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THE TICK VECTORS OF *COWDRIA RUMINANTIUM* (IXODOIDEA, IXODIDAE, GENUS *AMBLYOMMA*) AND THEIR DISTRIBUTION

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ABSTRACT

WALKER, JANE B., with illustrations by OLWAGE, A., 1987. The tick vectors of *Cowdria ruminantium* (Ixodoidea, Ixodidae, genus *Amblyomma*) and their distribution. *Onderstepoort Journal of Veterinary Research*, 54, 353–379 (1987).

Twelve species of *Amblyomma* are presently known to be capable of transmitting *Cowdria ruminantium*. Of these *A. variegatum* is the most important and widely distributed vector in Africa. It has also extended its range considerably outside this continent, eastwards to the Yemen Arab Republic and to the islands of Madagascar, Réunion and Mauritius, and westwards to the Cape Verde islands and to some of the West Indian islands. *A. hebraeum* is probably the only field vector in most parts of southern Africa. A 3rd species, *A. lepidum*, is known to have been involved in field outbreaks of heartwater in the Sudan. Two other species are also currently regarded as field vectors of *Cowdria*: *A. astrion* on the islands of São Tomé and Principe, and *A. pomposum* in Angola. Another 5 African species (*A. cohaerens*, *A. gemma*, *A. tholloni*, *A. sparsum* and *A. marmoreum*) have proved to be capable of transmitting heartwater in the laboratory, as have 2 American species (*A. maculatum* and *A. cajennense*), but none of these ticks have been implicated in field outbreaks of the disease.

INTRODUCTION

This paper is dedicated with respect and affection to the memory of 3 of my old colleagues and friends: Gertrud Theiler (11 September 1897–2 May 1986) of Onderstepoort; Harry Hoogstraal (24 February 1917–24 February 1986) of NAMRU$_3$, Cairo, and Glen M. Kohls (23 October 1905–3 August 1986) of the Rocky Mountain Laboratories, Hamilton, Montana.

Gertrud Theiler was the pioneer of studies on the zoogeography of African ticks and the work presented in this paper was built on foundations that she laid. Glen Kohls made most, but not all, of his contributions to our knowledge of ticks in his studies on the New World species, some of which will be mentioned later.

Harry Hoogstraal needs no introduction to anyone who has even heard of ticks or tickborne diseases. He was described by Keirans (1986) as: "one of the outstanding medical entomologists of this or any generation and, without question, the greatest authority on ticks and tickborne diseases who ever lived". I should like to begin this paper with the short story with which he opened his Presidential Address to the American Society of Parasitologists in August 1985: "Two scientists, Joan and John, were strolling on the beach one sunny day. Suddenly something scurried in the sand beside their feet. 'What's that?' asked John. 'Why, don't you know', Joan replied, 'that's a sandcrab . . . you've been studying its synapses for four years' " (Hoogstraal, 1985). The moral of that story is obvious: although a full understanding of heartwater undoubtedly demands ever-increasingly sophisticated laboratory studies the control of this disease in the field will depend also on a thorough knowledge of the natural history of its vectors. This paper deals simply with their distribution.

SOURCES OF INFORMATION

Africa, Yemen Arab Republic and Madagascar

Information on the distribution of the *Amblyomma* species occurring in the Afrotropical region as a whole (Fig. 1) is given in Theiler (1962), Morel (1969) and Keirans (1985). Records of those species that occur in West Africa were plotted primarily from Morel (1969). The following publications, listed under the countries (Fig. 1) to which they refer, were also consulted:

Angola (Sousa Dias, 1950; Serrano, 1963).

Botswana (Walker, Mehlitz & Jones, 1978; Paine, 1982).

Ethiopia (Morel, 1980; Pegram, Hoogstraal & Wassef, 1981).

Kenya (Walker, 1974; FAO, 1975).

Madagascar (Uilenberg, Hoogstraal & Klein, 1979).

Mozambique (Santos Dias, 1960).

Somali Democratic Republic (Pegram, 1976).

Sudan (Hoogstraal, 1956; Karrar, 1960, 1966).

Tanzania (Yeoman & Walker, 1967).

Uganda (Matthysse & Colbo, 1987).

Yemen Arab Republic (Pegram, Hoogstraal & Wassef, 1982).

Zaïre (Elbl & Anastos, 1966).

Zambia (MacLeod, 1970; MacLeod & Colbo, 1976; MacLeod, Colbo, Madbouly & Mwanaumo, 1977; MacLeod & Mwanaumo, 1978; Pegram, Perry, Musisi & Mwanaumo, 1986).

Zimbabwe (Norval, 1983).

North and South America and the West Indies

My basic reference for information on the distribution of the 2 potential vectors of heartwater in the New World, *A. maculatum* and *A. cajennense*, was Doss, Farr, Roach & Anastos, 1978. Further details were obtained from Bishopp & Hixson, 1936, Cooley & Kohls, 1944; Hoffmann, 1962; Jones, Clifford, Keirans & Kohls, 1972; Ivancovich, 1973; Strickland, Gerrish, Hourrigan & Schubert, 1976; Guglielmone & Hadani, 1982; Guglielmone, Mangold & Hadani, 1982, and Uilenberg, Barré, Camus, Burridge & Garris, 1984.

RESULTS

***Amblyomma variegatum* (Fig. 2–6)**

Of the 12 species of *Amblyomma* known to be capable of transmitting *Cowdria ruminantium* the tropical bont tick is undoubtedly the most important. Not only is it an extremely efficient vector but it is also far more widely distributed than any of the other species.

In Africa *A. variegatum* occurs south of the Sahel regional transition zone (White, 1983, Fig. 1), right across the continent from Senegal through West Africa, the Central African Republic, southern Sudan and Ethiopia to the extreme north-western tip of Somalia. It is excluded by the aridity of the environment from most

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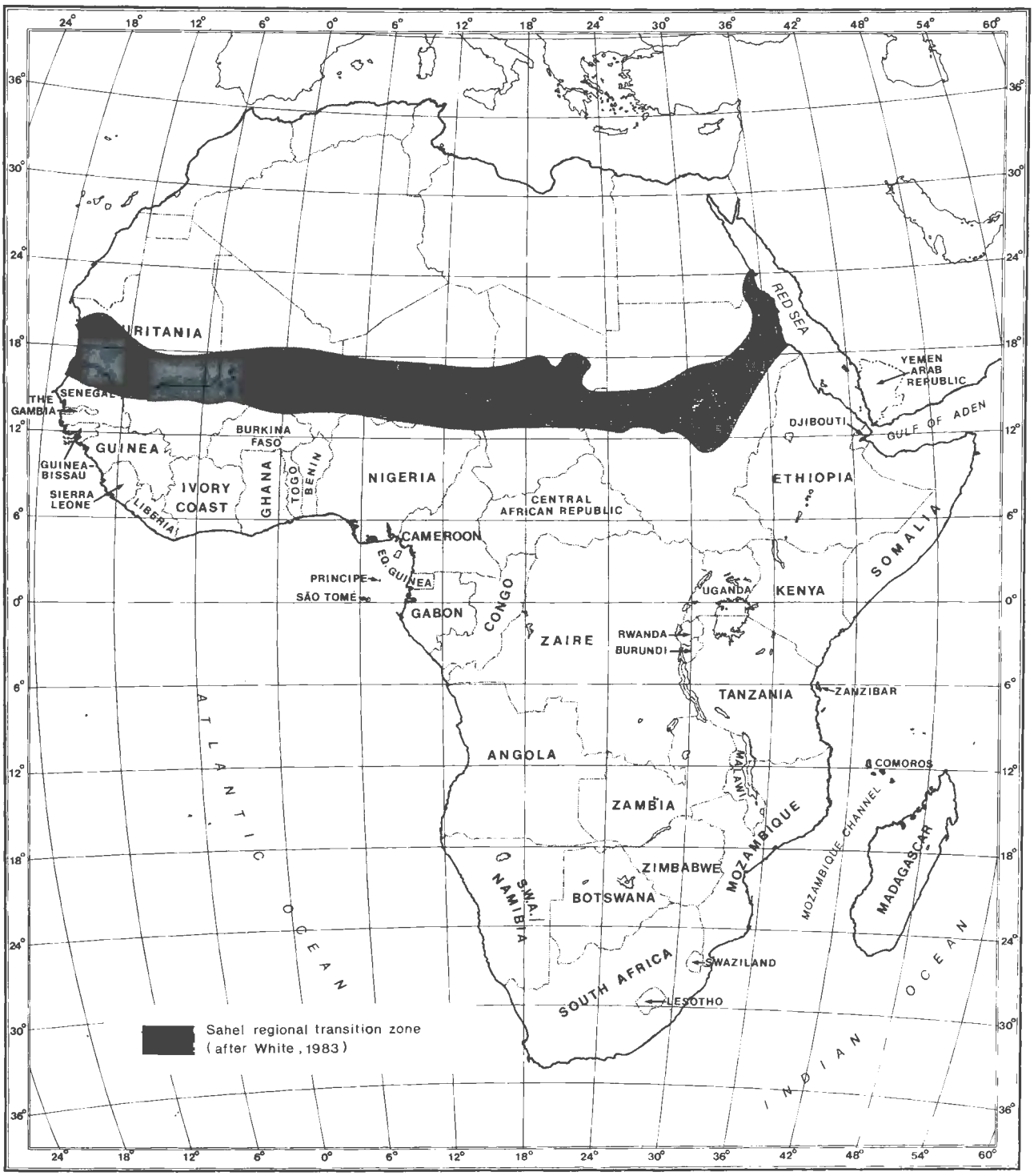

FIG. 1 Political divisions in the Afrotropical region, the Yemen Arab Republic and Madagascar

parts of the horn of Africa, comprising the greater part of Somalia, south-eastern Ethiopia and northern Kenya. It is prevalent in most of East Africa, as it is in Rwanda, Burundi, Malawi, much of Zambia, and eastern Angola. [Note that in Purnell (1984, Fig. 1) the names *A. variegatum* and *A. pomposum* in the key were inadvertently switched (Purnell, personal communication, 1986)]. South of Zambia its range extends through the Caprivi strip into the extreme north-eastern corner of Botswana and thence into north-western Zimbabwe, where it overlaps *A. hebraeum*.

In the case of Mozambique there is a difference of opinion that remains to be resolved regarding the identity of the *Amblyomma* species present. Despite the findings of Theiler & Salisbury (1959) and Tendeiro (1963), amongst others, regarding the taxonomy of the *A. variegatum* group, Dr Santos Dias still thinks that *A. variegatum* itself is confined to a few areas in the north of the country and that the tick he calls *A. pomposum* is the more prevalent species, ranging from the northern boundary with Tanzania on the Ruvuma River to approximately latitude 22° S. There is no doubt that this entity, which is thought to be the one described as *A. variegatum* var. *nocens* by Robinson (1926) and subsequently discussed by Theiler & Robsinson (1959) and Tendeiro (1963), does differ somewhat morphologically from what is regarded as typical *A. variegatum*. But whether it really is a separate species, or subspecies, or whether its

morphological differences are merely manifestations of clinal variation, remains to be determined. It occurs in some parts of southern Tanzania and the eastern border areas of Zimbabwe as well as in Mozambique. On Fig. 4 it has been mapped as *A. variegatum*.

A few of the empty areas on the map within the distribution zone shown in Africa for *A. variegatum* (Fig. 4) deserve special mention. The 2 blank areas in Tanzania coincide with parts of that country's major tsetse-infested woodland areas. Cattle, sheep and goats are virtually absent from these, consequently tick collections were not made there during the Tanzania survey (Yeoman & Walker, 1967). In various other countries from which there are as yet relatively few collections of this tick, for example Zaïre, the Central African Republic, the Congo Republic and Gabon, domestic animal populations are also relatively small (Schoenherr & Dobath, 1969). In addition there are few veterinary personnel and communications are on the whole poor. So it must not be assumed that an absence of records of *A. variegatum* in a particular area necessarily means that it is ecologically unsuitable for the tick. A variety of factors may militate against the accuracy of the distribution picture shown here.

A. variegatum is as yet the only African vector of heartwater that has established itself extremely successfully outside this continent. In the Yemen Arab Republic it has been recorded in a number of localities. It is thought to have been introduced into Madagascar, where it was first recorded by Neumann (1899), with cattle imported from Africa and now occurs virtually throughout the island (Uilenberg *et al.*, 1979). In the extreme south-west of the country, though, the rainfall is extremely low and G. Uilenberg (personal communication, 1986) said it would be surprising if the tick could survive there. He also questioned its presence in he highlands and in the eastern coastal zone of rain forest (indicated on Fig. 4 by smaller symbols). It has also been recorded from the Indian Ocean islands of Grande Comore, one of the Comoros Islands (J. B. Walker, unpublished data, 1987); Réunion (Neumann, 1911) and Mauritius [Moutia & Mamet (1947); Webb, Nadeau & Maurice (1963), both references cited by Doss *et al.*, 1978].

West of the African continent Doss *et al.* (1978) quote several references to the presence of *A. variegatum* on the Cape Verde Islands. Its introduction to, and subsequent establishment on, islands in the eastern Caribbean has been well documented by Uilenberg *et al.* (1984). They comment: "It has now been found on Guadeloupe (Grande Terre and Basse Terre), Antigua, Martinique, St. Croix, Puerto Rico, St. Lucia, Nevis, Galante and La Désirade. All of these islands are probably still infested today, except possibly St. Croix and La Désirade".

Fortunately *A. variegatum* has not as yet managed to spread to the American mainland, either north or south. Should it ever do so, though, Sutherst & Maywald (1985), who developed the computer-based CLIMEX system for matching climates in ecology, have predicted that it would find conditions to its liking in many parts of the continent, and in other parts of the world. The accompanying updated version of their CLIMEX map for this species (Fig. 6) is reproduced with the kind permission of these authors.

Further information regarding *A. variegatum* in the western hemisphere is given by Barré, Uilenberg, Morel & Camus (1987).

Amblyomma hebraeum (Fig. 4, 7–8)

The South African bont tick is the major vector of heartwater in the southern part of the African continent, i.e. in South Africa itself and in adjacent areas in eastern Botswana, southern Zimbabwe and southern Mozambique.

The isolated record of *A. hebraeum* in western Botswana is based on the collection of a single male from a bovine on Ncojane Ranches (Paine, 1982). It seems likely that this represents a chance introduction only; it is not known whether this species has since managed to establish itself in this area. Two isolated collections of the tick were also made from cattle during the Tanzania survey: 2 males on the Mahiwa Agricultural Department Farm, Lindi District, Southern Province, and 1 male on Rubisho Island, in south-west Lake Victoria (not shown on Fig. 4). Yeoman & Walker (1967) speculated that these ticks had been introduced, as engorged nymphae, on migrating birds. I know of no confirmed collections of this tick from elsewhere in Africa, although there are a few records from Kenya in some of the older literature (Walker, 1974). But in this connection it is worth remembering that, although the males of *A. hebraeum* and *A. gemma* can easily be separated, the females of these 2 species are, to my mind anyway, almost indistinguishable.

Amblyomma pomposum (Fig. 4, 9–10)

Theiler & Salisbury (1959), Tendeiro (1963) and myself, amongst others, think that this is the correct name for the species in the *A. variegatum* group that occurs across central Africa from the southern end of Lake Tanganyika through southern Zaïre and parts of Zambia to Angola. Except in the western half of Angola, where *A. pomposum* alone is prevalent, the distribution of the Angola bont tick quite often overlaps with that of *A. variegatum*. [The inadvertent switching of the names of these 2 species in Purnell (1984, key to Fig. 1) has been mentioned above].

Santos Dias (1953) described this tick as *Amblyomma superbum*, as he thinks the name *A. pomposum* refers to an eastern African species (see above, under *A. variegatum*). Both of us have seen the type male of *A. pomposum* (Zoological Museum, Berlin, No. 15965) collected at "Bismarkberg", which is now called Kasanga (08° 27′ S, 31° 08′ E), in Ufipa, southern Tanzania (Polhill, 1970). Unfortunately we disagree about the affinities of this specimen, so this nomenclatural problem remains to be solved.

Amblyomma lepidum (Fig. 11–13)

This species is widespread in eastern Sudan, Ethiopia, southern Somalia, eastern Uganda, Kenya and thence southwards through central Tanzania as far as the southern part of the Ruaha valley and the Lake Rukwa trough. It fades out at approximately latitude 08° S, as indicated by the smaller symbols on Fig. 13.

A. lepidum is known to have been involved in the transmission of heartwater to sheep and goats in the Kassala Province, Sudan (Karrar, 1960, 1966). This area lies between latitude 14°–16° N and longitude 34°–36° E, near the Ethiopian border.

Amblyomma astrion (Fig. 14–16)

This species resembles *A. cohaerens* closely in appearance, to the extent that the 2 species have sometimes been confused (Elbl & Anastos, 1966). In most parts of its range *A. astrion* is primarily a parasite of the African buffalo *(Syncerus caffer)*. With few exceptions records of the tick come from localities to the west of longitude 24° E, in the Central African Republic, the Congo Republic, western Zaïre and Angola, and on the West African islands of São Tomé and Principe. On these islands it is the principal tick on domestic ruminants (Uilenberg, Corten & Dwinger, 1982).

One record of *A. astrion,* from "Kawa (Lac Albert)" 31° 00′ E, 2° 00′ N, has been omitted from Fig. 16 because Elbl & Anastos (1966) are doubtful of its validity. This locality lies considerably to the east of this tick's usual range.

***Amblyomma cohaerens* (Fig. 17–18)**

Originally this species is thought to have been a parasite of the African buffalo, which animal is still its commonest host in parts of its range such as western and southern Uganda, where *A. cohaerens* is numerous in some areas. It has also been recorded, often but by no means always from buffaloes, in various places east of longitude 24° E in Zaïre, Rwanda, Burundi, northern Tanzania and south-western Kenya.

In western Ethiopia, in areas where Pegram *et al.* (1981) thought that dense populations of buffalo probably occurred originally, they noted that *A. cohaerens* is now "the most prevalent and abundant tick on cattle". Earlier, though, Pegram (1979) referred to a suggestion (made originally by G. C. Backhurst) that, because Ethiopian specimens of *A. cohaerens* from cattle are very much smaller than specimens seen in Kenya, they might belong to a separate species. No-one has as yet pursued this possibility further.

Although both *A. astrion* and *A. cohaerens* are closely associated with the African buffalo, neither tick has been recorded in very large parts of this animal's range in Africa (Smithers, 1983).

***Amblyomma gemma* (Fig. 19–21)**

This tick is prevalent in many parts of eastern Ethiopia (see below), Somalia, Kenya and Tanzania, southwards as far as the southern part of the Ruaha valley and the Lake Rukwa trough, i.e. to much the same latitude as *A. lepidum* where, as indicated by the smaller symbols on Fig. 21, it fades out. It also occurs in eastern Uganda but is not as well established there as is *A. lepidum*.

In their extensive survey of Ethiopian ticks, Pegram *et al.* (1981) state that *A. gemma* "was found only in the Rift Valley and eastward". Although Morel (1969, 1980) recorded this species from several points west of the Rift Valley in Ethiopia, R. G. Pegram (personal communication, 1986) does not believe that it is permanently established there.

According to Pegram *et al.* (1982) *A. gemma* was not found on 1320 domestic animals examined in Ta'izz district, Yemen Arab Republic, in 1978–79. They comment: "The single male of *A. gemma* taken from a cow at Ta'izz in 1951 was obviously introduced from Africa . . .". This record, which was mapped by Morel (1969), was therefore omitted from Fig. 21.

***Amblyomma sparsum* (Fig. 22–24)**

There are extremely few records of this species from domestic animals. Most adults have been collected from hosts that fall into 2 strikingly disparate groups: the African buffalo, the black or hook-lipped rhinoceros *(Diceros bicornis)* and occasionally other large game animals on the one hand, and various reptiles such as tortoises, monitor lizards and some of the larger snakes on the other.

The majority of records come from eastern and central Africa with a few scattered outliers, 3 in western Angola and 1 in SWA/Namibia. In northern Zimbabwe the distribution zones of *A. sparsum* and *A. marmoreum* overlap at much the same latitude as do those of *A. variegatum* and *A. hebraeum*.

***Amblyomma marmoreum* (Fig. 24–26)**

In its adult stage the South African tortoise tick is almost exclusively a parasite of reptiles, including various species of tortoises, snakes and monitor lizards (Theiler, 1962; Norval, 1975). Field collections of *A. marmoreum* adults from domestic animals are rare.

It has been recorded in much of South Africa, in southern Mozambique and in Zimbabwe, where its distribution overlaps that of *A. sparsum* in the north of the country. The few records that are available from Botswana and SWA/Namibia probably do not reflect the true range of this tick there.

***Amblyomma tholloni* (Fig. 27–29)**

The distribution of the elephant bont tick is linked with that of its main host, the African elephant, *Loxodonta africana* (Hoogstraal, 1956), though it has not as yet been recorded throughout the range of this animal (Smithers, 1983). The 2 small symbols on Fig. 29, in western Kenya and central Uganda, indicate places where *A. tholloni* has been collected in the past from elephants but these animals no longer exist there.

I do not know of any records of the adults from domestic animals, but MacKenzie & Norval (1980) reported that cattle, sheep and goats at the Rekomitjie Research Station in the Zambezi Valley were frequently infested with *A. tholloni* larvae and nymphae.

***Amblyomma maculatum* (Fig. 30–32)**

The common name of this species, the Gulf Coast tick, reflects its occurrence primarily in the hot, humid coastal areas bordering the Gulf of Mexico. It has also been recorded in a few places on the west coast of Mexico, in Belize, Colombia and Venezuela, and on the island of Jamaica.

Cooley & Kohls (1944) listed various records of *A. maculatum* from isolated areas outside its known normal distribution zone in the United States. Later Strickland *et al.* (1976) noted that it was established in several counties in north-eastern Oklahoma. Sonenshine (1979) referred to 5 collections of *A. maculatum* from various places in Virginia. He added: "it is unlikely that this tick is established in Virginia, and the few instances of its recovery in the state may reflect its transport by migratory birds. However, the possibility of its establishment in the less extreme climatic conditions of the south-eastern coastal areas cannot be discounted".

Doss *et al.* (1978) quote numerous references to the presence of *A. maculatum* in other parts of South America but these are thought to represent misidentifications and have been omitted. Earlier Kohls (1956), who studied *A. maculatum* and several related species, commented: "The numerous specimens of *A. maculatum* that I have examined all come from no further south than Colombia and Venezuela, . . .". Its absence in Argentina was confirmed by Guglielmone *et al.*, 1982.

***Amblyomma cajennense* (Fig. 33–35)**

According to the distribution map published by the American Geographical Society (1954), on which Fig. 35 is largely based, *A. cajennense* occurs from Mexico and southern Texas, at approximately latitude 30° N, through central and South America as far as northern Argentina (Ivancovich, 1973; Guglielmone & Hadani, 1982). It is also present on some of the Caribbean islands, e.g. Cuba, Jamaica and Trinidad.

The cayenne tick is apparently absent, according to the original map, from the major mountain ranges of the Sierra Madre Occidental in Mexico and the Andes in South America. D. E. Evans (personal communication, 1986) commented that he had no records of *A. cajennense* from either Chile or Uruguay. He also observed that, in the southernmost part of Brazil (Rio Grande do Sul), this tick has apparently not been reported on cattle

and horses, which are 2 of its commonest hosts elsewhere. But it was quite frequently found there on some wildlife species present in the same fields with these domestic animals (e.g. capybaras, *Hydrochaerus hydrochaeris*). Dr Evans suggested that this interesting situation should be investigated in detail.

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REFERENCES

AMERICAN GEOGRAPHICAL SOCIETY OF NEW YORK, 1954. Atlas of diseases. Plate 12. Distribution of rickettsial diseases. 3. Tick and mite vectors. New York.

BARRÉ, N., UILENBERG, G., MOREL, P. C. & CAMUS, E., 1987. Danger of introducing heartwater onto the American mainland: potential role of indigenous and exotic *Amblyomma* ticks. *Onderstepoort Journal of Veterinary Research*, 54, 405–417.

BISHOPP, F. C. & HIXSON, H., 1936. Biology and economic importance of the Gulf Coast tick. *Journal of Economic Entomology*, 29, 1068–1076.

COOLEY, R. A. & KOHLS, G. M., 1944. The genus *Amblyomma* (Ixodidae) in the United States. *Journal of Parasitology*, 30, 77–111.

DOSS, MILDRED, A. FARR, MARION M., ROACH, KATHARINE F. & ANASTOS, G., 1978. Index Catalogue of Medical and Veterinary Zoology Special Publication No. 3. Ticks and tick-borne Diseases. IV. Geographical distribution of ticks. United States Department of Agriculture.

FAO, 1975. Research on tick-borne cattle diseases and tick control, Kenya. Epizootiological survey on tick-borne cattle diseases. Rome: United Nations Development Programme, Food and Agriculture Organization of the United Nations, AG:DP/KEN/70/522, Technical Report 1.

ELBL, ALENA & ANASTOS, G., 1966. Ixodid ticks (Acarina, Ixodidae) of Central Africa. Volume 1. General introduction. Genus *Amblyomma* Koch, 1844. *Annales du Musée Royal de l'Afrique Centrale, Série in 8vo, Sciences Zoologiques*, 145, xiv + 275 pp.

GUGLIELMONE, A. A. & HADANI, A., 1982. *Amblyomma* ticks found on cattle in the northwest of Argentina. Preliminary Report. *Annales de Parasitologie, Paris*, 57, 91–97.

GUGLIELMONE, A. A., MANGOLD, A. J. & HADANI, A., 1982. *Amblyomma tigrinum* Koch, 1844 en la Argentina. Su diagnóstico erróneo como *Amblyomma maculatum* y su distribución geográfica. *Gaceta Veterinaria, Buenos Aires*, 44 (No. 367), 57–63.

HOFFMANN, ANITA, 1962. Monografia de los Ixodoidea de Mexico. *Revista de la Sociedad Mexicana de Historia Natural*, 23, 191–307.

HOOGSTRAAL, H., 1956. African Ixodoidea. I. Ticks of the Sudan (with special reference to Equatoria Province and with preliminary reviews of the genera *Boophilus*, *Margaropus* and *Hyalomma*). Research Report NM 005. 050.29.07, Washington D.C., Department of the Navy, Bureau of Medicine & Surgery.

HOOGSTRAAL, H., 1985. The American Society of Parasitologists: its historic role and modern opportunities. *Journal of Parasitology*, 71, 686–692.

IVANCOVICH, J. C., 1973. La garrapatas de Chaco y Formosa. Primera comunicación. *Revista de Investigaciones Agropecuarias, Serie 4, Patologia Animal*, 10, 9–24.

JONES, ELEANOR K., CLIFFORD, C. M., KEIRANS, J. E. & KOHLS, G. M., 1972. The ticks of Venezuela (Acarina: Ixodoidea) with a key to the species of *Amblyomma* in the Western Hemisphere. *Brigham Young University Science Bulletin, Biological Series*, 17, iv + 40 pp.

KARRAR, G., 1960. Rickettsial infection (heartwater) in sheep and goats in the Sudan. *British Veterinary Journal*, 116, 105–114.

KARRAR, G., 1966. Further studies on the epizootiology of heartwater in the Sudan. *Sudan Journal of Veterinary Science and Animal Husbandry*, 6, 83–85.

KEIRANS, J. E., 1985. George Henry Falkiner Nuttall and the Nuttall tick catalogue. *United States Department of Agriculture Miscellaneous Publication* No. 1438, 1785 pp.

KEIRANS, J. E., 1986. Harry Hoogstraal (1917–1986). *Journal of Medical Entomology*, 23, 342–343.

KOHLS, G. M., 1956. Concerning the identity of *Amblyomma maculatum*, *A. tigrinum*, *A. triste*, and *A. ovatum* of Koch, 1844. *Proceedings of the Entomological Society of Washington*, 58, 143–147.

MACKENZIE, P. K. I. & NORVAL, R. A. I., 1980. The transmission of *Cowdria ruminantium* by *Amblyomma tholloni*. *Veterinary Parasitology*, 7, 265–268.

MACLEOD, J., 1970. Tick infestation patterns in the southern province of Zambia. *Bulletin of Entomological Research*, 60, 253–274.

MACLEOD, J. & COLBO, M. H., 1976. Ecological studies of ixodid ticks (Acari, Ixodidae) in Zambia. I. Cattle as hosts of the larvae of *Amblyomma variegatum* (F.) and *Rhipicephalus appendiculatus* Neum. *Bulletin of Entomological Research*, 66, 65–74.

MACLEOD, J., COLBO, M. H., MADBOULY, M. H. & MWANAUMO, B., 1977. Ecological studies of ixodid ticks (Acari: Ixodidae) in Zambia. III. Seasonal activity and attachment sites on cattle, with notes on other hosts. *Bulletin of Entomological Research*, 67, 161–173.

MACLEOD, J. & MWANAUMO, B., 1978. Ecological studies of ixodid ticks (Acari: Ixodidae) in Zambia. IV. Some anomalous infestation patterns in the northern and eastern regions. *Bulletin of Entomological Research*, 68, 409–429.

MATTHYSSE, J. G. & COLBO, M. H., 1987. The ixodid ticks of Uganda. Washington, D. C.: Entomological Society of America.

MOREL, P. C., 1969. Contribution à la connaissance de la distribution des tiques (Acariens, Ixodidae et Amblyommidae) en Afrique Ethiopienne Continentale. Annexe Cartographique. Paris: Institut d'Élevage et de Médecine Vétérinaire des Pays Tropicaux.

MOREL, P. C., 1980. Study on Ethiopian ticks (Acarida, Ixodida). Maisons-Alfort: Institut d'Élevage et de Médecine Vétérinaire des Pays Tropicaux. 332 pp. Mimeographed.

NEUMANN, L.-G., 1899. Révision de la famille des Ixodides. 3e mémoire. *Mémoires de la Société Zoologique de France*, 14, 249–372.

NEUMANN, L.-G., 1911. Ixodidae. *In:* SCHULZE, F. E. (ed). Das Tierreich, 26. Lieferung, xvi + 169 pp. Berlin: R. Friedländer und Sohn.

NORVAL, R. A. I., 1975. Studies on the ecology of *Amblyomma marmoreum* Koch 1844 (Acarina: Ixodidae). *Journal of Parasitology*, 61, 737–742.

NORVAL, R. A. I., 1983. The ticks of Zimbabwe. VII. The genus *Amblyomma*. *Zimbabwe Veterinary Journal*, 14, 3–18.

PAINE, G. D., 1982. Ticks (Acari: Ixodoidea) in Botswana. *Bulletin of Entomological Research*, 72, 1–16.

PEGRAM, R. G., 1976. Ticks (Acarina, Ixodoidea) of the northern regions of the Somali Democratic Republic. *Bulletin of Entomological Research*, 66, 345–363.

PEGRAM, R. G., 1979. Ticks (Ixodoidea) of Ethiopia with special reference to cattle. M. Phil. Thesis, University of Brunel, Uxbridge, England.

PEGRAM, R. G., HOOGSTRAAL, H. & WASSEF, HILDA Y., 1981. Ticks (Acari: Ixodoidea) of Ethiopia. I. Distribution, ecology and host relationships of species infesting livestock. *Bulletin of Entomological Research*, 71, 339–359.

PEGRAM, R. G., HOOGSTRAAL, H. & WASSEF, HILDA Y., 1982. Ticks (Acari: Ixodoidea) of the Yemen Arab Republic. I. Species infesting livestock. *Bulletin of Entomological Research*, 72, 215–227.

PEGRAM, R. G., PERRY, B. D., MUSISI, F. L. & MWANAUMO, B., 1986. Ecology and phenology of ticks in Zambia: Seasonal dynamics on cattle. *Experimental and Applied Acarology*, 2, 25–45.

POLHILL, DIANA, 1970. Flora of Tropical East Africa Index of Collecting Localities. London: Royal Botanic Gardens, Kew.

PURNELL, R. E., 1984. Control of heartwater in cattle in southern Africa using Terramycin/LA. *Preventive Veterinary Medicine*, 2, 239–254.

ROBINSON, L. E., 1926. Part IV. The genus *Amblyomma*. xii + 302 pp., plates I–VII. *In:* NUTTALL, G. H. F., WARBURTON, C., COOPER, W. F. & ROBINSON, L. E. (1908–1926). Ticks. A monograph of the Ixodoidea. Parts I–IV and Bibliographies [I] & II. London: Cambridge University Press.

SANTOS DIAS, J. A. T., 1953. Sobre a posição systemática de algumas espécies africanas do género *Amblyomma* C. L. Koch (Acarina—Ixodoidea). *Moçambique*, No. 73, 119–139.

SANTOS DIAS, J. A. T., 1960. Lista das carraças de Moçambique e respectivos hospedeiros. III. *Anais dos Servicos de Veterinária e Industria Animal de 1953–1954*, No. 6, 213–287.

SCHOENHERR, S. & DOBATH, H., 1969. Domestic animals in the world 1959–1965. *The Blue Book*, 16, 2–14.

SERRANO, F. M. H., 1963. Consideracoes sobre a morfologia, ecologia e biologia dos ixodideos dos géneros *Amblyomma* e *Dermacentor*

assinalados em Angola. *Revista de Ciências Veterinarias*, 58, 181–204.

SMITHERS, R. H. N., 1983. The mammals of the southern African subregion. Pretoria: University of Pretoria.

SOUSA DIAS, V., 1950. Subsidios para o estudo dos ixodideos de Angola. *Pecuaria, Luanda (1947–1948)*, 2, 127–280.

SONENSHINE, D. E., 1979. The insects of Virginia: No. 13. Ticks of Virginia (Acari: Metastigmata). *Virginia Polytechnic Institute and State University, Research Division Bulletin* 139,44 pp.

STRICKLAND, R. K., GERRISH, R. R., HOURRIGAN, J. L. & SCHUBERT, G. O., 1976. Ticks of veterinary importance. *Animal and Plant Health Inspection Service, United States Department of Agriculture, Agriculture Handbook No. 485*, 122 pp.

SUTHERST, R. W. & MAYWALD, G. F., 1985. A computerised system for matching climates in ecology. *Agriculture, Ecosystems and Environment*, 13, 281–299.

TENDEIRO, J., 1963. Sur quelques ixodidés du Mozambique et de la Guinée Portugaise. III. *Boletim Cultural da Guiné Portuguesa*, No. 70, 223–229 + 32 photographs.

THEILER, GERTRUD & SALISBURY, LOIS E., 1959. Ticks in the South African Zoological Survey Collection. Part IX. "The *Amblyomma marmoreum* group". *Onderstepoort Journal of Veterinary Research*, 28, 47–124 + map.

THEILER, GERTRUD, 1962. The Ixodoidea parasites of vertebrates in Africa south of the Sahara (Ethiopian Region). Project S 9958. Report to the Director of Veterinary Services, Onderstepoort. 255 pp., mimeographed.

UILENBERG, G., HOOGSTRAAL, H. & KLEIN, J. M., 1979. Les tiques (Ixodoidea) de Madagascar et leur rôle vecteur. *Archives de l'Institut Pasteur de Madagascar, Numéro spécial*, 154 pp.

UILENBERG, G., CORTEN, J. J. F. M. & DWINGER, R. H., 1982. Heartwater (*Cowdria ruminantium* infection) on São Tomé. *Veterinary Quarterly*, 4, 106–107.

UILENBERG, G., BARRÉ, N., CAMUS, E., BURRIDGE, M. J. & GARRIS, G. I., 1984. Heartwater in the Caribbean. *Preventive Veterinary Medicine*, 2, 255–267.

WALKER, JANE B., 1974. The ixodid ticks of Kenya. London: Commonwealth Institute of Entomology.

WALKER, JANE B., MEHLITZ, D. & JONES, G. E., 1978. Notes on the ticks of Botswana. Eschborn: German Agency for Technical Cooperation (GTZ).

WHITE, F., 1983. The vegetation of Africa. A descriptive memoir to accompany the Unesco/AETFAT/UNSO vegetation map of Africa. Paris: Unesco.

YEOMAN, G. H. & WALKER, JANE B., 1967. The ixodid ticks of Tanzania. London: Commonwealth Institute of Entomology.

FIG. 2 *Amblyomma variegatum* male (from preserved specimen, Zambian strain)

FIG. 3 *Amblyomma variegatum* female (from preserved specimen, Zambian strain)

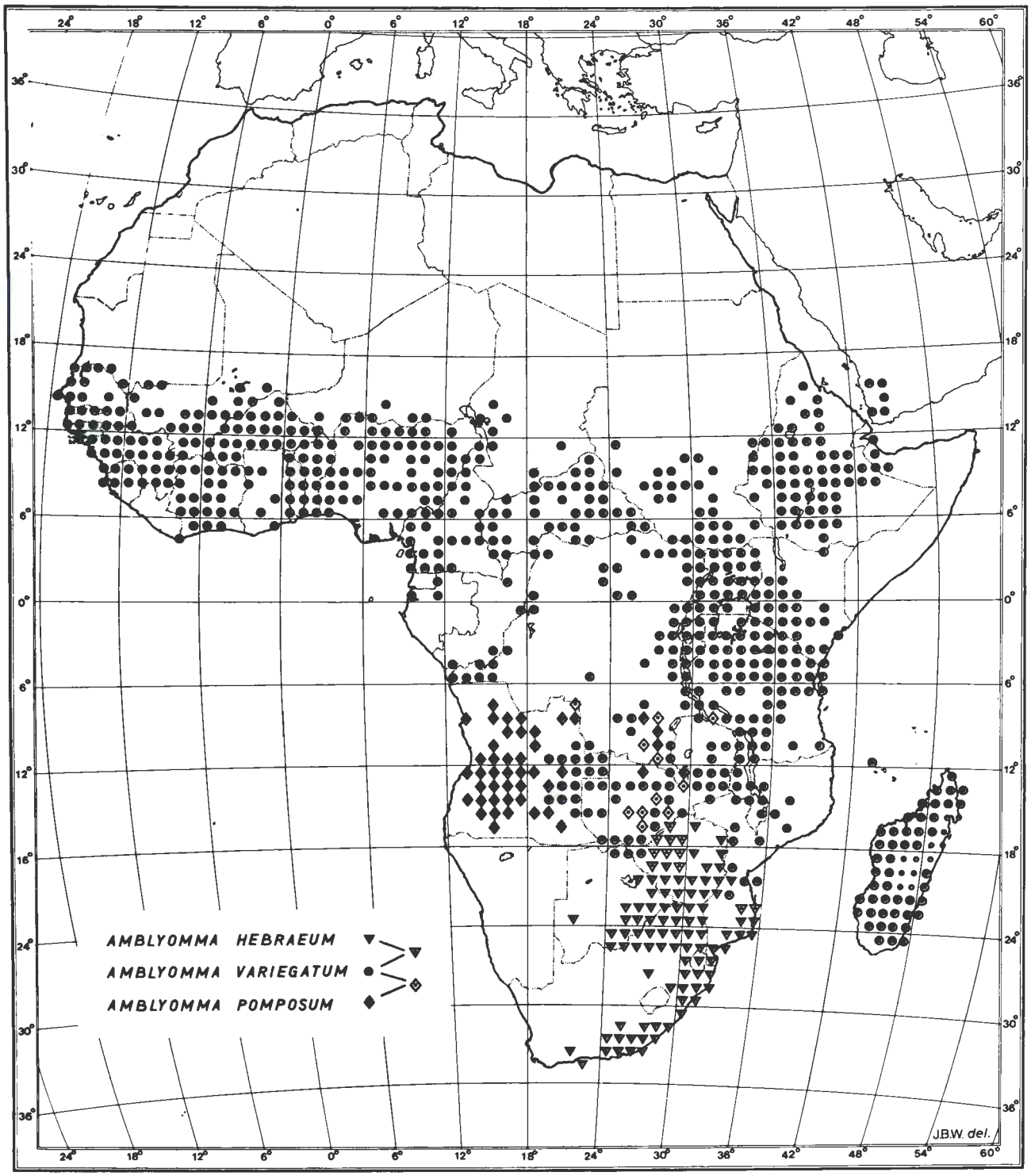

FIG. 4 Distribution of *Amblyomma variegatum*, *A. hebraeum* and *A. pomposum* in the Afrotropical region, the Yemen Arab Republic and Madagascar. The small symbols for *A. variegatum* in Madagascar indicate highland and coastal rain forest areas where the presence of this tick is questioned (G. Uilenberg, personal communication, 1986)

FIG. 5 Distribution of *Amblyomma variegatum* in the West Indies

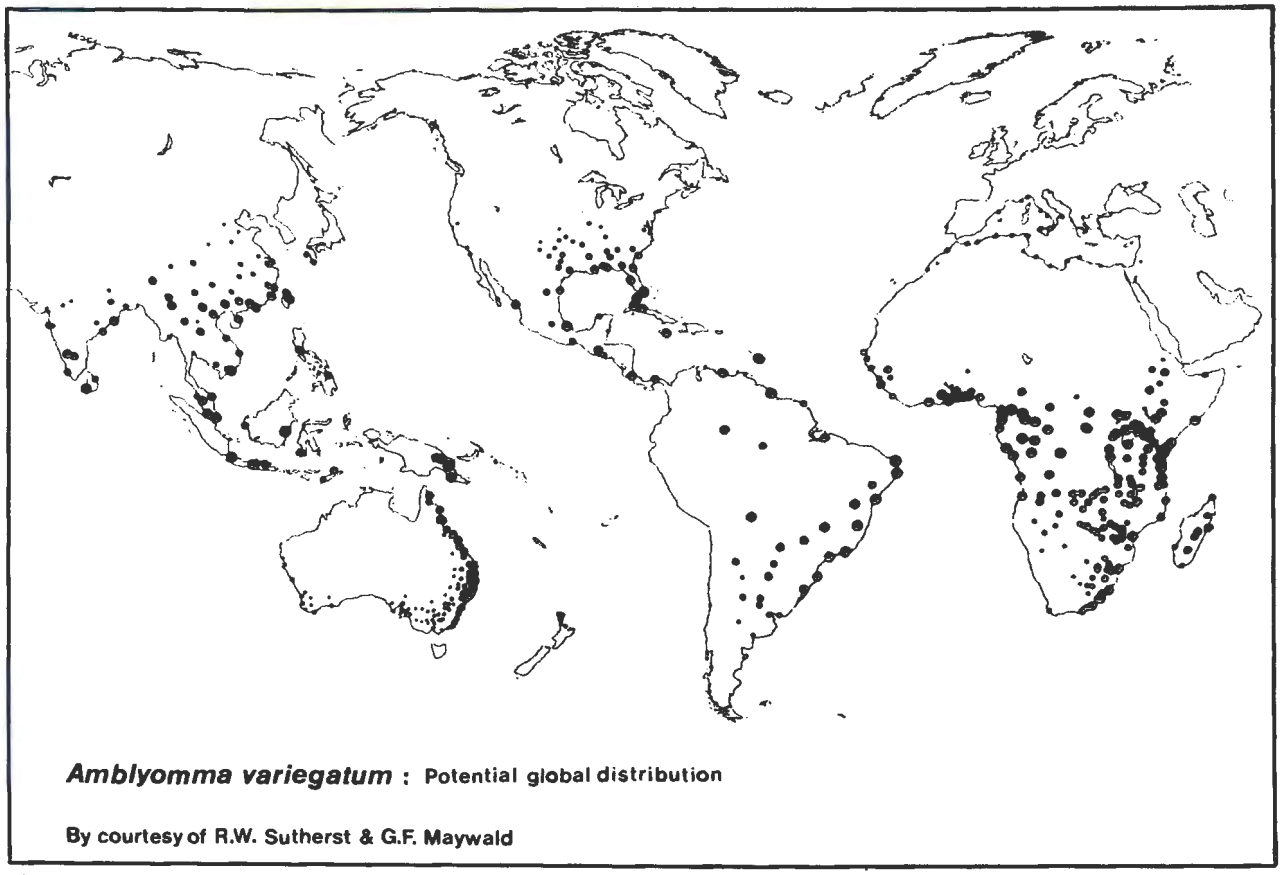

FIG. 6 Potential global distribution of *Amblyomma variegatum* as predicted with the CLIMEX computer-based system developed by R. W. Sutherst and G. F. Maywald. (Reproduced by courtesy of these authors.)

FIG. 7 *Amblyomma hebraeum* male (from live specimen, South African strain)

FIG. 8 *Amblyomma hebraeum* female (from live specimen, South African strain)

FIG. 9 *Amblyomma pomposum* male (from preserved specimen, Angola strain)

FIG. 10 *Amblyomma pomposum* female (from preserved specimen, Angola strain)

FIG. 11 *Amblyomma lepidum* male (from preserved specimen, Kenya strain)

FIG. 12 *Amblyomma lepidum* female (from preserved specimen, Kenya strain)

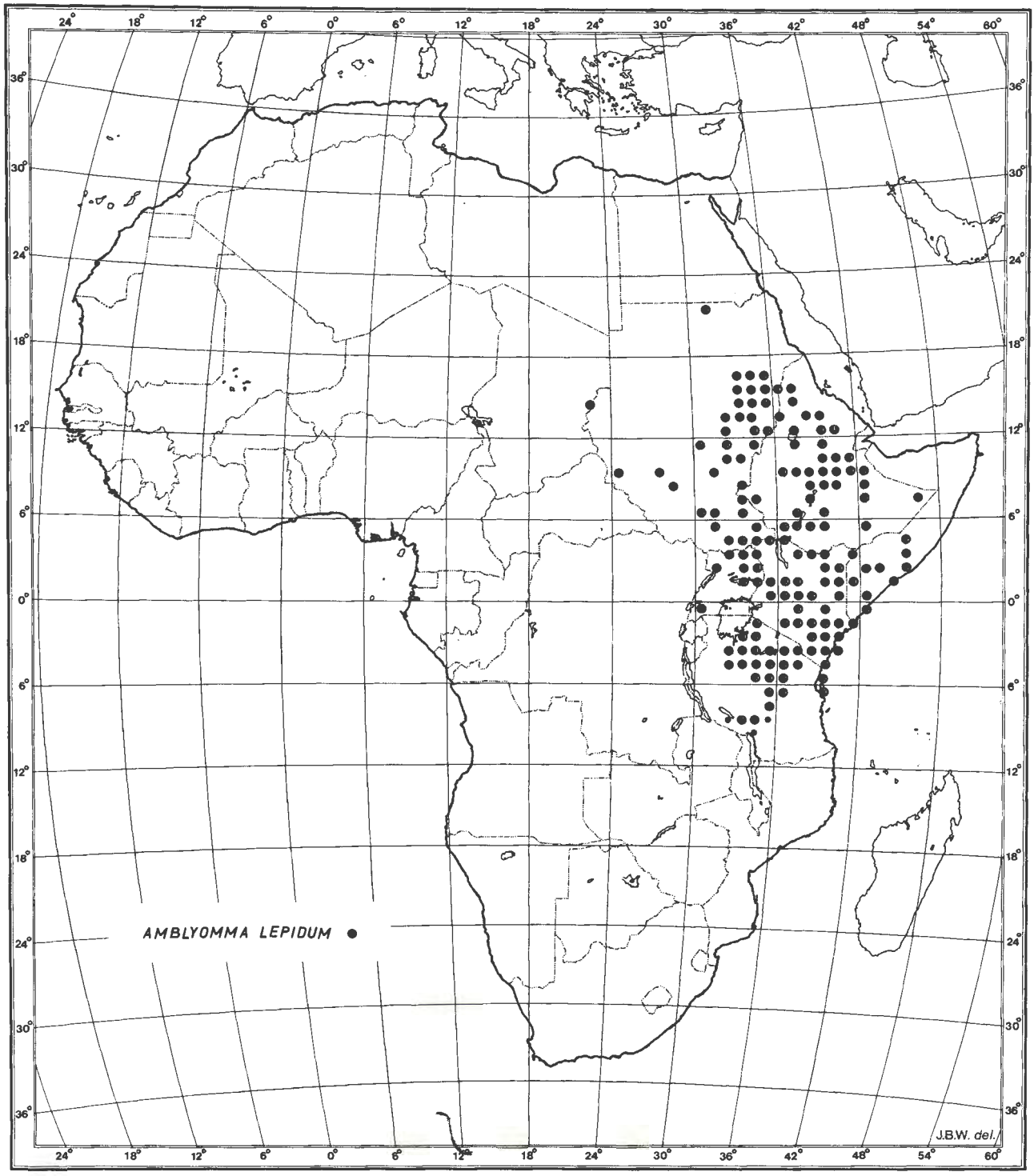

FIG. 13 Distribution of *Amblyomma lepidum*. Small symbols show areas where the tick fades out

FIG. 14 *Amblyomma astrion* male (from preserved specimen)

FIG. 15 *Amblyomma astrion* female (from preserved specimen)

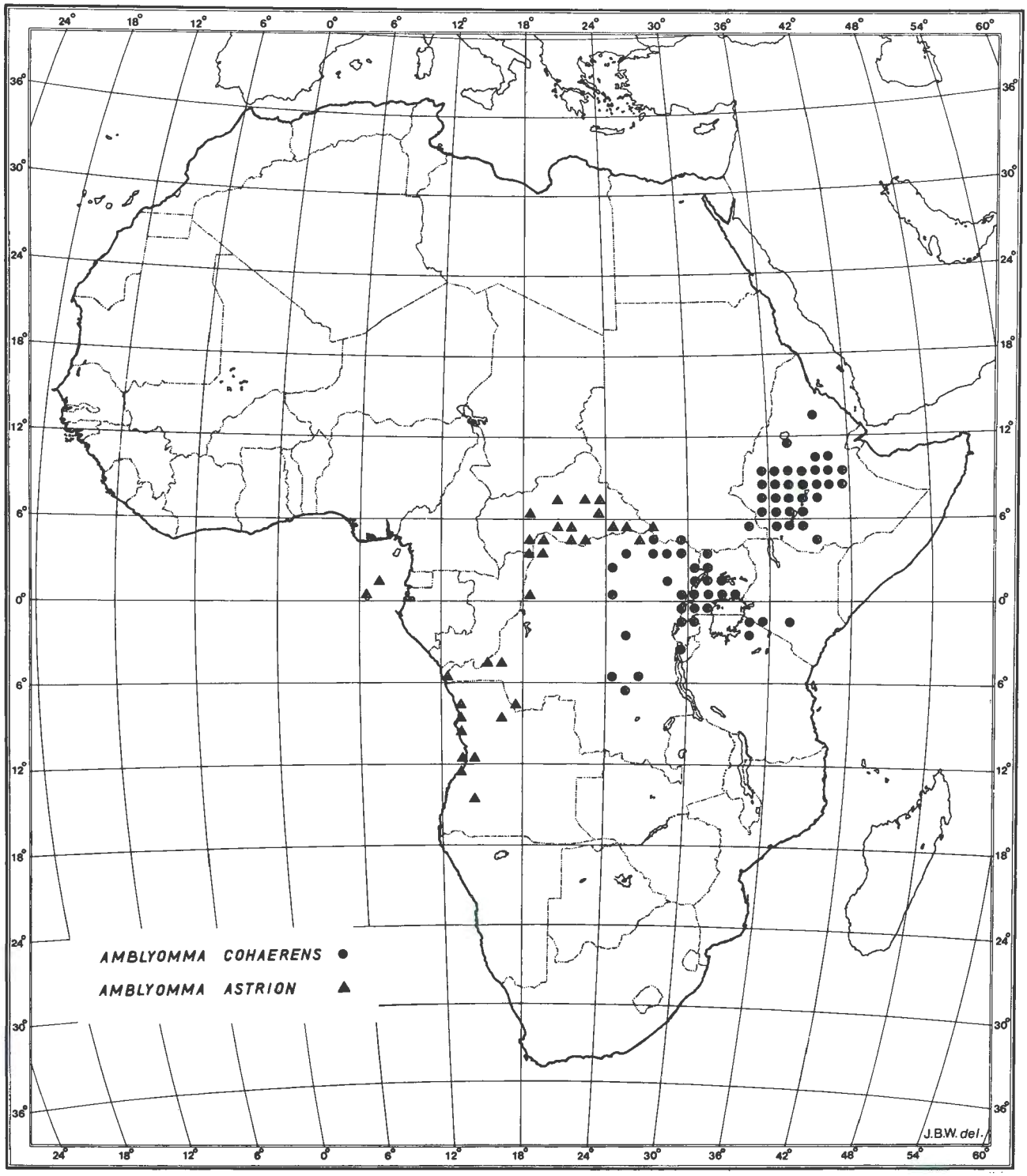

FIG. 16 Distribution of *Amblyomma astrion* and *A. cohaerens*

FIG. 17 *Amblyomma cohaerens* male (from preserved specimen)

FIG. 18 *Amblyomma cohaerens* female (from preserved specimen)

FIG. 19 *Amblyomma gemma* male (from preserved specimen, Kenya strain)

FIG. 20 *Amblyomma gemma* female (from preserved specimen, Kenya strain)

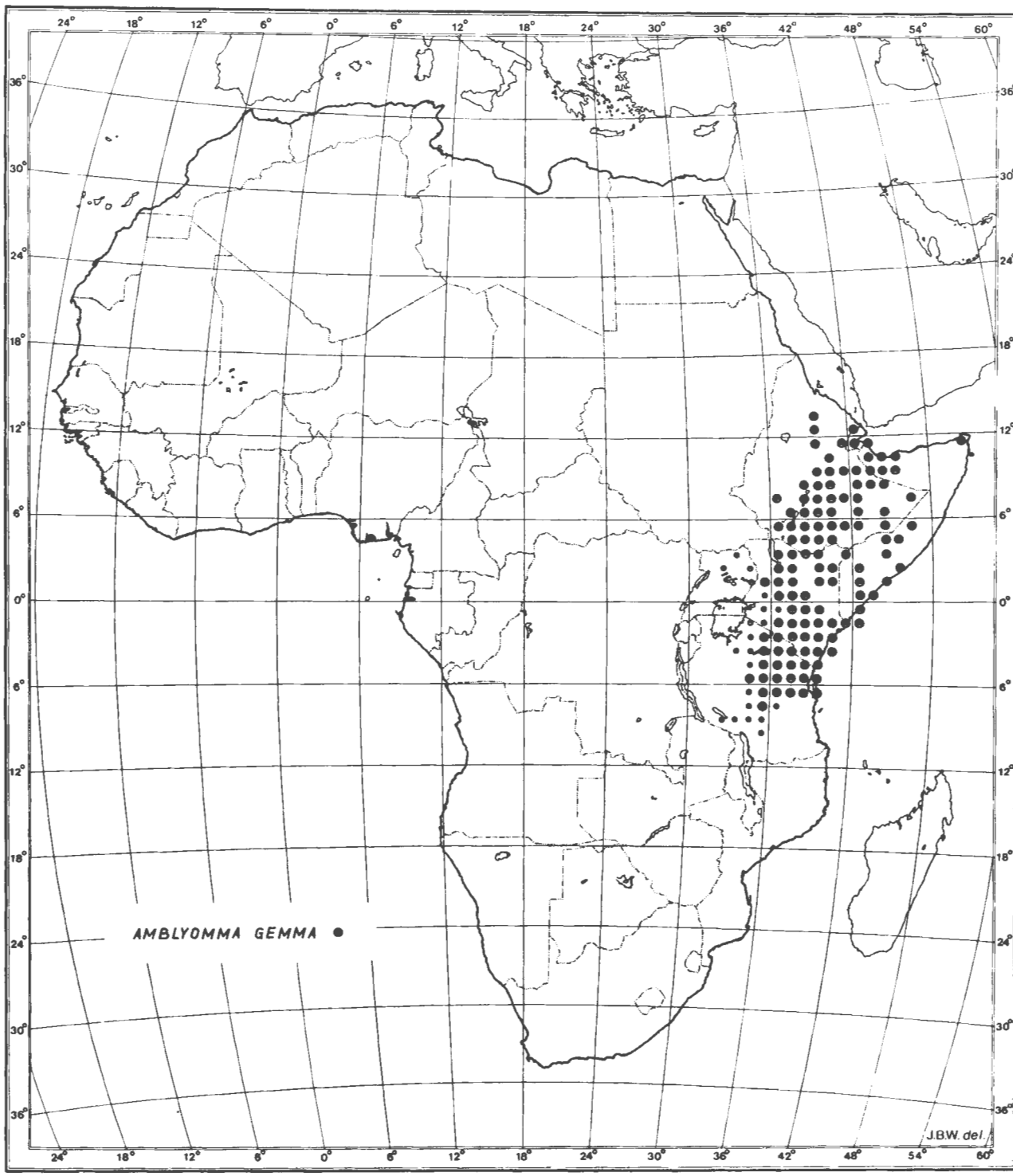

FIG. 21 Distribution of *Amblyomma gemma*. Small symbols show areas where the tick fades out

FIG. 22 *Amblyomma sparsum* male (from preserved specimen, Kenya strain)

FIG. 23 *Amblyomma sparsum* female (from preserved specimen, Kenya strain)

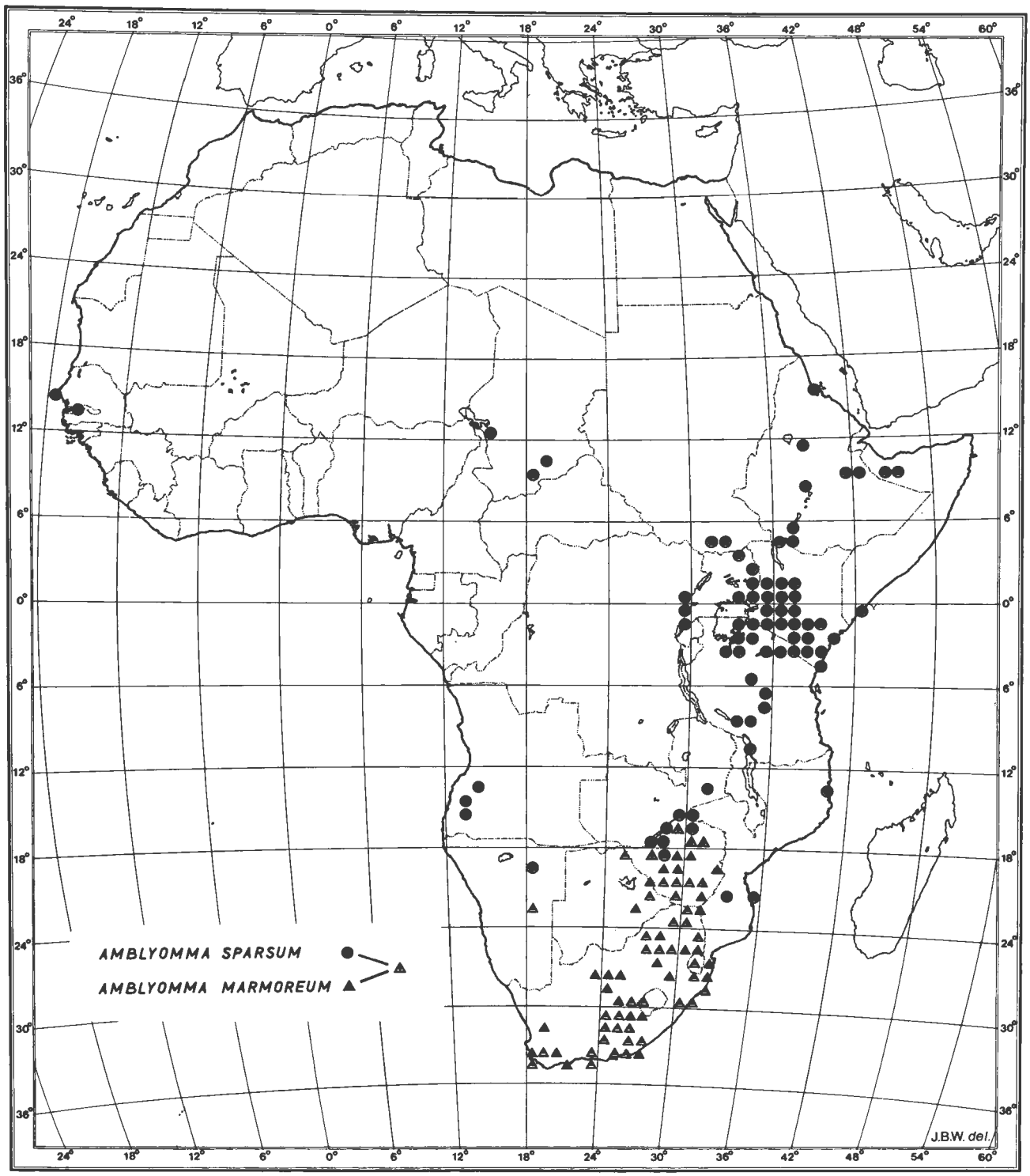

FIG. 24 Distribution of *Amblyomma sparsum* and *A. marmoreum*

a b

FIG. 25 *Amblyomma marmoreum* males, (a). light-coloured specimen, (b). dark specimen (from live specimens, South African strains)

FIG. 26 *Amblyomma marmoreum* female (from live specimen, South African strain)

FIG. 27 *Amblyomma tholloni* male (from preserved specimen, Uganda strain). Note that not all males of this species have such an extensive colour pattern as that shown here

FIG. 28 *Amblyomma tholloni* female (from preserved specimen, Uganda strain). Note that not all females of this species have such an extensive colour pattern as that shown here

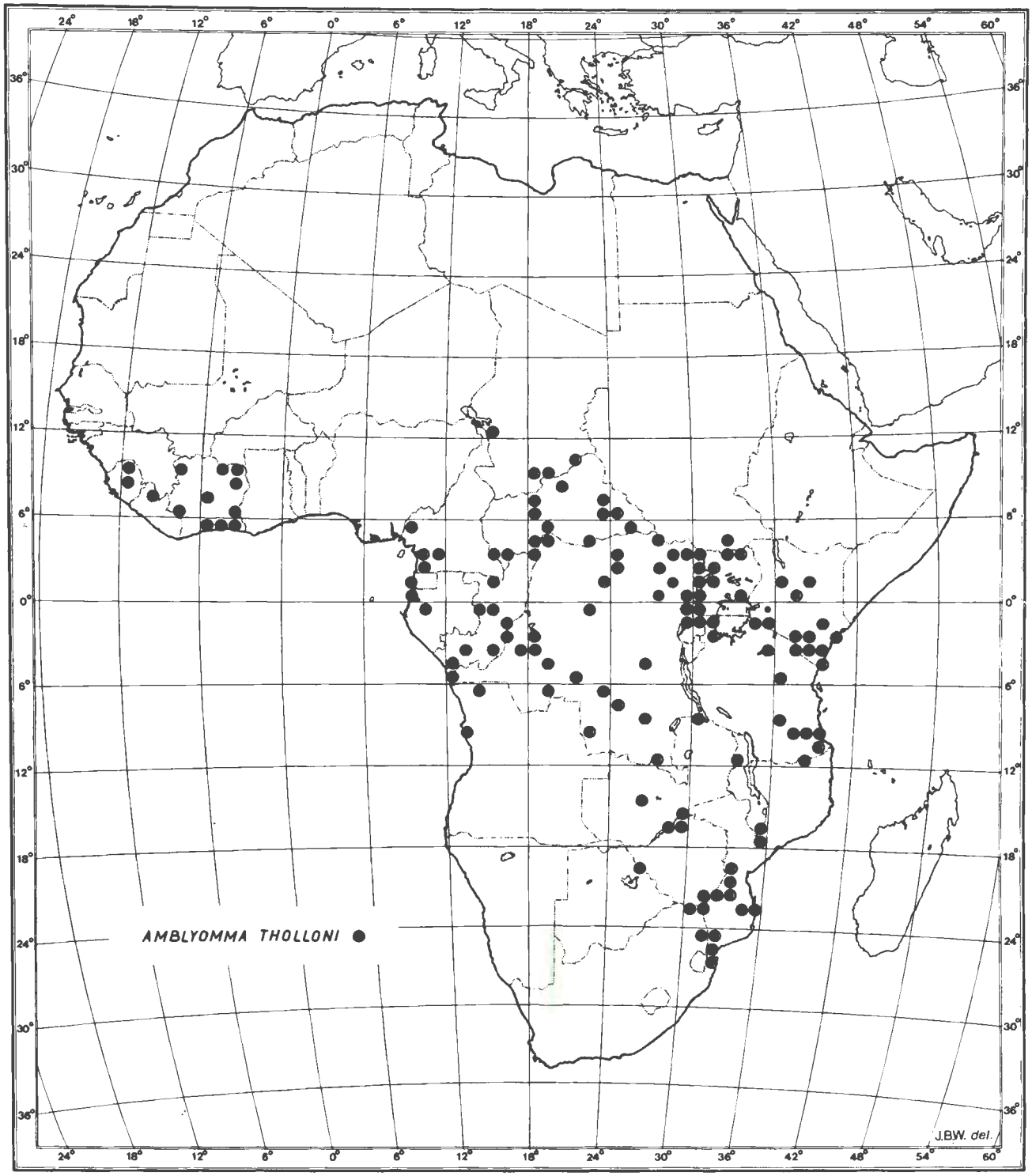

FIG. 29 Distribution of *Amblyomma tholloni*. Small symbols show areas where this tick was collected in the past but where elephants, and presumeably the tick, no longer exist

FIG. 30 *Amblyomma maculatum* male (from preserved specimen)

FIG. 31 *Amblyomma maculatum* female (from preserved specimen)

FIG. 32 Distribution of *Amblyomma maculatum*

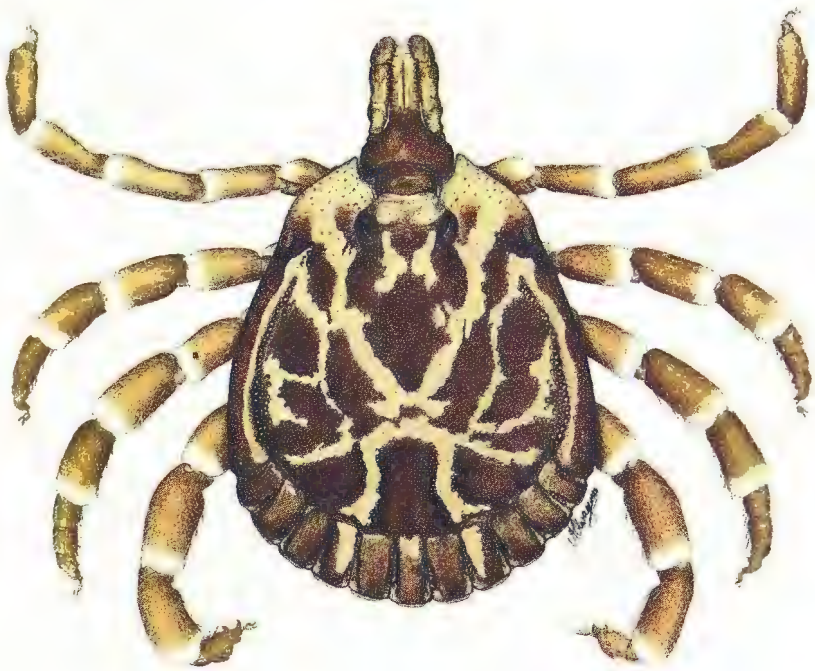

FIG. 33 *Amblyomma cajennense* male (from preserved specimen)

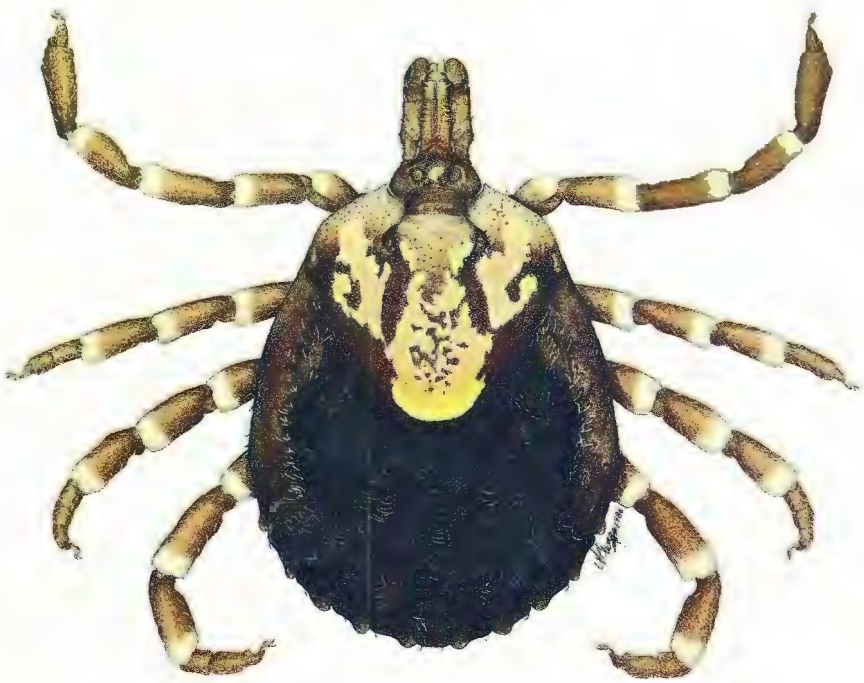

FIG. 34 *Amblyomma cajennense* female (from preserved specimen)

FIG. 35 Distribution of *Amblyomma cajennense*