ON SOME ADAPTIVE STRUCTURES IN SIPHONAPTERA

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Abstract. The degree of development of the pretarsal unguis of fleas is shown to be correlated with the type of skin cover of the host animal. Similarly, the influence of the dermecos on the development of etenidia, especially the pronotal etenidium, is discussed. The new term "dermecos" is coined for the micro-habitat created by the skin and its outgrowths of a mammal or bird. Pseudosetae of the pronotal or mesonotal collar are stated to be vestiges of etenidial spines, not rudiments. Some examples of the atavistic nature of teratological anomalies in fleas are given. A new subgenus is described for the only mammal-infesting species of Ceratophyllum, a large genus of bird-fleas.

The ancestral insect which eventually gave rise to the monophyletic order of fleas (Siphonaptera) is assumed to have been associated with a mammalian environment rather than the avian one which subsequently became available. Present evidence corroborates this assumption as only 6% of the 2000 known forms of fleas are parasites of birds and clearly derivatives of mammal-fleas (one-sixth of them are actually still congeneric with mammal-infesting species). The phylogeny of this order of insects is obscure and no firmer statement can still be made than that they are apparently a sister-group of one of the orders of the Panorpoid complex.

The habitus of the ancestral insect is a matter of conjecture and dependent on the depth of probing into the ancestry. On the basis of the dominant characters of the extant species the prototype, probably quite a small insect, may be presumed to have had: (a) an intregripit hypognathous and sessile head, (b) mouthparts with maxillae better developed than mandibulae and capable of piercing (in any case, damaging) mammalian skin, (c) short antennae (possibly already in rudiments of fossae), (d) a primitive type of thorax with relatively unmodified segments and undeveloped wings, (e) legs unmodified for jumping, with a five-unit tarsus bearing two pretarsal ungues, (f) simple segmentation of abdomen (except for the male genital segments), (g) a dorso-apical sensory organ on abdomen, (h) no etenidia on any sclerite.

Palaeontological evidence of a prototype is lacking. Two fleas are known from eocene Baltic amber of an estimated age of 50—60 million years and are presumed to be genuine inclusions although both specimens (from two different collections) happen to belong seemingly to the recent genus Palaeopsylla Wagner (vide Peuls 1968). Fossil rock imprints of supposed "ancestral fleas" have been recorded also twice. De Serres (1828) mentioned specimens (presumably now lost) which were "peut-être des Aptrées de l'Ordre des Suceurs" from Aix-en-Provence, France, from the lower Oligocene (which
followed the Eocene period); for no apparent reason Keferstein (1834) referred to those specimens more positively as "Pulcex, zwei Arten" but Handlirsch (1908) is more careful and lists the material as " / Pulcex". Recently Riek (1970) stated that "Two fleas have been collected in association with abundant remains of fish, plants, phyllopod Crustacea and other insects in a Lower Cretaceous [feldspathic] siltstone at Koonwarra, southern Gippsland, Australia." The age of these two fossils would therefore be 110—125 million years, according to present-day estimates. One of the two specimens is "of normal pulicid form and size" and "in many respects it is ancestral to the modern stick-fast fleas (Echidnophaga)." The second insect is larger (7 mm.) and Riek refers to it as a flea mainly because the askew squashed specimen has "a typical flea abdomen and male genitalia. There are a good many other insects whose squashed abdomen would superficially be similar in appearance, while Riek's evaluation of the "male genitalia" [a dark blob] seems to overstretch imagination. In my opinion it is unwarranted to call this fossil imprints a "flea" without any qualifications, instead of referring to it, for instance, as an insect belonging to an ancestral stock from which fleas may perhaps have been derived. The strata where the Australian fossil "fleas" have been found are obviously the site of a former lake, an environment that would not seem to have been an ideal one even for ancestral fleas, except for insects that may have been associated with a monotreme platypus-like host, but stickfast fleas such as an Echidnophagoid form are for obvious reasons not found on aquatic mammals and the recent platypus also has no specific flea. Another difficulty: would a highly advanced flea (the Echidnophagoid insect) occur more or less together with an extremely primitive ancestral "flea"? Riek deduced (a) from the nematoeorous-type of antennae of his primitive ancestral "flea" that fleas evolved from "nematocereous Diptera in the late Triassic or early Jurassic, at about the same time as the first warm-blooded vertebrates"; and (b) from his assumption that the primitive "flea" occurred on a furred animal "that marsupials must have been present in Australia at a very much earlier period than has hitherto been conceded". These deductions are based on unsatisfactory evidence. Interpretation of facts, or the attempt thereon, is useful when the facts are indisputable.

Qualiter taliter, the ancestral insects may well have acquired a flea-like habitus not too long after the emergence of mammals and their evolution very likely kept pace with that of the hosts (though perhaps lagging a step, as pointed out by Wagner (1932)). Assuming that at first the flea-ancestors were nidicolous scavengers, a closer association—in all its gradations—with the body of the nidifying mammal developed later. The closer this association—which is primarily and mainly required by the female flea—the greater the morphological changes in the flea (and, in Pulicids, the greater the reduction in size). At present the main stages of the range are: a) species that are still almost entirely nidicolous in habits (visiting the host only for relatively short feeds), (b) species whose representatives linger in the dermeocos* but also utilize the nest as abode, (c) species that remain in the dermeocos for most of their adult lives (e.g. bat-fleas), (d) semi-sedentary fleas, the females of which remain on the host for most of their life in the cold season of the year, sucking blood fairly constantly (Vermipyllids), (e) sedentary fleas, the females of which attach themselves by the strongly developed mouthparts to the skin of the host till the end of their egg-producing period (stickfast fleas), (f) sedentary fleas, the females of which bury themselves under the skin of the host, remaining imprisoned until death (jiggers).

*) The word "nest" or "nidus" (and the derivations "nidicole" and "nidicolous") is in use for one of the two main flea milieux. There appears to be no similar word for the other milieu, namely the microhabitat created by the host-skin and its outgrowths, and for which I suggest "dermeocos" (and the derivations "dermeicoile" and "dermeicoilous") [from derma (Gr.) = skin; oiko (Gr.) = house; dermoikes, simplified through dermeokes and dermekos to dermeocos].
The adaptations in response to these changes from nidicole to dermecicole are manifest first and foremost in the outer organization of the flea body but sedentary fleas, especially jiggers, are internally also affected.

Of prime importance for any flea is the ability to reach its food supply and to hang on to it. In order to get hold of the host animal, often a moving object, the legs are modified for jumping, especially in dermecicous fleas of larger hosts which do not nidificate properly. In the case of bat-fleas the legs are very long and slender which enables them to crawl up vertical surfaces to reach the host (after emergence from cocoon). For true nidicolous fleas the contacting of the usually small host is more or less a walk-over and such fleas have generally poor saltatorial powers. It does not seem that the simplified structure of thorax and legs of recent nidicolous fleas is still of a rudimentary (albeit modified) nature rather than of a vestigial one. Assuming the evolutionary sequence was, broadly speaking, scavenging nidicole (non-jumper) — dermecicole (jumper) — parasitic nidicole (poor or non-jumper), the extant poor jumpers are — on the basis of the structure of thorax and legs — no direct descendants from the primitive scavenging nidicoles, bypassing the jumping phase. However, certain nidicoles (e.g. Anomiopsyllus Baker, Rhadinopsylla Jordan & Rothschild) quitted the jumping phase much earlier than others (e.g. Libyastus Jordan, certain species of Ceratophyllus Curtis, Ichneumopsyllidae).

For retaining a hold of the host, the flea uses the pretarsal unguis except — for the sedentary fleas which attach themselves to the host by means of mouthparts, although initially they will have employed the partly degenerate unguis prior to anchoring the proboscis. It is to be expected that the gripping ability of the unguis is correlated with the texture and diameter of the hairs of the host (although there is a good deal of variation in those hairs). This is the case, but no comparative studies have yet been made on this subject. Two extreme cases of development of distitarsomere and pretarsus are illustrated here:

(a) In Malacopsylla grossiventris (Weyenbergh), a specific free-living flea of armadillos (Dasypodid Edentates), the legs are among the most powerful in fleas; the unguis (Figs. 1—3) are stout and very strongly ridged, not only the long main part but also the shorter basal “tooth” (for which I propose the name “allex”). Fleas of armadillos are confined to the ventral dermecos, which is liable to be brushed regularly against the substrate and therefore fleas can be expected to require the ability to cling very firmly to the hairs of these hosts. Hairs are gripped between the raised unguis and the strong lateral plantar setae of the distitarsomere. Powerful unguis have a well-developed unguitractor selerite sliding into a very distinct somewhat flattened cylinder inside the distitarsomere. The normal relaxed position of the unguis (which only have a very long and thin tendon, attached to the back of the sclerotic tubercle at the posterior side of the unguitractor, see Figs. 1, 3, of the depressor muscle in the femur; there is no antagonistic musculature) is at about a right angle with the longitudinal axis of the distitarsomere. The fully relaxed position, as shown in Figs. 1, 8, 9, does not appear to be a normal one in the living non-sedentary flea and is—in preparations perhaps due to accidents of mounting; actually, this position stretches the flexor tendon to such an extent that in a number of mounted specimens (e.g. Malacopsylla grossiventris and Brachiopsylla echidnae (Denny)) it has snapped. The fully retracted position of the unguis is shown in Fig. 2. It should be noted that the paired minute fimbriate and squamose setae just below the two minute sensory pores and between the preapical lateral setae and the apico-median plantar setae*) are presumably characteristic of Malacopsylla grossiventris — in other species (I have not examined all on this point) there is a curved microseta in this position (Fig. 8, but often virtually invisible). These minute structures

*) These have always been referred to as preapical plantar setae, but they are actually situated at or near the apical edge of the plantar side of the distitarsomere (see Fig. 1) which is shorter than the opposite (dorsal) side.
are not vestiges of pulvilli as they arise from an alveolus on the distitarsomere and do not belong to the pretarsus.

(b) In *Tunga penetrans* (L.), the well-known skin-burying jigger, as well as in the other species of the *penetrans*-group (which are parasites of Edentates), an opposite extreme in tarsal development is reached (Figs. 4, 5). These female jiggers favour relatively hairless skin for their site and they do not dwell among hair for any length of time. It is not known if or how often the free-living male visits the host for feeding, but he will do so to copulate with embedded females. In those species the distitarsomere is greatly simplified by the reduction of the lateral plantar setae to two pairs of short thin hairs, while the unguenae are curved, slender, entirely smooth and without an allex, and the unguitractor sclerite is hardly discernible. The unguenae cannot be retracted to grip a hair between them and the distitarsomeral planta; it seems that at most they can be pulled up to a position of a right angle with the distitarsomere (Fig. 5) while the angle between the two unguenae is then at least also a right angle. A similar condition, if not even more extreme, is seen in *Neotunga euloides* Smit (on pangolin), *N. inexpectata* (Smit) (on warthog) and *Echidnophaga biopus* Jordan and Rothschild (on echidna). In the *caecata*-group of *Tunga*, parasites of murid rodents, the unguenae are also smooth and slender and without an allex, but the lateral plantar setae are quite well developed (at least three pairs) and the unguenae can be retracted for gripping hairs.

Specimens of *Echidnophaga gallinacea* (Westwood) anchor themselves with their strongly serrated mouthparts to the skin of the host and consequently the unguenae, not being used regularly for gripping hairs, are smooth and lack an allex (as in Fig. 10). Other species of *Echidnophaga* provide an instructive example of the inverse correlation between development of mouthparts and that of the pretarsus: in *E. ambulans* Olliff (Fig. 10) and several other species those structures are similar to those of *E. gallinacea* (i.e. powerful mouthparts and degenerate unguenae), but in *E. aranka* Rothschild and *E. macronychia* Jordan and Rothschild (Fig. 13) the reverse is true (i.e. relatively weakly serrated mouthparts and, especially in the latter, fairly typical unguenae); between these two extremes are bridging species like *E. perlis* Jordan (Fig. 11) and *E. bradyta* Jordan and Rothschild (Fig. 12) in which the development of these structures is more or less intermediate. One might assume, therefore, that *E. aranka* and *E. macronychia* are not markedly stickfast in their behaviour. In *Spilopsyllus* Baker and *Chimacropsylla* Rothschild, which also have strongly serrated mouthparts, the unguenae (including the allex) is still well-ridged which indicates that these fleas remain ambulatory to a certain degree and are not stickfast all their lives. Similarly, in *Pulex echidnophagoides* (Wagner), with more powerful mouthparts than in these two genera, the unguenae are ridged but the allices are much reduced in size.

The majority of fleas have a normal distitarsomere and distinctly ridged unguenae. Exceptionally the two unguenae of a pretarsus are asymmetrical, i.e. of unequal stoutness (of all legs in *Pamallus galeanus* (Jordan), of only the fore leg in *Rhopalopsyllus lutizi* sspp.). This does not seem to have any connection with a certain type of dermecos as in these instances this is shared with fleas of other species (of the same family) which have perfectly normal unguenae. Such ungual asymmetry is also sporadically found in several other orders of insects.

The various types of pretarsal development mentioned above all relate to mammal-fleas. In bird-fleas — which are all derived from mammal-fleas — unguenae obviously do not grip hairs (although they can) and, for whatever structures they hang on to, the unguenae do not require a ridged surface to increase gripping ability. Bird-fleas have either lost those ridges or are in process of losing them. The ridges of the allex are the first to disappear. A careful study of the unguenae of good series of e.g. the various species of *Ceratophylus* specific to the house-martin *Delichon urbica* may give a clue to their
respective chronological history (*C. delichoni* Nordberg, for example, has weaker ungues than *C. hirundinis* (Curtis), *C. rusticus* Wagner and *C. farreni* Rothsechild and is presumably older than those three species). Species of bird-fleas that are still congeneric with mammal-fleas are presumably not as old as those that are generically distinct from their nearest relatives and their ungules usually still show traces of ridges as mere lines, often quite faint, while the mammal-infesting species of their genus have well-ridged ungules. Good examples are e.g. *Stivalius insolli* Traub, *Xenopsylla gratiosa* Jordan and Rothsechild (Fig. 9, cf. Fig. 8), *X. trispinis* Waterston and *X. mouchei* Smit, the only bird-fleas in their respective large genera. A similar contrast is seen in *Callopsylla*; Fig. 6 shows the pretarsus of a mammal-infesting species (*C. caspia* (Toff and Argyropulo)) and Fig. 7 the same structure of a bird-infesting species (*C. waterstoni* (Jordan)). The bird-flea *Xenopsylla gratiosa*, parasitic on various sea birds in the Mediterranean area, is derived from some species of the *conformis*-group (rodent-fleas in the Mediterranean subregion). Actually, the "*gratiosa*-group" of *Xenopsylla* should be demoted to a subgroup of the *conformis*-group. A comparison of Figs. 8 and 9 shows

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clearly the change that takes place in the distitarsonere and pretarsus by a drastic change of host.

The only other way in which the bird-flea *X. gratiosa* differs from a related mammal-flea, e.g. *X. conformis mycerini* (Rothschild), is that the size of the abdominal spiracular fossae is greater in the former. I have pointed out before (Smit 1960) that "there seems to be a correlation between the size of the spiracular fossae and the humidity of the fleas' habitat—the size becoming greater with an increase in relative humidity." Thus the species of the *conformis*-group, associated with rodents that live in deserts, have extremely small spiracular fossae, being of equal size as the alveoli of the large tarsal setae (Fig. 14), while in the derivative fleas *X. gratiosa* (on sea birds) and *X. cunicularis* Smit (on rabbits) these fossae are considerably enlarged (Fig. 15). Likewise, the spiracles of the bird-flea *Ceratophyllus vagabundus alpestris* Jordan, occurring in the Alps, are of a normal size and so are the ones of *C. vagabundus insularis* Rothschild when living well away from the sea coast, but specimens from nests of sea birds have larger fossae, similar to the ones in *C. vagabundus vagabundus* (Bohemian) which occurs mainly in nests of sea birds. Large spiracular fossae are e.g. also found in fleas of Arctic sea birds, *Mioctenopsylla* spp., derivatives of *Megabothris*, a genus of rather hygrophilic mammal-fleas.

A change of host can also have a marked effect on the chaetotaxy of a flea. Wagner (1932) noticed that mammal-fleas living in dry sandy habitats usually have some prolonged tarsal setae. Among bird-fleas the parasites of the sand-marten *Riparia riparia* (viz. *Ceratophyllus styx* spp., *C. celsius* spp. and *Frontopsylla tapponica* (Nordberg))—living in a very sandy habitat—are overall much more hirsute than their congeners. Primitive nest-fleas have a greatly reduced vestiture and so have jiggers. This indicates that setae have a protective function, apart from a tactile one, as nest-fleas and jiggers do not spend much time wriggling (through dense pile of hair. It is of interest to note that e.g. with the virtual disappearance of the eye in *Xenopsylla georgyi* (Fox) the protective ocular setae has been reduced to a minute hair. Most setae do not lie flat against the surface of the body wall but they stand off, being inserted at an angle of up to about 45°. Thus they ward off host hairs from the body wall of the flea, a contact apparently to be avoided; at the same time the long setae may also act as cat’s whiskers.

More conspicuously sensitive than setae to change of host are ctenidia of fleas. A ctenidium is a comb-like arrangement of pseudo-spines, in fleas situated along an edge of the pre-antennal part of the head and/or a dorsal sclerite of pro- or metathorax (exceptionally, in *Chiropteropsylla* Oudemans, along the posterior margin of the metepimeron) and/or at most six dorsal sclerites of the abdomen.

Approximately 20% of the 2000 known forms of fleas lack developed ctenidia; 60% are without a cephalic ctenidium; 40% have a protonal ctenidium but lack a cephalic one; 40% have both a cephalic and a protonal ctenidium (the combination “cephalic ctenidium present, protonal ctenidium absent” does not exist, at least not as a normal condition). No less than 80% of all fleas possess a protonal ctenidium. The occurrence of fully developed ctenidia on metanotum and/or abdominal terga is confined to certain members of the families Ischnopsyllidae, Hystrichopsyllidae, Stephanocircidae and Pygiopsyllidae.

The function of the genal ctenidia was assumed by Roesele (1749) “to make room between the hairs of the host to facilitate the usage of the proboscis”, while Tschendenberg (1880) stated that “These spines give the flea a stronger hold in the skin of the host during the act of feeding.” Kolenati (1836) observed that “By gripping hair between combs and nota or terga the fleas hold themselves to the host animals”, while in 1863 (p. 34) the same author suggests that “The adults hold themselves in the fur by pressure of the mesonotal [recte: pronotal] ctenidium.” Ever since, the comb-likeness
of the structures has induced students of fleas to assume that their function is the 
gripping of mammalian hair. Humphries (1967) observed specimens of two small-
rodent fleas and one bird-flea moving about on a piece of shrew's fur and asserted 
that "the spacing between [the very tips of] the etenidial spines [of the pronotum] 
corresponds to the diameter of the host's hairs, which tend to enter the etenidial spaces 
when the flea is in a resting posture but not during locomotion." He concluded that the 
etenidial resist backward movement through the fur and therefore capture by the host. 
Traub and Evans (1967) also expressed their belief that "the combs of fleas obviously 
aid in preventing dislodgement from or by the host" and that the "variation in the 
shape of spines is adaptive to the type of hair or feather" of the host animal.

As an antithesis, to provoke further study and discussion of the subject, I would 
like to suggest that etenidia serve no anchoring function at all and that any correlation 
between shape and spacing of the etenidial spines and the greatly variable diameter 
of host hairs is of a preventive nature, obviating the slight, virtually hypothetical, 
chance of hairs getting caught between them. Etenidia are mainly protective devices. It 
seems mechanically impossible for hairs to get caught between the spines of e.g. a normal 
pronotal etenidium. The spines are more or less adpressed against the mesonotum 
and even if there were ample room between etenidium and notum, the semicircular 
construction of the etenidium makes it impossible for a straight hair to become lodged 
between the spines. Moreover, if a flea should move backwards (an unlikely event), or 
carefully be pulled backwards by the host (the careful element being equally unlikely), 
hairs of the host would be caught between some of the numerous setae of the body as, 
in most fleas, these stand off at a marked angle to the body wall. Rothschild (1917) 
already called attention to this. If etenidia were meant to act as hair catchers one 
would expect some tactile organist to be associated with them as these rigid structures 
do not appear to be very tactile themselves; no such association is known. Among the 
hundreds of thousands of fleas that I have examined I have never seen a host hair be-
tween etenidial spines; it is not unusual to find such hairs in the grasp of the pretarsal 
ungues in preserved specimens.

As the pronotal etenidium is the commonest etenidium in fleas, occurring in 80% of 
them, it is presumably the most important one. Precursory to discussing the function 
of this etenidium, it should be noted that as regards mobility the actual body of a flea 
consists of two main units: a) head and prothorax (with fore-legs), b) remainder of 
thorax (with mid- and hind-legs) and abdomen. The first unit is a compact structure 
and little movement is possible between head and prothorax; the fore-legs have a tactile 
and wading function. The second unit allows for some movement between the abdominal 
segments (the abdomen can e.g. be curved upwards in the more slender species, especially 
in the male) and the mid- and hind-legs have an ambulatory and saltatorial function. 
The degree of movement between the two units, i.e. between pro- and mesothorax, can 
be very considerable, especially nutating. The greatly developed intersegmental 
membrane between the two nota makes this movement possible. The functioning of 
this membrane can easily be seen by observing e.g. cat- or dog-fleas moving among 
hairs. Jutting out well over the white membrane are the spines of the pronotal etenidium 
which thus protect this otherwise very vulnerable joint. Spines are probably stronger 
than a thin collar-like notal flange which in fleas without a pronotal etenidium covers 
the short intersegmental membrane which in this case cannot be exposed and such 
fleas apparently do not require a great degree of movement between the two units; 
this may be related with the position of first and/or second unit during the act of feeding. 
Rothschild (1917) was also aware of the fact that "incisions between the segments of 
the body and legjoints are points of danger; the hairs of the host might slip into the 
sutures and the parasites thus become entangled." He suggested that "parrying" setae
fend off the hairs of the host and he ascribed a similar function to etenidia. In fleas with compact bodies, i.e. with a rounded abdomen (typical of many Pulicids and Rhopalopsyllidae), not much movement seems to be possible between the various segments and such fleas have no etenidia. The abdomens of the stickfast Vermipsyllid and Hectopsylla females — all without any etenidia — can swell enormously, the tergal and sternal sclerites becoming quite widely separated from one another; etenidia would here obviously be useless and also superfluous as the intersegmental membrane is thick and tough and stickfast fleas do not move about in the dermecos in expanded condition. It is worth nothing that the main setae of Vermipsyllids are all recurved and host hairs can therefore not be trapped by them.

A genal etenidium protects the base of mouthparts and/or the basal joint of the fore coxa. The spines of a helmet-etenidium in Stephanocircidae are on each side inserted at about 45° and, following the wafer-thin helmet-plate, act like the bow of a ship and also protect the sensitive cephalic organs that are situated posterior to this etenidium. Jordan (1950) puzzled why the posterior margin of the head never bears a etenidium. As I have pointed out above, the head of fleas is fairly sessile and the posterior part, which connects with the pronotum and exposed a little in some fleas if the head were bent downwards fully, is the true occiput and this is not membraneous. There is therefore no need for any special kind of protection. Females of some species of Echidnophaga Olliff have developed a short lobe at the posterior margin of the head and it is possible that they stick out their necks more so than do other fleas.

Bird-fleas need no protection against hair and — feathers being coarser structures (down does not seem to trouble fleas) — therefore do not need etenidia (just as fleas of mammals with very coarse or spine-like hairs are either without etenidia, e.g. Pariodontis riggenbachii (Rothschild) (on porcupine), or in process of discarding them as e.g. in Archaeopsylla erinacei (Bouché) (on hedgehog) and Bradiopsylla echinidae (Denny) (on echidna) ). These species are derived from mammal-fleas which (a) apparently never had etenidia, (b) possessed at least a protonal etenidium. To the first category belong bird-fleas of the Pulicid genera Xenopsylla Glinkiewicz, Echidnophaga Olliff and Hectopsylla Frauenfeld, and of the Rhopalopsyllid genera Parapsyllus Enderlein and Listronius Jordan (L. robertsonianus (Jordan), the only supposed bird-flea in the small genus (3 species), is known from only two specimens and has unguis and distitarsosomal chaetotaxy virtually as in the other two species which are mammalian parasites; if L. robertsonianus eventually proves to be a true bird-flea, it must be one of relatively recent standing). The ancestors of these fleas were thus pre-eminently suited for a transfer to birds as, apart from tarsal changes, no structural modification was required. Bird-fleas without etenidia (whether derived from species that possessed them or not) are mostly parasites of sea birds (Sphenisei and Tubinares) which are among the oldest orders, at the bottom of a phylogenetic tree of birds; the flea/bird associations can consequently also be very old and etenidia have had time to disappear. Higher up in this tree are Laro-Limicolae, Columbce and Psittacidae and e.g. associated species of Ceratophyllus (derived presumably from a Monopsyllus-like stock) such as C. columbae (Gervais) and C. fionnus Usher, with their shortening etenidia, are likely older than the fleas that are parasites of the most recent order Osceines (land birds) to which the bird-fleas belong that still have a well-developed pronoatal etenidium although this is in an inchoate process of being done away with.

The second category can be subdivided into (a) species that still possess a pronotal etenidium, (b) species that have lost this etenidium. To (a) belong bird-fleas of the Ceratophyllid genera Callopsylla Wagner, Ceratophyllus Curtis, Dasypyllus Baker and Miocenopsylla Rothschild, of the Amphipsyllid genera Frontopsylla Wagner and Ioff and Ornithophaga Mikulin and of the Pygiopsyllid genera Stivalius Jordan
and Rothschild and Hooistraalia Traub. It is a well-known fact that bird-fleas with a pronotal ctenidium have more numerous spines in it than is the case in related mammalian parasites. This, I believe, is aimed at closing the gaps between the spines in order to create a pseudo-collar. Bird-fleas apparently do not require a high degree of mobility between head/prothorax unit and rest of body unit. The next evolutionary step after densation of the pronotal ctenidium is a shortening of the spines, the chitinous material

Fig. 23a–f. Ceratophyllus gallinae (Schräck), sternum VIII, ♂.

being used to lengthen the pronotal collar. A shortening of pronotal spines can be seen in e.g. Ceratophyllus columbae, which therefore may be assumed to be a somewhat older bird-flea than other species of Ceratophyllus (with longer spines), and especially in Mioctenopsylla spp. The pronotal ctenidium of Mioctenopsylla is most instructive (Fig. 24). As mentioned above, these fleas of arctic sea birds are derived from a Megabothris-like ancestor who presumably had a normal ctenidium, as all extant members of that genus of rodent-fleas. The pronotal spines in Mioctenopsylla are well on their way out and are already very short and poorly selerotized. The most ventral spines of a pronotal ctenidium are usually smaller than the others and they are the first to disappear. In Mioctenopsylla these ventral spines show that in downward direction they become gradually shifted from the normal marginal position on to the underside of the natal collar where eventually they (the lowermost) become strongly attenuated, resembling the pseudosetae which are commonly found under the mesonotal collar (Fig. 25).

To subcategory (b) belong bird-fleas of the Pulicid genera Actenopsylla Jordan and Rothschild and Ornithopsylla Rothschild, of the Ceratophyllid genus Glaciopsyllus Smit and Dunnet and of the Pygiopsyllid genus Notiopsylla Rothschild. In the two Pulicid genera and in the Pygiopsyllid genus there are no traces of a pronotal ctenidium left. In Glaciopsyllus, nearest related to Dasysyrripus (which still has a ctenidium), the pronotum bears a number of slender pseudosetae under the collar or at the margin. Here
we have additional proof that such pseudoetae are vestiges of ctenidial spines, not rudiments. In specimens of some species of Parapsyllids (which have no ctenidia) such pseudoetae still occur sporadically and these species must have been among the last in their family to lose their pronotal ctenidium. I must recall here my statement in the description of *Glaciopsyllus* that “there may conceivably be a partial correlation between temperature and the development of ctenidia” as this has now proved to be an incorrect supposition.

Finding two slightly abnormal specimens (which were subsequently mislaid) in which one of the mesonotal pseudoetae had developed into a ctenidial spine, Jordan (1947) became convinced that these mesonotal pseudoetae are the rudimentary spines of the mesonotal ctenidium. These specimens, as well as several others showing a similar abnormality, have since been rediscovered in the Tring collection; some of these abnormal mesonotal spines are shown here in Figs. 17—22. Jordan assumed that pseudoetae are incipient spines which for some reason or other were halted in their development, only anomalously growing into proper spines. Teratological anomalies, however, are usually of an atavistic nature. A good example was recently provided by a series of *Ceratophyllum gallinae* (Schrank) collected from the nest of a sand-martin *Riparia riparia* at Maulden, Bedfordshire, England, and kindly presented by Mr. R. S. George. Sternum VII of 11 of 33 males of these fleas shows gradations from the normal modified slender form (Fig. 23a) to a rather primitive and little modified one (Fig. 23f); this series also clearly illustrates the development of the vexillum. The genitalia of these specimens are also somewhat abnormal. These specimens developed in the nest of a “wrong” host. It is noteworthy that in general fleas that somehow managed to develop in a “foreign” environment are much more prone to structural abnormalities than those that develop in their specific niche. The specimens of *C. gallinae* seem to be infected with nematodes and these are known to be able to cause malformations in fleas; would it be possible that these nematodes are less harmful to the specific fleas of *Riparia riparia* than to straggling species?

Another example of an atavistic monstrosity that recently came my way, through the courtesy of Mrs Gunvor Brinck-Lindroth, is a case of floating genitalia in a male *Rhadinopsylla integella* Jordan and Rothschild (from Krape, Lycksele lappmark, Sweden). As is shown in Fig. 27, in this specimen the phallosome and the parameres are situated as a unit upside down inside the abdominal cavity. Normally the parameres are united with tergum IX and the phallosome occupies a central position partly between or just below the parameres. In the abnormal male tergum IX is a narrow sclerite without setae and with thickened ventral apices (where normally the parameres would have joined); sternum IX is shortened and somewhat modified, connected to the anal sternum by means of an intersegmental membrane which extends between the two arms of sternum IX and thus effectively closes the opening which would otherwise have been occupied by the phallosome (Fig. 26). Apart from the presence of genitalia, the terminal segments of this male are exactly similarly deformed as the ones in fully castrated males (where no trace is visible of phallosome and parameres). Smits (1970) supported Snodgrass’s views on the origin of the male genitalia, referring to fully castrated specimens. The abnormal male of *R. integella* lends support to the theory that both phallosome and parameres are derived from a common structure, the primary phallic lobes (the inner pair of these lobes normally uniting to form the phallosome, the outer lobes developing into parameres which unite with the ventral ends of tergum IX). Claassens (1967) described a similar abnormality in a male *Ceratophyllum gallinae* (from Blarney, Ireland) but his specimen was not in as good a condition as the one from Sweden and the nature of the abnormality was then not clearly understood.

Reverting to mesonotal pseudoetae, these are present in no less than 84% of all
species of fleas. If these structures are indeed vestiges of spines, one of the ancestral stages must have had a developed mesonotal ctenidium which, in turn, would mean that the joint between meso- and metathorax will have been movable to a higher degree than what it is now. Did an increase in saltatorial powers tighten up the connection between those two nota, thereby obviating the need for a protective ctenidium? Why do these vestiges of spines persist for so long? Are the Pulicidae, Coptopsyllidae and Xiphopsyllidae, the only families without a trace of mesonotal pseudosetae, derived from an ancestor that never possessed a mesonotal ctenidium or are they in an evolutionary more advanced stage than the members of the other families? The latter may be true for the Pulicidae, for the most highly specialized fleas belong to this family. Moreover, ctenidial spines that are discarded in Pulicidae leave no pseudosetal remnant, the pronotal ctenidium of Archaeopsylla erinacei (consisting of 9-0 spines) is a good example (Fig. 16a—c).

A study of unguis and ctenidia is not only of interest per se, but it may enlighten taxonomic obscurities or solve a dormant puzzle, such as there was in Ceratophyllus, a genus of 44 species, all but one being parasites of birds. The exception, C. lunatus spp., is a specific flea of the stoat Mustela erminea. Superficially C. lunatus strongly resembles other species of Ceratophyllus and its generic status has never been questioned. However, C. lunatus is the only species in the genus that has, as was to be expected, strongly ridged unguis. Its pronotal ctenidium consists of ‘more than 24 spines’ (the usual criterion for a bird-flea ctenidium) and this must have been the main reason for including this taxon in Ceratophyllus, although the spines are markedly longer than in the average bird-infesting species of the genus. However, the two other species with a pronotal ctenidium that are specific parasites of Mustela (viz. Neactopsylla (Neactopsylla) brooksi (Rothschild) and Callopsylla (Paracallopsylla) kaznakovi (Wagner)) also have a greatly increased number of pronotal spines in comparison with their congeners and they are in fact the only representatives of their subgenera. From a flea’s pronotal ctenidium point of view, the dermecos of a Mustelid is like that of a bird. In C. lunatus we have a case of parallel development with bird-infesting species of Ceratophyllus. Obviously they all share some Monopsyllus-like ancestor. It is warranted to place C. lunatus in a separate subgenus:

Rosickyiana* subg. nov. (of Ceratophyllus Curtis, 1832)

Differing from the nominate subgenus by the strongly striated and ridged pretarsal unguis and in the male by the presence of two well separated subsiniform setae on the telomere and the small size of the squarish aedeagal hamulus.

Type species: Ceratophyllus lunatus Jordan and Rothschild, 1920.

The subgenus is named in honour of Prof. Dr. B. Rosický as a token of esteem and appreciation of his valuable contributions to the study of fleas.

A number of Ceratophyllid genera are in need of careful revision and revaluation and it may eventually seem advisable to place some species of Monopsyllus into a separate subgenus of Ceratophyllus (M. anius (Rothschild), for example, parallels C. lunatus but has fewer than 24 pronotal spines, being a rodent-flea). If a good reason were forthcoming (which I doubt) for retaining them as a subgenus in Monopsyllus, then Rosickyiana could also be treated as a subgenus of Monopsyllus. In recent years there has been a tendency towards stressing differences instead of relationships by creating many new genera where subgenera might have sufficed. Is it really not preferable to stress relationships rather than differences, which are often sufficiently apparent?

*) Pronounced: Rositskiana.
Fig. 27. *Rhadinopsylla integella* J. & R., floating genitalia of male (from Krajpe, Sweden).
О НЕКОТОРЫХ АДАПТИВНЫХ СТРУКТУРАХ БЛОХ (ОТРЯД SIPHONAPTERA)
Ф. Г. А. М. Смит

Резюме. В статье устанавливается, что степень развития претарзальных коготков у блок связана с типом кожного покрова хозяина. Также обсуждается влияние дермекоса на развитие ктенидий, особенно ктенидий переднеспинки. Новый термин 'дермекос' обозначает образовавшуюся на коже мlekонитающего или питающего микроструктуру. Установлено, что псевдовесна валика переднеспинки или среднеспинки являются остатками зубцов и не рудIMENTАМи ктенидий. Приводятся примеры атавистического характера тератологических аномалий у блок. Дается описание нового подрода для единственного поражающего мlekонитающего вида, относящегося к крупному роду питьсяных блок Ceratophyllum.

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