Notes on the systematics of two species of *Heterodoxus* (Mallophaga, Boopidae)

By

N. J. B. PLOMLEY, B.Sc.

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PLATES III-VI

The problems here considered are, first, the systematics of the lice of the genus *Heterodoxus* Le Souëf and Bullen, occurring on the domestic dog and certain other monodelphian mammals, and, secondly, the question of their identity with members of the genus occurring on didelphian mammals (marsupials). Upon marsupials, apparently the true hosts, the genus appears to be confined to the Macropodidae.

DIAGNOSIS OF SPECIES; HOST RECORDS

Genus **Heterodoxus** Le Souëf and Bullen

Heterodoxus longitarsus (Piaget). Genotype

Menopon longitarsus Piaget (1880), pp. 504-506, pl. XLI, f. 7; *Halmaturus giganteus*. (Zoo. Rotterdam).

Heterodoxus macropus Le Souëf and Bullen (1902), p. 159, f. 11; 'Kangaroos, Wallabies, &c.'.

Type host: *Halmaturus giganteus* = *Macropus major* (Shaw).

Notes: The Piaget Collection in the British Museum (Natural History) includes four slides marked '*Menopon longitarsus*', a total of 3 ♂♂, 3 ♀♀, 3 ⊙⊙. Two slides, with 1 ♂, 1 ♀ mounted on each, are labelled '*Menopon longitarsus*, sur un Kangourou, *Halmaturus giganteus*', the other slides, '*Menopon longitarsus*, sur un Kangourou'; the former are to be considered the types since a definite host is designated.

Unfortunately, I have not been able to examine these specimens critically, nor have I been able to obtain any material from the type host. Since it is more than likely that *Heterodoxus* will show definite host specificity, I consider that *Heterodoxus longitarsus* (Piaget) from *Macropus major* (Shaw), is a definite species and distinct from *H. spiniger* (Enderlein) and from *H. ualabati*, sp. nov.

Heterodoxus spiniger (Enderlein)

Menopon spiniger Enderlein, (1909), pp. 80-81, pl. VIII, f. 4, 5; ('von Haushund eines Betschuanen, auf den es wohl von einem Beuteltiere gelangt ist.')

Heterodoxus armiferus Paine, (1912), p. 362, f. A-D; (dog).

Heterodoxus longitarsus auctorem (non-marsupial hosts).

Type Host: 'Haushund' = *Canis familiaris* Linné.

Hosts: (A) Marsupial: *Wallabia bicolor* (Desmarest); (B) Non-marsupial: (*Canis ochropus* Eschscholtz ('Coyote'), *Herpailurus salinarum* Thomas ('*Oncifelis salinarum*') 'Jackal' 'Man', *Canis familiaris* Linné.

Specimens examined: *Note*:—Certain of these specimens are those upon which previous authors have based descriptions, records, &c., and are indicated accordingly.

'Jackal', Uganda, Arua, 2.iii.1931, T. W. Chorley, 1 ♂, 2 ♀♀; '*Canis famil.* (juv.)', Belgian Congo, Katanga, Bukama, 18.x.1931 series ♂♂, ♀♀; 'Cocker Spaniel', Tasmania, Launceston, 24.i.1934, N. J. B. Plomley, 1 ♂, 2 ♀♀; 'Dogs', Dutch New Guinea, Geelvink Bai, iv.1929, Malte von Kuhlewein, 1 ♂, 3 ♀♀; 'Puppies', Australia, N.S.Wales, Gulargambont 18.vi.1933, R. N. McCulloch, 1 ♂, 1 ♀, 1⊙ (McCulloch, (1933)); 'Dog', Japan, Yokohama, 24.iv.1902, 1 ♀; 'Dog', China, Hangchow, 1 ♀; 'Dog', Brasil, Rio de Janeiro, 2 ♂♂, 5 ♀♀; 'Dogs', Malaya, Kelantan, Kota Bharu, 12.xi.1912, 1 ♂, 1 ♀; 'Dog', Dutch New Guinea, N. coast Schoutein Is., Warsa, 1.ii.1930, M. von Kuhlewein, 2 ♂♂, 7 ♀♀; *Wallabia bicolor* (Desmarest), Australia, Victoria, 2 ♂♂; 'Coyote', U.S.A., California, Santa Cruz, 1916, G. F. Ferris, 1 ♂, 1 ♀ (Ferris (1922)); 'Dog', U.S.A., California, Berkeley, 7.x.1909, Herms, 1 ♂, 1 ♀ (types *Heterodoxus armiferus* Paine) (Paine (1912)); 'Man', Fed. Malay States, Kuala Lampur, xi.1915, S. T. Darling, 1 ♀ (Ferris (1922)); 'Domestic Dog', Columbia, Villeta Dept., Cundinamarca, 1936, J. Bequaert, 1 ♂; 'Dog', Hawaii, Honolulu, 15.iii.1933, C. E. Pemberton, 1 ♂, 2 ♀♀; 'Dog', Java, Toeloengogoeng, 21.ix.1932, C. J. Louwerens, 4 ♂♂, 1 ♀; 'Dog', Java, Toeloengogoeng, 6.x.1932, C. J. Louwerens, 2 ♂♂, 1 ♀; 'Dog', Cuba, Havana, 6.x.1932, Dr. Terez Vigueira, 3 ♂♂; 'Off large, black, short-haired, adult ♀ dog', Canal Zone, R. Chagres, Gatuncillo, 19.i.1932, L. H. Dunn, 1 ♂, 1 ♀; *Oncifelis salinarum*, Argentina, Jujuy, F. L. Werneck, 1 ♂, 1 ♀ (Werneck (1936)); 'Dog', U.S.A., Missouri, State College, iv.1935, F. W. Stafford, 5 ♂♂, 5 ♀♀; 'Dog', U.S.A., Oklahoma City, 5.vi.1933, J. W. Ward, 1 ♂, 1 ♀ (Ward (1934)); *Canis familiaris*, S. Africa, Kalahari, 1910, (error = 1904), 1 ♀ (type *Menopon spiniger* Enderlein) (Enderlein (1909)); 'Chien Terre Neuve', Martinique, i.1896, 1 ♀ (Neumann (1912b)); 'Chien', Japan, Yokohama, 1909, C. N. Rothschild, 1 ♂, 1 ♀ (Neumann (1912b)); *Canis familiaris*, Formosa, Kosempo, vii.1911, 1 ♂, 1 ♀ (Neumann (1913)); *Canis familiaris*, Malay Peninsula, xi.1912, Dr. Gimlette, 1 ♀ (Neumann (1913)); 'Chien de laboratoire', Mozambique, Lourenço Marques, 9.iv.1910, Howard, 2 ♂♂, 1 ♀ (Neumann (1912b)); 'Dog', Australia, Queensland, Goondiwindi, 28.v.1936, F. H. S. Roberts, 3 ♂♂, 11 ♀♀, 6 ⊙⊙ (Roberts (1936)); 'Dog', India, Calcutta School of Tropical Medicine, 63 ♂♂, 74 ♀♀, 59 ⊙⊙; 'Dog', Porto Rico, Mayaguez, 22.iv.1936, 22 ♂♂, 43 ♀♀, 10 ⊙⊙.

Diagnosis. General facies typical of genus. Plate III, figs. A-J; Plate IV, figs. A-B, D-K; Plate V, figs, A, C-G; Plate VI, figs. B, C: show details of head, thorax and abdomen; Table 1 gives an analysis of measurements and counts. Distinguished from other species on the structure of the phallus in the male. Posterior border of tergite of last abdominal segment in ♂ bears 12·63 (S.D.n-1 = 1·54) spines; that of last abdominal sternite in ♀ 17·77 (S.D.n-1 = 1·75) spines; the setae are arranged in a discontinuous band or nearly so in both sexes, there being a median gap in the row dividing it right and left. Metathoracic sternal sclerite bears six setae, with intersetal distances as tabled. Setae arranged on metathoracic tergite as figured.

Heterodoxus ualabati sp. nov.

♂ *Heterodoxus macropus* Paine (1912) (nec Le Souëf and Bullen, (1902)), p. 361, f. E-G; 'Black Wallaby'.

? *Heterodoxus longitarsus* Harrison and Johnston (1916) (nec Piaget, (1880)), f. 11; *Macropus dorsalis* (= *Wallabia dorsalis* (Gray)).

Type Host: 'Black Wallaby', Victoria = *Wallabia bicolor* (Desmarest) (1).

Specimens examined: 'Black Wallaby', Victoria, A. S. Le Souëf, 2 ♂♂, ("type specimens" *Heterodoxus macropus* Paine) (Paine (1912)); *Wallabia bicolor* (Desmarest), Sydney Zoo, 10.v.1927, 5 ♂♂; *Wallabia bicolor* (Desmarest), Victoria, 4 ♂♂.

Diagnosis. General facies typical of genus. Plate III, fig. K; Plate IV, figs. (A), C. (E), L; Plate V, figs. (A), B, H; Plate VI, fig. A: show details of head, thorax and abdomen. Table 1 gives an analysis of measurements and counts. Distinguished from other species on the structure of the phallus in the male. Posterior border of tergite of last abdominal segment in ♂ bears about 22 spines, arranged in a continuous band. Metathoracic sternal sclerite bears six setae, with intersetal distances as tabled. Setae arranged on metathoracic tergite as figured. Female not known.

Description

Head. Shape conical, bluntly rounded anteriorly and the postero-lateral angles acute. Chaetotaxy very constant in disposition, but setae subject to some variation in relative length and strength. Plate III shows these features for a number of individuals of *H. spiniger* and *H. ualabati*. The head structure appears generically constant.

Thorax. Plate IV, figs. A, E show dorsal and ventral views of the thorax of an *H. spiniger*; the thorax has a similar structure in *H. ualabati*, and, except for the chaetotaxy of the metathorax, appears to be generically constant. Three segments are to be distinguished dorsally and ventrally. The chaetotaxy of the prothoracic and mesothoracic tergites is constant, that of their sternites variable. The prothoracic tergite is an oval plate (Plate IV, figs. A-C); on the sternite is a heart-shaped sclerite (2) bearing a number of setae (Plate IV, figs. E-H). These setae comprise:—(1) a series of three on each side (Plate IV, fig. F, 'x', 'y', 'z'), which are of almost constant occurrence, and (2) others of very variable disposition, though they show some tendency to comprise a few longer setae posteriorily and a row of shorter ones anteriorly. The width of this plate (see Table 1, intersetal distance 'xx') is expressed by the distance between the two anterior spines 'x'.

The mesothorax is poorly developed dorsally, where it bears only a pair of spines; ventrally it is more extensive, and bears a variable number of spines, which show little regularity of arrangement though a tendency to occur in two bands which diverge anteriorly.

The metathoracic tergite is of rectangular shape (Plate IV, figs. A, D). In *H. spiniger and H. ualabati* (♂) it bears posteriorly a median pair of long hairs with a pair of short spines at the lateral angles, and centrally a row of six long setae with some short ones laterally. In both species the sternum bears an ill-defined plate upon which there are three pairs of setae, the occurrence and disposition of which are very constant; only very occasionally are extraneous setae present (Plate IV, figs. E, I-L).

(1) Personal communication from Mr. A. S. Le Souëf.

(2) The pair of hairs situated at the anterior margin of the sclerite, sometimes included in it and sometimes outside it, and the similar pair between the plate and the mesothorax, occur regularly. They are not considered in counts for Table 1.

Abdomen. (Plate V, fig. A). The tergum, sternum and pleura of each segment bear setae, those of the tergum tending to be merged with those of the pleura. The spiracles are dorso-lateral; on segments 1-8 there are dorso-lateral sense organs (Plate IV, fig. A; Plate V, fig. A; 'so'). Though the lengths of the setae intergrade, in contrast to great variability among the smaller, the largest show constancy of numbers and distribution. Dorsally the setae of each segment form an irregular row, the smaller ones scattered amongst the largest, while ventrally they tend to be arranged in two rows, the largest in a posterior row which has no interspersed smaller setae. Thus a formula may express the numbers of these largest setae on tergum and sternum; for segments 1-6 inclusive, in *H. spiniger* and *H. ualabati*, it is:— (dorsal/ventral) 4/4, 6/6, 6/6, 6/8, 6/8, 6/8.

Terminalia. (Plate V, figs. B-H; Plate VI, figs. A, B). The terminalia in *H. spiniger* and *H. ualabati* are of the same general type, and consist of the modified terminal segments of the abdomen in male and female, and of the external genitalia in the male. Terminology is that used by Snodgrass (1935).

The terminal abdominal segments in male and female have their tergal and sternal plates modified as copulatory processes by the development of a row of stout setae ('sr') along the posterior border of the sclerite (Plate V, figs. B-D). It is probable that these setae help to hold the individuals in copulation, the two series becoming interlocked. This row of setae occurs on the tergum in the ♂ and on the sternum in the ♀, and so it is to be expected that the ♀ rides on the ♂ during copulation (c.f. Werneck (1936), pl. 1).

In *H. spiniger* and *H. ualabati*, the external genitalia of the ♂ (Plate V, figs. E-H; Plate VI, figs. A, B) consist of an apodemal plate and a phallus. The apodemal plate (Plate V, fig. E, 'ap') has upraised sides posteriorly; to these sides are hinged the parameres (Plate V, fig. E, 'pm'), and posterodorsally, a flap Plate V, fig. E, 'f'). Near the hinge points of the flap arise a pair of lightly-chitinized bars (Plate VI, fig. A, 'b'), so that the base of the phallus is supported by the bars and the apodemal plate ventrally and by the flap dorsally. The flap does not appear to be hinged directly to the apodemal plate, but indirectly via a pair of rods shaped like blunt thorns, which are hinged in turn to the apodemal plate, above the hinge points of the parameres.

The phallus is a thin-walled tube, bearing a series of processes and spines (Plate V, figs. E, 'ph'; F-H). In general its structure is the same in *H. spiniger* and *H. ualabati*, but there are differences of detail in the two species. Unfortunately, owing to lack of material, dissections were possible only for *H. spiniger*, so that the details of the phallus structure (particularly the central area) in *H. ualabati* were not followed as thoroughly as was hoped, Plate V, fig. H, being a diagrammatic reconstruction from the introvert phallus, based on the structure of the extrovert phallus in *H. spiniger*.

The phallus in *H. spiniger* (Plate V, figs. E-G; Plate VI, fig. B) may be divided into a lightly-chitinized basal region ('r' 1), a central region bearing various processes ('r' 2), and a lightly-chitinized terminal region ('r' 3). The basal region is a simple tube. The central region bears two prominent lateral processes ('lp'), and a ventral beak-like structure ('bk') having at its sides two small processes ('p'); there are no processes dorsally. The lateral processes bear distally on their outer edges heavily-chitinized concavities; they do not bear teeth. The lateral processes and the beak-like structure are strengthened by sclerotizations (Plate V, fig. G, 'sc' 1-'sc' 4). The terminal region of the phallus bears two rows of three spines ('st') and is covered, over most of its area, with small spinules; this character of the two rows of spines is a specific one in this species. The retracted phallus

has its processes lying within the tube, and, in situ, therefore shows inversion of the tube only; on eversion, the processes come to lie on the outer surface of the tube so formed.

The phallus in *H. ualabati* (Plate V, fig. H; Plate VI, fig. A) differs from that in *H. spiniger* as follows. The central region, of which the detailed structure was not determined, bears two prominent lateral processes ('lp' 1), which have their distal margins toothed. The terminal region of the phallus bears two sac-like structures ('ss') covered with spinules; no spines are to be found such as occur on this region in *H. spiniger*.

Measurements and Counts

In Table 1 is set out a summary of measurements and counts referring to *H. spiniger* and *H. ualabati*. The measurements were made with an ocular micrometer; This was calibrated against a stage micrometer and the absolute measurements interpolated after summarizing. The setal counts refer to the total number of setae occurring on the sclerite, except those made in connexion with the terminalia which refer only to a particular row of setae (Plate V, figs. B-D, 'sr'). Only mature males and females were considered. The selection of individuals for statistical analysis was qualitative, the criteria being the structure of the phallus for the male, and occurrence on non-marsupial hosts for females of *H. spiniger* (since only one type of male was found on such hosts; the results of the analyses support such selection). It must always be remembered that the measurements were made on specimens mounted on slides; such mounting results in some degree of distortion.

It is seen that while characters such as the number of setae sternal plate 1st thoracic segment, number of setae 1st tergite abdomen, are generic characters, significant differences exist for other characters. It is impossible to assess the value of such differences in the absence of material representing the genus as a whole, for until the whole has been examined the possibility that intermediate types may exist must always be kept in mind. Should difficulties arise when the whole genus has been surveyed, it may still be possible to characterize species by a group of measurements.

Table 1

	Number.	Mean.	Max.	Min.	S.D. (n-1).
H. spiniger: head width mm.	70 ♂ ♀	0·640	0·700	0·568	0·031
	29 ♂ ♂	0·638	0·700	0·581	0·031
	41 ♀ ♀	0·642	0·700	0·568	0·031
H. ualabati:	11 ♂ ♂	0·698	0·719	0·680	0·013
H. spiniger: head length mm.	70 ♂ ♀	0·423	0·462	0·383	0·021
	29 ♂ ♂	0·420	0·462	0·383	0·023
	41 ♀ ♀	0·426	0·462	0·383	0·020
H. ualabati:	11 ♂ ♂	0·480	0·502	0·462	0·019
H. spiniger: ratio: head width / head length (calculated from the separate values).	70 ♂ ♀	1·51	1·67	1·34	0·054
	29 ♂ ♂	1·52	1·60	1·43	0·042
	41 ♀ ♀	1·50	1·67	1·34	0·060
H. ualabati:	11 ♂ ♂	1·45	1·51	1·39	0·044
H. *spiniger*: setae sternite 1 thorax ($n = 2(x + y + z) + a$).	71 ♂ ♀	17·96	23	13	2·24
	28 ♂ ♂	18·04	21	13	2·20
	43 ♀ ♀	17·91	23	14	2·26
H. ualabati:	11 ♂ ♂	18·55	21	16	1·29

	Number.		Mean.	Max.	Min.	S.D. (n-1).
H. spiniger: sternite 1 thorax, intersetal distance xx. mm.	25 ♂ ♀		0·156	0·181	0·133	0·012
	15 ♂ ♂		0·153	0·169	0·133	0·010
	10 ♀ ♀		0·160	0·181	0·145	0·013
H. ualabati:	5 ♂ ♂		0·194	0·207	0·183	0·010
H. spiniger: sternite 3 thorax, intersetal distances mm.	75 ♂ ♀	a	0·189	0·215	0·138	0·016
		b	0·092	0·106	0·079	0·007
		c	0·087	0·106	0·068	0·009
	32 ♂ ♂	a	0·188	0·208	0·168	0·011
		b	0·093	0·105	0·081	0·007
		c	0·086	0·106	0·068	0·010
	43 ♀ ♀	a	0·191	0·215	0·174	0·010
		b	0·092	0·106	0·079	0·007
		c	0·087	0·103	0·071	0·008
H. ualabati:	7 ♂ ♂	a	0·224	0·242	0·211	0·012
		b	0·109	0·118	0·100	0·007
		c	0·121	0·134	0·108	0·010
H. spiniger: setae tergite 1 abdomen (n = 4 + a).	66 ♂ ♀		17·01	21	13	1·75
	27 ♂ ♂		16·74	19	13	1·51
	39 ♀ ♀		17·36	21	13	1·89
H. ualabati:	9 ♂ ♂		15·67	19	14	1·73
H. spiniger: setae tergite 8 abdomen ♂	30 ♂ ♂	Left	6·40	8	5	0·98
		Right	6·23	8	5	0·82
		Total	12·63	15	10	1·54
H. ualabati:	Total: Counts (latter four doubtful), 19, 22, 23, 23, 20, 20, 25, 25). Approx. mean ..... 22.					
H. spiniger: setae sternite 8 abdomen ♀	39 ♀ ♀	Left	8·95	11	7	1·05
		Right	8·82	11	7	0·97
		Total	17·77	21	14	1·75

Sex Ratio

A summary of data for specimens of *H. spiniger* infesting the dog shows a general preponderance of females over males. The only total count ('Dog', Canal Zone: 96 ♂ ♂, 122 ♀ ♀) gives a sex ratio of 79 ♂ ♂ to 100 ♀ ♀. However, in view of the findings of Buxton (1937) these results have little or no significance.

Notes

The genus *Heterodoxus* was defined by Le Souëf and Bullen (1902) for an amblycerous parasite of 'Kangaroos, Wallabies, &c.', *H. macropus*, which they described. Johnston and Harrison (1913) and Harrison and Johnston (1916) re-examined Le Souëf and Bullen's material and concluded that, in view of the wide range of variation found, *H. macropus* was identical with Piaget's *Menopon longitarsus*, also assigning to the species specimens from several macropods and from dogs. They direct attention, however, to the chaetotaxy of the thoracic sternites and to the genitalia.

Specimens examined include many of those upon which previous records have been based, and much of the Harrison and the Le Souëf and Bullen collections. Unfortunately, no material was available from several of the species listed by Harrison and Johnston (1916) as hosts of '*H. longitarsus*'. Material in the Le Souëf and Bullen collection labelled '*Heterodoxus macropus*' comprised more than one species, so that the status of *H. macropus* could not be determined definitely and the species must be ranked as a synonym of *H. longitarsus* (Piaget). Mr. A. S. Le Souëf informs me that no specimens of *H. macropus* were designated types. Froggatt (1907) labels his figure as 'drawn from the type', but this will be a mistake.

Discussion

The genus shows great constancy in the series examined; this, with the great individual variation, makes species diagnosis difficult. The parasites from a host individual tend to group together and to show some constancy; the body proportions, the number of setae on a particular sclerite, in a series from one host individual may differ markedly in that from another, but this definiteness is not apparent when the several series are considered together. Certain characters show much greater individual variation than others, and belong to the group as a whole rather than to the species.

A classification based on morphology alone is not possible for both sexes, for while the structure of the phallus permits species differentiation in the male, there is no one other character of absolute diagnostic value. This means that the female may be associated definitely with the male only after: (1) examination of long series of individuals, collected from known hosts, with special attention paid to the possibility of regional distribution on the host's body; (2) mating and breeding experiments (association of the sexes of *H. spiniger* is possible because of the abnormal host relations shown by this parasite). Although it may be found possible to delimit species by a series of characters considered together, and the findings for *H. spiniger* would indicate this, at present the number of individuals available for examination is so small that no attempt is warranted.

In elaborating a scheme of classification in the genus it would seem that attention should be paid to the following points:—(1) the structure of the phallus in the male, (2) arrangement of setae on the terminal abdominal segments, (3) arrangement of setae on the metathoracic tergite and sternite, the abdominal sternites and, doubtfully, the prothoracic sternite, (4) measurements for head and thorax, of which those considered here might form a basis. It may be argued that environment may influence the distribution of setae on the ventral surface, but this does not seem to hold since: (*a*) the tergal chaetotaxy of the metathorax and that of the terminal abdominal segment in the male, appear to have a specific value, (*b*) all specimens from non-marsupial hosts have the same chaetotaxy as well as phallus structure, and it seems reasonable to suppose that the environments offered are various, (*c*) a series from an individual *Wallabia bicolor* comprised two species on phallus structure, although the possibility of each being confined to a definite region of the body must be remembered.

To summarize, the investigation has done little but present a number of problems for future study and *until very much longer series, from all hosts, have been examined critically, the issue must remain indefinite.* Are the species here outlined but variants of the one natural group, the limits of which have yet to be defined, that is, but one species, 'a population the members of which form a genetically interlinked complex' (Ferris, 1935)? Or are we dealing with a case of convergence? The internal anatomy of the various forms has not been studied. Of 79 specimens from various marsupials (Macropodidae) I can assign only two males to the same group as those examined from non-marsupial hosts, *which all belong to the same group*, a fact which emphasizes our ignorance of the physiology of host specificity. No experimental infections and cross-infections were carried out. Finally, it is of interest that *Heterodoxus* has not been recorded from the Australian Dingo (*Canis dingo* Meyer), though admittedly there are but two records of ectoparasite examinations of this host, a *Trichodectes* being found in each case; I have seen a series of lice from a dingo and they were also a species of *Trichodectes*. Does *Heterodoxus* occur on the dingo; if not, why not? Mr. A. Arnold informs me that his trappers report ectoparasite infection of the dingo to be of rare occurrence in West Australia.

Ferris (1930) has recorded six parasite species from a single host individual. In the material examined by me four species of *Heterodoxus* (based on phallus structure) have *Wallabia bicolor* as host, a series from one host individual containing two species of *Heterodoxus*. It is to be emphasized, however, that some of the parasites were from animals in zoological gardens; moreover, a species may be confined to some region of the host's body, and hybridization may be possible.

Although it is not possible to assess much of the literature relating to *Heterodoxus*, records from non-marsupial hosts can all be assigned to *H. spiniger* with some degree of certainty.

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PLATE III

THE HEAD. A-J, *H. spiniger*. K, *H. ualabati*. A, ♀ from dog, Java, 'aa' head width, 'bb' head length. B, ♀ from dog, Brasil. C, ♂ from dog, Belgian Congo. D, ♂ from *Oncifelis salinarum*, Argentina. E, ♂ from dog, California; type *H. armiferus* Paine. F, ♀ from dog, California; type *H. armiferus* Paine. G, ♂ from coyote, California. H, ♀ from *Oncifelis salinarum*, Argentina. I, ♀ from dog, South Africa; type *M. spiniger* Enderlein. J, ♀ from jackal, Uganda. K, ♂ from "Black Wallaby", Victoria; type *H. macropus* Paine.

Convention all figures: dorsal to left, ventral to right.

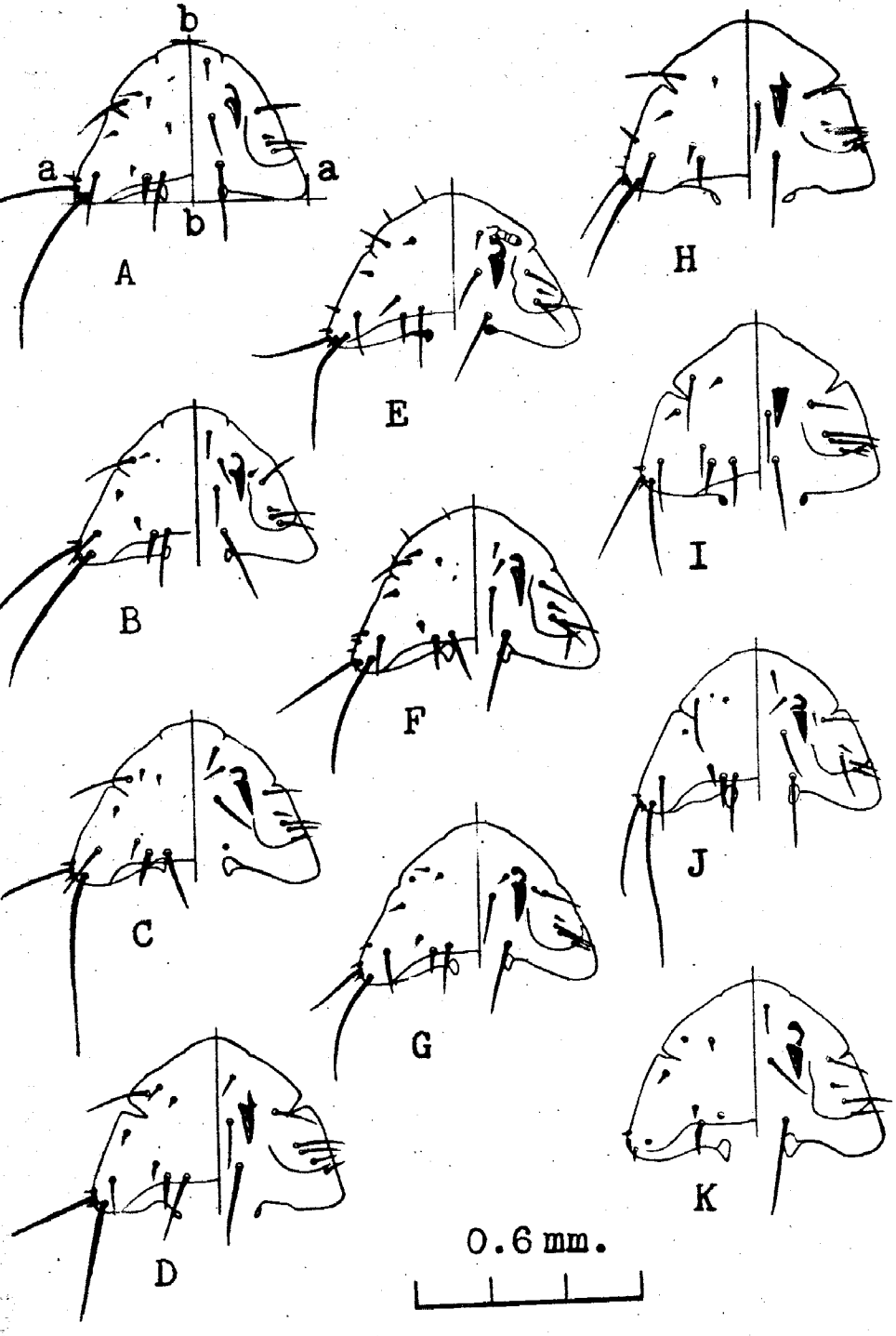

b
a
a
b
A
E
H
B
F
I
C
G
J
D
K
0.6 mm.

PLATE IV

THE THORAX. A, thorax from above, with first abdominal tergite, ♀ *H. spiniger*, dog, Java; 'so', sense organ first abdominal tergite. B, first thoracic tergite, ♂ *H. spiniger*, *Oncifelis salinarum*, Argentina. C, first thoracic tergite, ♂ *H. ualabati*, *Wallabia bicolor*. D, third thoracic tergite, ♂ *H. spiniger*, coyote, California. E, thorax from below, with first abdominal sternite, ♀ *H. spiniger*, dog, Java. F-H, plate first thoracic sternite: *H. spiniger*: F, ♀ from jackal, Uganda; 'x', 'y', 'z', three pairs generally occurring setae. G, ♀ from dog, Java; note seta 'x' duplicated on left. H, ♀ from dog, South Africa; type *M. spiniger* Enderlein. I-K, plate third thoracic sternite, *H. spiniger*; L. *H. ualabati*: I, ♀ from dog, South Africa; type *M. spiniger* Enderlein; intersetal distances 'a', 'b' (mean of 'b', 'b'1), 'c'; note extra pair of spines 'm', 'm'1, at sides of plate. J, ♂ from dog, Australia. K, ♀ from dog, Java; note extra spine 'n' on plate. L, ♂ from 'Black Wallaby', Victoria; type *H. macropus* Paine; note extra pair of spines 'o', 'o'1, on plate.

Scale: A-E, scale 'x'; F-L, scale 'y'.

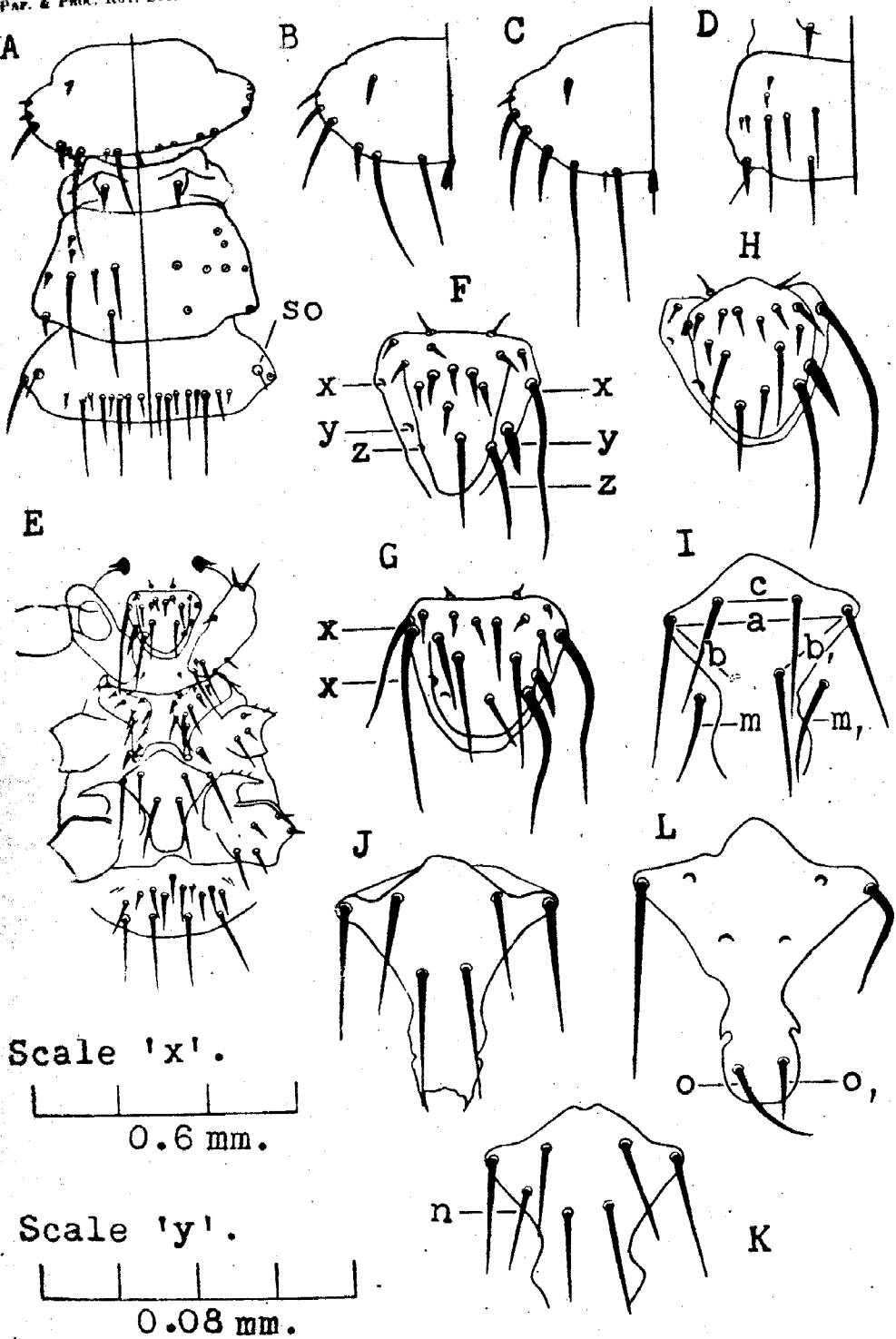

A
B
C
D
so
F
x
y
z
x
y
z
H
E
G
x
x
I
c
a
b
b,
m
m,
J
L
o
o,
n
K
Scale 'x'.
0.6 mm.
Scale 'y'.
0.08 mm.

PLATE V

THE ABDOMEN. A, Abdomen, omitting detail of terminal segment, ♀ *H. spiniger*, dog, Brasil; setae other than largest represented by dots for sternites 4, 5; 'so', sense organ; 'sp', spiracle. B-D, terminal abdominal segments, showing setal row, 'sr'. B, ♂ *H. ualabati*. C, ♀ *H. spiniger*. D, ♂ *H. spiniger*. E, external genitalia, with extrovert phallus, ♂ *H. spiniger*. F, phallus, ♂ *H. spiniger*, diagrammatic relief. G, extrovert phallus, ♂ *H. spiniger*. H, extrovert phallus, ♂ *H. ualabati*.

E-H: 'ap', apodemal plate; 'bk', beaklike structure; 'f', flap; 'lp', 'lp1', lateral process; 'p', process; 'ph', phallus; 'pm', paramere; 'r1', 'r2', 'r3', basal, central and distal regions of phallus; 'sc1', 'sc2', sclerotisations strengthening lateral processes; 'sc3', 'sc4', sclerotisations strengthening beaklike structure; 'ss', saclike structure; 'st', spine.

Convention: A-D, dorsal to left, ventral to right; E, from the side; F-H, from below. Scale: A, scale 'x'; B-D, scale 'y'; E-H, not to scale.

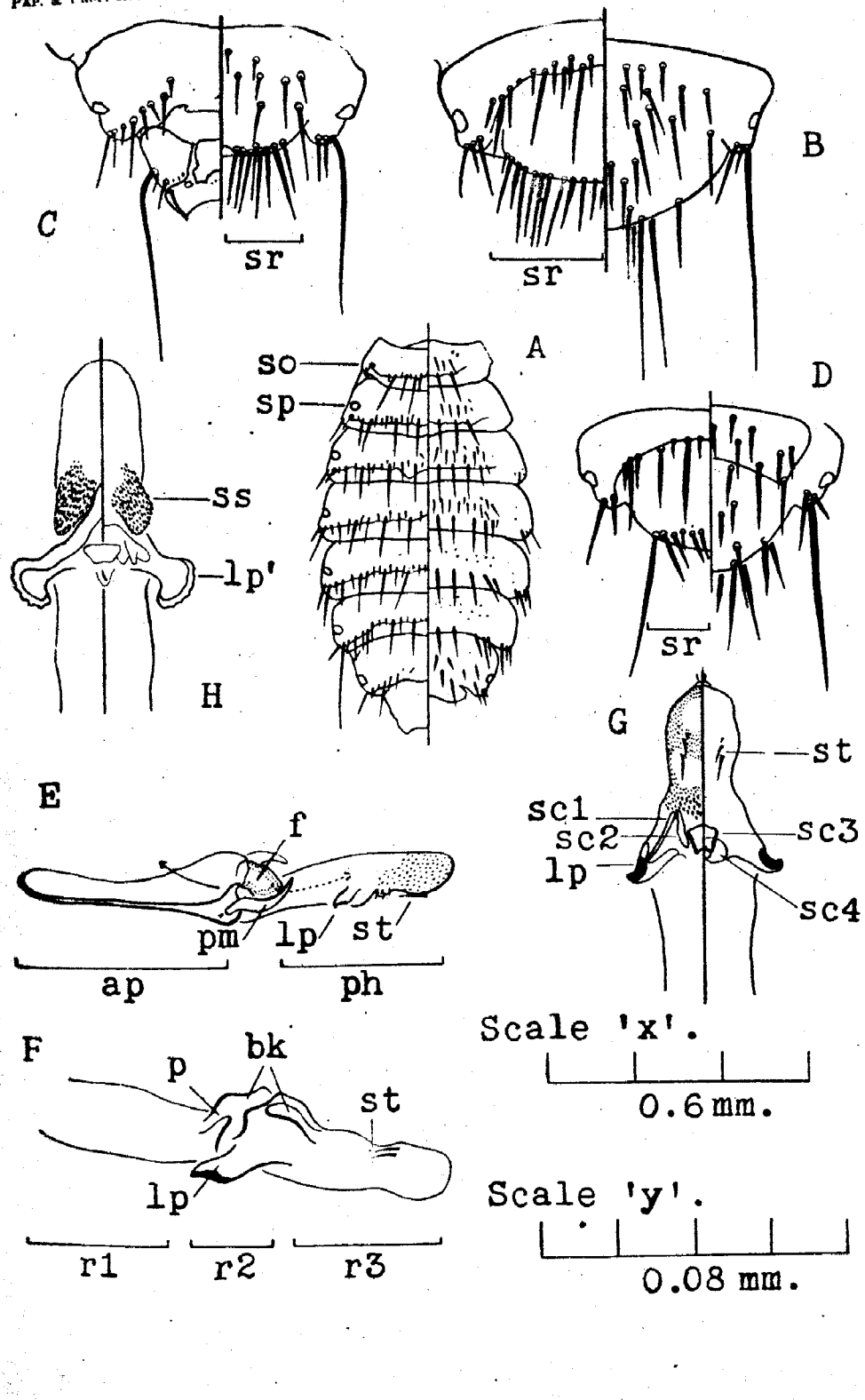
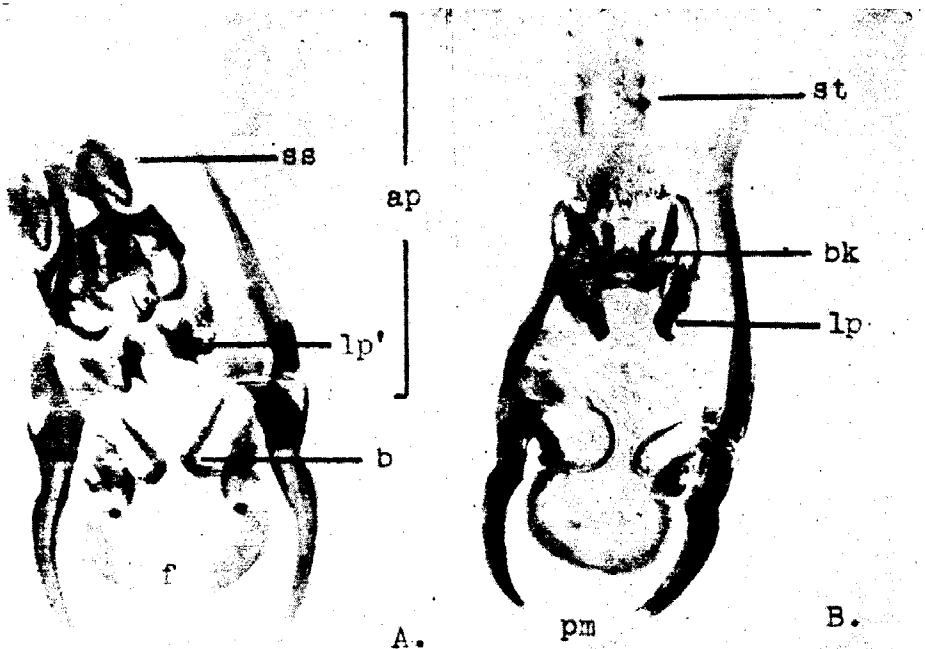
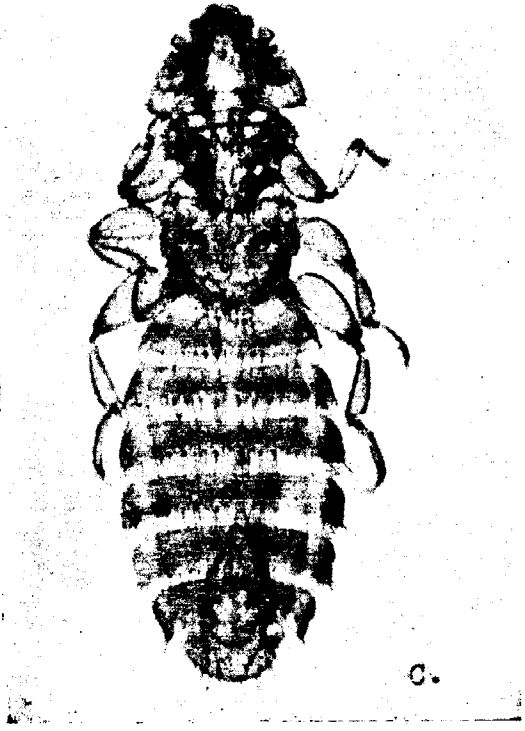

C
sr
B
sr
A
so
sp
D
sr
ss
lp'
H
G
st
sc1
sc2
sc3
lp
sc4
E
f
pm
lp
st
ap
ph
F
p
bk
st
lp
r1
r2
r3
Scale 'x'.
0.6 mm.
Scale 'y'.
0.08 mm.

PLATE VI

A, external genitalia *H. ualabati*, in situ. B, external genitalia *H. spiniger*, in situ. C, *Heterodoxus spiniger* (Enderlein) from *Herpailurus salinarum* Thomas. (Argentine, Jujuy, F. L. Werneck.).

A, B: 'ap', apodemal plate; 'b', bar; 'bk', beaklike structure; 'f', flap; 'pm', paramere; 'lp', 'lpl', lateral process; 'ss', saclike structure; 'st', spine.


ss
ap
lp'
b
f
A.
st
bk
lp
pm
B.


C.