Co-evolution of trichodecid lice (Insecta: Phthiraptera) and their mammalian hosts

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The cladogram of Trichodecidae produced by Lyal (1985) is interpreted, with reservations, as a phylogeny and is compared to such host phylogenies as are available. While the predominant pattern of louse relationships is broadly congruent with host relationships, indicating either phyletic tracking or a mixture of phyletic tracking and host-group-limited resource tracking by the lice, a substantial proportion (20-7%) of speciation events of the lice could only be explained by invoking secondary infestation of distantly related hosts by the lice.

The ancestor of the Trichodecidae almost certainly parasitized a eutherian, but the identity of the eutherian group is unclear. The primary host association of the Neotrichodecidae was with an American rodent, from which resource tracking onto Mephitidae and then Mustelidae, Procyonidae, Brachypodidae and Melinae took place. The Trichodecidae had an ancestral association with the ancestor of the Felidae, with subsequent secondary infestations of Mustelidae, Canidae, Ursidae and Procyonidae. The parasitism of the felid ancestor was probably derived by secondary infestation from a rodent or hyracoïd. The ancestral host of the Dasyonygidae may have been a hyracoïd, and two secondary infestations of primates are recorded in the subfamily. The exochosoid hosts of the Exocheirophilidae gained their lice from an unknown host. The ancestral host of the Bovicolaetidae is not known.

Future work to resolve these problems must involve: (1) Further collection of lice, with particular emphasis on Artiodactyla, Perissodactyla and Carnivora. (2) Further investigations of the clades of relationships of the Trichodecidae, particularly at the primary foci of the cladogram proposed by Lyal (1985), where synapomorphies have been very difficult to discern, and in the Bovicolaetidae. (3) Production of a more fully resolved cladogram of the Eutheria, and the identification of holophyletic mammalian groups at all levels.

Introduction
Most discussions of host-parasite co-evolution with respect to lice has been hampered by two factors: the dependence of louse classification on host classification, and the form of classification generally used for the vertebrate hosts. The detailed objectives of this paper are: (1) to provide a co-evolutionary history of the louse family Trichodecidae and their hosts, attempting to avoid the circularity of reasoning induced by the two factors mentioned above; (2) to discover the identities of the hosts parasitized by the stem-species of the major clades of Trichodecidae; (3) to discover the degree of non-congruence between host and parasite phylogenies.

For much of this century louse systematists have, implicitly or explicitly, followed the axiom that louse and host phylogenies are topologically identical ('Fahrenholz's Rule'). The desire to produce 'natural' classifications and a perhaps undue reverence for existing classifications of the vertebrate hosts led to a very close correspondence between host and parasite classifications. This in turn led to a reinforcement and general acceptance of the principles of Fahrenholz's Rule, and in some cases the use of louse relationships, themselves based on supposed host relationships, to support the original classification of the hosts (Traub, 1980).
The group of lice examined here, the Trichodectidae, has recently been the subject of a cladistic analysis performed without reference to host information, and a reclassification based exclusively on the cladistic analysis (Lyal, 1985). Thus the circularity of argument induced by the dependence of some louse classifications on the classifications of their hosts is avoided in the discussion below.

A comparison of the supposed trichodectid phylogeny and that of their mammalian hosts is still hampered by the second factor mentioned above, the methods of analysis and classification generally used by mammalian systematists. There has been very little cladistic work done on the groups of mammals parasitized by Trichodectidae, their relationships generally having been determined by palaeontological methods and their classifications having been produced following "evolutionary" principles (see Simpson, 1945, 1961). The classification of mammals is therefore predominantly "horizontal", comprising many paraphyletic "grade" groups which cannot be compared meaningfully with the holophyletic groups of lice. The phylogenies of mammals reconstructed from fossil evidence are rarely sufficiently complete for comparison with the trichodectid phylogeny to indicate a single most probable co-evolutionary hypothesis. Despite these difficulties some statements can be made, and certain correlations and differences between host and parasite phylogenies detected.

The phylogeny of the Trichodectidae used in this study is taken from Lyal's (1985) cladogram. Although the interpretation is sometimes challenged (Platnick, 1977), it is considered here that there is a topological correspondence between dichotomously branching cladograms and phylogenetic trees (following Wiley, 1979, 1981). A multiple forkation of the cladogram, however, is not taken as indicating the same topology on the corresponding phylogenetic tree, as a number of different arrangements would be equally possible.

Determining unequivocally the history of host-parasite associations is not possible. Extant associations between holophyletic and paraphyletic groups may be accounted for by transfer of lice between hosts, or by various combinations of parasite loss and independent speciation of louse and/or host (Lyal, 1986). No sure way is known of distinguishing between these possibilities, but in the cases discussed below it is felt that transfer is the most parsimonious hypothesis, and this will be discussed primarily. If transfer is assumed, the identity of the primary host of a holophyletic group of lice parasitizing members of more than one host taxon is determined by parsimony. The host taxa are treated as cladistic character states of the lice, but are given much less weight than the morphological character states used in the construction of the original cladogram. For example, in the Loriuscula paralacticus-unguicola clade (Fig. 17), paralacticus and laticeps parasitize Anasa paludibmnsicus while the sister-species of laticeps, L. mungos, is a parasite of Haemaphes sanguineus. In this case it is inferred that the association of L. mungos with H. sanguineus is apomorphic for the clade and may mark a speciation event associated with a secondary infestation, as this interpretation accords with the distribution of other apomorphies.

Clades of Trichodectidae are identified in the text by the names of the two "extreme" taxa of the clade, reading from the top of the page down.

The phylogenetic relationships of the lice and their hosts are discussed individually for each subfamily of Trichodectidae. This study formed part of the results of a research project submitted to the University of London for the degree of Doctor of Philosophy.

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**Bovicoline**

All species of Bovicoline other than *Tragoscelis", most *Werneckeia* and one *Bovicola* are associated with Bovidae and Cervidae (Artiodactyla: Pecora). For comparative purposes, possible phylogenies of the Artiodactyla and Bovidae are depicted in Figs 1–3. The phylogenetic relationships of the pecoran families (Moschidae, Cervidae, Antilocapridae, Capridae and Bovidae) are much disputed, almost every possible combination of sister-groups having been suggested (e.g., Hamilton, 1978; Leinders and Heintz, 1980; Eisenberg, 1981). For this reason no attempt is made in Fig. 1 to resolve the relationships of the Pecora beyond the initial pentauration. There are also problems in determining the relationships of the tribes of Bovidae, and two alternative phylogenies for the living members of the family are depicted in Figs 2 and 3.

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**Fig. 1.** Cladogram of the living Artiodactyla. Compiled from Hamilton (1978), Leinders and Heintz (1980) and Eisenberg (1981).

**Fig. 2.** Phylogeny and classification of the Bovidae. Compiled from Gentry (1978).
Genu Damalinia

Species of Damalinia are associated with hosts in the Bovidae and Cervidae. Those species of Damalinia associated with members of the latter family form two small clades in the subgenera D. (Cervicola) and D. (Tricholopera). The positions of these clades on the cladogram (Figs 4, 5) indicate the associations to be the result of independent transfers oflice to Cervidae from Bovidae. The primary host association of Damalinia, therefore, is believed to be with an ancestor of all or part of the Bovidae. Details of the host associations are discussed below by subgenus of Damalinia; the cladograms of the subgenera, associated with host identities, are depicted in Figs 4, 6, and 8.

Species of D. (Damalinia) are associated with Alcelaphini, Caprini, "Rupicaprini", Antilopini, Neotragini and Reduncini (Fig. 4). In no postulated phylogeny of the Bovidae do these tribes form a holophyletic group, although in Kingdom (1982) phylogeny the Reduncini are more closely related to the other tribes than is indicated by Gentry (1978). It is notable that Gentry (1990) does raise doubts about the bovid affinities of the Reduncini.

The two species of D. (Damalinia) parasitize on reduncines (D. adenota and D. halli), both associated with Kobus spp., form an unresolved dichotomy on the cladogram with D. pelae, a parasite of the ruminants Pelai capreolus. The position of D. pelae is tentative, as specimens have not been seen in this study. Pelae is placed by some authors in the Reduncini (Honacki et al., 1982), but it has also been placed in the Caprini (Gentry, 1970) and in the Neotragini (Gentry, 1978 and personal communication). If the phylogeny proposed by Kingdom (1982) is correct, Pelae might be a reduncine or neotragine without having to invoke secondary infestation by the lice, although if Gentry (1978) is correct some loose transfer must be invoked to permit Pelae to be anything other than a reduncine. The identities of the remaining hosts of D. (Damalinia), and their relative positions on the cladogram of lice, suggest that some secondary infestation has occurred, and that the association with Reduncini and Pelae is unlikely to be primary. Some secondary absence may be suggested. The two species of Kobus parasitized by D. adenota and D. halli form a paraphyletic group, possibly made paraphyletic by the exclusion of K. leche (Gentry, 1978), if D. adenota and D. halli are sister-species, the association may be explained by a single ancestral infestation from another bovid, with possible secondary absences from K. leche. The sister-group of the D. pelae-halla clade discussed above is the D. thompsoni-dimorpha clade. The host of D. dimorpha is not known, although Hopkins (1949) suggests that, as both Naemorhedus ceralis and Capricornis sumatraensis occur in the neighbourhood of its collection, one of these may be the host. Both D. thompsoni and D. orientalis parasitize Capricornis species, and a single ancestral association with the ancestor of these two hosts seems likely. Naemorhedus and Capricornis are generally placed in the 'Rupicaprai', but Gentry (1978) would like to transfer the hyoegenus of this tribe, Rupicaprai, to the Caprini, and Kingdom (1982) considers the whole tribe in the Caprini. Whichever the host of D. dimorpha, if it is one of the two suggested by Hopkins (1949), a single ancestral association of the D. thompsoni-dimorpha clade with either the ancestor of Capricornis or of Capricornis plus Naemorhedus seems probable. The latter group is almost certainly not sister-group to the hosts of any of the D. pelae-halla clade, nor of the D. fahremholzi-appendiculata clade, which is the sister-group of the D. thompsoni-halla clade. At least one more secondary association must be inferred, therefore, either by the ancestor of the D. thompsoni-dimorpha clade or that of the D. fahremholzi-appendiculata clade.

The hosts of the D. fahremholzi-appendiculata species pair belong to the genus Gazella. Species of this genus are among the few boids to span both Africa and Eurasia in their distribution (Groves, 1969), and this perhaps offers an explanation of the association of the sister-group of the lice with hosts in both Africa and China.

The D. theleri-ornata clade parasitizes the tribe Alcelaphini (Bovidae: Alcelaphinae), and comprises the only Trichodectidae known to do so. The sister-group of the Alcelaphini is the Aepycerotini (Vrba, 1979), which comprises only one species, Aepyceros melampus. This species is parasitized by two Trichodectidae, both of them in D. (Tricholopera) and not in a sister-group relationship with the lice of Alcelaphini.
These lice are discussed below. The cladogram of the lice of the Akelaphina (Fig. 4) may be compared to the cladogram of the hosts produced by Vrba (1979) (Fig. 5a). The two cladograms do not entirely accord, some of the differences arising from the lack of full resolution of the trichodectid cladogram. If this lack of resolution is corrected to a series of dichotomies by use of host relationships, a cladogram not dissimilar to that of the hosts is produced (Fig. 5b). The only anomaly in this cladogram is in the position of the species parasitizing Damalisicus, which is clearly not in accordance with any conception of Compsoceridae as a holophyletic genus. To achieve full accord between host and parasite cladograms a secondary infestation of Damalisicus from Compsoceridae is postulated. With this hypothesis, the association of the D. theiler-i-vena clade with the Akelaphina, with the exception of a single species, can be adequately described by reference to Fahrenholz's Rule. It is predicted that lice of the clade will be found on Sigmodon rufescens, but not necessarily on Damalisicus niger.

Species of *D. (Cervicina)* are associated with Tragelaphini, Reduncini, Cephalophini and Cervidae (Fig. 6). The association with Cervidae (except the *D. maui-*montanus clade) has been noted above as secondary. The four described and one undescribed species in the clade parasitize members of the Cervinae (Cervus, Axis), Odocoilinae: Capreolus (Capreolus), Muntiacinae (Muntiacus) and Hydropotini (Hydropotes). Because the *D. maui-*montanus clade has not been resolved fully, the hypothesis of a primary association of the clade with the most recent common ancestor of the Cervidae, followed by co-evolution, is not ruled out directly by the cladogram. Milling against this is (i) the absence of members of the clade from most Cervidae, including species very closely related to some of those parasitized (ii) the association of other members of *D. (Cervicina)* with hosts that evolved much more recently than the Cervidae, and (iii) the possible identity of the specimens from *Hydropotes* with *D. meyeri* from Capreolus. The hypothesis of several secondary infestations between cervids would also account for the host associations and is regarded as highly likely, especially as all of the deer concerned, other than *Axis* spp., are sympatric in China and the Far East, and *Axis* and *Muntiacus* are sympatric in India (Corbet, 1978; Corbet and Hill, 1980).

The *D. maui-*montanus clade is sister-group to the *D. hodgsoni-*martini clade, species of which are parasitic on Cephalophini and Reduncini. Species of the *D. reduncae-*larietii clade, which is the sister-group of the *D. hodgsoni-*martini clade are, surprisingly, also parasitic on members of the same two tribes. There are two possible explanations for this anomalous host distribution: (1) The ancestor of the *D. hodgsoni-*martini clade was associated with (at least) two host species, a primitive reducine and a primitive cephalophine. This association may have been from a common ancestor, or it may have been secondary on one of the two. Both host species and the louse species underwent speciation at roughly the same time. The two louse species resulting were both still associated with two host species, although further speciation may have followed fairly rapidly in the ancestor of the *reducana-*larietii clade. In the other branch, the ancestor of the *maui-*montanus clade may have moved from either the cephalophine or the reducine to a cervid. The course of these postulated evolutionary events is depicted in Fig. 7a. (2) The ancestor of the clade was parasitic on either an ancestral cephaline or an ancestral reducine for either tribe and the Cervidae followed to give the pattern of association seen today (Fig. 7b). The Cephalophini have very little ascertainable fossil history, and it is not known whether the group was ever distributed outside Africa. Fossils that probably represent primitive reducines have been found in Asia (Gentry, 1978), and perhaps account for the transfer of the lice to the Cervidae. The remaining two clades (three species) of *D. (Cervicina)* are associated with the Tragelaphini, although a single primary association with this tribe is not certain. The association of *D. hopkinsi* with species of *Taurotragus* and *Tragelaphus* may be the result of secondary infestation of the former genus from the latter, or may be the result of a single primary infestation of the common ancestor of the two genera (which

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**Fig. 5.** Cladograms of lice and their hosts. A. Cladogram of Akelaphina, after Vrba (1979). Extinct (fossil) species are marked by short branches. B. Cladogram of *Damaelius* theileri-fornata clade if unresolved trichodectid are resolved using host identity as an apomorphy (cf. cladogram in Fig. 4).

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**Fig. 6.** Cladogram and host associations of *Damaelius* (*Cervicina*).
Fig. 7. Two alternative possible phylogenetic associations between lice (broken line) in Damalinia (Cervidae) and their hosts (solid line) in the Reduncini (R), Cephalophini (Cep) and Cervidae (Cerv). Host and parasite phylogenies drawn close to one another indicate a single host-parasite association; a parasite phylogeny drawn equidistant from two host phylogenies indicates an association of the parasite with both of the two hosts concerned. In b the label R/Cep indicates that either family could be concerned.

may, if Tragelaphus is paraphyletic, lie within this genus). The association of D. ammoxeni and D. nasutus with different subspecies of Tragelaphus scriptus is not compatible with the cladogram, and neither is the association of D. ammoxeni and D. hopkinsi with T. spekei and T. angasi respectively, as these hosts are probably sister-species (Gentry, 1978).

Species of D. (Trichophorus) are associated with Antilopini, Aepycerotini, Neotragini, Cephalophini and Cervidae (Fig. 8).

The association with Cervidae (of the D. albimarginata-indica clade) has been noted above as secondary. Lice of this clade are associated with three genera of the New World Odocoleini (the D. albimarginata-parallela clade) and the Old World Muntiacinae (D. indica, parasitizing Muntiacus muntjac). The cladistic relationships of these two host groups (Fig. 1), coupled with the absence of lice from the other Cervidae examined, suggests that the hypothesis of a single ancestral infestation of the Muntiacinae-Cervidae clade is unlikely. The hypothesis of a single ancestral infestation of the Odocoleini before their migration to America is more likely, and may be tested by examination of more deer of this tribe for lice. The association may be derived by secondary infestation from Muntiacinae or vice versa, or of both from an unknown third host. The initial infestation of the Cervidae must have been from a bovid, and it is interesting in this context to note the suggestion of Gentry (1978) that the decline of the 'African' bovids in India may have been linked to the burgeoning of the deer. The association of both D. leiperioides and D. parallela with Odocoleus hemionus and O. virginianus indicates that speciation of the lice parasitizing the Odocoleini has not always followed the predictions of Fahrenholz's Rule.

The remaining hosts of the subgenus belong to the Aepycerotini, Antilopini, Neotragini and Cephalophini. Gentry (1978) regard the first three of these as having aegolion affinities and the last as bilodont (Fig. 2), in which case the two lice parasitic on Cephalophini (D. pakenhami and D. bedfordi) are almost certainly associated with their hosts as a result of transfer by their common ancestor from a neotragine. Kingdom (1982), however, figures the Cephalophini and Neotragini as sister-groups (Fig. 3), although referring in the text to a 'neotragine' ancestry of many of the bovines. If these two tribes are sister-groups, secondary infestation of Cephalophini or Neotragini is still the most likely explanation of the distribution of host associations on the cladogram (Fig. 8). If there have been no secondary infestations, Neotragini is either
paraphyletic with respect to the Cephalophini and some of the other neotragine genera, or there has been independent speciation of the lice on the common ancestor of the two subfamilies, followed by failure of one of the two resultant species to become associated with the ancestor of the Cephalophini on the division of the common ancestors of the two subfamilies. Lice have been collected from only eight of the 14 species of living Neotragini, and further collecting might elucidate the situation.

While both D. pakenhami and D. balfordi parasitize species of Cephalophus, one of them (D. pakenhami) is also associated with Sylvicapra grimmia. If the genus Cephalophus is holophytic, this association is likely to be secondary. There is very little fossil record of the Cephalophini (Gentry, 1978), and the acceptance by mammal systematists of paraphyletic groups makes it possible that Sylvicapra has an ancestry in Cephalophus. If this is so, the association with D. pakenhami may be primary. Cephalophus and Sylvicapra live in slightly different environments (Gentry, 1978).

The sister-group of the D. albimarginata-moschatus clade discussed above comprises a single species, D. elongata, parasitic on Aepyceros melampus (Alcelaphinae: Aepycerotini). The same host is also parasitized by D. (T.) aepycerus, a member of the single remaining clade in D. (Tricholophaeini), the D. aepycerus-spiner clade. Species of this clade are also associated with members of the Antilopini and Neotragini but, because of the poor resolution of the cladogram, no suggestion can be made of the primary host association on internal evidence alone.

A possible hypothesis of the primary host of the D. (T.) aepycerus-spiner clade (and of the subgenus Tricholophaeini) is suggested by the sister-group relationship of Aepyceros and the Alcelaphini, which are parasitized by the D. (D.) sheilerae-arnauze clade as described above. This hypothesis may be broken down into the following elements: (1) The ancestor of D. (Tricholophaeini) was associated with an aepycerotine ancestry, culminating in Aepyceros melampus, a primary infestation derived from its common ancestor with the D. (D.) sheilerae-arnauze clade, which itself parasitized the ancestor of the Alcelaphini. (2) The first speciation event in the history of D. (Tricholophaeini) to be discernible by study of living species gave rise to two species on Aepyceros melampus (D. elongata and D. aepycerus). (3) All other species of the D. (T.) aepycerus-spiner clade, the D. (T.) albimarginata-moschatus clade and the D. (D.) thompsoni-appendiculata clade became associated with their present hosts following secondary infestation from various Alcelaphinae.

An alternative hypothesis is available which explains the predominance of the association of the D. (T.) aepycerus-spiner clade with Antilopini and that of the D. (T.) linea-moschatus clade with Neotragini. The hypothesis depends on a sister-group relationship between these two tribes, as may be inferred from the phylogeny in Fig. 2, but which is denied by that in Fig. 3. The hypothesis postulates that the ancestor of D. (Tricholophaeini) was parasitic on the ancestor of the Antilopini plus Neotragini (Antilopinae sensu Gentry, 1978). The ancestor of the D. aepycerus-spiner clade was associated with the ancestor of the Antilopini, and secondary infestation of Aepyceros and Ourebia took place from antilopines. The ancestor of the D. (T.) elongata clade was associated with the ancestor of the Neotragini, and secondary infestations of Cervidae, Cephalophini and Aepyceros took place from members of this tribe. Speciation of the ancestor of the Neotragini and Antilopini might account for a primary association of D. (D.) damalina with this subfamily (Antilopinae sensu Gentry), and again division with the divergence into Neotragini and Antilopini took place (today represented by the lice on Pecos and Gazella). Secondary infestations of the Alcelaphini, Redunca and 'Rupicaprinae' took place.

The co-evolution of trichodectid lice and their hosts

The hypotheses of Alcelaphinae and Antilopinae (sensu Gentry) as ancestral hosts each require eight secondary infestations to be postulated, so no choice can be made between them on the grounds of parsimony. The problem will probably not be resolved without further phylogenetic research into relationships within the Bovidae.

It is notable that, if Gentry's (1978) revision of the Bovidae into agodont and biodont tribes (Fig. 2) is accepted, D. (Damalina) and D. (Tricholophaeini) are primarily associated with agodonts and D. (Cervina) is, as regards Bovidae, entirely associated with biodonts. If Kingdon's (1982) division of the Bovidae into subfamilies (Fig. 3) is accepted, all members of Damalina that are associated with Bovidae, except three species of D. (Cervina), are parasitic on members of the Antilopinae. The cladogram of Damalina does not support one phylogeny of the Bovidae rather than the other.

Genus Bovicola

Species of Bovicola are associated with Bovidae, Cervidae and Camalidae (Fig. 9). Only one species, B. breviceps, is parasitic on a camelid, this being the only trichodectid association with that family. This fact, together with the position on the cladogram of B. breviceps with respect to other species associated with Bovidae, suggests that this association with Camalidae is secondary.

The position on the cladogram of the species parasitic on Cervidae also suggests a secondary infestation of this family from a member of the Bovidae. The deer concerned belong to the Cervinae and the Rangiferini (Odocoileinae), and do not form a holophytic group (Fig. 1). The absence of lice of this clade from other species of Cervinae, particularly Cervus, suggests at least one and possibly two secondary
infestations within the clade to account for the present distribution of host associations. It is notable that the deer parasitized are all distributed in the Western Palaearctic and Neartic. The presence of lice on Elaphurus davidianus and Odobenus rosmarus results from secondary infestations.

The clade of species of *Bovicola* are associated with Caprini, *Rupicaprinae* and Bovini. The last-named tribe is not closely related to the other two (Fig. 2), and the position of the clade of the single species parasitizing a bovine (*B. bisus*, on domestic cattle) suggests the association to have been derived by secondary infestation from a caprine.

The poor resolution of the clade of *Bovicola* makes it difficult to speculate whether it is true or not that some of these are secondary infestations from wild species of *Capra*, but further collecting will be needed to confirm or refute this. The ancestor of *Bovicola* was almost certainly parasitic on an ancestor of one or all of the Caprinae.

**Genus Wernerckiella**

Members of this genus parasitise species of Equidae (Perissodactyla) and Bovidae (Artiodactyla), five of them being associated with the genus *Equus* and the other two with *Ammotragus* (Bovidae: Caprini) (Fig. 10).

Cladograms of *Equus* are provided by Bennett (1980) and Eisenmann (1980) (Fig. 11). Although the poor resolution of the cladogram of *Wernerckiella* makes detailed comment impossible, the postulated sister-species relationship of *W. equi* and *W. ocellata* is not compatible with either of the host cladograms. The primary hosts of these two species have been established by Moreby (1978). He notes that *W. equs* commonly found on the domestic horse *E. (E.) caballus*, has been taken from captive specimens of *E. (A.) hemionus kulan* but suggests that, as these may have come into contact with domestic horses, the association is probably secondary and *E. caballus* is the primary host (subgeneric placements of Bennett, 1980). Moreby (1978) is uncertain of the identity of the primary host of *W. ocellata*, but notes that numerous samples have been taken from the domestic ass *E. (A.) asinus* and only one from the zebra *E. (E.) burchelli* (the type-host). The most probable primary host is therefore the ass. Compatibility with both cladograms can be obtained by postulating a transfer of lice between the domestic horse and domestic ass, followed by speciation. If Bennett's cladogram is correct, the most likely direction of the transfer would be from *E. caballus* to *E. asinus*, leaving *Wernerckiella* primarily associated with one branch of the cladogram (comprising the species of the nominate subgenus). Discovery of species of *Wernerckiella* on *E. hemionus*, *kiang* and *onager* would not necessarily be expected. An alternative hypothesis is also possible if this cladogram is correct. This is that the ancestor of the *E. zebra-caballus* clade was parasitic by an ancestor of *W. equi*, *ocellata* and *zebra*, but speciation did not occur at an early stage of the cladogram. Speciation of the louse did occur when the ancestor of *E. zebra* diverged from the ancestor of the *E. asinus-hemionus* clade, and when *E. asinus* and *E. hemionus* diverged. If this is the case, *E. hemionus* will be found to be naturally infested with *W. equi* or a sister-species to this or *W. ocellata*, and *W. zebra* will be found to be the sister-species to these two or three species.

In the absence of a large number of secondary infestations of horses from other hosts, the association of *Wernerckiella* with *Equus* may date to the Hemphillian (earliest Pleistocene) period in North America, as Bennett (1980) suggests this origin for the genus.

The remaining two species of *Wernerckiella* both parasitise *Ammotragus lervia* (Caprini lervia of Gentry, 1978). Although the two lice are not indicated as sister-species on the clade diagram, they are very close morphologically, the females apparently being indistinguishable. The association of *Wernerckiella* with *Ammotragus* may be primary and that with *Equus* secondary, or vice versa. *Ammotragus* being infested once or twice from horses. Gentry (1978) refers to late Pleistocene fossils of *Ammotragus lervia* in North Africa, and Newbiggin (1936) suggests a Central Asian origin for the species. A North American origin for *Ammotragus* seems unlikely, therefore, so the hypothesis of an origin for a host is rejected. Further still is the *Ammotragus* acquired *Wernerckiella* once or twice from a more recent equid in North Africa where it is, or has been, sympatric with several species (Ansell, 1971).

**Other Bovicolinae**

The host associations of two of the five genera of Bovicolinae have not so far been discussed. *Bovicola* comprises one species (with two subspecies) parasitic on the bison and the buffalo (*Bovidae: Bovini*), and *Tragulicola* comprises a single species parasitic on the mouse deer (*Tragulidae*). Both of these associations must be considered primary for the modern host species, but the poor resolution of the cladogram does not allow any statement regarding the acquisition of the parasites by the ancestors of the modern hosts.
**Estrichophilinae**

The single genus is parasitic in New World porcupines (Erethizontidae: Rodentia). The origin of this association will be discussed further below. No attempts have been made to resolve the relationships of the lice in this subfamily, and therefore little comment can be made. The presence of the same three species of *Estrichophila* on *Coendou prehensilis* and *C. spinosus* is notable.

**Dasyoponginae**

The initial dichotomy of the clade divides *Ceboidea*, parasitic on Cebidae (New World Primates), from the hyrax lice of the Old World. No phylogenetic implications for the hosts can be drawn from this, and it must be that one or both infestations are secondary. This will be discussed further below. The uncertainties attached to the taxonomy and systematics of Procaviidae (Hyaenidae) and the dubious nature of some of the host identifications for the lice preclude any discussion of host-parasite co-evolution in this group, although with one exception secondary infestations, if there have been any, have been confined to members of the Hyaenidae. The single exception is the presence of *P. (Meganarianoides) colubri* on a monkey (Lay, 1983). This association must be secondary, as all other members of the clade (the *Procoptodaeus*—*Eurytrichodectes* clade) are parasites of hyraxes.

**Trichodectinae**

Almost all Trichodectinae parasitize Carnivora. For comparative purposes, a cladogram of living carnivorous families is presented in Fig. 12.

**Fig. 12. Phylogeny of the living Carnivora. Compiled from Tedford (1976), Eisenberg (1981) and Flynn and Galván (1983).**

**Co-evolution of trichodectid lice and their hosts**

**Fig. 13. Cladogram and host associations of Trichodectina. Host family Mustelidae is indicated by X.**

**Fig. 14. Cladogram and host associations of Trichodectes (Strobilidae).**

**Genus Trichodectes**

Species of this genus parasitize the canid families Ursidae, Canidae, Procyonidae and Mustelidae, the predominance association being with the latter (Figs 13, 14). Although all these families comprise a paraphyletic group, and thus the association might have resulted from a single primary infection, the distribution of the host taxa on the cladogram suggests a more parsimonious hypothesis of secondary infestation in some cases.
The three species parasitizing Procyonidae comprise a single clade in *T. (Stachyrella)*, and are sister-group of some of the musteline lice (Fig. 14). The Procyonidae are not the sister-group of some of the Mustelinae, but of the Mustelidae plus Phocidae (Tedford, 1976). The incompatibilities between host and host clades (clans) can be resolved by postulating that the association with Procyonidae follows secondary infestation from a mustelid. The sister-species relationship between the two species parasitizing *Procyon* is suggestive of a primary infestation, although the relationship between the two races is not known. Further collecting from other species of *Procyon*, coupled with a cladistic analysis of the genus, would enable the degree of phylogenetic association to be determined. Without such collecting and analysis the status of the association with *Lutricia* is difficult to assess. Simpson (1945) suggests that this genus is an early offshoot from the line which gave rise to other Procyonidae but, if this were so and the infestation with *Trichodectes* were primary, the other genera of Procyonidae might be expected to be parasitized by members of the genus also. A resolution of the problem must await further collection and a cladistic analysis of procyonid relationships.

The remaining species of *Trichodectes* (Stachyrella) are associated with mustelines of the closely related genera *Martes* and *Mustela*. However, if *Martes* is holophyletic, a secondary infestation of *Mustela* from this genus must be inferred.

The three species of *T. (Paratrichodectes)* are associated with three closely related African Mustelinae, and may have co-evolved with them. The host associations of the species of *T. (Trichodectes)* are rather more confusing. One species, *T. varius*, is parasitic on a number of Canidae and a single species of Viverridae; there is no doubt that the latter association is secondary. All but one other species of the subgenus are parasitic on Mustelidae, which are not thought to be paraplectic with respect to Canidae, and it is therefore probable that the association with Canidae is secondary. The same argument holds for the species parasitic on Ursidae, although the existence of two host-related (and morphologically distinct) subspecies of lice suggests that the infestation was initially with the ancestor of the bears concerned. The possible primary association of the *P. pinguis-voalabei* clade lies therefore with the Mustelidae, either with the Melinae or the Mellivoraecidae. The other two clades of *T. (Trichodectes)* are associated with Melinae and Galictinae (the latter is sometimes incorporated into the Mustelinae) respectively, but the poor resolution of the cladogram at this level makes conjecture difficult. The association with the South American Galictidae and Grisonidae is anomalous, as most of the lice in the subgenus (excepting only *P. ericeti*) are Old World, and Galictinae may be more closely related to the hosts of *T. (Paratrichodectes)* than to other Mustelinae. The relationship of Melinae and the monobiotic Mellivoraecidae is not known, but may be close.

The host of the ancestor of *Trichodectes* was therefore almost certainly a mustelid, although possibly not a member of one of the modern subfamilies.

The primary host of the *Trichodectes*

The primary host associations of the Trichodectes seem to be with Mustelidae (*Trichodectes, Neotrichodectes, Lutridia, Ursidae* (Werneckodectes) and Hyaenidae (*Prototeilicola*). The most parsimonious explanation for the association with Ursidae (*one species parasitizing a South American bear*), given that the Mustelidae are not paraplectic with respect to the Ursidae, is that it is secondary, and the primary host association of the *Trichodectes-Lutridia* clade is with the Mustelidae. The cladistic position of *Lutridia* and *Neotrichodectes* (both comprising species parasitic on *Lutrinae*) is confusing, and suggests that either the *Lutrinae* is paraplectic with respect to the rest of the Mustelidae, or that a secondary infestation of *Lutra* or *Pteronura* has taken place. The association of *Lutridia matzeckii* with both *Lutra* and *Onyctereutes* suggests a secondary infestation of the latter genus from the former, as the two other species concerned are at least partially sympatric, and the sister-species of *L. matzeckii* is also associated with *Lutra*. Collection from other species of *Lutra* may clarify the situation.

The *Trichodectes-Lutridia* clade, therefore, is believed here to have a primary association with Mustelidae, and secondary associations with Ursidae in Neotropical and Holarctic Regions, Procyonidae in the Neotropical Region, and Canidae at an unknown site. The association with Mustelidae has proceeded partially by co-evolution, but some secondary infestation must be invoked to explain discrepancies in the phylogenies. The cladistic relationships of some species of *T. (Trichodectes)* are difficult to reconcile with the relationships and distributions of their hosts.

The single genus of the *Trichodectes* not yet considered, *Prototeilicola*, has been recorded from two of the four living species of Hyaenidae. The discovery of further louse species on the other hyaenids and analysis of their relationships is necessary before any comment on co-evolution can be made. The significance of the host association of this clade with hyaenids will be discussed below.

**Genus Felicola**

Species of this genus parasites Herpestidae, Viverridae, Felidae and Canidae, most species being parasitic with members of the first family listed (Figs. 15, 16).

The parasitism of Canidae form a single clade in *F. (Sarcicolaeformis)*, and the most parsimonious explanation of the association is a single infestation of a canid from a

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FIG. 15. Cladogram and host association of *Felicola* (*Felicola*). The sister-group, *Felicola* (*Sarcicolaeformis*), is treated in Fig. 16.
Fig. 16. Cladogram and host associations of Felicola (Sarcoptiformes). The sister-group, Felicola (Felicola), is treated in Fig. 15.

The phylogenetic relationships of the species of felicola is difficult to determine. **Otocyon** is generally considered distinct from other Canidae (Van Gelder, 1978; Eisenberg, 1981), but the other canids infested may be placed in a single genus (Van Gelder, 1978). The typological and phenetic basis of canid systematic prohibited useful discussion at this level.

The positions on the cladogram of species parasitizing Viveridiae (F. viveridiae, F. hopkinsi, and *F. subrostratus*) suggest that these associations are secondary, resulting from two or three secondary infections of viverids from herpestids. A further species of Felicola, an undescribed member of the *F. zootoca*–viverid clade, parasitizes the viverid *Paradendrophorus hermaphroditus*. Paradoxurus and Viveridiae (the host of *F. viveridiae*) are not closely related, and even if *F. viveridiae* and the undescribed species are found to be sister-species, a single primary infection of Viveridiae by the common ancestor of these lice seems unlikely. The status of the associations with Viveridiae of *F. hopkinsi* and its sister-species, *F. subrostratus*, are discussed below.

**Felicola subrostratus** is the only species of the genus to parasitize Felidae, and its position on the cladogram indicates that this association is secondary. However, the host range of this louse includes members of the Felidae, Viveridiae and Herpestidae (Fig. 15), and the identity of the primary host is not certain. The sister-species of *F. subrostratus*, *F. hopkinsi*, parasitizes the viverid *Nandusia bonasia*. This species is not closely related to either of the two viverid hosts of *F. subrostratus*, and these two are not closely related to each other (Gregory and Hellman, 1939). Hopkins (1949) identifies the association of *F. subrostratus* with one of the three *Civettictis* civet, as the secondary association, by personal observation. Unless secondary association is not the result of a primary association by the common ancestor of *F. subrostratus* and *F. hopkinsi* with the ancestor of *Nandusia* and *Euploes* (the remaining viverid hosts of *F. subrostratus*) seems unlikely. The association of each of these lice is therefore believed to result from independent secondary infections of the present viverid hosts. The two remaining hosts of *F. subrostratus* are the herpestids *Ichneumia albiceps* and *Salamonea concolor*, either of which may be identified as the primary host of the louse. *Salamonea* is placed in the Madagascar subfamily *Galidactinae* (Petter, 1962), from which no other lice are known, whereas *Ichneumia* is African and more closely related to the other genera parasitized by Felicola. Further, *Ichneumia* is frequently domesticated whereas *Salamonea* is not (Walker, 1964), and therefore the chances of its lice coming into contact with potential hosts, especially other domestic animals such as the cat, are enhanced. For these reasons *Ichneumia* is identified as the primary host of *F. subrostratus*.

The remaining species of Felicola are associated with Herpestidae, and most genera of the family have been recorded as hosts to lice of the genus. There is a clear inference that the association of *Felicola* and Herpestidae is primary. Despite this, there are indications of secondary infestation. The *F. congorensis–occidentalis* clade is associated with *Crossarchus* and *Helogale* but, if both of these genera are considered to be holophyletic, at least one secondary infection must be postulated (Fig. 15). The most parsimonious hypothesis is that the association of *F. congorensis* and *Crossarchus* is secondary, although the existence of an undescribed sister-species to either *F. congorensis* or *F. helogale* and parasitic on *Crossarchus obscurus* poses problems.

Two of the *F. rani–viverid* clade have been identified above as having a secondary association with Viveridiae. Apart from these, one species is parasitic on *Atias paludinosus* and the others on Herpestidae. The distribution of species of this clade on the cladogram suggests at least a primary association with *Herpestes*, and therefore a secondary infestation of *Atias* might be suspected. However, *Herpestes* may be paraphyletic with respect to *Atias* (Gregory and Hellman, 1939), and the association therefore primary. Additional evidence suggesting a secondary infestation of *Atias paludinosus* from *Herpestes sanguineus* is discussed below under *Lorincola*. At least two secondary infestations of *Atias paludinosus* with *Felicola* must be postulated, as lice associated with this species appear at three points on the cladogram (Figs 15, 16).

The lack of a cladistic treatment of the Herpestidae precludes further comment.

**Genus Lorincola**

Species of this genus are associated with Viveridiae, Felidae, Herpestidae and Primates (Fig. 17). The distribution of host associations on the cladogram suggests

![Diagram](image-url)

**Fig. 17. Cladogram and host associations of Lorincola.**
clearly that the last two groups named are associated with Loricula following secondary infestations. The association with a primate probably took place in South East Asia, as both the louse concerned and its sister-species are distributed there, and that with Herpestidae in Africa as, again, both the clade concerned and its sister-group are sympatric in that continent.

Further comment must be made on the three species parasitic on Herpestidae, the L. paralaticeps-mungos clade. Two of them are parasitic on Atisal paludosus and the third on Herpestes sanguineus, their postulated clastic relationship suggesting an ancestral association with the former host. Herpestes may be paraphyletic with respect to Atisal, as noted above, but this relationship is not compatible with the clastic relationships of the species in the L. paralaticeps-mungos clade. A secondary infestation of Herpestes sanguineus from Atisal paludosus is the most parsimonious hypothesis to explain the distribution of lice on the host taxa. This being the case, the associations of the Felicola ramhi-viveridiae clade may be re-examined. In this clade there is also a sister-species relationship between lice parasitic on Atisal paludosus and Herpestes sanguineus. Although the possibility of the association of F. ramhi and Atisal being primary due to the paraphyly of Herpestes cannot be dismissed, the identification of a transfer of lice from Atisal paludosus to Herpestes sanguineus in Loricula must increase the likelihood attached to the proposition of a similar transfer, in the reverse direction, taking place in Felicola.

The association of the L. bengalensis-jucul clade with their hosts may have involved co-evolution, as Paguma and Paradoxurus are sometimes placed together in the subfamily Paradoxurinae (Gregory and Hellman, 1939; Honacki et al., 1982). Nadaba, parasitized by Felicola hopkinsi, is also placed in the same subfamily, as are several genera not known to be parasitized at all. In these cases either secondary absence or failure in collection may be suggested to explain the apparent absence of Loricula. However, an initial secondary infestation of the common ancestor of the two genera parasitized (which may, with Atisal, form a holophytic group) is also possible. Notably, Paradoxurus is also parasitized by an undescribed Felicola (F. inaqualee-zeylonicus clade), so multiple infestation is quite possible in the Viveridiae.

The identity of the primary host of Loricula is not certain, even though the associations with Primates and Herpestidae have been identified as secondary. A single species of viverid and 11 species of felid are known to be parasitized by species of L. (Loricula), the lice associated with the two families being (if L. nipobergi on the loris is ignored) sister-groups. If the Viveridiae are assumed to be holophytic (or at least not paraphyletic with respect to the Felidae) and if the clastic relationships of Loricula species are accepted, a secondary infestation of either Viveridiae of Felidae must be postulated. The clastic relationship between Felidae and Viveridiae is not certain (Fig 12), but the association of Loricula with the two families could be primary (possibly with one secondary infestation of Viveridiae); even if the two families form a paraphyletic group, secondary absence from other families may be involved to preserve the hypothesis of primary infestation. The relatively large number of Felidae parasitized, and their wide distributions, support the hypothesis of an early association of lice with members of this family, although all of the species concerned are in the genus Felis; collection of further species of lice from other genera of Felidae would strengthen the proposition. The clastic position of the viverid Conopopus (the louse of which is in the sister-group of the lice of Felis) is not known, but Gregory and Hellman (1939) suggest that it lies in the 'Hemigalida', which they put in a sister-group relationship to the 'Paradoxurida' (including Paradoxurinae but not Genetta or Priomodon); they also imply a closer phylogenetic relationship between Genetta and Priomodon than between either of these and the Hemigalida or Paradoxurida. If the relationships suggested by Gregory and Hellman are correct, the association of Loricula with Genetta and Priomodon can be considered primary, dating to their common ancestor, and two alternative hypotheses proposed to explain the host distribution of Loricula: (1) The association of Loricula with the Hemigalida plus Paradoxurida dates from their common ancestor, the lice being derived either from their common ancestor with the Viveridiae or by secondary infestation from the Herpestidae. If the lice are primary on the Viveridiae, they must be secondarily absent from groups other than the two named. The common ancestor of Genetta and Priomodon was colonized by lice from the Paradoxurida and the ancestor of Felis by lice from the Hemigalida. Lice of the genus Loricula will be found on other Viveridiae and possibly on other Felidae; if the association of Felicolini with Felicola is primary, Herpestidae and Viveridiae may be found to be cladistically closer to each other than either is to the Felidae. (2) The association of Loricula with the common ancestor of Viveridiae is primary. The association of Cynogale and L. malayanus must be secondary, the louse being acquired from a felid, or primary. If the association is primary, this association of a paraphyletic louse group with a holophytic host group may have resulted from an independent speciation of lice on the common ancestor of The Felidiae and Viveridiae followed by independent speciation of this ancestor into the spec-species of the two families, and appropriate loss of lice in some Viveridiae. In either case lice will be found on other Viveridiae and Felidae; Felidiae will be found to be cladistically closer to Viveridiae than either of these families is to Herpestidae.

The resolution of this problem awaits further collecting and a cladistic analysis of the Felicolinae.

The primary host of the Trichodectinae

The association of the ancestor of the Felicolini with the common ancestor of the Herpestidae and the Viveridiae, or possibly with that of the Herpestidae, Viveridiae and Felidae, seems likely. Further collecting is needed to determine the presence or absence of Felicolini on Cryptopodidae. The primary host of the Trichodectinae—Luridiae clade was an ancestor of some or all of the Mastilidae (Canoidea), but that of its sister-group (Proteolicea) is a member of (or the ancestor of) the Hyaenidae (Feliformes). Allowing that any primary association of Trichodectinae with Canoidea and Phocidae would have been lost on the assumption by these mammals of an aquatic life, no family of terrestrial Canoidea other than the Mustelidae (i.e., the Ursidae, Procyonidae, Ailuridae, Ailuropodidae and Canidae) is known to have a primary association with Trichodectinae. If the hypothesis is made of a primary association between the ancestor of the Trichodectinae and that of the Carnivora, the association between Hyaenidae and Proteolicea must be deemed to have resulted from a secondary infestation, and lice must be secondarily absent from the families named above. The alternative hypothesis is that the Trichodectinae are primarily associated with the Felicolini, and became associated with the ancestor of the Mustelidae by secondary infestation from the ancestor of the Hyaenidae; no further secondary absences need be postulated. The latter hypothesis is favored on the grounds of parsimony.
Neotrichodectine

Genus Geomydoecus

Geomydoecus is restricted to rodents of the family Geomyidae. The cladistic relationships between most of the members of the genus were not analysed by Lyal (1985), and those between the hosts are completely unknown. Timm (1983) suggests that there has been a marked degree of co-evolution between pocket gophers and lice, and uses the (phenetic) relationships of the Geomydoecus species to support postulated relationships of their hosts. Timm considers that "the Geomyzo-Geomydoecus system is consistent with Fahrenholz's Rule" (i.e., strict co-accommodation and co-specialization). If this were so, no host taxonomic divergence would be parasitized by more than one louse taxon, and no single taxonomic divergence would be associated with more than one host taxon (Lyal, 1986). Within Geomyza and Geomydoecus this is not the case, and the system is not compatible with Fahrenholz's Rule. The data presented by Timm (1983) are, however, consistent with resource tracking by Geomydoecus within Geomyza. The distributions of lice and hosts given by Timm and summarized in his fig 2 indicate a largely independent geographical distribution of Geomyza species and their lice. It is suggested here that the association of Geomydoecus and populations of Geomyza can be described using the island biogeography model of MacArthur and Wilson (1967). Because populations of the same species tend to be "closer" to one another (i.e., providing more opportunities for lice to colonize one from another) than populations of different species, and because geographical boundaries that delimit gopher species must delimit the distribution of lice, taxon boundaries of gopher and louse frequently coincide. It is therefore believed here that there has been repeated secondary infestation between members of the Geomyzidae. It is notable that several instances have been recorded of muscid predators being found with straggling specimens of Geomydoecus (Timm and Price, 1980; Timm, 1983).

Genus Neotrichodectes

Species of Neotrichodectes parazitize Mustelidae and Procyonidae (Carnivora) and Bradypodidae (Edentata) in the New World (Fig. 18). The two species parasitic on sloths (subgenus Lakshminarayanaella) are the only lice known from Edentata, and their position on the cladogram makes it virtually certain that lice have been secondarily acquired by sloths from a member of the Carnivora. Speciation within N. Lakshminarayanaella may have proceeded according to Fahrenholz's Rule, although if the rule has been fully adhered to further species of the subgenus must be expected from the other members of Bradypus and Choloepus. The supposed similarity of the sloth lice to hyrax lice, particularly Procaviola (Hopkins, 1949; Vanzolini and Guimarães, 1953; Eichler, 1963), does not reflect any phylogenetic relationship, and the suggestion that the association of sloths and Trichodectidae is "primary and ancient" (Vanzolini and Guimarães, 1955) is unfounded.

The remaining 11 species of Neotrichodectes are associated with members of the Procyonidae and Mustelidae, and within the latter family to members of the Mustelinae, Melineae and Mephitinae.

The positions on the cladogram of the two species parasitic on Procyonidae suggest these associations to be the result of independent secondary infestations from Mustelidae. This suggestion is supported by the lack of any close relationship between the procyonids (Simpson, 1945).

The position on the cladogram of the single species parasitizing a badger (Melineae), which is the sister-species of a parasite of the mephitine genus Conopatus, suggests a secondary infestation from Conopatus to Taxidea (Fig. 18).

The two remaining subfamilies parasitize, Mephistinae and Mustelinae, both appear on the two branches of the primary dichotomy on the Neotrichodectes cladogram, so some secondary infestation is almost certain. The number of secondary infestations is minimized by postulating that the lice were primarily parasitic on members of the Mephistinae, transferring to Mustelinae twice, and possibly once between different members of the Mephistinae (to account for the host association of N. wolfsoulti). If Conopatus is paraplethystic with respect to a holophyletic group comprising the other two skunk genera, no secondary transfer between members of the Mephistinae need be postulated at all. If Neotrichodectes is primarily parasitic on Mustelinae, four secondary infestations are necessary to explain the distribution of host associations on the cladogram. The two mustelines parasitized are not closely related, Eira being more closely related to some African genera than it is to Mustela (Ray et al., 1981), but the mephistine genera probably form a holophyletic group, restricted to the New World. The identifications of the Mephistinae as the probable ancestral hosts of Neotrichodectes is consistent with the geographical distribution and probable origin of the Geomydoecus-Neotrichodectes clade.

The primary host of the Trichodectidae

A cladogram of the Eutheria is depicted in Fig. 19 for comparative purposes.

The primary associations cited above for each major clade of the Trichodectidae are depicted in Fig. 20 and, as can be seen, are not immediately compatible with the host cladogram.

The associations of Trichodectidae with Primates have, apart from the three species of Cebocochla, been identified as secondary. If this remaining association is an indication of a primary association with the order, secondary absence of the lice on a large scale must be postulated. For this reason, the association is believed to be primary.
been a geomyid or a mephitine. The primary host association of the sister-group of this clade, the Trichodectinae, has been identified as the ancestor of either the Feloidea or the Carnivora. If the primary host association of the Neotrichodectinae is postulated to be with Mephitinae or even Mustelinae, and is believed to be derived with that of the Trichodectinae from a common ancestral host, this ancestral host must have been a member of the Canoidea. As the primary host association of the Trichodectinae-Lutridia clade has been identified as a musitellid, the most parsimonious identification of the common ancestral host is also as a musitellid. This hypothesis demands that infestation of the Feloidea took place twice from a Musitellid, once to give rise to the Feliscoinae and once to give rise to Protocricetidae. Considering that the primary host association of the Feliscoinae is with a postulated ancestor of most of the Feloidea, and that the Felidae is the sister-group of the Canoidea, the additional hypothesis must be made that the Mustelidae are the sister-group of most of the rest of the Canoidea. This is necessary to allow the Mustelinae to be distinct from the other Canoidea at an early enough period to provide a source of lice to the ancestor of the Herpestidae, Viverridae and Felinea. This hypothesis is not supported by the cladogram of Carnivora (Fig. 12). The alternative hypothesis is that the two clades of lice parasitizing Mustelidae became associated with their hosts independently, one as described from the Feloidea, the other from an unknown host. It is notable that the plesiomorphic form of the female external genitalia in Neotrichodectes and Geomyodescus is found in most species of the latter genus but in few of the former. If the form of the female genitalia is determined at least partially by the form of the host hair on which the egg must be cemented, as seems probable (Lyal, 1983), the assumption can be made that the form of the female genitalia found in numerous species of geomyid lice is adapted to oviposition on Geomyoidae, and that selection pressure on lice of other hosts (Neotrichodectes) has caused modification to this (plesiomorphic) form. If the plesiomorphic form of the female genitalia is an adaptation to oviposition on geomyid rodents, it follows that the primary host of the Neotrichodectinae was a geomyid or an ancestor of that family, from which the ancestor of Neotrichodectes was acquired by an ancestor of the Mephitinae.

The primary associations of the major clades of the Bovicolinae (including each subgenus of Damaena) comprise the Bovidae, Tragulidae and Equidae. The identity of the host of the ancestor of the subfamily is not clarified by the cladogram because of poor resolution. There is an early association with the Bovidae, and, if the association of Tragulidae with Tragulidae is primary, the ancestor of this group and the rest of the Bovicolinae (with the possible exception of Werneriella) may have parasitized the ancestor of the Ruminantia (Fig. 1). If this is the case, lice must be secondarily absent from the Cervidae, Moschidae, Giraffidae and Antilocapridae. If the association between Werneriella and Equidae is primary, an infestation of the common ancestor of the Perissodactyla and Artiodactyla might be postulated, in which case lice are secondarily absent from perissodactyla and the artiodactyla Suidae, Tayassuidae, Hippopotamidae and Camelidae as well as those mentioned above. The sister-group of the Perissodactyla has been held to be the Hyracoidae (McKenna, 1975; Eisenberg, 1981) and, if the second hypothesis above is correct, the association of Trichodectinae with the hyracoids as secondary for the cladogram of lice and Eutheria to be compatible. If it is not correct, and the primary association of the Bovicolinae lies within the ancestry of the Artiodactyla, the association of lice with the Hyracoidae can only be primary if an initial association with the Perissodactyla was lost, to be replaced by a secondary infestation with Werneriella from an artiodactyl.
The apparent restriction of Trichodectidae to Equus does not suggest a primary association with Perissodactyla, although the environment provided by the dermoceros of Rhinocerotidae may not be suitable for Trichodectidae. Specimens of the other family of extant Perissodactyla, the Tapiridae, have been examined for lice without success (Hopkins, 1949), but further examination of these hosts must be made to provide more evidence of the status of the association between Trichodectidae and Perissodactyla. The poor resolution of the cladogram of Bovicolinae prohibits further hypothesis, but it is clear that either secondary absence or secondary infestation must be invoked to explain the present associations of Trichodectidae with Artiodactyla, Perissodactyla and Hyracoidea, or the structure of the host or parasite cladograms must be changed.

No clear hypothesis can yet be proposed regarding the ancestral host association of the Trichodectidae, other than that it was with an eutherian and probably not an insectivore, primate, dermopteran, chiropteran or tupaiid. The primary host association of the Neo-trichodectidae was probably with a rodent in America, from which a predaceous ancestor of the Mephitidae acquired the ancestor of Neo-Trichodectidae. The primary host association of the Trichodectinae was with the ancestor of the Felidae; either the Canidae were also parasitized but lost their Trichodectidae, or the Felidae acquired their lice, as the Mephitidae are likely to have done, through predation on another animal. If the latter hypothesis is correct, this prey animal may be postulated also to be the rodent ancestor of the Geomyidae. The hypothesis of independent secondary infestation of this geomyid ancestor and of the Erethizontidae is maintained, but the source of these infestations cannot be identified. The large number of extinct Hyracoidea may have included these hosts, but it is difficult to see how this hypothesis can be tested. The Cebidae (or an ancestor of the Platyrrhine monkeys) may have acquired their lice from a byranx just as has the colobus more recently, and must have done this in Africa, as no fossil record of the byranxes exists outside this continent. The primary host association of the Bovicolinae is still more confusing. Although the strongest evidence is perhaps for a primary association with an ancestor of the Bovidae, the earliest fossil occurrence of this family is in the Miocene (Patterson, 1957), later than the most recent common ancestor of the Felidae (Flynn and Galindo, 1982) and thus after the initial dichotomy of the cladogram of the Trichodectidae. An earlier host of the Bovicolinae, and thus some secondary absence, must be postulated, although the identity of this host is not known.

Congruence of host and parasitic phylogenies

As noted in the introduction, louse and host phylogenies are frequently considered to be linked, and by this hypothesis the prediction is made that host and parasitic phylogenies are absolutely congruent. The discussion above indicates clearly that this prediction is not fulfilled within the Trichodectidae. If all speciation events recorded on the cladogram of Trichodectidae are considered for their possible compatibility with host speciation, 25% are clearly incompatible, of which 20% are associated with secondary infestations and the remaining 5% are speciation events of the parasites without concomitant host speciation. The rest of the history of the family is consistent with the operations of Fahrenholz's Rule given the most ‘favourable’ possible resolution of the host and host cladograms when these are not fully known at present. The figure of 25-50% is thus a minimum of incompatibilities, and will almost certainly rise with greater knowledge of host phylogeny and resolution of the louse cladogram.

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References


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