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Review

Functional morphology as an aid in determining trophic behaviour: the placement of astigmatic mites in food webs of water-filled tree-hole communities

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ABSTRACT

The arthropod communities of phytotelmata (plant-held waters) are considered excellent subjects for studying and testing community theory. Food webs constructed for phytotelm communities, however, usually exclude mites or determine their placement based on little, if any, actual knowledge of their trophic behaviour. Although individually small, many acarine species attain high population levels and therefore may be important as prey for other inhabitants, as processing chain species in commensal relationships and as competitors of the larger tree-hole inhabitants. An understanding of the trophic relationships of acarine inhabitants is therefore essential to an understanding of the dynamics of phytotelm communities. Studies emphasizing the functional morphology of mouth parts of astigmatic species inhabiting water-filled tree holes in the eastern USA and in Queensland, Australia, reveal a diversity of trophic groups. Among these are 'shredders' who ingest leaf material and associated microbes by biting off chunks of leaves, 'scrapers' (= grazers) who crop fungal hyphae and/or other microbes and detritus from the substrate surface and 'collectors' who filter microbes and fine particulate matter from the water. This information allows for the more exact placement of acarine inhabitants in food webs of water-filled tree holes.
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INTRODUCTION

It has been known for well over 100 years that a number of terrestrial plant species possess morphological attributes that collect and retain water and that these bodies of water often house communities of aquatic arthropods (Fish, 1983). The term phytotelmata is used to describe such habitats, which include the internode spaces

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of broken bamboo stems, inflated leaf axils of plants such as bromeliads and palms, modified leaves of pitcher plants, water-collecting flowers such as *Heliconia* and the water-collecting depressions on trees (treeholes) (Fish, 1983). In recent years phytotelmata have been lauded as excellent subjects for testing community theory since they are natural microcosms that can be easily manipulated, provide for replication and contain relatively few species (Kitching, 1971, 1983, 1987; Maguire, 1971; Frank and Lounibos, 1983; Kitching and Pimm, 1985; Pimm and Kitching, 1987; Jenkins and Kitching, 1990; Kitching and Beaver, 1990; Naeem, 1990; Sota, 1996). Such studies, however, normally require a knowledge of food web structure.

The development of a food web hypothesis requires a knowledge of the feeding behaviour of the various community inhabitants. For phytotelm communities, such information is generally based on laboratory studies and/or an examination of the literature. Due to their larger size, the trophic relationships of insect inhabitants are more readily established than are those for smaller arthropods; insect trophic relationships are therefore often detailed in publications on food web structure. Mites are common inhabitants of water-filled tree holes and of the fluid-filled pitchers of *Nepenthes*, the most extensively studied phytotelm communities (Fashing, 1973, 1974, 1994; Nesbitt, 1979; Fashing and Wiseman, 1980; Beaver, 1983, 1985; Smith and Harvey, 1989), but they often are excluded from community studies. In many cases this is simply due to the use of sampling techniques that exclude the recovery of mites. In other cases mites are intentionally ignored even though their presence is known. Paradise and Dunson (1997), for example, discussed the dominant insect inhabitants of water-filled tree holes in deciduous forests in Pennsylvania as well as the presence of protozoans and microbes. However, they did not mention acarine inhabitants, even though previous research conducted at the same study site by Barrera (1996) discussed their high frequency of occurrence in tree holes as well as their abundance. Even when their high numbers elicit an acknowledgement of their presence, mites often are omitted from the actual community analysis. Although Barrera (1996, p. 72) recognized that the high number of mites in water-filled tree holes made them an important component of the community, he did not include them in his food web analysis ‘because of uncertainty about their local distribution within natural tree holes’. Other authors have included mites in their food web analyses, but made no attempt to determine their trophic relationships and simply relegated all non-predaceous species to common trophic categories (Kitching and Callaghan, 1982; Beaver, 1983, 1985; Kitching, 1983).

It is undoubtedly due to their small size that mites are either omitted from phytotelm community studies or are relegated to positions of minor importance. Small size makes most mites difficult study subjects and leads to the erroneous assumption that their presence could not contribute in any substantial way to overall community dynamics. Acarine populations can, however, attain high levels in phytotelm communities and what they lack in size is often compensated for by their numbers. An understanding of the trophic relationships of acarine inhabitants is therefore essential to an understanding of the dynamics of phytotelm communities.

The research reported in this paper is an attempt to understand better the trophic relationships of the acarine component of water-filled tree-hole communities, with special emphasis on astigmatic species. Over the years, several investigative methods have been used to study acarine feeding behaviour. Of these, direct observation of behaviour through a dissecting microscope and/or an inverted compound microscope has proved useful (e.g. Walter and Kaplan, 1990), as has the microscopic examination of expelled faecal pellets and/or food boluses dissected from the guts of particulate-feeding mites (e.g. Goddard, 1982; Walter *et al*., 1988). However, each of these methods have their drawbacks. Behavioural study requires laboratory cultures of mites to be maintained on their natural substrates and the bright light required for microscopic observation often inhibits normal behaviour and can stimulate mites to move rapidly away from it. The latter method is mostly restricted to determining the diets of animals that engulf their food and is biased towards food items possessing easily recognized structures that resist digestion (Walter *et al*., 1988; Evans, 1992). Walter *et al*. (1988) summed up the difficulty of using gut content studies by pointing out that a common category in reporting results is ‘amorphous materials’.

Mites often exhibit a wide range of variation in mouth part morphology and such variation often reflects dietary differences (Karg, 1966, 1983; Akimov, 1979; Theron, 1979; Woolley, 1988; Evans, 1992). The size and shape of the rutellar lobes of the subcapitulum can vary between species, but how this variation affects food procurement is not well understood (Evans, 1992). The chelicerae are the primary food gathering components of the mouth parts and it is much easier to relate their structure to known function. Examples of cheliceral differences between six species of the aquatic/semi-aquatic family Algophagidae are illustrated in Fig. 1. All chelicerae are standardized to a common idiosomal length to accentuate the dramatic size differences found among the species. Levator muscles of the movable digit originate in the cheliceral shaft (Evans, 1992) and the size of the cheliceral shaft therefore reflects the muscle allocation dedicated to activating the digit. Chelicerae with enlarged cheliceral shafts have a powerful bite, as illustrated by *Algophagopsis* sp. (Fig. 1F), an algophagid that crushes the silicious cell walls of diatoms to extract nourishment. Levator muscles insert on the base of the movable digit and, all else being equal, the shorter the digit, the more force it can exert against the opposing fixed digit. The size, shape and alignment of the movable digit and the opposing fixed digit are also important attributes for food procurement. Therefore, an examination of the mouth parts in an attempt to relate structure to function (i.e. functional morphology) can be an important tool in determination of trophic behaviour. An optimal instrument for investigating functional morphology is the scanning electron microscope (SEM), but differential interference and phase microscopy may also provide useful information, particularly in distinguishing between thinner hyaline and thicker sclerotized structures. When specimens are available only as slide mounts, differential interference and phase microscopy

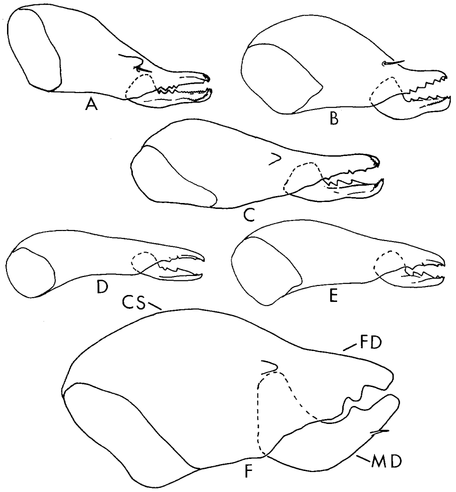

Fig. 1. Paraxial view of the chelicerae of six species of the family Algophagidae demonstrating variability in cheliceral morphology. All are standardized to a common idiosomal length to accentuate size differences. (A) *Hericia* new species from sap flux of oak tree (Virginia, USA). (B) *Fusohericia* new species from water in *Heliconia imbricata* bract (Costa Rica). (C) *Algophagus pennsylvanicus* from water-filled tree hole (Virginia, USA). (D) New genus, new species 1, from water-filled tree holes (Queensland, Australia). (E) New genus, new species 2, from water-filled tree holes (Queensland, Australia). (F) *Algophagopsis* new species from algal mats in lake (Oregon, USA). CS, cheliceral shaft; FD, fixed digit; MD, movable digit.

provide the primary methods of study. The results reported in this study utilize all of the above methods, but rely most heavily on the use of gnathosomal morphology.

METHODS AND MATERIALS

Acarines from water-filled tree-hole communities in temperate deciduous forests around Williamsburg, Virginia, USA and in semi-tropical box forests in Lamington National Park, Queensland, Australia, were examined. To obtain mites for study, samples consisting of water, detritus and associated arthropods were collected and maintained in finger bowls in the laboratory.

Food boluses excised from the guts of cultured mites, as well as collected faecal pellets, were squashed between a cover slip and microscope slide and examined utilizing phase contrast and Nomarski DIC microscopy. Direct observations on feeding behaviour were made through a dissecting microscope and through an inverted compound microscope when available. Although some observations were made on slide-mounted specimens using phase and Nomarski DIC microscopy, mouth-part morphology was primarily investigated using scanning electron microscopy. Live specimens were removed from laboratory cultures and put through several baths of distilled water in an attempt to cleanse them of debris. Low frequency sonication was also used to aid in cleaning when possible. Living mites were then briefly submerged in distilled water near the boiling point in order to force protraction of appendages such as the chelicerae. Specimens were then dehydrated in ethyl alcohol, dried using the critical point procedure, individually affixed to stubs using double-sided sticky tape and coated with gold palladium in a sputter coater. Microscopy was performed on an AMR 1200.

Additional insight into the feeding behaviours of two species from the eastern USA, *Naiadacarus arboricola* Fashing and *Algophagus pennsylvanicus* Fashing and Wiseman, was gained through laboratory experiments. Dried leaves were collected during the autumn leaf shed and conditioned by soaking in water for several days. Small pieces of leaves were then split into three groups and placed in Syracuse watch glasses containing water. One group was left as a control to determine the extent of microbial growth on leaves in the absence of mites. The second group contained ten adult *N. arboricola* in each culture and the third group had ten adult *A. pennsylvanicus* in each. The cultures were maintained at 25°C for a period of 40 days. The leaves were then examined using the dissecting microscope and SEM to determine any differences due to the presence of mites.

RESULTS AND DISCUSSION

A water-filled tree hole may be defined as any cavity or depression on the surface of a tree that is capable of collecting and retaining water for an extended period of time. Shed leaves provide the primary energy source for the tree-hole community, although some nutrients may be added by materials that are dissolved or suspended in rainwater as it runs down the bark into the tree hole (stem flow) (Carpenter, 1982). The tree-hole community is therefore a detritus-based system. Microorganisms play a vital role in this system since most of them synthesize extracellular enzymes (e.g. cellulase and pectinase) that break down leaves and thereby increase the available nutrient content through detritus cycling (Suberkropp and Klug, 1976). In many cases, microorganisms utilizing detritus as an energy source are themselves the primary diet of macroinvertebrate inhabitants. In other cases, the by-product of the combined activity of macroinvertebrates and microorganisms consists of suspended and/or deposited fine particulate matter which provides an additional nutrient source (Suberkropp and Klug, 1976). Thus, there are trophic resources available in water-filled tree holes for detritus feeders that are specialized as ‘shredders’, ‘scrapers’ and/or ‘collectors’. Shredders ingest leaf material and any associated microbes by biting chunks out of leaves, whereas scrapers (= grazers) feed by cropping fungal hyphae and/or other microbes and detritus from the leaf surface. Filtering collectors strain microbes and fine particulate matter suspended in the fluid and gathering collectors remove microbes and fine particulate matter that are on the detrital surface (Cummins and Klug, 1979).

The North American food web

In the eastern deciduous forest of North America, water-filled tree holes are the exclusive habitat for at least three species of astigmatic mites (Fashing, 1994). *Naiadacarus arboricola* (Acaridae) occurs in approximately 80% of the tree holes, *A. pennsylvanicus* (Algophagidae) in approximately 40% and *Hormosianoetus mallotae* (Fashing) (Histiostomatidae) in only 5%. All three species may be found occupying the same tree hole and all feed on microbes and/or detritus (Fashing, 1994). In their literature-based food web analysis for water-filled tree holes in the eastern USA, Kitching and Pimm (1985, p. 134) grouped all three species together and indicated that all probably feed on 'suspended detritus and associated microorganisms' as well as on 'fine detritus and associated microorganisms'. As detailed below, this is not the case.

A microscopic examination of food boluses excised from *H. mallotae* provided no clues to diet, but mouth part morphology was quite revealing. Like all members of the Histiostomatidae, the gnathosoma and mouth parts of *H. mallotae* differ considerably from the typical sarcoptiform plan (Hughes, 1953; OConnor, 1982; Evans, 1992). As with other histiostomatids, only the terminal segment of the pedipalp is movable (Hughes, 1953) and in *H. mallotae* it bears a very long, distal, flagella-like seta directed anteriorly and a shorter seta directed posteriorly (Fig. 2A and B). Both the movable and the fixed digits of the non-chelate chelicerae are flattened laterally. The fixed digit is serrated and rake like, bearing 18–20 small teeth (Fashing, 1994) and the distal end curves mesially (Fig. 2B–D). Most members of the Histiostomatidae are thought to be filter feeders that collect fine particulate matter from a fluid medium (Hughes, 1953; Krantz, 1978; OConnor, 1982; Walter and Kaplan, 1990; Evans, 1992) and *H. mallotae* is no exception. The long terminal setae of the pedipalps are beat in such a manner that a vortex is created in the fluid medium, drawing small particulate matter and microorganisms towards the anterior region of the subcapitulum. Here the food is raked into the gnathosoma by alternate protraction and retraction of the chelicerae. Individuals are often observed standing on detritus just below the water surface with their mouth parts working the surface film, an area rich in microorganisms and fine particulate matter (Fashing, 1994). This mode of feeding classifies *H. mallotae* as a filtering collector (Cummins and Klug, 1979). The whip-like pedipalpal setae are also used to stir up microorganisms and fine particulate matter from the leaf surface and the chelicerae are again used to rake them into the gnathosoma (Fashing, 1994). This trophic behaviour also classifies *H. mallotae* as a gathering collector (Cummins and Klug, 1979) in the tree-hole community.

The mouth parts of the other two acarine inhabitants, *N. arboricola* and *A. pennsylvanicus*, are typical of sarcoptiform mites in that both have chelate

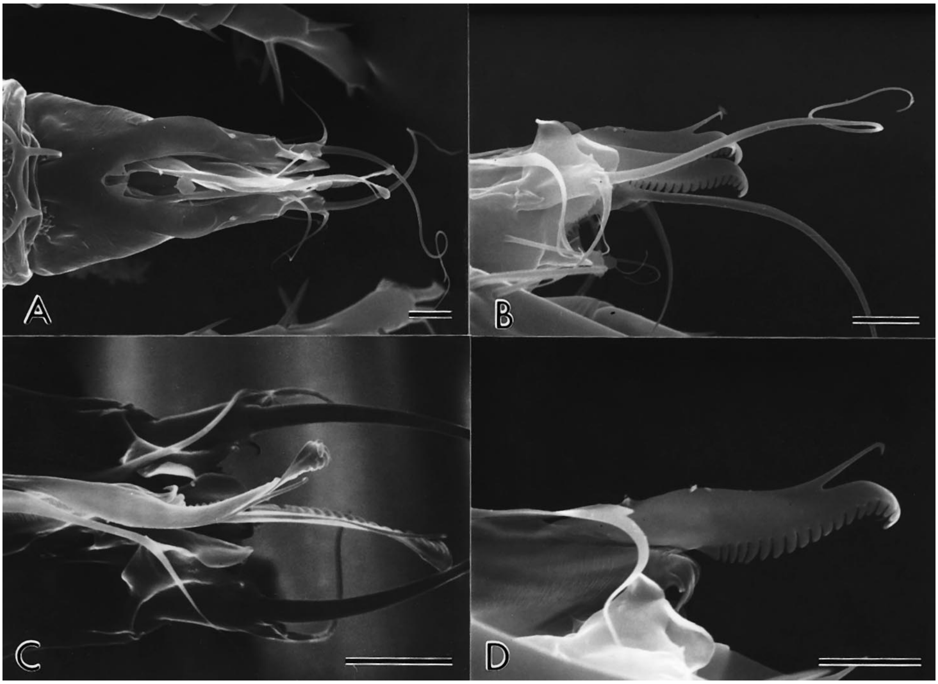

Fig. 2. Mouth parts of *H. mallotae*. (A) Dorsal view of gnathosoma. (B) Lateral view of chelicerae and pedipalps. (C) Dorsal view of chelicerae. (D) Lateral view of chelicera. Scale bar = 10 μm.

chelicerae and short solenidia/setae on the terminal pedipalpal segment. While all saprophagous astigmatids with chelate chelicerae are capable of retrieving and ingesting small particulate matter from substrate surfaces, some species have also evolved adaptations which allow them to specialize in other trophic categories and, therefore, gnathosomal morphology may differ in many respects. Although mouthpart functional morphology is addressed separately below for each species, figures of homologous structures for cohabiting species are paired to accentuate differences.

The subcapitulum dorsally houses the chelicerae within its cheliceral grooves when they are retracted or not in use (Evans, 1992). The size and shape of the subcapitulum is therefore at least partially determined by the chelicerae it accommodates and the relatively broad subcapitulum of *N. arboricola* (Fig. 3A) implies robust chelicerae. A close examination reveals this to be true; the cheliceral shafts are relatively large in all dimensions (Fig. 3B and C). An enlarged cheliceral shaft in turn reflects a large muscle mass operating the movable digit. In addition, the fixed digit is relatively short in relation to cheliceral length (Fig. 3C). These two characteristics indicate that the movable digits can exert a strong force against their opposing fixed digits, i.e. *N. arboricola* has a powerful bite. Further examination of

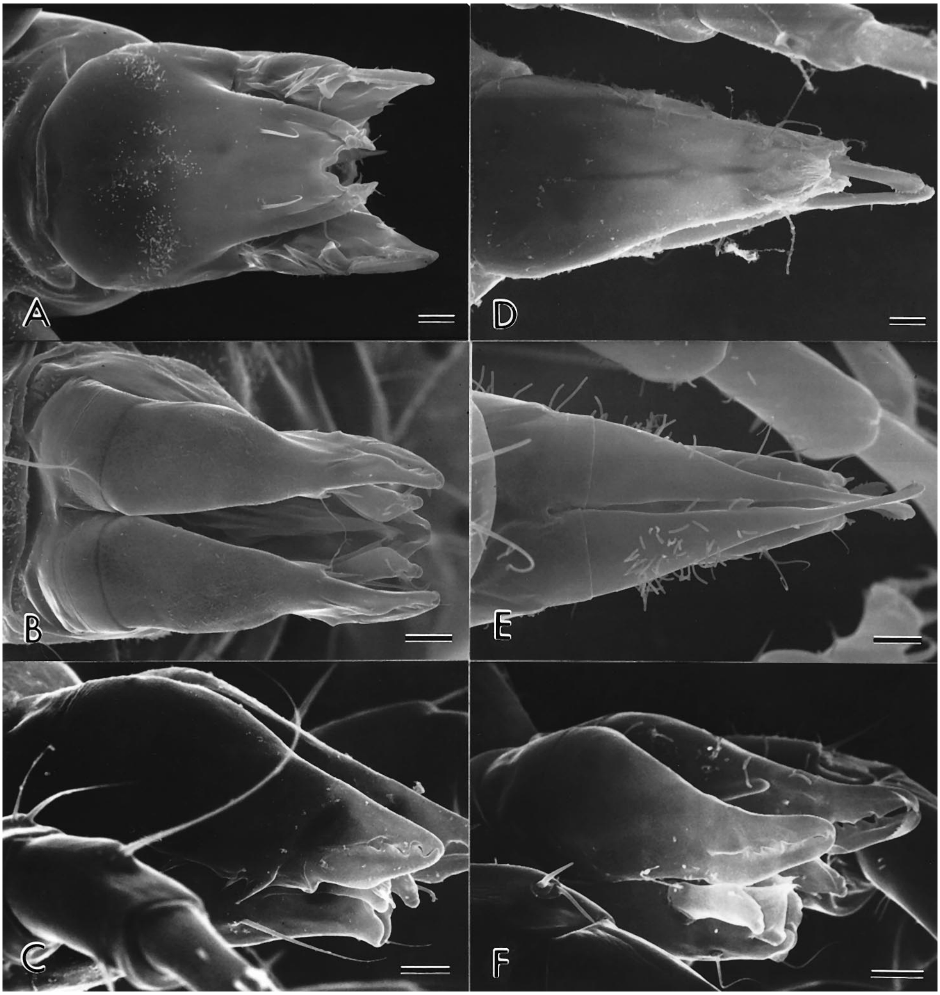

Fig. 3. Mouth parts of (A)–(C) *N. arboricola* and (D)–(F) *A. pennsylvanicus*. (A) and (D) Ventral view of gnathosoma. (B) and (E) Dorsal view of chelicerae. (C) and (F) Lateral view of chelicerae. Scale bar = 10 μm.

the movable and fixed digits reveals that both have sharp, robust teeth over their entire biting surfaces and that these teeth interdigitate when the digits close (Fig. 4A and B). The chelicerae are therefore well adapted for biting and/or tearing off pieces from a solid substrate. The rutella of the subcapitulum may aid in this process; they are well separated (Fig. 3A) and allow the chelicerae to move freely between them during protraction and retraction. It has been suggested that such rutella may be used for cutting as the chelicerae pull solid food towards the gnathosoma (Theron, 1979).

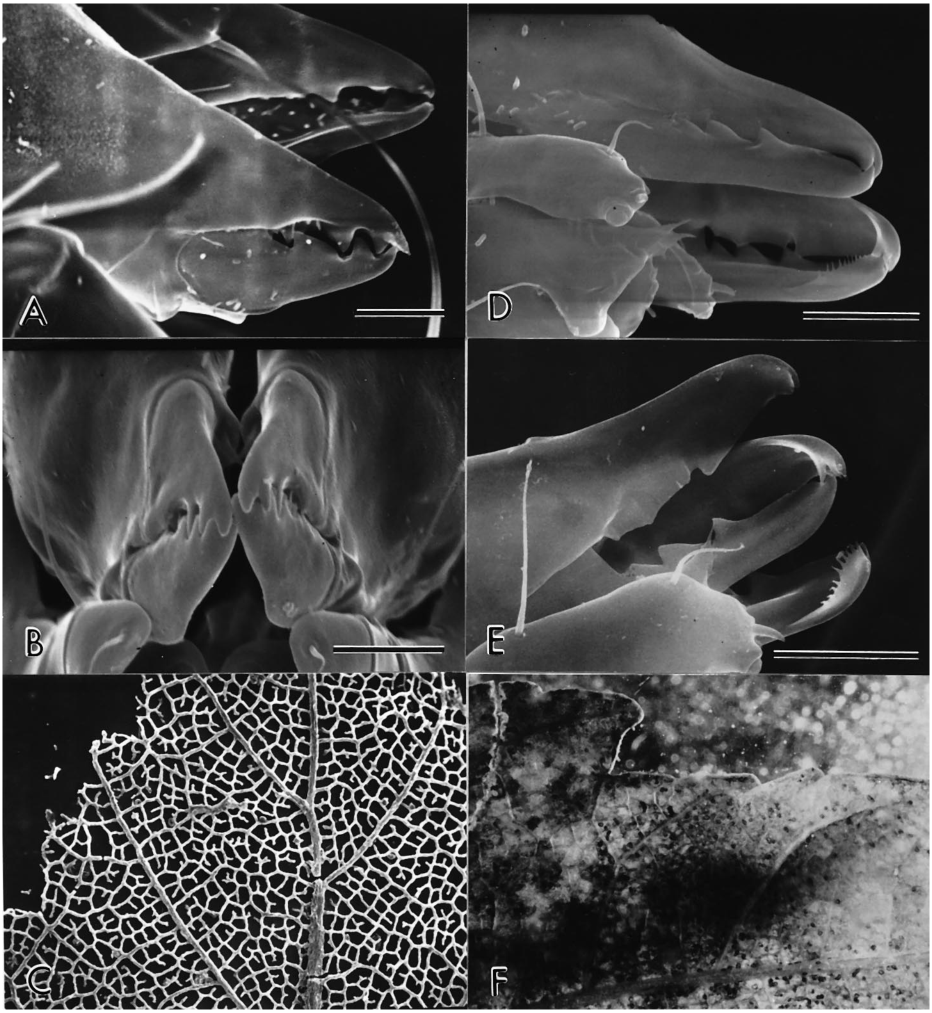

Fig. 4. Fixed and movable cheliceral digits of (A) and (B) *N. arboricola* and (D) and (E) *A. pennsylvanicus*. (A) and (D) Lateral view of closed digits. (B) Frontal view of closed digits. (E) Lateral view of open digits. (C) Surface of leaf on which *N. arboricola* was cultured (note skeletonization). (F) Surface of leaf on which *A. pennsylvanicus* was cultured (note lack of fungal hyphae and lack of skeletonization). Scale bar = 10 µm.

Mouth-part morphology strongly indicates that *N. arboricola* is a ‘shredder’ (Cummins and Klug, 1979) and feeds by biting chunks out of decomposing substrate. Although a microscopic examination of food boluses and faecal pellets was inconclusive, other laboratory observations bear out this mode of feeding. Control leaves without mites remain intact and soon become covered with fungal hyphae (Fashing and Campbell, 1992), whereas leaves with *N. arboricola* present are skeletonized and only the epidermis and veins remain (Fig. 4C). *Naiadacarus arboricola* therefore ingests the mesophyll of the decomposing leaf along with any associated microorganisms. Other laboratory studies indicate that nutrition is derived from the leaf mesophyll as well as from the associated microorganisms (Fashing, 1975).

In contrast to *N. arboricola*, the subcapitulum of *A. pennsylvanicus* is relatively narrow (Fig. 3D) since it houses slender chelicerae (Fig. 3E). In fact the cheliceral shaft is relatively narrow in all dimensions (Fig. 3E and F), which is indicative of a smaller muscle mass operating the movable digit. In addition, the digits are long relative to the total cheliceral length (Fig. 3F). These two characteristics imply that the bite of *A. pennsylvanicus* is not very powerful. The movable and fixed digits are slender (Figs 3F and 4D) and the fixed digit and the dorsal portion of the movable digit are thin and blade like (Fig. 4E). The dorsal portion of the movable digit bears retrose teeth in the proximal region (Fig. 4E). The thin, blade-like digits slide past each other like scissors when closing (Figs 3F and 4D), shearing food from the substrate. The ventral portion of the movable digit extends mesially to form a shelf (Figs 3F and 4D and E) onto which the sheared food falls. The distal ends of both digits have serrations that interdigitate to form a ‘cap’ at the cheliceral tip when the chelicera is closed (Figs 3F and 4D), thereby preventing food collected on the shelf from moving forward and falling off the chelicera when it is retracted. The narrow distal end of the subcapitulum (Fig. 3D) reflects the fact that the tips of the rutella touch rather than being separated as in *N. arboricola* (Fig. 3A), thereby creating an enclosure or ‘trough’ behind the rutella. It is surmised that the trough prevents food from escaping once it is brought into the preoral cavity. In a species with mouth parts adapted for shearing, it would not be necessary for the rutella to function in cutting.

Mouth-part morphology suggests that *A. pennsylvanicus* is a scraper (= grazer) (Cummins and Klug, 1979) and feeds by shearing fungal hyphae from the substrate. Although intact hyphae have been observed in food boluses, the fungal diet is better corroborated by an examination of the surfaces of decomposing leaves on which *A. pennsylvanicus* have been cultured. Control leaves with no mites are rich in fungal growth (Fashing and Campbell, 1992), whereas leaves harbouring *A. pennsylvanicus* reveal few fungal hyphae (Fig. 4F). Furthermore, laboratory studies have demonstrated that fungal hyphae may be utilized as a food source by this species (Fashing and Campbell, 1992).

It is likely that *A. pennsylvanicus* has yet another mode of feeding. Individuals are often observed near the water surface where they rapidly protract and retract their chelicerae through the surface film, an area rich in suspended particulate matter and microbes. Examination of the tips of both cheliceral digits reveals that not only do they possess serrations that interlock to form a cap at the tip when closed, but that the movable digit has smaller serrations that continue on mesially (Figs 3F and 4D and E). This cheliceral modification allows for filtering of fine particulate matter and microbes from the surface film and would also allow for collection of such material from the leaf surface. *Algophagus pennsylvanicus* is, therefore, probably a filtering and gathering collector as well as a scraper (Fashing and Campbell, 1992).

As shown above, feeding behaviour and diet differ for the three acarine inhabitants of water-filled tree holes in the eastern USA. *Naiadacarus arboricola* is a shredder, the most common functional group in a detritus-based community (Barlocher and Kendrick, 1973; Cummins and Klug, 1979). *Hormosianoetus mallotae* is a highly specialized filtering and gathering collector and therefore represents the least common functional group (Barlocher and Kendrick, 1973; Cummins and Klug, 1979). *Algophagus pennsylvanicus* fits into two functional groups: it is primarily a scraper (= grazer), the second most common functional group, but morphological and behavioural observations indicate that it may also feed as a filtering and gathering collector. In their proposed food web for water-filled tree holes in eastern North America, Kitching and Pimm (1985) placed all three acarine inhabitants into two functional categories: 'fine detritus and micro-organisms' and 'suspended detritus and microorganisms'. The modified food web (Fig. 5) not only removes *N. arboricola* from the suspended detritus and micro-organisms group but places it in the coarse detritus and microorganisms group, thereby reflecting its primary role in the community as a shredder. *Naiadacarus arboricola* can attain high population levels and is therefore an important competitor of both scirtid beetle larvae and syrphid fly larvae. Although *A. pennsylvanicus* is a member of the suspended detritus and microorganisms group, this is a

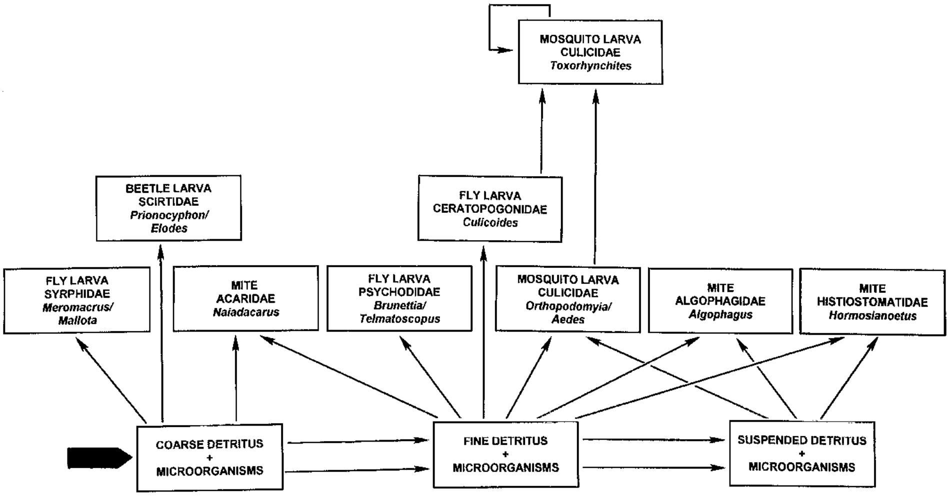

Fig. 5. Proposed food web for the arthropod community in water-filled tree holes in the eastern USA. Modified from Kitching and Pimm (1985) to include updated information on acarine trophic relationships.

secondary role; its primary role is as a member of the fine detritus and micro-organisms group where it is a competitor for a number of insect species. *Hormosianoetus mallotae* is an efficient filtering and gathering collector, but it is rare in tree-hole communities and therefore probably of relatively minor importance.

Naiadacarus arboricola may also play another indirect but important role in its trophic relationships with other tree-hole inhabitants. As a by-product of feeding, scirtid beetle larvae release unconsumed shredded leaf particles into the water, thereby indirectly making leaf material available to microbes and particulate-consuming arthropods (Paradise and Dunson, 1997). In addition, scirtid faeces may be utilized as nutrients by other species. Scirtid larvae are therefore considered 'processing chain' commensal inhabitants of the tree-hole community (Paradise and Dunson, 1997), a role which may be shared with *N. arboricola* since it is also a shredder and produces copious amounts of faeces.

The Australian food web

The arthropod communities of water-filled tree holes in Lamington National Park, Queensland, have been studied extensively (Kitching and Callaghan, 1982; Kitching, 1983, 1987; Kitching and Pimm, 1985; Pimm and Kitching, 1987; Jenkins and Kitching, 1990; Kitching and Beaver, 1990; Jenkins *et al*., 1992). These tree holes contain four species of acarine inhabitants (Kitching and Callaghan, 1982; Kitching, 1983), two of which are astigmatids in an undescribed genus of Algophagidae. For the purpose of this paper, the smaller species which is characterized by short dorsal setae is called species 1 and the larger species characterized by long, serrated dorsal setae species 2. Species 2 is the most common, being found in more tree holes and in larger numbers. Justifying the placement of these species in a food web, Kitching and Callaghan (1982, p. 67) stated that 'these mites occur in the detritus layer of the tree holes and, on the basis of information on other members of the family elsewhere, are considered to be saprophagus exploiting the small particle component of the resource'. No references were cited to support the presumed feeding behaviour and, at the time of their publication, the only literature concerning a possible diet for any algophagid species only speculated a diet of algae (see Fashing and Campbell (1992) for details). Kitching and Callaghan (1982) undoubtedly accepted the common stereotyped opinion that all non-predaceous, non-parasitic astigmatic mites were saprophagous and fed on small particulate matter.

The research reported below is an attempt to determine the trophic behaviour of the Australian tree-hole species. Due to time and equipment limitations while in Australia, only minimal information was gathered from living specimens. Most of the conclusions are therefore based on mouth-part morphology and on functional analogies drawn from comparison with North American species.

The subcapitulum of species 1 is very narrow (Fig. 6A), reflecting its extremely slender chelicerae (Fig. 6B). In fact the cheliceral shaft is extremely slender in all

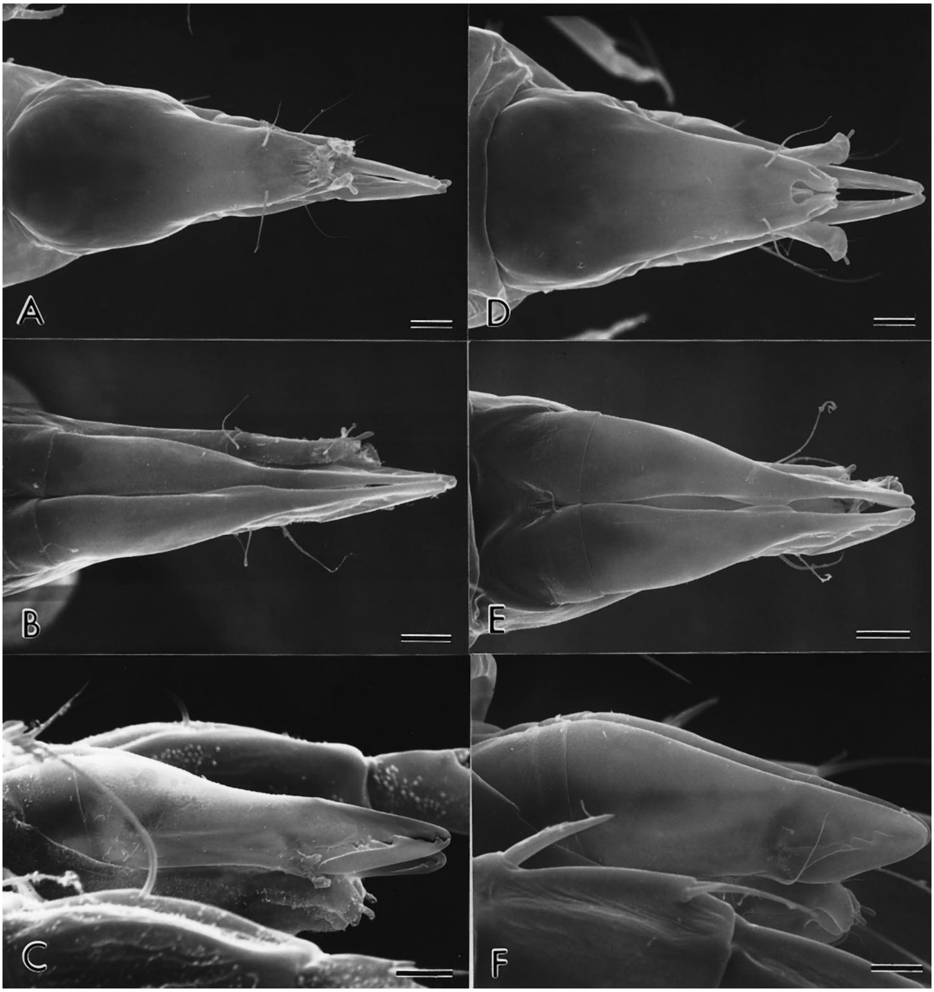

Fig. 6. Mouth parts of (A)–(C) Australian species 1 and (D)–(F) Australian species 2. (A) and (D) Ventral view of gnathosoma. (B) and (E) Dorsal view of chelicerae. (C) and (F) Lateral view of chelicerae. Scale bar = 10 µg.

dimensions (Fig. 6B and C), indicating that only minimal musculature operates the movable digit and that it can exert only a weak bite. It is therefore unlikely that species 1 is able to bite and/or tear pieces from a solid substrate. In addition, both the movable and fixed digits are slender and thin (Fig. 7A and B), with biting surfaces quite similar to those of *A. pennsylvanicus* (Fig. 7B versus Fig. 4E). As in *A. pennsylvanicus* (Figs 3F and 4D), the digits do not abut one another when closed, but rather slide past each other in a scissor-like manner when closing (Fig. 7A). Structural similarities suggest that species 1, like *A. pennsylvanicus*, is a scraper

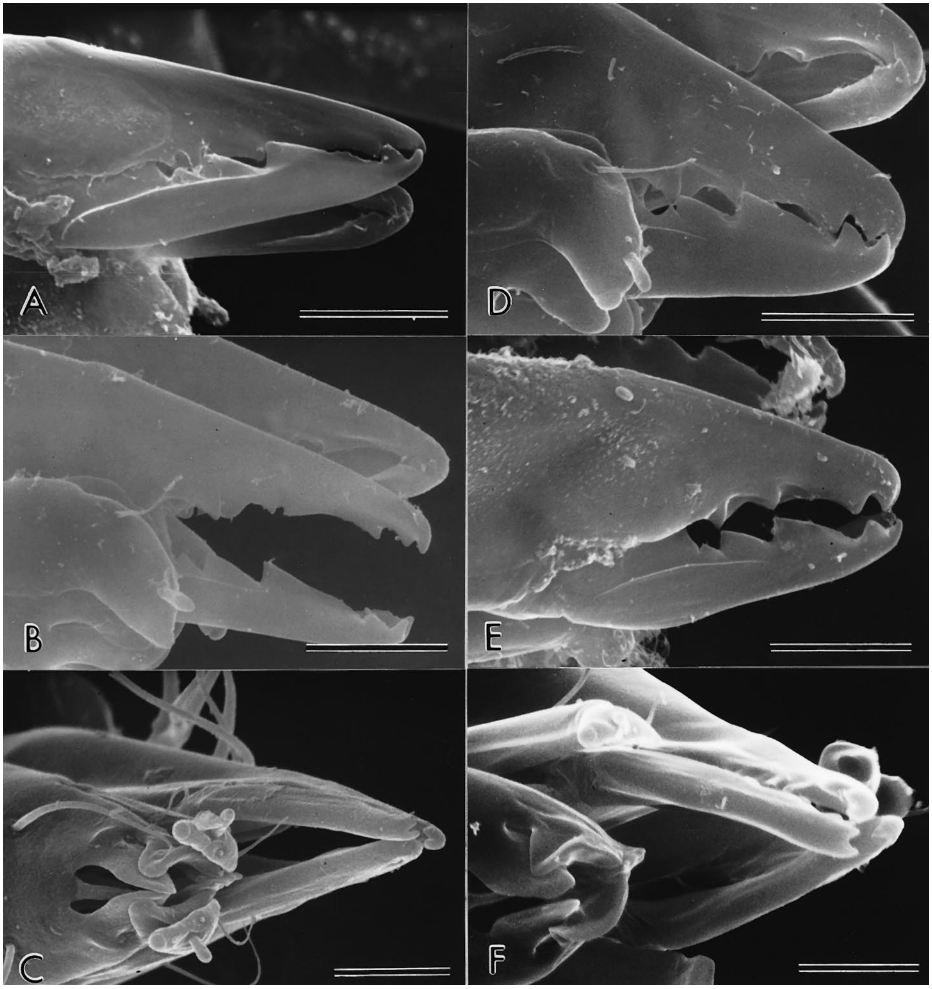

Fig. 7. Fixed and movable cheliceral digits of (A)–(C) Australian species 1 and (D)–(F) Australian species 2. (A) and (D) Lateral view of closed digits. (B) and (E) Lateral view of open digits. (C) and (F) Ventral view. Scale bar = 10 μm.

(= grazer) and feeds by cropping fungal hyphae from the substrate. This mode of feeding is corroborated, at least in part, by the presence of discernible fungal hyphae in food boluses. Unlike *A. pennsylvanicus*, however, species 1 is not a filtering and/or gathering collector. The tips of the movable and fixed digits (Fig. 7B and C) do not form a filtering apparatus as found in *A. pennsylvanicus* (Figs 3F and 4D and E).

Species 2 has many similarities in mouth-part morphology with *N. arboricola*. The subcapitulum is broad (Fig. 6D versus Fig. 3A) and the cheliceral shafts robust

(Fig. 6E and F versus Fig, 3B and C), indicating a large musculature to operate the movable digit and therefore a powerful bite. Both the fixed and movable digits have sharp teeth over the entire biting surface (Fig. 7E versus Fig. 4A) and the teeth interdigitate when the digits close (Fig. 7D and E versus 4A and B). An examination of food boluses and faecal pellets was inconclusive as with *N. aboricola*, revealing only amorphous material. Structural similarities suggest that species 2, like *N. arboricola,* is a shredder and feeds by biting and tearing off pieces from a solid substrate.

In his proposed food web for water-filled tree holes in Lamington National Park, Queensland, Australia, Kitching (1983) categorized the two algophagid species as feeding on small particle detritus and suspended matter. In later food-web scenarios this was changed to 'fine detritus and microorganisms' (Kitching and Pimm, 1985; Kitching and Beaver, 1990). Mouth-part morphology indicates that it is quite improbable that either species is able to filter suspended detritus and microorganisms from the water, but that it is likely that species 2 is a shredder and species 1 a scraper as illustrated in the modified food web (Fig. 8).

Two other acarine species, both non-astigmatids and both predators, have been recorded from water-filled tree holes at Lamington National Park (Kitching and

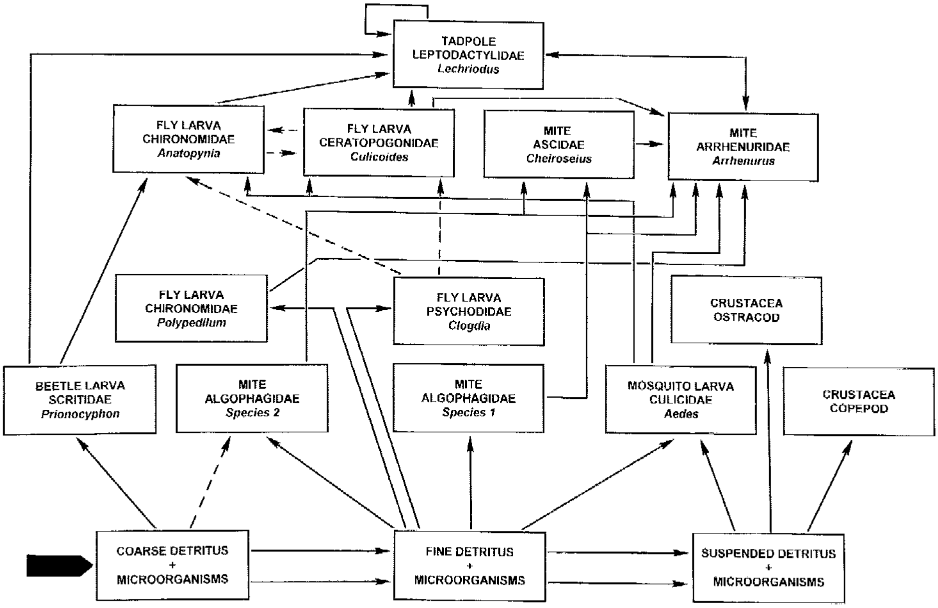

Fig. 8. Proposed food web for the arthropod community in water-filled tree holes in Lamington National Park, Queensland, Australia. Modified from Kitching and Pimm (1985) and Jenkins and Kitching (1990) to include updated information on acarine trophic relationships. Solid arrows indicate observed relationships and dashed lines putative ones.

Callaghan, 1982; Kitching, 1983). An unidentified species of *Cheiroseius* (Mesostigmata: Ascidae) has been observed to prey on the algophagid inhabitants (Kitching and Callaghan, 1982). In examining the arthropods from 102 samples collected by Kitching from 11 different tree holes over a 12 month period, I found *Cheiroseius* to occur in only five samples with a total of seven individuals and that it was present in only three of the 11 tree holes he routinely sampled. In addition, none of the samples I collected contained this species. Although *Cheiroseius* is often found in aquatic and subaquatic habitats (E. Lindquist, personal communication), its rare occurrence in tree holes would suggest that it is only an occasional visitor rather than a typical inhabitant. There is no doubt, however, that *Arrenurus kitchingi* Smith and Harvey (Prostigmata: Arrenuridae) is a permanent member of the tree-hole community. Of the 102 samples mentioned above, adult *A. kitchingi* occurred in 21, with a total of 41 individuals in six different tree holes and I recovered both adults and larvae from my samples. Although early publications speculated that tree-hole mites (algophagids and *Cheiroseus*) as well as ceratopogonid and mosquito larvae were probable prey for non-larval *A. kitchingi* (Kitching and Callaghan, 1982; Kitching, 1983), food-web illustrations in later publications imply that these predator–prey relationships are now firm (Kitching and Pimm, 1985). Kitching and Pimm (1985) also indicated that tadpoles of *Lechriodus fletcheri* (Boulenger) are preyed upon by *A. kichingi*. Proctor (personal communication) corroborated that ceratopogonid larvae, mosquito larvae and mosquito pupae are utilized as prey and she added chironomid larvae to the list. Although members of the genus *Arrenurus* often feed on crustaceans (B. Smith and H. Proctor, personal communication), Proctor was unable to entice *A. kitchingi* to feed on the ostracod inhabitants. She also found that scirtid beetle larvae are not part of their diet. In trials with three starved adults, I was unable to induce predation on either species of algophagid and Proctor (personal communication) was unsuccessful as well. It is quite probable that algophagid mites are only rarely utilized as prey by *A. kitchingi*.

CONCLUSIONS

The acarine inhabitants of a community may vary substantially in trophic behaviour as exemplified by those from water-filled tree holes. Although individually small, many species attain high population levels and are therefore important competitors of much larger arthropod inhabitants. Mites may also serve as prey for other tree-hole inhabitants and some species may play an important role in processing chain commensal relationships by indirectly converting leaves to particulate matter that may be utilized by other tree-hole inhabitants. The role of mites must therefore be considered in assessing community dynamics and mouth-part functional morphology is a valuable method for aiding in the determination of trophic relationships.

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