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DESCRIPTIONS OF NEW SPECIES OF HYSTRICHOPSYLLID FLEAS WITH NOTES ON ARCHED PRONOTAL COMBS, CONVERGENT EVOLUTION AND ZOOGEOGRAPHY (Siphonaptera)[1]

By Robert Traub[2] and Thomas M. Evans[3]

Abstract: It is suggested that the peculiar arched or flared pronotal comb, now known to occur in 8 genera and 5 families of fleas, is an example of convergent evolution in shrew-fleas or macroscelid-fleas. The following new species are described and illustrated, and are cited as exhibiting modifications in the genal or pronotal spines which are associated with the phylogeny of the host, or else with its habits or environment: *Palaeopsylla recava* n. sp. ex shrews in Taiwan; *P. apsidata* n. sp. ex *Crocidura* in the mountains of Malaya; *P. setzeri* n. sp. ex *Hyperacrius* burrowing-voles in the Himalayas of W. Pakistan; *P. remota nesicola* n. ssp. primarily ex Taiwanese *Anourosorex*; *Doratopsylla wissemani* n. sp. ex *Sorex* in W. Pakistan; and *Corrodopsylla barrerai* n. sp. ex *Sorex* in Guerrero, Mexico. The hitherto unknown female of *Xenodaeria telios* Jordan 1932, ex shrews, etc. in the Himalayas, is described and illustrated. Discussions on the geographic and host-distribution of some fleas in W. Pakistan and on "adaptive" modifications of the pronotal and genal spines of shrew-fleas are presented. The genus *Corrodopsylla* is shown to be highly unusual in possessing pseudosetae on the first tergum and comments are made about this structure, on apical spinelets and combs of spines in certain fleas.

Fleas of the family Hystrichopsyllidae are intimately associated with rodents and insectivores and hence are frequently encountered in field studies on vectors and reservoirs of viral and rickettsial infections, such as those undertaken by field teams of the Department of Microbiology of the University of Maryland School of Medicine conducted in West Pakistan and elsewhere. Some of the hystrichopsyllid fleas encountered in these investigations, or in similar programs undertaken by other organizations, have proven to be new or little-known species, and are of unusual interest in biology or evolution because of morphological modifications of the pronotal or genal ctenidia and these are described and illustrated in this paper. Examples of convergent evolution, such as the flared or arched pronotal comb are discussed and notes on zoogeography, comparative morphology and phylogeny are also included.

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Holotypes and allotypes are deposited in the U. S. National Museum, Washington, D. C. Paratypes are distributed amongst various collections, as available, including British Museum (Tring), Bishop Museum (Honolulu), U.S. National Museum, and Traub collection.

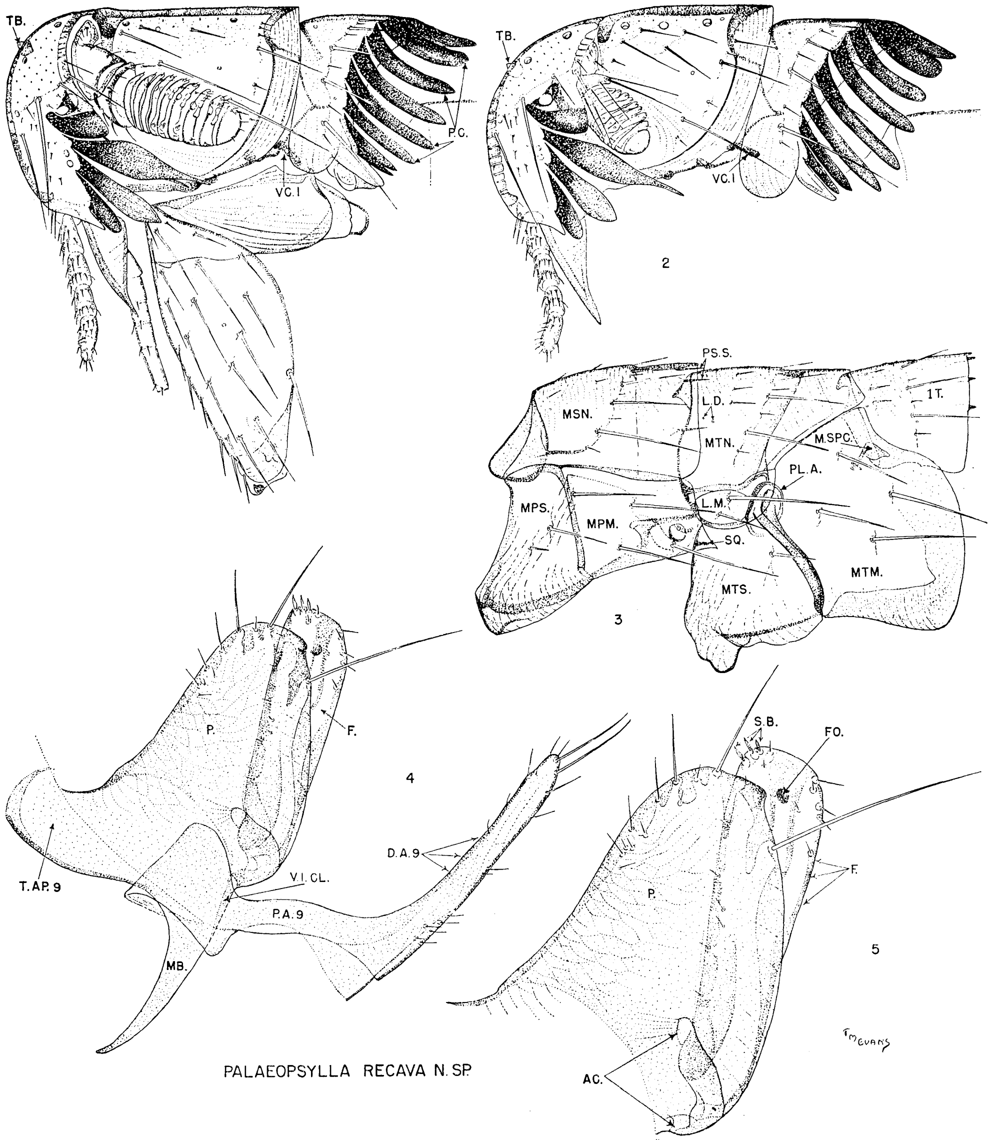
An outline of the species and topics presented, and the sequence in which they are treated, are as follows:

Subfamily CTENOPHTHALMINAE

1. **Palaeopsylla recava** Traub and Evans, new species Figs. 1-12 & 77.

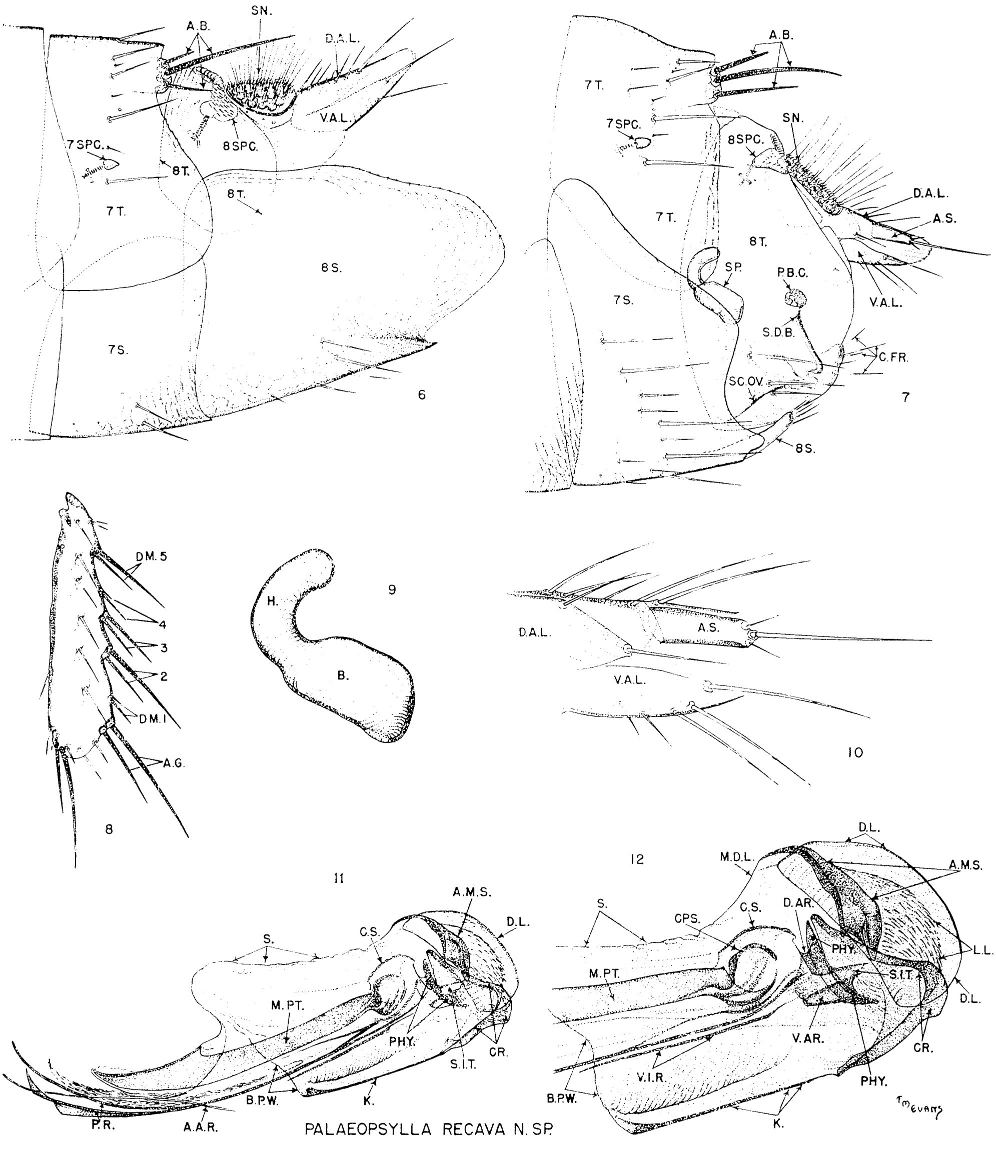
Type Material: Holotype ♂ and allotype ♀ (B-54839) ex *Soriculus caudatus fumidus*; Taiwan: Nan Tou Hsien, Yin Feng; 2090 m (6800 ft) elev.; 31.I.1962; coll. C. M. Yoshimoto & M. C. Thompson. Paratypes, all from Taiwan, as follows: 1♂, *S. c. fumidus*; Nan Tou Hsien, Yin Feng; 2185 m (7100 ft); 2.II.62; C. M. Yoshimoto & M. C. Thompson. 1♂, 1♀, *S. c. fumidus*; Nan Tou Hsien, Tsui (Chuei) Feng; 1815 m (5900 ft); 23.I.62; Yoshimoto & Thompson. 1♀, Small shrew; Nan Tou Hsien, 2 km E of Tsui (Chuei) Feng; 2245 m (7300 ft); 2.XI.61; R. Traub & R. E. Kuntz. 1♂, *S. c. fumidus*; Chia I Hsien, Alishan; 1845 m (6000 ft); 18.II.62; Yoshimoto & Thompson. 3♂, 3♀, *S. c. fumidus*; Chia I Hsien, Alishan; 1845 m (6000 ft); 22.II.62; Yoshimoto & Thompson. 1♂, *S. c. fumidus*; Chia I Hsien, Alishan; 1845 m (6000 ft); 2.III.62; Yoshimoto & Thompson.

Diagnosis: Unique among all described members of the genus (but agreeing with the next-described species) in that the pronotal ctenidium (figs. 1, 77, P. C.) is markedly arched, the base of the comb (lateral aspect) forming a distinct arc, so that the bases of the uppermost 2 spines are about in line with the apices of the ventralmost 2 spines, and the vertical axis of the ctenidium curves over the mesonotum, recalling *Xenodaeria telios* Jordan 1932 (fig. 83) and *Meringis altipecten* Traub & Hoff 1951, but the pronotum not



Figs. 1-5, *Palaeopsylla recava* n. sp.: 1, Head and prothorax (♂); 2, Head and prothorax (♀); 3, Meso- and metathorax, abdominal tergum 1 (♂); 4, ♂ sternum 9 and clasper; 5, Immovable and movable process of clasper.

quite as flared. In other *Palaeopsylla* the axis of the comb is generally virtually straight, and the bases form a vertical line (figs. 33, 76, P. C.) although in *P. sinica* Ioff 1953, *P. incurva* Jordan 1932, and *P. laxata* Jordan 1933, the comb is slightly arched, while in *P. miyama* Sakaguti & Jameson 1959, the axis of the comb is quite concave, but the bases of the uppermost spines are in line with those of the lowermost.



Figs. 6–12, ***Palaeopsylla recava*** n. sp.: 6, Segments 7, 8 and 10 (♂); 7, Modified abdominal segments (♀); 8, Metatibia (♂); 9, Spermatheca; 10, Dorsal and ventral anal lobes of proctiger; 11, Aedeagus; 12, Apex of aedeagus.

Belonging to the *P. soricis*-group of Smit (1960) (including *P. soricis* sspp., *P. sinica*, and *P. vartanovi* Ioff 1950) by virtue of: 1) the shape of the spines of the genal ctenidium (figs. 1, 2, G. C.); 2) the reticulated pattern of the abdominal segments with marginal microserrations (figs. 6, 7)[4]; 3) the absence of a striarium on the immovable process of the clasper (fig. 5, P.); and 4) distal arm of sternum 9 (fig. 4, D. A. 9) of subequal width throughout its length, etc., but differing from the *P. soricis*-group (as defined) in that the ♀ sternum 8 (fig. 7, 8 S.) is relatively long and thin, its sclerotized portion more than 9× as long as broad subapically, its apex therefore appearing narrow; and with 4 or 5 apical bristles, most of which are 2× as long as segment is broad. In *P. soricis*-group, ♀ sternum 8 relatively broad apically, the segment only about 5× as long as broad subapically, and apical bristles very short, their length only about 1/4 width of segment. Agreeing with *P. soricis*-group in that most of the spines of the pronotal comb are somewhat upcurved, their dorsal margin concave, but in the new species the uppermost 2 spines of this comb are only slightly concave or almost straight, somewhat shorter than the others and almost spatulate, whereas in *P. soricis*, the uppermost spines are as long and thin as the subdorsals and middle ones, and just as curved. Male sternum 9 differing from *P. soricis* and allies in that the distal arm is 8× or more as long as broad at midpoint (fig. 4, D. A. 9) instead of 6× or less.

Description—Head (figs. 1, 77, ♂; fig. 2, ♀): Frontoclypeal margin shallowly convex; tubercle (TB.) at upper 1/5, short and distinct, with exterior portion an equilateral triangle with altitude equal to about 1/2 of more-sclerotized inner portion. With preantennal row of 6 bristles, of which 3 are long, the others quite short; 1st (ventralmost) long bristle frontomarginal, at level of 3rd genal spine (counting ventral spine as 1st as in fig. 19A); 2nd long bristle median, at level of vestigial eye; 3rd long bristle along margin of antennal groove, at or somewhat below level of tubercle; 1 of short bristles between 1st 2 long ones; remaining 2 inserted dorsad of vestigial eye, 1 above and 1 below adjacent long one. Eye greatly reduced, its margin indistinct; located immediately above uppermost genal spine. First (ventralmost) genal spine digitoid, about 4.5× as long (measured along dorsal margin) as broad at midpoint. Second spine longer and broader than 1st; narrowed slightly at proximal 1/3 and margins thereafter somewhat convex; apically subacute; (shorter and more rounded apically in ♀ than in ♂). Third spine about 5× as long as broad at maximum; about 1.4× as long as 2nd; proximally narrow; beyond midpoint gradually narrowing to long acute apex; extending slightly beyond apex of acuminate genal process. Fourth spine broadening from base to truncate apex which is about 2× as broad as basal region; somewhat shorter than ventralmost spine. Maxillary lobe extending to slightly beyond base of last segment of maxillary palpi. Segments 1, 2 and 4 of maxillary palpi subequal; 3 only slightly smaller. Labial palpi 5-segmented, about 2/3 length of fore-coxae; apical segment more than 1.5× as long as segments 3 and 4. Scape of antenna with short proximal and dorsomarginal bristles. Antennal segment 2 with marginal bristles short in ♂; these scarcely exceeding width of segment; in ♀, bristles much longer, extending 1/2-3/4 length of club. Postantennal region with 3 rows of bristles but each row incomplete, viz: bristles arranged 2-2-2(3), of which lowest (ventralmost) are the largest in ♂, and those of last 2 rows very long, bordering antennal groove, but in ♀ 2nd row with ventralmost median in position and scarcely longer than dorsal one; each sex with broad gap between ventral 2 bristles in last row.

Thorax: Pronotum with row of about 4 long bristles per side; for most its height, much narrower than its spines are long. Pronotal comb with total of about 16 spines; comb

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4. The possession of reticulations and microdenticulations on the abdominal segments further serve to separate the new species from *P. miyama*, *P. incurva* and *P. laxata*, which are in the *P. remota*-group.

arched so maximum portion of convexity is at level of base of 3rd or 4th spine; all but dorsal 2 spines long and narrow; middle spines about 8× as long as broad at midpoint and quite concave dorsally; upper 2 spines about 4.5× as long as broad. Mesonotum (fig. 3, MSN.) with 1 row of bristles and 2 or 3 pseudosetae (PS. S.) per side. Mesepisternum (MPS.) with 1 long median, subcaudal bristle and 1 smaller one near midpoint. Mesepimere (MPM.) with 4 bristles arranged 2-2; posterior margin shallowly concave, terminating in acute ventrocaudal angle. Lateral metanotal area (L. M.) well demarcated; with 2 bristles, dorsalmost the longer. Metepisternum (MTS.) with 1 subcaudal submedian bristle; with lightly sclerotized squamulum (SQ.). Pleural arch (PL. A.) well-developed. Metepimere(MTM.) generally with 4 bristles arranged 2-2, of which upper anterior one is near sagittate spiracular fossa (M. SPC.), which is almost as broad as long.

With most of stout dorsomarginal bristles of tibiae paired. Metatibia (fig. 8) with 5 pairs of dorsomarginal bristles arising from sclerotized bases or platelets (DM.1—DM. 5) and with apical group (A. G.) of 2 long bristles; with these groups of dorsomarginal bristles spaced relatively widely apart, i.e., interval between bases equal to about 2× diameter of their basal platelets; 1st pair of dorsomarginals (DM. 1) and DM. 4 each consisting of 1 medium-sized bristle and 1 small seta; DM. 2 and DM. 5 consisting of 1 long and 1 medium bristle; in DM. 3, both members medium-sized but basal member slightly longer than apical one; large dorsomarginal relatively straight, narrow and long, i. e. in DM.2, larger member about 24× as long as broad at midpoint. Longest apical bristle of pro- and mesotibiae extending to near apex of segment II of tarsus; in metatibia longest apical bristle not quite reaching apex of tarsal segment I. Segment II of metatarsus with an apical bristle reaching almost to apex of segment III. Distal segment of each tarsus with 4 pairs of lateral plantar bristles, and with 1 proximal pair displaced so as to be between bases of 2nd pair. Measurements (in micra) of tibiae and tarsal segments (petiolate base deleted) of allotype:

		Tarsal Segment				
Leg	Tibia	I	II	III	IV	V
Pro-	142	46	46	40	38	81
Meso-	233	71	73	57	43	81
Meta-	308	204	124	76	51	84

Abdomen: Terga with apical spinelets arranged approximately as follows (total number): ♂: 6-6-4-2-1; ♀: 6-6-3-3. Occasional specimens have 1 or 2 additional spinelets on same segments, or even 1 or 2 on terga 5 and 6. Typical terga with 1st row of bristles reduced in number; tergum 2 with only 3 or 4 bristles in ♂ and terga 3-6 often lacking bristles or at most with 1 or 2 bristles per side; in ♀, tergum 2 with 5 bristles, 3 with 4 and terga 4-6 generally bearing 1-3 subdorsal or submedian bristles in 1st row. Unmodified terga with ventralmost bristle of posterior row inserted just below sagittate spiracular fossa; reticulate and microdenticulate. Basal abdominal sterna with reticulated pattern well-developed but medially consisting largely of elongate subparallel curved lines; with single ventromarginal bristle. Unmodified sterna in ♂ with 1 ventromarginal bristle; in ♀ with vertical row of 3 bristles, of which ventralmost is marginal, preceded by small ventromarginal bristle; sterna somewhat reticulate and pattern microdenticulate. Male with middle antepygidial bristle (fig. 6, A. B.) about 4.5-5.0× as long as upper one; ventralmost bristle about 0.5× as long as upper. Female with middle antepygidial bristle (fig. 7, A. B.) about 2× length of upper and about 1.5× that of ventral. Insertion of plate of antepygidial bristles somewhat submarginal in each sex, not dorsomarginal.

Modified Abdominal Segments—♂: Tergum 8 (fig. 6, 8 T.) extending caudad only to level slightly beyond middle of sensilium (pygidium) (SN.) and ventrad to about level of dorsal margins of unmodified sterna; devoid of bristles. Spiracular fossa 8 (8 SPC.) broadest basally; this portion 2× as broad (long) as high, rapidly narrowing to vermiform curved region bordering dorsal margin of tergum. Sternum 8 (8 S.) very large, about 1.5× as long as high at midpoint; anterior margin straight; dorsal margin shallowly biconcave; posterior margin convex, but ventral portion quite straight, declivous, sloping towards short sharp sinus or notch at junction with ventral margin, at region where reticulate pattern is quite dense and ridged, its contours approximated, crowded; true ventral margin quite straight. Sternum 8 with 2 groups or vertical rows of subventral or ventromarginal bristles, 1st of 2, 2nd of 3 bristles.

Immovable process of clasper (figs. 4, 5, P.) broadly ovate but with apex relatively subtruncate; about 2× as long (measured from base of acetabulum, AC.) as broad at midpoint; anterior margin proximally slightly concave but curving gradually so as to be equally convex subapically; distal margin very slightly concave between shallow shoulders; with distinct apicocaudal angle due to excision at junction with caudal margin, which is evenly but shallowly convex. This shoulder well-sclerotized, thickened, apparently articulating with well-developed fovea (FO.) on movable process (F.). Immovable process with anterior margin bearing row of 4 thin bristles commencing distad of midpoint; with longer apical bristle at anterior shoulder, and yet-longer subapical one on posterior margin. Movable process or finger of clasper (F.) about 4.7× as long as broad at midpoint, its sides appearing subparallel for most their length but actually slightly sinuate proximally and diverging somewhat apically so that finger is slightly clavate but with apex quite flat. Movable process with group of 4 or 5 small "sensillary" bristles (S. B.) at anterior shoulder of apex and with row of 4 small thin bristles on posterior margin, ranging from shoulder to level of fovea (FO.). Manubrium of clasper (MB.) slightly curved and narrow, resembling lower 1/2 of a crescent. Sternum 9 with proximal arm (P. A. 9) anteriorly (dorsally) terminating in conspicuous large subtrapezoidal expansion which in length is more than 3×, and breadth, more than 2× breadth of major portion of arm. Apical margin of this expansion of P. A. 9 subtruncate, its ventral margin slightly concave, its dorsal margin convex. Remainder of P. A. 9 curved, so dorsal margin somewhat convex and sides subparallel for most of their length. Distal arm, of sternum 9 (D. A. 9) long and narrow, digitoid; longer than entire P. A. 9 and, in the main, narrower than arched part of proximal arm; with 2 long subventral bristles at apex; in addition with 2 very small, more dorsal, apical bristles and 3 or 4 widely spaced dorsomarginal bristles at distal 1/3 of arm; with group of about 4–6 subventral or marginal small bristles at basal 1/6, 3 or 4 widely-spaced thin bristles scattered along ventral margin, and 1–3 small median mesal bristles.

Lateral plates of aedeagal apodeme arched dorsad to produce weakly sclerotized sail (velum) (figs. 11, 12, S.) extending dorsad as high as apical portion of phallosome, and cephalad to anterior 1/3 of apodeme. Middle plate (M. PT.) with sclerotized portion long and narrow, about 12× as long as broad at midpoint and apically narrowed and somewhat upcurved. Aedeagal pouch with sclerotized basal wall (B. P. W.) and stout keel (carina) (K.). End-chamber dominated by huge sclerite, the apicomedian sclerite (A. M. S.), which arises high from region of median dorsal lobe (M. D. L.) or apex of dorsal wall and extending down on each side as a broadening sclerotized band terminating near sclerotized inner tube (S. I. T.). Largest structures of endophallus are semi-ellipsoidal distodorsal lobes (D. L.), which virtually enclose entire end-chamber, extending from M. D. L. down to near ventral margin, and from apex of inner tube caudad to a point well distad of other lobes; about 2× as high as long; with delicate, short semi-membranous tufts or spicules, especially apically. Crescent sclerite (C. S.) shallowly convex and narrow, about 1/6 diameter of capsula (CPS.) it encloses. On each side of sclerotized inner tube, a prominent, large crescentic sclerite, the phylax (PHY.), extending from tip of dorsally-recurved apical portion of A. M. S. to wall below ventral armature (V. AR.) of sclerotized inner tube. Dorsal armature (D. AR.) of inner tube broader but shorter than V. AR., encompassing approximately area of sclerotized inner tube (S. I. T.), which in turn is about 6× as long as broad at region of phylax. Crochets well-developed as prominent thickened lobes lying mesad near ventral portion of distodorsal lobes (D. L.), arising near apex of A. M. S., and ventrally associated with apex of keel; with a submedian patch of semimembranous tufts lying ventrad to apex of S. I. T. Lateral lobes (L. L.) lightly sclerotized, scarcely apparent but covering parts of ventral portion of end-chamber. Penis rods (P. R.) uncoiled. Vesicle at distal end of ventral intramural rod (V. I. R.) inapparent. Aedeagal apodemal rod (A. A. R.) weakly sclerotized.

Abdominal segment 10 with dorsal lobe of proctiger (D. A. L.) with dorsomarginal bristles, the subapical one largest. Ventral anal lobe (V. A. L.) lightly sclerotized, with 1 subapical dorsal and 1 subapical ventral bristle.

Modified Abdominal Segments— ♀ : Sternum 7 (fig. 7, 7 S.) with posterior margin emarginate for most its length with deep, broad sinus, and subventrally curving sharply cephalad so that ventral margin is apically excised. 7 S. with anterior margin straight, almost vertical; dorsal margin declivous but ends curved convexly; with subvertical row of about 6–8 bristles, of which 2 or 3 submedian ones are quite small; row preceded by about 3 small subventral bristles. Tergum 8 (8 T.) apparently devoid of bristles near spiracular fossa 8 (8 SPC.) ; with vertical, subventral row of 3 or 4 bristles and group of 4 or 5 small subventral bristles along a sinus on caudal margin; this clump herein designated the caudal fringe (C. FR.) and associated with sclerotized margins. Sternum 8 (8 S.) distinctive as a relatively long, digitoid sclerite exceeding in length adjacent bristles of 7 S.; with 4 small apical bristles. Dorsal anal lobe (D. A. L.) with dorsomarginal row of wide-spaced bristles and a ventral bristle below and anterior to anal stylet (A. S.). Ventral anal lobe (V. A. L. and fig. 10) narrow, acuminate; with long, thin, dorsal subapical bristle and 3 thin, subapical ones, 2 of these long and subapical; ventral margin mainly bare because of the thin nature and wide separation of the bristles. Anal stylet (fig. 10, A. S.) about 3.5× as long as broad at midpoint; gradually narrowing from base to apex, but distally broad enough for insertion of 3 bristles, of which middle one is very long. Spermatheca (SP. and fig. 9) with bulga (B.) nearly 2× as long as broad; dorsal and ventral margins quite straight, subparallel anteriorly but somewhat diverging caudally so that anterior portion somewhat broader than posterior; separation of hilla (H.) from bulga not clearly demarcated. Hilla broad, about 0.5× diameter of bulga and subequal to it in length; of equal breadth throughout its length; upturned but not recurved over bulga; apex broadly rounded, lacking sclerotized papilla. Bursa copulatrix with duct (S. D. B.) relatively lightly sclerotized, straight; perula (P. B. C.), or bursa proper, subovate and indistinct. Walls of oviduct apparently sclerotized in part (SC. OV.), the ridge-like thickening often appearing paired but virtually contiguous, simulating mesal ridges of 8 T. of certain fleas, but variable in shape and position; at times sinuate and oblique, not horizontal.

Comments: The specific name *recava* is a Latin adjective meaning arched inward, or concave, and refers to the characteristic shape of the pronotal comb, which is vaulted or curved back over the mesonotum (figs. 1, 2), instead of having a straight perpendicular axis as in most fleas. The name is also applicable to the majority of the individual spines in the pronotal comb, for these too are concave.

2. **Palaeopsylla apsidata** Traub and Evans, new species Figs. 13–18.

Type Material: Holotype ♀ (B-47634-1) ex *Crocidura* sp.; W. Malaysia: Malaya, Perak, Maxwell Hill; 1355 m (4400 ft) elev.; 20.III.1958; Coll. R. Traub (U. S. Medical Research Unit, Malaya) & T. C. Maa (Bishop Museum, Honolulu). No other specimens known.

Diagnosis: In the *P. soricis*-group. Agrees with *P. recava* n. sp. in possessing a pronotal comb (fig. 13, P. C.) which is conspicuously arched over the mesonotum; thereby immediately separable from all other described species. Distinct from *P. recava* n. sp. as follows: 1) 1st (ventralmost) spine of genal comb (fig. 13, G. C.) as long as or longer than 2nd spine. 2) Apex of 2nd spine of genal ctenidium rounded. 3) Spiracular fossa of metepimere (fig. 17, M. SPC.) very broad (dorsoventrally), 1.4× as broad as long. 4) Sternum 7 (fig. 15, 7 S.) with caudal margin bearing deep subventral notch above conspicuous ventral lobe, which is more than 2× as long as broad. In *P. recava* n. sp. in contrast: 1) 1st spine of genal comb (fig. 2, G. C.) definitely longer than 2nd. 2) 2nd spine apically pointed or angulate. 3) Spiracular fossa of metepimere (fig. 3, M. SPC.) virtually as long as broad. 4) Caudal margin of sternum 7 (fig. 7, 7 S.) bearing shallow, broad sinus, while ventral lobe is about as long as broad. Like *P. recava* n. sp., further separable from other members of *P. soricis*-group in that upper 2 spines of pronotal comb (fig. 13, P. C.) are relatively thick, spatulate, instead of long, thin and somewhat pointed. Unique in *P. soricis*-group in that internal marginal sclerotizations or incrassations of frontoclypeal region are broad, i.e., some of individual patches 2× as long as high, instead of being subequal or higher than long.

Description[5]—*Head* (fig. 13): Ventralmost incrassation of frontoclypeal margin more than 2× as high (broad) as long; above this 2 small thin bristles. Ventralmost spine of genal ctenidium more than 6× as long as broad at maximum; gradually widening from base to apex. Second spine broader but somewhat shorter than ventralmost, spatulate. Third spine more than 2× length of 2nd, distal portion very narrow. Uppermost spine more than 0.5× length of ventralmost and subapically almost 2× as broad as that spine. Labial palpi extending somewhat beyond midpoint of 1st coxa; apical 2 segments subequal and slightly longer than segments 2 and 3. Postantennal rows of longish bristles arranged 1-2-3.

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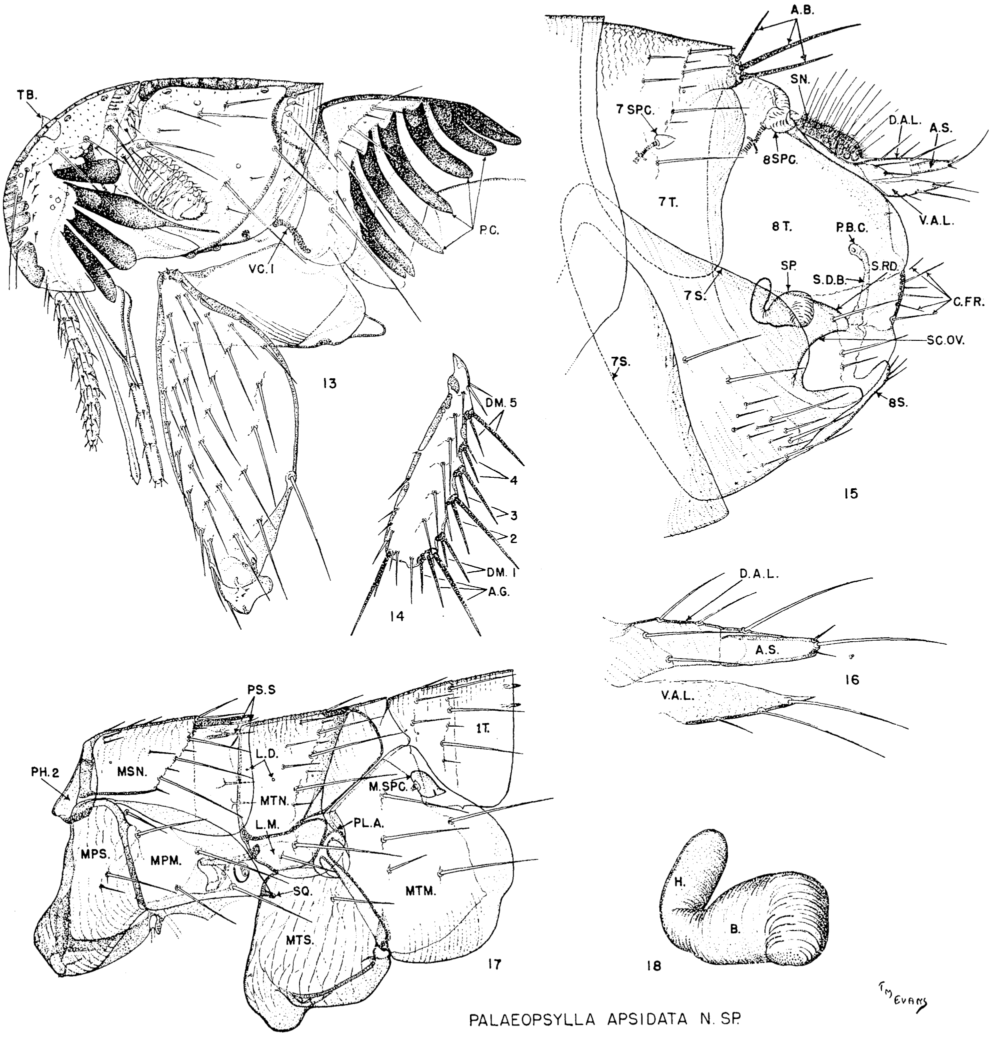
[5] In the description of this and the following species, only significant differences from *P. recava* n. sp. are cited.



Figs. 13–18, *Palaeopsylla apsidata* n. sp.: 13, Head and prothorax (♀); 14, Metatibia (♀); 15, Modified abdominal segments (♀); 16, Dorsal and ventral anal lobes of proctiger; 17, Meso- and metathorax, abdominal tergum 1 (♀); 18, Spermatheca.

Thorax: Pronotal comb of about 14 spines; strongly arched over mesonotum so that base of dorsalmost spines nearly in line with apices of ventralmost; maximum arc of convexity at level of base of 3rd spine. Lower 4 spines long and narrow, concave, apically subacuminate. Dorsal 3 spines broader, bluntly rounded. Mesonotum with 3 or 4 pseudosetae (fig. 17, PS. S.) per side. Metepimere (MTM.) with bristles arranged 3–2; its spiracular fossa (M. SPC.) broader than long, with apex ventral in position. Metatibia (fig. 14) with 3 long bristles in apical group (A. G.) but smallest, lateralmost, not really on same platelet; with 5 pairs of dorsomarginal bristles (DM.1–DM.5) but with an additional marginal seta between DM.1 and DM. 2; interstice between DM.1–DM.2 about 3× length of their basal platelets, and those between other dorsomarginal pairs about 2× their length. The larger bristle of pairs DM.1–DM.5 long, narrow and fairly straight, i.e. for M.2, 24× as long as broad at middle. Longest bristle of mesotibia not reaching beyond midpoint of segment II of tarsus; slightly further in hind leg. Tarsal segments with approximately same proportions as in *P. recava* n. sp.

Abdomen: Apical spinelets: 4–6–4–2. First row of tergal bristles as follows, per side: 2(3)–5–3(2)–2–1–2(1)–2. Sterna 2–5 with vertical subventral row of 3 bristles preceded by 1 or 2 smaller ones; 6 with 5 bristles in row, 1 of these small. Middle antepygidial bristle (fig. 15, A. B.) slightly more than 2× length of upper one and about 1.7× length of lower.

Modified Abdominal Segments: Sternum 7 (fig. 15, 7 S.) with broad deep subventral sinus; ventromarginal lobe below sinus narrower than sinus; lobe above very broadly convex; with a subvertical row of 3 or 4 large bristles and an additional ventromarginal one displaced somewhat cephalad; with a group of about 6–9 small bristles preceding row or with 1 or 2 of these intermingled with row.

Tergum 8 (8 T.) with a group of 3 median bristles of which ventralmost is small; with caudal fringe (C. FR.) consisting of a row of 6 bristles on a shallow sinus; sclerotized ridge (S. RD.) almost straight. Sternum 8 (8 S.) with sclerotized apical portion about 2× as long as broad; with total of 5 bristles of which bottom 2 are paired, representing 2 per side of sternum. Dorsal anal lobe (fig. 16, D. A. L.) with 3 widely spaced dorsomarginal bristles and 2 lateral ones. Ventral anal lobe (V. A. L.) with 3 ventromar ginal, thin bristles, of which 2 are long (that at apical 1/3 and 1 subapical). Spermatheca (SP. & fig. 18) distorted in position in specimen but with bulga (B.) apparently less than 2× as long as broad and with hilla (H.) more than 0.5× diameter of bulga and perhaps subequal in length. Perula of bursa copulatrix (P. B. C.) with a somewhat elongate base.

Comments: Relatively little is known about the shrews and shrew-fleas of the Indo-Malayan region, and this is particularly true for the hills of Malaya. In all probability these insectivores are common, but they are infrequently collected, largely because the trapping methods employed are generally designed for rats or equally large mammals which are of interest in research on scrub typhus and other infections. The snap-traps designed for mice and shrews are not practical for use in such terrain because they are apt to be sprung by mammals too large to be restrained by them, and are dragged away, or else the bait is eaten by ants, beetles or slugs. Persistent and large-scale use of mouse-traps in the hills of Thailand during some of our investigations have resulted in the capture of mice and shrews which previously were not known to occur there, and it seems likely that similar results might be obtained in Malaya.

Since 1944, Traub has examined at least 50 specimens of *Crocidura*, *Suncus*, *Anourosorex* and other shrews in Southeast Asia, i.e., North Burma, Assam, Malaya, Thailand and North Borneo, virtually almost all of which had been taken in the lowlands, but, except for one or two *Xenopsylla cheopis* (Rothschild 1903), the only flea ever collected was this new species. (In certain portions of the Himalayas, *Xenodaeria telios* is definitely associated with *Crocidura*, as mentioned below.) It seems likely that *Crocidura* may be the correct host for *P. apsidata* n. sp. since, as a member of the *P. soricis*-group, it is closely related to other shrew-infesting *Palaeopsylla*, and since *Crocidura* in the mountains of Malaya have been little-examined for fleas.

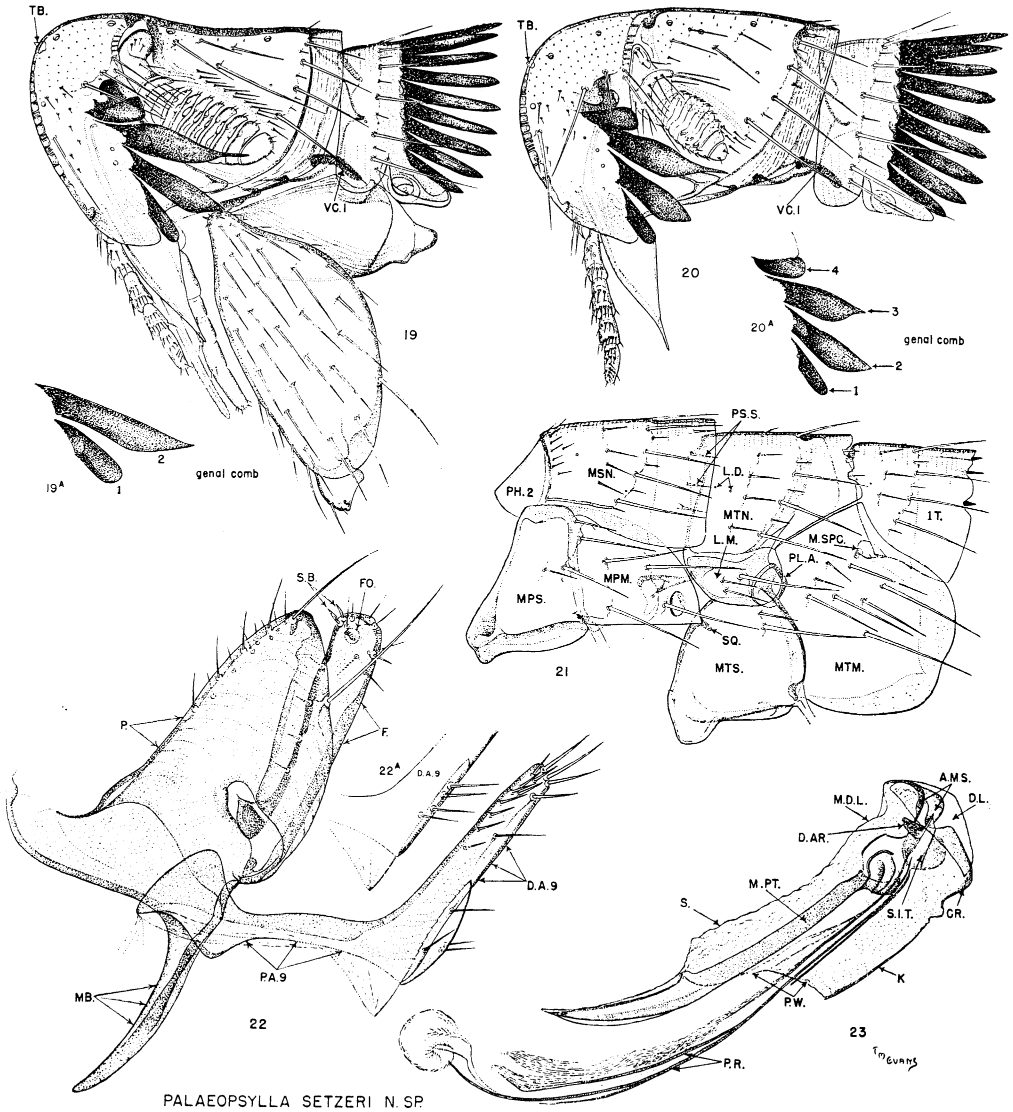
As mentioned below (Section 11), the rounded apices of the ventral genal spines suggest that *P. apsidata* n. sp. really is a shrew-flea and not a parasite of the Malayan mole (which is known only from a few specimens taken in the Cameron Highlands, and which theoretically may occur on Maxwell Hill, the type-locality of this flea).

The specific name is derived from the Latin term *apsis* (*-idis*), meaning an arch or vault, and refers to the highly modified concave pronotal comb of this species.

3. **Palaeopsylla setzeri** Traub and Evans, new species. Figs. 19–28, 30–31 & 78.

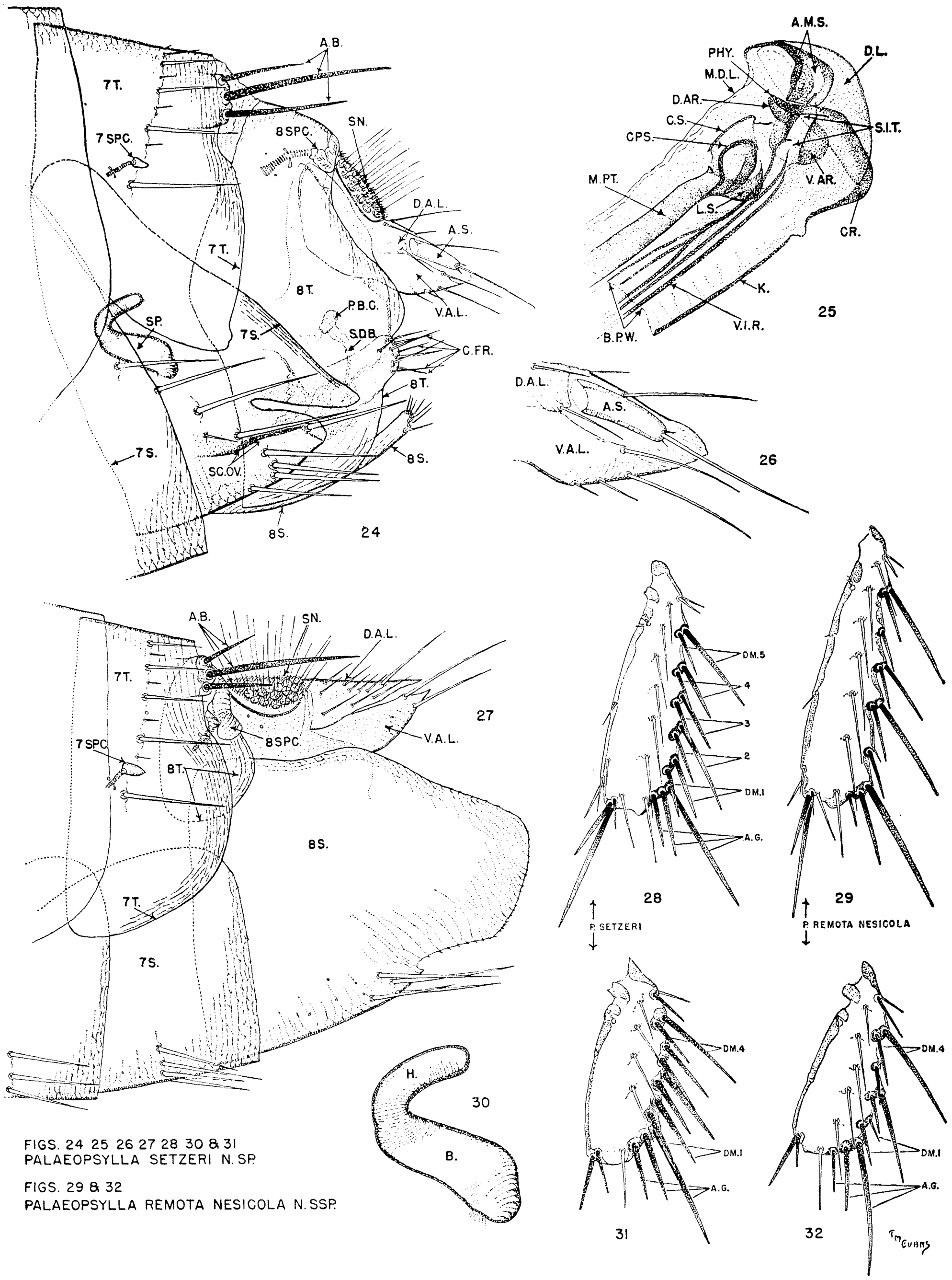
Type Material: Holotype ♂ and allotype ♀ (B-66031) ex *Hyperacrius* sp.; W. Pakistan: Hazara Dist., Kaghan Valley, Shogran; 2310 m (7500 ft) elev.; 29.VII.1963; coll. R. Traub & A. B. Mirza. Paratypes, all from W. Pakistan, as follows:

♂	♀	Host	Locality	Elev.	Date	Collector
—	3	*Hyperacrius* sp.	Hazara Dist., Kaghan Valley, Shogran	2310 m (7500′)	29.VII.63	R. Traub & A. B. Mirza
—	2	″	″ ″ ″	2615 m (8500′)	27.VII.63	″
—	5	″	″ ″ ″	2385 m (7750′)	1–3.VII.65	Mirza
1	10	″	″ ″ ″	″	3.VIII.64	J. J. O'Keefe
9	12	*H. wynnei*	″ ″ ″	…	23.V.66	″
2	1	″	″ ″ ″	2385 m (7750′)	23.IX.64	Traub
—	1	″	″ ″ ″ Mt. Makra	3170 m (10300′)	″	″
1	4	″	″ , Murree Hills, Dunga Gali	2460 m (8000′)	23.IX.62	Mirza & H. W. Setzer
—	2	*Hyperacrius* sp.	″ ″ ″	″	″	Traub & Mirza
—	1	″	″ ″ ″	…	28.VI.65	A. C. Risser
1	1	*Apodemus* sp.	″ ″ ″	…	27–28.VI.65	″
9	12	*Hyperacrius* sp.	″ , Nathia Gali	…	27–29.VI.65	″
1	—	*Crocidura* sp.	″ ″	…	29.VI.65	″
3	7	*H. fertilis*	Dir State, 26 km (16 mi.) N of Dir,	2615 m (8500′)	30.IX.66	Traub & Mirza
—	3	*Hyperacrius* sp.	″ 29 km (18 mi.) N of Dir, 3km (2 mi.) S of Lowari Top	…	28.IX.66	″
1	1	*H. fertilis*	″ , Lowari Top, 32 km (20 mi) N of Dir	2770 m (9000′)	27.IX.66	″
23	18	″	″ ″ ″	3200 m (10400′)	28–30.IX.66	″
7	6	″	Swat State, 10 km (6 mi.) SW of Utror, Sandoz Farm	2740 m (8900′)	6.X.66	Traub & O'Keefe
3	7	″	″ ″	″	8.X.66	Traub & Mirza
5	3	*Hyperacrius* sp.	″ ″	″	7–8.X.66	″



Figs. 19–23, *Palaeopsylla setzeri* n. sp.: 19, Head and prothorax (♂); 19A, Genal comb (1st and 2nd spine) (♂); 20, Head and prothorax (♀); 20A, Genal comb (♀); 21, Meso- and metathorax, abdominal tergum 1 (♂); 22, ♂ sternum 9 and clasper; 23, Aedeagus.

Diagnosis: 1) Characterized by the fact that the movable finger of clasper (fig. 22, F.) is clearly narrower at its proximal 1/3 than subapically. 2) Distinctive in that sternum 7 of ♀ (fig. 24, 7 S.) bears a very long narrow sinus which is horizontal in position, while the margin of the sternum above the sinus is relatively straight, not deeply emarginate or sinuate, and the upper lobe is almost as broad as the lower one. 3) Exceptional



Figs. 24–28, *Palaeopsylla setzeri* n. sp.: 24, Modified abdominal segments (♀); 25, Apex of aedeagus; 26, Dorsal and ventral anal lobes of proctiger; 27, Segments 7, 8, and 10 (♂); 28, Metatibia (♂). Fig. 29, *P. remota nesicola* n. ssp., Metatibia (♂). Figs. 30–31, *P. setzeri* n. sp.: 30, Spermatheca; 31, Protibia (♂). Fig. 32, *P. remota nesicola* n. ssp.: Protibia (♂).

in the genus and perhaps unique amongst known forms[6] in that: A) There is a "false comb" on each of the tibiae due *not* to the presence of supernumerary dorsomarginal bristles, but to the hyperdevelopment and slight downwards displacement of the smaller member of the usual dorsomarginal pairs (cf. fig. 31, 32). Thus, the 1st and 4th groups of dorsomarginals on the metatibia are both well-developed and stout (fig. 28, DM. 2 and DM. 4), instead of only 1 bristle being developed per group while the other is minute (fig. 29), and the bases of the pairs well separated and inclined obliquely instead of being virtually horizontal and close-set. B) The pairs of dorsomarginal tibial bristles relatively close together, i. e. the interval between the plates of the bases relatively narrow, being subequal in size to that of the platelets instead of being 2× as large, or greater. C) The metatibia relatively short in proportion, being definitely shorter than metafemur and only about 1.4× length of segment 1 of its tarsus, whereas in *P. remota* Jordan 1929 for example, the metatibia (fig. 29) and metafemur are subequal and the tibia/tarsus I ratio is 1.65; in *P. setzeri* n. sp., metatibia 261 μ or much less than 3× length of metatarsal V, while in *P. recava* n. sp. the corresponding ratio is much greater than 3. (Trait C above presumably accounts for B.) 4) Bearing a larger number of body bristles than is typical of the genus, and these unusually long and thin. Thus, on the unmodified segments, there are 2 bristles below the spiracular fossa, not 1, and there are 3 (♂) and 4 (♀) ventromarginals instead of 1-2 (♂) and 3 (♀).

Does not readily conform to any of the species-groups established by Smit (1960), but perhaps fits best with the *P. remota*-group, as follows. Since the surface sculpture of the abdominal segments is not well-reticulated and their margins are quite smooth, not serrate, the species does not belong to the *P. soricis*-group[7]. Since the longest (3rd from ventral) spine of the genal comb does not gradually taper to a long narrow apex but instead rapidly narrows at distal 1/3, it does not fit in the *P. minor*-group. Agrees with definition of *P. remota*-group in that 1) the abdominal segments are essentially non-reticulate and non-microdenticulate; 2) the distal arm of ♂ sternum 9 (fig. 22, D. A. 9) is gradually narrowed towards the apex, which bears shortish bristles, not subspiniforms; 3) the posterior margin of ♀ tergum 8 bears a caudal fringe (fig. 24, C. FR.) which is on a convexity, not a sinus; 4) apical 1/2 of ♀ sternum 8 (8 S.) is free and bears relatively long apical setae, and 5) 3rd genal spine fairly abruptly narrows to a long narrow apex. However, there are significant differences from the *P. remota*-group, viz: 1) there is no striarium on immovable process of clasper (cf. fig. 22, P. with figs. 35, 36, STR.-P.); 2) the sclerotization bordering the internal margin of the frons below level of tubercle is not broken up into conspicuous haemocoeles[8] (figs. 19, 20); 3) posterior margin of ♂ sternum 8 is subtruncate, not rounded (fig. 27, 8 S.); 4) ventral 1/2 of ♀ tergum 8 bears only 1 or 2 stout bristles, not a row of 3 (fig. 24, 8 T.) and 5) the spines of the pronotal comb (figs. 19, 20) are intermediate between the 2 types seen in the *P. remota*-group. Thus, they are not

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6. The new species is unique in this regard amongst all those species known to us, viz. *P. kohauti* Dampf 1910, *P. minor* (Dale 1878), *P. miyama*, *P. nippon* Jameson & Kumada 1953, *P. remota*, *P. similis* Dampf 1910, *P. sinica*, *P. soricis* (Dale 1878), and the new species herein described.
7. The ♂ sternum 8 is slightly reticulate in the new species; other sterna and ventral part of abdominal terga may be microreticulate and microdenticulate.
8. As Smit (1960) points out, the haemocoeles are not well-developed in certain specimens of *P. remota* (cf. our figs. 33, 33A, 34, 79) and *P. miranda* Smit 1960, in contrast to the condition in other species in the group.

as long, thin, pointed and straight as in *P. remota* (figs. 33, 34) nor as broad, rounded and upcurved as *P. incurva* and *P. miyama.*

Description—Head—(fig. 19, ♂; fig. 20, ♀; 78): Frontal row of 5 bristles, of which 1st is ventromarginal, 2 at level of upper portion of vestigial eye and 2 along antennal groove. Second genal spine usually slightly more than 2× as long as 1st spine (measured along middle of longitudinal axis) and not quite 2× as broad as 1st at maxima; its greatest breadth at apical 1/5 and thereafter ventral margin sharply angling toward apex, which is usually somewhat pointed but fairly abrupt, not acuminate (the tips usually blunter in ♀ than in ♂, somewhat variable in each sex (figs. 19A, 20A.)). Third genal spine somewhat longer than 2nd; its margin evenly diverging towards basal 1/4 (♂) or 1/3 (♀) and thereafter dorsal margin becoming markedly sinuate, especially in ♂, ventral margin curving upwards more gradually; spine terminating in highly acuminate apex, the long narrow portion equaling about 1/4 or 1/5 length of spine. (1 specimen with 3rd spine aborted on 1 side, as in fig. 20A). Fourth spine with usual truncate apex, shorter but somewhat broader than 1st spine. Segment 2 of maxillary palpus somewhat shorter than 1 but longer than 3; and subequal to 4. Segments 1 and 5 of labial palpus about 2× as long as 2 and 3; segment 4 somewhat longer than 3. With 4 or 5 bristles in 3rd postantennal row, ventralmost 3 or 4 equally spaced.

Thorax: Pronotum (figs. 19, 20) equal in length to about 2/3 that of spines of its comb; with 5, rarely 6 long bristles per side[9]. Pronotal comb with total of about 18 spines; axis of comb vertical, essentially straight; ventral 4 or 5 spines slightly concave, dorsal ones straight, middle spines about 8× as long as broad; apices of spines quite pointed. Mesonotum (fig. 21, MSN.) with 2 rows of setae, the 1st at times abbreviated; with about 4 pseudosetae (PS. S.) per side. Mesepisternum (MPS.) generally with 1 long caudomarginal bristle near midline and with 1 smaller, more median, adjacent bristle; with 1 or 2 bristles at dorsocaudal angle, these may appear as if on mesepimere (MPM.). Lateral metanotal area (L. M.) with 1 long and 1 or 2 smaller bristles. Metepimere (MTM.) generally with 7 or 8 bristles, of which 6 are usually long and appearing in 2 irregular rows of 3 each.

Tibiae (figs. 28, 31) with 5 pairs of stout dorsomarginal bristles, the smaller (lateral or anterior) member of each pair (DM. 1, etc.) usually relatively stout and long and inserted well apicad and somewhat ventrad of larger member. DM. 1 with anterior (subventral) bristle almost as long and stout as dorsal; in DM. 4 corresponding ratios for breadth and length are each 0.75 : 1. With 3 well-developed bristles in apical group (A. G.). Longest apical bristle of pro- and mesotibiae extending to about 3/4 length of tarsal segment II; in metatibia, this bristle not quite reaching apex of tarsal segment I. Measurements (in micra) of tibiae and tarsal segments (petiolate base deleted) of holotype:

		Tarsal Segments				
Leg	Tibia	I	II	III	IV	V
Pro-	129	46	43	38	33	88
Meso-	202	68	63	51	35	91
Meta-	261	192	114	78	43	96

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[9] Ventralmost bristle in fig. 20 is aberrant and is of its customary small size on the other side of the allotype and on other specimens.

Abdomen: Terga with apical spinelets frequently as follows (total numbers): ♂: 6-6-3-3; ♀: 6-4-1, but numbers variable and extreme patterns such as 1-5-3-1 in ♂ and 3-2-0 in ♀ are seen. Typical terga with anterior row of bristles reduced in number, usually (per side) 3-3-2-2-0-0-0 in ♂; 3-3-3-2-0-0-0 in ♀. With 2 bristles of 2nd row ventrad to sagittate spiracular fossa. Ventral portions of terga mildly microdenticulate and microreticulate; sterna more so; caudal margins somewhat denticulate. Cuticular whorls on basal sternum particularly well-developed in ♀. Sterna 3-6 generally with 3 bristles in vertical row in ♂, 4 in ♀. Male with middle antepygidial bristle (fig. 27, A. B.) slightly less than 3× as long as upper bristle, which in turn is somewhat longer than ventral one. In ♀ (fig. 24, A. B.) lower bristle nearly 2/3 length of middle and somewhat longer than upper one. Plate of antepygidial bristles submarginal in position.

Modified Abdominal Segments—♂: Tergum 8 (fig. 27, 8 T.) nude; extending ventrad for distance equivalent to only about 1/3 height of body and caudad only slightly behind level of anterior portion of sensilium (SN.). Spiracular fossa 8 (8 SPC.) dilated behind and below entrance of atrium of spiracle, which is flared at point of junction; dorsal portion of fossa elongate-ovate, narrowing only gradually and terminating at dorsal margin, near level of plate of antepygidial bristles. Sternum 8 (8 S.) very large, extending dorsad above ventral portion of anal lobes; about 1.25× as long as broad (high) at midlines; dorsal margin the shortest, sinuate. Caudal margin of 8 S. oblique for nearly 1/2 its length, then curving sharply and plunging ventrocephalad, only to become recurved ventrally, running cephalad to join ventral margin at a notch distad of insertion of group of 3 ventromarginal bristles; the resulting large lobe of 8 S. with microserrate margins. Ventral margin of 8 S. shallowly but evenly convex to sinus marking junction with caudal margin.

Immovable process of clasper (fig. 22, P.) broadly ovate, apically obtuse but with a hint of a pointed tip; about 1.9× as long as broad at midpoint; evenly and gradually tapering from midline; lacking striarium. Anterior margin of P. bearing row of short thin marginal bristles commencing at midpoint and terminating in a fairly long subapical bristle; row accompanied by contiguous but scattered smaller bristles. With a long marginal bristle near apical 1/4 of posterior margin of P. Movable finger (F.) long and narrow, nearly 7× as long as broad at midpoint; sides almost parallel but finger actually broadening slightly above midpoint; apex truncate; with a group of 3 sensillary bristles (S. B.) at cephaloapical angle; with about 2 short, thin bristles near caudoapical angle and 3-4 on distal portion of caudal margin. Manubrium (MB.) and proximal arm of sternum 9 (P. A. 9) essentially as in ***P. recava*** n. sp. (cf. fig. 4). Distal arm of sternum 9 (D. A. 9) about 2× as broad at base as subapically; dorsal margin almost straight; ventral margin with basal 1/3 fairly straight or else quite convex and then becoming straight, almost paralleling dorsal margin for apical 1/2; with 3 small thin bristles on ventral convexity; a group of small dorsomarginal subapical bristles; a fairly long dorsoapical bristle and 2 contiguous ventroapicals; with 1 smaller, thinner, mesal ventromarginal bristle and another such at apical 1/3.

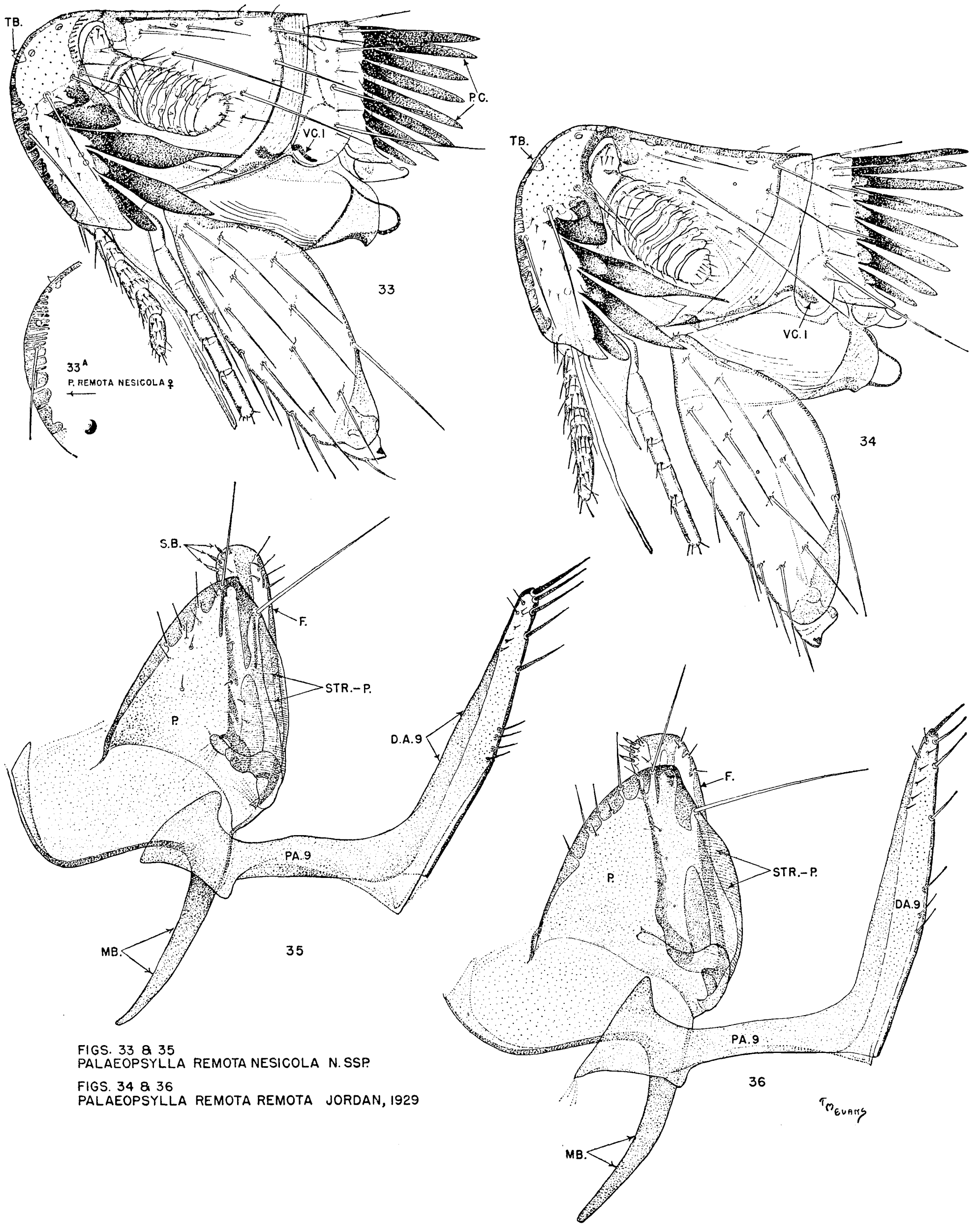
Aedeagal apodeme with sail (fig. 23, S.) so lightly sclerotized as to be almost inapparent; arched dorsad for distance less than 2× diameter of middle plate (M. PT.) at that point. Middle plate about 17× as long as broad; apically acute and somewhat upcurved. Keel (fig. 25, K.) of aedeagal pouch well-sclerotized. Apicomedian sclerite (A. M. S.) prominent; subapically somewhat more than 1/2 as broad as sclerite is long, but only dorsal (anterior) region well-sclerotized here, appearing as a tube-like structure. Distodorsal lobes (D. L.) semi-elliptical, about 2.5–3.0× as broad (high) as long, virtually as broad at apex of end-chamber. Crescent sclerite (C. S.) quite straight. Phylax (PHY.) rod-like; with only dorsal portion well-sclerotized and lying across sclerotized inner tube (S. I. T.) near apex of latter. Dorsal armature (D. AR.) of inner tube with most sclerotized region contiguous to and paralleling upper half of PHY. Ventral armature (V. AR.) of inner tube evenly convex. Sclerotized inner tube (S. I. T.) nearly 6× as long as broad at midpoint. Crochets (CR.) conspicuous as a pair of mesal, apically truncate lobes terminating at level of apex of S. I. T. Lateral lobes inapparent. Ventral intramural rod (V. I. R.) distinct. Penis rods (P. R.) uncoiled.

Dorsal anal lobe (fig. 27, D. A. L.) shaped like a narrow right-triangle with dorsal margin straight; with scattered thin bristles and a long dorsomarginal subapical one. Ventral anal lobe (V. A. L.) almost a mirror-image of D. A. L. but with ventral margin convex and only bearing 2 bristles, these subapical and long,—1 dorsal, the other ventral.

Modified Abdominal Segments—♀: Sternum 7 (fig. 24, 7 S.) with caudal margin deeply cleft ventrally by a long, narrow oblique sinus; lobe above sinus subacute; that below it, subtruncate and shorter; with an oblique row of about 7 large bristles, last 3 of which are approximated, subvertical and terminating at ventral margin; 3rd bristle (from top) at level of sinus; with 1 long ventromarginal bristle somewhat anterior to ventralmost of row and a small median one anterior to 4th bristle of row. Tergum 8 (8 T.) extending nearly to ventral margin; about 2× as high as long; devoid of bristles except for a single large subventral one and clump of 8 or 9 small bristles (about 4 mesal) in caudal fringe (C. FR.). Sternum 8 (8 S.) as in previous species; with distal group of about 6 bristles. Dorsal anal lobe (D. A. L. & fig. 26), ventral anal lobe (V. A. L.), and bursa copulatrix (P. B. C. and S. D. B) as in *P. recava* n. sp. Anal stylet (A. S.) similar also, but more curved, dorsal margin somewhat convex and ventral margin almost paralleling it. Spermatheca (SP. & fig. 30) with bulga (B.) relatively long, about 2.4× as long as broad at maximum level, which is at caudal 3/4. Ventral margin slightly concave; dorsal margin tapering obliquely towards hilla (H.) from height of bulge; caudal 1/4 curving sharply towards obtusely ovate rear. Hilla with sides evenly curved and parallel, inclined slightly over apex of bulga; about 3.5× as long as broad. Lacking conspicuously sclerotized walls in oviduct (cf. fig. 7).

Comments: It is apparent that subspecies of *P. setzeri* n. sp. exist, for fairly consistent differences can be noted in the convexity of the basal 1/3 of the ventral margin of the male sternum 9 (vide figs. 22, 22A) and in the relative breadth of the immovable process of the clasper, depending upon whether the specimens are from Shogran, Dir or certain parts of Swat. However, the significance of these observations cannot be evaluated without more material from the Murree Hills and certain regions of Swat, to say nothing of the need for specimens of both *Hyperacrius* and its fleas from Indian portions of Kashmir.

The species is named for Dr Henry W. Setzer of the Division of Mammalogy, U. S. National Museum, Washington, D. C., who by his extensive collection of African and Middle Eastern mammals and their ectoparasites, and by his studies on the distribution of the mammals, has contributed a great deal to the science of medical ecology. We are also indebted to Dr Setzer for the identification of the Pakistani mammals taken in our



Figs. 33–33A, *Palaeopsylla remota nesicola* n. ssp.: 33, Head and prothorax (♂); 33A, Frons (♀). Fig. 34, *P. r. remota*: Head and prothorax (♂). Fig. 35, *P. r. nesicola* n. ssp: ♂ sternum 9 and clasper. Fig. 36, *P. r. remota*: ♂ sternum 9 and clasper.

research on rickettsial and viral infections in that country, and for directly participating in the 1962 field-trip.

Although the hosts of all the *Palaeopsylla* described heretofore are either shrews (soricids) or moles (talpids), zoogeographic data and morphological evidence (the pattern of genal and pronotal spines) indicate that the true host of *P. setzeri* n. sp is indeed the burrowing-vole *Hyperacrius*. These points are discussed further in Sections 10 and 11 below.

The supernumerary and unusually long thin bristles in *P. setzeri* n. sp. are suggestive of the condition in fleas of certain other burrowing hosts, i. e. the ceratophylline *Foxella* Wagner 1929 and *Dactylopsylla* Jordan 1929 of U. S. pocket-gophers (Geomyidae).

4. **Palaeopsylla remota** Jordan 1929

P. remota, considered a flea of burrowing-shrews (*Anourosorex*) in the Burma-China region, exhibits structural modifications relevant to studies on zoogeography, convergent evolution and comparative morphology. It also is important as the representative member of the *P. remota*-group of *Palaeopsylla* of Smit (1960). A new subspecies from Taiwan, also from *Anourosorex*, is therefore figured in some detail, and certain structures described at length (not necessarily at subspecies level), while figures of *P. r. remota* are included for purposes of comparison.

4A. **Palaeopsylla remota remota** Jordan 1929 Figs. 34, 36 & 42.

Palaeopsylla remota Jordan 1929, Novit. Zool. **35**: 41, fig. 2; 1932, *Ibid.* **38**: 270, fig. 26; 1939, *Ibid.* **41**: 374, fig. 296.—Smit, 1960, Bull. Brit. Mus. (N. H.), Ent. **9**: 371, figs. 1, 3, 5, 7.—Traub & Barrera, 1966, J. Med. Ent. **3** (2): 141.—Hopkins & Rothschild, 1966, Cat. Roths. Collect. Fleas **4**: 199, figs. 303-4, 307, 309, 311.

4B. **Palaeopsylla remota nesicola** Traub and Evans, new subspecies
Figs. 33, 35, 37-41, 43 & 79.

Type Material: Holotype ♂ and allotype ♀ (B-54817-1) ex *Anourosorex* sp. (*Chodsigoa sodalis* misident.); Taiwan: Nan Tou Hsien, Wu-she; 985 m (3200 ft) elev.; 21.I.1962; coll. C. M. Yoshimoto & M. C. Thompson. Paratypes, all from Taiwan, as follow:

♂	♀	Host	Locality	Elev.	Date	Collector
1	1	*Anourosorex* sp.	Nan Tou Hsien, Wu-she	985 m (3200′)	21.I.62	C. M. Yoshimoto & M. C. Thompson
4	8	〃	〃 〃	675 m (2200′)	24.I.62	〃
—	1	Shrew	〃 , 11 km (7.5 mi) E of Wu-she	2000 m (6500′)	31.X.61	R. Traub & R. E. Kuntz
—	1	*Mogera insularis*	〃 , 12 km (8 mi) 〃 〃	2060 m (6700′)	〃	〃
1	9	*Anourosorex* sp.	〃 , Tsui (Chuei) Feng	1845 m (6000′)	26.I.62	Yoshimoto & Thompson
2	—	〃	〃 〃	...	4.XI.61	Kuntz
—	3	*Mogera insularis*	〃 , 6 km W of Tsui Feng (97 km mark)	2000 m (6500′)	2.XI.61	Traub & Kuntz
—	1	〃	〃 , 2 km E of Tsui Feng (101 km mark)	2245 m (7300′)	〃	〃
2	—	*Anourosorex* sp.	Chia I Hsien, Alishan	1940 m (6300′)	17.II.62	Yoshimoto & Thompson

Diagnosis: Separable from *P. r. remota* (Asian mainland—China, Burma, etc.) as follows: 1) Immovable process of clasper (fig. 35, P.) narrow, about 1.8× as long (measured from level of base of acetabulum) as broad at midline. In *P. r. remota*, caudal margin of P. (fig. 36) more convex, so that corresponding ratio is only 1.4. 2) Movable finger (fig. 35, F.) proportionately narrower in new subspecies, about 6× as long as broad at level of large subapical bristle on caudal margin of P. instead of 4.5× (fig. 36)[9A]. 3) Upper protuberance on apex (anterior margin) of expanded, cephalic portion of proximal arm of sternum 9 (P. A. 9) shorter and more obtuse, about as high as broad at base, instead of being subacute apically and definitely higher than broad. 4) Lobate sector (fig. 43, LO. S.) of apicomedian sclerite (A. M. S.) of aedeagus broadly rounded anteriorly, its height 1.5× that of adjacent lobe of dorsal armature (D. AR.) instead of being more upturned and hence more ovate anteriorly (fig. 42, LO. S.) and more than 2× the height of D.AR. 5) Caudal fringe of bristles on ♀ tergum 8 (fig. 39, C. FR.) with ventral 3 dark bristles relatively close together, i. e. separated by a distance less than that of subapical diameter (height) of sternum 8 (8 S.) instead of being well separated, the distance between them greater than that of the diameter of 8 S.

Some of the diagnostic features of *P. r. nesicola* n. ssp. suggest those of *P. miranda*, notably the relatively narrowed P. and subrounded apex of F., the rounding of the upper protuberance on the apex of P. A. 9 and the broadness of the lobate sclerite of A. M. S. of the aedeagus. The fundamental characters that Smit (1960) used to separate the 2 species still hold, however, such as the comb of 16 spines in *P. remota* s. lat. versus 20–22 in *P. miranda*; somewhat shorter and broader spines in *P. remota*, etc. Further, in *P. r. nesicola* n. ssp., the breadth of the base of the ventral armature of the sclerotized inner tube of the aedeagus (fig. 43, V.AR.) is much greater than the diameter or arc of the base of the sclerotized inner tube (S. I. T.) instead of being subequal.

Descriptive Notes—Head and Pronotum—(figs. 33, 79, ♂; figs. 33A, 37, ♀): Internal sclerotization of margin of frons divided by a series of hameocoeles, the inner margins of the fragments often convex or irregular (haemocoeles longer and narrower in ♀). First (ventralmost) genal spine shortest, relatively oblique, straight and apically fairly blunt. Second spine much longer, oblique, widening to maximum at apical 1/3, then gradually narrowing to a subacute apex. Third spine longest, horizontal, widest near midpoint, then abruptly tapering to a pronouncedly acuminate apex. Fourth spine horizontal, short, apically broad and subtruncate, intimately associated with vestigial eye above it. Pronotum slightly less than 1/2 as long (at midline) as spines of comb at that level; with 1 row of bristles. With about 16 (total) pronotal spines; straight, narrow (3rd from bottom about 9× as long as broad at midpoint) and sharply pointed; most spines inclined obliquely at angle of about 20° from horizontal.

Abdomen: Segments essentially devoid of cuticular reticulations, microdenticulations and apical microserrations (figs. 39, ♀, 41, ♂). Spiracular fossae of unmodified terga (i.e. 7 SPC.) subglobular but slightly broader (taller) than long; about 2× diameter of

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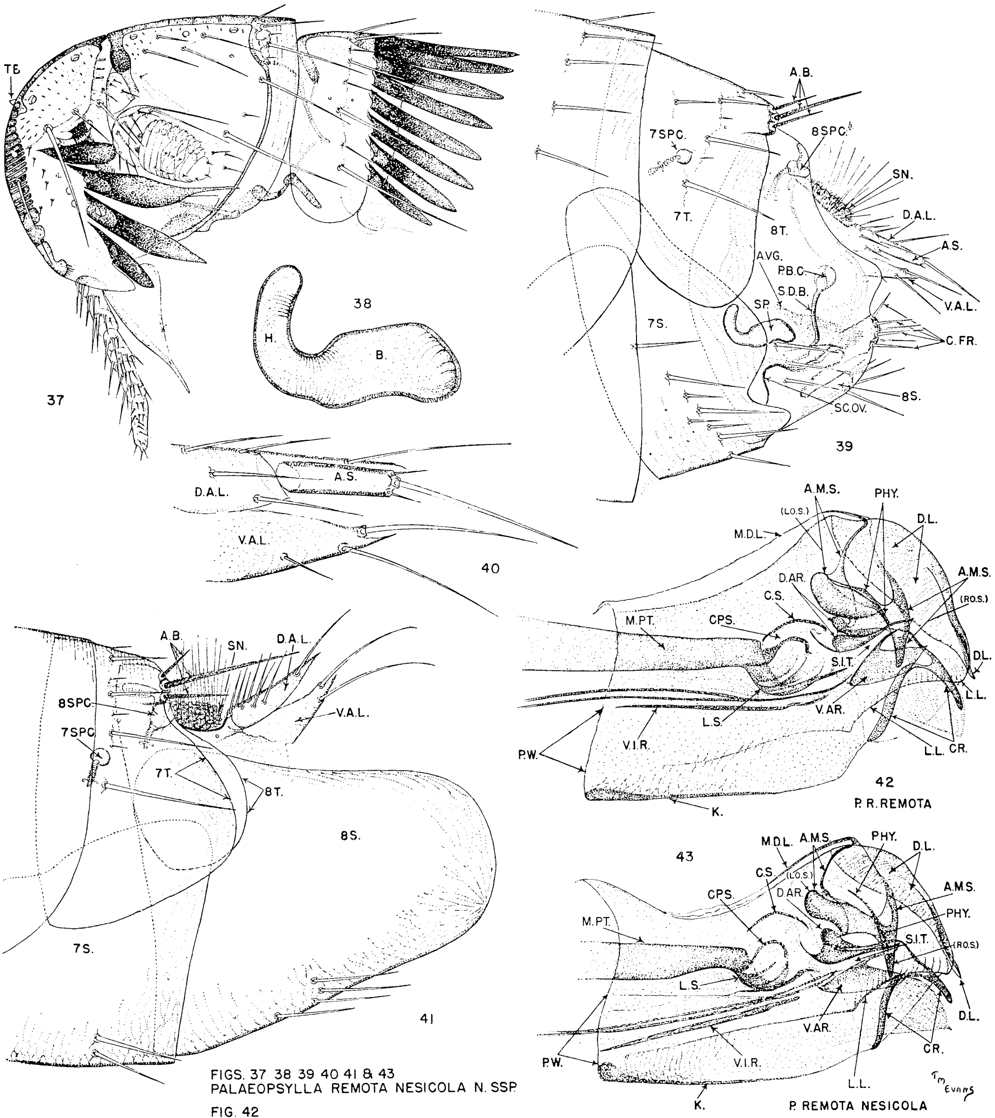
[9A] The apex of F. in the specimen drawn is atypical; it is usually subtruncate. Also, if F. is not lying flat, it may appear foreshortened and hence broader than it actually is. Usually F. on the other side is normal in appearance in such cases.



FIGS. 37 38 39 40 41 & 43
PALAEOPSYLLA REMOTA NESICOLA N. SSP.
FIG. 42
PALAEOPSYLLA REMOTA REMOTA JORDAN, 1929

Figs. 37–41, *Palaeopsylla remota nesicola* n. ssp.: 37, Head and prothorax (♀); 38, Spermatheca; 39, Modified abdominal segments (♀); 40, Dorsal and ventral anal lobes of proctiger; 41, Segments 7, 8 and 10 (♂). Fig. 42, *P. r. remota*: Apex of aedeagus. Fig. 43, *P. r. nesicola* n. ssp.: Apex of aedeagus.

adjacent setal bases. Fossa of tergum 8 ovoid in ♂ (fig. 41, 8 SPC.) and in ♀ (fig. 39, 8 SPC.) with a horizontal subrectangular portion and a longer, narrowed, upright, slightly recurved section more distad, bordering dorsal margin. Male sternum 8 apically subrounded and posterior margin merging smoothly with dorsal and ventral ones. Proximal 3/4 of posterior region of immovable process of clasper (fig. 35, P.) with a series of parallel, closely approximated striae forming the striarium (STR.-P.) of Smit (1960). Distance between ventrocaudal angle of movable finger (F.) and base of manubrium (MB.) subequal (or less) to breadth of base of F.

Aedeagal end-chamber more specialized than in *P. recava* n. sp. and *P. setzeri* n. sp. due to hyperdevelopment of apicomedian sclerite and of phallosomal labia. Sail of aedeagal apodeme lightly sclerotized; near its arched base about 1.7× breadth of middle plate at that level. Middle plate (M. PT.) about 14× as long as broad at midpoint. Keel (fig. 43, K.) well-sclerotized, especially basally, and here with a somewhat laminated pattern. Apicomedian sclerite (A. M. S.) the largest item in end-chamber; paired, with each side greatly expanded apically into 2 distinctive parts at somewhat different levels: 1) a more lateral and posterior section conspicuous as a beak-like extension, herein termed the rostrate sector (RO. S.), flanking apex of sclerotized inner tube (S. I. T.), pointing ventrad and terminating at level of ventral armature (V. AR.) of inner tube. 2) A more mesal, massive subtrapezoidal structure, herein termed the lobate sector (LO. S.), lying above dorsal armature (D. AR.) of S.I.T., extending anterodorsad and articulated with rod-like portion of A. M. S. running upwards to median dorsal lobe (M. D. L.). Phylax (PHY.) reduced to a narrow subvertical rod mesad to and near anterior portion of RO. S., and extending dorso-apicad so that it often appears as the upper anterior arm of a V-shaped structure formed by RO. S. Distodorsal lobes (D. L.) a large narrow cap-like sclerite at apex of end-chamber, ranging from tip of M. D. L. to anteroventral angle of aedeagus, here terminating in a short snout-like projection by site of dorsal curve of lateral lobes (L. L.). Dorsal armature (D. AR.) of S. I. T. a triangular sclerite along upper margin of S. I. T.; basally bilobed and dorsal margin concave, sloping towards apex of S. I. T. and here acuminate. Ventral armature (V. AR.) mainly apparent as a broad winglike or quadrate sclerite whose long axis is oblique to that of S. I. T., extending caudad for a distance equal to 2× its breadth; upper basal angle of quadrant with a narrow extension, which is highly acuminate and is contiguous with ventral wall of S. I. T. to apex. Crochets (CR.) highly modified and readily apparent as a 2nd pair of beak-like structures in the end-chamber, this one near the ventro-apical angle. Crochets arising dorsally immediately above apical portion of S. I. T., and ventrally from ventrocaudal angle of keel (K.) of pouch wall; ventral wall of crochets thickened and vaulting dorsad and then ventrocaudad, free end of resulting arch joining thickened dorsal member curving down from apex of S. I. T. and continuing together ventrad as an acuminate snout-like projection. With a series of semimembranous tufted projections associated with apical portion of arch of crochet. Lateral lobes (L. L.) fairly well-sclerotized apically and crossing apex of V. AR. and arch of crochet, then curving dorsad above ventral tip of distal lobe (D. L.). Ventral intramural rod (V. I. R.) well-sclerotized. Penis rods (P. R.) uncoiled.

Sternum 7 of ♀ (fig. 39, 7 S.) biconvex caudally; upper lobe broad and quite shallow; lower lobe somewhat longer, almost as long as broad at base; mouth of sinus about 1.5× that of lower lobe. Sternum 8 (8 S.) with submedian, subventral vertical row of 3 bristles.

Caudal fringe (C. FR.) with about 6 small bristles. Ventral anal lobe (V. A. L. & fig. 40) with greatly reduced chaetotaxy—only 3 bristles, 1 at middle of ventral margin, the others subapical (1 dorsal, 1 ventral). Spermatheca (SP. and fig. 38) with bulga (B.) somewhat longer than hilla (H.) and with dorsal margin flattened for most its length; ventral margin somewhat flattened anteriorly. Sclerotized portion of oviduct (SC. OV.) usually arched or sinuate. Accessory gland of vagina (A. VG.) large and well-developed.

Comments: The name of the subspecies is derived from the Latin (and Greek) term for an island, *nesis*, combined with the Latin suffix for an inhabitant, referring to the insular status of this subspecies.

5. Comments on some Morphological Features of the Genus *Palaeopsylla* Wagner 1903

It is possible that what we have designated as the crochet (hamulus of authors) in the aedeagus of the various *Palaeopsylla* (figs. 12, 25, 42, CR.) may not be truly homologous with the crochet of other fleas, even in the family Hystrichopsyllidae. The crochets in ceratophyllid, leptopsyllid and certain other groups of fleas are paired, large, articulated and freely movable structures that are generally unmistakable in appearance and arise from the ventral part of the aedeagal end-chamber. In hystrichopsyllids, the paired crochets usually are ventral to the sclerotized inner tube and generally relatively small, not clearly articulated and apparently movable to only a limited extent, although in some genera such as *Strepsylla* Traub 1950 and *Xenodaeria* Jordan 1932 (fig. 68, CR.), the crochets are quite large. What we term the crochets in *Palaeopsylla* are large lobe-like structures arising dorsad of the sclerotized inner tube (S. I. T.), extending ventrad and caudad as a flap, and apparently joining the apex of the keel (K.) of the pouch wall. Like Smit (1960), we have interpreted this specialized structure in *P. remota* as the crochet ("hamulus") and our reasons are as follows: 1) In this species there are no other sclerites present which could logically be designated as crochets. 2) The attachment as crochets to the keel occurs in some other hystrichopsyllid fleas, namely *Epitedia cavernicola* Traub 1957, and in *Xenodaeria* (figs. 65, 68) there is an especially intimate relationship between the pouch wall (P. W.) and crochets and even sternum 9 as well (figs. 66, 70). In the genus *Ctenophthalmus* Kolenati 1856, related to *Palaeopsylla*, there is often a small lightly sclerotized "crochet" on each side of the end-chamber distad of the inner tube, but in some species which lack such crochets, i.e., *C. calceatus* Waterston 1912, there is instead a pair of apical flaps bearing thickened rims and termed by Traub (1963) "phallosomal labia." These last-named structures are highly suggestive of the arrangement seen in *P. recava* n. sp. and appear as a step in the development of the specialized form exhibited by *P. remota*. It would therefore seem logical that the labial type of ventral aedeagal flaps in *Palaeopsylla* are really crochets, but if it proves that we are wrong, the term can be considered topographic or as a useful label whereby characters of obvious taxonomic value can be discussed and compared.

The structure of the phallosome of *P. recava* n. sp., and the other species herein described, emphasizes the relationship of this genus with *Ctenophthalmus*. In both genera the lateral plates of aedeagal apodeme are arched dorsally to produce a sail (velum) (figs. 11, 23, S.), and the end-chamber is equally expanded dorso-apically; there is a well-developed keel (K.); the crochets may appear as labiate lobes in the ventroapical region of the phallosome; the large apicomedian sclerite (A. M. S.) arises from median dorsal lobe (M. D. L.) extending down to vicinity of sclerotized inner tube (S. I. T.). The penis rods are at least typically uncoiled; the lobes of end-chamber often bear filamentous tufts or spicules, and the lateral plates are long and narrow. The conspicuous distodorsal lobes (D. L.) of *Palaeopsylla* apparently have their homologous counterpart in *Neopsylla* Wagner 1903, *Rothschildiana* Smit 1952 and *Strepsylla* in subfamily Neopsyllinae, where they are much smaller in size. It is interesting to note that in certain *Ctenophthalmus*, the lateral lobes are extremely well-developed and extend far dorsad, suggesting that the distodorsal lobes represent modifications of the lateral lobes, especially since the true lateral lobes in *Palaeopsylla* are at times reduced and lightly sclerotized and often difficult to see.

The presence of a large crescentic sclerite, the phylax (PHY.), flanking the sclerotized inner tube on each side is not typical of the subfamily Ctenophthalminae, but occurs sporadically in various kinds of fleas, and is quite common in Pygiopsyllidae, as in *Stivalius* (*Gryphopsylla*) *hopkinsi* Traub 1957. The presence of paired apicomedian sclerites (A. M. S.) in *P. recava* n. sp. (and other members of the genus) is noteworthy because ordinarily the component parts of this sclerite are fused, as in *Ctenophthalmus*.

The homologies of the sail (velum) of the aedeagus of ctenophthalmine fleas are rather confusing due to the facts that: 1) in some species (i.e., *P. setzeri* n. sp.) the structure definitely appears paired, suggesting modifications of the lateral plates of the aedeagus, while in others the sail is single; 2) morphological elements from both the middle plate and the lateral plates join the sail in some species, and 3) the ventral margins of the lateral plates are absent or invisible. It would appear that the sail is actually derived from the lateral plates and that in some instances the two components have fused to form a single structure or else are so contiguous that they look like a unit when seen under the microscope (Traub 1950). That this view is correct is suggested by the presence of paired acuminate projections of the lateral plates flanking the apodemal strut and overlapping the base of the end-chamber as seen in many ceratophyllid or other fleas. Presumably it is this "extra length" of the lateral plates, or that of the anterior projection of the apodeme seen in other fleas (the "apical appendage") that is utilized in the formation of the sail. Also supporting this contention is the fact that in species with a sail, the ventral convex extensions of the lateral plates, which in other fleas are usually clearly seen below the middle plate and on each side of it, are apparently absent; only the anterior portions can be seen and these curve dorsally as part of the sail. The apodemal strut is of complex composition, with its sclerotized portion derived mainly from the middle plate, and perhaps even paired structures like the lateroventral sclerites arise mainly from that plate. However, in other genera, the lateral plates generally fuse with the middle one near the strut (vide figs. 48, 68) and in other fleas, semimembranous elements of the lateral plates extend to the middle plate, suggesting that the strut here too is intimately associated with both parts of the apodeme. Major tissues linking the two are apt to be lost when the specimen is treated with caustic potash in preparation for mounting, and a close association may actually be present even when not apparent. For these reasons, the original views of homology presented by Traub (1950) are believed to be correct, while in subsequent descriptions of *Ctenophthalmus* portions of the lateral and median plates at times have been confused (Traub 1963; Traub & Barrera 1966).

Mesal to the female tergum 8 and generally under the overlapping caudal region of sternum 7, there can be seen in these species of *Palaeopsylla* a rod-like sclerotization which frequently appears to be a paired structure (vide figs. 7, 39, SC. OV.). At first it was assumed that these were the internal ridges regularly seen in that position in certain genera and which presumably are internal thickenings of the wall of the sterna, in a site which is generally conspicuously browner or darker in hue than are the adjacent areas. However, in *Palaeopsylla* it was noted that these sclerotizations were unusual in that: 1) they were always intimately associated with, or even arose from, the oviduct at a fixed distance from the bursa copulatrix, and other genitalic organs, regardless of where or how the various components of the female internal genitalia had been displaced in the process of clearing and mounting the specimen. 2) Their shape at times varied from specimen to specimen of the same species. Thus in *P. r. nesicola* n. ssp., in some specimens the "ridge" was straight; in others, somewhat arched; in yet others, strongly arched or even looped. 3) In some instances, one end or the other appeared frayed, as if consisting of fused tendrils. 4) The sclerotizations were deep in the body cavity, at the level of the oviduct and vagina, and not near the lateral surfaces. 5) The "paired" rods were virtually contiguous and each was in focus under the microscope simultaneously with the vaginal glands and other parts of the internal genitalia, indicating the sclerotizations could have been lining the walls of a tube and enclosing a lamina. 6) In one species (*P. apsidata* n. sp.), both types of sclerotized ridges were present (vide fig. 15, S. RD. & SC. OV.).

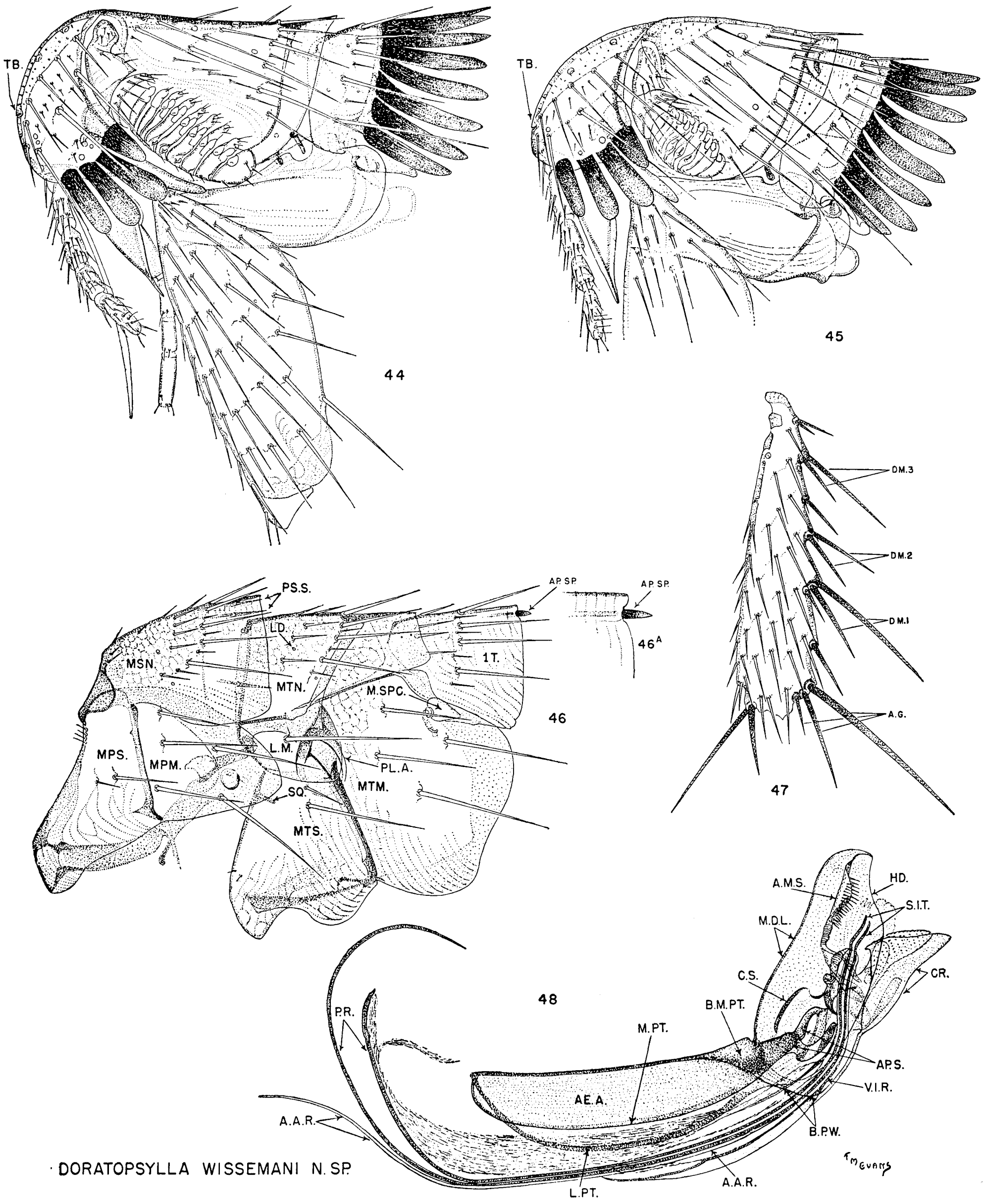
For these reasons we have interpreted the rod-like sclerotizations as being genitalic modifications, and have termed them "sclerotizations of the oviduct" (SC. OV.). The relative lengths of these structures, their degree of sclerotization and even their shape (as seen in a series) show variations of use in taxonomy. For example, in *P. recava* n. sp., SC. OV. is relatively shorter, thinner and more lightly sclerotized than in *P. remota*, and the anterior portion is weakly sclerotized, apically somewhat dilated and here partially membranous. In *P. remota*, SC. OV. is usually convex or sinuate in appearance; in *P. setzeri* n. sp. and *P. recava* n. sp., generally quite straight. As will be shown, a similar structure is present in *Xenodaeria*, but here the sclerotization is much shorter and lighter than in *Palaeopsylla*.

In this article, mention is made of the independent course in evolution followed by various taxa of fleas, whereby certain characteristic structural modifications appear which may be absent or undeveloped in other members of the tribe or subfamily. Thus, in *Palaeopsylla* the trend is toward a relative large number of long, thin and acute spines in the pronotal comb and highly tapered ones in the genal comb, as compared to its kin, *Ctenophthalmus*. Another example is the unusual shape of the mesepimere seen in *Palaeopsylla*, in which the ventral margin and lower portion of the caudal margin are straight, and the dorsoventral angle acute (cf. figs. 3, 17, 21 MPM.; with figs. 46, 64).

Subfamily DORATOPSLLINAE

6. **Doratopsylla wissemani** Traub and Evans, new species Figs. 44-56.

Type Material: Holotype ♂ (B-66442-2) ex *Hyperacrius* sp.; Pakistan: Hazara Dist., Kaghan Valley, Gitidas; 3690 m (12,000 ft) elev.; 25.VII.1964; coll. R. Traub & A. B.



Figs. 44–48, *Doratopsylla wissemani* n. sp.: 44, Head and prothorax (♂); 45, Head and prothorax (♀); 46, Meso- and metathorax, abdominal tergum 1 (♂); 46A, Apical spinelet (♂); 47, Metatibia (♂); 48, Aedeagus.

Mirza. Allotype ♀ (B-66441-1) ex *Sorex* sp.; ibid. but 26.VII.1964. Paratypes, all from Pakistan: Hazara Dist., Kaghan Valley, as follows:

♂	♀	Host	Locality	Elev.	Date	Collector
1	–	*Hyperacrius* sp.	Gitidas	3690 m (12,000′)	25.VII.64	R. Traub & A. B. Mirza
–	3	*Sorex* sp.	〃	〃	26–28.VII.64	〃
1	–	〃	Besal	3290 m (10,700′)	26.VIII.63	〃
1	–	〃	Saif ul Maluke	3230 m (10,500′)	5.VIII.63	〃
–	1	〃	Shogran	2460 m (8000′)	22.IX.64	Traub

Diagnosis: Agrees with *D. coreana* Darskaya 1949 in general configuration, in that the 4th (dorsalmost and caudalmost) genal spine is straight, triangular, and much shorter than 3rd spine, and in that the ventral margin of the spermatheca of the ♀ is somewhat concave. Readily separable from that species as follows: 1) Immovable process of clasper with larger (caudal) process (figs. 49, 50, P_2) much narrower than in *D. coreana*, viz. more than 3× as long as broad at midpoint (length measured from lowest level of sinus between P_1 and P_2 to apex), instead of only about 2× as long. 2) Distal arm of ♂ sternum 9 (figs. 49, 51, D.A. 9) apically much longer and narrower in new species, viz. portion distad of conspicuous spiniform-bearing convexity is distinctly longer than proximal portion, instead of being subequal. 3) Apex of aedeagal crochet (figs. 48, 53, CR.) subacuminate instead of ovate. 4) Sternum 7 of ♀ (fig. 56, 7 S.) with ventral 1/2 of caudal margin biconcave, bearing a long proboscoid lobe; the sinus below the lobe broader than long and directed mainly ventrad. In *D. coreana* 7 S. with only a long, narrow subventral sinus, this directed caudad, while lobe above is obtuse and indistinct.

Description—Head—(fig. 44, ♂; fig. 45, ♀): Frontoclypeal margin of ♂ subvertical and slightly convex; preantennal region more than 2× as high as long at level of reduced eye; in ♀ 2/3 of margin curving much more caudad, thus more ovate than elliptical, and preantennal region distinctly less than 2× as high as long. Tubercle (TB.) in ♂ just above level of penultimate (2nd from ventral) bristle of 1st row at eye level; in ♀ just below this bristle. With 6 fairly small, thin bristles in 1st preantennal row. With 3 long bristles in 2nd row, the uppermost at level above apex of antennal segment 1; middle one extending beyond apex of genal spine. Eye virtually vestigial, an ovoid shadow above and in front of uppermost genal spine. Axis of 1st 3 spines of genal comb making an angle of 55° with horizontal in ♂, 45° in ♀; uppermost (4th) spine in ♂ out of line with main axis, more vertical in insertion so that its base would make a 65° angle with horizontal; in ♀, 4th spine less dorsad in position, fairly well in line with others. Fourth genal spine about 1/2 length of others and narrower, but apex ovate, other genal spines rounded apically; 2nd and 3rd spines somewhat broader subapically than proximally. Genal process long and narrow, extending well beyond apex of 3rd spine and about 1/2 as broad. Maxillary lobe extending to middle of segment 2 of labial palpi and to middle of apical segment of maxillary palpi. Labial palpi 4-segmented, extending only somewhat beyond middle of forecoxae; segments 2 and 3 subequal and each shorter than 4th. Antennal segment 2 with marginal bristles short in ♂, about 2× length of segment; only slightly longer in ♀. With 3 complete rows of longish postantennal bristles; the numbers per row somewhat variable but usually: ♂: 3(4)–3(4)–6; ♀: 4(5)–5(6)–7(8); penultimate in last row the longest.

Thorax: Pronotum with single row of 5–6 long bristles per side; with dorsal spines 1.7× longer than notum at that level, and middle spines 1.8× longer at their level.

Pronotal comb with base subvertical; with a total of about 16 spines, these somewhat concave dorsally (except for ventralmost which is fairly straight); middle spines with bases inclined ventrocaudad, 30° from horizontal in ♂, somewhat more in ♀. Spines about 7× as long as broad near base; apices fairly blunt. Mesonotum (fig. 46, MSN.) with 2 rows of bristles and usually 3 pseudosetae (PS.S.) per side—viz. 1 median and 2 (sometimes 3) subdorsal and dorsal. Mesepisternum (MPS.) with 1 long and 1 short submedian bristle. Mesepimere (MPM.) with 5 bristles arranged 3-2; its caudal lobe overlapping lateral metanotal area (L.M.) but ventrocaudal corner relatively subrounded. L.M. with 1 long subdorsal bristle, somewhat longer than broad. Metepisternum (MTS.) with 1 long subdorsal bristle and 1 small one above it; with a long narrow squamulum (SQ.); ventral margin appearing deeply sinuate although caudal lobe lateral to cephalic. Metepimere (MTM.) with 4 bristles arranged 2-2; upper anterior one at level of large cordate spiracular fossa (M.SPC.); caudal margin deeply concave where contiguous with fossa, then becoming convex and curving ventrad; posterior portion slightly concave for ventral 1/3, ventral margin evenly convex.

Metacoxa with a group of scattered, small, thin mesal bristles from near apex upwards to about middle, the patch submarginal distally and moving towards 2nd 1/4 as it proceeds dorsad. Metatibia (fig. 47) with apical group (A.G.) of 3 dorsomarginal bristles, of which inner one is quite small and outer member very long; with dorsomarginal notches bearing 3 pairs of unequal bristles (DM.1-DM.3). Between A.G. and DM.1, a notch with a single stout bristle; ditto between DM.2 and DM.3. Longest bristle of protibia reaching to about apex of tarsal segment II, almost likewise for mesotibia; in metatibia reaching to near apex of segment I. Apical bristles of tarsal segments all short, only on metatarsal I, II and III do they reach middle of following segment. Distal segment of each tarsus with 4 pairs of thin lateral plantar bristles plus a medially-displaced proximal pair between bases of 1st lateral pair. Measurements (in micra) of tibiae and tarsal segments (petiolate base deleted) of ♂ paratype (B-66442-1):

		Tarsal Segments				
Leg	Tibia	I	II	III	IV	V
Pro-	152	63	56	46	40	94
Meso-	241	106	81	66	46	96
Meta-	329	222	139	94	63	101

Abdomen: Terga usually with total of 2 apical spinelets (fig. 46A) on each of 1st 5 segments in both sexes. Cuticula of all non-genitalic terga and sterna (including 8th) reticulate, at least proximally or dorsally and ventrally; caudally usually with vertical ridges. Reticulations often bearing microserrations, especially along posterior margins. Sternum 2 with a caudal striarium in ♂ and nearly entirely striate in ♀. Unmodified terga 2-6 with 2 rows of bristles but 1st row at times reduced in number (to 0-2) on lattermost of these terga; tergum 7 with only 1 row; in each, ventralmost bristle in 2nd row well below sagittate spiracular fossa (e.g. figs. 52, 56, 7 SPC.). Unmodified sterna 2-3 usually with 1 ventromarginal bristle per side; remainder with an additional subventral above it. Male with ventral antepygidial bristle (fig. 52, A.B.) almost 2× length of dorsal one and about 1/2 length of middle one; ♀ with almost same proportions (fig. 56, A.B.), but uppermost somewhat smaller so that ventral is slightly more than 2× its length. Insertion of plate of antepygidial bristles dorsal in position.

Modified Abdominal Segments—♂: Tergum 8 (fig. 52, 8 T.) subrectangular, nearly 3× as high (broad) as long; extending caudad only to level slightly beyond base of anal segments and ventrad only to subdorsal portion of sternum 8 (8 S.). Spiracular fossa 8 with swollen basal portion about as high (broad) as long; its anterior and posterior margins converging dorsally so that upper 2/3 of fossa is acute, extending to dorsum. Sternum 8 (8 S.) slightly higher (subproximally) than long at middle, extending dorsad to cover ventral portion of anal segments. Dorsal margin of 8 S. becoming slightly concave at basal 1/5 or 1/6 but soon straightening and becoming convex; caudal margin evenly convex except near ventral margin, where slightly incised; these margins microdenticulate at edges of reticulations; ventral margin with proximal 2/3 slightly convex and then becoming straight. 8 S. with 1 long submedian bristle; 1 short subventral and 1 short ventromarginal.

Immovable process of clasper with anterior lobe or process (figs. 49, 50, P_1) very short —only about as high (long) as broad[10]; or only slightly longer than spiracular fossa 7; relatively inconspicuous except for its 2 long terminal bristles (accompanied by 2 short, thin subapical ones), the sinus between it and anterior margin of long subrectangular posterior process (P_2) only about 1/2 breadth of P_1. Process P_2 about 3.5–4.0× as long as broad at middle, somewhat rectangular although actually slightly narrower at middle than at either end; anterior margin quite flat; posterior margin more membranous and somewhat undulating or irregularly doubly sinuate; apical margin shallowly and broadly convex; with a small bristle near antero-apical angle. With 1 very long, stout acetabular bristle (AC.B.) arising near ventrocaudal angle of immovable process; this accompanied by a contiguous, but more ventral or posterior small thin bristle. Movable process or finger (F.) upright, digitoid, somewhat longer than P_2, which reaches level of fovea (FO.) (as usual); about 7.5× as long as broad at level of 3rd longish bristle of posterior margin (near apical 1/3 of F.). Movable finger broadest near mid-line because anterior margin shallowly biconcave; posterior margin slightly convex at extremities but otherwise quite flat for most its length; anterior margin with a thin bristle near mid-line, about as long as P_2 broad; shortly above this, a similar bristle and then 2 or 3 shorter ones between those and level of fovea; with 1 short thin subapical bristle. Convex apical margin of F. narrow and bearing 3 short bristles. Caudal margin of F. with a short subapical bristle; a long thin one above level of fovea and another below it; with a shorter one at anterior 1/3 and a small one at proximal 1/5. F. with a median row of scattered small mesal setae. Body of clasper short, and that portion ventrad to dorsal internal incrassation of clasper (D.I.CL.) and to acetabulum forming an equilateral triangle whose vertical (anterior) arm is the margin of the short manubrium (MB.) and whose oblique ventral (posterior) arm consists of the caudal margin of MB. plus lower margin of ventral internal incrassation of clasper (V.I.CL.); base of triangle an imaginary line connecting ventral angle of tergal apodeme of segment 9 (T.AP.9) and acetabular

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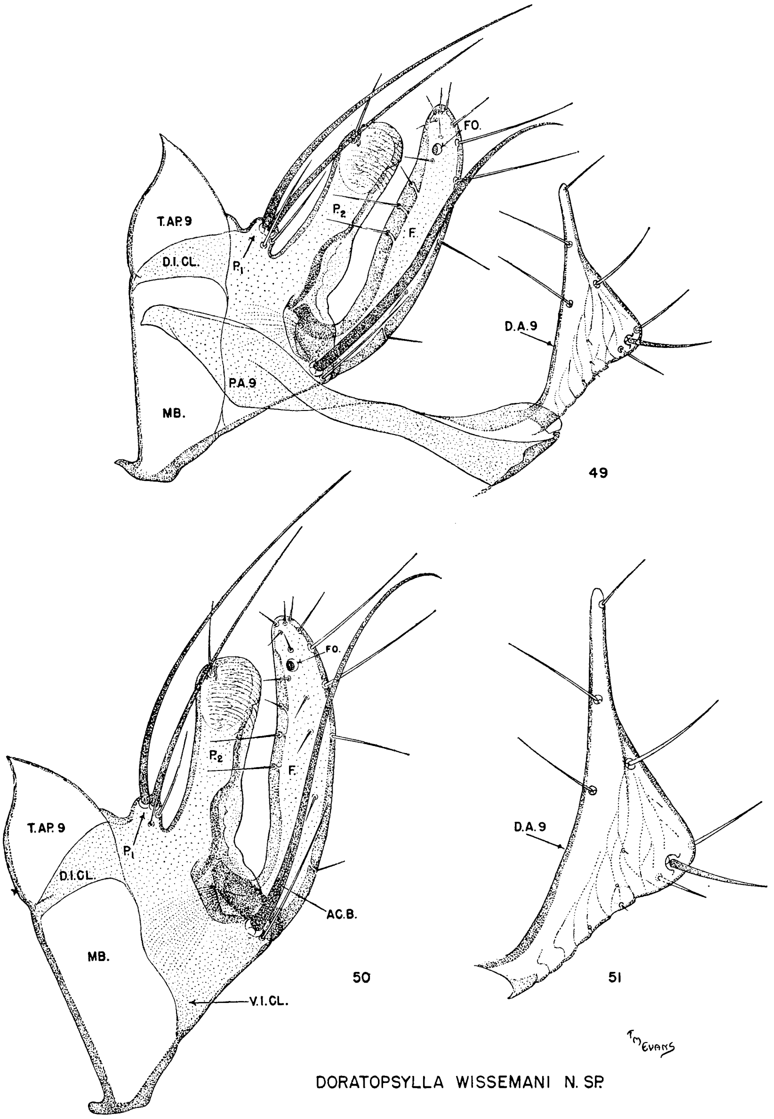
[10] The ventral-dorsal dimensions of the immovable and movable processes in most fleas, especially in Doratopsyllinae, are spoken of as the *length*, and the anterior-posterior axis as the *breadth*, although strictly speaking the opposite should perhaps be the case. The movable finger is usually so digitoid or rectangular that it would be confusing to refer to the long axis as "breadth" and the short one as "length."

bristle (AC.B.); altitude of this triangle subequal to lobe P_2 in length; apex of triangle flattened, and this truncate apex of MB. with a short anterior-directed spur. T.AP.9 also somewhat equilateral-triangular but anterior side sinuate and posterior rather convex; apex subacute, its altitude subequal to 3× length of lobe P_1.

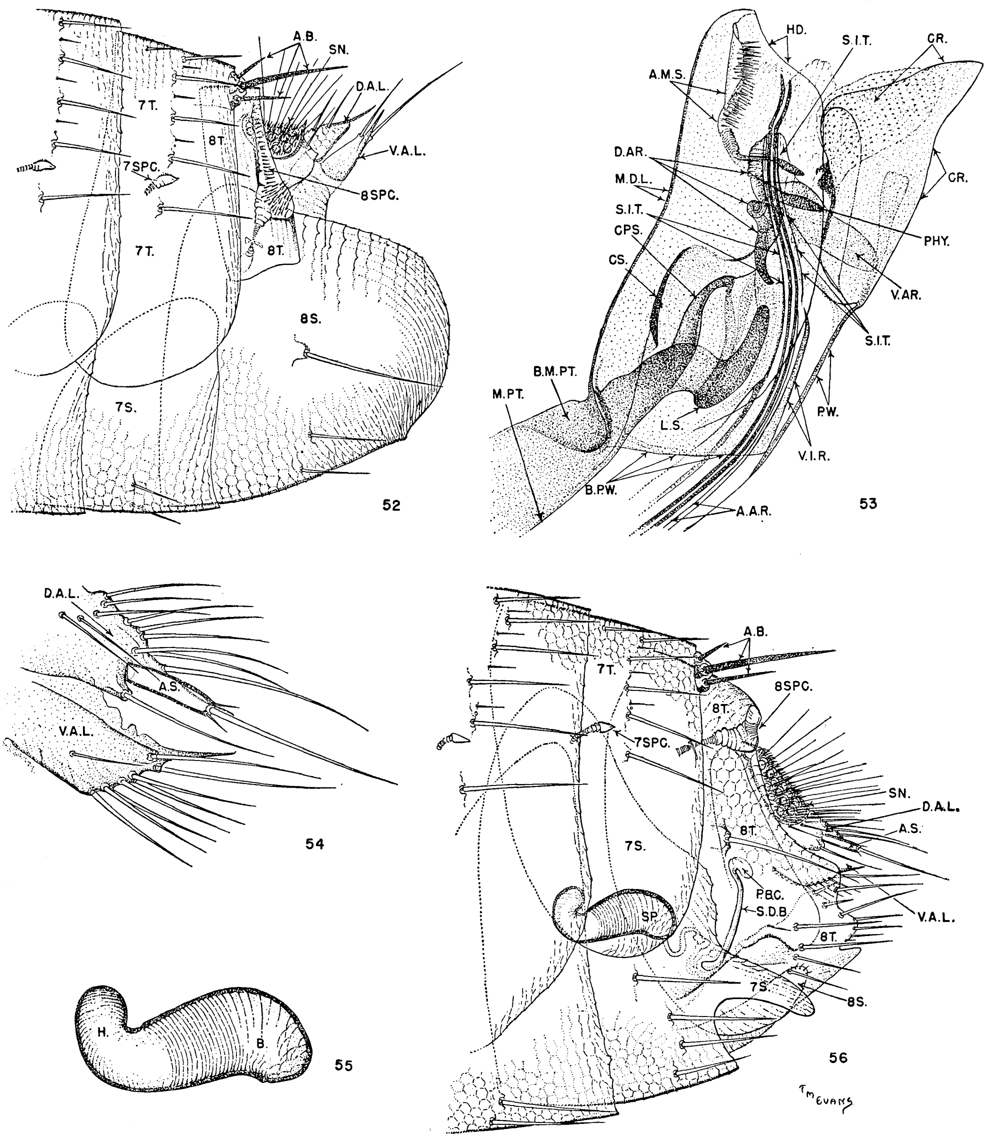
Sternum 9 with proximal arm (fig. 49, P.A.9) long and medially narrow; much longer than entire distal arm (D.A.9 & fig. 51); about 13× as long as broad at middle;



Figs. 49–51, *Doratopsylla wissemani* n. sp.: 49, ♂ sternum 9 and clasper; 50, Immovable and movable processes of clasper; 51, Distal arm of ♂ sternum 9.

expanded at anterior 1/4 and again near base; anterior 1/2 about 2× as long as wide at maximum (at level of ventral angle); apex subtruncate. Distal arm of sternum 9 (D.A.9) apically produced into a long narrow vertical process; with a median caudal rounded lobe. Height of D.A.9 above maximum convexity of median lobe (level of stout submarginal bristle) somewhat longer (1/7th) than length from that level to base of D.A.9; about 1/2 this length taken up by markedly narrow, rod-like distal portion. D.A.9 with an apical thin bristle; with 2 such anteromarginals—1 at midline and 1 half-way between this and apex; with 1 caudomarginal bristle midway between apex and caudal lobe; with 1 thin mesal bristle immediately above and another just below stout bristle on lobe.

Aedeagal apodeme fairly broad; its middle plate (fig. 48, M.PT.) nearly 5× as long (measured at base of apodemal strut, AP.S.) as broad at middle, and subtruncate at anterior end (apex). Lateral plates (L.PT.) extending below middle plate about 1/3 its breadth; ventral margin shallowly convex. Dorsal margin of aedeagal apodeme straight, terminating at apex. Bay of middle plate (B.M.PT. & fig. 53) fairly small, its length at middle about 1/2 that of crescent sclerite (C.S.) and somewhat broader (deeper) than long at this level. End-chamber very long—that portion of aedeagus caudal to posterior margin of B.M.PT. and base of pouch wall (B.P.W.) almost as long as apodeme cephalad of that level. End-chamber proportionately narrow—folds of hood (HD.) extending ventrad to level of dorsal part of crochet (CR.) and here chamber only about 2× breadth of middle plate (M.PT.) of aedeagal apodeme. Median dorsal lobe (M.D.L.) very long, somewhat biconvex. Ventral margin of folds of hood (HD.) slightly concave for apical 3/4, then becoming concave (emarginate) to join short apical margin. Apicomedian sclerite (A.M.S.) conspicuous because of long distal narrow portion which is subapically fringed or subpectinate due to a partly doubled row of fine, parallel, short and acute, evenly separated projections facing ventrocaudad; the "teeth" becoming smaller and blunter proximally, so that sclerite here appears fluted or ridged. A.M.S. with a ribbon-like anterior sector curving across apical portion of sclerotized inner tube (S.I.T.). Crescent sclerite (C.S.) long, narrow and fairly straight, flatter than capsula (CPS.) below it. Sclerotized inner tube fairly short, extending from levels of posterior end of C.S. to near anterior line of pecten of A.M.S.; fairly broad and oblique; with a well-developed dorsal armature (D.AR.) consisting of 1) a fluted or grooved apical portion which medially is of same girth as aperture of tube, 2) a smooth sector of nearly equal length and breadth, 3) a recurved or looped, broad, median portion dorsally astride a curved flask-like section extending cephalad (proximad) for remainder of length of S.I.T. D.AR. thus broadest at middle of S.I.T. and partially overlapping it here. Ventral armature (V.AR.) of sclerotized inner tube apically of same girth as D.AR. but rapidly curving deeply ventrad so that anterior portion consists of a large lobate keel-like structure 5× as long as diameter of S.I.T. and 2× as broad. Phylax (PHY.) a narrow sclerite flanking caudal margin of base of long lobe of V.AR.; extending across S.I.T. to anterior margin of D.AR. Crochets (CR.) very large, equal in length to entire end-chamber distad of apodemal strut and somewhat more than 2× as long as high (broad) at maximum level (near apical 1/3); ventral margin shallowly sinuate; dorsal margin basally somewhat sinuate, but medially terminating in a bilobed convexity, of which posterior hump is subacute, and then margin quite straight to near apex, where recurved to form a sharp spur pointing cephalad or anteroventrad; caudal margin arising from this spur and becoming medially somewhat concave but curving ventrad subapically to bluntly rounded apex. Crochet with a long



DORATOPSYLLA WISSEMANI N. SP.

Figs. 52–56, *Doratopsylla wissemani* n. sp.: 52, Segments 7, 8 and 10 (♂); 53, Apex of aedeagus; 54, Dorsal and ventral anal lobe of proctiger; 55, Spermatheca; 56, Modified abdominal segments (♀).

subventral rod-like thickening extending 1/2 its length. Lateral lobes inapparent. Penis rods (P.R.) uncoiled. Lacking a distinct vesicle at end of ventral intramural rod (V.I.R.). Aedeagal apodemal rod (A.A.R.) largely paralleling penis rods.

Abdominal segment 10 with dorsal anal lobe (fig. 52, D.A.L.) terminating in a long narrow apical stylar projection subequal in length to rest of segment; with 2 dorsomarginal bristles. D.A.L. shaped like isosceles triangle (excluding projection) with its altitude equal to length of acute projection. Ventral anal lobe (V.A.L.) more acutely triangular, slightly longer than D.A.L. and also terminating in a long narrow style; with 2 long subapical bristles, of which ventralmost is the longer.

Modified Abdominal Segments—♀: Sternum 7 (fig. 56, 7 S.) with posterior margin bearing a subventral long narrow lobe, the projection subequal in length to bulga of spermatheca (SP.) and about 3× as long as broad at middle; margin immediately above lobe quite straight (and microserrate); sinus below lobe 2× diameter and directed ventrocaudad; with a vertical row of 4 subventral bristles. Tergum 8 (8 T.) devoid of bristles near spiracular fossa 8 (8 SPC.); with a long median bristle at level of anal stylet (A.S.); a group of 4 submedian, subventral ones, of which ventral 2 are fairly small; with 2 short mesal bristles below ventral anal lobe; with a vertical row of 3 adjacent caudomarginals at this level, along broad sinus of tergum; lobe below this sinus with a group of 3 or 4 small marginal bristles, above the notch demarking ventrocaudal angle. Spiracular fossa 8 (8 SPC.) with axis of horizontal portion at right angles to vertical, these subequal in length but horizontal one somewhat broader than vertical, upright portion with length 3× subapical diameter. Dorsal anal lobe (fig. 54, D.A.L.) with a dorsomarginal row of bristles and an anterior row flanking posterior margin of sensilium (SN.); with a long bristle at ventrocaudal angle, below base of anal stylet (A.S.) and usually another long one dorsad to base of A.S. Ventral anal lobe (V.A.L.) with a long dorsocaudal acute projection, at base of which is a long bristle; with a submedian thin bristle; ventral margin nude and perpendicular to caudal margin, which bears about 4 long, basally broad, apically flagellate, bristles; at times these bristles almost contiguous with those of V.A.L. of other side. Anal stylet (A.S.) long and narrow; about 4× as long as broad; slightly arched, with dorsal margin convex; with 1 long apical bristle and a short one above and below it. Spermatheca (SP. & fig. 55) with very short and broad upturned hilla (H.); that portion of hilla extending above point of fusion with bulga (B.) shorter than its diameter; apex of hilla broadly rounded. Bulga elongate-ovate; base broad and flat; arched, with maximum height at caudal 1/4 of spermatheca, but here dorsal margin not quite reaching level of tip of hilla. Bursa copulatrix with its duct (S.D.B.) well-sclerotized on caudal margin, quite straight. Perula (P.B.C.) ovate.

Comments: The morphology of the aedeagus of *Doratopsylla* Jordan & Rothschild 1912 (figs. 48, 53) is basically very different from that of *Palaeopsylla* (figs. 11, 12, 43) and indicates that the two genera indeed are worthy of being placed in separate subfamilies as Hopkins & Rothschild (1966), Smit (1962) and Kishida (1939) have done on the basis of other taxonomic characters, in contrast to Wagner (1939) and Ewing & Fox (1943), who also used non-aedeagal features in their schemes of classification. Thus, the aedeagus of *Doratopsylla* is relatively unspecialized—there is an undifferentiated hood or mantle (fig. 53, HD.) enclosing the end-chamber, instead of there being modified structures like distodorsal lobes (fig. 11, D.L.); there is no sail, apical appendage or proximal strut. *Doratopsylla* possesses a bay in the middle plate (B.M.PT.), which is missing in *Palaeopsylla*, the curve in the plate presumably being used in the sail (thereby apparently also accounting for absence of spurs, etc., as mentioned above in the discussion of *Palaeopsylla*).

D. wissemani n. sp. is undoubtedly a true parasite of *Sorex* in the alpine and arctic alpine zones of the Kaghan Valley of the Himalayas, above elevations of 3075 m (10,000 ft), as is discussed below in Sections 10 and 11 on geographic and host-distribution and on the ctenidia of shrew-fleas, respectively.

The species is named for Prof. Charles L. Wisseman, Jr., M.D., Head of the Department of Microbiology, University of Maryland School of Medicine, among whose many outstanding contributions in the field of infectious disease is the highly successful field-program on viral and rickettsial infections in W. Pakistan, which also led to the collection of this fine species, as well as many other new taxa of ectoparasites.

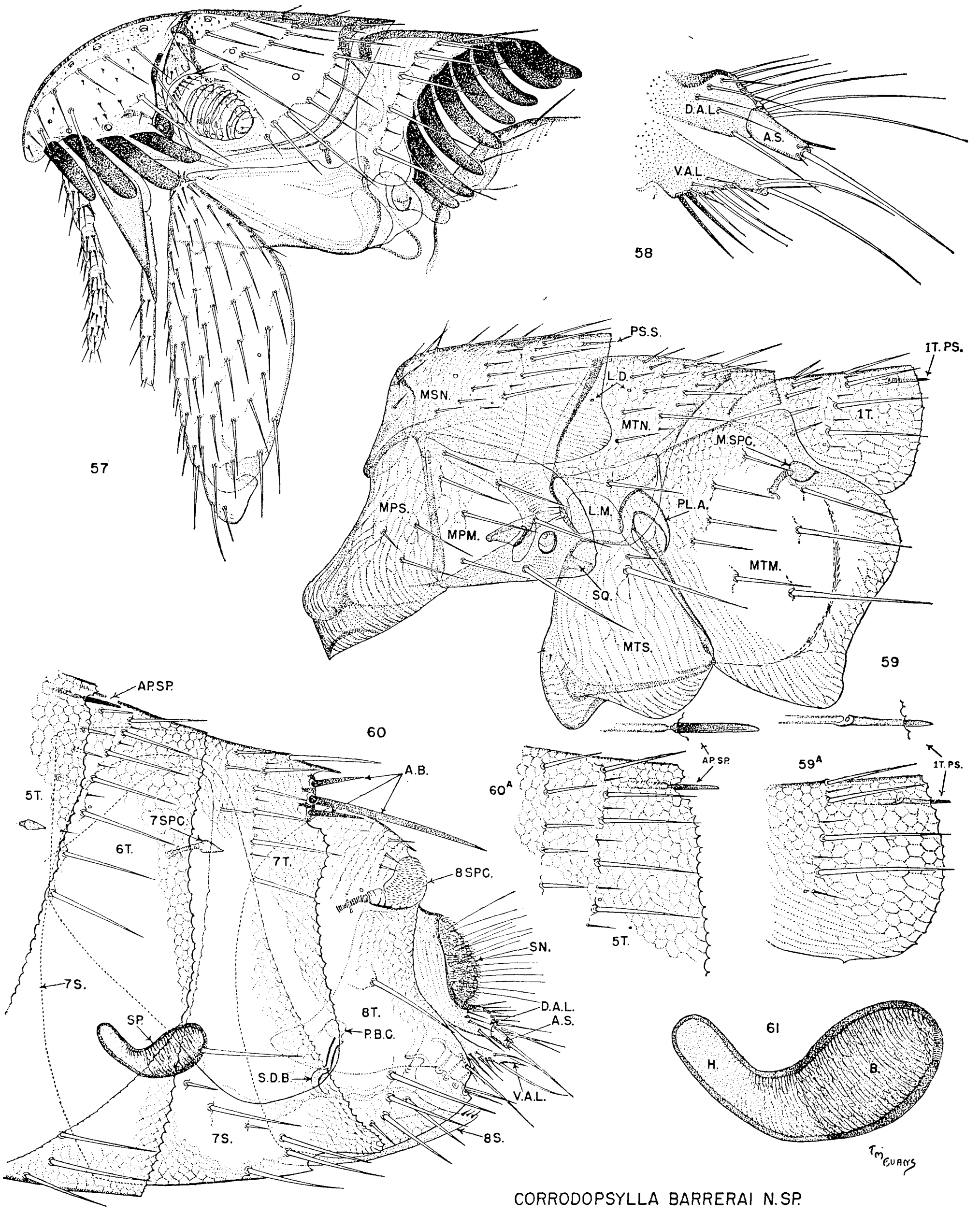
7. **Corrodopsylla barrerai** Traub and Evans, new species Figs. 57–61.

Type Material: Holotype ♀ (B-64949) ex *Sorex* sp.; Mexico: Guerrero, Omiltemi, (5 km SW); 2155 m (7000 ft) elev.; 6.IV.1963; coll. A.D. Stock & J. H. Shaw for the University of Maryland School of Medicine. No other specimens known.

Diagnosis: Unique amongst known members of the genus in that: 1) pronotal ctenidium (fig. 57) is markedly concave, its arc curving back over the pronotum; 2) 1st (anteriormost) genal spine removed from oral angle by a distance equal to its breadth; 3) ventral margin anterior to this spine bulges conspicuously and is almost snout-like; 4) apex of genal process caudad and somewhat ventrad to 4th genal spine. In the other species of *Corrodopsylla* Wagner 1929: 1) bases of spines of pronotal comb form only a slight curve and hence the axis of the comb is almost vertical; 2) 1st genal spine very close to the oral angle, separated by a distance distinctly less than breadth of the spine; 3) ventral margin anterior to this spine is quite straight; 4) apex of genal process below or beyond apex of 4th genal spine.

Further separable as follows from all subspecies of *C. curvata* (Rothschild 1915), the only other *Corrodopsylla* reported from Mexico: 1) lobe on the caudal margin of the sternum 7 of ♀ (fig. 60, 7 S.) is virtually ventral in position, its lower margin horizontal and separated from true ventral margin by only a slight excision; 2) preantennal region of head relatively long, i.e., longer than high at level of reduced eye. In *C. curvata*: 1) there is either a complete caudad-directed sinus on the posterior margin of sternum 7 or else the lobe is only subventral in position and the margin beneath the lobe is vertical; 2) preantennal region about 1.25× as high as long at level of eye.

Description—Head (fig. 57): Preantennal region relatively long, at level of eye, about 1.8× length of 2nd genal spine and 1.12× height of spine at that point; frontoclypeal margin accordingly gradually curving ventrad from vertex; this margin smooth (but perhaps bearing a rudiment of a deciduous tubercle at level of 3rd bristle of anterior, submarginal row of 7 bristles). With 4 bristles in an irregular 2nd row; 1 small, above 1st genal spine; 1 long, above 2nd genal spine; 1 long, above and anterior to greatly reduced eye; and 1 fairly long, along antennal groove at level of apex of scape. Eye represented by an indistinct ovate structure immediately above and behind last spine of genal comb. All spines of genal comb inclined ventrocaudad at same angle and essentially parallel; their bases almost in line and horizontal; all with rounded apices and the 4th especially spatulate. First genal spine narrower and shorter than 2nd and 3rd, tapering slightly for distal 1/5. Other spines of same length throughout to apex. Third spine slightly broader than 2nd. Fourth spine narrower than 3rd and somewhat shorter. Maxillary lobe extending to apex ofsegment 3 of maxillary palpus. Segment 1 of maxillary palpi the longest; 2× as long as segment 3 and 1.25× length of apical one, which is somewhat longer



Figs. 57–61, *Corrodopsylla barrerai* n. sp.: 57, Head and prothorax (♀); 58, Dorsal and ventral anal lobes of proctiger; 59, Meso- and metathorax, abdominal tergum 1 (♀); 59A, Pseudoseta on tergum 1; 60, Modified abdominal segments (♀); 60A, Apical spinelet; 61, Spermatheca.

than 2. Labial palpi 4-segmented; extending about 3/5 length of fore-coxae; segment 1 the longest; apical one nearly as long and slightly longer than subequal 2 and 3. Scape and segment 2 of antenna with short apical bristles. Antennal club fairly broad and ovate. Postantennal region with 3 full rows of bristles.

Thorax: Pronotum with a row of about 6 long bristles per side; anterior margin straight and vertical but posterior margin strongly curving dorsocaudad, the flare commencing at level of 2nd spine (counting ventralmost as 1st); dorsal margin accordingly nearly 2× as long as ventral (to base of spines). Spines of pronotal comb about 8 per side; all concave (with ventral and dorsal margins both concave) and bluntly rounded apically; all inclined more ventrad than caudad; 3rd and 4th spines 4.5× as long as broad near base; 5th and 6th shorter and proportionately broader; 7th spine and dorsalmost about 3× as long as broad. Mesonotum (fig. 59, MSN.) with 2 full rows of bristles and 1 pseudoseta (PS.S.) per side. Mesepisternum (MPS.) with about 3 bristles, median one small, submedian and caudomarginal ones longer. Mesepimere (MPM.) with bristles arranged 3-4; caudal margin oblate and lower 1/2 quite straight. Lateral metanotal area (L.M.) well demarcated; posterior margin much longer than anterior; with a median bristle near dorsal margin. Metepisternum (MTS.) with 1 short bristle near dorsocaudal angle and 1 long one below it; squamulum (SQ.) distinct; about 3× as long as broad. Pleural arch (PL.A.) well-developed. Metepisternum (MTM.) with a curved row of 5 bristles followed by a row of 3 longer ones, of which uppermost is below broadly sagittate spiracular fossa (M.SPC.); caudal margin relatively straight for upper and lower 1/5, intermediate portion markedly convex.

Metatibia with an apical group of 3 bristles of which innermost is small, middle one fairly long and outer one very long; with 3 pairs of dorsomarginal bristles arising from platelets; with a single dorsomarginal between apical group and 1st pair and another between 2nd and 3rd pairs; this last pair subproximal in position. Protibia with 1 ventromarginal distal bristle reaching to near apex of tarsal segment I; mesotibia with 2 long bristles at apex of anterior and posterior margins (each); of these, 1 member extending somewhat beyond middle of tarsal segment I and the longer member reaching just beyond apex of that segment; metatibia with a long bristle on each apical angle reaching slightly beyond middle of tarsal segment I. All tarsal segments with relatively short bristles-none on pro- and mesotarsi even approaching middle of following segment; on metatarsus I and II there are 1 or 2 distal bristles reaching to near middle of succeeding segments. Distal segments of each tarsus with 4 pairs of lateral plantar bristles and with 1 proximal pair displaced so as to lie between or slightly distad of bases of proximal lateral (true 2nd) pair. Measurements (in micra) of tibiae and tarsal segments (petiolate base deleted) of holotype:

		Tarsal Segment				
Leg	Tibia	I	II	III	IV	V
Pro-	157	58	56	43	33	76
Meso-	241	101	78	56	38	81
Meta-	348	228	157	101	58	94

Abdomen: Tergum 1 bearing a single pseudoseta (sic!) on each side (fig. 59, 1 T.SP.);

this subdorsal and submarginal in position; about 6× as long as broad at base and resembling mesonotal pseudosetae in appearance and apparent structure. Terga 2–5 each with a subdorsal apical spinelet about 5–6× as long as broad at base; appearing submarginal but caudal margin curving anteriorwards to meet base of spinelet (fig. 60, AP.SP.). Typical terga with 2 rows of bristles; 1st row terminating ventrally above sagittate spiracular fossa (fig. 60, 7 SPC.). Non-genitalic terga and sterna reticulate, the pattern usually a series of hexagons (at one level of focus; usually 1/3 of a hexagon at other level); caudal margins strongly scalloped and microdenticulate. Basal abdominal sternum with 1 very small submedian bristle and 1 ventromarginal per side. Sterna 3 and 4 with 2 ventromarginals per side; 5 and 6 with 3. With 3 antepygidial bristles (A.B.), middle one about 4.5× as long as upper and lower ones. Insertion of plate of A.B. subdorsal; tergum 7 (7 T.) produced into an acute lobe above plate, and extending straight caudad for a short distance below it.

Modified Abdominal Segments: Sternum 7 (fig. 60, 7 S.) with caudal margin bearing a short, fairly narrow, blunt ventral lobe; margin above lobe somewhat oblique but slightly concave; its lower 1/3 microdenticulate. Sinus below lobe incomplete—an elongate semi-ellipse with ventral margin missing. 7 S. with an oblique rows of 3 long, widely-separated bristles (ventralmost marginal) and a group of 2 contiguous, more posterior bristles near ventral margin; with 1 very small bristle above, and 1 below middle bristle of 1st row. Tergum 8 (8 T.) with group of 2 or 3 small bristles just anterior to spiracular fossa (8 SPC.) which in turn is largely broadly ovate but with anterior margin concave and much shorter than posterior, so that posterior margin is evenly and markedly convex. 8 T. with single large submedian bristle, a subventral almost vertical row of 3 long bristles, with a more posterior bristle in line with middle one and a short anterior one just below ventralmost of the 3; with 3 short, stout mesal bristles in an oblique row below ventral anal lobe (V.A.L.) close to an approximated pair on ventrocaudal sinus of posterior margin; with 1 long thin bristle above this, near V.A.L. Dorsal anal lobe (D.A.L. & fig. 58) with oblique row of 3 bristles near anterior margin; 1 submedian bristle, a dorsal fringe of bristles, of which posterior 2 are very long; 1 ventrocaudal bristle near base of anal stylet (A.S.). Ventral anal lobe with anterior 1/2 of ventral margin slightly sinuate and bearing 3 or 4 long bristles, 2 of these at anteroventral angle, stout; and with about 3 small bristles in a subhorizontal row near margin, commencing at 2nd long marginal bristle; posterior 1/2 with 3 nonapical bristles, of which 2 subapical ones are small and that near middle of margin fairly long and thin; with 2 very long apical bristles. Anal stylet (A.S.) slightly more than 2× as long as broad at maximum; dorsal and ventral margins quite straight; with a very long apical bristle, base of which is flanked by 2 tiny bristles, 1 subdorsal, 1 ventral. Spermatheca (SP. & fig. 61) flask-shaped, bulga (B.) forming broadly ovate, somewhat curved base of flask and hilla (H.) the fairly long, upturned neck. Hilla not clearly separated from bulga, but apparently slightly longer than bulga and with its apical 1/2 of equal diameter throughout and with parallel sides; apex bluntly rounded. Bursa copulatrix with duct (S.D.B.) fairly well-sclerotized and shaped like an inverse question mark; perula (P.B.C.) broad, oblate and indistinct.

Comments: The species is named for our good friend, Prof. Alfredo Barrera, Director, Museo de Historia Natural de la Ciudad de Mexico, one of the leading students of Siphonaptera, in acknowledgement of his contributions on the zoogeography of the Mexican ectoparasite fauna, particularly that of the fascinating Omiltemi region. It was only through

Prof. Barrera's cooperation and guidance that our field-team collected this unusual species of flea.

The difference in the shape of the thorax in the new species, as compared to other members of *Corrodopsylla*, is of the magnitude formerly used by some taxonomists in naming new genera. However, on the basis of what has been observed in other genera where one member has such an arched comb, it is doubted that this modification has been accompanied by other morphological distinctions (even in the male) which would warrant a change in its generic assignment.

Since all known *Corrodopsylla* and *Doratopsylla* are shrew-fleas, the host-data (*Sorex*) for this new species is almost undoubtedly correct. Additional reasons for regarding *C. barrerai* n. sp. as a soricid-flea are indicated in the notes on convergent evolution below, and are based on the structure of the genal and pronotal ctenidia.

8. Notes on the Status of *Corrodopsylla* Wagner 1929 Versus *Doratopsylla* Jordan & Rothschild 1912, with Comments on Pseudosetae, Apical Spinelets and Combs of Spines

Although *Corrodopsylla* and *Doratopsylla* are regarded as being closely related and share many features, there are significant and perhaps critical differences between the two that seem to have been overlooked. The similarities are discussed first.

Both genera infest shrews and are perhaps the most host-specific of all fleas, since they rarely have been collected on other mammals, even in the same microhabitat. They resemble one another so closely that Wagner originally designated *Corrodopsylla* as a subgenus of *Doratopsylla*, and subsequent authors frequently disregarded the name entirely (i.e., Kishida 1932; I. Fox 1940; Holland 1942; Hubbard 1947, etc.). Others have dealt with *Corrodopsylla* as a subgenus (Traub 1944; Ioff & Scalon 1954; Sakaguti & Jameson 1962). In recent years, however, most authors have regarded *Corrodopsylla* as a full genus, viz. Holland 1949; Traub 1950; Smit 1962; Sakaguti 1962 and Hopkins & Rothschild 1966.

In some respects, the new species herein described suggests that the two taxa really are quite closely related, but it also demonstrates a difference that may be fundamental. One of the features suggesting close affinity is that the 1st genal spine is further removed from the oral angle than in other *Corrodopsylla* (fig. 80), thereby approaching *Doratopsylla* (fig. 81); another is that the genal process is of the *Doratopsylla*-type. However, the new species resembles other *Corrodopsylla* in that: 1) the 4th genal spine is essentially in line with the others and not displaced dorsad to border the antennal fossa (fig. 57); 2) the apices of the terga and some sterna are distinctly serrated (fig. 60); and 3) the 7th tergum is extended as a process between the two sets of antepygidial bristles.

The important and perhaps fundamental differences between *Corrodopsylla* and *Doratopsylla*, illustrated by *C. barrerai* n. sp. and *D. wissemani* n. sp., concern the pseudosetae and apical spinelets, and the distinctions are present in other members of the respective genera. Thus, 1) it is reported for the first time that *Corrodopsylla* is highly unusual, if not unique, in that the 1st abdominal tergum bears, on each side, what is apparently a true pseudoseta (figs. 59 & 59A, 1 T.PS.), whereas *Doratopsylla* instead possesses only the apical spinelets (figs. 46 & 46A, AP.SP.) which are customarily present in ctenidia-bearing fleas. 2) The apical spinelets on terga 2-5 of *Corrodopsylla* (figs. 60 & 60A, AP.SP.) are exceptionally long, about 5-6 times as long as broad at the base and the caudal margins of the terga are obviously recessed or excised at points of origin of the spinelets, so that the structures appear as if they were non-marginal, while of course they actually are marginal. In contrast, in *Doratopsylla* the apical spinelets are only 1.5 or 2 times as long as broad at the base and actually are marginal in position, i.e., caudal margin entire and generally not appreciably recessed at those levels.

The presence of pseudoseta-like structures on the 1st tergum is so surprising as to warrant further discussion, first as to their identity and then as to their significance. Pseudosetae on the 1st tergum (or anywhere on the abdomen) are apparently exceedingly rare and for this reason, and because the pseudoseta-like structures on this segment in *Corrodopsylla* (figs. 59 & 59A, 1 T.PS.) superficially resemble the oddly long apical spinelets on terga 2-5 in that genus (figs. 60 & 60A, AP.SP.), it is tempting to regard the former as merely spinelets which are submarginal in position. Several factors militate against this view, viz. 1) they are definitely mesal in position, as are true pseudosetae, and are not caudomarginal or lateral in position like ctenidia or apical spinelets (the so-called "minor combs"). 2) They arise well anterior to the caudal margin, which can be discerned laterad to them, i.e., passing over the pseudosetae, instead of curving in scallopwise to meet their bases. 3) They are less discrete in structure than are the spinelets, especially at the base, although the basal canal-like extension is quite similar in both pseudosetae and spinelets in *Corrodopsylla* (which is unusual).

Pseudosetae seem to be of basic importance in the phylogeny and taxonomy of fleas. They are not known to occur in pulicids, tungids, rhopallopsyllines, and certain other genera of other families, as cited in part by Dampf (1945), using an outmoded scheme of nomenclature, and more fully by Jordan (1947), but in general (not always) are found in non-pulicids that bear a pronotal comb. There seems to be an inverse relationship between pseudosetae and ctenidia. Thus, 1) if present at all, pseudosetae are found on the mesonotum. However, no flea is known to bear a mesonotal comb. 2) If fleas have a true comb, it is on the pronotum, if nowhere else, but pseudosetae are rarely found on the pronotum, and if present, the pronotum lacks a comb (i.e., some parapsyllines).[11] 3) No flea is known to bear both pseudosetae and true combs on the same tergum. (*Glaciopsyllus* Smit & Dunnet 1962, is the only known flea bearing both pseudosetae and apical spinelets on one notum.[11]) 4) Abdominal terga frequently bear apical spinelets ("minor combs") or, occasionally, a true but miniature comb, and rarely a full or "major comb." Accordingly, one would expect that pseudosetae would be unusual on any of the abdominal segments, and *Corrodopsylla* is the only exception of which we are cognizant.[12]

Observations of this nature, and two instances in freakish fleas in which one of the pseudosetae resembled the spine of the pronotal comb, led Jordan (1947) to postulate that "...the pseudosetae are the spines of the pronotal comb." Jordan went on to say that "...pronotal pseudosetae represent like the mesonotal ones a primitive comb and can only be expected to occur in species of which the ancestor never had an external pronotal

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[11] In the highly anomalous ceratophyllid genus *Glaciopsyllus*, there are pseudosetae on all the thoracic nota, and apparently the pronotum bears seta-like spinelets as well, as shown in Smit's accurate figure in the original description.

[12] Holland (1964) stated that the 1st abdominal tergum in *Glaciopsyllus* bears pseudosetae, but we believe that this is due to a misinterpretation of the original description. Smit (in litt.) confirms that the abdomen in this genus bears spinelets, not pseudosetae, but points out that in *Glaciopsyllus* the two are quite similar in appearance.

comb." He regarded apical spinelets as vestigial combs and pointed out that in some groups of Siphonaptera, even the remnants of combs of certain segments have been lost completely. Holland (1964) stated that the condition in *Glaciopsyllus* warrants re-appraisal of the Jordan hypothesis, and our new observations of the presence of pseudosetae on tergum 1 in *Corrodopsylla* in lieu of the apical spinelets of the closely related *Doratopsylla*, are in accord with Holland's viewpoint. If *Corrodopsylla* and *Doratopsylla* had diverged before the evolutionary development of combs on the terga, then there would be no conflict with Jordan's theory that pseudosetae represent incipient or rudimentary combs, but the two taxa resemble one another too closely for that to have been the case. However, it must be added that the main tenet of Jordan's theory probably has a very sound basis, since it holds for practically all fleas, and the instances of *Corrodopsylla* and *Glaciopsyllus* are just other examples of the exceptions that invariably seem to plague systems of classification in the Order. We do not question the corollaries of Jordan's postulate, namely that vermipsyllid fleas never had ctenidia whereas comb-less pulicids and hystrichopsyllids are the descendants of comb-bearing fleas (Holland 1959).

The fundamental nature of the pseudosetae in phylogeny and taxonomy is exemplified by Dampf's action (1945) in stating that Ewing erred in his scheme of classification in placing *Megarthroglossus* Jordan & Rothschild 1915 (I-2)[13] with the pulicids, since that genus possessed pseudosetae, and pulicids lack them. Regardless, the morphological similarities between pseudosetae and apical spinelets in *Corrodopsylla* and the apparent presence of both pseudosetae and apical spinelets on the pronotum of *Glaciopsyllus*, demonstrate some fundamental but little-understood relationship between pseudosetae, ctenidia and apical spinelets.

Some of the figures in this article illustrate a point that seems to support the view that the apical spinelets are derived from true ctenidia and that both types of structures are lateral and marginal (or submarginal) in origin, not median or mesal. For example, in figs. 34, 97, 100 and 101, it can be seen that the ventral portion of the pronotum extends well caudad of the base of the lowest ctenidial spine. This pronotal extension (PR. EX.) presumably represents that part of the tergum which has not been concerned in the development of the ctenidial spines, as indicated by the following observations. When the comb is short (consisting only of a few spines and/or not reaching far down the notum, the extension is very high (broad), as in fig. 100. When the comb is long (figs. 97, 34), PR. EX. is short (narrow), and when the comb is full length, reaching the vinculum (fig. 44) then, by definition, there is no ventral extension. Further, the pronotal extension is generally subequal in length to that of the spine immediately above it.

It would therefore appear that the spines are an integral part of the notum, and observations on the relative lengths of the pronotum and its spines seem to bear this out. As can be seen in fleas with a simple or unmodified type of pronotal comb, the pronotum can be regarded as being of a " constant ", " unit " or " standard " length. That is, the length of the notum proper, plus the length of the spines, is an approximate constant (proportionate, of course, to the size of the flea). Thus, when the dorsal half of the notum is short (narrow), as in *P. remota* (fig. 34)(I-3) and in *Jellisonia klotsi* Traub 1950 (III-1), then the spines are long. In contrast, when the notum is long, then the spines are short, as in

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[13] The families and subfamilies of the genera cited are indicated by code-designation, such as I-2, and these are listed in Section 13.

Stivalius pomerantzi Traub 1950 (II-1). The genus *Mioctenopsylla* Rothschild 1922 (III-1) is most instructive in this regard since the pronotal spines are extremely short (and lightly sclerotized), while the tergum is exceptionally long. Accordingly, it is not surprising that in vermipsyllid fleas, which are believed to never have developed combs in their evolutionary course, the pronotum is of maximum length. In effect then, the length of the spines to a great extent represents that portion of the notum that has entered into their development, and the spines are not mere additions to existing structures. In other words, it is as if the entire comb were moved forward on the notum and thereby did not arise from the caudal margin. In instances where the spines are very long, as in mole-fleas (fig. 76) and *P. remota* (fig. 79), the length of the pronotum plus that of the spines seems to slightly exceed that of the theoretical ancestral notum, or that of the portion anterior to the level of the comb plus that of PR.EX. Nevertheless, the inverse relationship between length of spine versus that of notum suggests that the combs are submarginal in origin, and the narrow sclerotized band (fig. 97) and/or remnant of a suture (fig. 95) often seen at the base of the comb indicates that the anterior portion of the primitive *flange* of the pronotum may be the region involved in the production of the spines. This view is supported by the fact that in some species, such as *Pleochaetis soberoni* Barrera 1956 (III-1), the apical spinelets are quite long and the "canal" or "path" of the base of each is of exceptional length, extending forward to near the base of the flange. That the spines of these combs are lateral in origin and not mesal like pseudosetae, is indicated by the presence of a *mesal* sclerotized seam under the pronotal comb, near the bases of the spines.

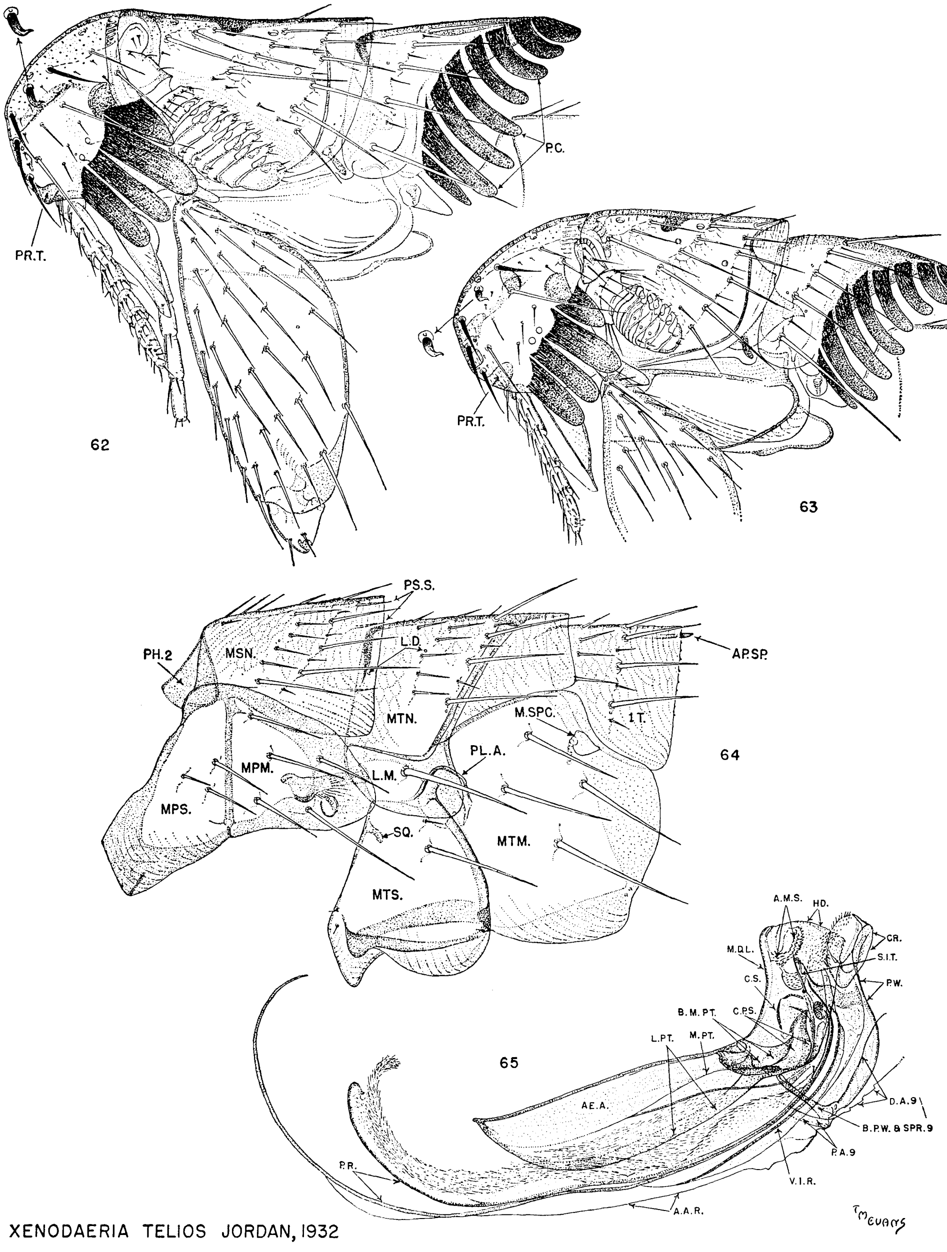
If this theory about the length of the pronotum being "constant" is correct, then one would expect that when the apical spinelets are unusually long, as in *C. barrerai* n. sp. (I-5), there would be a corresponding adjustment to compensate for the "additional" length, and this is actually the case. Thus, the abdominal tergal margins are recessed, and, as a result, the spinelets are physically (not homologically) submarginal. In *P. soberoni*, the caudal margins are relatively concave at the level of the spinelets. Similarly, when there is a major comb of large spines present on the abdomen, as in *Stivalius hopkinsi* (II-1) there is a notal extension beneath the comb equal to the length of the ventral spines (recalling the "pronotal extension") and the entire comb is therefore "recessed", as it were.

If the hypothesis about the pronotal comb arising from a flange on the notum is valid, then we may indeed be correct in our suspicions that in many fleas there may be some degree of movability in the entire comb whereby it can be appressed towards the body or partially lifted, as a flap (See Section 12 below).

9. **Xenodaeria telios** Jordan 1932 Figs. 62-73 & 83.

Xenodaeria telios Jordan, 1932, Novit. Zool. **38**: 273, figs. 31, 32 (Unique ♂ only.).—Smit, 1962, Proc. R. Ent. Soc. Lond. (B) **31** (9-10): 114.—Traub & Barrera, 1966, J. Med. Ent. **3** (2): 140, 142.—Hopkins & Rothschild, 1966, Cat. Roths. Collect. Fleas **4**: 85, figs. 120-21.—Traub, Wisseman & Nur Ahmad, 1967, Trans. R. Soc. Trop. Med. Hyg. **61** (1): 45.

This species is of considerable interest because of its structural modifications (incrassations on head, arched pronotal comb, etc.), its broad geographical range, doubt about the true host and because it has been known only from the unique male. The female is herein



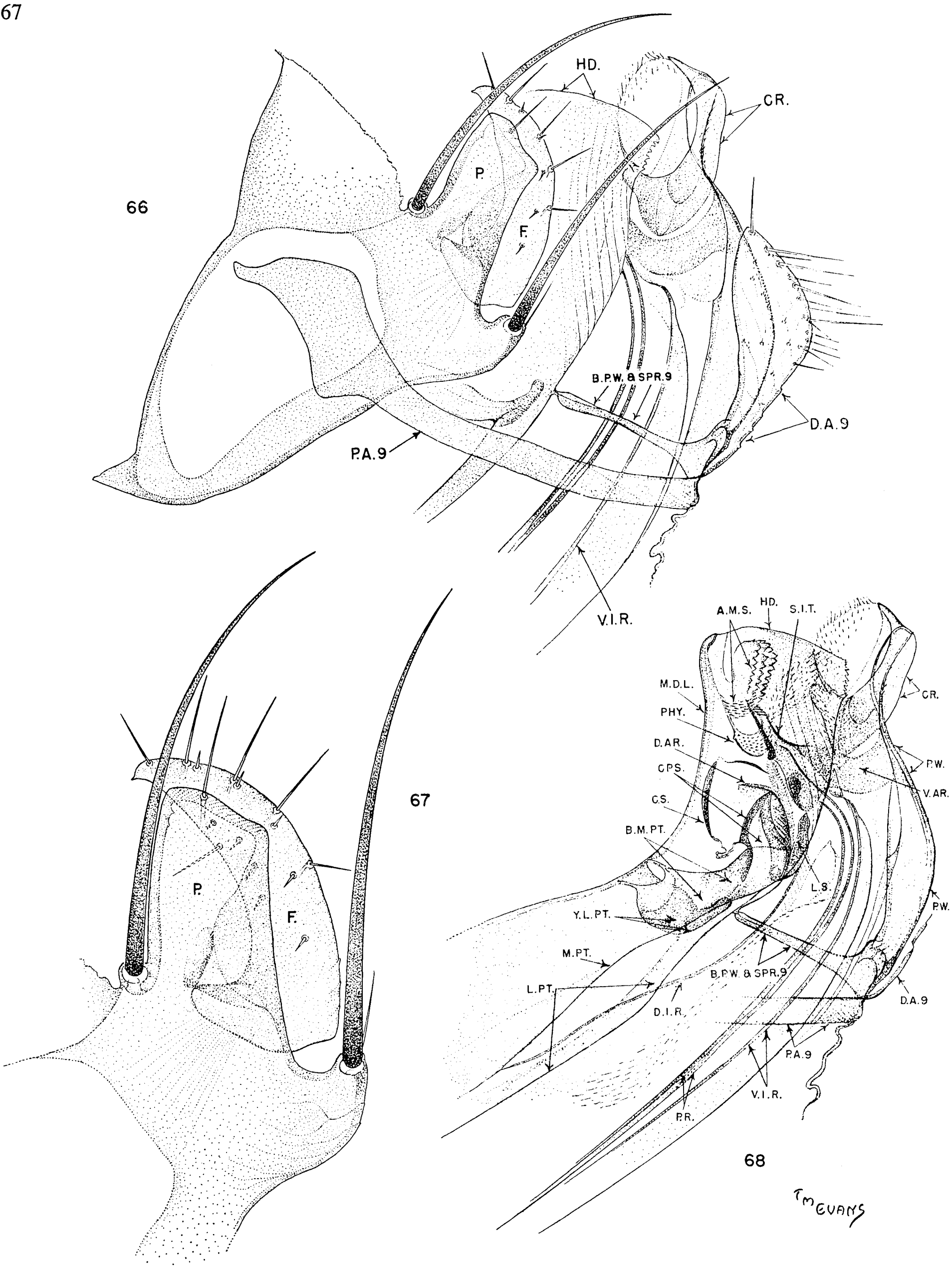
Figs. 62–65, *Xenodaeria telios*: 62, Head and prothorax (♂); 63, Head and prothorax (♀); 64, Meso- and metathorax, abdominal tergum 1 (♂); 65, Aedeagus.

described, as is the aedeagus. It is illustrated in detail for the above reasons and to emphasize its affinities. Host-relationships and zoogeographic notes regarding *X. telios* are discussed below in Section 10, features of the genal comb in Section 11, and the pronotal comb in Section 12.

Descriptive Notes—Head: With marked sexual dimorphism regarding internal incrassations, viz. 1) that extending from margin below frontal tubercle dorsocaudad towards region above eye. In ♂, the heavily incrassate portion reaches level of eye (fig. 62); in ♀ (fig. 63), median portion very light so that there appears to be 2 incrassations, with the upper one darker and more discrete (ovate, imposed on a subspherical background) than in ♂. 2) Median occipital dorsal incrassation broader and shallower (extending ventrad) in ♂, about 2.5× as long as deep; deeper in ♀—only 1.6× as long as deep. 3) Preoral tuber (PR.T.) cordate in ♂; dorsally convex in ♀. In both sexes, cuticular ridges on abdominal sternum 2 partly whorled and closely approximated and subparallel; true striarium absent.

Abdomen—♀ (fig. 73): Terga 1-5 each with total of 2 apical spinelets. Terga 2-4 with 1st row of bristles extending to near level of sagittate spiracular fossa; in 5 and 6, row only about 1/2 as long. Caudal row with ventralmost bristle inserted below spiracular fossa. Unmodified terga with caudal margin dorsally microdenticulate, the tiny serrations well-spaced. Unmodified sterna with caudal margins entire, smooth; with 2 bristles in a vertical row; 1 submarginal, 2nd ventromarginal. With middle of 3 antepygidial bristles (A.B.) about 1.6 or 1.7× length of lower one and about 4× or more length of upper. Insertion of plate of A.B. almost dorsomarginal and caudal margin of 7 T. only slightly incurved below plate.

Modified Abdominal Segments—♀: Sternum 7 (fig. 73, 7 S.) relatively tall and narrow, 1.8× as high as long at maximum; with a conspicuous squarish sinus 2× as long as high and with ventral margin slightly longer than dorsal (occasionally oblique in pitch); lobe above sinus broadly rounded and inclined more ventrad than caudad; ventral lobe fairly truncate and about 3× as broad as sinus; with an oblique vertical row of 3 bristles—uppermost just above level of sinus, lowermost near ventral margin; with a smaller bristle anterior to last bristle and ventromarginal. Tergum 8 (8 T.) apparently devoid of bristles anterior to or below spiracular fossa (8 SPC.) which is vertical in position and slightly more than 2× as high as broad subapically and medially somewhat constricted, but otherwise of subequal diameter; horizontal portion of fossa broad at base but rapidly constricting. 8 T. with 1 large median bristle and 2 submedian ones; preceded by an anterior row of 2 or 3 small bristles of which uppermost is at level of upper submedian and of dorsal lobe of 7 S.; with 2 very small bristles at ventrocaudal angle, just below sinus; with 2 caudomarginals above this sinus and upper of these flanked by 2 small mesal bristles near ventral anal lobe (V.A.L.). Caudal fringe (C.FR.) with 4 small bristles. Sternum 8 (8 S.) highly sclerotized, outlines indistinct, broadly ellipsoid. Dorsal anal lobe (D.A.L.) relatively short and dorsally convex; with a subproximal vertical row of thin bristles and 2 or 3 longish dorsal bristles, that above base of anal stylet (A.S.) longest; with 1 such bristle near anteroventral angle. Ventral anal lobe (V.A.L. & fig. 72) narrow and angled; devoid of bristles on proximal (subventral) margin; apical (caudal) margin with 2 long bristles, of which 1 is at angle; with a smaller subapical dorsal bristle. Anal stylet (A.S. & fig. 72) about 3× as long (dorsally) as broad at middle; slightly broader proximally than apically; ventral margin commencing distad of dorsal margin; sides straight; with long apical bristle flanked at base by 2 tiny ones. Spermatheca (SP. & fig. 71) sigmoid; bulga (B.) bulbous, gourd-shaped or like base of an ovoid curved flask; hilla (H.) broadly vermiform, upcurved and with dorsal pitch greater than ventral, apex broadly rounded. Bursa



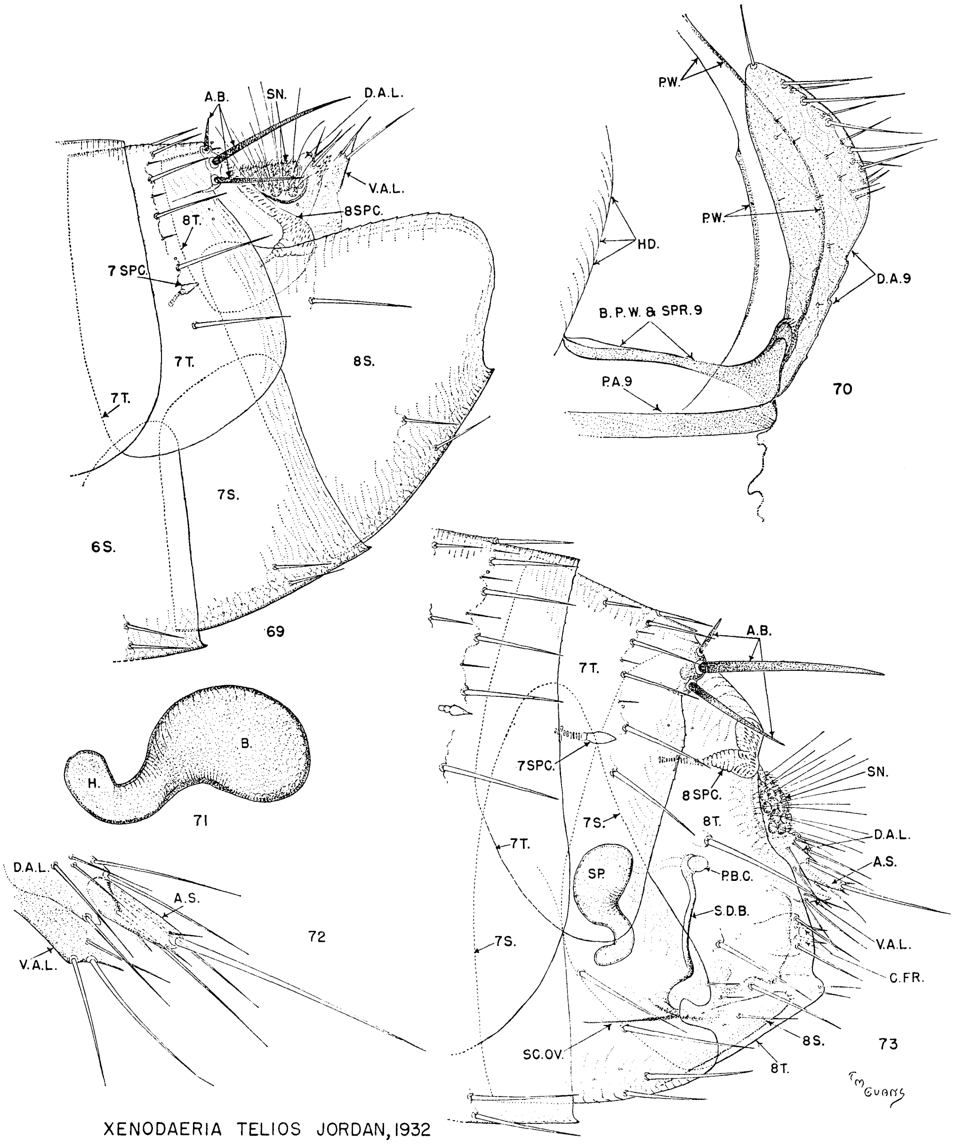
Figs. 66–68, *Xenodaeria telios*: 66, ♂ sternum 9, clasper and apex of aedeagus; 67, Immovable and movable processes of clasper; 68, Apex of aedeagus.

copulatrix with duct (S.D.B.) slender and mildly sinuate; perula (P.B.C.) lightly sclerotized and ovate. Sclerotized wall of oviduct (SC.OV.) apparent as a thin horizontal or oblique line usually terminating near sinus of 7 S., near ventral portion of indistinct slightly incrassate area.

Aedeagus (figs. 65, 68): Apodeme (AE.A.) fairly broad, as measured from base of apodemal strut (AP.S.), nearly 4× as long as broad; dorsal margin, as well as ventral margin of lateral plates (L.PT.) well-sclerotized, much more so than ventral margin of middle plate (M.PT.). Bay of middle plate (B.M.PT.) obscured by being overlain by well-sclerotized ovate yoke of lateral plates (Y.L.PT.). Base of pouch wall (B.P.W.) well-developed, straight (oblique) and rod-like and indefinably and intimately merging with a conspicuous dorsal spur (SPR.9) of base of distal arm of sternum 9 (D.A.9). Ventral margin of pouch wall (P.W.) well-sclerotized, sinuate and running along and intimately connected with D.A.9 and curving over ventro-apical portion of crochet (CR.). Median dorsal lobe (M.D.L.) shallowly concave to near apex and there joining light folds of unmodified hood (HD.) which extends down on sides of end-chamber. Apicomedian sclerite (A.M.S.) conspicuous as a subdorsal structure somewhat rectangular, spiculose at base and whose ventral 1/2 is rugose or bearing close rows of broad, approximated serrations, hence A.M.S. appearing like a large brush. Crescent sclerite (C.S.) long, exceeding capsule (CPS.), narrow and only slightly convex. Phylax (PHY.) apparently reduced to an indistinct tomentose or spiculose area arising from anterodorsal portion of A.M.S. and diverging and curving ventrad over sclerotized inner tube (S.I.T.). Dorsal armature (D.AR.) of inner tube relatively unspecialized; characterised mainly by a proximal tuber. Ventral armature (V.AR.) arising from basal 2/3 of tube; huge, more than 3× diameter of S.I.T. and extending down to ventral margin of pouch wall; about 1/3 as long as deep; anterior and posterior margins sinuate. Crochets (CR.) very long, equivalent to length of end-chamber distad of apodemal strut; arising from near center of caudal margin of V.AR. and extending past end of aedeagus for 1/2 its length; sclerotized portion shaped like a barge or scow; proximal upright region fairly broad but posterior one subacute apically; dorsal portion of CR. between terminal axes lightly sclerotized and spiculose dorsally. Penis rods (P.R.) completely uncoiled. Our records are as follows (all from Pakistan):

♂	♀	Host	Locality	Elev.	Date	Collector
7	5	Shrew	Hazara Dist., Dunga Gali	2495 m (8100′)	9-10.IX.63.	R. Traub & A. B. Mirza
1	—	*Hyperacrius wynnei*	〃 〃	2460 m (8000′)	23.IX.62	H. W. Setzer
1	—	*Crocidura* sp.	〃 〃	〃	〃	〃
12	9	〃	〃 Nathia Gali	—	27-29.VI.65	R.L. Amoureux
6	—	〃	〃 Thandiani	2460 m (8000′)	3.XII.66	Mirza
—	1	*Hyperacrius* sp.	〃 〃	〃	5.XII.66	〃
7	3	*Crocidura* sp.	〃 〃	2705 m (8800′)	6-7.XII.66	〃
—	1	〃	〃 Kaghan Valley, Shogran	—	31.VII.65	A.C. Risser
1	2	〃	〃 〃 〃	3075 m (10000′)	1.VIII.65	〃
1	—	*Apodemus*	〃 〃 〃 Mt. Makra	3045 m (9900′)	22.IX.64	Traub
—	1	*Rattus* sp.	〃 Murree Hills, 1.6 km E of Ghoradaka	—	21.IX.62	Setzer
—	1	*R. rattoides*	〃 Sathan Gali, Shakol	1955 m (6350′)	14.XII.66	Mirza
1	—	*Crocidura* sp.	Hazara Dist., Kund. Shaheed Pani	3075 m (10000)	20.XII.66	Mirza
2	4	*Hyperacrius* sp.	Swat State, Yakh Tangai	2125 m (6900′)	13.X.66	Traub & Mirza
1	—	*Crocidura* sp.	〃 3.4km SW of Yakh Tangai 8km E of Shangla	1940 m (6300′)	〃	Traub
3	3	〃	〃 8km S of Kalam	—	14.V.66	J.J. O'Keefe

It is our belief that *X. telios* is a true shrew-flea (ex *Crocidura*) as discussed below in Section 10.



Figs. 69-73, *Xenodaeria telios*: 69, Segments 7, 8 and 10 (♂); 70, Distal arm of ♂ sternum 9; 71, Spermatheca; 72, Dorsal and ventral anal lobes of proctiger; 73, Modified abdominal segments (♀).

The aedeagus of *Xenodaeria* (figs. 65, 68) may be characterized (on the generic level) as follows: Aedeagal apodeme (AE.A.) relatively broad; apical appendage and proximal spur absent, as are keel and sail; lateral plates (L.PT.) with ventral margins broadly yoking with bay of apodeme (Y.L.PT.). End-chamber relatively short and inclined posterodorsad. Base of pouch wall (B.P.W.) heavily sclerotized and intimately connected with spur-like dorsal extension (SPR.9) of base of distal arm of sternum 9 (D.A.9). Ventral portion of pouch wall (P.W.) conspicuous, closely associated with D.A.9 and extending caudad to crochet (CR.). Median dorsal lobe (M.D.L.) quite flat. Hood (HD.) simple. Apicomedian sclerite (A.M.S.) large and brush-like. Distodorsal lobes inapparent. Crescent sclerite (C.S.) quite flat and long. Phylax (PHY.) greatly reduced. Sclerotized inner tube (S.I.T.) short and oblique; its dorsal armature (D.AR.) unspecialized, but ventral armature (V.AR.) massive. Crochets unusually long, exceeding that of apodemal strut. Lateral lobes weakly developed. Penis rods (P.R.) uncoiled. Vesicle at end of ventral intramural rod (V.I.R.) unspecialized.

The genus *Xenodaeria* morphologically closely resembles other doratopsylline fleas, especially *Corrodopsylla*, in such features as the pattern of the genal ctenidium, the apical portion of the distal arm of sternum 9, the details of the clasper and the structure of the aedeagus. Amongst the last-named are the absence of any extensions of the plates of the aedeagus in the form of a sail or apical appendage, etc.; presence of a relatively unspecialized hood, a brush-like region of A.M.S., a very large crochet, etc. The pseudosetae and apical spinelets are of the type of *Doratopsylla*, not *Corrodopsylla*. However, *Xenodaeria* is quite unique in the family in some respects, i.e., the notable incrassations on the frons and occiput; the presence of spiniform bristles on the frons, and the distinct connections between the aedeagal pouch wall and sternum 9. The arched pronotal comb is discussed in Section 11.

An excellent account of the affinities and classification of *Xenodaeria* and allies (*Idilla* Smit 1957; *Acedestia* Jordan 1937; *Doratopsylla*, etc.) at the subfamily and tribal levels is presented in Smit (1962). Hopkins & Rothschild (1966) also provide sound views in this regard.

10. **Notes on the Geographic and Host-Distribution of Some Fleas in West Pakistan**

Study of the affinities and distribution of fleas (and chiggers) and their hosts in W. Pakistan, undertaken by the University of Maryland School of Medicine, has contributed to the demonstration of the presence of scrub typhus infection in highly unusual types of terrain and in unexpected geographical areas (Traub, Wisseman & Nur Ahmad 1967). The results reported there also included significant and distinctive zoogeographic patterns exhibited by the fleas (and chiggers) and their hosts, which actually served as the basis for selecting specific habitats and areas for microbiological study regarding tick typhus and scrub typhus.

However, more recent data permit us to extend those observations, and to clarify the host-relationships of some of the species (*P. setzeri* n. sp. and *X. telios*) discussed in the present article, as well as to suggest that the genal and pronotal spines of certain of these fleas are modified in a characteristic manner. However, before attempts are made to show that the patterns of genal and pronotal spines exhibited by these fleas are associated with certain kinds of hosts or with the host-environment, it is necessary to determine the specific host, and this in turn requires a brief review of salient points made in the above article and a discussion of our records of some of the fleas and their hosts in the mountains of W. Pakistan.

The ecological features of the Kaghan Valley, the Murree Hills and the mountain-deserts and forests of Gilgit were presented by Traub, Wisseman & Nur Ahmad (1967), along with notes on the habits and distributional records of such hosts as voles, field-mice, rats, hamsters, flying-squirrels and shrews. In that article it was pointed out that the flea- and chigger-fauna of Shogran, near the mouth of the Kaghan Valley, appeared to be significantly different in some respects from those of the more northern two-thirds of the 160 km long Valley, despite superficial similarities in topography, flora, elevation and climate. The flea- and vole-fauna of the Shogran region were said to resemble that of the Murree Hills more closely than that of the bulk of the Kaghan Valley, where apparently there is a greater degree of rainfall and where the terrain is more subject to glaciation during cold weather.

The arid mountains and valleys of Gilgit, in the rain-shadow of the lee side of the Himalayas and Karakorams, were shown to have an ectoparasite fauna more suggestive of the xeric stretches of Central Asia than that of the mesic slopes on the other side of the mountains. However, it was stressed that "... in the midst of the desolate mountain deserts of Gilgit occur 'ecological islands' atop of peaks or in sheltered valleys watered by glacial streams, where the major elements of the flora and fauna are the same as those in the Kaghan Valley..." It was prognosticated that similar specialized habitats, with a concomitant comparable rodent-, insectivore-, ectoparasite-fauna (and microbial flora) were scattered throughout much of Central Asia, despite the intervention of deserts, broad rivers and mountain peaks.

The present article is based not only upon the records of fleas and mammals collected in the field-programs reported in the above-cited article on scrub typhus, but those of more recent studies on rickettsial and viral infections in W. Pakistan. Of special interest here are the collections made in the mountains of Swat and Dir States in an attempt to verify the hypothesis of "ecological islands" just outlined. Both of these states are west of the Indus River and are separated from the Kaghan Valley by many miles of semidesert and several valleys. Suffice it to say for our present purpose that in the temperate and alpine zones of Dir and Swat were found much the same type of terrain as in the Kaghan Valley, along with floral signs of a somewhat milder and drier climate.

The numbers of specimens of certain mice and shrews collected in these mountainous areas are shown in Table 1, whence it can be seen that specimens of the burrowing-voles, *Hyperacrius*, were taken in all the regions studied save Gilgit.[14] In all, 839 specimens were examined, representing three species or forms, and it is noteworthy that one, *H. wynnei*, was never collected in the relatively well-studied northern parts of the Kaghan Valley (i.e., Naran, Battakundi, etc.) but was found at Shogran, the Murree Hills and parts of Swat. Significantly, *H. fertilis* was also found at Shogran (often within a meter's distance from *H. wynnei*) and was abundant north of Shogran, as well as in Dir and near Kalam,

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[14] Mount Babusar, the pass connecting the Kaghan Valley with the mountain-deserts of Gilgit is technically in Gilgit Agency but ecologically is the same as the Kaghan and here is so considered.

Table 1. The numbers of specimens of certain mammals examined in some mountainous areas in W. Pakistan.

Name of Host	Total Collected	Kaghan Valley		Murree Hills	Dir	Swat	Gilgit
		Shogran	Northern Sectors				
Hyperacrius wynnei	57	14/57†	—	36/57	—	7/57*	—
Hyperacrius fertilis	728	18/728	567/728	—	69/728	74/728**	—
Hyperacrius indet. (*fertilis* or *wynnei*)	37	37/37	—	—	—	—	—
Hyperacrius sp. #3	17	—	—	—	—	17/17@	—
Alticola sp.	436	23/436	324/436	—	32/436	19/436	38/436
Apodemus flavicollis	2175	106/2175	1160/2175	30/2175	135/2175	369/2175	375/2175
Crocidura sp.	319	8/319	162/319	15/319	17/319	42/319	75/319
Sorex sp.	36	1/36	35/36	—	—	—	—

†*Numerator* indicates number of specimens from indicated area. *Denominator* indicates total number of specimens collected for that species.

*=From Shangla area only; **=From Kalam area only; @=From Yakh Tangai area only.

Swat. It has not been taken by us in the Murree region. The third type of *Hyperacrius* was encountered only at Yakh Tangai in Swat. The common name "Kashmir Vole" formerly applied to *Hyperacrius*[15] is shown by these data to be a misnomer, for *Hyperacrius* is now known to be common in certain habitats west of the Indus River.

Alticola roylei voles were fairly common in the Kaghan Valley and were also collected in Dir and Swat, but the *Alticola* in Gilgit may prove to be a different species. No *Alticola* were trapped in the Murree Hills. The field-mouse *Apodemus* was found in all the mountains surveyed, as were shrews of the genus *Crocidura*, but only at elevations below 2925m (9500 ft.). *Sorex* shrews were collected only in alpine and subarctic habitats.

Table 2 list certain fleas which were collected on *Hyperacrius*, at least occasionally, but which may also have been associated with some of the other mammals included in Table 1. The areas represented in the collections are also cited, and it is apparent that none of these fleas had been encountered at Gilgit (where *Hyperacrius* was never taken either). Two species, *Ctenophthalmus golovi* ssp. (I-3) and a new *Amphipsylla* #1)(IV-2), were collected only in the northern Kaghan Valley. Three forms (*D. wissemani* n. sp. (I-5) ; New Genus #3, n. sp. #1, n. ssp. 'A' (III-1) ; and *Amphipsylla* n. sp. #2) were found both at Shogran and elsewhere in the Kaghan Valley, but not in the other areas. The new *Rhadinopsylla* (I-8) and *Stenischia* (I-8) were widely distributed, but the second subspecies of New Genus #3, n. sp. #1 was collected only at one locality in Swat.

Of particular interest and relevance is the distribution of *P. setzeri* n. sp. (I-3) and *X. telios* (I-5). Both of these were taken at Shogran but not elsewhere in the Kaghan Valley, even though those northern areas were the most intensively studied sites in our four-year program. Further, these two species were also collected in the Murree Hills and Swat. In

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[15] *H. fertilis* True can properly be called True's vole, but we believe terms like true shrew, tree-shrew, vole-mole, shrew-mole and mole-shrew are confusing enough without adding a name that might easily be printed as true vole, yet refer to an untrue or burrowing-vole.

Table 2. Fleas collected from *Hyperacrius* in some mountainous areas in W. Pakistan.

Name of Flea	Total Collected	Kaghan Valley		Murree Hills	Dir	Swat	Gilgit
		Shogran	Northern Sectors				
Ctenophthalmus golovi spp. (?)	12	—	12/12*	—	—	—	—
Doratopsylla wissemani n. sp.	8	1/8	7/8	—	—	—	—
Palaeopsylla setzeri n. sp.	33	10/33	—	10/33	9/33	4/33	—
Rhadinopsylla n. sp.	21	2/21	18/21	—	—	2/21	—
Stenischia n. sp.	12	1/12	4/12	1/12	2/12	4/12	—
Xenodaeria telios Jord., 1932	16	3/16	—	10/16	—	3/16	—
New Genus #3, n. sp. #1, ssp. 'A'	33	1/33	32/33	—	—	—	—
New Genus #3, n. sp. #1, ssp. 'B'	1	—	—	—	—	1/1	—
New Genus #3, n. sp. #2	4	—	—	—	—	4/4	—
Amphipsylla n. sp. #1	13	—	13/13	—	—	—	—
Amphipsylla n. sp. #2	55	12/55	43/55	—	—	—	—

**Numerator* indicates numbers of "collections" (or occasions on which collected) for designated species from specified area. *Denominator* indicates total numbers of "collections" of that species made from all listed areas.

addition, *X. telios* was collected in Dir (and in the mountains between the Kaghan Valley and Swat).

From the distribution-data in Tables 1 and 2, it is clear that certain common rodents and fleas were found in all of the major, widely-separated (geographically and topographically) mountainous areas studied. Since it is unlikely that these temperate and alpine animals could have crossed barriers like vast deserts and peaks of eternal snow, these observations support the hypothesis of Traub, Wisseman & Nur Ahmad (1967) that there are relict faunas of mammals and ectoparasites in suitable pockets of forest-remnants scattered throughout the mountains of southwestern Asia. Thus, these isolated populations are presumably descendants of animals that in the geological past (Tertiary) were widely and regularly distributed in a continuous belt of coniferous or temperate forest which was first broken by the Pliocene upheavals of the formation of the Himalayas, and subsequently, if in the rain-shadows of the massive peaks, largely converted into desert areas.

Analysis of the host-flea data reinforce this contention, since, in general, in our study-areas, the same species of flea frequently parasitizes the same species of host if the local environment is similar, regardless of the *geographic* area involved. Thus, *Alticola* was infested with *Amphipsylla montana* Argyropulo 1946 (IV-2) in Gilgit, Swat and Dir, and *Leptopsylla* (*Pectinoctenus*) *pamirensis* (Ioff 1946)(IV-1) had a similar distribution, but on *Apodemus*. *Callopsylla* (*C.*) *fragilis* Mikulin 1953 (III-1), was common on *Apodemus* in all areas save Swat, and *Frontopsylla* (*Profrontia*) *ambigua* Fedina 1946 (IV-2), was abundant on that host in all five. A new genus and species of flea (III-1) and *Macrostylophora*

Table 3. The numbers of "collections" of species of fleas reported from *Hyperacrius* and other hosts in some mountainous areas of W. Pakistan.

Name of Flea	*Hyperacrius*=Burrowing Voles					Voles	Shrews		Other Genera
	All spp. (Total)	*fertilis*	*wynnei*	Indet. (*fertilis* or *wynnei*	Species #3	*Alticola*	*Crocidura*	*Sorex*	
Ctenophthalmus golovi ssp. (?)	11/12	11/12				1/12			
Doratopsylla wissemani n. sp.	1/6	1/6						5/6	
Palaeopsylla setzeri n. sp.	30/33	7/33	10/33	13/33				1/33	2/33*
Rhadinopsylla n. sp.	10/21	10/21				11/21			
Stenischia n. sp.	12/12	8/12	1/12	1/12	2/12				
Xenodaeria telios Jord. 1932	2/16		1/16		1/16		10/16		4/16*@
New Genus #3, n.sp. #1, ssp. 'A'	33/33	33/33							
New Genus #3, n.sp. #1, ssp. 'B'	1/1	1/1							
New Genus #3, n. sp. #2	4/4				4/4				
Amphipsylla n. sp. #1	12/13	12/13				1/13			
Amphipsylla n. sp. #2	3/55	3/55				48/55			4/55@

†Indet.=Not determined to species but undoubtedly either *H. wynnei* or *H. fertilis*.

*=Ex *Rattus rattoides*; @=Ex *Apodemus flavicollis*; *@=2 ex *R. rattoides* and 2 ex *Apodemus*.

Table 4. The numbers of specimens of designated species of fleas collected from specified hosts in some mountainous areas of W. Pakistan.

Name of Flea	*Hyperacrius*=Burrowing Voles					Voles	Shrews		Other Genera of Rodents
	Hyper. All spp. (Total)	*Hyper. fertilis*	*Hyper. wynnei*	Indet. (*fertilis* or *wynnei*)	*Hyper.* Species #3	*Alticola*	*Crocidura*	*Sorex*	
Ctenophthalmus golovi ssp. (?)	12/13	12/13				1/13			
Doratopsylla wissemani n. sp.	2/9	2/9						7/9	
Palaeopsylla setzeri n. sp.	161/164	53/164	54/164	58/164			1/164		2/164*
Rhadinopsylla n. sp.	15/32	15/32				17/32			
Stenischia n. sp.	13/13	9/13	1/13	1/13	2/13				
Xenodaeria telios J., 1932	7/59		1/59		6/59		48/59		4/59*@
New Genus #3, n.sp. #1, ssp. 'A'	92/92	92/92							
New Genus #3, n.sp. #1, ssp. 'B'	2/2	2/2							
New Genus #3, n. sp. #2					8/8				
Amphipsylla n. sp. #1	53/54	53/54				1/54			
Amphipsylla n. sp. #2	4/163	4/163				153/163			6/163@

*=Ex *Rattus rattoides*; @=Ex *Apodemus flavicollis*; *@=2 ex *R. rattoides* and 2 ex *Apodemus*.

fimbriata (Jordan & Rothschild 1921)(III-1) both associated with *Hylopetes* flying-squirrels, as well as another new genus of flea (III-1) infesting *Petaurista* flying-squirrels, were all collected in the Kaghan Valley, Dir and Swat.

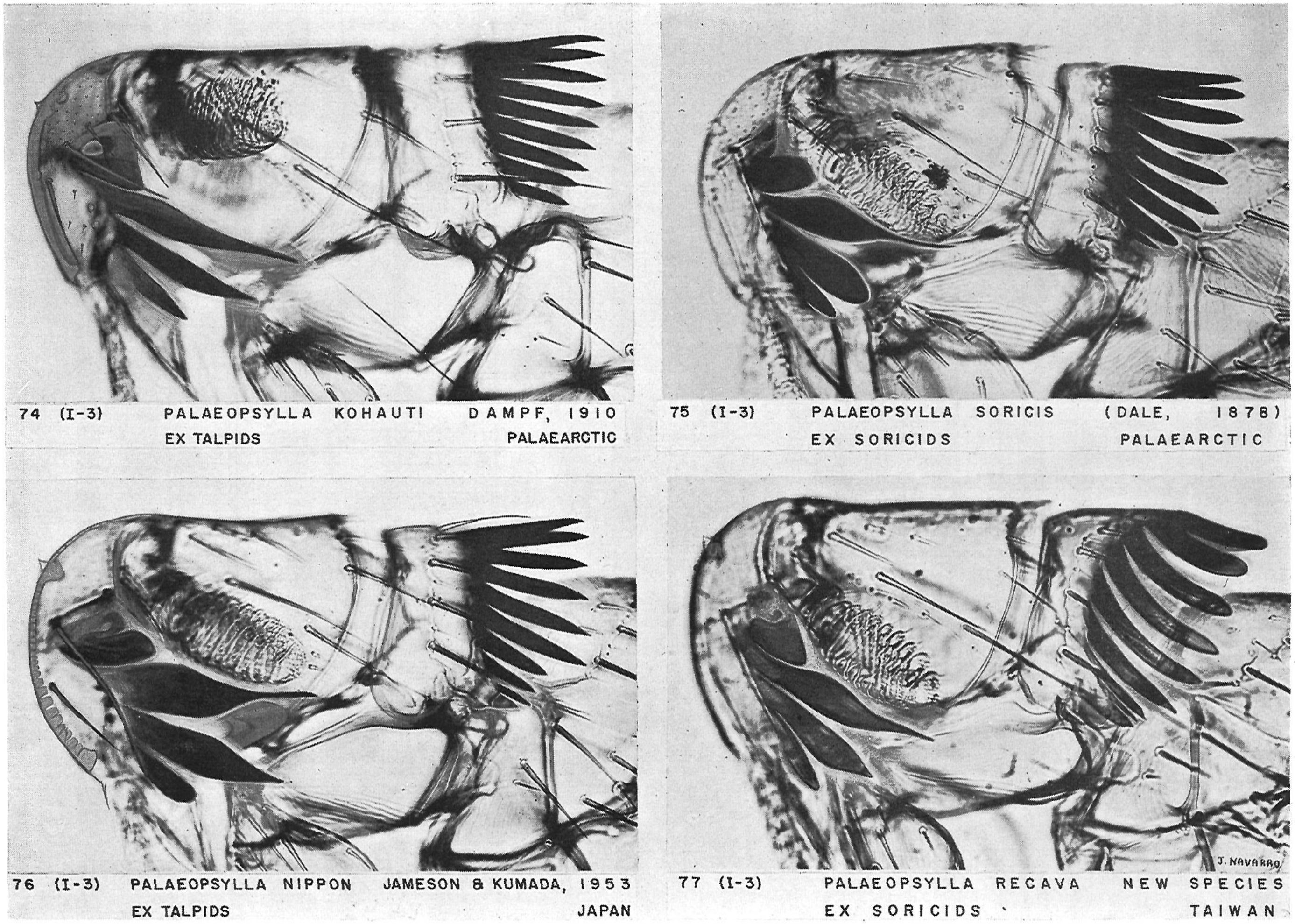
Data regarding the host-affinities of the species of fleas listed in Table 2 as having been taken on *Hyperacrius* burrowing-voles, are presented in Tables 3 and 4. In discussing host-relationships, it is important to consider not only the actual number of *specimens* of fleas associated with a species of mammal in an area, but also the *frequency* with which it was collected on that host. This is necessary to avoid assigning undue weight to an exceptionally large number of specimens that may have been taken on one individual and yet represent an unusual infestation. Therefore, Table 3 considers only the numbers of " collections " from each kind of host, and this term is defined as each instance or occasion when the designated species was taken from a host (or pool of hosts of the same species bearing identical data and accessioned as a unit). The " collection " may thus consist of more than one specimen of the species of flea under discussion, and its frequency of occurrence for a host is regarded as an indicator of host-preference. Of course, the total numbers of *specimens* per species collected from each kind of host are also important, and hence these are listed in Table 4.

The data on *Ctenophthalmus golovi* and *Stenischia* n. sp. indicate the need for considering the numbers of " collections." As shown in Table 3, 11 of 12 collections of *C. golovi* and all 12 of *Stenischia* came from *H. fertilis*, but only 13 specimens of each were taken in all (Table 4). Obviously there is some significant connection with *Hyperacrius* in contrast to *Apodemus*, etc., but the small numbers of specimens involved indicate there is much to be learned about these two species (which may be nest-forms and hence seldom collected on the host). Most species of the holarctic genus *Rhadinopsylla* Jordan & Rothschild 1912 (I-8) have a markedly discontinuous distribution and are relatively rarely collected. They too may prove to be nest-fleas, but it is of interest that all of our records of the new species in the mountains of W. Pakistan were from *Hyperacrius* or *Alticola* and were nearly equally divided between the two.

In contrast, *D. wissemani* n. sp. (I-5) is apparently a *Sorex* flea (as one would except from its generic assignment and morphology, including pronotal and genal spines. *Vide* below.) *Amphipsylla* n. sp. ♯2 is clearly an *Alticola* flea (48/55 ; 153/163).

X. telios (I-5) was collected on 16 occasions, and 10 of these collections were from *Crocidura* (48 of 59 specimens). The remaining specimens of *X. telios* were scattered on three other hosts (2 collections each). These records indicate that shrews (*Crocidura*) are the true host of *X. telios*, as Hopkins & Rothschild suggested (1966) based upon a knowledge of the anatomy and affinities of the species, and as reported by Traub & Barrera (1966). Since this species had been known but from a single specimen, from the linsang, a weasel-like viverrid in Sikkim, its preferred host had been a matter of doubt. As has been pointed out by Traub & Barrera (1966) and as mentioned below, the pattern of genal and pronotal combs in *Xenodaeria* likewise suggest that it is a true shrew-flea.

Altogether 10 species of fleas are listed in these tables as having been collected on *Hyperacrius*, an impressive figure since at present only a total of 74 species of fleas are known to us from all types of hosts examined in W. Pakistan. At least four of these species of Siphonaptera seem to be associated with the burrowing-voles, sufficiently so that *Hyperacrius* may be cited as the preferred host. Thus, all the collections (33) and all the specimens



Figs. 74–77, Head and pronotal comb: 74, *Palaeopsylla kohauti* Dampf 1910; 75, *P. soricis* (Dale 1878); 76, *P. nippon* Jameson & Kumada 1953; 77, *P. recava* n. sp.

(92) of the new genus designated as #3, new species #1, were from *Hyperacrius*; the same is true for the second undescribed species of that genus, and virtually all of the *Amphipsylla* n. sp. #1 (12 of 13 collections; 53 of 54 specimens) came from that host.

The fourth species, *P. setzeri* n. sp. merits discussion since all other known *Palaeopsylla* infest shrews and moles, yet 30 of 33 collections and 161 of 164 specimens of *P. setzeri* n. sp. were from this microtine burrowing-vole, while only 1 specimen was collected from shrews despite our having examined a total of 355 shrews. (Moles are not known to occur in the regions under consideration). These data strongly suggest that *Hyperacrius* is the real host of *P. setzeri* n. sp. In this regard, the odd pattern of the distribution-data of certain of these fleas and hosts are worth emphasizing since they are unusual enough to indicate validity of the observations, viz: 1) the apparent absence of *P. setzeri* n. sp. and *X. telios* at Naran and other northern localities in the Kaghan Valley and their presence at Shogran near the mouth of that Valley (and in the Murree Hills, Swat or Dir); 2) our failure to collect *H. wynnei* north of Shogran; and 3) the absence at Shogran (as well as in Dir, Swat and Gilgit) of a new species of *Leptopsylla* (*Pectinoctenus*), which is the most common flea of *Apodemus* at Naran and other northern parts of the Kaghan Valley. The type of genal and pronotal comb exhibited by *P. setzeri* n. sp. also indicates that it is a *Hyperacrius*-flea, as pointed out in Section 11.

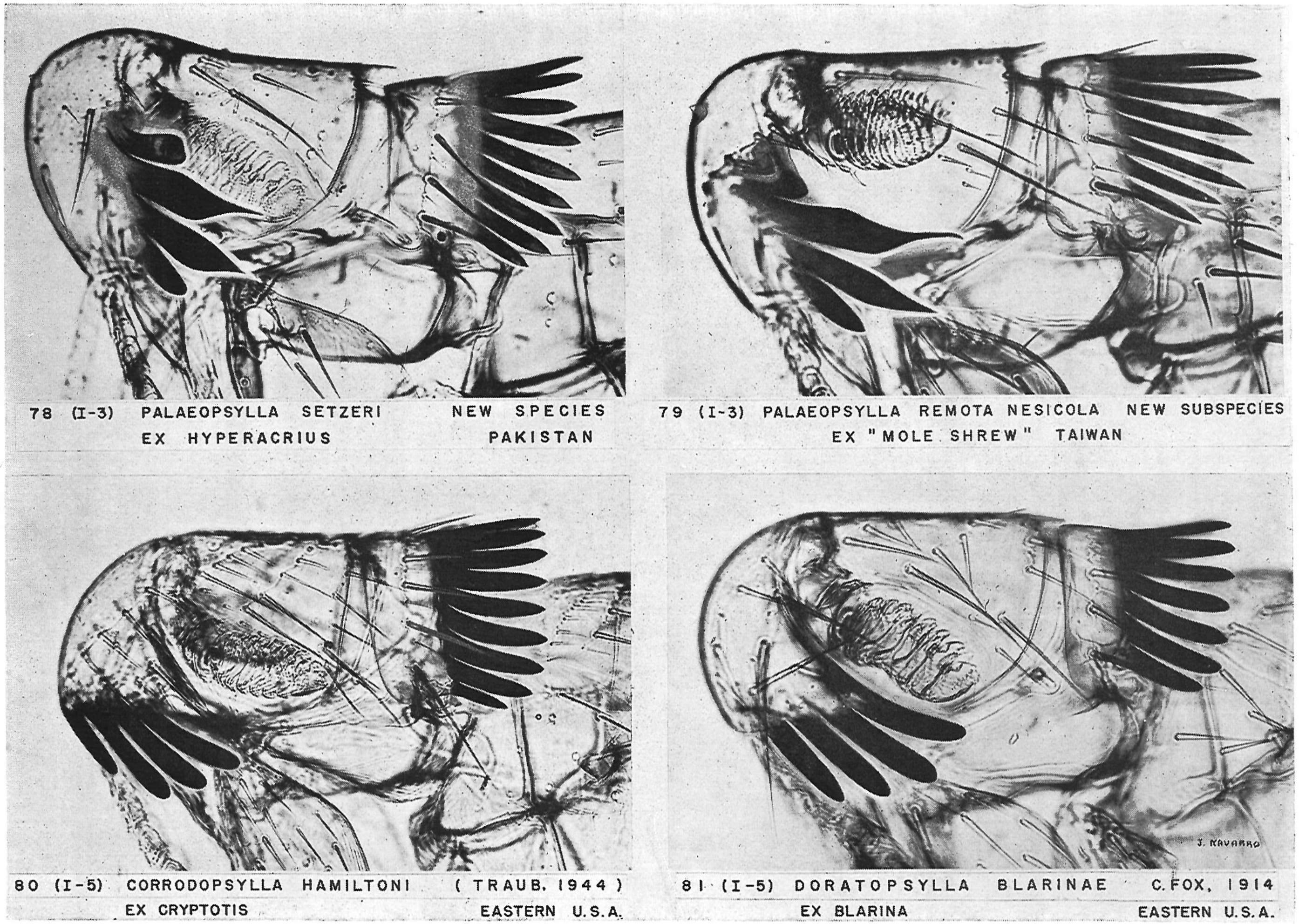
11. Notes on Convergent Evolution of the Pronotal and Genal Combs of Shrew-Fleas

As indicated by Traub & Barrera (1966) and by Traub (1967), both the genal and pronotal combs of shrew-fleas tend to be modified in a fairly characteristic manner, regardless of the genus, subfamily or family of flea represented. They hence appear to be "adaptive" and are excellent examples of convergent evolution. A review of this point is now presented in order to show how some of the new species, herein described, support this contention, and to serve as background for discussing the flared pronotal comb.

In many shrew-fleas, the *genal* spines are typically broad and spatulate as in *Doratopsylla* Jordan & Rothschild 1912 (I-5) (fig. 44) and *Corrodopsylla* Wagner 1929 (I-5) (fig. 57). However, in certain genera there has been an evolutionary development of a specialized type of genal comb in which some of the spines are long, narrow and apically acuminate or tapering. This has occurred in *Palaeopsylla* Wagner 1903 (I-3), *Corypsylla* C. Fox 1908 (I-8) and *Nearctopsylla* Rothschild 1915 (I-8), and it is noteworthy that in the representatives of these genera which infest shrews, one or more of these spines (usually the 2nd or 3rd) are consistently shorter, blunter and less attenuated than in their relatives infesting talpids (cf. figs. 75, 77, 84, 86 - shrew-fleas; versus figs. 74, 76, 85, 87 - talpid-fleas). From fig. 13, it can be seen that *P. apsidata* n. sp. bears a genal ctenidium of the type found in *Palaeopsylla* shrew-fleas and this suggests that the species really is a parasite of *Crocidura* and not of moles.

Comparison of the genal spines of *Xenodaeria* (figs. 62 & 83) with those of the shrew-infesting doratopsylline fleas (I-5) *C. barrerai* n. sp. (fig. 57), *C. hamiltoni* (Traub 1944) (fig. 80) and *D. blarinae* C. Fox 1914 (fig. 81), emphasizes that they are fundamentally of the same type.

That this trend towards blunting of the genal spines is a definite phenomenon in shrew-fleas is further suggested by the Mexican subgenus *Alloctenus* Traub & Barrera 1966 of the



Figs. 78–81, Head and pronotal comb: 78, *P. setzeri* n. sp.; 79, *P. remota nesicola* n. ssp.; 80, *Corrodopsylla hamiltoni* (Traub 1944); 81, *Doratopsylla blarinae* C. Fox 1914.

genus *Ctenophthalmus* Kolenati 1856 (I-3) (fig. 92). Here, in all three members of the subgenus, as in the case of the only other *Ctenophthalmus* known to specifically infest shrews (*C. particularis* Berteaux 1949, fig. 93), the first two of three genal spines are fairly broad and blunt, instead of being angulate, pointed and narrow as in the 100 or more species of the genus parasitizing murids (i.e., fig. 91), cricetids or talpids (fig. 90).

According to this hypothesis, then, if *P. setzeri* n. sp. were really a shrew-flea instead of a *Hyperacrius*-flea, it would be expected that the second (from ventral) genal spine would be spatulate as in *P. apsidata* n. sp. (fig. 13) or *P. soricis* (Dale 1878) (fig. 75) or else bear only a short, tapered tip as in *P. recava* n. sp. (figs. 1, 2, 77). Actually, in *P. setzeri* n. sp., this spine is longer and more acuminate (figs. 19, 19A, 78) than in shrew-*Palaeopsylla*, but yet not as narrow and pointed as is typical of mole-fleas (figs. 74 & 76). In fact, the demonstrated variability in the degree of acuteness of the second genal spine in *P. setzeri* n. sp. (fig. 19A) suggests a character that is still plastic or flexible in the evolutionary sense.

The case of *P. r. nesicola* n. ssp. and *P. r. remota* on the surface appears to contradict the theory, since the genal (and pronotal) spines (figs. 33, 34, 79) are acuminate and suggestive of mole-fleas, and yet the true host of the mainland form is reported to be the soricid, *Anourosorex*, (Hopkins & Rothschild 1966), and most of our records are likewise from this host. However, some of the specimens of the Formosan form came from the mole, *Talpa* (or "*Mogera*") and further study may show that *P. remota* regularly infests that host. Even if *P. remota* actually is a flea of *Anourosorex*, the fact that it bears genal spines suggestive of talpid-fleas may paradoxically support our hypothesis, since *Anourosorex* is supposed to be a burrowing-shrew and quite mole-like in habit, hence the popular name "Mole Shrew" (Walker 1964)[16] and, as pointed out by Traub & Barrera (1966) and Traub (1967), the pattern of genal (and pronotal) spines exhibited by various fleas may in reality represent responses to the *environment* of the host rather than to its phylogenetic position. Therefore, it is not surprising that the genal comb of a *Palaeopsylla* infesting burrowing-voles (i.e., *P. setzeri* n. sp.) resembles that of a talpid-flea instead of one like shrew-fleas.

Thus far we have been discussing primarily genal spines and now reference is made to the *pronotal* ctenidium. As indicated by Traub & Barrera (1966) and Smit (1958), in many shrew-fleas, at least some of the spines of the pronotum are fairly broad, concave dorsally and the apices rounded, ovate or blunt (figs. 75, 80, 83, 92). In contrast, as Traub & Barrera (1966) have stated, in fleas which have talpids for hosts, the pronotal spines are narrow, straight and sharply pointed (figs. 74, 76, 90). The genera *Corypsylla* and *Nearctopsylla* have developed pronotal combs characterized by having many narrow spines, and it is interesting to note that the modifications associated with infestation of shrews versus moles are superimposed on that evolutionary foundation. Thus, in *Corypsylla*, the shrew-

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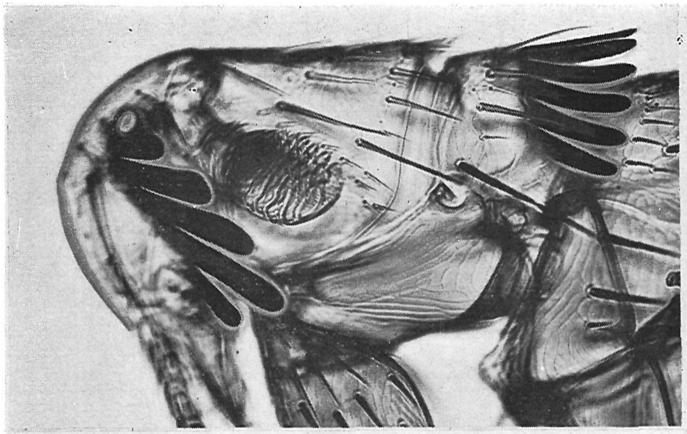
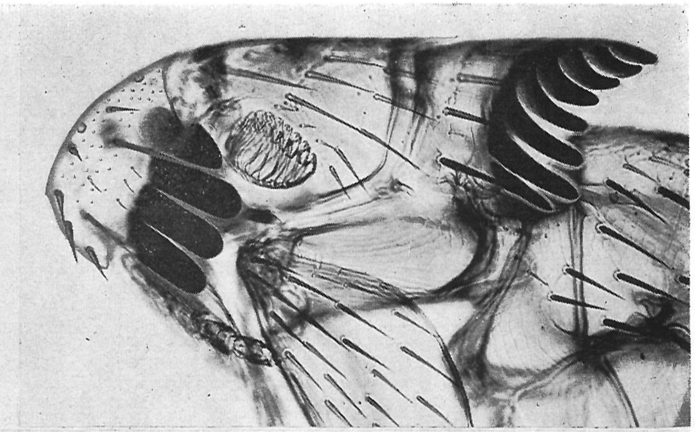
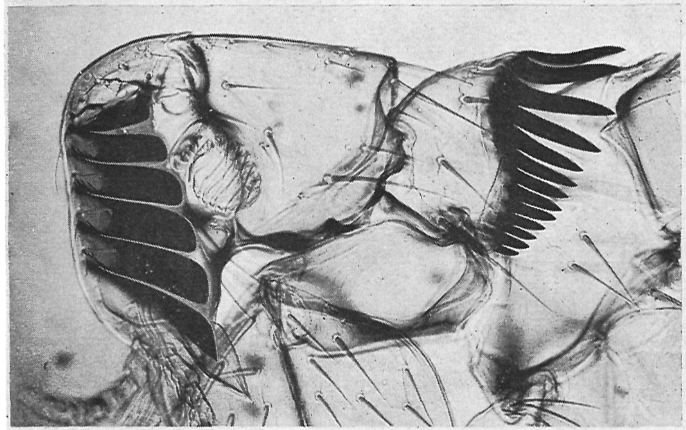
[16] There is much to be learned about the habits of *Anourosorex*. Its body-build suggests a burrowing creature, and the only direct observation in the literature refers to the shrews restricting their activities to underground burrows in Szechwan. Unpublished records of Traub when with the United States of American Typhus Commission in World War II in Assam indicated that this shrew was most readily trapped when the traps were placed in burrows that had been excavated rather than when set on the surface of the ground. Limited observations by Traub suggest the same is true in Taiwan. Dr E. W. Jameson, Jr., who has had much more experience trapping *Anourosorex* in Taiwan, writes (in litt.) that he does not regard this shrew to be any more mole-like than are *Blarina* in the U.S.



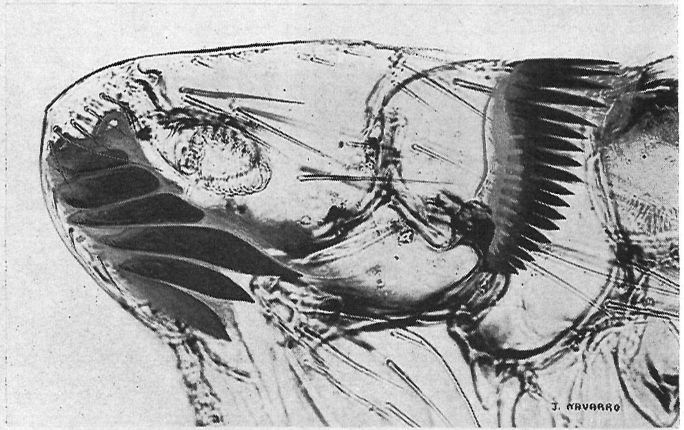
82 (XI-1) HYPSOPHTHALMUS CAMPESTRIS JORDAN & ROTHSCHILD, 1913
EX SORICIDS AFRICA



83 (I-5) XENODAERIA TELIOS JORDAN, 1932
EX CROCIDURA HIMALAYAS



84 (I-8) CORYPSYLLA KOHLSI HUBBARD, 1940
EX SORICIDS WESTERN NORTH AMERICA



85 (I-8) CORYPSYLLA ORNATA C. FOX, 1908
EX TALPIDS NEARCTIC

Figs. 82–85, Head and pronotal comb: 82, *Hypsophthalmus campestris* J. & R. 1913; 83, *Xenodaeria telios* Jordan 1932; 84, *Corypsylla kohlsi* Hubbard 1940; 85, *Corypsylla ornata* C. Fox 1908.

infesting species (fig. 84) has fewer, shorter, more concave, and blunter spines in the pronotal comb than the mole-flea (fig. 85). The same tendency is seen in *Nearctopsylla genalis* (Baker 1904) (fig. 86), but to a lesser degree, perhaps because this species is found both on shrews and moles, unlike *N. traubi* Hubbard 1949, which is a mole-flea (fig. 87). It is noteworthy that the only *Ctenophthalmus* truly restricted to talpids also possesses a pronotal comb of narrow, sharply pointed spines (fig. 90), which is in contrast to the types seen in vole-fleas (fig. 91) and shrew-fleas (fig. 92) of that genus.

The new taxa of fleas described in the present article have pronotal combs that support this hypothesis concerning differences in the shape of the spines of shrew-fleas. Thus, the spines of the pronotal ctenidium of shrew-infesting *D. wissemani* n. sp. (fig. 44), *C. barrerai* n. sp. (fig. 57) and *X. telios* (figs. 62 & 83), *P. apsidata* n. sp. (fig. 13) and *P. recava* n. sp. (figs. 1 & 77) all fit this description, at least insofar as concerns dorsal spines, and even though the pronotal comb of some of these are arched over the mesonotum. (In Section 12 are presented additional arguments for believing the fleas with flared combs are shrew-fleas.)

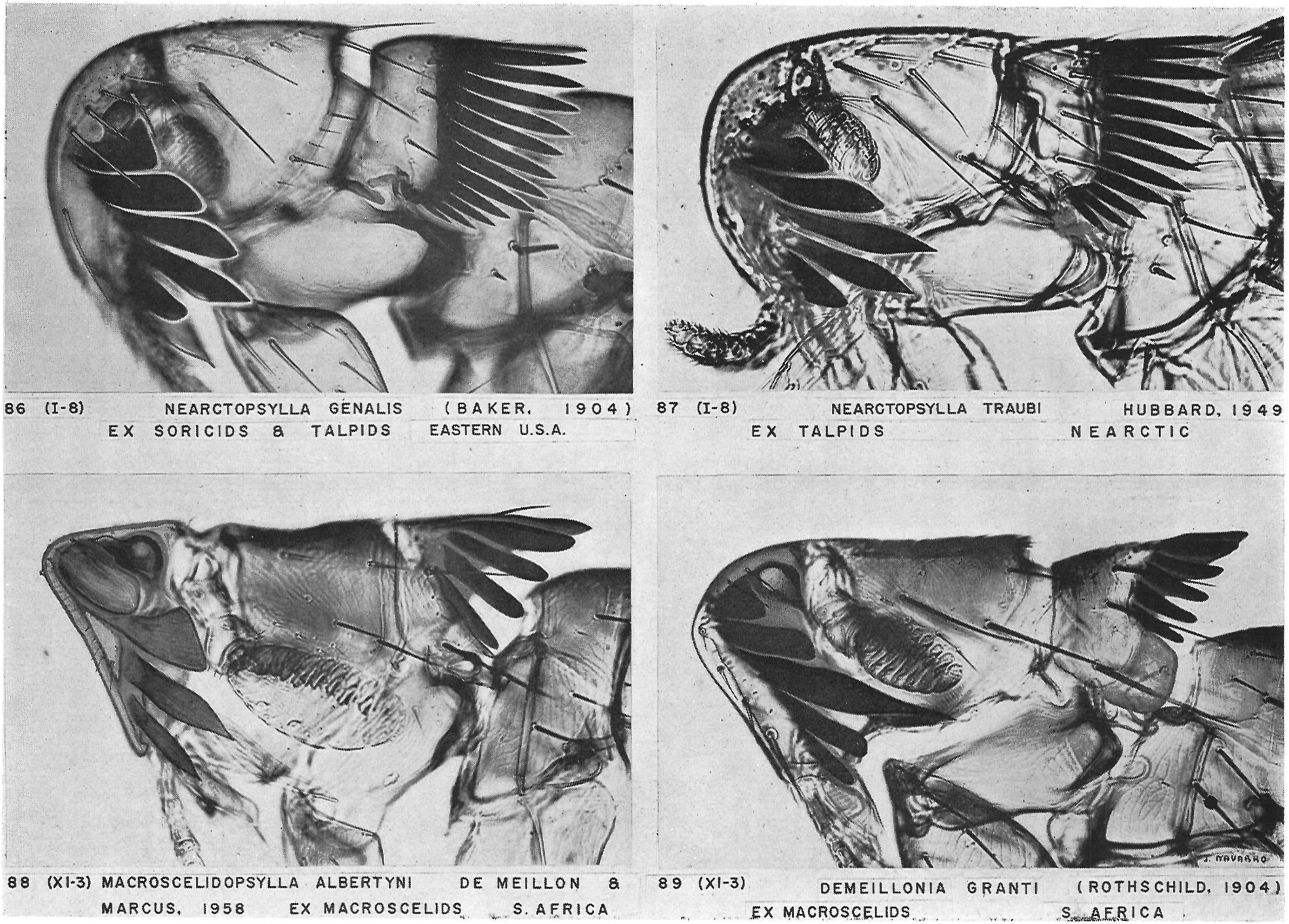
Once again, *P. r. nesicola* n. ssp. (figs. 33 & 79) appears anomalous, since the pronotal comb of this flea suggests a mole-flea (figs. 74 & 76) rather than a shrew-flea (fig. 75) and here too we feel that the explanation lies in the mole-like habits of the host (or else that it also infests talpids, as mentioned above). Similarly, the pronotal comb of *P. setzeri* n. sp. (figs. 19 & 78) resembles that of a mole-flea, thus supporting our contention that the burrowing-vole, *Hyperacrius*, and not a shrew, is the true host of this flea, even though all other known species of *Palaeopsylla* infest insectivores, not rodents.

The shape of the genal and pronotal spines thus support the conclusions suggested by the host-data and distributional records cited in earlier sections for the various taxa discussed.

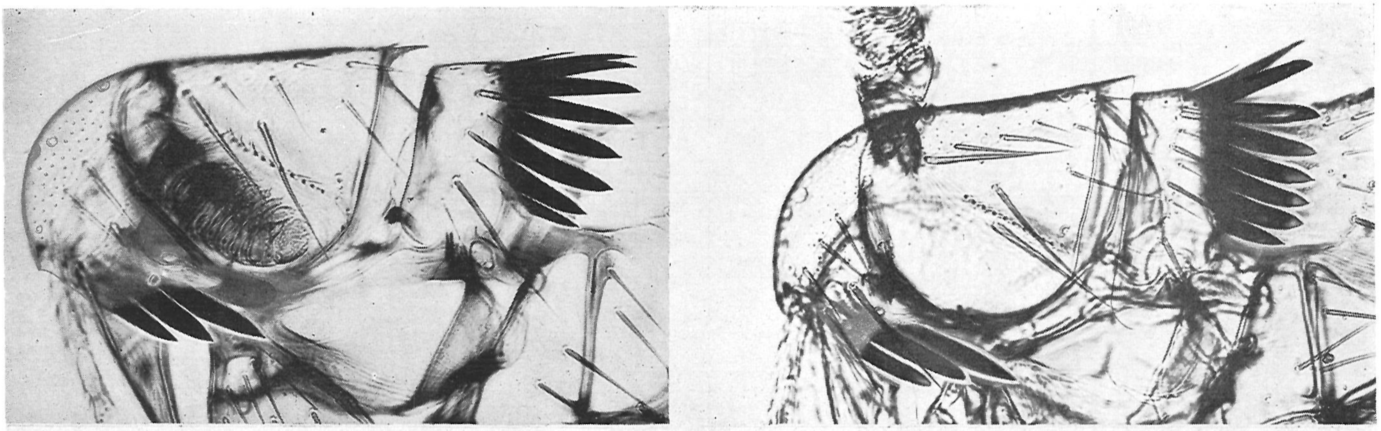
12. **Notes on the Arched Pronotal Comb**

In the great majority of ctenidium-bearing fleas, the axis of the pronotal comb is vertical, as in *P. setzeri* n. sp. (fig. 19) and *Ctenophthalmus pseudagyrtes* Baker 1904 (fig. 91). However, occasionally the comb is remarkable in that the axis is greatly curved, and as a result, the dorsal margin is usually longer than the ventral, and the ctenidium is flared or arched over the mesonotum (figs. 1, 13, 83, 93) in a peculiar manner, and the dorsal spines (at least) are spatulate. Because of the three species with such modifications, described in this paper, a total of ten species with arched combs is now known, representing nine genera, six subfamilies and four families, as shown in Table 5. It is noteworthy that in genera with a large number of species, only one or two species may be so modified (i.e., 1 of 111 *Ctenophthalmus*; 2 of 24 *Palaeopsylla*), and that in other respects the species closely resemble other members of the taxa. This suggests that the modification is of an " adaptive " nature. It also seems significant that this phenomenon has occurred in widely separated areas and habitats, viz. desert (*Meringis* Jordan 1937 in New Mexico and *Macroscelidopsylla* De Meillon & Marcus 1958 in South Africa), the rainy mountains of Malaya (*P. apsidata* n. sp.), and the forests of Central Africa (*Ctenophthalmus particularis*).

It has thus far not been possible to associate this type of flared comb with any environmental or host-factors (Hopkins 1957; Traub & Barrera 1966). However, further consideration and some new data lead us to discuss this feature in some detail. Since the pronotal comb in the monotypic genus *Barreropsylla* Jordan 1953 (fig. 98) is of such a bizarre type

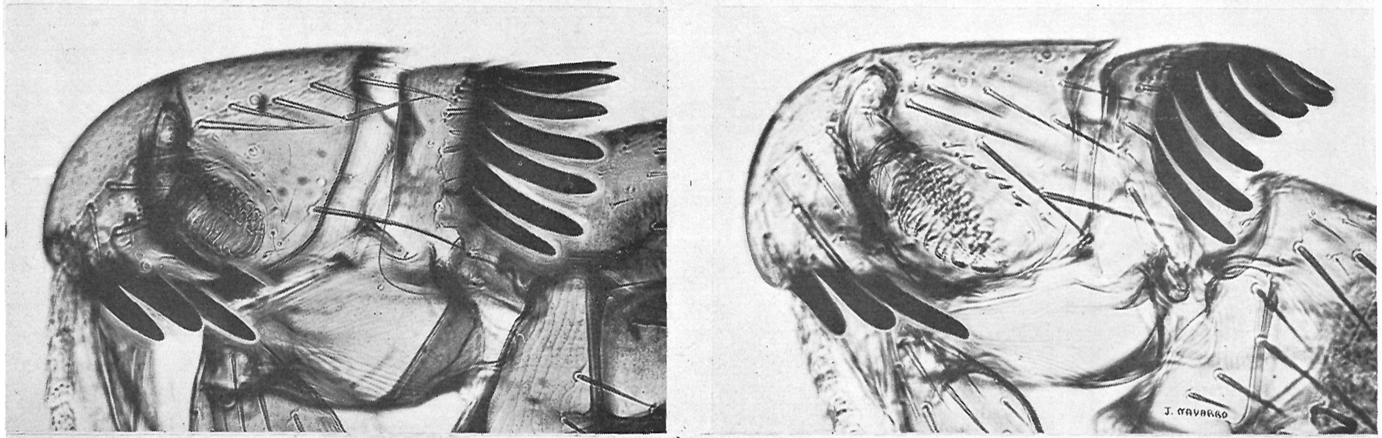


Figs. 86–89, Head and pronotal comb: 86, *Nearctopsylla genalis* (Baker 1904); 87, *Nearctopsylla traubi* Hubbard 1949; 88, *Macroscelidopsylla albertyni* De Meillon & Marcus 1958; 89, *Demeillonia granti* (Rothschild 1904).



90 (I-3) CTENOPHTHALMUS (CT.) BISOCTODENTATUS
KOLENATI, 1863 EX TALPIDS PALAEARCTIC

91 (I-3) CTENOPHTHALMUS (NEARCTOCTENOPHTHALMUS)
P. PSEUDAGYRTES BAKER, 1904 EX VOLES NEARCTIC



92 (I-3) CTENOPHTHALMUS (ALLOCTENUS) CRYPTOTIS
TRAUB & BARRERA, 1966 EX CRYPTOTIS MEXICO

93 (I-3) CTENOPHTHALMUS (IDIOCTENOPHTHALMUS)
PARTICULARIS BERTEAUX, 1949 EX CROCIDURA C. AFRICA

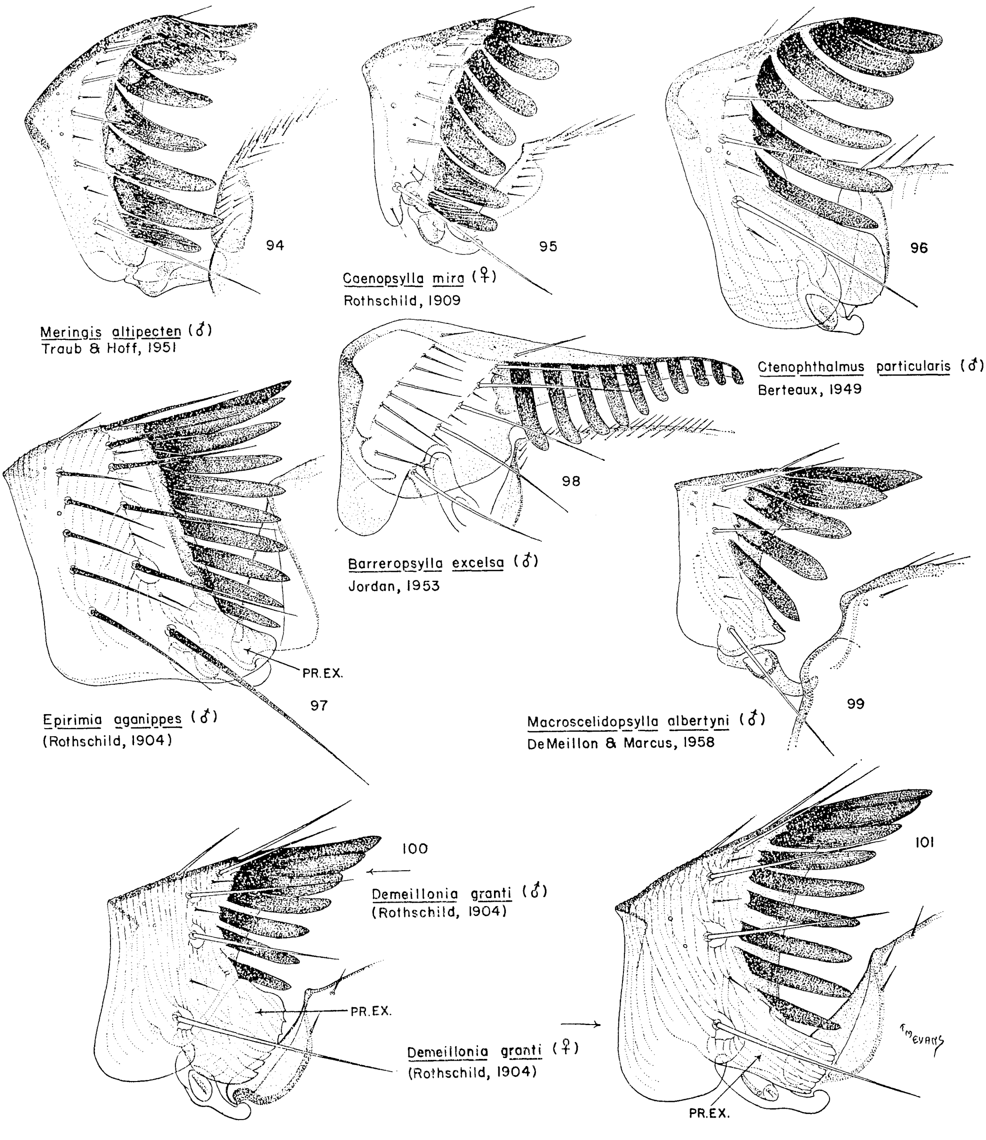
Figs. 90–93, Head and pronotal comb: 90, *Ctenophthalmus* (*C.*) *bisoctodentatus* Kolenati 1863; 91, *C.* (*Nearctoct.*) *p. pseudagyrtes* Baker 1904; 92, *C.* (*Alloctenus*) *cryptotis* Traub & Barrera 1966; 93, *C.* (*Idioct.*) *particularis* Berteaux 1949.

Table 5. Genera of fleas in which the pronotal comb is flared or arched over the pronotum.

Name	Fig. ref.	Family & subfamily	Code	No. of unmod. species in gen.	Locality	Usual Host
1. *Barreropsylla excelsa* Jordan 1953	98	Stephanocircidae Craneopsyllinae	VII–2	Monotypic	Argentina	*Akodon* (?)
2. *Caenopsylla mira* Rothschild 1909	95	Leptopsyllidae Amphipsyllinae	IV–2	2	North Africa	Elephant-Shrews (Macroscelids) and "*Ctenodactylus*"(?)
3. *Demeillonia granti* (Rothschild 1904)	89 100 101	Chimaeropsyllidae Epirimiinae	XI–3	Monotypic	South Africa	"Macroscelids"
4. *Macroscelidopsylla albertyni* DeMeillon & Marcus 1958	88 99	Chimaeropsyllidae Epirimiinae	XI–3	Monotypic	South Africa	"Macroscelids"
5. *Meringis altipecten* Traub & Hoff 1951	94	Hystrichopsyllidae Neopsyllinae	I–7	13	Southwest U.S.A.	Shrews (?) *Dipodomys*
6. *Ctenophthalmus particularis* Berteaux 1949	93 96	Hystrichopsyllidae Ctenophthalminae	I–3	111	Central Africa	Shrews
7. *Palaeopsylla apsidata* n. sp.	13	Hystrichopsyllidae Ctenophthalminae	I–3	24	Malaya	Shrews
8. *Palaeopsylla recava* n. sp.	1 2	Hystrichopsyllidae Ctenophthalminae	I–3	24	Taiwan	Shrews
9. *Corrodopsylla barrerai* n. sp.	57	Hystrichopsyllidae Doratopsyllinae	I–5	3	Mexico	Shrews
10. *Xenodaeria telios* Jordan 1932	62 63 83	Hystrichopsyllidae Doratopsyllinae	I–5	Monotypic	Himalayas	Shrews

that it probably does not share any evolutionary trend with the others cited, and because very little is known about the hosts or habits of that remarkable flea, *Barreropsylla* is not discussed further.

A glance at Table 5 indicates that "shrews" (or "elephant-shrews" or macroscelids)


94 Meringis altipecten (♂) Traub & Hoff, 1951

95 Caenopsylla mira (♀) Rothschild, 1909

96 Ctenophthalmus particularis (♂) Berteaux, 1949

97 Epirimia aganippes (♂) (Rothschild, 1904)

98 Barreropsylla excelsa (♂) Jordan, 1953

99 Macroscelidopsylla albertyni (♂) DeMeillon & Marcus, 1958

100 Demeillonia granti (♂) (Rothschild, 1904)

101 Demeillonia granti (♀) (Rothschild, 1904)

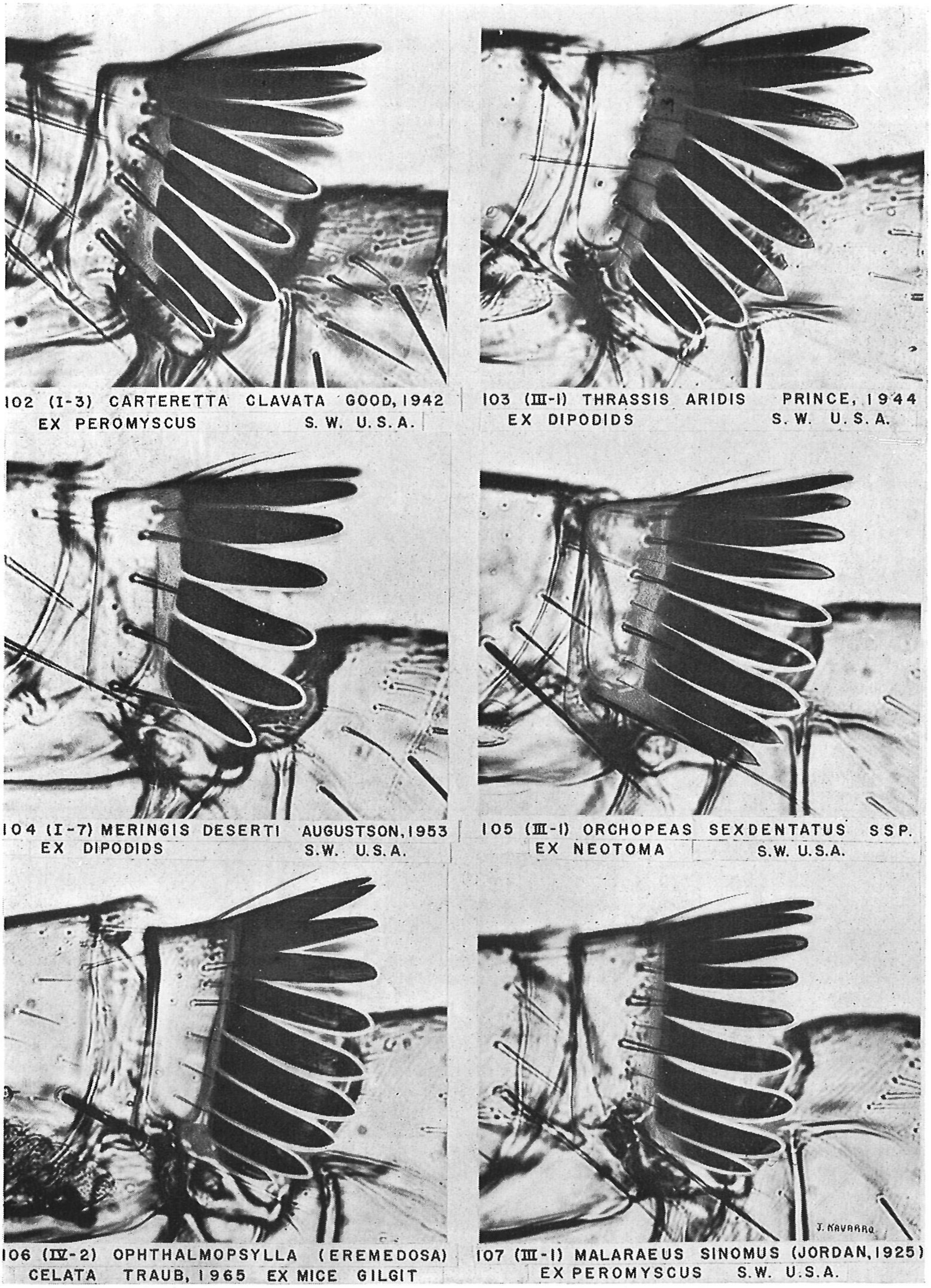
Figs. 94–101, Pronotal comb: 94, ♂ *Meringis altipecten* Traub & Hoff 1951; 95, ♀ *Caenopsylla mira* Rothschild 1909; 96, ♂ *C.* (*Idioct.*) *particularis* Berteaux 1949; 97, ♂ *Epirimia aganippes* (Rothschild 1904); 98, ♂ *Barreropsylla excelsa* Jordan 1953; 99, ♂ *Macroscelidopsylla albertyni* De Meillon & Marcus 1958; 100, ♂ *Demeillonia granti* (Rothschild 1904); 101, ♀ *Demeillonia granti* (Rothschild 1904).

are invariably among the usual hosts, suggesting the hypothesis that the fleas with arched pronotal combs may in reality be shrew-fleas. An alternate theory, which may be applicable for desert-fleas, is that they represent a peak in a special evolutionary trend in fleas found in a xeric environment. These hypotheses are discussed herewith ; that dealing with shrew-fleas is presented first.

It has already been pointed out in this article (Section 11) and stressed elsewhere (Traub & Barrera 1966 ; Smit 1958), that the pronotal spines of the shrew-fleas are generally dorsally concave and frequently relatively very broad, and (at leat in dorsal spines) apically blunt, rounded or ovate (figs. 80, 81, 92). This is precisely the condition found in all nine of the relevant species with arched combs listed in Table 5, and as illustrated in figs. 77, 83, 88, 89, 93–97, 99–101. Apparently unreported heretofore, is another suggestive modification in the pronotal comb, in which there is a pronounced curve in the axis of the ctenidium, as seen in certain *Palaeopsylla* which infest shrews, but not in any *Palaeopsylla* parasitizing moles. Thus, in *P. incurva* Jordan 1932, *P. laxata* Jordan 1933, and *P. miyama* Sakaguti & Jameson 1959, the bases of the spines of the pronotal comb form a markedly convex arc and the comb is somewhat curved over the mesonotum. In other words, the configuration approaches that of a truly flared comb. In these fleas too, the spines themselves are pronouncedly modified in the manner noted above as being characteristic of shrew-fleas. In these cases, it would appear likely, then, that the arched comb is an extension of this phenomenon of curving over the next tergum, the arc reaching a length whereby the dorsal spines actually are directed ventrad.

If macroscelids were considered shrews, then the only possible exception in the table regarding infestation of shrews would be *Meringis altipecten* Traub & Hoff 1951 (I–7). It must be stated, however, that while most mammalogists regard macroscelids as members of Insectivora, some consider the group more closely related to tupaiids (tree-shrews) than to shrews and moles. They are shrew-like in diet and somewhat so in behavior (although perhaps more diurnal than crepuscular). It is interesting and pertinent that the genal and pronotal combs of South African fleas associated with macroscelids have converged to a remarkable degree so as to resemble those of palaearctic and nearctic insectivore-fleas belonging to a different family. For example, the genal comb of *Hypsophthalmus* Jordan & Rothschild 1913 (XI–1) (fig. 82), *Demeillonia* Hopkins & Rothschild 1956 (XI–3) (fig. 89), and *Chimaeropsylla* Rothschild 1911 (XI–1), all members of the family Chimaeropsyllidae, are so similar to those of the hystrichopsyllid genera *Palaeopsylla* (I–3)(figs. 75–76), *Nearctopsylla* (I–8) (figs. 86–87) and *Corypsylla* (I–8) (figs. 84–85), that Ewing in 1929, relying on head characters alone, actually placed all five of these genera which had been described by that date, in a single family. Wagner was equally misled by these "adaptive" resemblances and hence proposed a similar scheme of classification (1939). Further, both the genal and pronotal spines in the above African genera, and also in *Macroscelidopsylla* (figs. 88 & 99), likewise associated with elephant-shrews, are definitely more like those of shrew-fleas (figs. 84 & 86) than mole-fleas (figs. 85 & 87) or than murid-fleas such as their compatriot and relative, *Epiremia* De Meillon 1940 (XI–3)(fig. 97). Such marked examples of convergence suggest that there must be some factor common to these diverse fleas ; the environment, physiology or physiognomy (vestiture) of the hosts, if not their phylogeny, are all possibilities.

It is important to discuss the hosts of *Macroscelidopsylla*, *Demeillonia* and *Caenopsylla*



Figs. 102–107, Pronotal comb: 102, ♂ *Carteretta clavata* Good 1942; 103, ♂ *Thrassis aridis* Prince 1944; 104, ♂ *Meringis deserti* Augustson 1953; 105, ♂ *Orchopeas sexdentatus* ssp.; 106, ♂ *Ophthalmopsylla (Eremedosa) celata* Traub 1965; 107, ♂ *Malaraeus sinomus* (Jordan 1925).

mira Rothschild 1909, a leptopsyllid (IV-2), before proceeding further with the thesis. All three are relatively rare in collections, and the first-named was, until recently, known only from the original material from *Macroscelides.* It has been collected three or four more times, always from an elephant-shrew. *Demeillonia* has been taken more often-De Meillon, Davis & Hardy (1961) record 20 collections, of which 16 were from elephant-shrews, one from *Crocidura* and the remainder from other hosts. These authors state: "... *D. granti* is clearly a flea of elephant-shrews..." Our few additional reports are also from *Macroscelides. C. mira* was described from a few specimens taken on the gundi *Ctenodactylus,* in the coastal region of North Africa, and apparently there has been no mention of subsequent collections. We have a few unpublished records, also from *Ctenodactylus,* but since only two specimens were collected from a minimum of 30 gundis examined under optimal circumstances, it seems to us unlikely that *Ctenodactylus* is the preferred host. Elephant-shrews, as well as true shrews of the genus *Crocidura,* are found in the same rock-piles as gundis, but they are seldom trapped and examined for fleas. It seems likely that the macroscelid *Elephantulus* (or else *Crocidura*) will turn out to be the correct host for *C. mira,* as is suggested, not only by its type of pronotal comb (fig. 95), but by the fact that the closely related *C. assimulata* (Weiss 1913) is a flea of *Elephantulus* and has a pronotal comb somewhat modified along the lines of *C. mira,* but not as arched.

It is worth considering the possibility that true shrews could be the actual host of all the fleas with flared pronotal combs. Admittedly, at first thought this would appear unlikely, since the ranges of these fleas include desert and semidesert areas in the southwestern U.S., North Africa and South Africa—habitats where most people would assume shrews could not survive. Actually, however, soricids do occur in all the areas where these fleas have been collected, but they have been inadequately trapped or examined for fleas. The case of *Meringis altipecten* (I-7) is pertinent in this regard. *M. altipecten* is a fairly common flea on *Dipodomys* in sandy habitats scattered throughout the southwestern U.S. and northern and central Mexico. The xerophilous shrew, *Notiosorex,* is found in the same area, but we know of no records of fleas from this shrew in those localities. Moreover, Professor Barrera informs us (in litt.) that he has just collected *M. altipecten* from both a shrew and *Dipodomys* at the base of Mt. Popocatépetl in Mexico at 2500 m elevation.

It has been mentioned above that *Crocidura* co-exists with *Elephantulus* and gundis in North Africa; representatives of this genus also occur in Iran and Central Asia where other species of *Caenopsylla* are present. The piebald shrew, *Diplomesodon,* occurs in semidesert stretches of Turkestan and Kazakhstan. Until adequate numbers of shrews from relatively xeric areas are examined for fleas, we will not know whether the above hypothesis is correct insofar as concerns the chimaeropsyllid fleas and *M. altipecten.* The association between the flared comb and being a parasite of shrews or shrew-like animals seems quite definite in the other instances.

Another possible explanation for this type of comb occurring in desert-fleas is that the phenomenon is the height of an evolutionary line characteristic of the majority of truly xeric species of sandy terrain. In fleas of such desert-hosts, the pronotal spines are typically closely set at the base and are long and narrow, and in properly mounted specimens, flare outward well above the mesonotum (Traub & McGoodwin, in prep.) (figs. 102-107). Examples include *Thrassis aridis* Prince 1944 (III-1) (fig. 103), *Carteretta clavata* Good 1942 (I-3) (fig. 102), *Ophthalmopsylla* (*Eremedosa*) *celata* Traub 1965 (IV-2) (fig. 106) and many others not illustrated. Further, in genera like *Monopsyllus* Kolenati 1857 (III-1) and *Orchopeas* Jordan 1933 (III-1) where the majority of species live in a mesic environment, this type of comb is found only in the species, or even subspecies, living in the xeric habitat, i.e., *M. exilis* (Jordan 1937) and *O. sexdentatus* (Baker 1904).

As mentioned in Section 8, we believe that the pronotal comb is derived from the flange of the ancestral tergum. Hence it may be that in certain fleas there may be limited movability in the flange whereby it and the comb it bears can be moved somewhat close to the body or " opened " slightly. The fact that fleas of desert animals have a flaring pronotal comb thus may be functional (physiological) as well as morphological and evolutionary and adaptive as a heat-control measure. If this were so, there would be an analogy with the behavior of ants and other insects active in the hot desert sands, i.e., running with the abdomen raised well off the ground. A movable flange would also explain why in some mounted specimens of desert-fleas—i.e., those where the cover glass is pressing tightly on the flea, the comb is flat, adpressed to the mesonotum, whereas in the majority the spines are inclined over or away from the body.

In summation it may be said that the flared pronotal comb seen in nine genera of fairly diverse fleas apparently is another example of convergence in Siphonaptera, occurring in shrew-fleas and perhaps in macroscelid-fleas. As in the examples of parallel modification in the shape of pronotal and genal spines cited here and elsewhere, the environment or habits or vestiture of the host, and not just its phylogenetic assignment (nor that of the flea), at times seems to be a critical factor in the association noted. While the similarities observed here and for genal spines may be adaptive, as one would theoretically expect, further study is required regardingtheir possible function.

The combs of fleas obviously aid in preventing dislodgement from and by the host (N. C. Rothschild 1917, Traub & Barrera 1966), and it may be that the noted variation in the shape of the spines is adaptive to the type of hair or feather constituting the environment of the flea on the infested animal. It is also possible that mammals with similar habits, or living in the same type of microhabitat, may also have converged to the degree of having analagous hair-structures or fur-patterns, and that this is why the fleas of mole-like animals have narrow sharp spines in the combs, for example. It therefore would be instructive to critically compare the fur of sundry moles, shrews, macroscelids and rodents to see if the features of the pelage could be correlated with the pattern of the genal and pronotal spines of the particular fleas infesting these hosts. However, it would also be necessary to study the hairs of different parts of the body of each animal, for they may vary conasiderbly, ranging from fine to coarse, or even spinose or stiff (as vibrissae), and to determine whether the various fleas regularly infest one area of the host more than another. Some fleas are associated with fairly specific sites of attachment or infestation on the host, but we lack data on this point insofar as most species are concerned. Even the time-factor may be important. Thus, Miriam Rothschild (1965) has shown that the European rabbit-flea, after passing an initial period of about 3 weeks among the vibrissae on the host's muzzle, remains attached to the ears of the rabbit for long periods of time, but when the young are born, the fleas leave the mother and transfer to the nestlings, and generally feed in the sacral region (in a different environment regarding pelage). The fleas then suddenly return to the doe-rabbit after a few weeks on the babies, once again attaching to the ears. Another factor complicating attempted correlation of ctenidial spines and pelage is that of the position of the flea when feeding. Certain comb-bearing fleas have greatly flattened heads, and this feature seems to be adaptive, especially in species with anchoring-type mouthparts. It seems likely that in such instances the ctenidia may also have become modified.

Important as the nature of the hairs or feathers of a host may be in the evolution of specialized ctenidial spines, there may very well be other contributory elements. The convergence in the pronotal combs of desert-fleas has been briefly indicated above, and it may prove difficult to correlate this with pelage, but there are other striking instances of parallel development in the pronotal combs of fleas which are associated with the *environment* of the host. This will be discussed in another article (Traub & McGoodwin, in prep.). Suffice it for present purposes to cite an example concerning fleas which are deemed to be characteristic inhabitants of rodent-nests, in contrast to fleas which regularly infest the fur of the hosts. Some nest-fleas are characterized by hyperdevelopment of mouthparts, marked loss of spines and bristles, reduction in jumping-ability, etc. Others have not become so specialized; such ctenidium bearing "nest-fleas" occur in a wide variety of unrelated genera, representing 4 families. All of these agree in possessing pronotal combs in which the number of spines has been reduced, but the spines themselves are exceptionally broad, and hence the size of the comb is the same as in related "fur-fleas." In contrast, the fleas normally found on the bodies of these highly varied rodents inhabiting such underground nests, however, have other kinds of pronotal combs.

13. List of Species Cited and Systematic Position of Genera Discussed in this Article

Name of Taxon	Code[17]	Family	Subfamily
Acedestia Jordan 1937	I-5	Hystrichopsyllidae	Doratopsyllinae
Amphipsylla montana Argyropulo 1946	IV-2	Leptopsyllidae	Amphipsyllinae
Barreropsylla excelsa Jordan 1953	VII-2	Stephanocircidae	Craneopsyllinae
Caenopsylla assimulata (Weiss 1913)	IV-2	Leptopsyllidae	Amphipsyllinae
Caenopsylla mira Rothschild 1909	IV-2	Leptopsyllidae	Amphipsyllinae
Callopsylla (C.) fragilis (Mikulin 1953)	III-1	Ceratophyllidae	Ceratophyllinae
Carteretta clavata Good 1942	I-3	Hystrichopsyllidae	Ctenophthalminae
Chimaeropsylla Rothschild 1911	XI-1	Chimaeropsyllidae	Chimaeropsyllinae
Corrodopsylla barrerai n. sp.	I-5	Hystrichopsyllidae	Doratopsyllinae
Corrodopsylla curvata (Rothschild 1915)	I-5	Hystrichopsyllidae	Doratopsyllinae
Corrodopsylla hamiltoni (Traub 1944)	I-5	Hystrichopsyllidae	Doratopsyllinae
Corypsylla kohlsi Hubbard 1940	I-8	Hystrichopsyllidae	Rhadinopsyllinae
Corypsylla ornata C. Fox 1908	I-8	Hystrichopsyllidae	Rhadinopsyllinae
Ctenophthalmus (Alloctenus) cryptotis Traub & Barrera 1966	I-3	Hystrichopsyllidae	Ctenophthalminae
Ctenophthalmus (C.) bisoctodentatus Kolenati 1863	I-3	Hystrichopsyllidae	Ctenophthalminae
Ctenophthalmus (Ethioct.) calceatus Waterston 1912	I-3	Hystrichopsyllidae	Ctenophthalminae
Ctenophthalmus (Medioct.) golovi Ioff & Tiflov 1930	I-3	Hystrichopsyllidae	Ctenophthalminae
Ctenophthalmus (Idioct.) particularis Berteaux 1949	I-3	Hystrichopsyllidae	Ctenophthalminae

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[17] Roman numerals refer to family and Arabic numerals to subfamily, in the classification we are following, which is essentially the one used by Hopkins & Rothschild, 1956.

Name of Taxon	Code	Family	Subfamily
Ctenophthalmus (*Nearctoct.*) *p. pseudagyrtes* Baker 1904	I-3	Hystrichopsyllidae	Ctenophthalminae
Dactylopsylla Jordan 1929	III-2	Ceratophyllidae	Foxellinae
Demeillonia granti (Rothschild 1904)	XI-3	Chimaeropsyllidae	Epirimiinae
Doratopsylla blarinae C. Fox 1914	I-5	Hystrichopsyllidae	Doratopsyllinae
Doratopsylla coreana Darskaya 1949	I-5	Hystrichopsyllidae	Doratopsyllinae
Doratopsylla wissemani n. sp.	I-5	Hystrichopsyllidae	Doratopsyllinae
Epiremia aganippes (Rothschild 1904)	XI-3	Chimaeropsyllidae	Epirimiinae
Epitedia cavernicola Traub 1957	I-7	Hystrichopsyllidae	Neopsyllinae
Foxella Wagner 1929	III-2	Ceratophyllidae	Foxellinae
Frontopsylla (*Profrontia*) *ambigua* Fedina 1946	IV-2	Leptopsyllidae	Amphipsyllinae
Glaciopsyllus Smit & Dunnet 1962	III-1	Ceratophyllidae	Ceratophyllinae
Hypsophthalmus campestris Jordan & Roths. 1913	XI-1	Chimaeropsyllidae	Chimaeropsyllinae
Idilla Smit 1957	I-5	Hystrichopsyllidae	Doratopsyllinae
Jellisonia klotsi Traub 1944	III-1	Ceratophyllidae	Ceratophyllinae
Leptopsylla (*Pectinoctenus*) *pamirensis* (Ioff 1946)	IV-1	Leptopsyllidae	Leptopsyllinae
Leptopsylla (*Pectinoctenus*) n. sp.	IV-1	Leptopsyllidae	Leptopsyllinae
Macroscelidopsylla albertyni De Meillon & Marcus 1958	XI-3	Chimaeropsyllidae	Epirimiinae
Macrostylophora fimbriata (Jordan & Roths. 1921)	III-1	Ceratophyllidae	Ceratophyllinae
Malaereus sinomus (Jordan 1925)	III-1	Ceratophyllidae	Ceratophyllinae
Megarthroglossus Jordan & Rothschild 1915	I-2	Hystrichopsyllidae	Anomiopsyllinae
Meringis altipecten Traub & Hoff 1951	I-7	Hystrichopsyllidae	Neopsyllinae
Meringis deserti Augustson 1953	I-7	Hystrichopsyllidae	Neopsyllinae
Mioctenopsylla Rothschild 1922	III-1	Ceratophyllidae	Ceratophyllinae
Monopsyllus exilis (Jordan 1937)	III-1	Ceratophyllidae	Ceratophyllinae
Nearctopsylla (*Beringiopsylla*) *genalis* (Baker 1904)	I-8	Hystrichopsyllidae	Rhadinopsyllinae
Nearctopsylla (*B.*) *traubi* Hubbard 1949	I-8	Hystrichopsyllidae	Rhadinopsyllinae
Neopsylla Wagner 1903	I-7	Hystrichopsyllidae	Neopsyllinae
Ophthalmopsylla (*Eremedosa*) *celata* Traub 1965	IV-2	Leptopsyllidae	Amphipsyllinae
Orchopeas sexdentatus (Baker 1904)	III-1	Ceratophyllidae	Ceratophyllinae
Palaeopsylla apsidata n. sp.	I-3	Hystrichopsyllidae	Ctenophthalminae
Palaeopsylla incurva Jordan 1932	I-3	Hystrichopsyllidae	Ctenophthalminae
Palaeopsylla kohauti Dampf 1910	I-3	Hystrichopsyllidae	Ctenophthalminae
Palaeopsylla laxata Jordan 1933	I-3	Hystrichopsyllidae	Ctenophthalminae
Palaeopsylla minor (Dale 1878)	I-3	Hystrichopsyllidae	Ctenophthalminae
Palaeopsylla miranda Smit 1960	I-3	Hystrichopsyllidae	Ctenophthalminae
Palaeopsylla miyama Sakaguti & Jameson 1959	I-3	Hystrichopsyllidae	Ctenophthalminae
Palaeopsylla nippon Jameson & Kumada 1953	I-3	Hystrichopsyllidae	Ctenophthalminae
Palaeopsylla recava n. sp.	I-3	Hystrichopsyllidae	Ctenophthalminae
Palaeopsylla r. remota Jordan 1929	I-3	Hystrichopsyllidae	Ctenophthalminae
Palaeopsylla r. nesicola n. ssp.	I-3	Hystrichopsyllidae	Ctenophthalminae
Palaeopsylla setzeri n. sp.	I-3	Hystrichopsyllidae	Ctenophthalminae
Palaeopsylla similis Dampf 1910	I-3	Hystrichopsyllidae	Ctenophthalminae
Palaeopsylla sinica Ioff 1953	I-3	Hystrichopsyllidae	Ctenophthalminae
Palaeopsylla soricis (Dale 1878)	I-3	Hystrichopsyllidae	Ctenophthalminae

Name of Taxon	Code	Family	Subfamily
Palaeopsylla vartenovi Ioff 1950	I-3	Hystrichopsyllidae	Ctenophthalminae
Pleochaetis soberoni Barrera 1958	III-1	Ceratophyllidae	Ceratophyllinae
Rhadinopsylla n. sp.	I-8	Hystrichopsyllidae	Rhadinopsyllinae
Rothschildiana Smit 1952	I-7	Hystrichopsyllidae	Neopsyllinae
Stenischia n. sp.	I-8	Hystrichopsyllidae	Rhadinopsyllinae
Stivalius (Gryphopsylla) hopkinsi Traub 1957	II-1	Pygiopsyllidae	Pygiopsyllinae
Stivalius (S.) pomerantzi Traub 1950	II-I	Pygiopsyllidae	Pygiopsyllinae
Strepsylla Traub 1950	I-7	Hystrichopsyllidae	Neopsyllinae
Thrassis aridis Prince 1944	III-1	Ceratophyllidae	Ceratophyllinae
Xenodaeria telios Jordan 1932	I-5	Hystrichopsyllidae	Doratopsyllinae
Xenopsylla cheopis (Rothschild 1903)	IX-1	Pulicidae	Pulicinae
New Genus #3, n. sp. #1, n. ssp. 'A'	III-1	Ceratophyllidae	Ceratophyllinae

14. List of Hosts of Fleas Mentioned

Akodon Meyen 1833
Alticola Blanford 1881
Alticola roylei Gray 1842
Anourosorex Milne-Edwards 1872
Apodemus Kamp 1829
Apodemus flavicollis Melchior 1834
Crocidura Wagler 1832
Cryptotis Pomel 1848
Ctenodactylus Gray 1830
Diplomesodon Brandt 1852
Dipodomys Gray 1841
Elephantulus Thomas & Schwann 1906
Hylopetes Thomas 1908
Hyperacrius Miller 1896
Hyperacrius fertilis True 1894
Hyperacrius wynnei Blanford 1881
Hyperacrius sp. #3
Macroscelides A. Smith 1829
Mogera insularis Swinhoe 1862
Notiosorex Coues 1877
Petaurista Link 1795
Rattus rattoides Hodgson 1845
Sorex Linnaeus 1758
Soriculus caudatus fumidus Thomas 1913
Suncus Ehrenberg 1833

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17. **List of Abbreviations**

A.A.R.	Third aedeagal rod (accessory apodemal rod).
A.B.	Antepygidial bristles.
A.G.	Apical group of dorsomarginal bristles on tibia.
A.M.S.	Apicomedian sclerite of aedeagus.
A.S.	Anal stylet.
A.VG.	Accessory gland of vagina.
AC.	Acetabulum.
AC.B.	Acetabular bristles.
AE.A.	Aedeagal apodeme.
AP.S.	Apodemal strut of aedeagus.
AP.SP.	Apical spinelets.
B.	Bulga (head) of spermatheca.
B.M.PT.	Bay of middle plate of aedeagal apodeme.
B.P.W.	Base of wall of aedeagal pouch.
C.FR.	Caudal fringe -characteristic group of small bristles along a subventral sinus or convexity of caudal margin of ♀ tergum 8.
C.S.	Crescent sclerite of aedeagus.
CPS.	Capsula.
CR.	Crochet of aedeagus.
D.A.L.	Dorsal anal lobe of proctiger.
D.A.9	Distal arm of ♂ sternum 9.
D.AR.	Dorsal armature of sclerotized inner tube.
D.I.CL.	Dorsal internal incrassation of clasper.
D.I.R.	Dorsal intramural rod of aedeagus.
D.L.	Distodorsal lobe of aedeagus.
DM.1-5	Pairs of dorsomarginal bristles arising from sclerotized bases of metatibia.
F.	Movable finger or process of clasper.
FO.	Fovea.
G.C.	Genal ctenidium.
H.	Hilla (tail) of spermatheca.
HD.	Unmodified mantle-like folds arising from dorso-apical region of aedeagus and hanging over sides of end-chamber.
K.	Keel of aedeagal pouch.
L.D.	Leuco disc.
L.L.	Lateral lobe of aedeagus.
L.M.	Lateral metanotal area of metathorax.
L.PT.	Lateral plates of aedeagal apodeme.
L.S.	Lateroventral sclerite of apodemal strut of aedeagus.
LO.S.	Lobate sector of apicomedian sclerite.
M.D.L.	Median dorsal lobe of aedeagus.
M.PT.	Middle plate of aedeagal apodeme.
M.SPC.	Mesothoracic spiracle.
MB.	Manubrium.
MPM.	Mesepimere.
MPS.	Mesepisternum.
MSN.	Mesonotum.
MTM.	Metepimere.
MTN.	Metanotum.
MTS.	Metepisternum.

P.	Immovable process of clasper.
P_1	Anterior process of immovable process of clasper.
P_2	Posterior process of immovable process of clasper.
P.A.9	Proximal arm of ♂ sternum 9.
P.B.C.	Perula-dilated portion of bursa copulatrix.
P.C.	Pronotal ctenidium.
P.R.	Penis rods.
P.W.	Wall of aedeagal apodeme.
PH.2	Second phragma; on mesonotum.
PHY.	Phylax. A crescentic sclerite on each side of inner tube of aedeagus.
PL.A.	Pleural arch of metathorax.
PR.EX.	Caudal extension of pronotum beneath ctenidium.
PR.T.	Preoral tuber.
PS.S.	Pseudosetae.
RO.S.	Rostrate sector- beak-like extension of apicomedian sclerite.
S.	Sail-of middle plate of aedeagal apodeme.
S.B.	Sensory bristles on movable process F.
S.D.B.	Sclerotized duct of bursa copulatrix.
S.I.T.	Sclerotized inner tube of aedeagus.
S.RD.	Internal sclerotized ridge of ♀ tergum 8.
SC.OV.	Sclerotized portion of oviduct.
SN.	Sensilium.
SP.	Spermatheca.
SPR.9	Dorsal spur of base of distal arm of sternum 9.
SQ.	Squamulum.
STR.-P.	Striarium of immovable process of clasper.
T.AP.9	Tergal apodeme of segment 9.
TB.	Frontal tubercle.
V.A.L.	Ventral anal lobe of proctiger.
V.AR.	Ventral armature of sclerotized inner tube.
V.I.R.	Ventral intramural rod of aedeagus.
V.I.CL.	Ventral internal incrassation of clasper.
VC.1	First vinculum.
Y.L.PT.	Yoke of lateral plates.
1 T.	Tergum 1.
1 T.PS.	Pseudoseta on abdominal tergum 1.
7 S.	Sternum 7.
7 SPC.	Spiracle (fossa) of abdominal segment 7.
7 T.	Tergum 7.
8 S.	Sternum 8.
8 SPC.	Spiracle (fossa) of abdominal segment 8.
8 T.	Tergum 8.