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

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(Accepted 17 March 1988)

The cladogram of Trichodecididae 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 phylectic tracking and host-group-limited resource tracking by the lice, a
substantial proportion (20 %) 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 Trichodecididae almost certainly paratanized a eutherian, but
the identity of the eutherian group is unclear. The primary host association of the
Nectrotrichodectes was with an American rodent; from which resource tracking
onto Mephitinae and then Mustelinae, Procyoninae, Brachypodinae and Felidae
took place. The Trichodecididae had an anomalous association with the ancestor
of the Felidae, with subsequent secondary infestations of Mustelidae, Canidae,
Ursidae and Procyonidae. The parasitism of the feloid ancestor was probably
derived by secondary infestation from a rodent or hyracoid. The ancestral host of
the Dasyoryginae may have been a hyracoid, and two secondary infestations of
primates are recorded in the subfamily. The eutherian hosts of the Eutrichocephal
lineae gained their lice from an unknown host. The ancestral host of the Bovicoline
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 investigation of the cladistic relationships of the Trichodecididae, parti-
cularly at the primary farcions of the cladogram proposed by Lyal (1985), where
apomorphies have been very difficult to discern, and in the Bovicoline. (3)
Production of a more fully resolved cladogram of the Eutheria and the
identification of holophyletic mammalian groups at all levels.

Introduction
Most discussion 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
Trichodecididae 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 Trichodecididae; (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 parapathic '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 (Plate 197), it is considered here that there is a topological correspondence between dichotomously branching cladograms and phylogenetic trees (following Wiley, 1979, 1981). A multiple fusionation 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 parapathic 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 Loricataclothrix—mungos clade (Fig. 17), paralactepe and latoeops parasitise Arland paludinosum while the sister-species of latoeops, L. mungos, is a parasite of Herpestes sangineus. In this case it is inferred that the association of C. mungos with H. sangineus is apotypic 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 below 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.
Genus Damalini

Species of *Damalina* are associated with hosts in the Bovidae and Cervidae. Those species of *Damalina* associated with members of the latter family form two small clades in the subgenera *D. (Cervicola)* and *D. (Tricholophaeus)*. The positions of these clades on the cladogram (Figs. 4, 8) indicate the associations to be the result of independent transfers of lice to Cervidae from Bovidae. The primary host association of *Damalina*, 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 *Damalina*; the cladograms of the subgenera, with associated host identities, are depicted in Figs. 4, 6, and 8.

Species of *D. (Damalina)* are associated with Alcelaphini, Caprini, 'Rupicaprinae', Antilopini, Neotragini and Reduncini (Fig. 4). In no postulated phylogeny of the Bovidae do these tribes form a holophyletic group, although in Kingdom's (1982) phylogeny the Reduncini are more closely related to the other tribes than is indicated by Gentry (1978). It is notable that Gentry (1980) does raise doubts about the bovid affines of the Reduncini.

The two species of *D. (Damalina)* parasitic on reduncines (*D. adneto* and *D. hili*, both associated with Kobus spp.) form an unresolved trichotomy on the cladogram with *D. pelea*, a parasite of the rheed *Pelea capreolus*. The position of *D. pelea* is tentative, as specimen have not been seen in this study. *Pelea* is placed by some authors in the Reduncini (Honokai 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, *Pelea* might be a rheed 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 *Pelea* to be anything other than a reduncine. The identities of the remaining hosts of *D. (Damalina)*, and their relative positions on the cladogram is, therefore, secondary infestation has occurred, and the association with Reduncini and *Pelea* is unlikely to be primary. Some secondary absence may be suggested. The two species of *Kobus* parasitized by *D. adneto* and *D. hili* form a monophyletic group, possibly made paraphyletic by the exclusion of *K. leche* (Gentry, 1978). If *D. adneto* and *D. hili* are sister-species, the association may be explained by a single ancestral infestation from another bovid, with possible secondary absence from *K. leche*.
These lice are discussed below. The cladogram of the lice of the Akelaphini (Fig. 4) may be compared to the cladogram of the hosts produced by Vrba (1979) (Fig. 5a). The two cladograms do not entirely agree; 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 Damalisus, which is clearly not in accordance with any conception of Cimicoides as a holophyletic genus. To achieve full accord between host and parasite cladograms a secondary infestation of Damalisus from Connochaetes is postulated. With this hypothesis, the association of the D. theileri-form species clad with the Akelaphini, with the exception of a single species, can be adequately described by reference to Fahrenholz’s Rule. It is predicted that lice of the clad will be found on Sigmodon hispidus, but not necessarily on Damalisus horteri.

Species of D. (Cervicola) are associated with Tragelaphini, Reduncini, Cephalophini and Cervidinae (Fig. 6).

The association with Cervidinae (of the D. mauli-muntiacus clad) has been noted above as secondary. The four described and one undescribed species in the clad parasitize members of the Cervinae (Cervus, Axis), Odocoileinae: Capreolus (Capreolus), Muntiacinae (Muntiacus) and Hydropotesinae (Hydropotes). Because the D. mauli-muntiacus clad has not been resolved fully, the hypothesis of a primary association of the clad with the most recent common ancestor of the Cervidae, followed by co-evolution, is not refuted directly by the cladogram. Mitigating against this is (i) the absence of members of the clad from most Cervidae, including species very closely related to some of those parasitized, (ii) the association of other members of D. (Cervicola) 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 present host associations, and is considered 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. mauli-muntiacus clad is sister-group to the *D. hervicki-taranga* clad, species of which are parasitic on Cephalophini and Reduncini. Species of the D. redunca-loricensis clad, which is the sister-group of the D. hervicki-muntiacus clad 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. hervicki-taranga clad was associated with (at least) two host species, a primitive reducine and a primitive cephaphine. This association may have been with 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 reducine-taranga clad. In the other branch, the ancestor of the mauli-muntiacus clad may have moved from either the cephaphine or the reducine to a cervid. The course of these postulated evolutionary events is depicted in Fig. 7a. (2) The ancestor of the clad was parasitic on either an ancestral reducine or an ancestral cephaphine, and speciation with secondary infestations of the other bovid tribe and of the Cervidinae followed to give the pattern of association seen today (Fig. 7b). The Cephaphineae 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. (Cervicola) are associated with the Tragelaphini, although a single primary association with this tribe is not certain. The association of D. hopkinsi with species of both *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...
may, if Tragelaphus is paraphyletic, lie within this genus). The association of D. ameotess and D. natalensis with different subspecies of Tragelaphus scriptus is not compatible with the cladogram, and neither is the association of D. ameotess and D. hopkinsi with T. spekei and T. angasi respectively, as their hosts are probably sister-species (Gentry, 1978).

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

The association with Cervidae (of the D. altimarginata-indica clade) has been noted above as secondary. Lice of this clade are associated with three genera of the New World Odocoileini (the D. altimarginata-paradela 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 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 Odocoileini 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 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. liperoxides and D. paradela with Odocoileus hemionus and O. virginianus indicates that speciation of the lice parasitizing the Odocoileini has not always followed the predictions of Fahrenholz's Rule.

The remaining hosts of the subgenus belong to the Aepycerotini, Antilocapridae, Cephalophini and Cervidae (Fig. 8).
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. bedfordi 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 (Alephasinae: Aepycerotini). The same host is also parasitized by D. (T.) aepyceros, a member of the single remaining clade in D. (Tricholipurus), the D. aepyceros-spinifer 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.) aepyceros-spinifer clade (and of the subgenus Tricholipurus) is suggested by the sister-group relationship of Aepyceros and the Alcelaphini, which are parasitized by the D. (D.) sheltleri-ornata clade as described above. This hypothesis may be broken down into the following elements: (1) The ancestor of D. (Tricholipurus) was associated with an aepycerotine ancestral to modern Aepyceros melampus, a primary infestation derived from its common ancestor with the D. (D.) sheltleri-ornata clade, which itself parasitized the ancestor of the Alcelaphini. (2) The first speciation event in the history of D. (Tricholipurus) to be discernible by study of living species gave rise to two species on Aepyceros melampus (D. elongata and D. aepyceros). (3) All other species of the D. (T.) aepyceros-spinifer 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.) aepyceros-spinifer clade with Antilopini and that of the D. (T.) lineata-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 denoted by that in Fig. 3. The hypothesis postulates that the ancestor of D. (Tricholipurus) was parasitic on the ancestor of the Antilopini plus Neotragini (Antilopinae, Gentry, 1978). The ancestor of the D. aepyceros-spinifer clade was associated with the ancestor of the Antilopini, and secondary infestation of Aepyceros and Cervidae took place from antilopines. The ancestor of the D. lineata-moschatus 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. (Damalini) with this subfamily (Antilopinae sensu Gentry), and again division with the divergence into Neotragini and Antilopini took place (today represented by the lice on Pelo and Gazella). Secondary infestations of the Alcelaphini, Reduncini and 'Rupicaprini' took place.

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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 investigations within relationships of Bovidae.

It is notable that, if Gentry's (1978) division of the Bovidae into aegodont and biiodont tribes (Fig 2) is accepted, D. (Damalini) and D. (Tricholipurus) are primarily associated with aegodonts and D. (Cervicola) is, as regards Bovidae, entirely associated with biiodonts. If Kingdom's (1982) division of the Bovidae into subfamilies (Fig 3) is accepted, all members of Damalini that are associated with Bovidae, except three species of D. (Cervicola), are parasitic on members of the Antilopinae. The cladogram of Damalini does not support any phylogeny of the Bovidae rather than the other.

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**Genus Bovicola**

Species of Bovicola are associated with Bovidae, Cervidae and Camelidae (Fig. 9). Only one species, B. breviceps, is parasitic on a camelid, being the only trichoecid association with that family. This fact, together with the position in the cladogram of B. breviceps with respect to other species associated with Bovidae, supports the hypothesis that Bovicola is associated with the Cervinae.

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 Cervidae, 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 Euphorbus davidianus and Odobenus columnarius results from secondary infestations.

The remainder of the species of Bovicola are associated with Caprini, Rupicaprinae and Bovini. The last-named tribe is not closely related to the other two (Figs 2, 3), and the position on the cladogram of the single species parasitizing a bovine (B. bovis, on domestic cattle) suggests the association to have been derived by secondary infestation from a caprine.

The poor resolution of the cladogram prohibits much further speculation, but it is notable that a number of species are associated with the domestic goat. It may be 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 some or all of the Caprinae.

Genus Werneckeia

Members of this genus are all species parasitize 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 Werneckeia makes detailed comment impossible, the postulated sister-species relationship of W. equi and W. ocellatus 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. equi, 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. ocellatus, 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 Werneckeia primarily associated with one branch of the cladogram (comprising the species of the nominate subgenus). Discovery of species of Werneckeia on E. hemionus, kiang and onager would not necessarily be expected. If Eisenmann’s cladogram is correct, there is equal likelihood that the transfer took place in either direction, and associations between species of Werneckeia and E. hemionus, kiang and onager would be expected. An alternative hypothesis is also possible if this cladogram is correct. This is that the ancestor of the E. burchelli caballus clade was parasitized by an ancestor of W. equi, ocellatus and zebræ, but speciation did not occur at the primary dichotomy of the equid cladogram. Speciation of the louse did occur when the ancestor of E. zebræ diverged from the ancestor of 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 infected with W. equi or a sister-species to this or W. ocellatus, and E. zebræ 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 Werneckeia with Equus may date to the Hemphillian (early PD) period in North America, as Bennett (1980) suggests this origin for the genus.

The remaining two species of Werneckeia both parasite Ammotragus lervia (Capra lervia of Gentry, 1978). Although the two lice are not indicated as sister-species on the cladogram, they are very close morphologically, the females apparently being indistinguishable. The association of Werneckeia with Ammotragus may be monophyletic, 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 Newbigging (1936) suggests a central or south central, or a north American origin for the species. A North American origin for Ammotragus seems unlikely, therefore, so the hypothesis of an infestation of horses from this host is rejected. Far more likely is the Ammotragus acquired Werneckeia 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 (two subspecies) parasitic on the bison and the buffalo (Bovidae: Bovini), and Tragulicolae 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.
Estrichophiliinae
The single genus is parasitic on New World porcupines (Erethizonidae: Rodentia). The origin of this association will be discussed further below. No attempt has 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 Estrichophilius on Coendou prehensilis and C. spinosus is notable.

Dasypodinae
The initial dichotomy of the clade divides Cebidcola, 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 (Hyracoidae) 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. (Meganariomorphus) colobus on a monkey (Lyal, 1985). This association must be secondary, as all other members of the clade (the Procaviidae–Eurypodinae clade) are parasites of hyraxes.

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

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**Fig. 13. Cladogram and host associations of Trichodectini. Host family Mustelidae is indicated by M.**

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

**Genus Trichodectes**
Species of this genus parasitize the canid families Ursidae, Canidae, Procyonidae and Mustelidae, the predominant 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 infestation, the distribution of the host taxa on the cladogram suggests a more parsimonious hypothesis of secondary infestation in some cases.
The three species parasitizing Procynoidae comprise a single clade in T. (Stachyaella), and are sister-group of some of the musteline lice (Fig. 14). The Procynoidae are not the sister-group of some of the Mustelinae, but of the Mustelidae plus Phocidae (Telford, 1976). The incompatibilities between host and host clades in primates cannot be resolved by postulating that the association with Procynoidae follows secondary infestation from a mustelid. The sister-species relationship between the two species parasitizing Procynus is suggestive of a primary infestation, although the relationship between the two races is not known. Further collections from other species of Procynus, 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 of Panus is difficult to assess. Simpson (1945) suggests that this genus is an early offshoot from the line which gave rise to other Procynoidae but, if this were so and the infestation with Trichodectes were primary, the other genera of Procynoidae 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 procynoid relationships.

The remaining species of Trichodectes (Stachyaella) 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. sausa, 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 Mustelinae, 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 T. pinguis-viverrinii clade lies therefore with the Mustelidae, either with the Melesinae or the Mellivorinae. The other two clades of T. (Trichodectes) are associated with Melesinae and Galictinae (the latter is sometimes incorporated into the Mustelinae) respectively, but the poor resolution of the cladogram at this level makes convection difficult. The association with the South American Galictis and Grisonella is anomalous, as most of the lice in the subgenus (excepting only T. p. sausa) are Old World, and Galictinae may be more closely related to the hosts of T. (Paratrichodectes) than to other Mustelinae. The relationship of Melesinae and the monobasic Mellivorinae 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, Neotaristria, Lutridia), Ursidae (Vermecocotylus) and Hyaenidae (Protecion). 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 Neotaristria (both comprising species parasitic on Lutridia) is confusing, and suggests that either the Lutridinae is paraphyletic with respect to the rest of the Mustelidae, or that a secondary infestation of Lutra or Pteronura has taken place. The association of Lutridia martreii with both Lutra and Aonyx 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. martreii is also associated with Lutra. Collection of other species of otter 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, Procynoidae in the Neotropical Region, and Canidae as 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 Trichodectinae not yet considered, Protelicia, has been recorded from two of the four living species of Hyaenidae. The discovery of furtherouse 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 parasitize Herpestidae, Viverridae, Felidae and Canidae, most species being associated with members of the first family listed (Figs 15, 16).

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

![Diagram](attachment:Figure_15.jpg)

**FIG. 15. Cladogram and host association of Felicola (Felicia).** The sister-group, Felicola (Sarcocoryne), is treated in Fig. 16.
Co-evolution of trichodectid lice and their hosts

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 *Ichnuemia* 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 that, there are indications of secondary infestation. The *F. congoensis-occidentalis* clade is associated with *Crocuta* and *Helogale* but, if both of those genera are considered to be holophyletic, at least one secondary infestation must be postulated (Fig. 15). The most parsimonious hypothesis is that the association of *F. congoensis* and *Crocuta* is secondary, although the existence of an undescribed sister-species to either *F. congoensis* or *Helogale* is parasitic on *Crocuta* is discussed below under *Loriccula*. At least two secondary infestations of *Atelax 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 Loriccula**

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

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**Fig. 16. Cladogram and host associations of *Felicola* (Viveridae).** The sister-group, *Felicola* (*Felidae*), is treated in Fig. 15.

The phylogenetic relationships of the species of *F. hopkinsi* and *F. subrostratus* suggest that these associations are secondary, resulting from two or three secondary infestations of viverids from herpestids. A further species of *Felicola* is tentatively assigned to the *F. hopkinsi-*viveridae clade, parasites the viverid *Paradoxurus hermaphroditus*. *Paradoxurus* and *Viveridae* (the host of *F. viveridae*) are not closely related, and, even if *F. viveridae* and the undescribed species are to be sister-species, a single primary infestation of *Viveridae* by the common ancestor of these lice seems unlikely. The status of the associations with *Viveridae* 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, Viveridae and Herpestidae (Fig. 15), and the identity of the primary host is not certain. The sister-species of *F. subrostratus*, *F. hopkinsi*, parasites the viverid *Nandinia bengalensis*. This species is closely related to either of the two viverid hosts of *F. subrostratus*, and these two species are not closely related to each other (Gregory and Hellman, 1939). Hopkins (1949) identifies the association of *F. subrostratus* with one of the three: *Crocuta* (*viveridae*), and a secondary association by the common ancestor of *F. subrostratus* and *F. hopkinsi* with the ancestor of *Nandinia* and *Eupleres* (the remaining viverid hosts of *F. subrostratus*) seems unlikely. The association of each of these two lice is therefore believed to result from independent secondary infestations of the present viverid hosts. The two remaining hosts of *F. subrostratus* are the herpestids *Ichnuemia albicuda* and *Salamone concolor*, either of which may be identified as the primary host of the louse. *Salamone* is placed in the Madagascar subfamily Gaudichaudinae (= Galidinae) (Petter, 1962), from which no other lice are known, whereas *Ichnuemia* is African and closely related to the other genera parasitized by *Felicola*. Further, *Ichnuemia* is frequently domesticated whereas *Salamone* is not (Walker, 1964), and
clearly that the last two groups named are associated with *Lorisidea* 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 *Atelis paludumosus* and the third on *Herpestes sanguinipes*, their postulated cladistic relationship suggesting an ancestral association with the former host. *Herpestes* may be paraphyletic with respect to *Atelis*, as noted above, but this relationship is not compatible with the cladistic relationships of the species in the *L. paralaticeps--mungos* clade. A secondary infestation of *Herpestes sanguinipes* from *Atelis paludumosus* is the most parsimonious hypothesis to explain the distribution of lice on the host taxa. This being the case, the associations of the *Felicia rahmi--viveridiae* clade may be re-examined. In this clade also there is a sister-species relationship between *louse parasitic on Atelis paludumosus and Herpestes sanguinipes*. Although the possibility of the association of *F. rahmi* and *Atelis* being primary due to the paraphyly of *Herpestes* cannot be dismissed, the identification of a transfer of lice from *Atelis paludumosus* to *Herpestes sanguinipes* in *Lorisidea* must increase the likelihood attached to the proposition of a similar transfer, in the reverse direction, taking place in *Felidea*.

The association of the *L. bengalensis--jucil* clade with their hosts may have involved co-evolution, as *Pygama* and *Paradoxurus* are sometimes placed together in the subfamily *Paradoxurinae* (Gregory and Hellman, 1939; Honacki et al., 1982). *Nandina*, parasitized by *Felodia 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 *Lorisidea*. However, an initial secondary infestation of the common ancestor of the two genera parasitized (which may, with *Arctis*, form a holophylytic group) is also possible. Notably, *Paradoxurus* is also parasitized by an undescribed *Felicia* (*F. inaquata--zeleus* clade), so multiple infestation is quite possible in the *Viveridiae*.

The identity of the primary host of *Lorisidea* 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. (Lorisidea)*, the lice associated with the two families being (if *L. nippebergi* or the louse is ignored) sister-groups. If the *Viveridiae* are assumed to be holophylytic (or at least not paraphyletic with respect to the Felidae) and if the cladistic relationships of *Lorisidea* species are accepted, a secondary infestation of either *Viveridiae* of Felidae must be postulated. The cladistic relationship between *Felidae* and *Viveridiae* is not certain (Fig. 12), but the association of *Lorisidea* 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 cladistic position of the viverid *Conopale* (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 'Hemigalidea', which they put in a sister-group relationship to the 'Paradoxurida' (including *Paradoxurinae* but not *Genetta* or *Prionodon*); they also imply a closer phylogenetic relationship between *Genetta* and *Prionodon* than between either of these and the *Hemigalidea* or Paradoxurida. If the relationships suggested by Gregory and Hellman are correct, the association of *Lorisidea* with *Genetta* and *Prionodon* can be considered primary, dating to their common ancestor, and two alternative hypotheses proposed to explain the host distribution of *Lorisidea*: (1) The association of *Lorisidea* with the *Hemigalidea* 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 *Prionodon* was colonized by lice from the Paradoxurida and the ancestor of *Felis* by lice from the *Hemigalidea*. Lice of the genus *Lorisidea* will be found on other *Viveridiae* and possibly on other Felidae; if the association of *Felicojini* with *Felidea* 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 *Lorisidea* with the common ancestor of *Viveridiae* is primary. The association of *Cynopale* and *L. malayensis* may 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 holophylytic host group may have resulted from an independent speciation of lice on the common ancestor of the *Felidae* and *Viveridiae* followed by independent speciation of this ancestor into the two 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; Felidae 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 Felidea.

The association of the host of the *Trichodectinae* is the common ancestor of the *Herpestidae* and *Viveridiae*, or possibly with that of the *Herpestidae*, *Viveridiae* and Felidae, seems likely. Further collecting is needed to determine the presence or absence of *Felicojini* on *Cryptoproctidae*. The primary host of the *Trichodectinae*--*Luridinae* was an ancestor of one or all of the Mustelidae (Carnivora), but that of its sister-group (*Proteolocidae*) is a member of (or the ancestor of) the Hyaenidae (Feloidea). Allowing that any primary association with *Trichodectinae* with *Oxudidae* and *Phocidae* would have been lost on the assumption by these mammals of an aquatic life, no family of terrestrial Carnivora other than the *Mustelidae* (i.e., *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 *Proteolocidae* 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 *Felidea*, 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 favoured on the grounds of parsimony.
Neotrichodectinae

Genus Geomydectes

*Geomydectes* 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 Geomydectes species to support postulated relationships of their hosts. Timm considers that 'the Georyzis-Geomydectes system is consistent with Fahrenholz's Rule' (i.e., strict co-accommodation and co-specialisation). If this were so, no host taxon would be parasitized by more than one louse taxon, and no louse taxon would be associated with more than one host taxon (Lyal, 1966). Within Geomyz and Geomydectes this is patently 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 *Geomydectes* within Geomyz. The distributions of lice and hosts given by Timm and summarized in his fig 2 indicate a largely independent geographical distribution of Geomyz species and their lice. It is suggested here that the association of *Geomydectes* and populations of *Geomyz* 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 invasion between members of the Geomyzidae. It is notable that several instances have been recorded of mustelid predators being found with strangling specimens of *Geomydectes* (Timm and Price, 1980; Timm, 1983).

Genus Neotrichodectes

Species of *Neotrichodectes* parasitize Mustelidae and Procyonidae (Carnivora) and Bradypodidae (Edentata) in the New World (Fig. 18). The two species parasitic on sloths (subgenus *Lakshminarayana*) 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. (Lakshminarayana)* 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 Bradypodinae and Choloepinae. The supposed similarity of the sloth lice to hyrax lice, particularly *Pecarinola* (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, Melinei and Mephitinae.

The positions on the cladogram of the two species parasitic on Procyonidae suggest that these associations to be the result of independent secondary infestations from Mustelinae. 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 (Melinei).

Co-evolution of trichodectid lice and their hosts

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<tr>
<th>Louse Family</th>
<th>Host Family</th>
<th>Genus</th>
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<td>N. (N. tigris)</td>
<td>Procyonidae</td>
<td><em>N. tigris</em></td>
</tr>
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</table>

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 parasitized, Mephitinae 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 Mephitinae, transferring to Mustelinae twice, and possibly once between different members of the Mephitinae (to account for the host association of *N. fulvus*). If *Conopatus* is paraphyletic with respect to a holophyletic group comprising the other two skunk genera, no secondary transfer between members of the Mephitinae 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 mephitine genera probably at least form a holophyletic group, restricted to the New World. The identification of the Mephitinae as the probable ancestral hosts of *Neotrichodectes* is consistent with the geographical distribution and probable origin of the *Geomydectes-Neotrichodectes* clade.

The primary host of the Trichodectidae

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

The primary association depicted 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 *Cebuella*, 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 Trichodectidae, has been identified as the ancestor of either the Fleoidea or the Carnivora. If the primary host association of the Neotrichodectidae is postulated to be with Mephitidae or even Mustelidae, and is believed to be derived with that of the Trichodectidae from a common ancestral host, this ancestral host must have been a member of the Canoidea. As the primary host association of the Trichodectidae clade has been identified as a mustelid, the most parsimonious identification of the common ancestral host is also as a mustelid. This hypothesis demands that infestation of the Fleoidea took place twice from a Mustelid, once to give rise to the Felicicolina and once to give rise to Prodocida. Considering that the primary host association of the Felicoidea is with a postulated ancestor of most of the Fleoidea, and that the Fleoidea 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 Mustelidae 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 Felidae. 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 Fleoidea, the other from an unknown host. It is notable that the pleisiomorphic form of the female external genitalia in Neotrichodectes and Geomyodes is found in most species of the latter genus but in very 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, 1985), the assumption can be made that the form of the female genitalia found in numerous species of geomyid lice is adapted to oviposition on Geomyidae, and that selection pressure on lice of other hosts (of Neotrichodectes) has caused modification to this (pleisiomorphic) form. If the pleisiomorphic form of the female genitalia is an adaptation to oviposition on geomyid rodents, it follows that the primary host of the Neotrichodectidae 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 Domesticus) comprise the Bovicidae, 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 clearly an early association with the Bovicidae, and, if the association of Tragulinae with Tragulidae is primary, the ancestor of this genus and the rest of the Bovicola (with the possible exception of Weermeeckelina) 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 Weermeeckelina 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 other Perissodactyla and the artiodactyla Suidae, Tayassuidae, Hippopotomidae and Camelidae as well as those mentioned above. The sister-group of the Perissodactyla has been held to be the Hyracoida (McKenna, 1975; Eisenberg, 1981) and, if the second hypothesis above is correct, the association of Trichodectidae with the hyracoida must be 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 Hyracoida can only be primary if an initial association with the Perissodactyla was lost, to be replaced by a secondary infestation with Weermeeckelina from an artiodactyl.
The apparent restriction of Trichodectidae to Equus does not suggest a primary association with Perissodactyla, although the environment provided by the dermecos of Rhinoceridae may not be suitable for Trichodectidae. Specimens of the other family of extinct 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 Hyracoidae, 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 tapir. The primary host association of the Neotrichodectidae was probably with a rodent in America, from which a predatory ancestor of the Mephitidae acquired the ancestor of Neotrichodectidae. 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 Mephitinae 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 Hyracoidae may have included these hosts, but it is difficult to see how this hypothesis can be tested. The Ceboidea (or an ancestor of the Platyrhine monkeys) may have acquired their lice from a byraux just as has the colobus more recently, and must have done this in Africa, as no fossil record of the byrauxes 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 Galgano, 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 tightly linked, and by this hypothesis the prediction is made that host and parasite phylogenies are absolutely congruent. The above discussion 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 specialization events of the parasites without concomitant host speciation. The rest of the history of the family is consistent with the operations of Fahrenheit's Rule given the most 'favorable' possible resolution of the louse and host cladograms when these are not fully known at present. The figure of 25-30% is thus a minimum of incompatibilities, and will almost certainly rise with greater knowledge of host phylogeny and resolution of the louse cladogram.
Co-evolution of trichodectid lice and their hosts


