

## Redescription of *Haemaphysalis (Rhipistoma) elliptica* (Koch, 1844), an old taxon of the *Haemaphysalis (Rhipistoma) leachi* group from East and southern Africa, and of *Haemaphysalis (Rhipistoma) leachi* (Audouin, 1826) (Ixodida, Ixodidae)

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### ABSTRACT

APANASKEVICH, D.A., HORAK, I.G. & CAMICAS, J-L. 2007. Redescription of *Haemaphysalis (Rhipistoma) elliptica* (Koch, 1844), an old taxon of the *Haemaphysalis (Rhipistoma) leachi* group from East and southern Africa, and of *Haemaphysalis (Rhipistoma) leachi* (Audouin, 1826) (Ixodida, Ixodidae). *Onderstepoort Journal of Veterinary Research*, 74:181–208

Koch (1844) originally described only the male of *Haemaphysalis (Rhipistoma) elliptica* (Koch, 1844), which he named *Rhipistoma ellipticum*. For the past century, however, this name has been considered a junior synonym of *Haemaphysalis (Rhipistoma) leachi* (Audouin, 1826), or a *nomen nudum*. We redescribe here the male and larva of *H. (R.) elliptica* and describe the female and nymph for the first time. Our redescription is based on the male holotype, plus numerous specimens from southern and East Africa. The adults of this tick parasitize domestic and wild carnivores, and the immature stages infest rodents in these regions. For comparative purposes redescrptions of all parasitic stages of *H. (R.) leachi* are provided. It parasitizes the same hosts as *H. (R.) elliptica* in Egypt, and in north-eastern, Central, West and East Africa.

**Keywords:** Descriptions, geographic distribution, *Haemaphysalis (Rhipistoma) elliptica*, *Haemaphysalis (Rhipistoma) leachi*, hosts

### INTRODUCTION

For those involved in their identification, the systematics of the African *Haemaphysalis (Rhipistoma) leachi* group of ticks has been fraught with problems. Before the studies of Hoogstraal and Camicas practically all ticks in the group were considered to belong to a single species, namely *Haemaphysalis (Rhipistoma) leachi* (Audouin, 1826). However, a redescription of an Egyptian population of *H. (R.) leachi* by Hoogstraal (1958), and his designation of a neotype, stimulated taxonomic studies of ticks belonging to this cluster of species. During the 1970s and 1980s Camicas and Hoogstraal and their co-workers elucidated taxonomic problems associated with this group and described or re-established a number

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of species. Hoogstraal & Kim (1985) consolidated the accumulated data on *Haemaphysalis* Koch, 1844 and on the subgenus *Rhipistoma* Koch, 1844 as well as on the *H. (R.) leachi* group. They placed these ticks in three subgroups, namely *H. (R.) leachi*, *Haemaphysalis (Rhipistoma) pedetes* and *Haemaphysalis (Rhipistoma) spinulosa*. Camicas, Hervy, Adam & Morel (1998) concurred with this decision and updated the species composition of the three subgroups. The *H. (R.) leachi* subgroup now consisted of five species, namely *H. (R.) elliptica* (Koch, 1844), *H. (R.) leachi* (Audouin, 1826), *Haemaphysalis (Rhipistoma) moreli* Camicas, Hoogstraal & El Kammah, 1972, *Haemaphysalis (Rhipistoma) para-leachi* Camicas, Hoogstraal & El Kammah, 1983, and *Haemaphysalis (Rhipistoma) punctaleachi* Camicas, Hoogstraal & El Kammah, 1973. The *H. (R.) pedetes* subgroup contained two species, viz. *H. (R.) pedetes* Hoogstraal, 1972 and *Haemaphysalis (Rhipistoma) zumpti* Hoogstraal & El Kammah, 1974, while the *H. (R.) spinulosa* subgroup incorporated four species, namely *Haemaphysalis (Rhipistoma) muhsamae* Santos Dias, 1954, *Haemaphysalis (Rhipistoma) norvali* Hoogstraal & Wassef, 1983, *H. (R.) spinulosa* Neumann, 1906 and *Haemaphysalis (Rhipistoma) subterra* Hoogstraal, El Kammah & Camicas, 1992.

There are only two synonyms for species within the *H. (R.) leachi* group, and these are *Haemaphysalis leachi* var. *humerosoides* Theiler, 1943, that has been synonymized with *H. (R.) leachi*, and *Haemaphysalis ethiopica* Santos Dias, 1958, that has been synonymized with *H. (R.) spinulosa*. Camicas *et al.* (1998), in their review of the ticks of the world, created two problems within the taxonomy of the *H. (R.) leachi* group by re-establishing two names, namely *H. (R.) elliptica* and *H. (R.) muhsamae*. The present paper addresses the taxonomic status of *H. (R.) elliptica*, while that of *H. (R.) muhsamae*, which for several decades has been considered a junior synonym of *H. (R.) spinulosa*, will be tackled in a future communication.

Koch (1844) originally described *Haemaphysalis (Rhipistoma) elliptica* (Koch, 1844) as *Rhipistoma ellipticum*. Neumann (1897) placed this species in the genus *Haemaphysalis* Koch, 1844 and synonymized it with *H. (R.) leachi* (Audouin, 1826). Thereafter the majority of tick taxonomists considered *H. (R.) elliptica* to be a junior synonym of *H. (R.) leachi*, or a *nomen nudum* (Nuttall & Warburton 1915; Camicas *et al.* 1972). Little more than a century later Camicas *et al.* (1998) re-established this taxon, but gave no reasons for their decision, thus begging the question, is *H. (R.) elliptica* a valid taxon or not?

After an exhaustive study of many collections of *Haemaphysalis* that had been identified as *H. (R.) leachi*, and a comparison of these ticks with true *H. (R.) leachi* from North Africa and with the holotype specimen of *H. (R.) elliptica*, we concluded that many of the southern and East African ticks previously identified as *H. (R.) leachi* are actually *H. (R.) elliptica*. Furthermore, these studies enabled us to delimit the geographic distributions of both ticks. We here redescribe the male [the first description is given by Koch (1844), under the name *Rhipistoma ellipticum*], and the larva [the first description is given by Bedford (1934), under the name *Haemaphysalis leachi*], and describe the female and nymph of *H. (R.) elliptica* for the first time. For comparative purposes we have also redescribed all stages of development of *H. (R.) leachi*.

## MATERIAL EXAMINED

The material examined is summarized in Tables 1, 2 and 3. Specimens from South Africa and Mozambique were studied by IGH, or by IGH and DAA, and the remainder were examined by DAA. Because of difficulties experienced in the identification of specimens we used the following material for the present study:

- (i) All primary identifications have been based on males.
- (ii) With the exception of collections from Egypt and South Africa, collections containing only females have been excluded.
- (iii) Females in collections containing males of two or more species have been excluded.
- (iv) The immature stages that we have studied come only from laboratory-reared specimens from allopatric localities within the distribution ranges of the two ticks, namely South Africa for *H. (R.) elliptica*, and Egypt and the Central African Republic for *H. (R.) leachi*.

The records of JLC have not been included because they need to be rechecked in relation to the new characters that we have found.

The descriptions of the adults of various *Haemaphysalis* species by Hoogstraal and his co-authors are characterized by the use of proportions between measurements of particular structures, mainly those of the gnathosoma. However, we could not find any exact description of the scheme of measurements taken by Hoogstraal and his co-workers, who gave only brief explanations in the texts. The exact features or structures between which some of the meas-

measurements were made are for the most part quite easily recognizable, but for several they are not. Consequently, we have taken those measurements that we consider are the most suitable for describing the species. Except for the measurements for which an explanation is given in the text, a scheme of the measurements that we have taken is illustrated in Fig. 1.

Because the larva and nymph have sometimes been inadequately described or not described at all, our set of measurements for them does not differ substantially from that used for these stages of development of previously described species. For the

adults we tried to follow Hoogstraal's format so that our measurements would at least approximate those that had been used before.

Measurements for the male conscutum and female scutum and their total lengths are given in millimetres (mm), and those for the immature stages in micrometres ( $\mu\text{m}$ ). The measurements are arranged as follows: minimum – maximum (average  $\pm$  standard deviation,  $n$  = number of specimens measured).

When measuring the dorsal and ventral spurs on palpal segments II and III, it must be noted that they are not in the same plane as the gnathosoma as they are directed either dorsally or ventrally. Con-

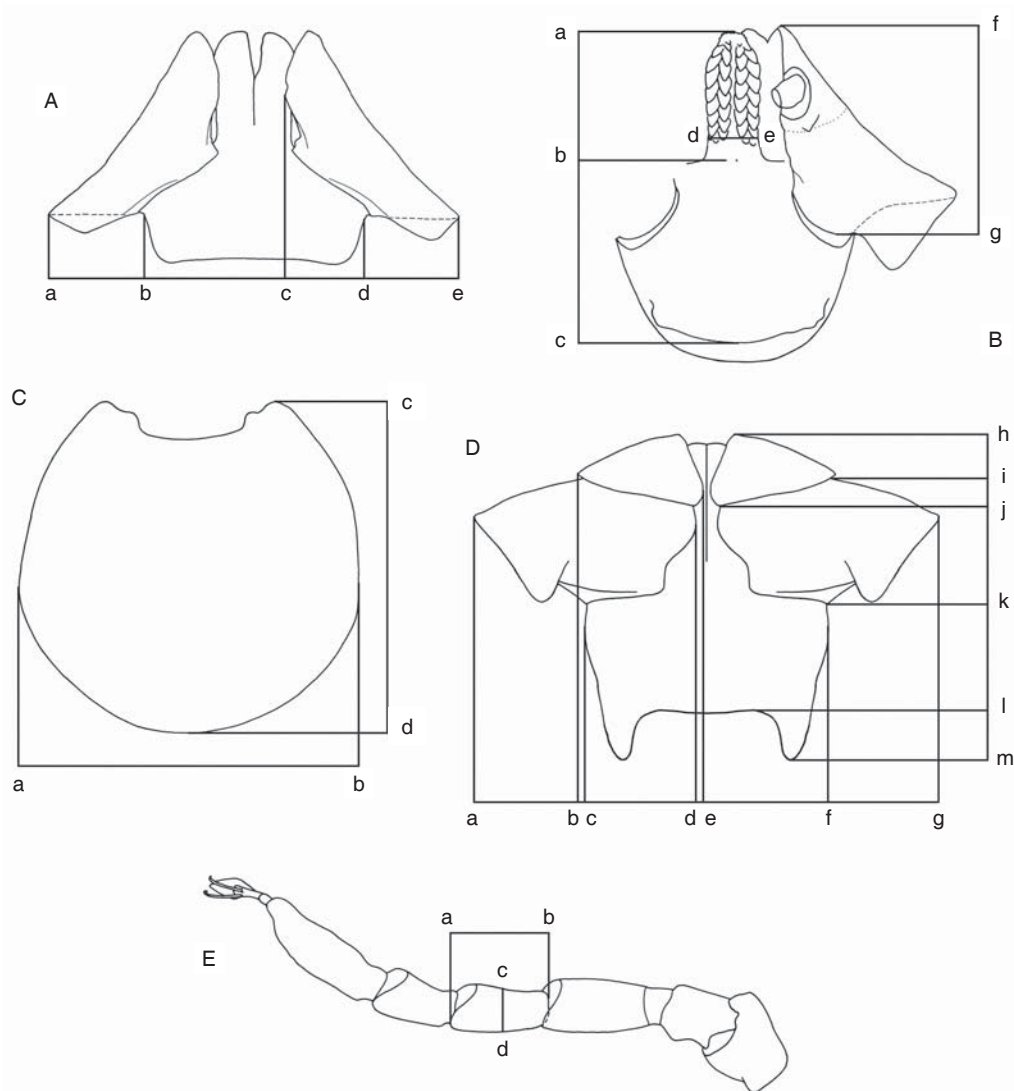


FIG. 1 Scheme of measurements for *Haemaphysalis*. A, nymph, gnathosoma dorsally: a-e—combined palpal width, b-d – width of basis capituli, c-e – width of palp; B, nymph, gnathosoma ventrally: a-b – length of hypostome, a-c – length of gnathosoma, d-e – width of hypostome, f-g – length of palp; C, nymph, scutum: a-b – width, c-d – length; D, male, gnathosoma dorsally: a-d – width of palpal segment II, a-g – combined palpal width, b-e – width of palpal segment III, c-f – width of basis capituli, h-j – length of palpal segment III, i-k – length of palpal segment II, k-m – length of basis capituli, l-m – length of dorsal cornua; E, nymph, leg I: a-b – length of genu, c-d – width of genu

sequently, the shape and the length of these spurs vary according to the plane along which they are observed. DAA's illustrations of the gnathosoma of the larvae and nymphs are based on slide-mounted specimens, but because of the differences in planes even in these preparations, the spurs on the palpal segments are in reality longer than illustrated. This observation has been verified by scanning electron microscopy. Furthermore, in order to simplify identification for persons who may in future examine these species we have attempted to use a minimum of poorly defined diagnostic characters.

***Haemaphysalis (Rhipistoma) elliptica*  
(Koch, 1844)**

THE SOUTH AFRICAN CARNIVORE  
HAEMAPHYSALID

(Fig. 2–7)

**Synonym**

*Haemaphysalis leachi humerosoides* Theiler, 1943  
*sensu* Theiler, 1943.

The collection lot (no. 2754), identified as *Haemaphysalis leachi* var. *humerosoides* by G. Theiler, contains nine vials. In the catalogue listing the specimens in the Onderstepoort Veterinary Institute tick collection the first vial (i) is marked as "Type": i (13 ♂, 17 ♀) – Bilene, Macia [Mozambique], 25.V.1940, PEAf Collection, XIII, Banino. According to its label, the second vial may also contain specimens of the original type series: ii (10 ♂, 15 ♀) – Angonia, Massoane [Mozambique], 12.VII.1940, PEAf Collection, XXV, Banino. DAA and IGH have identified all the specimens in these vials as *H. (R.) elliptica*. The other vials contain various ticks of the *H. leachi* group as well as *Rhipicephalus* Koch, 1844 collected from localities in Africa at a later stage.

**Holotype**

Male, Cape of Good Hope (Western Cape Province, South Africa), deposited in the Natural History Museum of Berlin, Berlin, Germany; collection no. ZMB 1099. This specimen has been examined by all of us and studied by DAA and JLC.

**DESCRIPTION AND REDESCRIPTION**

**Male** (Fig. 2A–C, 3A–F)

*Length* from palpal apices to posterior margin of conscutum 2.41–3.54 (3.00 ± 0.19, *n* = 323); *breadth* of conscutum (at widest point) 1.19–1.75 (1.47 ±

0.10, *n* = 322); ratio 1.78–2.32 (2.05 ± 0.10, *n* = 319). *Colour* reddish brown.

*Conscutum* (Fig. 2A–C): *ca* 1.9 times as long as broad; margins slightly convex, broadest at level of

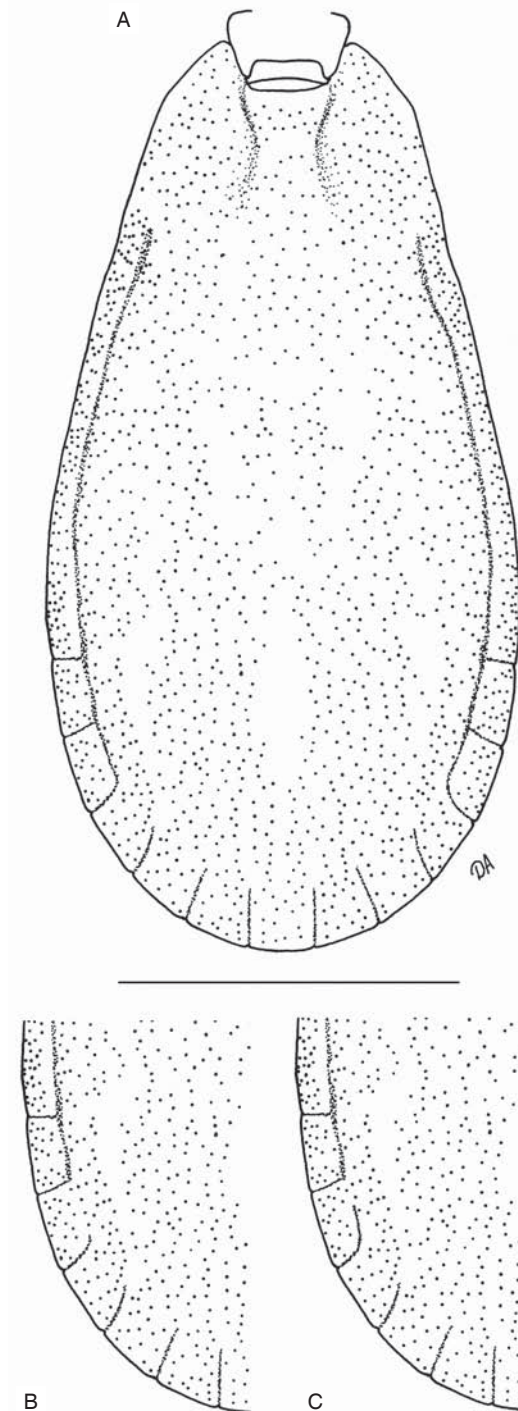


FIG. 2 *Haemaphysalis elliptica*, male, A, conscutum. Bar = 1 mm; B, C, left posterior half of conscutum. Bar = 1 mm. All setation is omitted



spiracular plates, smoothly rounded posteriorly. *Cervical pits* narrow, deep, converging. *Cervical grooves* indistinct, short, shallow, diverging. *Lateral grooves* deep, distinct, extend to anterior 1/4 of scutal length;

enclose first or first and second festoons. *Punctations* dense, medium-sized, discrete, relatively deep. *Festoons* number 11. *Genital structures* (Fig. 3A): as illustrated. *Spiracular plates* (Fig. 3B): variable in

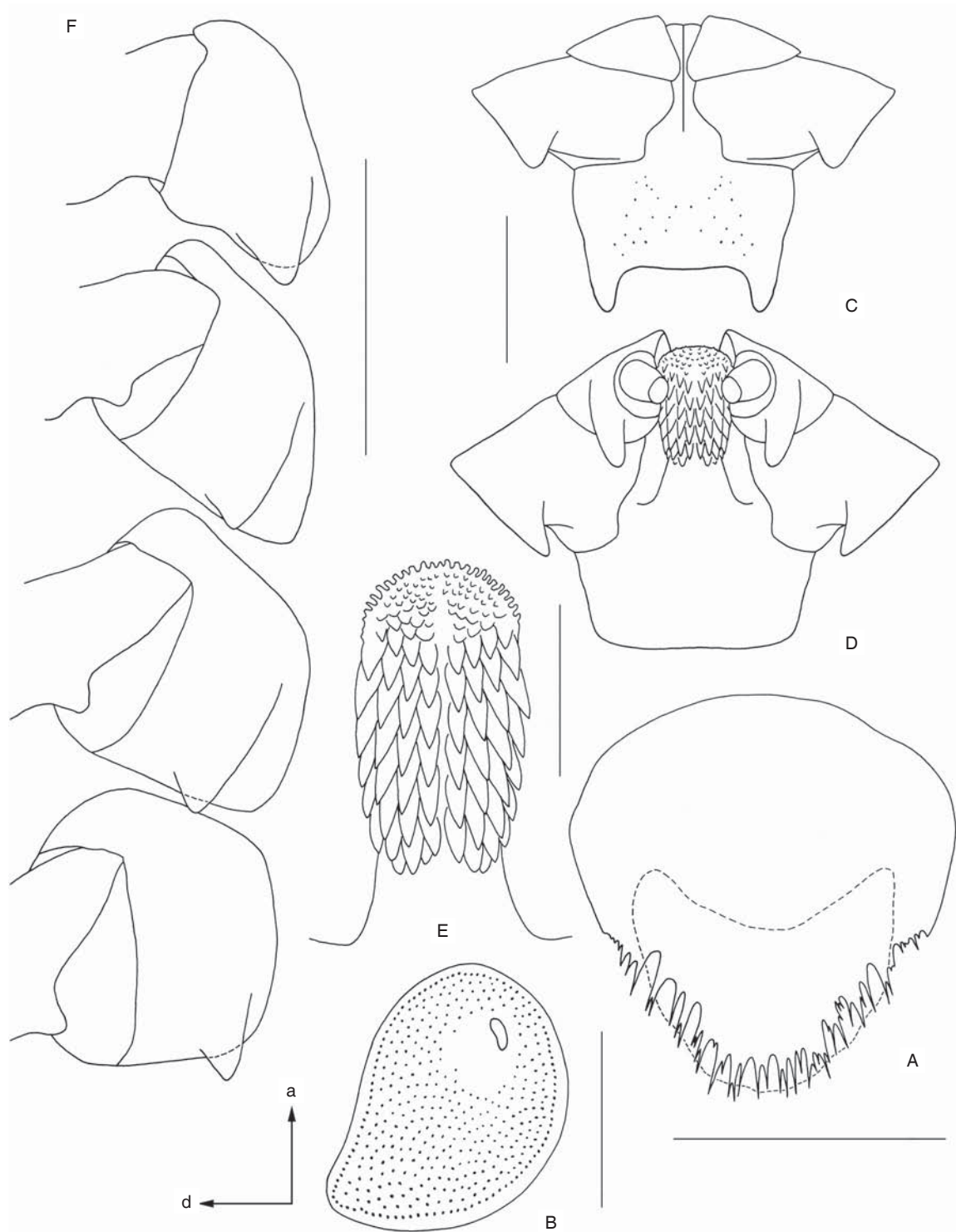


FIG. 3. *Haemaphysalis elliptica*, male, A, genital structures: apron and postgenital sclerite. Bar = 200 µm; B, spiracular plate (a – anterior; d – dorsal). Bar = 200 µm; C, gnathosoma dorsally. Bar = 200 µm; D, gnathosoma ventrally. Bar = 200 µm; E, hypostome. Bar = 100 µm; F, coxae. Bar = 500 µm. All setation is omitted

size, usually slightly broader than long; suboval; dorsal projection triangular.

**Capitulum** (Fig. 3C, D): *Basis capituli* dorsally ca. 1.7 times as broad as long; lateral margins diverging anteriorly; cornua elongately triangular, apices rounded, ca. 1/3 as long as length of basis capituli; ventrally as illustrated. *Palps* broadly salient (*leachi* type); combined breadth ca. 1.9 times breadth of basis capituli. Segment II ca. 1.7 times as broad as long; dorsomedian margin of segment II gradually widening anteriorly at level of its mid-length; postero-dorsal spur large, triangular; posteroventral spur large, triangular, with straight lateral margin. Segment III ca. 1.6 times as broad as long; ca. 1/2 the length of segment II; ventral spur of segment III narrowly elongate, U-shaped apex at level of anterior 1/4 of length of segment II. **Hypostome** (Fig. 3E): slightly shorter than palps; dental formula 4/4; denticles in subequal-length files of 6 or 7.

**Coxae** (Fig. 3F): I to IV each with a short, subtriangular, more or less bluntly pointed spur, extending somewhat beyond coxal margin; spur of coxae IV usually subequal to that of coxae III.

#### Female (Fig. 4, 5A–F)

**Length** from palpal apices to posterior margin of scutum 1.42–1.92 ( $1.73 \pm 0.10$ ,  $n = 131$ ); **breadth** of scutum (at widest point) 0.82–1.14 ( $1.02 \pm 0.06$ ,  $n = 133$ ); **ratio** 1.50–1.86 ( $1.70 \pm 0.07$ ,  $n = 131$ ).

**Scutum** (Fig. 4): ca. 1.3 times as long as broad; anterior margins diverging for anterior 1/5 of total length, subparallel 1/5 of the length, thence gradually converging, bluntly rounded posteriorly; slight postero-lateral angles. **Cervical grooves** narrow arcs extending 2/3 of total scutal length. **Punctations** moderately dense, denser on lateral fields, absent in cervical grooves; medium-sized, discrete, relatively deep. **Posterior lip of genital aperture** (Fig. 5A): broadly U-shaped. **Spiracular plates** (Fig. 5B): varying in size; irregularly suboval or subcircular; dorsal projection short, broadly triangular.

**Capitulum** (Fig. 5C, D): *Basis capituli* dorsally ca. 2.4 times as broad as long; external margins diverging anteriorly; cornua short, broadly triangular, bluntly pointed, ca. 1/6 as long as the length of the of basis capituli; porose areas elongate-oval, tilted inwards, moderate size, widely spaced. *Basis capituli* ventrally as illustrated. *Palps* broadly salient (*leachi* type); combined breadth ca. 1.6 times breadth of basis capituli. Segment II ca. 1.4 times as broad as long; dorsomedian margin of segment II gradually

widening anteriorly at level of its midlength; postero-dorsal spur large, triangular; posterolateral margin straight; posteroventral spur reduced to short rounded projection or curve. Segment III ca. 1.2 times as broad as long; ca. 0.7 times as long as segment II; ventral spur of segment III narrowly U-shaped, elongate, apex at level of anterior 1/3 of length of segment II. **Hypostome** (Fig. 5E): nearly as long as palps; dental formula 4/4; denticles usually in files of 9 or 10.

**Coxae** (Fig. 5F): I to IV each with a short, subtriangular, more or less bluntly pointed spur, extending somewhat beyond coxal margin; spur on coxae IV subequal to that of coxae III.

#### Nymph (Fig. 6A–E)

**Length** (unengorged) from palpal apices to posterior body margin 1 366–1 683 ( $1 543 \pm 77.93$ ,  $n = 32$ ); **breadth** of idiosoma (at widest point) 756–988 ( $896 \pm 62.33$ ,  $n = 32$ ); **ratio** 1.60–1.85 ( $1.73 \pm 0.06$ ,  $n = 32$ ).

**Scutum** (Fig. 6A): length 431–510 ( $472 \pm 20.95$ ,  $n = 32$ ), breadth 421–549 ( $427 \pm 27.71$ ,  $n = 32$ ), ratio 0.92–1.08 ( $1.00 \pm 0.04$ ,  $n = 32$ ); irregularly circular. **Spiracular plates** (Fig. 6B): suboval.

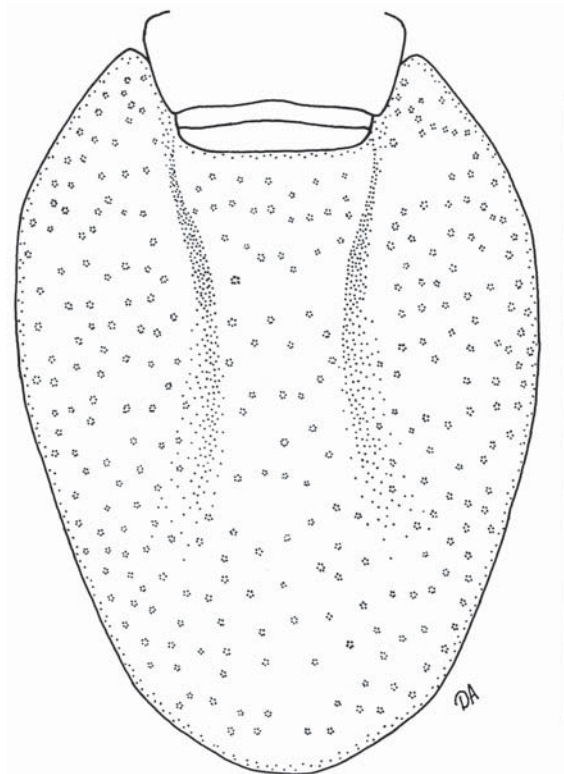


FIG. 4 *Haemaphysalis elliptica*, female, scutum. Bar = 1 mm. All setation is omitted

*Capitulum* (Fig. 6C, D): length 240–284 ( $265 \pm 11.91$ ,  $n = 32$ ), breadth (palps combined) 336–402 ( $371 \pm 16.97$ ,  $n = 32$ ), ratio 0.69–0.79 ( $0.71 \pm 0.004$ ,  $n = 32$ ). *Basis capituli* dorsally subrectangular; cornua slight bulges; ventrally as illustrated. *Palps*: length 167–198 ( $182 \pm 8.69$ ,  $n = 32$ ), breadth 147–181

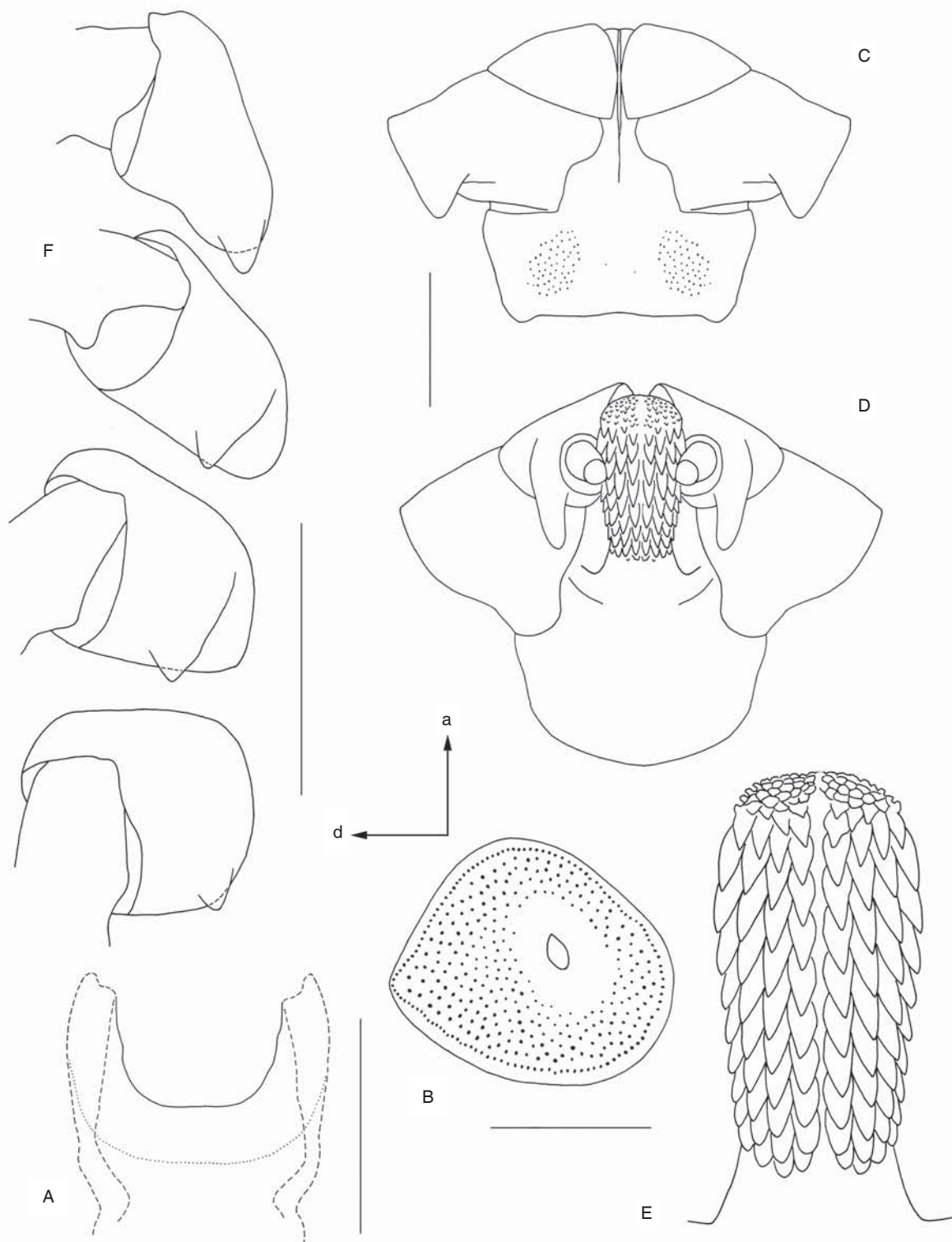


FIG. 5 *Haemaphysalis elliptica*, female, A, genital structures: posterior lip of the genital aperture and vestibular part of vagina. Bar = 200  $\mu$ m; B, spiracular plate (a – anterior; d – dorsal). Bar = 200  $\mu$ m; C, gnathosoma dorsally. Bar = 200  $\mu$ m; D, gnathosoma ventrally. Bar = 200  $\mu$ m; E, hypostome. Bar = 100  $\mu$ m; F, coxae. Bar = 500  $\mu$ m. All setation is omitted

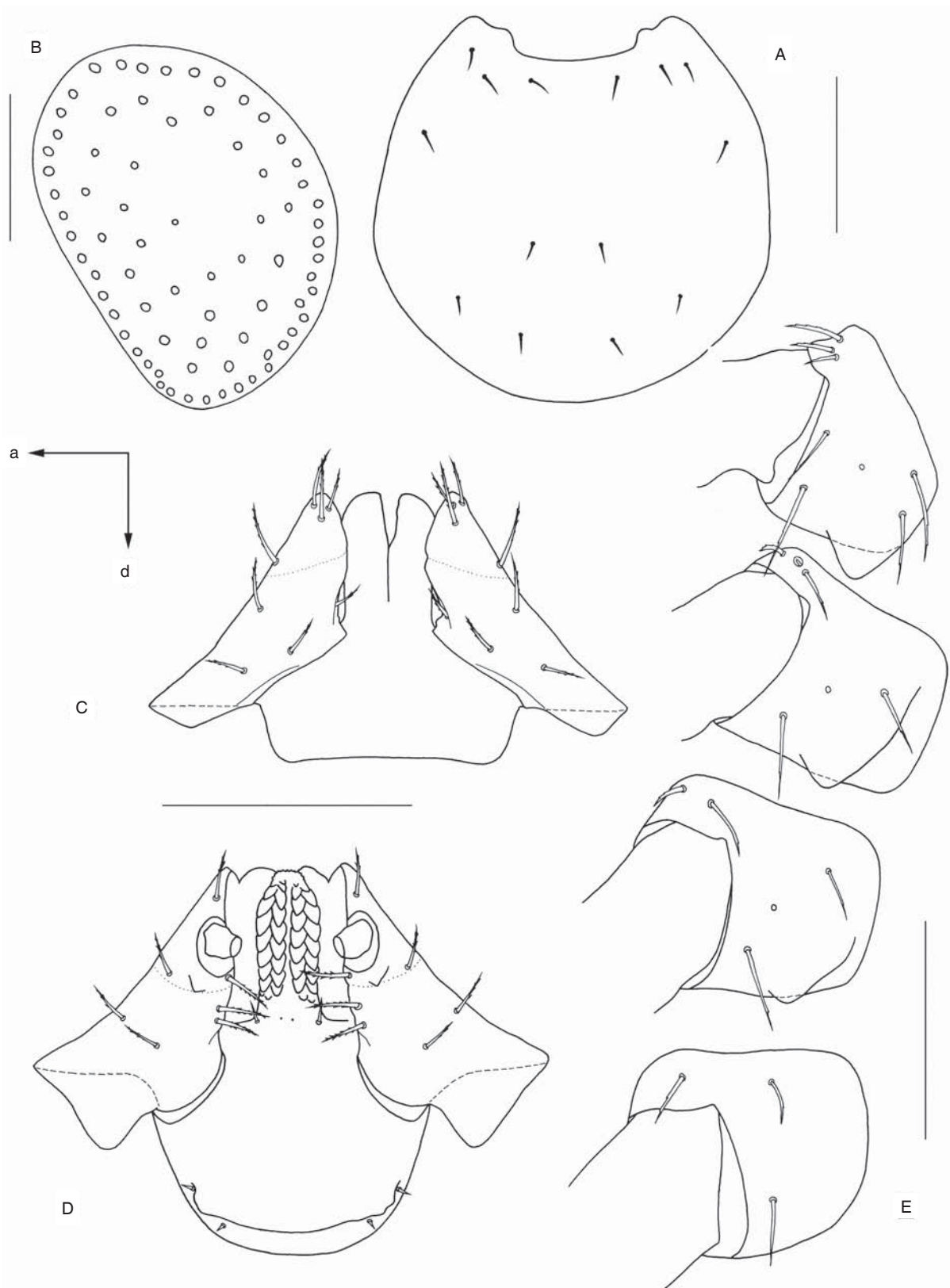


FIG. 6 *Haemaphysalis elliptica*, nymph, A, scutum. Bar = 200 µm; B, spiracular plate (a – anterior; d – dorsal). Bar = 50 µm; C, gnathosoma dorsally. Bar = 200 µm; D, gnathosoma ventrally. Bar = 200 µm; E, coxae. Bar = 200 µm. Setation of palpal segment IV is omitted



( $160 \pm 7.77$ ,  $n = 32$ ), ratio 1.08–1.21 ( $1.14 \pm 0.03$ ,  $n = 32$ ); broadly salient; anterolateral margin slightly concave. Dorsomedian margin of segment II gradually widening anteriorly at level of its midlength; dorsal spur moderate; ventral spur large, broad; lateral margin of spur slightly concave. Ventral spur of seg-

ment III distinct, broadly triangular, with sharp apex. *Hypostome* (Fig. 6D): length 97–116 ( $107 \pm 5.47$ ,  $n = 32$ ), breadth 40–48 ( $45 \pm 2.05$ ,  $n = 32$ ), ratio 2.20–2.67 ( $2.39 \pm 0.10$ ,  $n = 32$ ); nearly as long as palps; dental formula 2/2; denticles in files of 7 to 9 (usually 8).



FIG. 7 *Haemaphysalis elliptica*, larva, A, scutum. Bar = 200  $\mu$ m; B, gnathosoma dorsally. Bar = 100  $\mu$ m; C, gnathosoma ventrally. Bar = 100  $\mu$ m; D, coxae. Bar = 100  $\mu$ m. Setation of palpal segment IV is omitted

**Coxae** (Fig. 6E): coxae I spur prominent, triangular; coxae II and III spur small, triangular; no spur on coxae IV. *Genu*: length 168–212 ( $193 \pm 8.92$ ,  $n = 32$ ), breadth 78–93 ( $86 \pm 4.06$ ,  $n = 32$ ), ratio 2.08–2.43 ( $2.26 \pm 0.09$ ,  $n = 32$ ).

#### Larva (Fig. 7A–D)

*Length* (unengorged) from palpal apices to posterior body margin 657–755 ( $704 \pm 22.01$ ,  $n = 90$ ); *breadth* of idiosoma (at widest point) 461–529 ( $498 \pm 16.80$ ,  $n = 90$ ); *ratio* 1.31–1.53 ( $1.41 \pm 0.04$ ,  $n = 90$ ).

**Scutum** (Fig. 7A): length 220–269 ( $237 \pm 10.24$ ,  $n = 90$ ), breadth 294–372 ( $324 \pm 14.60$ ,  $n = 90$ ), ratio 0.66–0.80 ( $0.73 \pm 0.02$ ,  $n = 90$ ); margins markedly diverging to level of ca. anterior 1/3 of scutal length, subparallel along mid-third; thence abruptly converging, bluntly rounded posteriorly.

**Capitulum** (Fig. 7B, C): length 126–159 ( $143 \pm 6.21$ ,  $n = 90$ ), breadth (palps combined) 189–221 ( $206 \pm 6.25$ ,  $n = 90$ ), ratio 0.65–0.76 ( $0.70 \pm 0.02$ ,  $n = 90$ ). *Basis capituli* dorsally subrectangular; cornua as slight marginal bulges; ventrally as illustrated. *Palps*: length 90–111 ( $99 \pm 4.47$ ,  $n = 90$ ), breadth 74–87 ( $82 \pm 2.92$ ,  $n = 90$ ), ratio 1.12–1.37 ( $1.21 \pm 0.04$ ,  $n = 90$ ); broadly salient; lateral margin slightly concave. Dorsal spur of segment II prominent, broadly rounded; ventral spur of segment II long, broad; lateral margin of spur slightly concave. Ventral spur of segment III distinct, fold-like. *Hypostome* (Fig. 7C): length 57–74 ( $66 \pm 3.43$ ,  $n = 90$ ), breadth 25–30 ( $28 \pm 1.17$ ,  $n = 90$ ), ratio 2.08–2.70 ( $2.38 \pm 0.13$ ,  $n = 90$ ); longer than palps; dental formula 2/2; denticles in files of 7 or 8.

**Coxae** (Fig. 7D): coxae I spur moderate, triangular; coxae II and III spur short, fold-like. *Genu*: length 99–129 ( $112 \pm 5.69$ ,  $n = 90$ ), breadth 48–61 ( $54 \pm 2.82$ ,  $n = 90$ ), ratio 1.83–2.22 ( $2.06 \pm 0.09$ ,  $n = 90$ ).

### *Haemaphysalis (Rhipistoma) leachi* (Audouin, 1826)

THE YELLOW DOG HAEMAPHYSALID  
(Fig. 8–13)

#### Synonyms

*Haemaphysalis leachi humerosoides* Theiler, 1943  
*sensu* Hoogstraal 1956.

*Haemaphysalis leachi humerosoides* Theiler, 1943  
*sensu* Santos Dias, 1958.

*Haemaphysalis leachi humerosoides* Theiler, 1943  
*sensu* Theiler, 1962.

*Haemaphysalis leachi humerosoides* Theiler, 1943  
*sensu* Camicas *et al.* 1998.

#### Neotype

Male, collected as an engorged nymph in a nest of *Arvicanthis niloticus niloticus* (Desmarest, 1822) at Kirdasa, Imbaba, Giza, Egypt, 14 June 1953 by H. Hoogstraal (moulted to adult in laboratory, 28 June 1953). The neotype was selected by Hoogstraal and

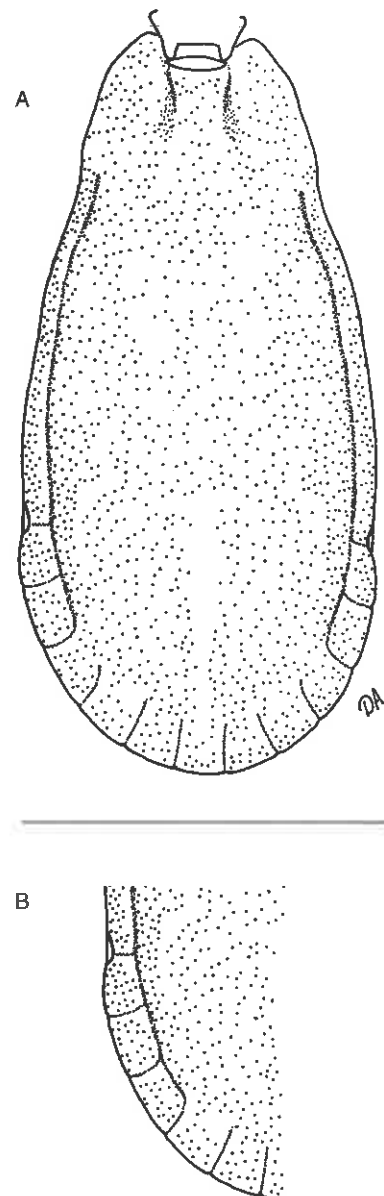


FIG. 8 *Haemaphysalis leachi*, male, A, conscutum. Bar = 1 mm; B, left posterior half of conscutum. Bar = 1 mm. All setation is omitted

deposited in the United States National Tick Collection, Georgia Southern University, Statesboro, USA; collection number: 56757. This specimen has been examined by DAA.

## REDESCRIPTION

### Male (Fig. 8A, B, 9A–F)

*Length* from palpal apices to posterior body margin 1.88–2.97 ( $2.45 \pm 0.15$ ,  $n = 714$ ); *breadth* of conscutum (at widest point) 0.82–1.29 ( $1.06 \pm 0.07$ ,  $n = 718$ ); *ratio* 1.94–2.78 ( $2.30 \pm 0.12$ ,  $n = 698$ ). *Colour* yellowish brown.

*Conscutum* (Fig. 8A, B): ca. 2.1 times as long as broad; margins slightly convex, broadest at level of spiracular plates, smoothly rounded posteriorly. *Cervical pits* narrow, deep, converging. *Cervical grooves* indistinct, short, shallow, diverging. *Lateral grooves* deep, distinct, extend to anterior 1/4 of scutal length; enclose first two or three festoons. *Punctations* dense, medium-sized, discrete, walls vertical, relatively deep. *Festoons* number 11. *Genital apron* (Fig. 9A): as illustrated. *Spiracular plates* (Fig. 9B): variable in size, usually slightly longer than broad; suboval or subrectangular; dorsal projection bluntly triangular.

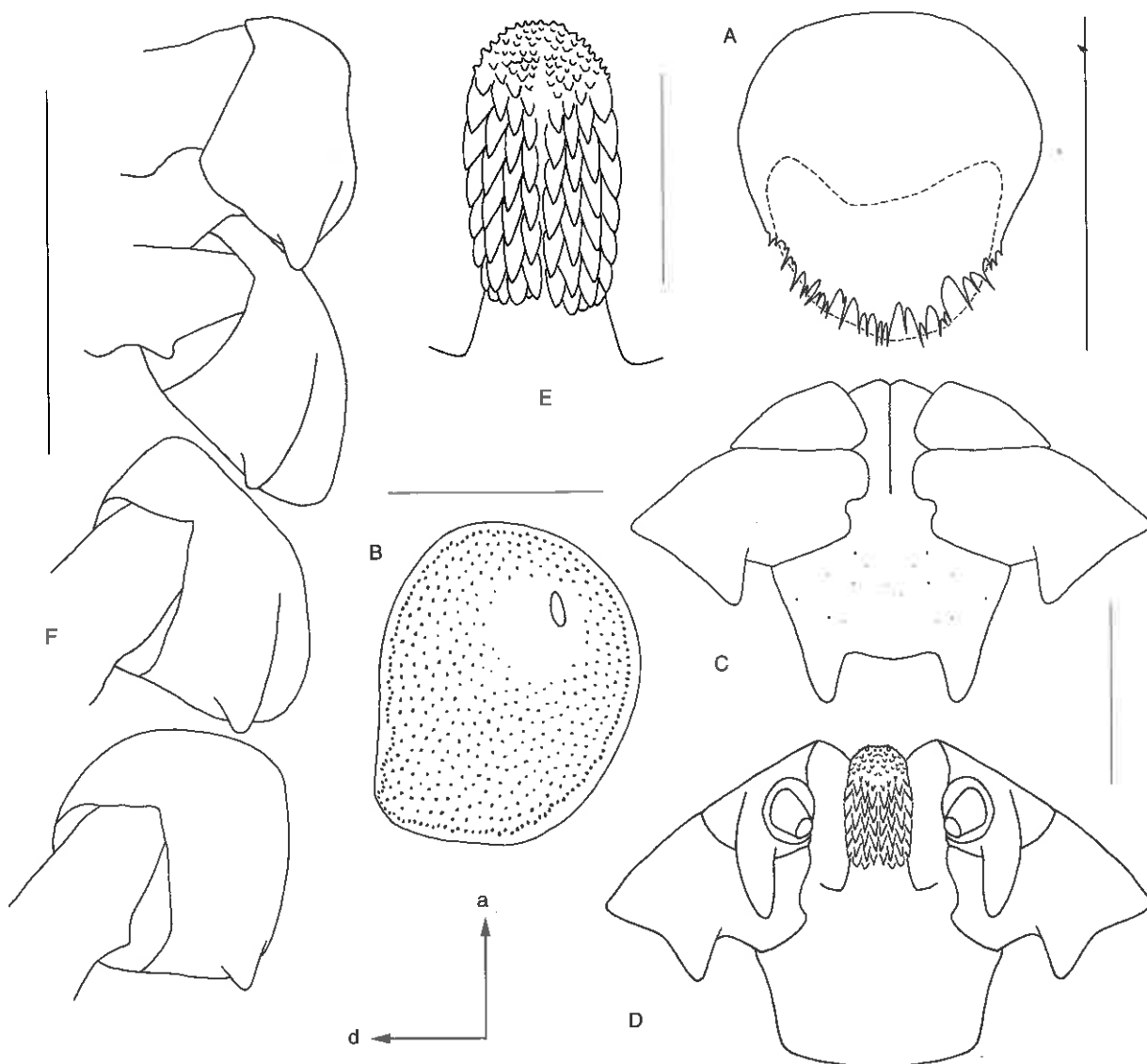


FIG. 9 *Haemaphysalis leachi*, male, A, genital structures: apron and postgenital sclerite. Bar = 200  $\mu$ m; B, spiracular plate (a – anterior; d – dorsal). Bar = 200  $\mu$ m; C, gnathosoma dorsally. Bar = 200  $\mu$ m; D, gnathosoma ventrally. Bar = 200  $\mu$ m; E, hyposome. Bar = 100  $\mu$ m; F, coxae. Bar = 500  $\mu$ m. All setation is omitted

**Capitulum** (Fig. 9C, D): *Basis capituli* dorsally ca. 1.7 times as broad as long; lateral margins diverging slightly anteriorly; cornua elongately triangular, apices rounded, ca. 1/3 as long as length of basis capituli; ventrally as illustrated. *Palps* broadly salient (*leachi* type); combined breadth ca. 2.1 times breadth of basis capituli. Segment II ca. 1.8 times as broad as long; dorsomedian margin of segment II sharply bulging anteriorly at mid-length; postero-dorsal spur large, triangular; posteroventral spur large, triangular; lateral margin of spur markedly concave. Segment III ca. 1.7 times as broad as long; ca. 1/2 as long as segment II; ventral spur of segment III narrowly elongate, apex at level of mid-length of segment II. *Hypostome* (Fig. 9E): slightly shorter than palps; dental formula 4/4; denticles in subequal-length files of 6 or 7.

**Coxae** (Fig. 9F): I to IV each with a short, subtriangular, more or less bluntly pointed spur, extending somewhat beyond coxal margin; spur of coxae IV usually shorter than that of coxae III.

#### Female (Fig. 10, 11A–F)

*Length* from palpal apices to posterior scutal margin 1.17–1.70 ( $1.53 \pm 0.08$ ,  $n = 267$ ); *breadth* of scutum

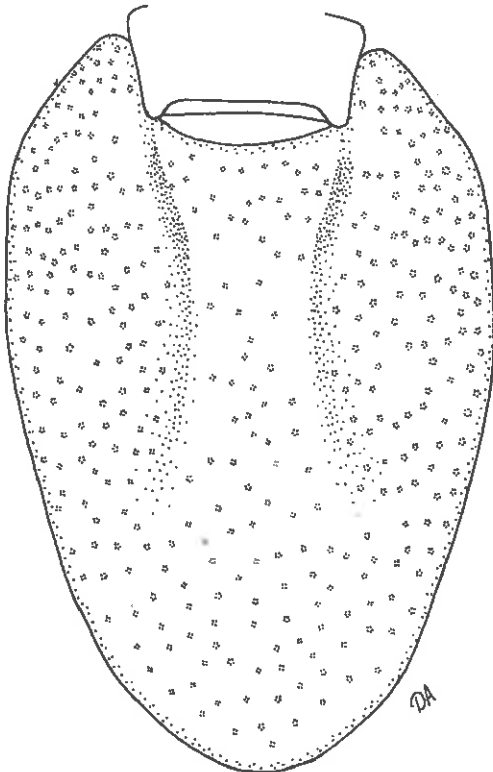


FIG. 10 *Haemaphysalis leachi*, female, scutum. Bar = 1 mm. All setation is omitted

(at widest point) 0.66–0.96 ( $0.84 \pm 0.04$ ,  $n = 267$ ); *ratio* 1.58–2.14 ( $1.81 \pm 0.08$ ,  $n = 267$ ). *Colour* yellowish brown.

**Scutum** (Fig. 10): ca. 1.4 times as long as broad; margins diverging for anterior 1/5 of total length, subparallel 1/5 of length, thence gradually converging, bluntly rounded posteriorly; slight postero-lateral angles. *Cervical grooves* narrow arcs extending 2/3 of total scutal length. *Punctations* moderately dense, denser on lateral fields, absent in cervical grooves; medium-sized, discrete, walls vertical, relatively deep. *Genital aperture* (Fig. 11A): posterior lip broadly U-shaped. *Spiracular plates* (Fig. 11B): variable in size; irregularly subcircular; dorsal projection short, broadly triangular.

**Capitulum** (Fig. 11C, D): *Basis capituli* dorsally ca. 2.2 times as broad as long; external margins slightly diverging anteriorly; cornua relatively long, broadly triangular, bluntly pointed, ca. 1/4 as long as length of basis capituli; porose areas elongately-oval, tilted inwards, moderate size, widely spaced. *Basis capituli* ventrally as illustrated. *Palps* broadly salient (*leachi* type); combined breadth ca. 1.8 times breadth of basis capituli. Segment II ca. 1.5 times as broad as long; dorsomedian margin of segment II sharply bulging anteriorly at mid-length; postero-dorsal spur large, triangular; posterolateral margin slightly concave; posteroventral spur reduced to short, rounded projection or curve. Segment III ca. 1.4 times as broad as long; ca. 0.6 times as long as segment II; ventral spur of segment III narrowly elongate, apex at level of mid-length of segment II. *Hypostome* (Fig. 11E): nearly as long as palps; dental formula 4/4; denticles in files usually of 8 or 9.

**Coxae** (Fig. 11F): I to IV each with a short, subtriangular, more or less bluntly pointed spur, extending somewhat beyond coxal margin; spur on coxae IV subequal or shorter than that on coxae III.

#### Nymph (Fig. 12A–E)

*Length* (unengorged) from palpal apices to posterior body margin 1 293–1 427 ( $1 344 \pm 45.04$ ,  $n = 8$ ); *breadth* of idiosoma (at widest point) 707–817 ( $755 \pm 36.55$ ,  $n = 8$ ); *ratio* 1.66–1.84 ( $1.78 \pm 0.06$ ,  $n = 8$ ).

**Scutum** (Fig. 12A): length 392–431 ( $412 \pm 13.86$ ,  $n = 10$ ), breadth 402–446 ( $416 \pm 12.53$ ,  $n = 10$ ), ratio 0.95–1.02 ( $0.99 \pm 0.02$ ,  $n = 10$ ); irregularly sub-circular. *Spiracular plates* (Fig. 12B): suboval.

**Capitulum** (Fig. 12C, D): length 208–252 ( $236 \pm 11.62$ ,  $n = 10$ ), breadth (palps combined) 326–363 ( $339 \pm 13.53$ ,  $n = 10$ ), ratio 0.64–0.72 ( $0.70 \pm 0.02$ ,



$n = 10$ ). *Basis capituli* dorsally subrectangular; cornua slight bulges; ventrally as illustrated. *Palps*: length 152–167 ( $158 \pm 4.48$ ,  $n = 10$ ), breadth 142–162 ( $150 \pm 6.68$ ,  $n = 10$ ), ratio 1.00–1.12 ( $1.06 \pm 0.04$ ,  $n = 10$ ); broadly salient; anterolateral margin markedly concave. Dorsomedian margin of segment II widening sharply anteriorly at level of its midlength; dorsal spur moderate; ventral spur large, narrow; posterolateral margin distinctly concave. Ventral spur of segment III distinct, triangular, with sharp apex.

*Hypostome* (Fig. 12D): length 76–94 ( $87 \pm 5.68$ ,  $n = 10$ ), breadth 36–41 ( $38 \pm 1.63$ ,  $n = 10$ ), ratio 1.94–2.50 ( $2.28 \pm 0.16$ ,  $n = 10$ ); nearly as long as palps; dental formula 2/2; denticles in files of 5 or 6.

*Coxae* (Fig. 12E): coxae I spur moderate, triangular; coxae II and III spur small, triangular; no spur on coxae IV. *Genu*: length 160–184 ( $167 \pm 7.24$ ,  $n = 10$ ), breadth 71–80 ( $76 \pm 2.92$ ,  $n = 9$ ), ratio 2.03–2.42 ( $2.19 \pm 0.11$ ,  $n = 9$ ).

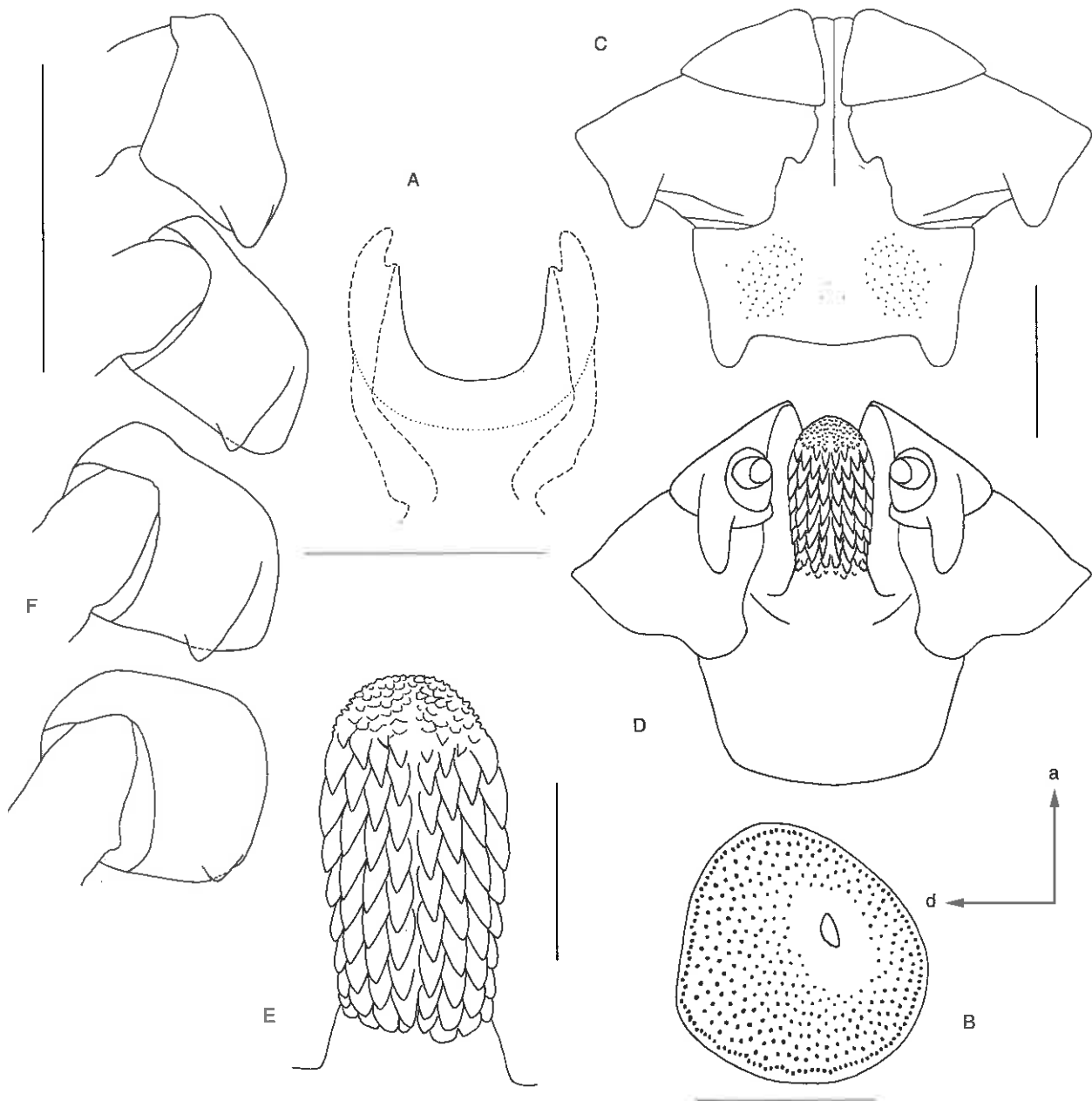


FIG. 11 *Haemaphysalis leachi*, female, A, genital structures: posterior lip of the genital aperture and vestibular part of vagina. Bar = 200  $\mu\text{m}$ ; B, spiracular plate (a – anterior; d – dorsal). Bar = 200  $\mu\text{m}$ ; C, gnathosoma dorsally. Bar = 200  $\mu\text{m}$ ; D, gnathosoma ventrally. Bar = 200  $\mu\text{m}$ ; E, hypostome. Bar = 100  $\mu\text{m}$ ; F, coxae. Bar = 500  $\mu\text{m}$ . All setation is omitted

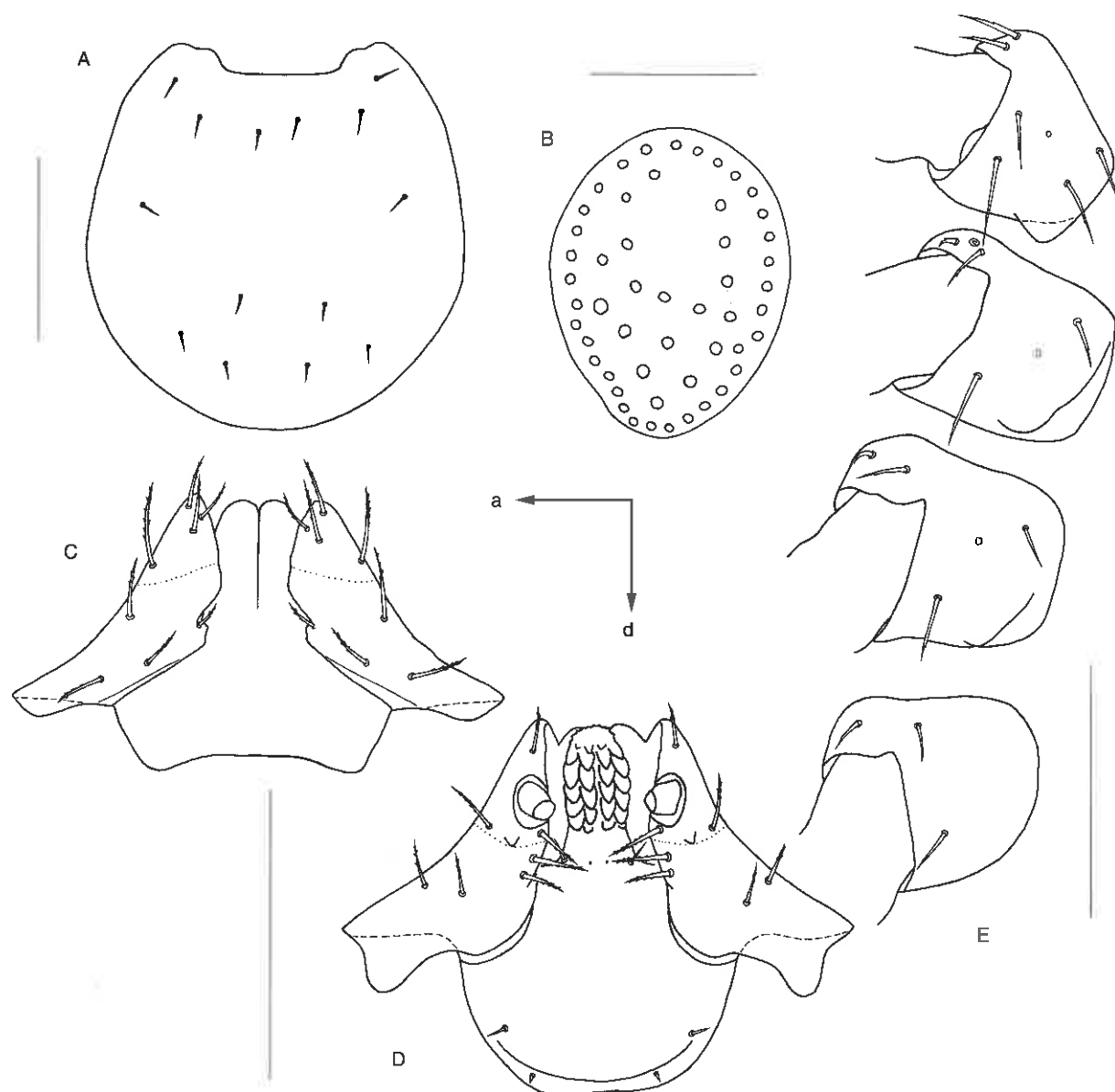


FIG. 12 *Haemaphysalis leachi*, nymph, A, scutum. Bar = 200  $\mu$ m; B, spiracular plate (a – anterior; d – dorsal). Bar = 50  $\mu$ m; C, gnathosoma dorsally. Bar = 200  $\mu$ m; D, gnathosoma ventrally. Bar = 200  $\mu$ m; E, coxae. Bar = 200  $\mu$ m. Setation of palpal segment IV is omitted

### Larva (Fig. 13A–D)

*Length* (unengorged) from palpal apices to posterior body margin 608–681 ( $652 \pm 17.56$ ,  $n = 116$ ); *breadth* of idiosoma (at widest point) 431–559 ( $457 \pm 16.05$ ,  $n = 112$ ); *ratio* 1.14–1.50 ( $1.43 \pm 0.05$ ,  $n = 112$ ).

*Scutum* (Fig. 13A): length 196–225 ( $208 \pm 6.64$ ,  $n = 117$ ), breadth 279–323 ( $302 \pm 9.30$ ,  $n = 120$ ), ratio 0.62–0.74 ( $0.69 \pm 0.02$ ,  $n = 117$ ); margins sharply diverging to level of ca. anterior 1/3 of scutal length, subparallel along mid-third; thence abruptly converging, bluntly rounded posteriorly.

*Capitulum* (Fig. 13B, C): length 117–140 ( $128 \pm 4.74$ ,  $n = 119$ ), breadth (palps combined) 177–205 ( $192 \pm 4.78$ ,  $n = 118$ ), ratio 0.61–0.73 ( $0.67 \pm 0.02$ ,  $n = 117$ ). *Basis capituli* dorsally subrectangular; cornua as slight marginal bulges; ventrally as illustrated. *Palps*: length 87–108 ( $97 \pm 4.25$ ,  $n = 120$ ), breadth 67–80 ( $73 \pm 2.61$ ,  $n = 120$ ), ratio 1.18–1.44 ( $1.32 \pm 0.06$ ,  $n = 120$ ); broadly salient; lateral margin slightly concave. Dorsal spur of segment II prominent, slightly tapering to apex; ventral spur of segment II long, relatively narrow; lateral margin of spur distinctly concave. Ventral spur of segment III dis-

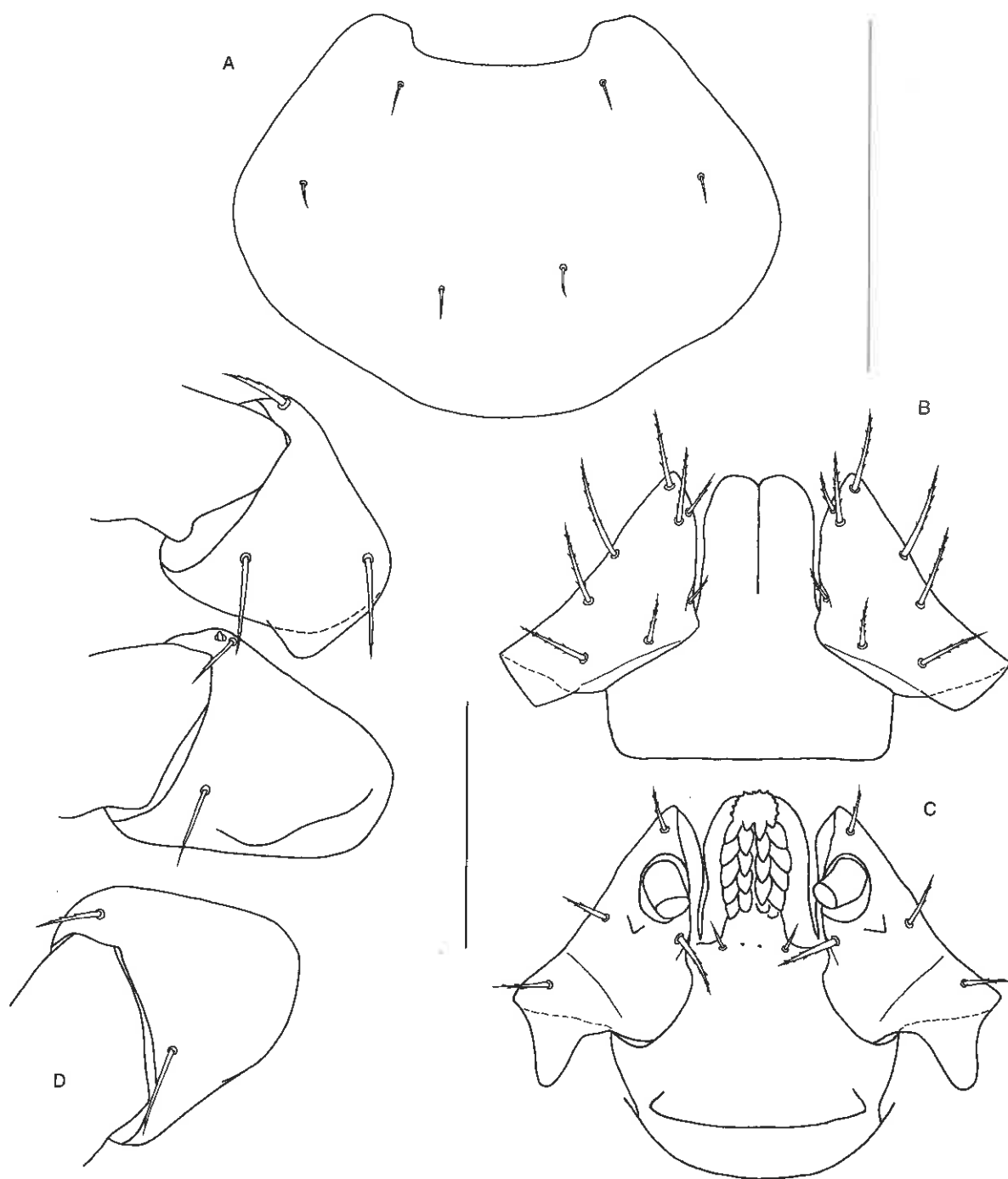


FIG. 13 *Haemaphysalis leachi*, larva, A, scutum. Bar = 200  $\mu$ m; B, gnathosoma dorsally. Bar = 100  $\mu$ m; C, gnathosoma ventrally. Bar = 100  $\mu$ m; D, coxae. Bar = 100  $\mu$ m. Setation of palpal segment IV is omitted

tinct, triangular, pointed apex. *Hypostome* (Fig. 13C): length 52–62 ( $57 \pm 2.36$ ), breadth 22–28 ( $25 \pm 1.53$ ,  $n = 120$ ), ratio 1.92–2.74 ( $2.28 \pm 0.19$ ,  $n = 119$ ); longer than palps; dental formula 2/2; denticles in files of 4 to 6 (usually 5).

*Coxae* (Fig. 13D): coxae I spur moderate, triangular;

coxae II and III spur short, fold-like. *Genu*: length 103–120 ( $114 \pm 3.51$ ,  $n = 119$ ), breadth 48–60 ( $54 \pm 2.27$ ,  $n = 110$ ), ratio 1.88–2.38 ( $2.11 \pm 0.11$ ,  $n = 110$ ).

The differential diagnosis of the two species is summarized in Table 4.

TABLE 1 *Haemaphysalis (Rhipistoma) elliptica* (Koch, 1844), material examined

No. of ticks		Host	Locality	Date of collection	Collector	Collection no.*
♂	♀					
<b>Democratic Republic of Congo</b>						
13	10	Domestic dog	Monigi	05 Aug 1949	F. Schoenaers	027837
<b>Kenya</b>						
1		<i>Lepus capensis</i>	Nairobi	09 Jan 1968	J.E.C. Flux	095065
	2	Domestic dog	Nairobi airport	22 Sep 1954	C.B. Philip	032318
1	2	Domestic dog	Nairobi-Kilimani area	22 Sep 1953	C.B. Philip	032319
1	1	Domestic dog	Rift Valley, Nakuru dist., Subukiya	26 Jun 1948	H. Hoogstraal	123754
28	12	<i>Civettictis civetta</i>	Rift Valley, Narok, Langata	Mar 1964	R. Harmsen	095064
3		<i>Civettictis civetta</i>	Sultan Hamud	26 Sep 1953	C.B. Philip, Barnett	032320
1				1976	A.E. Bianco	123755
1	2			1976	A.E. Bianco	123756
<b>South Africa</b>						
10	12	Domestic cat	Grahamstown	23 Jul 1936	F. Zumpt	123748
4+	2*	<i>Otomys irroratus</i> (nest of)	Johannesburg	Aug 1957		123759
2		<i>Canis mesomelas</i>	Johannesburg (imported into USA: Missouri, Jackson County, Kansas City, Kansas City Zoo)	1995	E.C. Greiner	121742
	1		Kruger National Park, Krugertabletkop	03 Mar 1989	J.E. Keirans	119549
2	7	<i>Canis mesomelas</i>	Kruger National Park, Skukuza	20 Feb 1969		123749
	1	Domestic dog	North Transvaal, Naboomspruit			123750
1			Transvaal, Bon Accord	Nov 1951	R.A. Cooley	120362
	1		Transvaal, Bon Accord, Onderstepoort	Nov 1951	R.A. Cooley	120364
2	1	<i>Canis mesomelas</i>	Transvaal, Bon Accord, Onderstepoort	14 Apr 1952		120368
	4	<i>Tatera nest</i>	Transvaal, Potchefstroom	06 Oct 1965		123751
2	1		Transvaal, Randfontein			123752
						123747
<b>Tanzania</b>						
4		<i>Civettictis civetta</i>	Coast, Dar es Salaam, University campus	15 Sep 1974	K.M. Howell	106728
3	4	<i>Panthera leo</i>	Mara, Serengeti National Park	16 Oct 1966	G.R. Schaller	094949
1		<i>Canis mesomelas</i>	Mara, Serengeti Plains, Seronera	25 Sep 1974	D. Schmidt	095204
1	1	<i>Canis mesomelas</i>	Mara, Serengeti Plains, Seronera	22 Nov 1974	D. Schmidt	094955
	1	<i>Panthera leo</i>	Serengeti National Park	21 Aug 1985	L. Herbst	118227
	1	<i>Panthera leo</i>	Serengeti National Park	21 Aug 1985	L. Herbst	118254



TABLE 1 (cont.)

No. of ticks		Host	Locality	Date of collection	Collector	Collection no.*
♂	♀					
<b>Tanzania (cont.)</b>						
	2	<i>Panthera leo</i>	Serengeti National Park	21 Aug 1985	L. Herbst	118206
1		<i>Panthera leo</i>	Serengeti National Park	02 Oct 1985	L. Herbst	118219
1	4	<i>Panthera leo</i>	Serengeti National Park	21 Aug 1985	L. Herbst	118251
2	1	<i>Panthera leo</i>	Serengeti National Park	11 Sep 1985	L. Herbst	118235
	3	<i>Panthera leo</i>	Serengeti National Park	26 Sep 1985	L. Herbst	118237
4	1	<i>Panthera leo</i>	Serengeti National Park	25 Aug 1985	L. Herbst	118226
	2	<i>Panthera leo</i>	Serengeti National Park, along Seronera River	03 Oct 1985	L. Herbst	118215
1	2	<i>Panthera leo</i>	Serengeti National Park, at Downey's Dam	26 Sep 1985	L. Herbst	118257
	1	<i>Panthera leo</i>	Serengeti National Park, base of Nyamanga River	02 Aug 1985	L. Herbst	118248
3	1	<i>Panthera leo</i>	Serengeti National Park, base of Nyamanga River	02 Aug 1985	L. Herbst	118246
	1	<i>Panthera leo</i>	Serengeti National Park, base of Nyamanga River	05 Sep 1985	L. Herbst	118225
	6	<i>Panthera leo</i>	Serengeti National Park, base of Nyamanga River	05 Sep 1985	L. Herbst	118212
4	3	<i>Panthera leo</i>	Serengeti National Park, Loliondo South Kopjes	02 Sep 1985	L. Herbst	118218
	1	<i>Panthera leo</i>	Serengeti National Park, near Masai Marsh	31 Aug 1985	L. Herbst	118220
3	1	<i>Panthera leo</i>	Serengeti National Park, near Masai Marsh	31 Aug 1985	L. Herbst	118229
	1	<i>Panthera leo</i>	Serengeti National Park, Simba Kopjes	21 Sep 1985	L. Herbst	118240
	1	<i>Panthera leo</i>	Serengeti National Park, Simba Kopjes	21 Sep 1985	L. Herbst	118209
<b>Uganda</b>						
22	3	<i>Canis aureus</i>	Ruwenzori National Park		M.H. Woodford	088635
<b>Zambia</b>						
Many	Many	<i>Canis adustus</i>	Chipata, Susa Camp	08 Aug 1980	S.G.A. Weak	123753
1		<i>Civettictis civetta</i>	Lochinvar	Jul 1959		123757
4		<i>Civettictis civetta</i>	Lochinvar	Jul 1959	F. Zumpt	091302
1		<i>Panthera leo</i>	Southern, Namwala	19 Aug 1951	J.G. Matthysse	091294
<b>Zimbabwe</b>						
2	2	Domestic cat	Manicaland, Umtali, Maranke T.T.L.	1976	R.A.I. Norval	103030
5	4	Domestic dog	Mashonaland North, Mukwichi T.T.L., Kadunga Dip	19 Aug 1976	R.A.I. Norval	103028
2+	2+	<i>Canis familiaris</i>	Mashonaland South, Salisbury	1980	R.A.I. Norval	121602
21		<i>Civettictis civetta</i>	Mashonaland South, Salisbury, Atlantica Foundation Research Station	07 Jul 1977	R.A.I. Norval	107272
5		<i>Civettictis civetta</i>	Mashonaland South, Salisbury, Calgary Farm	16 May 1977	R.A.I. Norval	107096
1		<i>Civettictis civetta</i>	Mashonaland South, Salisbury, Calgary Farm	14 Feb 1977	R.A.I. Norval	121599

TABLE 1 (cont.)

No. of ticks		Host	Locality	Date of collection	Collector	Collection no.*
♂	♀					
<b>Zimbabwe (cont.)</b>						
3	2	<i>Felis silvestris</i> (= <i>lybica</i> )	Mashonaland South, Salisbury, Mazoe Vet. Farm	06 Sep 1976	R.A.I. Norval	103029
10	10	<i>Canis mesomelas</i>	Mashonaland South, Salisbury, Mt. Pleasant	10 Sep 1976	R.A.I. Norval	103026
30	14	<i>Canis adustus</i>	Mashonaland South, Salisbury, Wingate Club	23 Dec 1976	R.A.I. Norval	107097
1		<i>Atelrix albiventris</i>	Matabeleland, Bulawayo	04 Feb 1981	R.A.I. Norval	121600
5	3	<i>Felis silvestris</i> (= <i>lybica</i> )	Matabeleland, Bulawayo, Khami prison	05 May 1976	R.A.I. Norval	103032
3	6	Domestic dog	Matabeleland, Shashani, Tribal Trust Land (T.T.L.), Sinti Dip	14 Oct 1976	R.A.I. Norval	103027
16	2	<i>Civettictis civetta</i>	N Rhodesia, Chizarira Nat. Park, Manzituba Camp	03 Jun 1976	R.A.I. Norval	103033
2	1	<i>Panthera pardus</i>	NW Rhodesia, Matetsi, Safari Area, Dibangombe Siding	18 Jun 1976	R.A.I. Norval	103031
<b>I.G. Horak collection (South Africa &amp; Mozambique)</b>						
23	18	Vegetation	Kruger National Park (KNP) 2510 S, 3144 E (Horak <i>et al.</i> 2006)	Jan to Dec 1999	I.G. Horak	Burnplots
31	28	Vegetation	KNP 2508 S, 3138 E (Horak <i>et al.</i> 2006)	Jan to Dec 1999	I.G. Horak	Burnplots
358	327	Vegetation	KNP 2510 S, 3144 E (Horak <i>et al.</i> 2006)	Jan to Dec 2000	I.G. Horak	Burnplots
287	316	Vegetation	KNP 2508 S, 3138 E (Horak <i>et al.</i> 2006)	Jan to Dec 2000	I.G. Horak	Burnplots
65	77	Vegetation	KNP 2510 S, 3144 E (Horak <i>et al.</i> 2006)	Jan to Dec 2001	I.G. Horak	Burnplots
116	95	Vegetation	KNP 2508 S, 3138 E (Horak <i>et al.</i> 2006)	Jan to Dec 2001	I.G. Horak	Burnplots
24	29	Vegetation	KNP 2510 S, 3144 E (Horak <i>et al.</i> 2006)	Jan to Mar 2002	I.G. Horak	Burnplots
43	45	Vegetation	KNP 2508 S, 3138 E (Horak <i>et al.</i> 2006)	Jan to Mar 2002	I.G. Horak	Burnplots
167	194	Vegetation	KNP 2516 S, 3204 E (Spickett <i>et al.</i> 1992)	Aug 1988 to Mar 2002	I.G. Horak	Burnplots
98	100	Vegetation	KNP 2458 S, 3136 E (Spickett <i>et al.</i> 1992)	Aug 1988 to Mar 2002	I.G. Horak	Burnplots
77	573	<i>Canis familiaris</i>	Maputaland, KwaZulu-Natal (Horak <i>et al.</i> 2001)	Feb 1999 to Apr 2000	I.G. Horak	Zone 17N
107	100	<i>Canis familiaris</i>	Maputo 2557 S, 3235 E and vicinity, Mozambique (Neves <i>et al.</i> 2004)		Various	Zone 4
410	826	<i>Canis familiaris</i>	Individual owners, Stellenbosch 3355 S, 1850 E (Horak & Matthee 2003)	Sep 2000 to Dec 2001	Owners	WP Dogs
560	4 566	<i>Canis familiaris</i>	Vet. clinics and animal shelter, Stellenbosch 3355 S, 1850 E (Horak & Matthee 2003)	Oct 2000 to Dec 2002	Vet. assistants	WP Dogs
506	449	<i>Canis familiaris</i>	Animal shelter, Franschoek 3350 S, 1907 E (Horak & Matthee 2003)	Dec 2001 to Dec 2002	Assistants	WP dogs
25	168	<i>Canis familiaris</i>	Eastern Eastern Cape Province (Nyangiwe <i>et al.</i> 2006)	Jan 2004 to May 2005	N. Nyangiwe	OP dogs
1 184	843	<i>Canis familiaris</i>	Vet. Faculty Clinic, Onderstepoort (Horak 1995)	Jun 1991 to May 1994	Vet. students	OP dogs

TABLE 1 (cont.)

No. of ticks		Host	Locality	Date of collection	Collector	Collection no.*
♂	♀					
<b>I.G. Horak collection (South Africa &amp; Mozambique) (cont.)</b>						
2 426	3 720	<i>Canis familiaris</i>	Grahamstown 3319 S, 2632 E (Horak <i>et al.</i> 1987)	Aug 1983 to Jul 1986	Owners	
87	269	<i>Canis familiaris</i>	Boschkop, North West Province	Oct 1999 to May 2000	Z. v.d. Merwe	
6	9	<i>Canis familiaris</i>	Luala, 1744 S, 3615 E, Zambesia Prov. Mozambique (Neves <i>et al.</i> 2004)		G. Bester	
2	2	<i>Canis familiaris</i>	Xai-Xai, 2506 S, 3334 E Gaza Prov. Mozambique (Neves <i>et al.</i> 2004)		G. Bester	
70	65	Domestic cats	Vet. clinic Stellenbosch 3355 S, 1850 E (Horak & Matthee 2003)	Oct 2000 to Dec 2002	Assistant	Cats
604	663	Domestic cat	Pretoria	Sep 2003 to May 2006	N. Donkin	Cats
3	1	<i>Canis mesomelas</i> (1)	KNP (Horak <i>et al.</i> 2000)		I.G. Horak	
4	5	<i>Canis mesomelas</i> (1)	Vekeerdevlei, Free State (Horak <i>et al.</i> 2000)			
159	34	<i>Acinonyx jubatus</i> (3)	KNP (Horak <i>et al.</i> 2000)		I.G. Horak	
2 198	831	<i>Panthera leo</i> (19)	KNP (Horak <i>et al.</i> 2000)		I.G. Horak	
63	26	<i>Panthera pardus</i> (3)	KNP (Horak <i>et al.</i> 2000)		I.G. Horak	
1	6	<i>Panthera pardus</i> (1)	Roodplaat Dam, Gauteng (Horak <i>et al.</i> 2000)			
85	23	<i>Civettictis civetta</i> (4)	KNP (Horak <i>et al.</i> 2000)		I.G. Horak	
8	7	<i>Parahyaena brunnea</i> (1)	Bon Accord, Gauteng (Horak <i>et al.</i> 2000)		I.G. Horak	

\* All the collection numbers are those of specimens in the United States National Tick Collection

+ Reared specimens

TABLE 2 *Haemaphysalis (Rhipistoma) leachi* (Audouin, 1826), material examined

No. of ticks		Host	Locality	Date of collection	Collector	Collection no.*
♂	♀					
<b>Cameroon</b>						
1		Domestic dog		26 Dec 1949		094716
<b>Central African Republic</b>						
4	4	<i>Panthera leo</i>	Bamingui Bangoran, Bamingui, Gazao		J. Thal	096988
2	3	Domestic dog	La Topia	12 Aug 1969	G. Uilenberg	096991
3	18	Domestic dog	Nana Nambere, Bouar	23 Jul 1969	M. Giret	096982
6	16	Domestic dog	Nana Nambere, Bouar	24 Jul 1969	M. Giret	096977
22	31	Domestic dog	Nana Nambere, Bouar	Late Aug 1969	M. Giret	096990
12	46	Domestic dog	Nana Nambere, Bouar	Aug 1969	M. Giret	096996
16	51	Domestic dog	Nana Nambere, Bouar	Aug 1969	M. Giret	096987
1	2	Domestic cat	Nana Nambere, Bouar	27 Jul 1969	M. Giret	096995
3	2	Domestic cat	Nana Nambere, Bouar	Aug 1969	M. Giret	096985
2	4	Domestic cat	Nana Nambere, Bouar	07 Jan 1970	R. Lacotte	096984
8	4	Domestic cat	Nana Nambere, Bouar	11 Jan 1970	R. Lacotte	096986
1	5	Domestic cat	Nana Nambere, Bouar	18 Jan 1970	G. Uilenberg	096993
13	5	<i>Civettictis civetta</i>		14 Apr 1971	J. Thal	097149
28	7	<i>Panthera leo</i>		26 Feb 1971	J. Thal	097150
<b>Democratic Republic of Congo</b>						
1	1	<i>Panthera leo</i>	Bodio	15 Dec 1950		086264
6	1	<i>Genetta maculata</i>	Garamba Park	16 Sep 1951	H. de Saeger	036711
2		<i>Panthera pardus</i>	Kasai, Luluaburg	1925	C. Waert	046717
1			Katanga (N), Muhilo	1966	J. Bafort	123771
1	3	<i>Crocuta crocuta</i>		12 Apr 1951	P. Schoemaker	037461
19	2	<i>Leptailurus serval</i>		17 Aug 1951	J.V.	037454
8	3	<i>Leptailurus serval</i>		29 Sep 1951	H. de Saeger	037452
<b>Egypt</b>						
1		<i>Felis chaus</i>	Alexandria, Amiriya road	29 Jan 1965	I. Helmy, D. Osborn	078789
5		<i>Felis chaus</i>	Alexandria, 14 km SW of Alexandria	09 Nov 1965	I. Helmy, D. Osborn	078791
35	6	<i>Vulpes vulpes</i>	Beni Suef, Beni Suef, Al Hakamnah	20 Jan 1982	Local hunter	123769
2	3	<i>Arvicanthis niloticus</i> nest	Daqahiya, Aga, Minshat El Ikhwa	12 Nov 1953	H. Hoogstraal	078732
4		<i>Vulpes vulpes</i>	Daqahiya, Village of Tanboul (5 miles W of Simbillawein)	24 Feb 1947		025480



TABLE 2 (cont.)

No. of ticks		Host	Locality	Date of collection	Collector	Collection no.*
♂	♀					
<b>Egypt (cont.)</b>						
	1	<i>Felis silvestris</i> (= <i>lybica</i> )	El Wadi El Gedeed, Dakhla Oasis, Mut	26 Apr 1974	I. Helmy, S. Tawfik	094366
1	9	<i>Canis aureus</i>	Faiyum, Faiyum	15 Aug 1956	H. Hoogstraal	078760
1		<i>Canis aureus</i>	Faiyum, Faiyum (near)	02 Feb 1955	H. Hoogstraal	078756
4		<i>Vulpes vulpes</i>	Faiyum, Ibshawai, Abu Dinqash	09 Feb 1983	Local hunter	123768
12	3	<i>Vulpes vulpes</i>	Faiyum, Ibshawai, El Nazla	09 Feb 1983	Local hunter	123773
24		<i>Canis aureus</i>	Faiyum, Ibshawai, Qasr El Gibali	09 Feb 1983	Local hunter	121756
1		<i>Vulpes vulpes</i>	Faiyum, Kom Oshim	06 Feb 1948	H. Hoogstraal	078759
1		<i>Felis chaus</i>	Faiyum, Kom Oshim (1 mile North of)	28 Dec 1953	H. Hoogstraal	078761
1	1	<i>Felis chaus</i>	Faiyum, Tamiya, Fanus	12 Apr 1954	H. Hoogstraal	078763
5		<i>Felis chaus</i>	Faiyum, Tamiya, Fanus	12 Apr 1954	H. Hoogstraal	078764
5	4	<i>Felis chaus</i>	Faiyum, Tamiya, Fanus	12 Apr 1954	H. Hoogstraal	034583
1			Giza, Aiyat, Kafr Ammar		H. Hoogstraal	078755
2	2	<i>Arvicanthis niloticus</i> nest	Giza, Imbaba, Beni Magdul	14 Jun 1953	H. Hoogstraal	078737
6		<i>Felis chaus</i>	Giza, Imbaba, El Baragil	04 Nov 1958	H. Hoogstraal	078784
1	2	<i>Vulpes vulpes</i>	Giza, Imbaba, Gizzaya	30 Apr 1954	H. Hoogstraal	078785
5	5	<i>Arvicanthis niloticus</i> nest	Giza, Imbaba, Kirdasa	14 Feb 1957	H. Hoogstraal	078730
3	3	<i>Arvicanthis niloticus</i> nest	Giza, Imbaba, Kirdasa	14 Jun 1953	H. Hoogstraal	078738
9+	11+	<i>Arvicanthis niloticus</i> nest	Giza, Imbaba, Kirdasa	28-29 Jun 1953	H. Hoogstraal	078736
1		<i>Arvicanthis niloticus</i> nest	Giza, Imbaba, Kirdasa	15 Jul 1953	H. Hoogstraal	078741
1+	2+	<i>Arvicanthis niloticus</i> nest	Giza, Imbaba, Kirdasa	14 Jun 1953	H. Hoogstraal	056757
1		<i>Arvicanthis niloticus</i> nest	Giza, Imbaba, Kirdasa	03 Jan 1955	H. Hoogstraal	078731
1		<i>Vulpes vulpes</i>	Giza, Imbaba, Tanash	14 Jan 1960	H. Hoogstraal	078765
	2	<i>Arvicanthis niloticus</i> burrow	Miniya, Maghagha, Maghagha	12 Mar 1952	H. Hoogstraal	078744
1		<i>Vulpes vulpes</i>	Miniya, Maghagha, Saft	01 Jan 1979	Local hunter	123772
1		<i>Canis aureus</i>	Miniya, Minya	11 Jan 1981	Local hunter	123767
13	7	<i>Felis chaus</i>	Qalyubiya, El Amar El Kubra	15 Jan 1954	H. Hoogstraal	078757
4	2	<i>Canis aureus</i>	Qalyubiya, Qalyubiya, Sanatir, Ezbet Ihsan	03 Feb 1966	I. Helmy, D. Osborn	078790
4		<i>Felis chaus</i>	Qena, Isna, Wadi Nassim	07 Apr 1953	H. Hoogstraal	078762
<b>Ethiopia</b>						
1		Vegetation	Gamo-Gofa, Arba Mineh	14 Jan 1966	H. Hoogstraal	092735
5	1	<i>Colobus polykomos</i>	Harer, Hirna valley, Dire Dawa College (80 km W of)	21 Sep 1962	B. Glass	092730
1		<i>Canis mesomelas</i>	Harer, Rd. between Dacata and Erer Rivers		B. Glass	092732

TABLE 2 (cont.)

No. of ticks		Host	Locality	Date of collection	Collector	Collection no.*
♂	♀					
<b>Ethiopia (cont.)</b>						
9	1	<i>Ichneumia albicauda</i>	Harer, Rd. between Dacata and Erer Rivers	04 Jul 1962	B. Glass	092731
1	2	Domestic cat	Ilibabor, Gambella		J.S. Ash	092741
1		Human	Ilibabor, Gambella	30 Jul 1972	J.S. Ash	092742
17	10	<i>Civettictis civetta</i>	Kefa, Mezan Tefari	10 Mar 1980	H.K. Lall	123760
7	3	<i>Vulpes</i> sp.	Kefa, Sokoru/Deke	Aug 1979	H.K. Lall	123770
19		<i>Hyaena hyaena</i>	Rock Valley		B. Glass	092733
1	3	Domestic dog	Shashamani	25 Jun 1961	L.W. Teller	092726
1	1	Human	Shoa, Addis Ababa	11 Mar 1970	J.S. Ash	092743
1		"Black-tailed mongoose"	Shoa, Koka	25 Feb 1973	R. Traub, J.S. Ash	092747
22	11	<i>Leptailurus serval</i>	Shoa, Lake Langono Rd (10 miles N of)	28 Dec 1974	L. Sholdt	092746
<b>Kenya</b>						
16	2	<i>Civettictis civetta</i>	Central, Muranga, Mitubiri	08 Feb 1953	D.G. MacInnes	095066
<b>Liberia</b>						
1	1	Domestic dog	Bolahim	1930	T. Kolbe	046716
8	5	Domestic cat	Harbel		R. Fox	087923
<b>Mali</b>						
64	5	<i>Civettictis civetta</i>	Kayes, Niore du Sahel, Lorak Banc	12 Feb 1956		084578
14	2	<i>Leptailurus serval</i>	Kayes, Niore du Sahel, Lorak Banc	06 Feb 1956		089579
3		<i>Panthera pardus</i>	Sikasso, Sikasso	20 Aug 1954		089576
<b>Senegal</b>						
1		<i>Leptailurus serval</i>	Casamance, Bignona	21 Oct 1945	From P.C. Morel	088278
1		Vegetation	Sangalkam	05 Apr 1945	L. Kartman	021793
3		<i>Felis silvestris</i> (= <i>lybica</i> )	Senegal Oriental, Niokolo Koba, Badi	Mar 1957	From P.C. Morel	088277
7		<i>Civettictis civetta</i>	Senegal Oriental, Niokolo Koba	Feb 1956	From P.C. Morel	088276
9	39	<i>Leptailurus serval</i>	Thies, Mbour, Sandiara	18 May 1956	From P.C. Morel	088279
<b>Sudan</b>						
1		<i>Hyaena hyaena</i>	Bahr El Ghazal, Tirol	21 Jan 1955	E.T.M. Reid	093012
1	3	Domestic cat	Bahr El Ghazal, Wau	Oct 1953	S.V.S.	093025
2	1	<i>Arvicanthis</i> sp. burrow	Equatoria, Juba, Juba	10 Dec 1952		093013
8		<i>Civettictis civetta</i>	Equatoria, Torit, Obbo	09 Apr 1950	H. Hoogstraal	093031

TABLE 2 (cont.)

No. of ticks		Host	Locality	Date of collection	Collector	Collection no.*
♂	♀					
<b>Sudan (cont.)</b>						
13	5	<i>Canis aureus</i>	Equatoria, Torit, Torit	25 Nov 1949	H. Hoogstraal	094959
14		<i>Canis aureus</i>	Equatoria, Torit, Torit	06 Dec 1949		093014
22	2	<i>Canis aureus</i>	Equatoria, Torit, Torit	02 Dec 1949		093016
1		<i>Canis aureus</i>	Equatoria, Torit, Torit	06 Dec 1949	H. Hoogstraal	093015
1	1	<i>Civettictis civetta</i>	Equatoria, Torit, Torit	08 Feb 1951	H. Hoogstraal	093023
1	4	Domestic dog	Equatoria, Torit, Torit	04 Jan 1952		093024
1		<i>Mungos mungo</i>	Equatoria, Torit, Torit	13 Apr 1950	J. Owen	093011
6		<i>Panthera leo</i>	Equatoria, Torit, Torit	15 Mar 1952		093028
14	3	<i>Canis mesomelas</i>	Equatoria, Ubo	08 May 1948		093018
1		<i>Canis adustus</i>	Upper Nile, Malakal (near)	14 Mar 1964	H. Hoogstraal, S. Gaber	094960
2		<i>Canis adustus</i>	Upper Nile, Malakal, Malakal (7 miles N of)	01 Feb 1962	H. Hoogstraal, S. Gaber	094961
1	8	<i>Panthera leo</i>	Upper Nile, 40 mi S of Malakal, Abwong	27 Feb 1961	H. Hoogstraal	092978
		<i>Canis adustus</i>	Upper Nile, Paloich, Gelhak Forest	23 May 1962	H. Hoogstraal, S. Gaber	092881
1		<i>Felis silvestris</i> (=lybica)	Upper Nile, Paloich, Paloich (5 miles N of)	27 Feb 1962	H. Hoogstraal, S. Gaber	094962
2		<i>Felis silvestris</i>	Upper Nile, Paloich, Tir (near)	23 Feb 1961	H. Hoogstraal, S. Gaber	092973
2	1	<i>Leptailurus serval</i>	Upper Nile, Paloich, Tir (near)	07 Feb 1961	H. Hoogstraal, S. Gaber	094958
<b>Tanzania</b>						
1		<i>Canis mesomelas</i>	Mara, Serengeti Plains, Seronera	25 Sep 1974	D. Schmidt	095204
1		<i>Connochaetes taurinus</i>	Yeida, Swamps	04 Oct 1938	L.R. Paddock	115774
<b>Uganda</b>						
11	1	<i>Panthera leo</i>	Ankole, Nyabushozi	22 Oct 1965	J. Matthyse	123763
1	2	<i>Panthera leo</i>	Ankole, Nyabushozi	09 Oct 1965	J. Matthyse	120367
7	6	<i>Panthera pardus</i>	Ankole, Mbarara	09 Aug 1965	J. Matthyse	123762
2		<i>Panthera leo</i>	Ankole, Mbarara (35 miles SW of)	14 Apr 1962	Major Price	089542
7	2	Domestic dog	Baganda, Entebbe	27 Apr 1966	J. Matthyse	053826
3	1	Domestic dog	Karamoja, Kampala	05 Feb 1940	G.H.E. Hopkins	120365
		<i>Panthera pardus</i>	Karamoja, Moroto, Labwor	16 Aug 1965	J. Matthyse	123764

TABLE 2 (cont.)

No. of ticks		Host	Locality	Date of collection	Collector	Collection no.*
♂	♀					
<b>Uganda (cont.)</b>						
2			Kigezi, Nakabande	25 Oct 1940		
1	1	Domestic dog	Pacota, Aswa, Acholi	21 Jun 1966	J. Matthyse	120366
10	2	<i>Panthera leo</i>	Ruwenzori National Park	31 Jul 1969	M.H. Woodford	053835
3		<i>Panthera leo</i>	Ruwenzori National Park, Mweya	19 Jun 1974	M.H. Woodford	088634
21		<i>Civettictis civetta</i>	W. Mengo, Entebbe	Apr 1979	M.N. Kaiser	120363 123761
<b>Zambia</b>						
10	17	<i>Panthera leo</i>	Southern, Namwala	19 Aug 1951	J.G. Matthyse	091294
1	10	Domestic dog	Barotseland, Kalabo (E of)	Apr 1965	R.G. Japp	091297
1	1	<i>Felis silvestris</i> (= <i>lybicus</i> )	Barotseland, Kalabo (E of)	30 Dec 1964	R.G. Japp	091296
1		<i>Mastomys natalensis</i>	Mt. Makulu	16 Jun 1970	M.H. Colbo	091300
6		<i>Civettictis civetta</i>	Eastern, Lundazi, Chibembe Pontoon (10 mi N of)	07 Aug 1962	G. Corbet, J. Ingles	091304
15	1	<i>Civettictis civetta</i>	Lochinvar	Jul 1959		123765
1		<i>Potamochoerus porcus</i>	Susa Camp, Chipata, Eastern	24 Jul 1980	S.G.A. Weak	123766
<b>Zimbabwe</b>						
16		<i>Civettictis civetta</i>	Mashonaland South, Salisbury, Atlantica Foundation Research Station	07 Jul 1977	R.A.I. Norval	107272
13		<i>Civettictis civetta</i>	Mashonaland South, Salisbury, Calgary Farm	16 May 1977	R.A.I. Norval	107096
3		<i>Civettictis civetta</i>	Mashonaland South, Salisbury, Calgary Farm	14 Feb 1977	R.A.I. Norval	121599
6		<i>Leptailurus serval</i>	Mashonaland South, Salisbury, Calgary Farm	09 Feb 1977	R.A.I. Norval	121603
7		<i>Felis silvestris</i> (= <i>libyca</i> )	Mashonaland South, Salisbury, Mazoe Veterinary Farm	06 Sep 1976	R.A.I. Norval	103047
8	9	<i>Leptailurus serval</i>	Mashonaland South, Sinoia	25 May 1977	R.A.I. Norval	121595

\* All the collection numbers are those of specimens in the United States National Tick Collection

+ Reared specimens from engorged nymphs found in *Arvicanthis niloticus* nests



TABLE 3 *Haemaphysalis (Rhipistoma) elliptica* and *Haemaphysalis (Rhipistoma) leachi*, immature stages examined

No. of ticks		Host	Locality	Date of collection	Collector	Collection no.*
N	L					
<b><i>Haemaphysalis (Rhipistoma) elliptica</i></b>						
16 <sup>+</sup>	30 <sup>+</sup>	Domestic dog	South Africa	13 Jul 2005	K. Junker	IGH
16 <sup>+</sup>	30 <sup>+</sup>	<i>Acinonyx jubatus</i>	South Africa, Pretoria	21 Feb 2006	I. Hubmer	IGH
<b><i>Haemaphysalis (Rhipistoma) leachi</i></b>						
8 <sup>+</sup>		Domestic dog	Central African Republic, Nana Nambere, Bouar	10 Oct 1969 to 14 Jan 1970	R. Lacotte	096992
	30 <sup>+</sup>	Domestic dog	Central African Republic, Nana Nambere, Bouar	16 Oct to 10 Dec 1969	R. Lacotte	096979
	30 <sup>+</sup>	Domestic dog	Central African Republic, Nana Nambere, Bouar	02 Aug to 03 Sep 1969	M. Giret	096980
2 <sup>+</sup>	30 <sup>+</sup>	Domestic dog	Egypt, El Wadi El Gedeed, Dakhla Oasis, El Hindaw	20 Nov 1972	I. Helmy	078801
	30 <sup>+</sup>	<i>Arvicanthis niloticus</i> nest	Egypt, Giza, Imbaba, Ausim	Sep 1953	H. Hoogstraal	078734
	30 <sup>+</sup>	<i>Vulpes vulpes</i>	Egypt, Giza, Imbaba, Saft El Laban	06 Mar 1958	H. Hoogstraal	078749

\* All the collection numbers are those of specimens in the United States National Tick Collection

+ Reared specimens

TABLE 4 Differential diagnosis between *Haemaphysalis (Rhipistoma) elliptica* and *Haemaphysalis (Rhipistoma) leachi*

<i>Haemaphysalis (R.) elliptica</i>	<i>Haemaphysalis (R.) leachi</i>
<b>Male</b> (Fig. 2, 3, 8 and 9)	
1. Longer and broader tick: <ul style="list-style-type: none"> <li>– Length (from palpal apices to posterior margin of conscutum) avg. 3.00 mm</li> <li>– Width (of conscutum) avg. 1.47 mm</li> <li>– Ratio length to width avg. 2.05</li> </ul> 2. One or two of first festoons enclosed by marginal groove           3. Dorsally median margin of palpal segment II gradually widening anteriorly from the segment's mid-length           4. Lateral margin of ventral spur on palpal segment II straight	1. Shorter and more slender tick: <ul style="list-style-type: none"> <li>– Length (from palpal apices to posterior margin of conscutum) avg. 2.45 mm</li> <li>– Width (of conscutum) avg. 1.06 mm</li> <li>– Ratio length to width avg. 2.30</li> </ul> 2. Two or three of first festoons enclosed by marginal groove           3. Dorsally median margin of palpal segment II abruptly widening anteriorly from the segment's mid-length           4. Lateral margin of ventral spur on palpal segment II concave
<b>Female</b> (Fig. 4, 5, 10 and 11)	
1. Longer and broader tick: <ul style="list-style-type: none"> <li>– Length (from palpal apices to posterior margin of scutum) avg. 1.73 mm</li> <li>– Width (of scutum) avg. 1.02 mm</li> <li>– Ratio length to width avg. 1.70</li> </ul> 2. Dorsal cornua shorter, approximately 1/6 length of basis capituli           3. Dorsally median margin of palpal segment II gradually widening anteriorly at segment's mid-length	1. Shorter and more slender tick: <ul style="list-style-type: none"> <li>– Length (from palpal apices to posterior margin of scutum) avg. 1.53 mm</li> <li>– Width (of scutum) avg. 0.84 mm</li> <li>– Ratio length to width avg. 1.81</li> </ul> 2. Dorsal cornua longer, approximately 1/4 length of basis capituli           3. Dorsally median margin of palpal segment II abruptly widening anteriorly at segment's mid-length
<b>Nymph</b> (Fig. 6 and 12)	
1. Larger (see description)           2. Dorsally median margin of palpal segment II widening gradually anteriorly           3. Ventral spur of palpal segment II broad           4. Denticles of hypostome in files of 7 to 9 (usually 8)	1. Smaller (see description)           2. Dorsally median margin of palpal segment II widening sharply anteriorly           3. Ventral spur of palpal segment II narrow           4. Denticles of hypostome in files of 5 or 6
<b>Larva</b> (Fig. 7 and 13)	
1. Larger (see description)           2. Ventral spur of palpal segment II broad           3. Ventral spur of palpal segment III indistinct, fold-like           4. Denticles in files of 7 or 8	1. Smaller (see description)           2. Ventral spur of palpal segment II narrow           3. Ventral spur of palpal segment III distinct, triangular           4. Denticles in files of 4 to 6 (usually 5)

## REMARKS ON IDENTIFICATION

Our study has shown that *H. (R.) elliptica* is an independent species belonging to the *H. (R.) leachi* subgroup and that it is clearly distinguishable from *H. (R.) leachi*. However, the value of diagnostic characters varies from stage to stage.

The easiest stage to distinguish is the larval. All the larval characters that we have chosen clearly differentiate the larvae of *H. (R.) elliptica* from those of *H. (R.) leachi*. Males of *H. (R.) elliptica* are also quite easily distinguishable from those of *H. (R.) leachi*. The main differentiating characters are the shape of

the lateral margin of the ventral spur on palpal segment II and total size of the ticks. The most obvious character for nymphs is the number of denticles per file on the hypostome, and total size. Females are the most difficult to distinguish. The main characters are total size and the size of the dorsal cornua, and because both characters have a metric value, difficult specimens do not have to be excluded during routine examinations. The females of most closely related species within the *H. (R.) leachi* group are difficult to distinguish interspecifically. However, because of the morphological stability of *Haemaphysalis* species, the size of various structures is of consid-

erable value for discriminating between all the parasitic stages of closely related species.

Finally, unpublished molecular data confirm our opinion on the species independency of *H. (R.) elliptica*.

## DISTRIBUTION AND HOSTS

*Haemaphysalis (R.) elliptica* is present in East and southern Africa, and DAA and IGH have recorded it in the *Democratic Republic of Congo, Kenya, Mozambique, South Africa, Tanzania, Uganda, Zambia* and *Zimbabwe* (Table 1). JLC adds *Ethiopia, Malawi* and *Rwanda* to this list.

*Haemaphysalis (R.) leachi* has chiefly been recorded from North (Egypt) and East Africa south to the north of Zimbabwe. Judging by collection data this species is probably quite common in Central Africa. A few collections have been made in West Africa. DAA and IGH record this species from *Cameroon, Central African Republic, Democratic Republic of Congo, Egypt, Ethiopia, Kenya, Liberia, Mali, Senegal, Sudan, Tanzania, Uganda, Zambia* and *Zimbabwe* (Table 2). JLC adds *Burundi, Chad* and *Guinea* to this list. Both species share a large area of sympatry in East Africa.

The hosts of adult *H. (R.) elliptica* are various carnivore species, amongst which are the domestic dog, domestic cat, lion, *Panthera leo*, and leopard, *Panthera pardus* (Table 1). The hosts of the immature stages are diverse rodent species, and they may very occasionally be present on the same hosts as the adults. The hosts of adult *H. (R.) leachi* are similar to those of *H. (R.) elliptica*, namely domestic and wild carnivores (Table 2). The immature stages use various rodents and other small mammals as hosts. It will, however, only be possible to determine the actual host range of the immature stages of *H. (R.) elliptica* and *H. (R.) leachi* once a taxonomic revision of the whole *H. (R.) leachi* group has been completed.

The adults of both species have been found in a number of collections taken from a single host. Both geographic and host sympatry indirectly confirm the specific independency of *H. (R.) elliptica* and *H. (R.) leachi*.

## DISEASE RELATIONSHIPS

*Haemaphysalis (R.) elliptica* (then referred to as *H. leachi*) is the vector of *Babesia canis rossi*, the

cause of virulent babesiosis in domestic dogs in South Africa (Lewis, Penzhorn, Lopez-Rebollar & De Waal 1996). We are, however, unable to find any records of *H. (R.) leachi* transmitting *Babesia canis* in Egypt. In South Africa, *H. (R.) elliptica* (as *H. leachi*) has been recorded as transmitting *Rickettsia conori*, resulting in tick bite fever in humans (Gear 1954). Possibly because of its preference for carnivores, adult *H. (R.) elliptica* (then recorded as *H. leachi*) is one of the tick species most frequently collected from humans working in the field (Horak, Fourie, Heyne, Walker & Needham 2002).

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