*, *guasayana* and *patagonica*, none is known to have migratory habits, that could explain their current distribution.

Another possibility is that they dispersed actively, by flight. Although there are no published flight records for *T. guasayana* or *T. patagonica*, field and laboratory studies have demonstrated that under favourable climatic conditions *T. sordida* has a higher dispersive capacity than *T. infestans* and is able to fly longer distances (McEwen, 1991; Schofield et al., 1991). Following from the conclusions of Forattini et al. (1982), that *T. sordida* originated in the central cerrado of Brazil, we would speculate that its subsequent dispersal southwards brought contact with a new host – guinea

pigs – promoting minor evolutionary modifications (*guasayana*) which became progressively more accentuated further southwards (*patagonica*). Under this hypothesis, *sordida* would be evolutionary ‘oldest’ and *patagonica* ‘youngest’ of the group, a hypothesis which may be amenable to further analysis by DNA studies.

ACKNOWLEDGEMENTS

To Dr R. Blackman (NHM) for use of the image processor, to the Servicio Nacional de Chagas (Argentina) and to Dr Patricia Munday for providing specimens, to Instituto Miguel Lillo and the Museum für Naturkunde der Humboldt (Universität zu Berlin) for the loan of *T. guasayana* and *T. sordida* types and to the Electron Microscope Unit staff of the NHM.

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