Ancestral transfer of symbionts between cockroaches and termites: an unlikely scenario†

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SUMMARY

Thorne's (Proc. R. Soc. Lond. B 241, 37 (1990)) studies of the laboratory behaviour of extant woodroaches (Cryptocercus) and termites (Zootermopsis) suggest that transfaunation of hindgut protozoans potentially could occur by aggression and consumption in the field. However, existing literature suggests no overlap in protozoan species composition for these two taxa. Furthermore, it is doubtful that transfaunation would occur in the solitary ancestral 'termitoid' and 'roachoid' lines proposed by Thorne; not only is it unlikely that such insects would encounter each other, but it is doubtful that they would show the degree of aggression exhibited by the termite soldiers in her study. Inheritance from an ancestor common to Cryptocercus and the lower termites remains the most logical explanation for the presence of the unique cellulolytic oxymonad, trichomonad and hypermastigote flagellates in these two groups.

1. INTRODUCTION

Thorne (1990) conducted laboratory experiments in which she showed that aggressive and consumptive behaviour occurs in termites of the genus Zootermopsis when a nymph of the woodroach Cryptocercus punctulatus is introduced into their chamber. Soldier termites quickly kill the intruder, and the corpse is then consumed by the remainder of the colony. In the reverse situation, woodroaches were not observed killing a Zootermopsis intruder, but they did feed on freshly killed termite corpses. Based on these observations, Thorne postulates that in sympatric populations of these two genera, opportunities for aggressive encounters and consequent transfaunation of hindgut protozoans exist because Cryptocercus and Zootermopsis occasionally occur in the same log. Thorne argues that there is no known close match between protozoan species in Zootermopsis and Cryptocercus because no one has surveyed sympatric populations, and because transfaunation, even if temporarily persistent, is likely to be a rare event.

Currently, the prevailing hypothesis for the presence of similar cellulolytic gut fauna in Cryptocercus and the lower termites is one of association by descent: they were inherited from a common ancestor of the two taxa (Cleveland et al. 1934; Kirby 1937; Bobyleva 1975). Based on her studies, however, Thorne presents an alternative hypothesis: aggression and consumption in the solitary ancestors of Cryptocercus and the termites are responsible for the presence of protozoans in the modern lineages of these two groups. The following evolutionary scenario is presented (Thorne 1990, p. 40). 'Cockroaches' and prototermites diverged from a common ancestor as solitary detritivores lacking intestinal symbionts as early as the Carboniferous or Permian. Over time, one or the other taxon acquired cellulolytic gut protozoans; transfaunation of the protozoans to the other taxon then occurred via aggression and consumption. Termites and cockroaches continued to evolve, and their intestinal physiology, anatomy and life histories became more specialized.

I contend that there is no evidence for transfer of gut protozoans via aggressive and consumptive behaviour in natural populations of extant Cryptocercus and Zootermopsis and, more importantly, it is unlikely that the solitary, non-woodfeeding ancestors proposed by Thorne would share the behavioural attributes of extant social woodfeeders.

2. PROTOZOA OF CRYPTOCERCUS AND ZOOTERMOPSIS

The flagellates in question are sufficiently well studied to suggest that those in the woodroach are not any more closely related to the protozoans of Zootermopsis than to the protozoans of allopatric genera of termites. Cleveland et al. (1934) and Cleveland (1953) described the flagellates of the Pacific coast Cryptocercus. The samples were collected in Cottage Grove, Glendale, and Divide, Oregon, Willow Creek and Crescent City, northern California, and Chehalis, Washington. All of these sites are within the current range of both Zootermopsis angusticollis and Z. nevadensis (Castle 1934; Weesner 1965). Much of the work on the hindgut fauna of Zootermopsis was from material collected in California (Kofoid & Swezy 1919e, d; Kirby 1930, 1932). Specific locations are cited in Kofoid & Swezy (1919a, b) and Kirby (1932): Berkeley, San Francisco

† A reply to this paper by Thorne (Proc. R. Soc. Lond. B 246, 191 (1991)) will appear in the next issue.
Table 1. Protozoan hindgut fauna of sympatric Cryptocercus and Zootermopsis

<table>
<thead>
<tr>
<th>Pacific coast</th>
<th>Zootermopsis angusticollis and Zootermopsis nevadensis</th>
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<tbody>
<tr>
<td>Cryptocercus punctulatus</td>
<td>Hexamastix termopsidis</td>
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<tr>
<td></td>
<td>Streblomastix strix</td>
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<tr>
<td></td>
<td>Tricercomitus termopsidis</td>
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<td></td>
<td>Trichonotopsis termopsidis</td>
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<td></td>
<td>Trichonympha camppanula</td>
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<td></td>
<td>Trichonympha collaris</td>
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<td>Trichonympha sphaerica</td>
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<td>Barbulanympha laurabuda</td>
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<td>Barbulanympha ufalula</td>
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<td>Barbulanympha estaboga</td>
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<td>Barbulanympha wenyonb</td>
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<tr>
<td>Eucromonympha tula</td>
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<tr>
<td>Hexamita cryptocerci</td>
<td></td>
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<tr>
<td>Leptospironympha rudisb</td>
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<tr>
<td>Macrospironympha xyloplethab</td>
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<tr>
<td>Monocercomonoides globus</td>
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<td>Naisla proteus</td>
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<tr>
<td>Oxymonas nana</td>
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<td>Paranotila lata</td>
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<td>Prophoramomas tocopola</td>
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<tr>
<td>Rhyehonympha tarda</td>
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<tr>
<td>Saccinobaculus ambloaxostylus</td>
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<tr>
<td>Saccinobaculus lata</td>
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<td>Trichonympha acuta</td>
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<td>Trichonympha okolona</td>
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<td>Trichonympha algou</td>
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<td>Trichonympha lata</td>
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<td>Trichonympha chula</td>
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<td>Trichonympha parva</td>
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<tr>
<td>Trichonympha grandisb</td>
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<tr>
<td>Uryonympha taelu</td>
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</table>

a After summaries in Bobyleva (1975) and Yamin (1979).

b Absent in the Appalachian population of Cryptocercus punctulatus.

and Carmel, all of which are south of the Pacific coast range of Cryptocercus. Andrews (1925), however, studied Zootermopsis from Oregon, and Cleveland (1925) stated that the hindgut fauna of the Zootermopsis he examined from Oregon did not differ from those collected in California. It is likely, then, that table 1 is an accurate reflection of the protozoan hindgut symbionts present in Cryptocercus and Zootermopsis in their current zone of sympatry.

Z. angusticollis and Z. nevadensis share the same seven protozoan species (Yamin 1979), and 24 species of protozoan are found in the Pacific coast population of C. punctulatus (described by Cleveland and summarized in Bobyleva (1975); this paper, table 1). There is no overlap in species composition of the gut fauna in Cryptocercus and Zootermopsis. They share but one genus of flagellate: the primitive hypermastigote Trichonympha, which is widespread but unevenly distributed in the Isoptera (Kirby 1932, 1937). Of 205 lower termites examined, 27% are hosts of at least one of the 36 known species of Trichonympha (Yamin 1979). Additionally, termites exist that share two genera of flagellates (Oxymonas and Trichonympha) with Cryptocercus (Kalotermitidae: Glyptotermes uelenensis, Incisitermes immigrans, I. marginipennis and I. tabogae (Yamin 1979)). The range of none of these termites overlaps with the Pacific coast Cryptocercus (Emerson 1955; Weesner 1970).

There is, then, no evidence of aggressive and consumptive transfaunation in the known hindgut fauna of Pacific coast Cryptocercus or Zootermopsis. One of several factors may be responsible for this lack of close similarity.

1. The aggressive and consumptive behaviour demonstrated by Thorne in the laboratory does not occur in the field. Territorial behaviour does not necessarily include fierce combat. Defence can be subtle, with individuals maintaining exclusive areas by mutual avoidance of each others' territorial signals, such as scent or sound (Davies & Houston 1984). Laboratory studies of Cryptocercus suggest that they will use their enlarged pronotum to block galleries or engage in pushing contests with intruders. They are not, however, known to bite, and in nearly 150 observed encounters the opponent was never injured. When barriers are removed between family groups, they show alarm behaviour and rapidly begin building a structural boundary (Seelinger & Seelinger 1983). In the field, adjacent families of Cryptocercus may be separated by physical barriers erected by the insects (Nalepa 1984, figure 1). Some termite species are known to avoid mutual contact rather than attack each other (Nel 1968); such a strategy makes sense for such soft bodied insects. Additionally, termites are known to initiate building behaviour when they are alarmed (Stuart 1967). Bouillon (1970) attributes the aggressive responses of termites in laboratory experiments to the stress of the unnatural conditions, including the forced confrontation of 'opponents' without the structural or ethological barriers that exist in nature.

2. Aggressive and consumptive behaviour occurs in the field, but transfaunation is not successful. Laboratory experiments conducted by Cleveland et al. (1934) and Nutting (1956) suggest that the protozoans of Cryptocercus and Zootermopsis can be successfully
transfaunated to the alternate host. In all cases, however, the recipient of the alien gut protozoans was defaunated before inoculation. Unless a termite is approaching moult, or has recently moulted, its hindgut is densely packed with a resident fauna. It may be unrealistic to expect that consumed protozoans would find an open niche or be able to replace the flagellates already established in a host.

3. Aggressive and consumptive behaviour occurs in the field, transfaunated protozoans become established in their new host, and further study of the hindgut contents of sympatric populations of Cryptocercus and Zootermopsis will disclose protozoan species overlap. The protozoans of these two taxa are reasonably well studied (see beginning of section); it is possible, but unlikely, that evidence for species overlap is forthcoming.

Further observation and experimentation may provide support for one of the above scenarios. Regardless of the results of these studies, however, they will bring us no closer to an understanding of the origins of the cellulolytic protozoans in woodroaches and termites. There are fundamental problems associated with using laboratory experiments on extant, social, woodfeeding insects to postulate the field behaviour of solitary detritivores that lived during the Permian.

5. COEXISTENCE OF ANCESTORS

Thorne's hypothesis is based on the assumption that, some time after the divergence of cockroaches and insects to postulate the field behaviour of solitary cellulolytic protozoans in woodroaches and termites. The taxon that lacked symbionts may have nested within logs collapsed (Thorne 1990, p. 38). A problem, however, is that only the ancestor that first acquired cellulolytic protozoans is likely to have used wood as an exclusive food source. The taxon that lacked symbionts may have occasionally sheltered in logs, but would have spent the majority of their time in the forest litter foraging for food they could digest (probably plant-derived material and animal debris (Cochran 1985)). The chances of the woodfeeder encountering the other taxon, then, are no higher than its chances of encountering any other contemporary inhabitant of forest litter.

4. BEHAVIOUR OF ANCESTORS

If both 'termitoid' and 'roachoid' lines were solitary and detritivores at the time of the proposed protozoan transfer, it is doubtful that they would show the aggression and consumption exhibited in Thorne's studies. The aggressive behaviour seen in Cryptocercus and Zootermopsis is correlated with the fact that: (i) they currently nest in wood and thus show territorial behaviour in defence of their galleries (Urbani 1979); and (ii) they both show some degree of sociality and thus defend their families (Cryptocercus) or colony (termites) (Hermann 1984).

It is unlikely that the hypothetical taxon that first acquired a functional symbiosis would remain solitary for any length of time. The need to transfer flagellates to neonates via anal trophallaxis dictates that some degree of subsociality is concomitant with the use of these protozoans for cellulose digestion. If, however, transfaunation is proposed between a subsocial wood-feeder and a solitary detritivore, it is likely that it would be the woodfeeder (who already has symbionts) that would be the aggressor in an encounter, not the non-woodfeeder (see previous paragraph).

An additional complication is that in every experiment conducted by Thorne, termite soldiers killed the Cryptocercus nymphs. Soldiers, however, are a defensive caste characteristic of eusocial termites, and therefore several evolutionary steps removed from a solitary or subsocial ancestor. Although worker termites can be aggressive (Bouillon 1970), their aggression is also correlated with eusociality (see first paragraph in this section).

5. TRANSFAUNATION IN OTHER TAXA

1. Termite-termite. A correlate of Thorne's aggression-consumption hypothesis is that extant sympatric species of termites would be expected to have similar hindgut fauna. Different species of termites are known to nest in the same log (Bouillon 1970), and transfaunation should be common because of the presence of soldiers in both participants of an encounter. In thousands of observations of termite flagellates, however, just one case of possible termite to termite transfaunation has been found (between Postelectrotermes (as Neotermites) longus and Neotermites gracilidens (Kirby 1949)).

2. Termite–mole rat. Thorne cites the work of Porter (1957) in suggesting that the naked mole rat Heterocephalus glaber acquired three species of gut protozoans by burrowing into termite mounds and ingesting the occupants. The observation of coprophagous behaviour and the existence of large numbers of ciliates in the gut of this vertebrate are used as support that these protozoans have a symbiotic relation with the mole rat.

Coprophagy occurs in a variety of rodents (McBee 1977), and it is likely that mole rats do have a symbiotic relationship with the ciliates, bacteria and fungi present in their hindgut (Jarvis 1991). The microorganisms cited by Porter (1957) as being shared by termites and mole rats, however, are amoebae of the genera Entamoeba and Endolimax, and the flagellate Entrichomasix. These protozoans are abundantly represented in a wide variety of both invertebrates and vertebrates: Entamoeba in reptiles, primates and rodents (Porter 1957), Endolimax in primates, fowl, craneflies, belostomatids, bees and cockroaches (Kirby 1927; Porter 1957), and Entrichomasix in vertebrates of all classes, trichopteran larvae and beetles (Kirby 1931). Although it is possible that mole rats may have acquired these three genera of protozoans from termites, the presence of these microorganisms in a wide array of different animals suggests that they are easily acquired from the environment. The unique genera and species of cellulolytic oxymonad, trichomonad and hypermastigote flagellates shared by the

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lower termites and the Cryptocercidae, however, are found nowhere else in nature but in these two groups (Honigberg 1970).

6. CONCLUSIONS

Thorne makes a valid point in that we are perhaps too complacent in our acceptance of the theory that the cellulolytic gut protozoans in *Cryptocercus* and the termites were inherited from a common ancestor. At this time, however, there is no evidence to support the contention that transfaunation occurs in extant woodroaches and termites, even though the current behaviour of these insects may allow it. Furthermore, it is unlikely that transfaunation occurred in geological history when the behaviour of the proposed solitary ancestors was almost certainly different. Thorne's data do not justify abandoning the theory that the cellulolytic protozoans currently found in *Cryptocercus* and the lower termites originated from an ancestor common to these two taxa.

Definitive proof of the historical origin of these protozoan symbionts undoubtedly will be difficult to obtain. Perhaps, then, we should turn our attention to a different symbiotic association shared by cockroaches and termites, one that is in the visceral fat body and unlikely to be transmitted by aggression and consumption. Measurements of DNA sequence similarity in the bacteroids of cockroaches suggest that the evolution of these fat body endosymbionts occurred in tandem with their host. This symbiotic system has been in existence since before cockroaches evolved the present day forms on which their taxonomy is based (Wren *et al.* 1989). The primitive termite *Mastotermes darwinianus* also has these endosymbionts, and they appear identical to those of cockroaches, including the minute details of transmission (transovarial) (summarized in Buchner (1965)). A molecular study of the endosymbionts in this termite, then, may suggest that they were inherited from an ancestor common to both termites and cockroaches, and strengthen the hypothesis that the symbiotic gut protozoans also originated in this way.

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